REVIEW PAPER

A survey of Antarctic cyanobacteria

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Abstract This review compiles principal data on Antarctic cynobacteria published in recent decades and focuses on the diversity, environmental adaptations, and ecotypes of these microorganisms. Multidisciplinary investigation of Antarctica is important especially in times of global climate change and anthropogenic threats to unaltered ecosystems. Antarctica, which has been disconnected from Gondwana for the last 65 Myr, harbors relict biota mainly including microorganisms adapted to multiextreme environments. Cyanobacteria represent the most well studied Antarctic microorganisms related to the cell biology, abundance, distribution, and symbioses. However, substantial drawbacks remain, e.g., (i) the diversity of Antarctic cyanobacteria has been evaluated without a consensus between bacteriologists and phycologists due to the intricate interplay of morphological records, genomic data and culturing restrictions as well as taxonomic obstacles; (ii) although the main strategy of Antarctic cyanobacteria is biofilms (in particular, microbial mats), detailed knowledge on these symbiotic systems is still fragmentary; (iii) the specificity of the 'Antarctic cyanobacteria biosphere' should be better understood in light of unresolved questions related to endemism in prokaryotes, and (iv) the strains of Antarctic cyanobacteria maintained in culture are not numerous and not very diverse. These issues are at the forefront of cyanobacteriology, which is supported by related biosciences and earth sciences.

Keywords Cyanoprokaryotes · Polyphasic taxonomy · Psychrophilic bacteria · Endemic bacteria · Biofilm · Microbial mat

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Introduction

The Antarctic microbiota is a highly important interdisciplinary topic, especially considering global climate change and anthropogenic threats to unaltered ecosystems (Gasparon & Burgess, 2000; Weisleitner et al., 2019). Antarctica is inhabited by microorganisms that have adapted themselves to extreme environments and rely on symbiotic associations such as biofilms (e.g., microbial mats). With regard to food webs, the Antarctic microbiota mainly depends on cyanobacteria (Convey, 2013; Chong et al., 2015). At present, Antarctica is possibly the best studied region

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with respect to the diversity, distribution and cell biology of these microorganisms (Taton et al., 2003, Jungblut et al., 2005; Taton et al., 2006; Wood et al., 2008; Pushkareva et al., 2018). Microbiologists describe Antarctic cyanobacteria via polyphasic taxonomy which evaluates phenotypic resemblance together with phylogenetic record similarity. Phycologists, who by compromise designate cyanobacteria as cyanoprokaryotes (Komárek & Anagnostidis, 1999), have also gradually shifted to polyphasic taxonomy (Komárek, 2016).

An account of principal data related to Antarctic cyanobacteria is given below, together with selected information on the essential accompanying microorganisms.

Antarctic climate and microbial ecogeography: general outline

Antarctica, as a whole can be subdivided in two biogeographic zones: continental (East Antarctica) and maritime (west Antarctic Peninsula sea costs and neighboring islands) (see Fig. 1). The Antarctic ecotope types are distinguished as aquatic, soil, bog, ice, snow, and bare ground ones (Convey, 2013).

A continental climate is typical for cryosphere: the temperature in summer rarely exceeds $+2°C$, while in winter it often falls to $-60°C$. The maritime Antarctic climate is more humid; in coastal regions, seasonal fluctuations are less pronounced, with a maximum value of approximately $+15°C$ (Convey, 2013). In addition to low temperature, there are other environmental factors that inhibit organic life, namely: aridity, intensive solar radiation in spring and summer, period of dark in winter, and recurrent freeze–thaw cycles (Singh & Elster, 2007; Prieto-Barajas et al., 2018).

The Antarctic ice sheet is edged with pack ice which partially melts even at negative temperatures (due to strong irradiance input through highly transparent air; the melted water feeds small lakes or, in spring and summer, brooks and rivers). Running water usually does not discharge into the sea; rather, it seeps through ice bodies and fills costal depressions that turn into Antarctic lakes (Quesada et al., 2006). The latter vary from ultrafresh to hypersaline (Sabbe et al., 2004). Even minute salinity fluctuations strongly affect the physiology and population parameters of microbiota (Jungblut et al., 2005).

