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Biodiversity of UV-Resistant Bacteria in Antarctic Aquatic Environments

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Abstract: Antarctica is an untapped reservoir of bacterial communities, which are able to adapt to a huge variety of strategies to cope with extreme conditions and, therefore, are capable of producing potentially valuable compounds for biotechnological applications. In this study, 31 UV-resistant bacteria collected from different Antarctic aquatic environments (surface sea waters/ice and shallow lake sediments) were isolated by UV-C assay and subsequently identified. A phylogenetic analysis based on 16S rRNA gene sequence similarities showed that the isolates were affiliated with Proteobacteria, Actinobacteria and Firmicutes phyla, and they were clustered into 15 bacterial genera, 5 of which were Gram negative (*Brevundimonas*, *Qipengyuania*, *Sphingorhabdus*, *Sphingobium*, and *Psychrobacter*) and 10 of which were Gram positive (*Staphylococcus*, *Bacillus*, *Mesobacillus*, *Kocuria*, *Gordonia*, *Rhodococcus*, *Micrococcus*, *Arthrobacter*, *Agrococcus*, and *Salinibacterium*). Strains belonging to Proteobacteria and Actinobacteria phyla were the most abundant species in all environments. The genus *Psychrobacter* was dominant in all collection sites, whereas bacteria belonging to Actinobacteria appeared to be the most diverse and rich in terms of species among the investigated sites. Many of these isolates (20 of 31 isolates) were pigmented. Bacterial pigments, which are generally carotenoid-type compounds, are often involved in the protection of cells against the negative effects of UV radiation. For this reason, these pigments may help bacteria to successfully tolerate Antarctic extreme conditions of low temperature and harmful levels of UV radiation.

Keywords: Antarctica; UV radiation; UV-C assay; UV-resistance; marine bacterium; lake microorganism; pigment

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1. Introduction

Although solar radiation represents one of the most important abiotic factors that allows life on Earth, excessive ultraviolet radiation (UV-R) of certain wavelengths can also threaten living organisms by causing damage to their molecular machinery. In fact, UV-mediated cellular stress produces an increase in reactive oxygen species (ROS), which damage DNA, lipids, and proteins [1,2]. Such deleterious processes can change aquatic ecosystems, thereby influencing biodiversity, ecosystem stability, trophic interactions, and global biogeochemical cycles [3].

Through evolution, aquatic microorganisms have developed unique metabolic, physiological, and adaptive strategies to survive in diverse and hostile environments. For

this reason, they are a huge source of unique chemical and biochemical diversity, and their metabolites are useful for counteracting environmental pressures [4]. Among others, aquatic microorganisms display important mechanisms to counteract UV damage, including avoidance mechanisms, the synthesis of UV-absorbing substances, the enzymatic and non-enzymatic quenching of ROS, and the activation of DNA repairing pathways [5].

Generally, local UV incidence is influenced by the total ozone column, cloudiness, ground reflectivity (i.e., albedo), and local aerosols, but, in Antarctica, surface UV is mostly driven by ozone and albedo effects [6]. In this context, the extreme and remote Antarctic environment offers a unique opportunity to isolate and study UV-resistant microorganisms. In fact, the Antarctic Ocean is characterized by a low attenuation of UV-R, especially during episodes of ozone holes, where surface incidence can increase by 35% [7]. In recent decades, over much of Antarctica, the "ozone hole" has grown in size (up to 27 million km^2 in 2006, which is almost double the area of the Antarctic continent) and duration (from August to early December). Although it recently seemed to be slightly on the decline (15–18 million km^2 in November 2017 [3]), the 2021 Antarctic ozone hole (24 million km^2 in November 2021) has ranked 13th largest since 1979, which is probably due to colder-than-average 2021 stratospheric conditions in the Southern hemisphere (https://www.noaa.gov/news/antarctic-ozone-hole-is-13th-largest-on-record-and-expected-to-persist-into-november, accessed on 16 March 2023).

Therefore, for Antarctic aquatic microorganisms living in one of most inhospitable scenarios on Earth, with extreme temperatures, UV-R, and ice, photoprotective defence mechanisms are fundamental to mitigate the effects of solar radiation of rays B (UV-B) [3]. In fact, UV-resistant Antarctic aquatic bacteria use a non-enzymatic antioxidant defence system, such as the synthesis of pigments, mostly carotenoids, to provide photo-oxidative protection to the cells [8–13]. Behind non-enzymatic antioxidants, other quenching mechanisms used by microorganisms for minimizing UV damage included an efficient enzymatic system to cope with ROS, represented by antioxidants, such as superoxide dismutase (SOD), catalase (CAT), glutathione peroxidase, and other enzymes that can neutralize the effects of radicals [14]. In some cases, the presence of more than one copy of these genes ensures an enhanced antioxidant capacity in the cold environment [14]. Since ROS are formed at a higher abundance as a result of increased oxygen solubility at low temperatures [15], the antioxidant enzyme system also plays an important role in the adaptation to low temperatures in marine cold-adapted microorganisms [3]. Moreover, Antarctic aquatic microorganisms have developed repair mechanisms to correct DNA damage induced by UV-B rays, such as cyclobutane pyrimidine dimers (CPD), photolyases, and 6,4-photolyases [16–20].

However, to date, there is still little information available on photoprotection products from Antarctic organisms, due to the limited accessibility to this extreme ecosystem. The current study aims to expand the still scarce knowledge on the biodiversity of UV-resistant bacterial communities inhabiting Antarctica. Several bacterial genera collected from different Antarctic aquatic sites have here been identified for their UV resistance and phylogenetically identified by molecular approaches.

2. Materials and Methods

2.1. Sampling

Marine surface water, ice, and sediment samples from different coastal areas in Antarctica, listed in Table 1, were collected during the Italian XXIX (January 2014), XXXIII (October–November 2017) and XXXIV (November–December 2018) expeditions at the Mario Zucchelli Station, including different sites in Tethys Bay and Road Bay near the Italian station and 2 sites, Edmonson Point and Inexpressible Island, reached by helicopter.

All samples were collected in duplicate into sterile 50 mL conical tubes and stored at +4 °C and −20 °C until further use. In some cases (where possible for logistical constraints), 5–10 L of surface water were also collected, filtered (0.45 μm) by a peristaltic pump, and stored in 20% glycerol at −80 °C.

Table 1. Collection sites, samples, expeditions, and geographic coordinates are reported.

Collection Site	Location	Samples	Expedition	Coordinates
Site 1	Tethys Bay	Surface sea water/ice	XXXIII	S 74°42′03.8″ E 164°02′32.5″
Site 2	Tethys Bay	Surface sea water [1]	XXXIII	S 74°42′00.2″ E 164°02′34.8″
Site 3	Tethys Bay	Surface sea water/ice	XXXIV	S 74°41′13.98″ E 164° 2′11.76″
Site 4	Road Bay	Surface sea water [1]	XXXIII	S 74°41′47.2″ E 164°07′16.1″
Site 5	Inexpressible Island	Surface sea ice	XXXIII	S 74°53′46.7″ E 164°44′26.3″
Site 6	Inexpressible Island	Surface sea water	XXXIII	S 74°53′47.1″ E 163°44′27.2″
Site 7	Inexpressible Island	Surface sea water/ice	XXXIV	S 74°53′45.60″ E 63°44′31.68″
Site 8	Inexpressible Island	Surface sea water/ice	XXXIV	S 74°53′47.94″ E 63°44′37.80″
Site 9	Edmonson Point	Surface sea water	XXXIII	S 74°19′57.4″ E 165°08′52.1″
Site 10	Edmonson Point	Surface sea water/ice	XXXIV	S 74°19′24″ E 166°07′12″
Site 11	Edmonson Point	Surface sea water/ice	XXXIV	S 74°19′44″ E 165°25′40″
Site 12	Edmonson Point	Shallow lake sediments	XXIX	S 74°20′11.12″ E 65°07′53.02″

[1] In these collection sites, 5–10 L of surface water were collected, filtered (0.45 µm) by a peristaltic pump, and stored in 20% glycerol.

2.2. Media

Marine Broth (MB) and R2A media were those of Conda Pronadisa (Madrid, Spain). The Luria–Bertani (LB) growth medium (per litre) contained bacto-tryptone 10.0 g (VWR, Leuven, Belgium), yeast extract 5.0 g (Applichem, Darmstadt, Germany), and sodium chloride 10.0 g (Applichem, Darmstadt, Germany). The TGY growth medium (per litre) contained bacto-tryptone 3.0 g (VWR, Leuven, Belgium), yeast extract 3.0 g (Applichem, Darmstadt, Germany), glucose 3.0 g (Applichem, Darmstadt, Germany). For solid media, 15 g of bacteriological agar (VWR, Leuven, Belgium) was added to 1 L of liquid medium.

2.3. Isolation and Selection of UV-Resistant Bacteria by UV-C Assay

The isolation of UV-resistant bacteria was carried out as previous described by [21]. Briefly, 100 µL of each marine water/melted ice sample or 100 µL aliquots stored in 20% glycerol were incubated into 0.9 mL of MB and R2A at 15 °C, 180 rpm, for 1 week. After that, bacterial cells were serially diluted ten-fold until 10^{-6} in MB and R2A. Moreover, 1 g of each sediment sample was suspended in 9 mL of sterile sea water, vigorously stirred by vortexing and incubated at 15 °C, 180 rpm, overnight. The supernatant was serially diluted tenfold until 10^{-6} in sterile sea water.

