




Biological Sciences

Cold-loving microorganisms in Antarctic glaciers: a review of South Shetland archipelago glaciers

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Abstract

Antarctic glaciers have been considered classically uninhabited. However, they constitute an authentic biome and are populated by microorganisms that not only survive in them but also maintain an active metabolism. The South Shetland archipelago is a good study model to observe the diversity and evolution of the microbial populations that inhabit its glaciers. From a geological point of view, this archipelago is of considerable interest due to the intense and relatively recent volcanic eruptions on Deception Island. Additionally, it has been a place of transit for human and animal populations over time. All of these factors have influenced the composition and diversity of the microbial communities inhabiting the glacial ice. Among these microorganisms, a great diversity of bacteria, archaea, viruses and microeukaryotes such as algae and unicellular fungi have been identified thanks to high-throughput technologies. These cold-adapted microorganisms develop molecular mechanisms of adaptation to the extreme environment they inhabit and contribute to global energy cycles through the processing of organic and inorganic compounds. This review summarizes current knowledge on the biodiversity, ecology and molecular mechanisms of adaptation of cold-adapted microorganisms, and it details the specific characteristics of the microbial populations housed in the Antarctic glaciers in the South Shetland archipelago.

Keywords: Archaea; bacteria; biodiversity; glacier; microbial communities; microeukaryotes

Introduction

Antarctic glaciers have been little explored until now. Historically, the Antarctic region has been prospected solely for lucrative economic purposes, especially for hunting, fishing and mining, but glacial areas have classically been considered to lack potential utility and to be uninhabited. The earliest research on the microorganisms that inhabit glaciers dates back to 1918, but these microorganisms were underestimated until the 1980s (McLean 1918). Subsequently, these microorganisms have been studied profusely for their great interest as survivors at the limits of life and for their remarkable biotechnological potential (Garcia-Descalzo *et al.* 2012).

It has been estimated that in the next decade the global temperature of Earth will rise by $\sim 2^{\circ}\text{C}$ (IPCC 2022). This increase will be especially significant in some Antarctic regions such as the Antarctic Peninsula, where this increment will be five times greater than the global average (Turner *et al.* 2013). Climate change is threatening the climatological stability of our planet, and glaciers are suffering ice reduction that produces serious consequences for the associated ecosystem processes. Severe shrinkage processes have been described in Arctic (Garcia-Lopez *et al.* 2019) and Antarctic glaciers (Garcia-Lopez *et al.* 2021), as well as in high

mountain glaciers such as those in the Alps (Sommer *et al.* 2020), Pyrenees (Moreno *et al.* 2021) and Himalayas (Mukhia *et al.* 2024).

Among all of the climatic indicators, glacial ice is one of the most effective because it contains a large amount of data, including its microbiological composition, which allows us to increase our knowledge of the palaeoclimatic history of these regions and to predict the future course of these environments (Varghese *et al.* 2023). Among microorganisms in glaciers, a great diversity of bacteria, archaea, viruses and microeukaryotes such as algae and unicellular fungi have been identified (Boetius *et al.* 2015). These glaciers constitute a biome, and they are populated by microorganisms that maintain the nutrient cycling pathways and form the basis of the ecosystem's food webs (Anesio & Laybourn-Parry 2012). These cold-adapted microorganisms develop molecular mechanisms of adaptation to the extreme environment they inhabit, and they contribute to global energy cycles through the processing of organic and inorganic carbon and nitrogen compounds. As there are nearly no plants or animals in these pristine environments, microorganisms, which maintain an active metabolism, are responsible for carrying out the biogeochemical cycles in these areas (Martinez-Alonso *et al.* 2019, Trejos-Espeleta *et al.* 2024).

The South Shetland archipelago is a good study model to observe the diversity and evolution of the microbial populations that inhabit its glaciers. It is located ~ 120 km off the coast of the Antarctic Peninsula, south of the American continent, and it has been a place of transit of human and animal populations over time. It was one of the areas first discovered by Antarctic explorers, and it was later used by whalers and researchers. At present, there are

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This article is dedicated to our colleague and friend Professor Andres Barbosa.

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17 Antarctic research stations belonging to 12 countries on the South Shetland archipelago. From a geological point of view, the South Shetland archipelago is of great interest due to the intense and relatively recent volcanic eruptions on Deception Island. This activity has conditioned the diversity of microbial populations throughout the archipelago (Garc a-Lopez *et al.* 2021, Hidalgo-Arias *et al.* 2023). Recently, tourism to exotic regions such as the poles is also significantly altering this delicate environment. Over 10 years, tourism to the South Shetland archipelago has grown from 35 000 to 105 000 visitors in the 4 months of the summer season, in addition to the presence of some 10 000 scientists. This represents a growing threat that is shifting the glacier microbiome composition (Garc a-Lopez *et al.* 2021).

Whereas Antarctic tourism is strictly restricted by the International Association of Antarctic Tour Operators (IAATO; Bauer & Dowling 2003), the Arctic does not have a body that is equivalent to IAATO, and its economic and touristic exploitation is much more intense. In the Arctic, the number of visitors has also increased significantly from 35 million in the year 1995 to 66 million in 2017 (Shijin *et al.* 2020). A study comparing Arctic and Antarctic microbial populations living in wet soil, small streams and ponds showed that the percentage of cosmopolitan taxa was higher in Arctic (43%) than in Antarctic samples (36%; Kleintich *et al.* 2017). These researchers concluded that the widespread distribution of polar microorganisms could be explained by natural or anthropogenic dispersal, and that this could favour the establishment of cosmopolitan genotypes and the loss of endemic taxa.

There are few studies on the impacts of tourists and researchers on microbial populations in Arctic glaciers. In a study that compared the microbial populations of seven glaciers in the Svalbard archipelago, microorganisms of human origin such as *Escherichia*

and *Helicobacter* species were also found in the surroundings of local research stations (Garc a-Lopez *et al.* 2019). However, these results demonstrated that the most abundant species in Arctic glaciers were related to the degradation of hydrocarbons and chemical pollutants (e.g. *Rhodococcus phenolicus*, *Pseudonocardia hydrocarbonoxydans*, *Polaromonas naphthalenivorans* and *Sphingomonas oligophenolica*). These microorganisms have been described as degraders of chlorobenzene, dichlorobenzene and phenol (Rehfuss & Urban 2005), hydrocarbons, naphthalene (Jeon *et al.* 2004) and phenolic acids (Ohta *et al.* 2004), respectively.

This review discusses the diversity and molecular mechanisms of adaptation that are being investigated from studies on cold-adapted microorganisms, and it details the specific characteristics of the microbial populations housed in the Antarctic glaciers of the South Shetland archipelago.