Water in the liquid state appears in Antarctica either due to seasonal snow melting in oases, i.e., ice-free territories (Komárek & Komárek, 2010) or in deep lakes covered with ice (Andersen et al., 2011). Ice capillaries filled with supercool water are known to approach the lower limmit for bacterial growth (D'Amico et al., 2006), and it was found that cyanobacteria in Antarctic lake ice water pockets (with temperatures always below zero) were metabolically active and retained their photosynthetic capacity (Paerl & Priscu, 1998). Antarctic cyanobacteria were also shown to metabolize even at $-20°C$ (Psenner & Sattler, 1998). The largest Antarctic oases—the McMurdo Dry Valleys, Bunger Oasis and Vestfold Hills—encompass oligotrophic and ultraoligotrophic lakes, as well as smaller water reservoirs with various pH and salinity values (Gillieson et al., 1990; Porcino et al., 2020). Oases are usually almost free of pack ice, while bays and fiords are so only in the summer (Quesada et al., 2006).

Antarctic microbiota: fundamentals, and analysis methods

Antarctic microbial communities are in fact 'The lost world', because they have long been subject to isolation with a relatively low disturbance level (Vincent, 2007).

Starting from pioneering scientific expeditions in the early 1900s, the Antarctic microbiota has been investigated by phycologists, protozoologists and mycologists (see Ruisi et al., 2007). Prokaryotic subsets except blue-green algae, later referred to as also cyanobacteria, began attracting broad attention from microbiologists only in the second half of the XX century (e.g., Herbert & Tanner, 1977; Franznann et al., 1988).

The noncyanobacterial moiety of the Antarctic microbiota is represented by other prokaryotes (anoxygenic photosynthetic bacteria, chemosynthetic bacteria, chemoheterotrophic bacteria, and archaea) as well as by unicellular eukaryotes (protozoa, microalgae and microfungi). Some of these taxa are primary producers, while others utilize cyanobacterial exometabolites and mortmass. Along with cyanobacteria, these microorganisms comprise the backbone of the food web on the sixth continent (Ji et al., 2017).
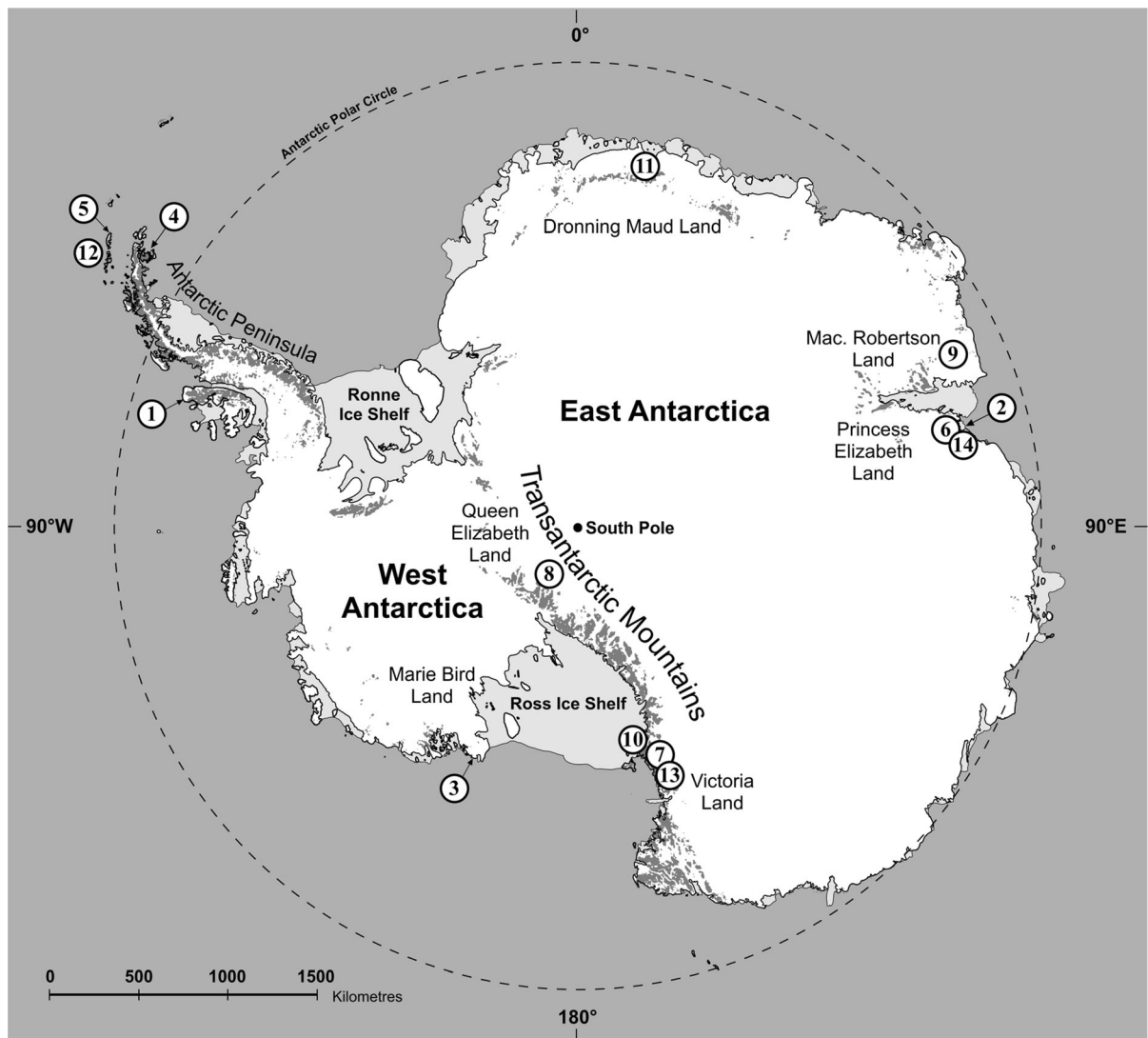
Fig. 1 Schematic map which shows the Antarctic cyanobacteria sampling sites. (1)—Alexander Island; (2)—Bølingen Islands; (3)—Edward VII Peninsula; (4)—James Ross Island; (5)—King George Island; (6)—Larsemann Hills; (7)—McMurdo Dry Valleys; (8)—Mount Howe; (9)—Mawson Rock; (10)—Pyramid Trough; (11)—Schirmacher Oasis; (12)—South Shetland Islands; (13)—Taylor Valley; (14)—Vestfold Hills. Shelf marked grey, glacier marked dark grey