Aliquots (100 µL) of each sample prepared as described above were spread in duplicate on Marine Agar (MA) and R2A agar plates. One plate for each sample was exposed to UV-C irradiation for 45 s (corresponding to 0.135 J/cm^2) inside a Bio-Link crosslinker and, subsequently, incubated at 15 °C for 1 week (or more, if necessary). After that, only the UV-resistant colonies were visible on plates. On the contrary, one plate for each sample was incubated directly at 15 °C without UV exposure and used as negative control.

A UV-C assay was performed as previously described by [21] to characterize the UV resistance of Antarctic bacteria. Identified bacterial isolates were grown in MB or R2A broth at 15 °C with constant shaking until an OD_{600} ~0.3 was reached [22]. Then, 100 µL of each culture were plated in MA or R2A agar (in triplicates). Each plate was exposed to UV-C irradiation for 0, 1, 2, and 3 min (corresponding to 0, 0.180, 0.360, and 0.540 J/cm^2, respectively) inside a Bio-Link crosslinker and then incubated at 15 °C for 1 week. Some strains, which were very resistant (showing more colonies on plates after 3 min of UV-C irradiation), were also exposed to UV-C for 4, 5, and 6 min (corresponding to 0.720, 0.900, and 1.08 J/cm^2, respectively) and incubated at 15 °C for 1 week [21]. The same protocol was used for *Escherichia coli* MG1655 (UV-C sensitive) and *Deinococcus radiodurans* (UV-C resistant), as negative and positive controls, respectively. They were grown at 37 °C in LB (*E. coli*) or at 30 °C in TGY (*D. radiodurans*); colonies were visible on plates after only 2–4 days [21].

2.4. PCR Amplification of 16S rRNA Gene of UV-Resistant Bacteria

Selected isolates (from the plates exposed to UV), resistant to UV-C irradiation for 45 s (0.135 J/cm2) (Section 2.2), were identified by 16S rRNA sequencing. UV-resistant Antarctic bacterial colonies, grown overnight at 15 °C on MA or R2A agar plates, were resuspended in 50 µL of sterile distilled water, frozen for 60 min, then heated to 95 °C for 10 min, and cooled on ice for 5 min. PCR amplification of 16S rDNA gene was carried out using universal primers 27F (5′-AGAGTTTGATCCTGGCTCAG-3′) and 1492R (5′-GGTTACCTTGTTACGACTT-3′) designed from the conserved bacterial sequences at the 5′ and 3′ ends of the 16S rRNA gene of *Escherichia coli* rDNA, thus allowing the amplification of nearly the entire gene [23]. The reaction mix consisted of 1 µL of PCR colony as template, 1.25 µL of each primer, 5 µL of Q5® High-Fidelity Reaction Buffer (New England Biolabs), 0.5 µL of dNTP, 0.25 µL of Q5® High-Fidelity DNA Polymerase (New England Biolabs) and 15.75 µL of molecular grade water. The amplification steps included initial denaturation at 98 °C for 3 min, 35 cycles at 98 °C for 10 s, 60 °C for 30 s, 72 °C for 40 s, and a final extension at 72 °C for 10 min.

The PCR products were analysed on 1% agarose gel and checked by sequencing of both strands by a commercial sequencing service (Eurofins Genomics, Ebersberg, Germany). Other universal bacterial primers were used to sequence the initial (518R: 5′-GTATTACCGCGGCTGCTGG-3′) and the final (967F: 5′-CAACGCGAAGAACCTTACC-3′) parts of the 16S rRNA gene [24].

2.5. Identification and Phylogenetic Analysis

The sequences of 16S rRNA obtained from the bacterial isolates were analysed with the BioEdit program and compared with sequences deposited in the NCBI GenBank database by using the BLASTn tool. Furthermore, evolutionary analyses were conducted using Molecular Evolutionary Genetics Analysis (MEGA) version 6 [25] with Clustal W sequence alignments [26]. The evolutionary history was inferred by using the Maximum Likelihood method based on the Jukes–Cantor model [27].

Each 16S rRNA gene sequence was deposited in the NCBI GenBank database under the accession numbers shown in Table 2 and in the phylogenetic trees.

3. Results ad Discussion

3.1. Sampling

Sampling was performed in several marine coastal sites in Victoria Land (Figure 1a,b), a region in eastern Antarctica, which fronts the western side of the Ross Sea (Southern Ocean) and is the most extensive continental shelf ecosystem South of the Antarctic Polar Front.

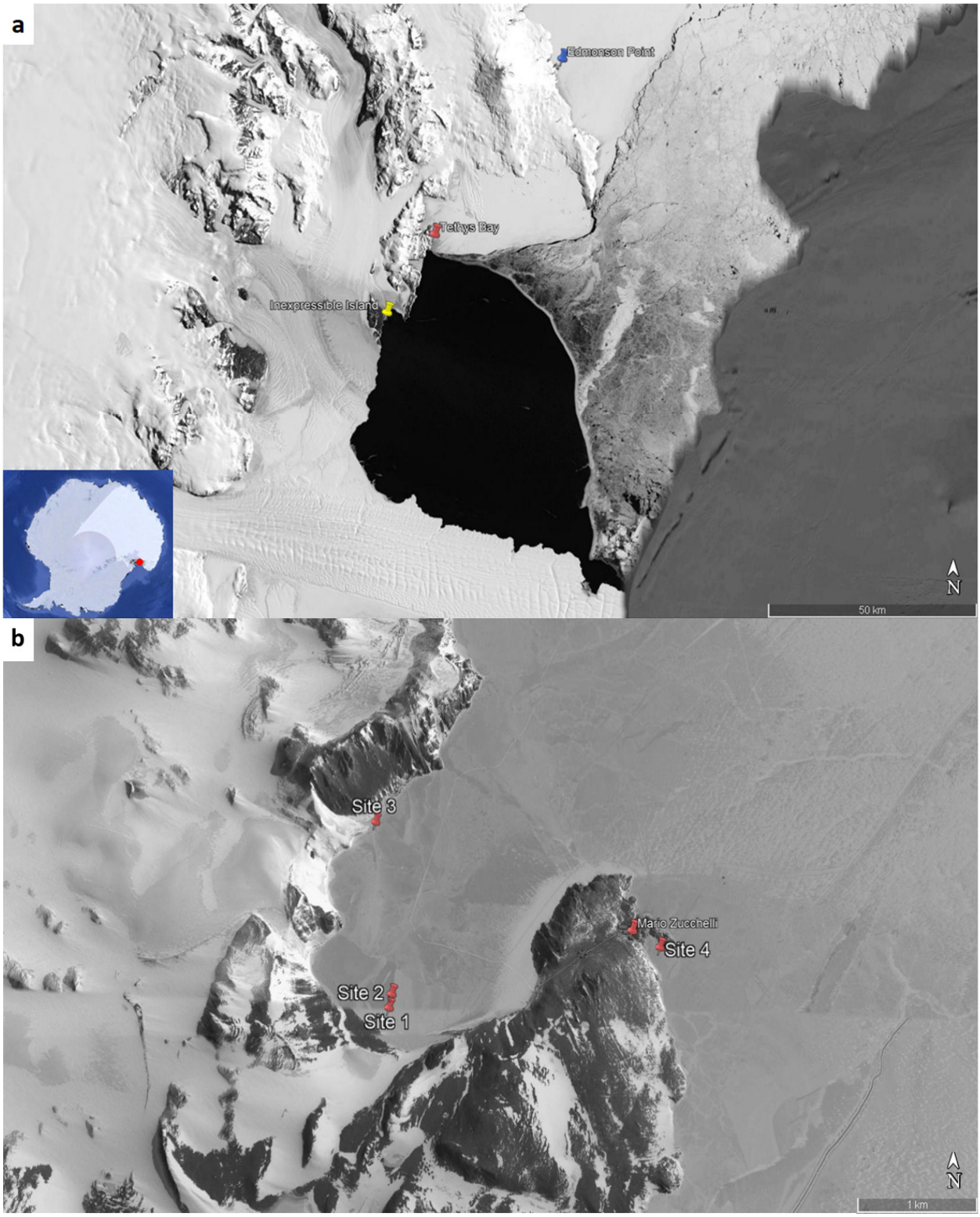

Figure 1. Map of Victoria Land, Ross Sea, Antarctica. (**a**) Collection coastal areas in Tethys Bay (red site), Inexpressible Island (yellow site), and Edmonson Point (blue site), scale bar = 50 km. (**b**) Collection sites in Tethys Bay: scale bar = 1 km. In each location, collection sites were numbered as indicated in Table 1.

This area is characterized by the rigid Antarctic climate, with the average monthly air temperature ranging between −25.9 °C (August) and −0.1 °C (January). Furthermore,

there is complete darkness during winter (from May to August) and 24 h of light during the summer (from October to February), with December and January showing the maximum monthly average radiation, corresponding to 320 and 300 Wm^{-2}, respectively [28].