Glacial habitats

Several reports have been published on the microbiology associated with glacial environments in Antarctica such as Lake Vostok (Shtarkman *et al.* 2013) and the Blood Falls (Fig. 1; Mikucki *et al.* 2009). Lake Vostok is one of the largest of the nearly 400 subglacial Antarctic lakes, and it has been continuously buried by glacial ice for 15 million years. Moreover, the Blood Falls is an iron-rich subglacial drainage that flows from the Taylor Glacier (Mikucki *et al.* 2009). The appeal of these two sites has encouraged research into other Antarctic glacial environments. The case of the perennially cold, anoxic hypolimnion of Ace Lake in the Vestfold Hills of Antarctica should be highlighted. In this extreme environment, methanogenic and psychrophilic microorganisms have been reported (Franzmann *et al.* 1997). In addition, in the interior

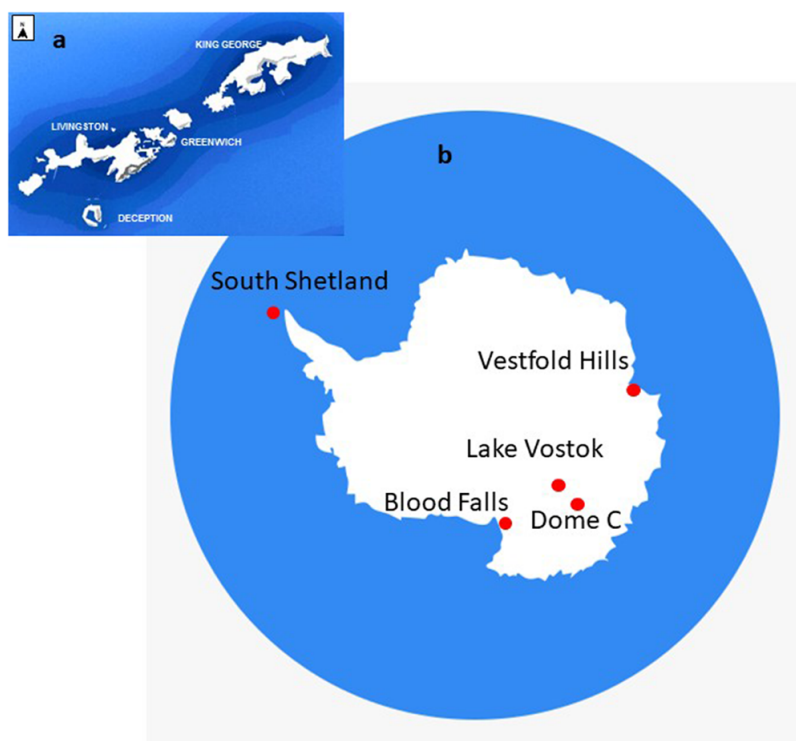


Figure 1. Map of Antarctica showing some of the glaciers where microorganisms have been explored to date. **a.** South Shetland archipelago. **b.** Antarctica. Details on the glaciers and references are summarized in Table I.

Table 1. Studies performed on microorganisms from Antarctic glaciers. The glaciers with samples shown in Figs 4 & 5 are highlighted in bold.

Geological area	Name	Location	Habitat	GPS coordinates	Reference
Lake	Ace Lake	Vestfold Hills	Subglacial	68°28'19"S, 78°11'16"E	Franzmann <i>et al.</i> (1997)
	Vostok	Pole of Cold	Subglacial	78°28'00"S, 106°48'00"E	Shtarkman <i>et al.</i> (2013)
Glacier	Dome C	Antarctic Plateau	Supraglacial	75°06'09"S, 123°20'09"E	Michaud <i>et al.</i> (2014)
	Blood Falls, Taylor Glacier	McMurdo Dry Valleys	Subglacial	77°28'00"S, 162°31'00"E	Mikucki <i>et al.</i> (2009)
	Mount Pond	Deception Island	Englacial	62°56'01"S, 60°35'44"W	Martinez-Alonso <i>et al.</i> (2019)
	Rojo	Deception Island	Englacial	62°57'30"S, 60°35'55"W	Garcia-Lopez <i>et al.</i> (2021)
	Macaroni	Deception Island	Englacial	62°54'09"S, 60°32'03"W	Garcia-Lopez <i>et al.</i> (2021)
	Johnson	Livingston Island	Englacial	62°38'60"S, 60°21'00"W	Garcia-Lopez <i>et al.</i> (2021)
	Hurd	Livingston Island	Englacial	62°41'00"S, 60°20'74"W	Garcia-Lopez <i>et al.</i> (2021)
	Quito	Greenwich Island	Englacial	62°27'00"S, 59°45'00"W	Garcia-Lopez <i>et al.</i> (2021)
	Traub	Greenwich Island	Englacial	62°27'59"S, 59°45'23"W	Garcia-Lopez <i>et al.</i> (2021)
	Ecology	King George Island	Englacial	62°09'60"S, 58°28'00"W	Garcia-Lopez <i>et al.</i> (2021)
	Machu Picchu	King George Island	Englacial	62°06'00"S, 58°28'00"W	Garcia-Lopez <i>et al.</i> (2021)
	Macaroni	Deception Island	Subglacial	62°54'27"S, 60°32'19"W	Garcia-Lopez <i>et al.</i> (2022)
	Kirkwood	Deception Island	Subglacial	62°59'56"S, 60°38'15"W	Garcia-Lopez <i>et al.</i> (2022)
	Mount Pond	Deception Island	Supraglacial	62°56'01"S, 60°35'44"W	-
	Johnson	Deception Island	Supraglacial	62°38'60"S, 60°21'00"W	-

of the Antarctic continent, microbial populations housed in the surface snow from the High Antarctic Plateau (Dome C) have been described, noting that polar microorganisms can not only be considered as deposited airborne particles but as an active component of the snowpack ecology (Michaud *et al.* 2014). Furthermore, many of the South Shetland archipelago glaciers have been investigated, especially the coastal glaciers that discharge into the sea (Martinez-Alonso *et al.* 2019, Garcia-Lopez *et al.* 2021, 2022). The distance of the glaciers from the shoreline has been reported to be of great importance to the composition and diversity of their microbial populations due to the exchange of microorganisms between terrestrial and marine ecosystems (Garcia-Lopez *et al.* 2019). Figure 2 shows some examples of these coastal Antarctic glaciers of the South Shetland archipelago.

In most glaciers, three habitats can be distinguished that condition the composition of microbial communities: a sunlit and oxygenated supraglacial habitat, an intermediate englacial habitat and a basal subglacial habitat (Boetius *et al.* 2015). These three environments differ greatly in terms of their physicochemical characteristics, nutrient concentration, temperature, solar radiation and pressure. Figure 3 presents a principal component analysis (PCA) of the microorganisms distributed in these three glacial habitats in glaciers. According to this analysis, significant differences exist between the diversity of the populations of the three glacial ecosystems.