The Antarctic microbiota, especially cyanobacteria, has been studied by morphological description combined with conventional microbiological methods (e.g., strain isolation and characterization in terms of ecology) and genomic analysis especially targeting the 16S rRNA gene large fragment (or full size gene). In recent years, the Antarctic microbiota has been extensively explored with next generation-high performance-sequencing (NGS), or 16S rRNA-barcoding, which performs high-throughput taxonomic identification of

commmunity members. The sum of these approaches has been used to obtain in-depth knowledge on the diversity, distribution, ecology and adaptations of Antarctic microbiota (Chong et al., 2015; Pessi et al., 2015, 2016; Achberger et al., 2016; Koo et al., 2017; Prieto-Barajas et al., 2018). The results obtained with the help of different metagenomic technologies strongly propelled our understanding of the diversity and distribution of Antarctic microbiota. For example, the survey of Lake Fryxell microbial mats revealed, in

addition to cyanobacteria, many members of the phyla Bacteroidetes, Chlorobi, Chloroflexi, Planctomycetes, Proteobacteria and Verrucomicrobia; it is noteworthy that the cyanobacterial 'stress' gene subset prevailed over these genes in Proteobacteria (Varin et al., 2012).

Cyanobacteria in Antarctic microbiota

For the most part, the Antarctic microbiota is represented by photosynthetic representatives of the phylum Cyanobacteria which support the entire ecosystem with energy sources as well as with fixed carbon and nitrogen (Singh & Elster, 2007; Komárek & Komárek, 2010; Bowman et al., 2012; Chrismas et al., 2015; Prieto-Barajas et al., 2018). In Antarctic ecosystems, cyanobacteria play the role of principal primary producers; their survival and development in extreme environments are mainly due to their ability to produce biofilms (especially microbial mats) (Convey, 2013; Chong et al., 2015).