Sea water/ice sampling was carried out in different sites of Tethys Bay (Figure 1a,b, red sites 1, 2, and 3) and Road Bay (Figure 1b, red site 4), in the surroundings of the Mario Zucchelli Station, the Italian seasonal research station, located at Terra Nova Bay, Ross Sea. The bay is a coastal marine area encompassing 29.4 km^2, which is very important for scientific investigations in Antarctica. It is generally free of ice during the summer due to the western katabatic winds that blow from the plateau towards the sea.

Sea water/ice sampling was also performed in the Inexpressible Island area (Figure 1a, yellow site). Site 5 is far from the others (around 30 km) whereas sites 6, 7, and 8 are about 200 m from each other. It is almost completely free from glaciers and culminates at 390 m.

Sea water/ice sampling was also performed in the Edmonson Point area (Figure 1a, blue site), located approximately 50 km NE of the Mario Zucchelli Station, in Wood Bay, Ross Sea. Site 10 is far at around 20 km from site 11, whereas site 11 is about 5 km from sites 9 and 12. These latter sites are about 500 m from each other. Edmonson Point is covered by hills, knolls, and moraines of volcanic material, and it is divided by small valleys with streams, ponds, and lakes [28]. In general, the soil is dark in colour, which favours the melting of snow in spring; in summer, there are some shallow lakes free of ice cover, while deeper lakes are permanently frozen. Generally, Antarctic lakes are dominated by microbial organisms, including bacteria, protozoa, and phytoplankton [29,30], of which little information is available. Interestingly, they include freshwater and saline systems that have experienced little or no anthropogenic impact and, therefore, harbour pristine biotopes. In this area, in addition to sea water sampling, sediments from a shallow lake, which was free of ice, were sampled as well (site 12).

3.2. Isolation and Identification of UV-Resistant Bacteria by UV-C Assay

In order to obtain cultivable UV-resistant bacteria, each sea water/melted ice sample or sediment sample collected from different sites in Antarctica was prepared as described previously (Section 2.2). Several colonies were present on all MA plates subjected to UV-C irradiation, whereas very few bacterial isolates were present on the R2A agar plates. On the contrary, bacteria, incubated directly at 15 °C for 1 week and not exposed to UV-C rays, grew to confluence on the plates (no UV-C control plate).

The tolerance to UV-R of all the isolates obtained was studied by exposing them to UV-C radiation for different times (from 1 to 3 min corresponding to 0.180, 0.360, and 0.540 J/cm^2, respectively), as shown in Table 2. The four most UV-C resistant isolates derived from surface sediment samples, which showed more colonies on plates after 3 min of UV-C irradiation, were exposed to UV-C for longer times (from 4 to 6 min) and compared with the positive control *D. radiodurans* (UV-C resistant) [21]. As shown in Table 2, these strains still displayed colonies after up to 6 min of exposure to UV-C.

All bacterial UV-C-resistant strains were identified by 16S rRNA sequencing, and their sequences were compared with the closest relatives of isolates deposited in the NCBI GenBank database using the BLASTn tool to determine their taxonomical relationships (Table 2). Comparative sequence analysis indicated that the UV-C resistant Antarctic bacteria were closely related to known bacteria with a 16S rRNA sequence homology >99%.

The bacterial strains belonged to Proteobacteria (class Alpha and Gammaproteobacteria), Actinobacteria (class Actinobacteria), and Firmicutes (class Bacilli) phyla (Table 2). The results revealed that the 31 isolates were representative of 15 bacterial genera: 5 of which were Gram negative (*Brevundimonas*, *Qipengyuania*, *Sphingorhabdus*, *Sphingobium*, and *Psychrobacter*) and 10 of which were Gram positive (*Staphylococcus*, *Bacillus*, *Mesobacillus*, *Kocuria*, *Gordonia*, *Rhodococcus*, *Micrococcus*, *Arthrobacter*, *Agrococcus*, and *Salinibacterium*).

Table 2. UV-resistant bacterial strains isolated from Antarctic marine and lake environments.

Strain	Pigmentation	Sample Source-Collection Site	Identification by 16S rRNA	UV-C Resistance (min)	Accession Number (AN)	Next Relative by GenBank Alignment (AN, Organism)	Sequence Homology (%)
Phylum PROTEOBACTERIA							
Class Alphaproteobacteria (Gram negative)							
RA4	Reddish orange	Lake sediments—Edmonson Point (site 12)	*Brevundimonas* sp.	6	OQ540805	EF093132.1, *Brevundimonas* sp. VTT E-052914	99.93
ED-ICE-A-RA1	Reddish orange	Sea ice—Edmonson Point (site 10)	*Brevundimonas* sp.	3	OQ540806	EF093132.1, *Brevundimonas* sp. VTT E-052914	99.79
IN-H2O-B-RA3	Reddish orange	Sea water—Inexpressible Island (site 8)	*Brevundimonas* sp.	3	OQ540807	AJ244710.1, *Brevundimonas* sp. V4.BP.05	100
H2O-2-80-G2	Brilliant yellow	Sea water/ice—Tethys Bay (site 1)	*Qipengyuania* sp.	3	OQ540808	MZ749497.1, *Qipengyuania aerophila* GH25	100
G5G	Yellow	Lake sediments—Edmonson Point (site 12)	*Sphingorhabdus* sp.	6	OQ540809	MN255826.1, *Sphingorhabdus soli* D-2Q-5-6	100
A1G	Yellow	Lake sediments—Edmonson Point (site 12)	*Sphingorhabdus* sp.	6	OQ540810	MN255826.1, *Sphingorhabdus soli* D-2Q-5-6	100
AM-0m-G3 [1]	Pale yellow	Sea ice—Tethys Bay (site 3)	*Sphingobium* sp.	3	OQ540811	CP016456.1, *Sphingobium* sp. RAC03	100
Class Gammaproteobacteria (Gram negative)							
IN-H2O-A-2BE6	Creamy	Sea water—Inexpressible Island (site 7)	*Psychrobacter* sp.	2	OQ540812	EU196303.1, *Psychrobacter* sp. NP52	99.64
IN-ICE-A-A1B	Beige	Sea ice—Inexpressible Island (site 7)	*Psychrobacter* sp.	2	OQ540813	CP012533.1, *Psychrobacter* sp. P11G5	99.87
H2O-1-80-BE1	Beige	Sea water—Edmonson Point (site 9)	*Psychrobacter* sp.	3	OQ540814	ON209525.1, *Psychrobacter okhotskensis* PCRB17b	99.86
IN-ICE-A-A1G	Creamy	Sea ice—Inexpressible Island (site 7)	*Psychrobacter* sp.	1	OQ540815	FR750957.1, *Psychrobacter nivimaris* CMS161	99.66
Gly6-2-BE4	Beige	Sea water—Tethys Bay (site 2)	*Psychrobacter* sp.	3	OQ540816	KU579272.1, *Psychrobacter nivimaris* OUCMDZ4219	99.93
Gly9-1-BE7	Beige	Sea water—Road Bay (site 4)	*Psychrobacter* sp.	1	OQ540817	CP106752.1, *Psychrobacter* sp. SC65A.3	100

Table 2. *Cont.*

Strain	Pigmentation	Sample Source-Collection Site	Identification by 16S rRNA	UV-C Resistance (min)	Accession Number (AN)	Next Relative by GenBank Alignment (AN, Organism)	Sequence Homology (%)
Phylum FIRMICUTES							
Class Bacilli (Gram positive)							
B-MEP	White	Sea water—Edmonson Point (site 9)	*Staphylococcus* sp.	2	OQ540818	CP054831.1, *Staphylococcus saprophyticus* UTI-045	99.93
G-MEP	Pale Yellow	Sea water—Edmonson Point (site 9)	*Staphylococcus* sp.	2	OQ540819	CP054831.1, *Staphylococcus saprophyticus* UTI-045	99.93
H2O-2-80-R3W	White	Sea water/ice—Tethys Bay (site 1)	*Staphylococcus* sp.	1	OQ540820	MN826459.1, *Staphylococcus saprophyticus* TA1	100
ED-ICE-B-R1B	Translucent white	Sea ice—Edmonson Point (site 11)	*Mesobacillus* sp.	1	OQ540821	KY202702.1, *Mesobacillus subterraneus* A9	99.86
ED-ICE-A-RA1B	Translucent white	Sea ice—Edmonson Point (site 10)	*Bacillus* sp.	3	OQ540822	MT332156.1, *Bacillus cereus* DBA1.1	100
Phylum ACTINOBACTERIA							
Class Actinobacteria (Gram positive)							
H2O-1-80-G1	Brilliant yellow	Sea water—Edmonson Point (site 9)	*Kocuria* sp.	3	OQ540823	AM237350.1, *Kocuria carniphila* OS-32.d1	99.93
IN-H2O-A-BE6R	Red coral	Sea water—Inexpressible Island (site 7)	*Kocuria* sp.	1	OQ540824	AM418390.1, *Kocuria* sp. 29Y1zhy	99.93
IN-ICE-B-MR1A	Red coral	Sea ice—Inexpressible Island (site 8)	*Kocuria* sp.	1	OQ540825	CP035103.1, *Kocuria rosea* ATCC 186	99.93
H2O-1-80-R1	Brilliant orange	Sea water—Edmonson Point (site 9)	*Gordonia* sp.	1	OQ540826	CP049836.1, *Gordonia terrae* RL-JC02	99.86
H2O-2-80-R4	Brilliant orange	Sea water/ice—Tethys Bay (site1)	*Gordonia* sp.	1	OQ540827	CP049836.1, *Gordonia terrae* RL-JC02	100
H2O-10-G4	Yellowish orange	Sea water—Tethys Bay (site 2)	*Rhodococcus* sp.	1	OQ540828	JX428873.1, *Rhodococcus* sp. ZS333	99.80
H2O-19-G5	Brilliant yellow	Sea water—Inexpressible Island (site 6)	*Micrococcus* sp.	3	OQ540829	CP097650.1, *Micrococcus yunnanensis* TT9	99.86