Supraglacial habitat

The supraglacial habitat is mainly composed of surface snow and ice that melt during the summer. This zone receives solar radiation and contains photosynthetic algae, fungi (Hu *et al.* 2023) and coloured bacteria (Garcia-Lopez & Cid 2016) that give the glacial surface reddish, greenish or brownish tones (Martín-Cerezo *et al.* 2015). The most abundant representatives of these microorganisms

are unicellular algae of the family Chlamydomonaceae (included in Archaeplastida), mainly the species *Chlamydomonas nivalis* (Garcia-Lopez & Cid 2016). The juvenile stages of these algae synthesize green pigments involved in photosynthesis. When mature, the algae produce reddish carotenoids that protect them from excess solar radiation (Lutz *et al.* 2014, Khan *et al.* 2021).

In the supraglacial habitat, the important role played by cryoconite holes must be emphasized. Cryoconite is defined as the sediment that forms due to the interaction of mineral particles deposited on the glacier surface and the microbial communities that inhabit them. Over time, the surface snow melts, giving rise to cryoconite holes filled with liquid water. These holes are true oases for the development of microbial communities, containing sufficient nutrients for their growth (Hassan *et al.* 2024). Cryoconite holes are populated mainly by primary producers such as cyanobacteria (Fig. 3a) and microalgae (Fig. 3b; Hodson *et al.* 2008). It has been demonstrated that significant metabolic heat is produced within cryoconite holes, which contributes to ice melting and in turn increases the size and depth of these pools (Gladkov *et al.* 2024). Some cryoconite holes generate at least 13% of the observed runoff on the one glacier for which this has been measured (Fountain *et al.* 2004).

Englacial habitat

The englacial habitat, consisting of the area and veins occurring within a glacier, is the least understood part of the glacial environment. It is also the most inhospitable area of these glaciers due to the presence of low temperatures, high pressures and total darkness. Researching this habitat is difficult as such research requires the extraction of ice cores under sterile conditions to avoid contamination. The first studies on the microbiology of these cores were carried out by Abyzov (1993). The microorganisms in this stratum could come from the upper layer and the marginal moraines by

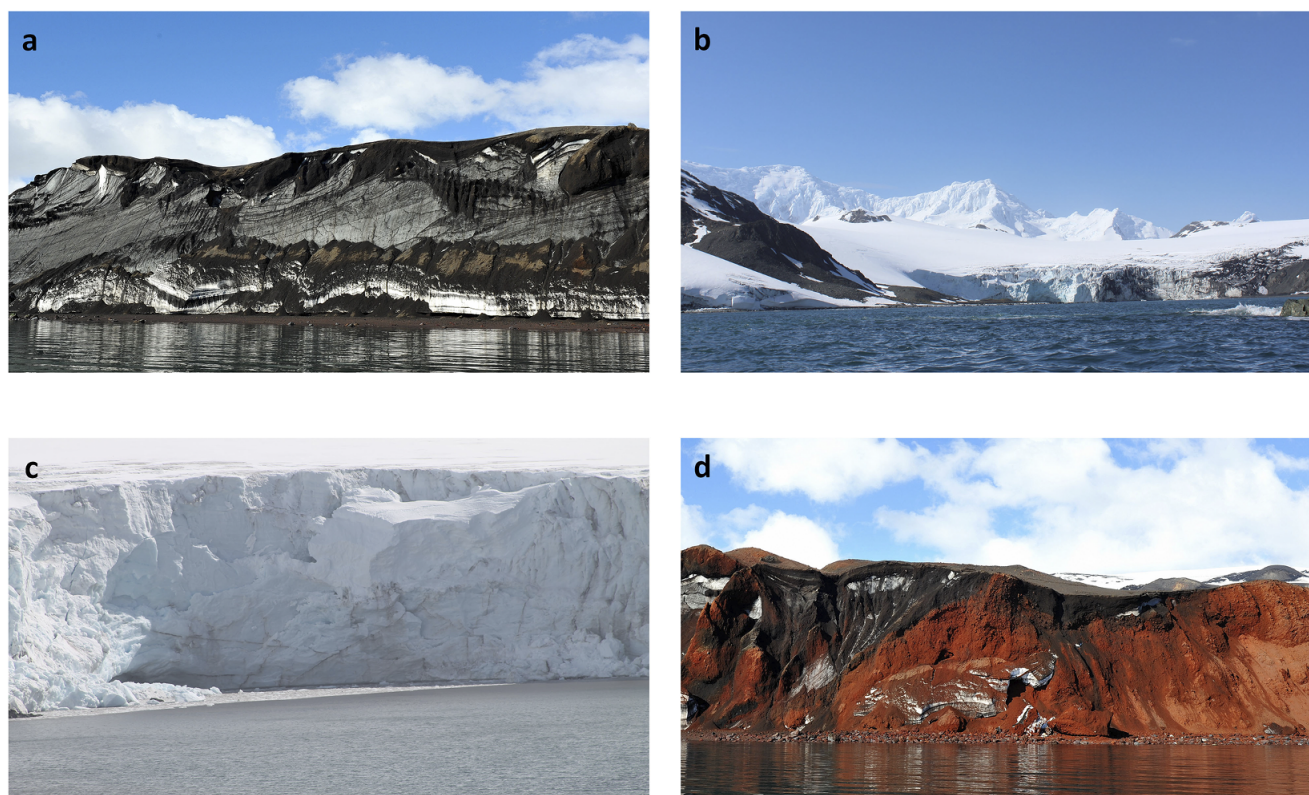


Figure 2. Examples of coastal Antarctic glaciers of the South Shetland archipelago: **a.** Mount Pond glacier, **b.** Johnson glacier, **c.** Quito glacier and **d.** Rojo glacier. The glaciers in images **a.** and **d.**, located on Deception Island, clearly show the remains of lava and volcanic ash that colour the glacial ice.