Cyanobacteria have been frequently observed in glaciers and cold deserts, where they employ molecular adaptations to mitigate the harshness of local environment (Vincent, 2007). Plankton strains are mainly represented by picocyanobacteria (although these are not abundant except in East Antarctic saline lakes where they accumulate at densities of up to $1.5 \cdot 10^7$ cells ml^{-1}), in contrast, microbial mat forming strains are ubiquitous and abundant (Vincent & Quesada, 2012a). Cyanobacteria were shown to dominate in the Antarctic microbial mat surface layers while deeper layers were inhabited by phototrophic bacteria of the phyla Chlorobi and Chloroflexi, as well as by sulfur-dependent heterotrophs from the class *Epsilonproteobacteria* (the latter were previously found only in the anoxic lower zone); at the same time, *Alphaproteobacteria*, *Betaproteobacteria*, *Gammaproteobacteria* and *Deltaproteobacteria* were shown to inhabit the entire mat (Jungblut et al., 2016).

Antarctic cyanobacteria closely coexist with heterotrophic satellites that particularily belong to the phyla Proteobacteria and Bacteroidetes (Zhu et al., 2016; Cornet et al., 2018). Multixenic cyanobacterial cultures were obtained from ice, snow and soil biofilms (Bowman et al., 2012; Pearce et al., 2012; Bottos et al., 2014; Lopatina et al., 2016). These represent a convenient model for the research of environmental relationships between cyanobacteria

and their heterotrophic partners (Zhu et al., 2016; Cornet et al., 2018). Satellite bacteria were suggested to supply cyanobacteria with indispensable growth factors (Singh & Elster, 2007; Cornet et al., 2018).

Nearly a half of cyanobacterial operational taxonomic units (OTUs; 24 of 42) associated with Antarctic ice-free areas correspond to uncultured objects. These OTUs display 87–97% similarity to the 16S rRNA genes of cultured cyanobacteria deposited at the NCBI GenBank database which offers an opportunity to propose new taxa (Namsaraev et al., 2010; Tindall et al., 2010). Importantly, environmental phylotypes outnumbered morphologically recorded ecospecies (and, all the more, cultured species); in other words, the majority of Antarctic cyanobacteria should be ascribed to 'microbial dark matter' of the planet (Lambrechts et al., 2019).

Diversity of Antarctic cyanobacteria

Cyanobacteria are simultaneously classified and identified according to botanical taxonomic system (Hoffmann et al., 2005; Komárek et al., 2014; Komárek, 2018) and bacteriological taxonomic system (Rippka et al., 1979; Castenholz, 2001). However, in both these cases, generic assignments are primarily based on the key criteria developed in the blue-green algae (Cyanophyceae) system by Lothar Geitler in 1930: unicellular or filamentous forms; branched or unbranched trichomes; inability or ability to produce differentiated cells, etc. The bacteriological approach to generic assignments of cyanobacteria is based on these morphological characters related to cultured strains while the routine phycological identification focuses on herbarium material (and also illustrative material until 1953) for this purpose.

The assignment of cyanobacteria to taxa above generic level is problematic. Thus, recent phycological system of cyanobacteria compromises on the phylum Cyanobacteria that contains the single class Cyanophyceae, which includes four subclasses: Gloeobacterophyceae (with a single 'phylogenetic' order), Nostocophycideae (also with a single 'phylogenetic' order), Oscillatoriophycideae and Synechococcophycideae (Komárek et al., 2014; Komárek, 2018). However, despite phylogenetic markers have been steadily addressed (Palinska & Surosz, 2014; Komárek, 2016, 2018), this system evidently

represents a transient state in cyanobacterial taxonomy. Notably, Synechococcophycideae and Oscillatoriophycideae are not monophyletic in phylogenies based on multigene sequence alignments (Hoffmann et al., 2005). The bacteriological system of cyanobacteria is more conservative, and it confines itself to the 'Geitlerian' taxonomy. Within the phylum Cyanobacteria, five non-nomenclatural units are distinguished that conditionally correspond to 'phenotypic' orders: Subsection I (unicellular cyanobacteria that reproduce by binary fission), Subsection II (unicellular cyanobacteria that reproduce by only multiple fission, or by binary and multiple fission), Subsection III (filamentous, unbranched or false branching cyanobacteria that cannot produce differentiated cells), Subsection IV (filamentous, unbranched or false branching cyanobacteria that can produce differentiated cells), and Subsection V (filamentous, true branching cyanobacteria that can produce differentiated cells) (Rippka et al., 1979; Castenholz, 2001). With few exceptions, and in contrast to the botanical system, the bacteriological system does not rely on taxonomic category of species; the reason for this is a difference between the provisions of Prokaryotic Code (ICNP) and Botanical Code (ICN), respectively (Oren & Ventura, 2017).