Table 2. *Cont.*

Strain	Pigmentation	Sample Source-Collection Site	Identification by 16S rRNA	UV-C Resistance (min)	Accession Number (AN)	Next Relative by GenBank Alignment (AN, Organism)	Sequence Homology (%)
ED-ICE-B-R1G	Brilliant yellow	Sea ice—Edmonson Point (site 11)	*Micrococcus* sp.	2	OQ540830	CP043842.1, *Micrococcus luteus* NCCP 16831	99.79
ED-ICE-B-G2	Brilliant yellow	Sea ice-Edmonson Point (site 11)	*Arthrobacter* sp.	2	OQ540831	KR085775.1, *Arthrobacter flavus* IHBB 9551	100
ED-ICE-B-R1	Brilliant red	Sea ice—Edmonson Point (site 11)	*Arthrobacter* sp.	1	OQ540832	JX949321.2, *Arthrobacter cheniae*	99.73
R5	Brilliant red	Lake sediments—Edmonson Point (site 12)	*Arthrobacter* sp.	6	OQ540833	KU921543.1, *Arthrobacter agilis* IHBB 9979	99.66
IN-ICE-A-G6 [1]	Creamy	Sea ice—Inexpressible Island (site 7)	*Agrococcus* sp.	2	OQ540834	MW580037.1, *Agrococcus* sp. AHE_PA_072	99.72
H2O-17-M1-G6	Brilliant yellow	Sea ice—Inexpressible Island (site 5)	*Salinibacterium* sp.	2	OQ540835	MK140978.1, *Salinibacterium* sp. s4a41-10	99.86

[1] These strains were isolated and grown in R2A medium.

Strains affiliated with Proteobacteria and Actinobacteria phyla were detected in all sites and were the most abundant species in all of the different environments included in this study, as has already been reported in other Antarctic environments [31–33]. Affiliates to the genera *Psychrobacter* (among the Gammaproteobacteria) appeared to be predominant in all investigated Antarctic sites. Conversely, isolates belonging to Actinobacteria appeared to be the most diverse and rich in species among all the collected sites. Interestingly, Alpha and Gammaproteobacteria species, which are more traditionally associated with the marine environment, were also isolated from the lake sediment (Edmonson Point, Sites 12). Considering the proximity of the lake to the sea, it is not excluded that there was a contribution of bacteria from the marine environment to the Antarctic Lake through atmospheric deposition (aerosols) and/or seabird droppings [30,34,35].

Interestingly, 20 of 31 isolates showed pigmentation exhibiting various colours with different shades ranging from brilliant red to brilliant orange, to reddish or yellowish orange, and from pale yellow to brilliant yellow and yellowish. The other 11 strains were not pigmented, showing from cream to translucent white colonies (Figure 2, Table 2). The colonies of *Arthrobacter* spp. exhibited different colors, including brilliant yellow (ED-ICE-B-G2) and brilliant red (ED-ICE-B-R1 and R5) with colonies of *Kocuria* spp. that were brilliant yellow (H2O-1-80-G1) and red coral (IN-H2O-A-BE6R and IN-ICE-B-MR1A), as has already been reported for both strains [36,37].

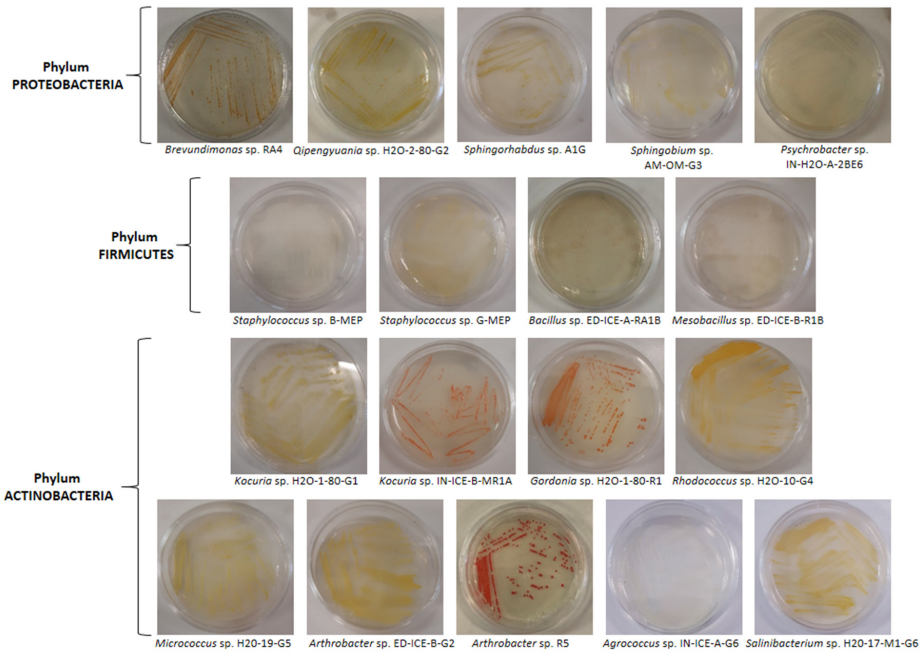

Figure 2. Representative Antarctic UV-resistant bacteria belonging to different genera and showing different pigmentation.

Bacterial pigmentation is determined by the expression of pigments that, in many cases, are represented by carotenoid-type compounds, which are often involved in the protective role against the negative effects of UV-R [3,12]. As chemical quenchers of singlet oxygen, they function as potent scavengers of ROS [38]. In addition to being essential constituents of photosynthetic organisms (e.g., plants, algae, and cyanobacteria) [39], in heterotrophic bacteria, carotenoids provide protection against exposure to solar UV and freeze–thaw cycles [40]. In the Antarctic environment, they may contribute to membrane stability by maintaining proton permeability and augmenting oxidative stress resistance [41,42]. The presence of carotenoids has been already reported in the literature for most genera studied in this work (see below Section 3.3).

Bacterial pigments are promising and sustainable bioactive compounds, which may be used in cosmetics, food, textiles, printing, and pharmaceutical products [43–45]. They

can be produced from bacterial sources easily and cheaply, compared to plant sources, obtaining a huge biomass by culturing them in controlled conditions in bioreactors [44,46]. For their wide range of applications in different industries, bacterial pigments are getting more attention in the global pigments market (https://www.grandviewresearch.com/industry-analysis/dyes-and-pigments-market, accessed on 16 March 2023) and in the global carotenoids market (https://www.researchandmarkets.com/reports/5682374/carotenoids-market-global-industry-trends, accessed on 16 March 2023). Among bacteria, marine species are a valuable source of these pigments with potential cosmeceutical and nutraceutical applications [46–49].

3.3. Diversity of UV-Resistant Antarctic Aquatic Bacteria and Phylogenetic Analysis

A phylogenetic tree made by using the 16S rRNA gene sequences of Antarctic marine and lake bacterial strains was constructed by using the Maximum Likelihood method based on the Jukes–Cantor model (bootstrap 500), Figure 3.