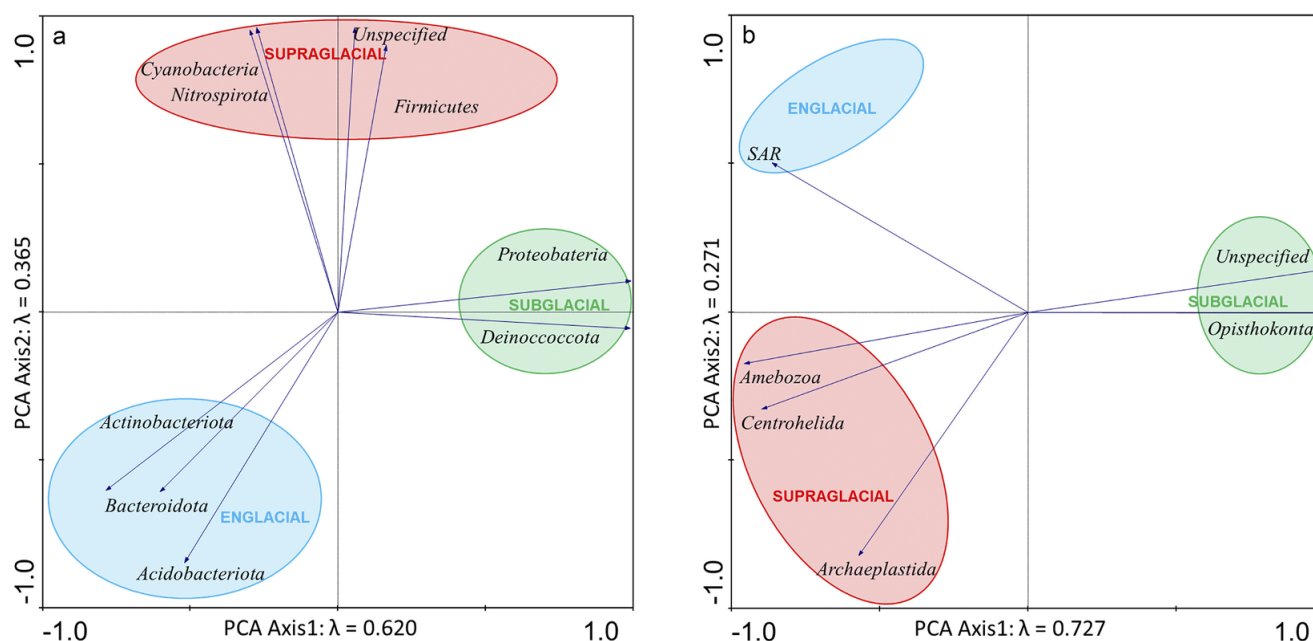


Figure 3. Principal component analysis (PCA) of the microorganisms distributed in the three glacial habitats: **a.** Bacteria and **b.** Eukaryota. The influence of the environment on the microbial community composition was investigated by PCA developed using *CANOCO 5* software (Leps & Smilauer 2003). The analyses were evaluated using a Monte Carlo test with 500 permutations. Data are from the glaciers highlighted in bold in Table 1.

dragging through the ice. They reside in the air bubbles, veins and water microchannels that form between the ice crystals. It has been shown that the populations inhabiting these environments are not in a quiescent state but are functional (Martinez-Alonso

et al. 2019). The microorganisms of this glacial zone are generally chemoautotrophs. They can also be heterotrophs that feed on the organic debris carried by the ice. They usually perform anaerobic respiration due to the lack of oxygen.

Subglacial habitat

Subglacial environments represent a largely unexplored component of Earth's biosphere. This environment is generated as a result of ice friction on rocks, fragmenting minerals and organic debris that, combined with subglacial water, create optimal niches for microbial life. It has been described that under glaciers there is often a stream of water. This water may originate from the melting of the ice by geothermal heat from the underlying rock or from supraglacial channels that cross these glaciers and form lakes on their bedrock (Anesio & Laybourn-Parry 2012). Although, as mentioned earlier, this ecosystem was one of the first glacial environments to come to the attention of researchers in the 1980s thanks to the exploration of the microbiology of Ace Lake (Franzmann *et al.* 1997) and Lake Vostok (Shtarkman *et al.* 2013), few studies have sampled subglacial environments given the difficulties associated with accessing these sites. In these surveys, several species of archaea, bacteria and fungi have been found (Garcia-Lopez *et al.* 2022).

Diversity of the microorganisms in Antarctic glaciers

Antarctic glacier microbiology has been extensively studied in recent years thanks to the development of omics techniques (Doytchinov & Dimov 2022, Vick-Majors *et al.* 2024). These methodologies have made it possible to elucidate the genomic compositions of microbial communities and their distributions in the various glacial ecosystems.

This review paper compares this previous knowledge with the microbial diversity results found in our previous works on 11 glaciers in the South Shetland archipelago by re-analysing the sequences from the amplicon sequencing of 16S and 18S rRNA genes (Martinez-Alonso *et al.* 2019, Garcia-Lopez *et al.* 2021, 2022). These DNA databases are becoming more complete, and they contain an increasing number of identified sequences. Therefore, fewer unspecified sequences have been obtained in this review than in previous analyses.

Bacteria

It has been reported that all major phyla of bacteria are represented in glaciers, especially Acidobacteriota, Actinobacteriota, Bacteroidota, Firmicutes, Gemmatimonadota, Planctomycetota, Proteobacteria and Verrucomicrobiota (Anesio & Laybourn-Parry 2012).

In this work, great bacterial diversity has been observed when compared with other Antarctic glaciers (Grzesiak *et al.* 2015). According to our results, it is confirmed that all major phyla of bacteria are represented in glaciers. Most of the phyla of the englacial ecosystem were identified as Firmicutes, Proteobacteria and Bacteroidota (Fig. 4, level 2), and the major genera in this habitat were *Polaromonas*, *Pedobacter*, *Sulfobacillus*, *Flavobacterium*, *Clostridium* and *Sphingomonas* (Fig. 4, level 6).

Regarding the subglacial ecosystem, samples from two glaciers on Deception Island were analysed (Garcia-Lopez *et al.* 2022). These samples were collected in the basal margins of the glaciers, in contact with the lower bedrock. The major phyla in the subglacial ecosystem were Actinobacteriota, Bacteroidota, Cyanobacteria and Proteobacteria (Fig. 4, level 2). Most of the bacterial genera of the subglacial habitat were *Hymenobacter*, *Pontibacter*, *Frankia*, *Cyanobacterium* and *Symploca* (Fig. 4, level 6).

It is worth highlighting the presence of sentinel microorganisms of human contamination inside the glacial ice, which have altered

the composition of native microbial populations. In a study comparing the gradient of microbial populations across the archipelago, it was observed that the western islands contained greater microbial diversity, possibly due to the existence of volcanic minerals that serve as nutrients for chemolithotrophic bacteria (Garcia-Lopez *et al.* 2021). However, in the eastern islands, where the number of research stations and tourists is higher, the diversity of chemolithotrophs decreased and the existence of microorganisms associated with human presence was observed. These microbial populations include various species of enterobacteria such as *Escherichia coli*, as well as other microorganisms such as *Helicobacter*, *Bacteroides*, *Streptococcus* and *Oscillospira* (Power *et al.* 2016). The presence of animal parasitic microeukaryotes such as *Cryptosporidium* was also observed (Kleinertz *et al.* 2014). The problems associated of human frequentation through tourism and the expansion of scientific operations have been reported previously, and these activities can have serious repercussions such as increased human-mediated antimicrobial resistance (Clark *et al.* 2025).