Generic and species assignment of cyanobacteria faces serious obstacles, such as: (i) the coexistence of two taxonomic systems; (ii) objective and/or subjective difficulties encountered at morphology-based identification; (iii) sometimes questionable correspondence between closely matching NCBI GenBank sequence and correct taxonomic attribution of this sequence.

Starting from the first botanical descriptions of Antarctic cyanobacteria as early as 1911 (e.g. West & West, 1911), floristic records have been confined to the morphology of fixed samples, this is exemplified by numerous descriptions of botanical species, e.g. *Leptolyngbya* spp., *Lyngbya murrayi* West and West, *L. scotti* var. *minor* Fritsch, *Microcoleus vaginatus*, *Nostoc* spp., *Oscillatoria priestleyi* West, *Phormidium autumnale*, *P. frigidum* Fritsch, *P. priestleyi* Fritsch, *P. tenue* (Menegh.) Gom., *P. uncinatum*, *Pseudanabaena* spp. and *Synechococcus* spp. (see Broady et al., 1984). Notably, earlier studies documented a limited local diversity, e.g. Lake Fryxell was shown to harbor only *Lyngbya* spp. and *Phormidium* spp. (Wharton et al., 1993).

In 2004–2015, Jiří Komárek and coauthors (e.g., Mataloni & Komárek, 2004) greatly extended the knowledge on Antarctic cyanobacteria; certain species, e.g. *Plectonema hodgsonii* sampled in Lake Progress (Larsemann Hills) were described via polyphasic analysis with support from molecular data (Taton et al., 2006).

The diversity of Antarctic cyanobacteria has been long studied from a single perspective: by morphological description of live or fixed samples. Today, these cyanobacteria provide an opportunity for metagenomic analysis, as well as polyphasic taxonomy, which encompasses: strain isolation; axenization (if possible); morphological, physiological, biochemical, molecular biological and phylogenetic analyses of cultured strains; and ecological description of microorganisms in their natural habitat (Vincent & James, 1996; Taton et al., 2006; Singh et al., 2008; Suman et al., 2010; Jungblut et al., 2016; Pessi et al., 2016; Koo et al., 2017; Pessi et al., 2018). Culture-based approaches have their own limitations, such as culturability restrictions and high degree of phenotypic difference between cyanobacteria in the free-living and cultured state (see the authors' participation to this field of research in Supplementary material S1).

Principal information on Antarctic cyanobacterial genera, which are structured according to the bacteriological system (Table 1), has been compiled from the publications that had different aims of research and different methodological capacities. Some of these publications described cultured (or preferentially not cultured) isolates analyzed by morphological and/or molecular phylogeny methods—Sanger sequencing of 16S rRNA gene fragments (rarely, full size gene) or sequencing of the 16S−23S ITS region of rRNA gene cluster. Other publications contained NGS data on the taxonomic composition of microbial communities.

Some notable aspects of the Antarctic cyanobacterial diversity

Species with uncommon pigment content

Chlorophyll *a* (Chl *a*) is the only chlorophyll in the majority of cyanobacteria, the exception is 'green' ones (also termed prochlorophytes), which additionally possess one or several chlorophylls (e.g., divinyl Chl *a*, Chl *b*, divinyl Chl *b*, Chl *c*, Chl *d* and Chl *f*). The

Table 1 Principal information on the Antarctic cyanobacterial genera (since the early 1970s)