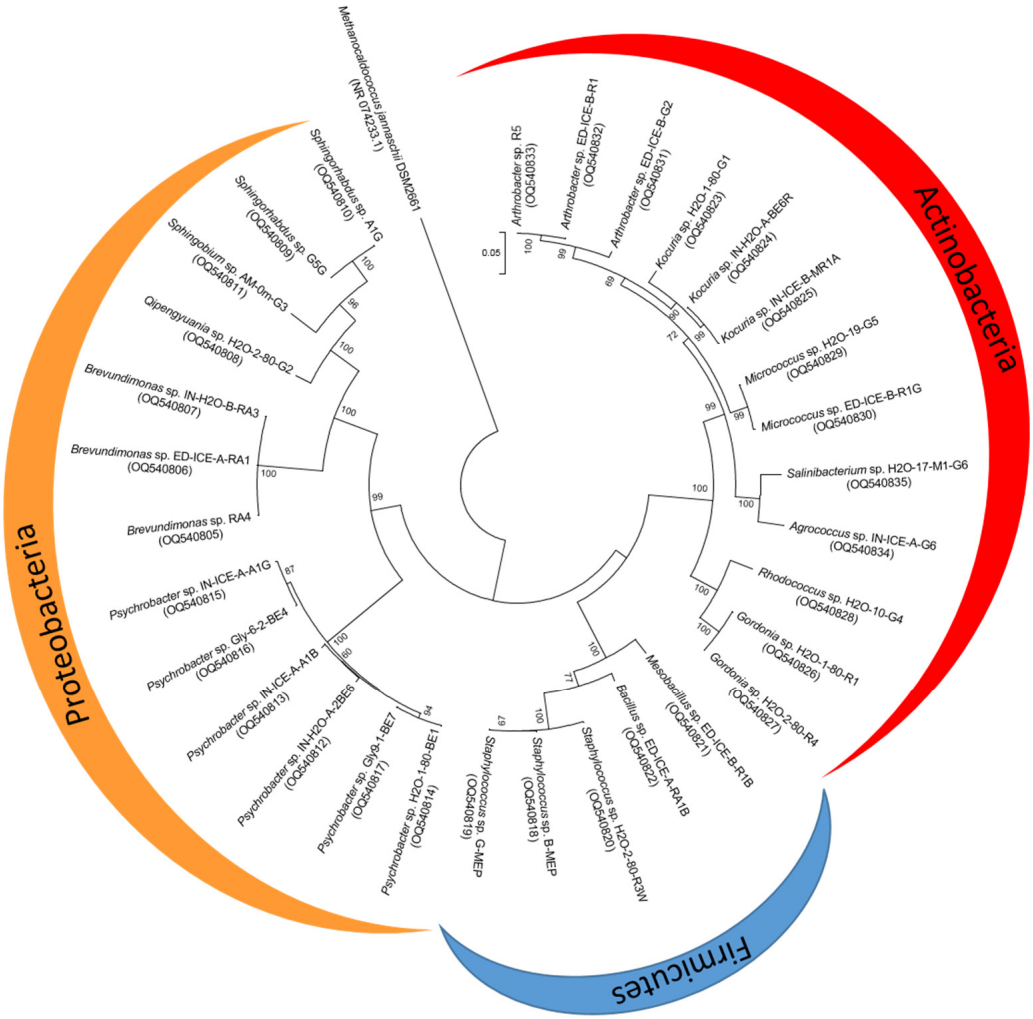

Figure 3. 16S rRNA genes phylogenetic tree created using the Maximum Likelihood method based on the Jukes–Cantor model of Antarctic UV-resistant bacteria isolated from marine and lake environments. The percentage of trees in which the associated taxa clustered together in the bootstrap test (500 replicates) is shown next to the branches (values below 50% are not shown). The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. The analysis involved 1257 positions in the final dataset. All positions containing gaps and missing data were eliminated. The tree was outgrouped with the 16S rRNA gene sequence of *Methanocaldococcus jannaschii* DSM2661 (NR_074233.1). All accession numbers are in parentheses.

The analysis of the phylogenetic tree revealed the presence of two distinct phylogenetic clusters, one split into Gram-negative Proteobacteria phylum and the other including Gram-positive Actinobacteria and Firmicutes phyla. In the cluster of Gram positive bacteria, the Firmicutes phylum was split into a separate group of *Staphylococcus*, *Bacillus,* and *Mesobacillus*.

To further investigate the evolutionary relatedness between each strain and other members of the same genus, representative sequences (5 for each strain with the highest percentage of identity sequence) were downloaded from the NCBI to build phylogenetic trees (Figures 4–6).

3.3.1. Actinobacteria

Phylogenetic studies of the bacteria belonging to the Phylum Actinobacteria revealed that the tree was split in two lineages. The first one divided in many subgroups comprising *Arthrobacter*, *Kocuria*, *Micrococcus, Agrococcus*, and *Salinibacterium* spp., whereas the second clade was divided in two subgroups represented by *Rhodococcus* and *Gordonia* spp. (Figure 4).

Arthrobacter, *Micrococcus*, and *Kocuria* species are aerobic Gram-positive bacteria of the family Micrococcaceae, and they all show interesting characteristics of UV-R resistance. Phylogenetic studies, supported by BLAST analyses of 16S rRNA gene sequences, indicated that the strains R5, ED-ICE-B-R1, and ED-ICE-B-G2 grouped together in the *Arthrobacter* clade, which was subdivided into two subgroups. One group comprised the red-pigmented R5 and ED-ICE-B-R1, which shared 99.53% of 16S rRNA gene sequence identity and were closely related to the red-pigmented *Arthrobacter agilis* strain IHBB 9979 [50] and *Arthrobacter cheniae* strain [51], respectively. The other group comprised the yellow-pigmented ED-ICE-B-G2, which was closely related to the yellow Antarctic *Arthrobacter flavus* strain IHBB 9551 [52] and shared 100% sequence identity with it (Figure 4).

Members of the genus *Arthrobacter* were among the most frequently isolated bacteria in extreme cold environments ranging from the Antarctic to Arctic and Himalaya, and they are well known for their metabolic versatility and wide prevalence in stressful environments [53–56]. This genus is a good carotenoid producer. For example, different carotenoids with high antioxidant activity and good stability under exposure to UV light were isolated from the Antarctic bacteria *Arthrobacter agilis* 50cyt and *Arthrobacter psychrochitiniphilus* 366 [57]. Other Antarctic isolates of *Arthrobacter agilis* produce the red carotenoid bacterioruberin and a C50 hydrocarbon known as tetraanhydrobacterioruberin [41]. The rare C50 carotenoid bacterioruberin in *Arthrobacter agilis* DSM 20550^{T} and *Arthrobacter bussei* DSM 109896^{T} has been reported to modulate membrane fluidity, thereby increasing cell resistance to freeze–thaw stress [58]. *Arthrobacter* sp. P40 strains, isolated from Fildes Peninsula in King George Island, produced C50 carotenoids, such as decaprenoxanthin and its glucosylated derivatives, as well as lycopene used as synthesis precursors of C50 carotenoids [59]. Other strains, *Arthrobacter* sp. QL17 and *Arthrobacter* sp. G20, produced carotenoids with possible applications in the food and pharmaceutical industries [60,61].

Arthrobacter genomes isolated from Antarctic soils contained several genes that conferred protection from free radical damage and from ROS. Among them, there were up to two copies of the SOD gene and up to three copies of the CAT gene, as well as several copies of the peroxiredoxin gene and thioredoxin genes [54]. Other Antarctic *Arthrobacter* strains showed the presence of genes encoding proteins involved in the DNA repair system in response to DNA damage caused by UV-R [62].

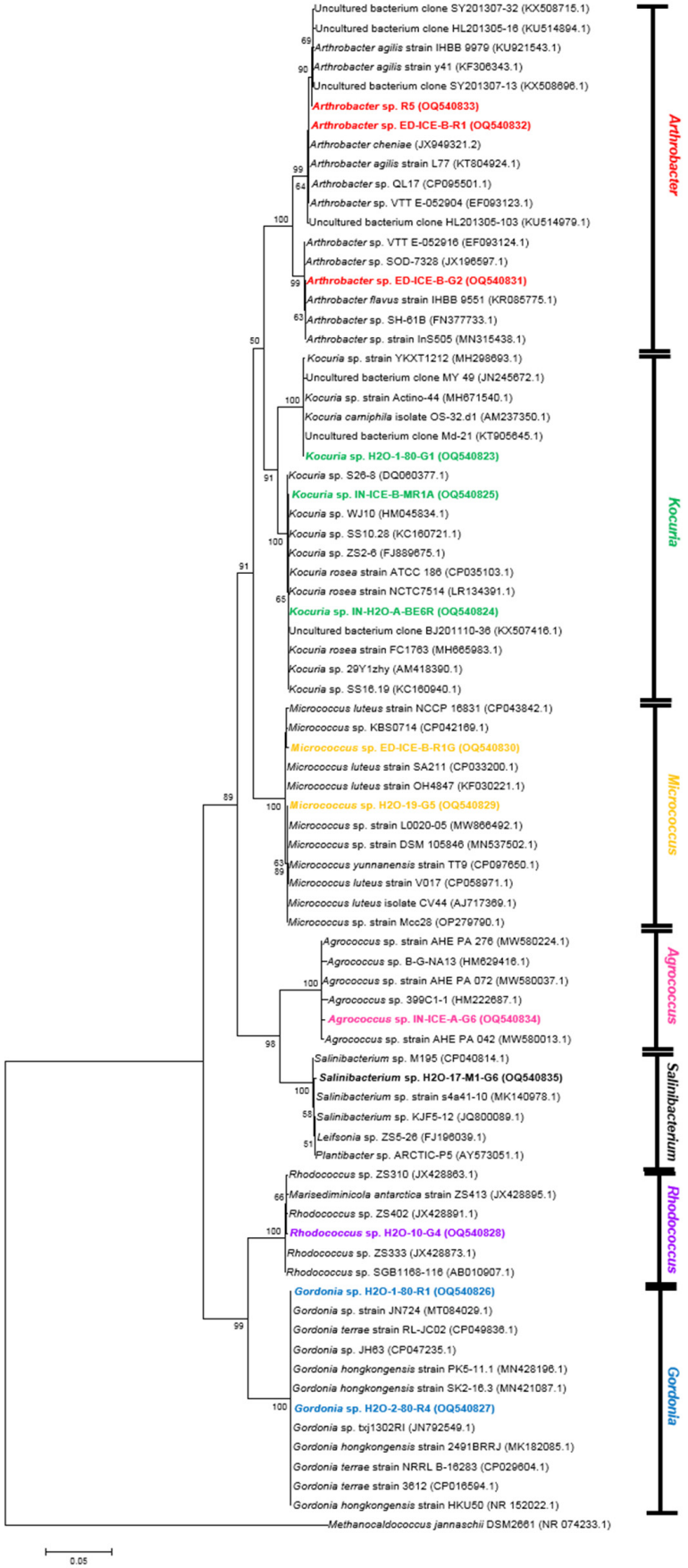

Figure 4. 16S rRNA genes phylogenetic tree created using the Maximum Likelihood method based

on the Jukes–Cantor model of Antarctic UV-resistant bacteria isolated from marine and lake environments affiliated with Actinobacteria. The percentage of trees in which the associated taxa clustered together in the bootstrap test (500 replicates) is shown next to the branches (values below 50% are not shown). The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. The analysis involved 1319 positions in the final dataset. All positions containing gaps and missing data were eliminated. The tree was outgrouped with the 16S rRNA gene sequence of *Methanocaldococcus jannaschii* DSM2661 (NR_074233.1). All accession numbers are in parentheses.