A comparison of the microbial populations of the glaciers at the two poles shows that the differences between the two geographical regions are significant, and these disparities condition their observed environmental microbiology. The Arctic is an ocean surrounded by continents. Arctic glaciers are heavily influenced by marine microorganisms that have colonized the land from the sea, and vice versa. Sentinel microorganisms of this transfer such as the genus *Hymenobacter* have been described (Garcia-Lopez *et al.* 2019). This process is less observed in Antarctica, where the continent is surrounded by the ocean. It is also significant that the microbial diversities at both poles are very different, and there are taxonomic groups that only exist in either one or the other of them. Also noteworthy is the presence of microorganisms of the same genus (e.g. *Psychrobacter*) but different species (e.g. *Psychrobacter frigidicola* and *Psychrobacter arcticus*) in the glaciers of both poles, which may be due to evolutionary convergence or past migrations (Bowman *et al.* 1996, Bakermans *et al.* 2006).

Archaea

The greatest number and diversity of archaea on the planet exist in cold environments (Caviccioli 2006). Archaea have been reported both within glacier ice and beneath glaciers (Skidmore *et al.* 2000). Methanogenic archaea represent one of the most abundant resident groups in glaciers, especially in the subglacial environment (Tung *et al.* 2005). For example, *Methanogenium frigidum* and *Methanococcoides burtonii* are two of the most studied such species, and they were isolated from samples from the aforementioned Ace Lake, Antarctica (Franzmann *et al.* 1997, Saunders *et al.* 2003). Other archaea that are not methanogenic have also been described, such as *Halorubrum lacusprofundi*, which was isolated from Deep Lake, Antarctica. This psychrophilic microorganism is also capable of living in a subglacial lake with a salinity that is 10 times higher than that of seawater (Caviccioli 2006). In our sequence analyses, although they were not specifically designed to search for archaea, some archaea of the Halobacterota and Euryarchaeota groups were identified (Fig. 4).

Microeukaryotes

Eukaryotic microorganisms mostly populate the surface of glaciers, especially cryoconite holes (Christner *et al.* 2003). However, eukaryotic microorganisms have also been found in the

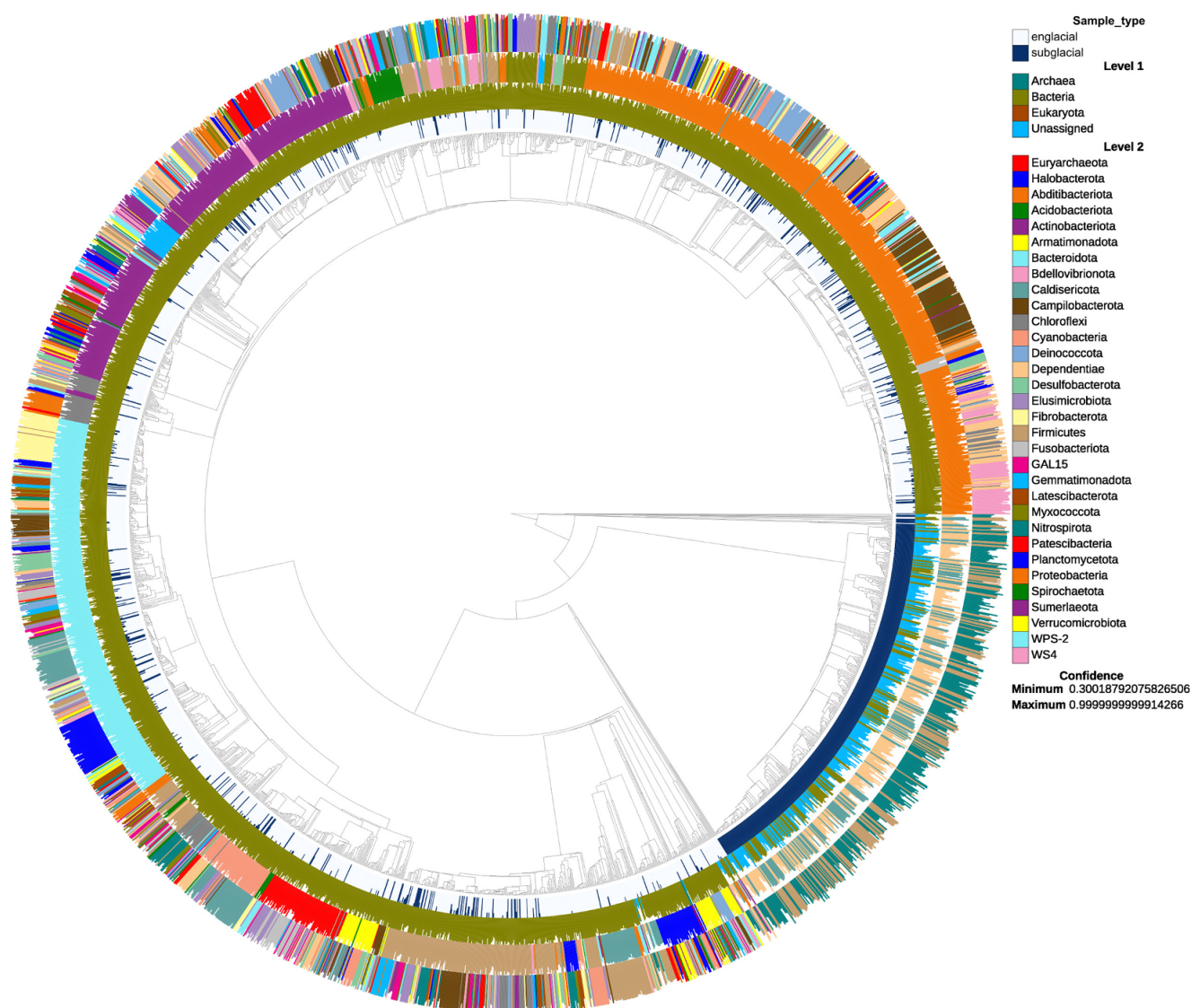


Figure 4. Phylogenetic tree and taxonomy of bacteria identified in South Shetland archipelago glaciers. The phylogenetic tree was generated from 16S amplicon sequences previously obtained for Martinez-Alonso *et al.* (2019) and Garcia-Lopez *et al.* (2021, 2022). Sequence analysis and tree construction were performed as previously described (Ruiz-Blas *et al.* 2023). Barplots were generated from taxonomic annotations using the SILVA rRNA database. The first barplot ring (closer to the tree) represents the glacial environments, the second barplot ring represents taxonomic level 1, the third barplot ring represents taxonomic level 2 and the most external barplot ring represents taxonomic level 6 (genus). The legend corresponding to the genera (level 6) has not been represented due to its large size, but the major genera are detailed in the text.

englacial ecosystem. The majority of the groups of the englacial ecosystem belonged to Opisthokonta (41.57%, of which 65.27% were fungi), SAR (38.09%) and Archaeplastida (12.58%), although 7.68% of the sequences were assigned as unspecified eukaryotes (Fig. 5, level 2).