Operational unit[a]	Genus	Ecotype	Sampling site[b]	Method of analysis	References
Subsection I	*Acaryochloris*	Endolithic and aquatic biofilms	MDV	Morphology; NGS	de los Rios et al. (2007) and Rego et al. (2018)
	Aphanocapsa	Benthic, endolithic, epilithic and soil biofilms; littoral mats	JRI; KGI; MA; MDV; MH; SSI	Morphology; 16S rRNA gene Sanger sequencing; NGS	Friedmann et al. (1988), Broady & Weinstein (1998), Mataloni & Pose (2001), Cockell & Stokes (2006), Fermani et al. (2007), Jungblut et al. (2010), Namsaraev et al. (2010), González Garraza et al. (2011), Allende & Mataloni (2013) and Komárek (2013)
	Aphanothece	Chasmoendolithic, cryoconite and hypolithic biofilms; stream mats	JRI; KGI; MA (also in Arctic); MDV; VH	Morphology	Broady (1981, 1986), Mataloni & Pose (2001), Mueller & Pollard (2004), Cockell & Stokes (2006), Komárek et al. (2008), Omelon (2008) and Allende & Mataloni (2013)
	Chamaesiphon	Cryoconite, epilithic, epiphytic, lichen and soil biofilms; pond, lake and stream biofilms	AI; HM; JRI; MA (also in Arctic); MDV; OS; QML; VL	Morphology (*C. austro-polonicus*, *C. arctowskii*); 16S rRNA gene Sanger sequencing	Broady (1979), Priscu (1998), Izaguirre & Pizarro (2000), Mataloni & Pose (2001), Liu et al. (2006), Brinkmann et al. (2007), Zakhia et al. (2008), González Garraza et al. (2011), Allende & Mataloni (2013), Martineau et al. (2013), Komárek (2013), Pessi et al. (2016), Segawa et al. (2017), Faluaburu et al. (2019) and Weisleitner et al. (2020)
	Chlorogloea	Ornithogenic soil biofilms	AP; MH	Morphology (*C. antarctica*)	Jungblut et al. (2010), González Garraza et al. (2011) and Komárek et al. (2014)
	Chroococcus	Cryptoendolithic biofilms; benthic mats	BI; JRI; LH; MD; VH	Morphology; 16S rRNA gene Sanger sequencing	Friedmann et al. (1988), Pandey et al. (2004), Taton et al. (2006) and Jungblut et al. (2010)
	Cyanosarcina	Ornithogenic soil biofilms	AP	Morphology	Mataloni & Pose (2001), González Garraza et al. (2011) and Allende & Mataloni (2013)
	Cyanothece	Chasmoendolithic, endolithic, epilithic and soil biofilms	AI; ED; MA; MDV	Morphology; NGS	Broady (1989b), Brinkmann et al. (2007), de los Ríos et al. (2007), Büdel et al. (2008), Namsaraev et al. (2010) and Komárek (2013)
	Gloeocapsa	Chasmoendolithic, cryoconite, cryptoendolithic, hypolithic and soil biofilms; benthic mats	BI; ED; LH; MA; MDV; MH; SO (also in Arctic); VH	Morphology; 16S−23S ITS sequencing; NGS; polyphasic approach	Broady (1981, 1986), Friedmann et al. (1988), Broady (1989a), Broady & Weinstein (1998), Cockell & Stokes (2004), Mueller & Pollard (2004), Pandey et al. (2004), Mataloni et al. (2005), Taton et al. (2006), Vincent (2007), Jungblut et al. (2010), Namsaraev et al. (2010), Komárek et al. (2014), Micheli et al. (2014)
	Synechococcus	Cryoconite, cryptoendolithic, epilithic, epiphytic, hypolithic, snow and soil biofilms; lake biofilms and marine phytoplankton	AI; DM; HM; MA; MDV (also in Arctic)	Morphology; 16S rRNA gene Sanger sequencing; NGS	Broady (1979), Ryan et al. (1989), Vincent (2000), Mueller & Pollard (2004), Liu et al. (2006), Brinkmann et al. (2007), Wilkins et al. (2013) and Pessi et al. (2016; 2018)
	Synechocystis	Rock subaerophytic biofilms; aquatic biofilms	JRI; KGI	Morphology	Komárek (2013)