In the phylogenetic tree (Figure 4), *Kocuria* species, IN-ICE-B-MR1A, IN-H2O-A-BE6R, and H2O-1-80-G1, grouped together within the genus *Kocuria* and shared a high sequence identity of 16S rRNA genes between them (from 96.3–99.9%) (Figure 4). As occurred for *Arthobacter*, they were subdivided into two groups—one group consisting of the yellow-pigmented H2O-1-80-G1, which is closely related to the yellow *Kocuria carniphila* [63], and a second group comprising the two red coral IN-ICE-B-MR1A and IN-H2O-A-BE6R, which are closely related to the pink *Kocuria rosea* (CP035103.1), which is capable of tolerating extreme conditions [64]. The genus *Kocuria*, which was generated by the taxonomic dissection of the genus *Micrococcus* [65], included species resistant to gamma-irradiation [66] and UV-C radiation [64] with the ability to produce relatively large quantities of CAT [67]. *Kocuria* sp. 301 showed high resistance against UV-R, comparable to the remarkably radiotolerant *D. radiotolerans*, free radicals and desiccation [68]. Studies conducted on the carotenoids extracted from the *Kocuria marina* DAGII strain showed a higher antioxidant activity compared to β−carotene, thus suggesting several potential applications [69].

In this study, the yellow H2O-19-G5 and ED-ICE-B-R1G isolates, which shared 99.6% of 16S rRNA gene sequence identity, were grouped within the cluster of the *Micrococcus* genus (Figure 4). The *Micrococcus* sp. ED-ICE-B-R1G was closely related to *Micrococcus luteus* NCCP 16831 and *Micrococcus* sp. KBS0714, and the latter is resistant to environmental stressors [70]. Strains belonging to the genus *Micrococcus* are commonly found in temperate soil, water, mammalian skin, Antarctic ice, and desert soil, which is probably due to the ability of these bacteria to form biofilms or enter dormant stages following conditions such as desiccation and starvation [70–72].

Agrococcus and *Salinibacterium* species belong to the same family Microbacteriaceae. In Figure 4, they were grouped together and subdivided in two subgroups. *Agrococcus* sp. IN-ICE-A-G6, isolated in R2A medium, clustered tightly with species of marine *Agrococcus* isolated from the North Sea (AHE_PA_276, AHE_PA_072, AHE_PA_042). The yellow *Salinibacterium* sp. H2O-17-M1-G6 grouped closely to *Salinibacterium* sp. KJF5-12, which were isolated from the subarctic glacial Fjord Kongsfjorden [73], and *Leifsonia* sp. ZS5-26 isolated from Antarctic sea ice.

The genus *Salinibacterium* has mainly been isolated from sea water samples from the East Sea, from frozen soil from a Chinese glacier, and from Antarctic sediments or green snow [74–77]. Members of the bacterial genus *Agrococcus* are globally distributed and found across diverse environments, including polar ones [78]. Both genera are potentially able to produce carotenoids. *Salinibacterium* strains isolated from the Fildes Peninsula in King George Island presented a pigment profile composed of the carotenoid C.p. 450 free form and its glucosylated derivatives [59]. The *Agrococcus pavilionensis* strain RW1, which was isolated from microbialite collected in Pavilion Lake, British Columbia, was screened for genes involved in carotenoid production, and they had the genetic potential to produce lycopene, β-carotene, canthaxanthin, echinenone, and zeaxanthin or astaxanthin [79]. In this study, the isolated strain of *Agrococcus* sp. IN-ICE-A-G6 showed no pigmentation with creamy colonies isolated on R2A agar (Figure 2).

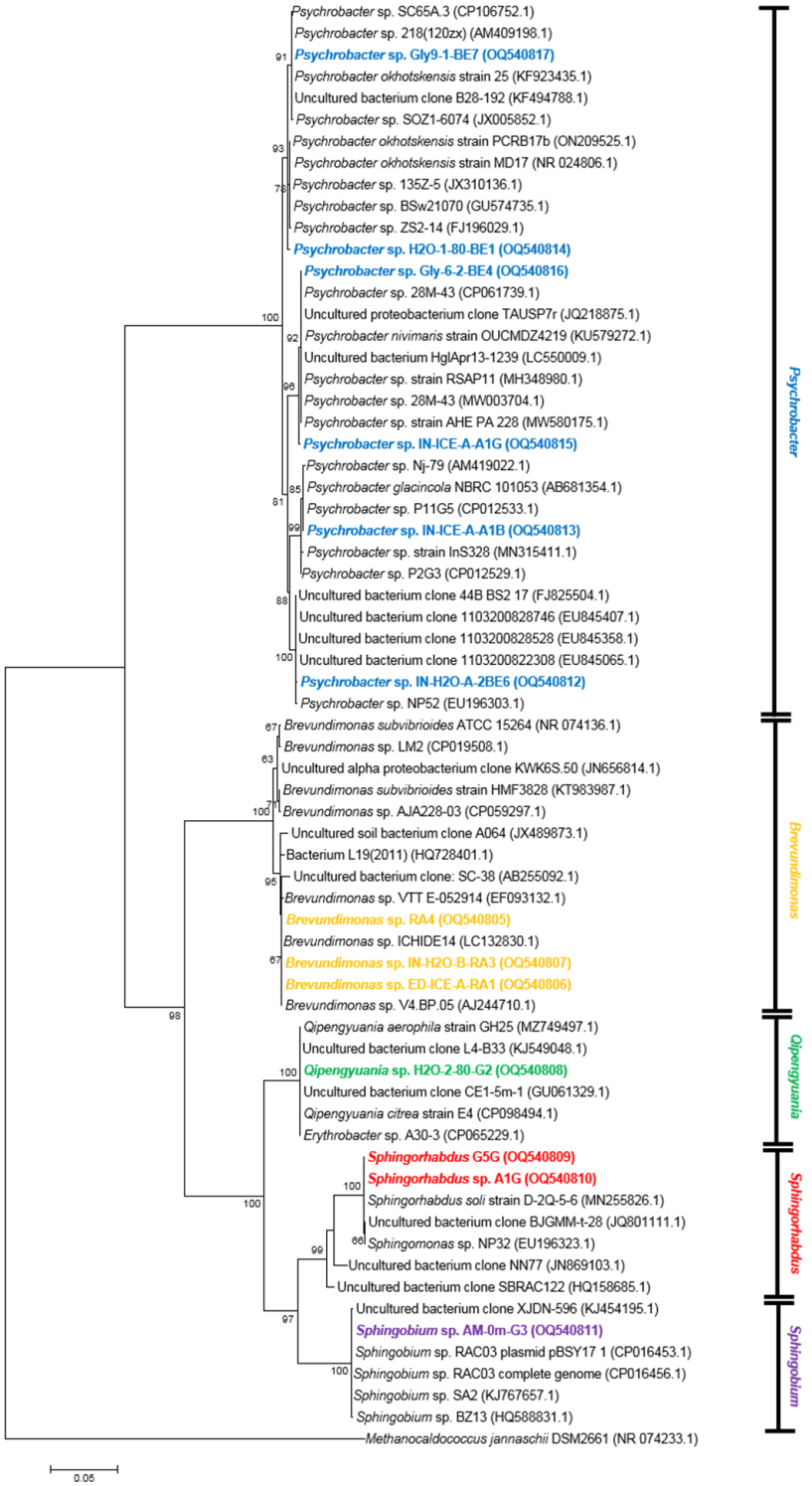

Figure 5. 16S rRNA genes phylogenetic tree created using the Maximum Likelihood method based on the Jukes–Cantor model of Antarctic UV-resistant bacteria isolated from marine and lake environments affiliated with Proteobacteria. The percentage of trees in which the associated taxa clustered together in the bootstrap test (500 replicates) is shown next to the branches (values below 50% are not shown). The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. The analysis involved 1274 positions in the final dataset. All positions containing gaps and missing data were eliminated. The tree was outgrouped with the 16S rRNA gene sequence of *Methanocaldococcus jannaschii* DSM2661 (NR_074233.1). All accession numbers are in parentheses.