The most abundant genera of eukaryotes in the englacial environment were diatoms such as *Thalassiosira* and *Cocconeis*, green algae such as *Hydrurus* and *Urospora*, cercozoa such as *Glissomonadida* and *Bodomorpha* and fungi such as *Phytophthora*, *Sporobolomyces* and *Hyphozyma* (Fig. 5, level 6). It has been previously reported that the lack of light and the anoxic conditions of the englacial and subglacial environments favour the growth of numerous fungal species (Anesio *et al.* 2012).

Some microorganisms that denote environmental contamination, such as the microeukaryote *Cryptosporidium*, a characteristic gastrointestinal parasite of emperor penguins, were identified in the glaciers Traub (Greenwich Island) and Ecology and Machu

Picchu (King George Island; Garcia-Lopez *et al.* 2021). The genus *Giardia*, an anaerobic flagellated parasite of vertebrates, was also detected in the englacial habitat of Mount Pond glacier (Martinez-Alonso *et al.* 2019).

Viruses

Most of the studies conducted on Antarctic viruses have been done using freshwater samples from lakes (Lopez-Bueno *et al.* 2009) or seawater samples taken under the Antarctic ice shelves (Lopez-Simon *et al.* 2023). However, very few studies exist on the diversity of viruses in Antarctic glacier ice. Yet, by analysing the genomes of bacteria and microeukaryotes, the presence of viruses that infect microorganisms (phages) can be detected (Boetius *et al.* 2015). It is known that viruses in cold environments play an important role in controlling the mortality and diversity of microbial communities, but further research is needed on ice-hosted viral populations,

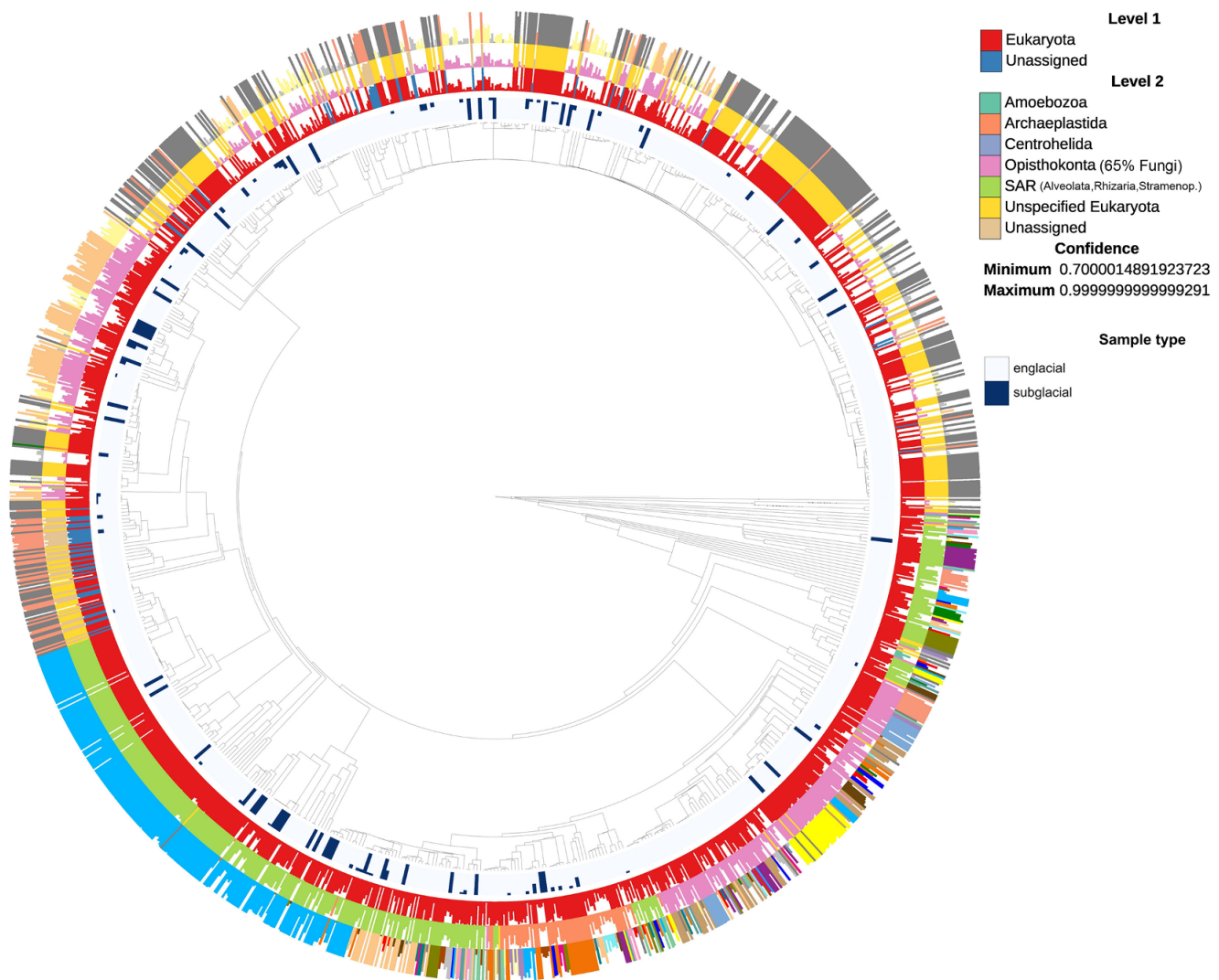


Figure 5. Phylogenetic tree and taxonomy of microeukaryotes identified in South Shetland archipelago glaciers. The phylogenetic tree was generated from 18S amplicon sequences previously obtained for Martinez-Alonso *et al.* (2019) and Garcia-Lopez *et al.* (2021). Sequence analysis and tree construction were performed as previously described (Ruiz-Blas *et al.* 2023). Barplots were generated from taxonomic annotations using the SILVA rRNA database. The first barplot ring (closer to the tree) represents the glacial environments, the second barplot ring represents taxonomic level 1, the third barplot ring represents taxonomic level 2 and the most external barplot ring represents taxonomic level 6 (genus). The legend corresponding to the genera (level 6) has not been represented due to its large size, but the major genera are detailed in the text.

which remain poorly understood (Anesio & Laybourn-Parry 2012). As a consequence of climate change, glaciers and permafrost are melting. This means that pathogenic viruses could awaken and infect the surrounding fauna and flora (Varghese *et al.* 2023).