Table 1 continued

Operational unit[a]	Genus	Ecotype	Sampling site[b]	Method of analysis	References
Subsection II	*Aliterella*	Epilithic, green algae-associated and ornithogenic soil biofilms; phytoplankton	KGI	Polyphasic approach (*A. antarctica*)	Rigonato et al. (2016)
	Chroococcidiopsis	Chasmoendolithic, cryptoendolithic, epilithic, hypolithic and soil biofilms	DM; ED; MA (also in Arctic); MDV; MR;VH	Morphology;16S and 23S rRNA gene Sanger sequencing; NGS	Broady (1981, 1986, 1989a), Friedmann et al. (1988), Ryan et al. (1989), Thompson (1989), Cockell & Stokes (2004), Bahl et al. (2011) and Komárek et al. (2014)
	Myxosarcina	Epilithic biofilms	MA	Morphology	Broady (1981)
	Pleurocapsa	Chasmoendolithic, epilithic and hypolithic biofilms; stream biofilms	AI; DM; HM; MA; MDV (also in Arctic)	Morphology (*P. antarctica*)	Broady (1981, 1986), Vincent (2007) and Komárek et al. (2014)
Subsection III	*Geitlerinema*	Freshwater phytoplankton; shallow wetlands; wet rocks and soil biofilms	JRI. MA, MDV	Morphology, NGS; polyphasic approach (*G. deflexum = Anagnostidinema deflexum*)	Taton et al. (2003), Allende & Mataloni (2013), Pessi et al. (2016) and Strunecký et al. (2017)
	Leptolyngbya	Chasmoendolithic, cryoconite, cryptoendolithic, epilithic, glacial ice, hypolithic, nunatac and soil biofilms; benthic mats	AI; BI (also in Arctic) LH; MA; MDV; PT QML; VH; VL	Morphology; 16S−23S ITS sequencing; NGS; polyphasic approach (*L. antarctica, L. fragilis, L. frigida, Leptolyngbya* sp.)	Friedmann et al. (1988), Priscu (1998), Mataloni et al. (2000), Mataloni & Pose (2001), Cavacini (2001), Taton et al. (2003), Mueller & Pollard (2004), Jungblut et al. (2005), Mataloni et al. (2005), Stibal et al. (2006), Brinkmann et al. (2007), Komárek (2007), Biondi et al. (2008), Jungblut et al. (2010), Martineau et al. (2013), Micheli et al. (2014), Zhang et al. (2015), Jungblut et al. (2016), Koo et al. (2017), Segawa et al. (2017), Pessi et al. (2018), Pushkareva et al. (2018), Rego et al. (2018) and Weisleitner et al. (2019)
	Lyngbya	Cryoconite, epilithic, glacial ice and soil biofilms; aquatic bodies biofilms	MA; MDV; MR,VL (also in Arctic)	Morphology; NGS	Broady (1981), Broady et al. (1984), Broady (1989a), Friedmann et al. (1988), Ryan et al. (1989), Nadeau et al. (2001), Sabbe et al. (2004), Brinkmann et al. (2007) and Pessi et al. (2018)
	Microcoleus	Cryoconite, epilithic and glacial ice biofilms; bentic mats	LH, MA, AI, MDV, QML (also found in Arctic)	Morphology; 16S rRNA gene Sanger sequencing; NGS; polyphasic approach (*M. vaginatus*)	Broady et al. (1984), Mueller and Pollard (2004), Casamatta et al. (2005), Stibal et al. (2006), Brinkmann et al. (2007), Komárek et al. (2008), Strunecký et al. (2010; 2012), Martineau et al. (2013), Archer et al. (2015), Segawa et al. (2017), Pessi et al. (2018), Pushkareva et al. (2018) and Faluaburu et al. (2019)
	Nodosilinea	Endolithic and soil biofilms	MDV	Morphology; 16S rRNA gene Sanger sequencing; NGS; polyphasic approach (*Nodosilinea* sp.)	Rego et al. (2018)
	Oscillatoria	Cryoconite, endolithic and soil biofoilms; benthic mats	MA; MDV; LH; SO (also Arctic); VH	Morphology; 16S rRNA gene Sanger sequencing	Cameron (1972), Broady et al. (1984), Broady (1989a), Broady & Kibblewhite (1991), Mataloni et al. (2000), Mataloni & Pose (2001), Nadeau et al. (2001), Mueller & Pollard (2004), Pandey et al. (2004), Jungblut et al. (2005), Taton et al. (2003, 2006), Vincent (2007), Brinkmann et al. (2007), Zhang et al. (2015) and Koo et al. (2017)
	Phormidesmis	Cryoconite biofilms; lake benthic mats	AI; DM; ED; LH; MA; MDV; PT (also in Arctic); VL	Morphology; 16S rRNA gene Sanger sequencing; NGS; draft genome sequencing; polyphasic approach (*P. priestleyi*)	Martineau et al. (2013), Archer et al. (2015), Chrismas et al. (2016), Lara et al. (2017), Segawa et al. (2017), Pessi et al. (2018) and Rego et al. (2018)