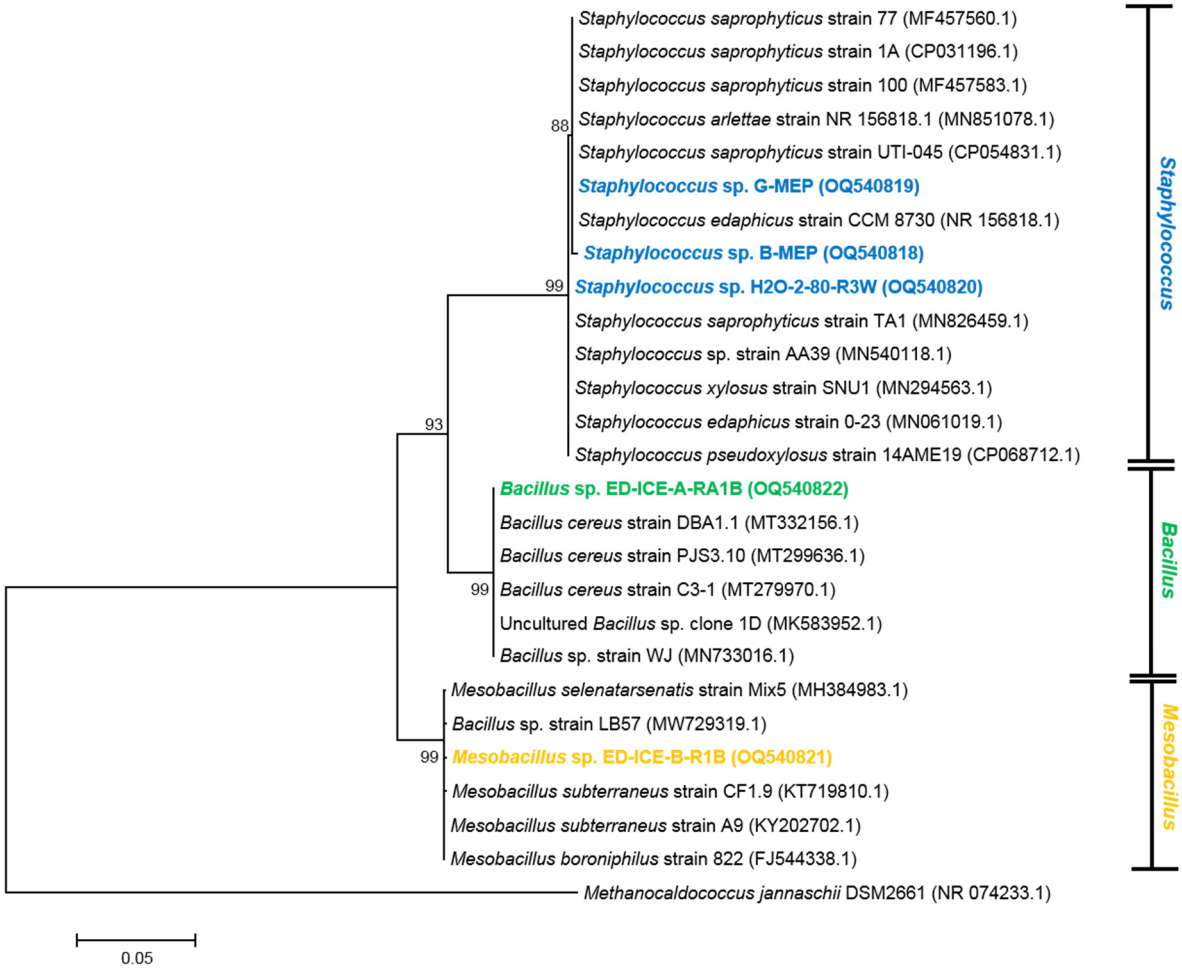

Figure 6. 16S rRNA genes phylogenetic tree created using the Maximum Likelihood method based on the Jukes–Cantor model of Antarctic UV-resistant bacteria isolated from marine and lake environments affiliated with Firmicutes. The percentage of trees in which the associated taxa clustered together in the bootstrap test (500 replicates) is shown next to the branches (values below 50% are not shown). The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. The analysis involved 1321 positions in the final dataset. All positions containing gaps and missing data were eliminated. The tree was outgrouped with the 16S rRNA gene sequence of *Methanocaldococcus jannaschii* DSM2661 (NR_074233.1). All accession numbers are in parentheses.

The 16S rRNA gene sequence analysis indicated that the yellowish orange strain H2O-10-G4 may be affiliated within the genus *Rhodococcus*, which belongs to the family Nocardiaceae, particularly with *Rhodococcus* sp. ZS333, which was isolated from Antarctic sandy intertidal sediments, as its closest relative (99.80% of 16S rRNA gene sequence identity) (Figure 4). However, the strain H2O-10-G4 shared 99.7% of 16S rRNA gene sequence identity also with the *Marisediminicola antarctica* strain ZS413^{T}, which belongs to the family Microbacteriaceae and was isolated from the coastal area off the Chinese Antarctic Zhongshan Station [80]. To date, only two strains have been reported belonging to this genus: *Marisediminicola antarctica* strain ZS413^{T} and *Marisediminicola senii* sp. nov., which was isolated from Queen Maud Land, Antarctica [81]. Comparison with 16S rRNA gene sequences (100 sequences showing the highest sequence identity with H2O-10-G4 strain) deposited in the NCBI GenBank database showed that the *Marisediminicola antarctica* strain ZS413^{T} was the only species belonging to this genus, whereas all other strains with high sequence identities (from 98.00 to 99.80%) belonged to the genus *Rhodococcus* sp. Species belonging to the *Rhodococcus* genus are reported in widespread environments, including deep-sea and sea level sediments, alpine soils, and Arctic and Antarctic regions.

They are able to survive under several stressful conditions, including UV irradiation [82]. The Antarctic marine bacterium *Rhodococcus* sp. NJ-530, which was isolated from floating ice, showed several UV adaptive characteristics, including significant repair activities of DNA damage induced by UV rays of the purified DNA photolyase [16]. The red-orange strain *Rhodococcus* sp. B7740, which was isolated from deep-sea water in the Arctic Ocean, is a promising source of natural carotenoids and isoprenoid quinones, which is interesting for their application in the food industry [83].

In Figure 4, the orange *Gordonia* species, H2O-1-80-R1, and H2O-2-80-R4, with a 99.7% of 16S rRNA gene sequence identity between them, were closely related to different strains of the *Gordonia* genus, *Gordonia terrae* and *Gordonia hongkongensis*, from the family Gordoniaceae. A strain of *Gordonia terrae* showing antimicrobial activity was already isolated from Antarctic volcanic soils in Deception Island [33]. Species belonging to the genus *Gordonia* are ecologically adaptable and produce a large variety and significant quantities of carotenoids that are recently gaining attention for their biotechnological potential [84]. An important example is provided by *Gordonia jacobaea* MV-1, which is capable of producing great amounts of carotenoids [85], including ketocarotenoid all-*trans*-canthaxanthin (4,4′-diketo-β-carotene) and all-*trans*-astaxanthin (3,3′-dihydroxy-4,4′-diketo-β-carotene), which are currently produced by Hoffmann-La Roche, Ltd. and used as food additives in feeding.

3.3.2. Proteobacteria

Proteobacteria constituted one of the most dominant phyla in Antarctica [31–33] and in this study comprised 5 Gram-negative genera *Brevundimonas*, *Qipengyuania*, *Sphingorhabdus*, *Sphingobium*, and *Psychrobacter*. The phylogenetic tree of bacteria affiliated with the Phylum Proteobacteria was split into two distinct phylogenetic lineages (Figure 5) that, in turn, were divided in other groups: two groups for the *Psychrobacter* genus and another two groups divided in other subgroups that comprised *Brevundimonas*, *Qipengyuania*, *Sphingobium*, and *Sphingorhabdus*.

In the current study, *Psychrobacter* was the most abundant genus and comprised 19% of the identified sequences. *Psychrobacter* spp. IN-H2O-A-2BE6, IN-ICE-A-A1B, H2O-1-80-BE1, IN-ICE-A-A1G, Gly6-2-BE4, and Gly9-1-BE7 were isolated from different sites, shared from 97.6 to 99.7% of 16S rRNA gene sequence identity, and were not pigmented. They grouped within the *Psychrobacter* genus, of the family Moraxellaceae, and were split into three groups. This genus is known to be widely distributed in different habitats, including fish, food, clinical specimens, Antarctic soils, and sea water [86]. *Psychrobacter* is a good producer of antioxidants involved in oxidative stress defence in Antarctic and Arctic environments [87–89].