Molecular mechanisms of the adaptation of microorganisms in Antarctic glaciers

Antarctic microorganisms have successfully coped with various stresses thanks to various molecular mechanisms of adaptation and evolutionary pressure that have selected certain species (Leo *et al.* 2021). Using proteomics techniques, the molecular machinery at work in Antarctic glacier inhabitants has been discovered and the molecular mechanisms of adaptation to the polar environment have been elucidated (Martinez-Alonso *et al.* 2019). The ability to determine the complete genomes of microorganisms has recently enabled the reliable identification of a large number of related proteins. But, even in the best-studied model microorganisms,

such as *E. coli*, there remain large numbers of genes with unknown functions (Ghatak *et al.* 2019). In glacier microorganisms, this proportion is even higher, and much more information is still needed on the metagenomes of glacier microorganisms because ~20–30% of the analysed proteins are listed in databases as hypothetical or unknown proteins. Many other proteins are identified by analogy with the proteomes of other types of microorganisms that have been much more studied, but this type of identification is not very reliable, as low significance scores are obtained from such searches in protein databases.

Adaptation to temperature changes

Antarctic glacier ice shows a wide temperature range. Average summer temperatures are close to 0°C, although temperatures of up to 18.3°C have been recorded on the surface of glaciers, where solar radiation amplified by the albedo heats the ice (Bergstrom *et al.* 2020). During the winter (March–September), there is little

to no incoming solar radiation, and temperatures average -30°C (Fountain *et al.* 1999). These enormous temperature variations must be added to the generalized temperature increase that the entire planet is undergoing due to climate change linked to anthropogenic greenhouse gases. Although this change is less pronounced in Antarctica than in other regions of Earth, the temperature increase in the South Shetland archipelago has been $\sim 3^{\circ}\text{C}$ since the middle of the 20th century (Gorodetskaya *et al.* 2023).

Microorganisms adapt to temperature changes by adopting various modifications in their cellular and molecular machinery. These adjustments include the synthesis of heat shock proteins (Hsps) and cold shock proteins (Csps) that are involved in several cellular processes such as transcription, translation, protein folding and the regulation of membrane fluidity (Garcia-Descalzo *et al.* 2011, Yusof *et al.* 2022). These proteins have been extensively investigated in the context of the adaptation of Antarctic yeasts and bacteria to temperature increases (Deegenars *et al.* 1997, Che *et al.* 2013, Garcia-Descalzo *et al.* 2022). For example, when the bacterium *Shewanella frigidimarina* is exposed to high temperatures, it accumulates Hsps, as well as other proteins related to stress, redox homeostasis or protein synthesis and degradation and the depletion of enzymes and cell envelope components. In addition, the entire cellular machinery is remodelled, and chaperone proteins, such as Hsps, reorganize their interaction networks with other proteins (Garcia-Descalzo *et al.* 2014).

Another adaptation of microorganisms to cold is the modification of the composition of their cell membranes. Cold reduces the fluidity of membranes, and to compensate for this effect, the fatty acid composition of the membranes of these microorganisms is different from that of membranes of other prokaryotes (Wang *et al.* 2017). Among the modifications to membrane fatty acids, the synthesis of lipids with *cis*-unsaturated double bonds has been described previously, as well as the incorporation of branched lipids and the incorporation of short fatty-acyl chains that reduce the contacts between adjacent chains (Feller 2007, Chen *et al.* 2022).

Recently, high-throughput technologies have been developed to determine the function of a large number of enzymes from psychrophilic microorganisms, combining proteomics techniques and the reconstruction of protein networks (Garcia-Descalzo *et al.* 2022, Ramasamy *et al.* 2023). It has been shown that living at low temperatures is benefitted by the ability to synthesize enzymes that continue to function at near-freezing temperatures. Psychrophilic enzymes constitute an important class of proteins in which structure-function relationships can be investigated by comparing their properties with those of homologous mesophilic and thermophilic counterparts (Ruggiero *et al.* 2007). In this comparison, it has been observed that psychrophilic enzymes are more flexible (the space available for amino acid side chains is larger than that for mesophilic enzymes), and this fact allows them to continue to function at low temperatures. The flexibility of these proteins sometimes affects the whole molecule, but it is sufficient if only the catalytic region has such flexibility (Hochachka & Somero 2002, D'Amico *et al.* 2006, Giordano *et al.* 2012).

Adaptation to high levels of radiation

Microorganisms that are highly resistant to radiation are called 'radiophiles'. Among them, representatives of the genus *Deinococcus* such as *Deinococcus radiodurans* and *Deinococcus radiophilus* have been described, which are mostly found on the surface of

glacial ice, where solar radiation and albedo are very intense (Zhang *et al.* 2020, Cheng *et al.* 2024). These microorganisms are also highly resistant to oxidative damage and dehydration. It has been observed that these bacteria utilize several repair mechanisms (Liu *et al.* 2023). The DNA of cells subjected to high doses of radiation is damaged and becomes non-functional, but these bacteria can repair such damaged DNA (Singh & Gabani 2011).

Another important resistance mechanism of microorganisms to protect themselves from solar radiation is the synthesis of pigments. Bacteria, as well as archaea and algae, are pigment producers (Garcia-Lopez & Cid 2016). For example, the bacterium *Sphingobacterium antarcticus* produces zeaxanthin, β -cryptoxanthin and β -carotene (Jagannadham *et al.* 2000). Another pigment capable of protecting organisms from radiation is xanthomonadin, which is exclusively produced by *Xanthomonas* (Rajagopal *et al.* 1997). Other pigments produced by halophilic archaea are bacterioruberin and bacteriorhodopsin (Rodrigo-Ba os *et al.* 2015). Among the microalgae, *Chlorella zofingiensis* and *Chlamydomonas nivalis* produce xanthophylls (Smaoui *et al.* 2021).