The 16S rRNA gene sequence analysis indicated that *Brevundimonas* spp. RA4, ED-ICE-A-RA1, and IN-H2O-B-RA3 shared more than 99.70% of sequence identity between them, and they were grouped together within the clade of the genus *Brevundimonas*, of the family Caulobacteraceae, which were close to species found from different sources (Figure 5). One of these, *Brevundimonas* sp. V4.BP.05, was identified as *Brevundimonas mediterranea* sp. nov., which was isolated from the Mediterranean Sea [90]. Although the majority of Antarctic *Brevundimonas* strains reported in the literature displayed no pigmentation [35,91–93], in this study, all three isolates, RA4, ED-ICE-A-RA1, and IN-H2O-B-RA3, showed a reddish orange pigmentation, as has already been reported in other environments [94,95]. Some orange *Brevundimonas* strains isolated from aquatic environments in Japan were producers of astaxanthin and adonixanthin [94]. Red 2,2′-dihydroxy-astaxanthin was the major carotenoid produced by *B. scallop* and has strong antioxidative activity and potential industrial use [96].

In Figure 5, the yellow species H2O-2-80-G2 aligned closely with *Erythrobacter* and *Qipengyuania* species in sharing 100% of 16S rRNA gene sequence identity with them. Both genera, *Erythrobacter* and *Qipengyuania*, belong to the family Erythrobacteraceae of the order Sphingomonadales within the class Alphaproteobacteria. Recently, the taxon-

omy of the family Erythrobacteraceae has been revised, thereby leading to the formation of many novel genera within the family. Some species of the genus *Erythrobacter* were proposed to be reclassified into the genus *Qipengyuania*. The genus *Qipengyuania* currently comprises 13 species with validly published names, thus showing a high degree of genetic diversity, metabolic versatility, and environmental adaptation [97–100], (https://lpsn.dsmz.de/genus/qipengyuania, accessed on 24 January 2023). For this reason, the species H2O-2-80-G2 was assigned to the genus *Qipengyuania*. Members of the genus *Qipengyuania* are heterotrophic bacteria generally that are found worldwide in diverse marine environments with great possible applications in several fields (e.g., carotenoid producer) [100,101].

In Figure 5, the three yellow *Sphingorhabdus* spp. A1G, G5G, and *Sphingobium* sp. AM-0m-G3 belong to the same family Sphingomonadaceae. The 16S rRNA gene analysis revealed that *Sphingorhabdus* spp. A1G and G5G shared 100% of 16S rRNA gene sequence identity with the *Sphingorhabdus soli* strain D-2Q-5-6, whereas 99.93% of 16S rRNA gene sequence identity was shared with species affiliated with the genus of *Sphingomonas* sp. NP32. *Sphingomonas* strains are highly UVC-resistant bacteria, which is probably due to their ability to produce carotenoids [102], as well as CPD photolyases and a 6,4-photolyase to repair DNA damage [18]. Members of *Sphingorhabdus* have been isolated from various habitats, including freshwater, sea water, and polar environments [103,104], and analysis of the genome sequencing of some strains revealed the presence of a terpenoid gene cluster with high similarity encoding the carotenoid astaxanthin [105].

Sphingobium sp. AM-0m-G3, which was isolated in R2A medium, shared a 100% sequence identity with *Sphingobium* sp. RAC03 (Figure 5). *Sphingobium* is one of the four genera commonly called *Sphingomonas*, together with *Sphingomonas*, *Novosphingobium*, and *Sphingopyxis*. Strains belonging to the genus *Sphingobium* have been found in different environments, including in Antarctica, where they have been characterized for their ability to degrade aromatic and aliphatic hydrocarbons [106,107]. Analysis of the carotenoids extracted from the yellow-pigmented carbazole-degrading bacterium *Sphingobium yanoikuyae* XLDN2-5 showed the production of zeaxanthin, which is likely involved in the modulation of membrane fluidity and protection against oxidative stress [108].

3.3.3. Firmicutes

The phylogenetic tree of bacteria affiliated with the Phylum Firmicutes was split into two distinct phylogenetic clusters (Figure 6).

The bigger clade was formed by *Staphylococcus* and some strains of *Bacillus* genera, which were split in a separate branch. The more recent clade was formed by other *Bacillus* genera of the family Bacillales. The genus *Bacillus* is a heterogeneous group of species exhibiting polyphyletic branching with other new genera of the family Bacillaceae that were recently proposed [109]. In fact, *Mesobacillus* sp. ED-ICE-B-R1B shared 99.86% of its sequence identity with other sequences of the group, with some of these belonging to *Mesobacillus* or *Bacillus* genera. *Mesobacillus* sp. ED-ICE-B-R1B and *Bacillus* sp. ED-ICE-A-RA1B shared 93.35% of 16S rRNA gene sequence identity between them. *Bacillus* sp. ED-ICE-A-RA1B was phylogenetically close to *Bacillus cereus*, which has been found in the waters of Lake Vostok, Antarctica [93]. *Staphylococcus* spp. B-MEP, G-MEP, and H2O-2-80-R3W shared 99.15% of 16S rRNA gene sequence identity and were closely related to the genus *Staphylococcus*, of the family Staphylococcaceae. Members of the genus *Staphylococcus* are widespread in nature, and their ability to act as pathogens is partly due to their ability to alleviate oxidative and nitrosative stress through the development of different protection, detoxification, and repair mechanisms, including the production of carotenoids or detoxifying enzymes [110]. *Staphylococcus saprophyticus*, which is the closest phylogenetic relative of the *Staphylococcus* strains isolated in this study, is an opportunistic pathogen that is able to infect humans, lower mammals, and birds, and it can cause human urinary tract infections, wound infections, and septicaemia [111,112]. The Antarctic *Staphylococcus*

edaphicus sp. nov., which is closely related to *Staphylococcus* sp. H2O-2-80-R3W, presented characteristics that are essential to adaptation to extreme environments [113].

Mesobacillus sp. ED-ICE-B-R1B and *Bacillus* sp. ED-ICE-A-RA1B exhibited no pigmentation. Only a few studies have reported the isolation of pigmented *Bacillus* isolates from marine sources [114]. However, marine *Bacillus* species showed good antioxidant activity by producing a wide range of enzymes and metabolites [115–117]. In the case of *Staphylococcus* species, only *Staphylococcus* sp. G-MEP exhibited pale yellow pigmentation, even though it shared 100% of its 16S rRNA sequence identity with the white B-MEP (Figure 2). This yellow pigment in G-MEP may be due to the formation of a carotenoid intermediate pigment found in the same *Staphylococcus* species [118,119].

4. Conclusions

The extreme conditions of the Antarctic aquatic environment have selected a high biodiversity within the bacterial communities, which are able to tolerate and survive to the constant exposure to UV-R. Our results highlight the importance of the Antarctic environment as a rich and novel source of pigmented UV-resistant Gram-positive and Gram-negative bacteria. In total, 42% of the UV-resistant strains isolated from the surface sea waters/ice and shallow lake sediments were assigned to the Phylum Proteobacteria that was represented by 5 genera (*Brevundimonas*, *Psychrobacter*, *Qipengyuania*, *Sphingorhabdus*, and *Sphingobium*); the other 42% was affiliated with Actinobacteria with 7 genera (*Kocuria*, *Gordonia*, *Rhodococcus*, *Micrococcus*, *Arthrobacter*, *Agrococcus*, and *Salinibacterium*), and the remaining 16% was assigned to the Phylum of Firmicutes represented by 3 genera, i.e., *Staphylococcus*, *Mesobacillus*, and *Bacillus*. Most of the Antarctic strains showed a close phylogenetic relationship to bacteria obtained from diverse Antarctic and non-Antarctic ecosystems, as well as marine and non-marine environments. However, many of them shared the harsh conditions in which they inhabited, which suggests that these species possessed adaptive features that allowed them to survive in these hostile environments.

It is widely reported that the bacterial genera selected in this work have been previously characterized as good producers of molecules that are able to minimize UV damage, including antioxidant molecules and enzymes. Many of them are represented by pigments, in particular carotenoids, that function as protection against UV-R and ROS, as well as modulate the membrane fluidity in the cold.

Antarctica is a huge reservoir of pigmented bacterial biodiversity but a still poorly explored resource for pigment discovery, production, and applications. There could be promising candidates for novel chemical structures and for cell factories of bio-pigments. Although the literature studies on Antarctic pigmented bacteria are increasing rapidly, currently, there are only few examples of Antarctic pigments that have been used in biotechnological applications, such as the carotenoids isolated from UV-resistant Antarctic bacteria used to develop green solar cells, called photosensitizers, in dye-sensitized solar cells [22]. Therefore, further studies are needed to investigate the potential of pigmented Antarctic bacteria and related molecular and enzymatic machineries to be used in biotechnological discovery pipelines and pharmaceutical applications.

Author Contributions: Conceptualization, D.C. and D.G.; collection of samples in the framework of Italian National Antarctic Research Program (PNRA) expeditions, D.C. and G.Z.; methodology, D.C., C.L., G.N., M.C. and D.G.; formal analysis, data curation, D.C., C.L., M.C. and D.G.; writing—original draft preparation, D.C., C.L., G.N., M.C. and D.G.; writing—review and editing, D.C., C.L., G.Z., G.N., A.F., A.I., M.C., C.V. and D.G.; funding acquisition, C.L., G.N., A.F., A.I., M.C. and D.G. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The datasets generated for this study can be found in the GenBank nucleotide repository, https://www.ncbi.nlm.nih.gov/nucleotide/, using either the strain names or accession numbers highlighted in Table 2 and Figure 3.

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