Adaptation to the lack of oxygen

The supraglacial habitat is populated by aerobic microorganisms that use oxygen as an electron acceptor (Maccario *et al.* 2015). Oxygen is the acceptor of choice for cells as the reduction of oxygen produces a large amount of energy compared to that produced by the reduction of other electron acceptors (Madigan *et al.* 2015). However, in the englacial and subglacial habitats, the oxygen concentration is very limited, and so the respiration of microorganisms in these habitats is anaerobic. These microorganisms use other electron acceptors, such as nitrate reduced to nitrite or nitrogen by *Pseudomonas* species (Martinez-Alonso *et al.* 2019). Other bacteria use other inorganic compounds, such as *Geobacter* using ferric iron and *Desulfovibrio* using sulphate (Martinez-Alonso *et al.* 2019). Some methanogenic microorganisms reduce carbonate to methane, whereas acetogens reduce carbonate to acetate. Even organic molecules such as fumarate can be used as electron acceptors in anaerobic respiration (Madigan *et al.* 2015). Similarly to aerobic respiration, anaerobic respiration requires electron transport and uses the enzyme ATPase to synthesize adenosine triphosphate (ATP). Most of the enzymes and proteins used in these cellular processes have been discovered only recently through proteomics analysis (Martinez-Alonso *et al.* 2019).

Adaptation to the lack of nutrients

Glacial microorganisms play an important ecological role as they participate in global geochemical fluxes. They are essential components of microbial food webs and are often dominant primary producers, playing important roles in chemical weathering and carbon and nitrogen cycling processes (Trejos-Espeleta *et al.* 2024).

In the supraglacial ecosystem, there is a large majority of photosynthesizing and heterotrophic microorganisms that feed on organic debris carried by the ice, and so the lack of nutrients is not a limiting factor to their survival (Maccario *et al.* 2015). However, in the lower layers of glaciers, microorganisms have adapted to nutrient scarcity by developing a chemoautotrophic metabolism in which they feed on rocks and soil (Harrold *et al.* 2016). Most of the microorganisms in these ecosystems are heterotrophic and chemoautotrophic (Hodson *et al.* 2008, Martinez-Alonso *et al.* 2019). The englacial and subglacial environments also favour the

growth of numerous fungal species. Such fungal growth facilitates the weathering of rocks and the opening of internal channels. These fungi have a heterotrophic metabolism and degrade organic matter remains. In turn, the carbon obtained from this degradation and its transport through the hyphae into the rocks would facilitate the growth of other microorganisms such as heterotrophic bacteria (Butinar *et al.* 2007).

The anaerobic metabolism of microorganisms also include methanogenesis. As stated earlier, the Archaea contain methane-producing microorganisms. There are two groups of methanogenic archaea: methylotrophic and hydrogenotrophic. Hydrogenotrophic methanogens produce methane from H_2 plus CO_2 (or formate). Methylotrophic methanogens produce methane from simple monocarbon compounds such as methanol, methylamines and methylthiols (Madigan *et al.* 2015). It has been documented previously that when glaciers retreat, the methane that had been retained beneath the glacier in pockets of gas, which had been produced by methanogenic microorganisms, escapes into the atmosphere (Kleber *et al.* 2023). Once these glaciers disappear, pedogenesis begins, and the organic matter in glacial forefields becomes subject to remineralization to CO_2 by microbial respiration (Tao *et al.* 2023). In this succession, fungi play a main role in the initial stabilization of the assimilated carbon (Trejos-Espeleta *et al.* 2024).

Adaptation to dryness

The Antarctic continent is extremely dry, averaging 166 mm of precipitation per year (Vaughan *et al.* 1999). The air in Antarctica is also dry, as the low temperatures result in very low absolute humidity levels. As a mechanism of adaptation to the lack of water, some species of bacteria, such as those of the genus *Bacillus*, produce structures called 'endospores'. These survival mechanisms enable these organisms to withstand unfavourable growth conditions, such as extreme temperatures, dryness or a lack of nutrients. In addition, these endospores are easily dispersed by wind and water (Ryan-Payseur & Freitag 2018).

Among eukaryotic microorganisms, fungi, such as the genus *Rhizopus* identified in the Mount Pond glacier, are also capable of resisting dryness through the formation of a zygosporangium, which can remain dormant and resist dryness and other unfavourable conditions (Gryganskyi *et al.* 2019).

Another mechanism of adaptation is the formation of biofilms. This mechanism has been investigated in bacteria of the genus *Bacillus*, which that can choose between two lifestyles: biofilm formation and flagellum-mediated swimming motility. This choice is made at the individual cell level, with bacterial cells in a population expressing either the genes required for biofilm formation or the genes required for flagellum-mediated swimming motility (Ryan-Payseur & Freitag 2018). Furthermore, to form a biofilm, the cells need to engage in intercellular communication (quorum sensing) that leads to a choice being made between living freely or forming a biofilm. It has been demonstrated previously that in the genus *Pseudomonas* quorum sensing induces the expression of a group of genes necessary for the synthesis of the exopolysaccharides that form a biofilm. Intracellular signalling is also involved in biofilm formation in *Pseudomonas aeruginosa* through the cyclic di-GMP messenger protein, which is unique to prokaryotes (Lichtenberg *et al.* 2022). In glaciers, biofilms can be observed on the surface of cryoconite holes in which there is a liquid water medium and in which cells can move and communicate with each other.

Conclusions

This review paper explores the diversity of the molecular mechanisms of adaptation of cold-loving microorganisms, and it details the specific characteristics of the microbial populations living in the Antarctic glaciers of the South Shetland archipelago. The main conclusions are as follows:

- Antarctic glaciers had classically been considered uninhabited, but they have in fact been colonized by a great diversity of bacteria, archaea, viruses and microeukaryotes such as algae and unicellular fungi.
- In this work, a great diversity of prokaryotic and eukaryotic microorganisms was observed in the glaciers of the South Shetland archipelago when compared with other Antarctic glaciers.
- DNA databases are becoming more complete, and they contain an increasing number of identified sequences. Therefore, fewer unspecified sequences have been obtained in this review than in previous analyses. Even so, ~40% of microeukaryote sequences remain unknown or unspecified.
- The South Shetland archipelago supports large numbers of scientists and tourists. The presence of prokaryotic and eukaryotic microorganisms of human origin can already be detected within the glacial ice of these islands.
- The identification of the complete genomes of some microorganisms has recently enabled the reliable identification of a large number of related proteins. However, much more information on the metagenomes of Antarctic glacier microorganisms is still needed, because ~20–30% of the analysed proteins are still listed in the relevant databases as hypothetical or unknown proteins.

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Nucleotide sequence accession numbers. The amplicon sequencing data are available at SRA (NCBI, Bethesda, MD, USA) under the project IDs PRJNA430179 (Martinez-Alonso *et al.* 2019); SAMN14863991, SAMN14868361, SAMN14868400, SAMN14868414, SAMN14868429, SAMN14868542, SAMN14868580, SAMN14868598, SAMN14868636, SAMN14868654, SAMN14868683, SAMN14868702, SAMN14868717, SAMN14868740, SAMN14868844, and SAMN14868902 (García-Lopez *et al.* 2021); SRS10910775-SRS10910778 (García-Lopez *et al.* 2022).

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