Table 1 continued

Operational unit[a]	Genus	Ecotype	Sampling site[b]	Method of analysis	References
	Phormidium	Chasmoendolithic, cryoconite, endolithic, epilithic, glacial ice, hypolithic, permafrost and soil biofilms; lake and pond littoral or benthic mats	AI; BI; DM; ED; LH; MA; MDV; SO (also in Arctic); QML; VL	Morphology; 16S rRNA gene Sanger sequencing; NGS; polyphasic approach (*P. autumnale, P. murrayi, P. priestleyi, P. pseudopriestleyi*)	Seaburg et al. (1979), Broady et al. (1984), Ryan et al. (1989), Thompson (1989), Broady & Weinstein (1998), Komárek (1999), Mataloni & Pose (2001), Nadeau et al. (2001), Priscu et al. (2005), Brinkmann et al. (2007), Comte et al. (2007), Vincent (2007), Biondi et al. (2008), Martineau et al. (2013), Zhang et al. (2015), Jungblut et al. (2016), Koo et al. (2017), Segawa et al. (2017), Pessi et al. (2018), Pushkareva et al. (2018), Weisleitner et al. (2019), Sohm et al. (2020) and Weisleitner et al. (2020)
	Plectolyngbya	Endolithic and soil biofilms	MDV (also in Arctic)	Morphology; 16S rRNA gene Sanger sequencing; NGS; polyphasic approach (*P. hodgsonii*)	Taton et al. (2011) and Rego et al. (2018)
	Plectonema	Chasmoendolithic, endolithic, hypolithic and soil biofilms; lake benthic mats	BI; LH; MA; MDV; MR; VH	Morphology; 16S rRNA gene Sanger sequencing; NGS; polyphasic approach (*Plectonema* sp.)	Cameron (1972), Broady et al. (1984), Broady (1986), Nienow & Friedmann (1993), Taton et al. (2006) and Micheli et al. (2014)
	Pseudanabaena	Soil biofilms; littoral and benthic mats	BI; LH; MA; MDV; PT, VH	Morphology; 16S rRNA gene Sanger sequencing; polyphasic approach (*Pseudanabaena* sp.)	Broady et al. (1984), Mataloni et al. (2000), Mataloni & Pose (2001), Taton et al. (2006), Brinkmann et al. (2007), Martineau et al. (2013), Zhang et al. (2015), Pessi et al. (2016); Koo et al. (2017), Pessi et al. (2018) and Weisleitner et al. (2020)
	Tychonema	Lake benthic mats	KGI; MDV	Morphology; 16S rRNA gene Sanger sequencing	Jungblut et al. (2005), Zhang et al. (2015), Koo et al. (2017) and Weisleitner et al. (2020)
Subsection IV	*Anabaena*	Cryoconite, endolithic, permafrost and soil biofilms; lake benthic mats	AI (also in Arctic); MA; MDV	Morphology; 16S rRNA gene Sanger sequencing; NGS	Friedmann et al. (1988), Thompson (1989), Mataloni et al. (2000), Mueller & Pollard (2004), Taton et al. (2006), Brinkmann et al. (2007), Vincent (2007), Namsaraev et al. (2010) and Archer et al. (2015)
	Calothrix	Chasmoendolithic, epilithic, hypolithic and soil biofilms; lake benthic mats	BI; ED; JRI; LH; MA; MDV; MR; SO; VH; VL	Morphology; 16S rRNA gene Sanger sequencing; NGS; polyphasic approach (*Calothrix* sp.)	Broady (1981, 1986, 1989b), Cavacini (2001), Pandey et al. (2004), Taton et al. (2006), Vincent (2007), Martineau et al. (2013), Komárek et al. (2015) and Pessi et al. (2018)
	Coleodesmium	Aquatic biofilms (including benthic mats)	BI; DV; LH; VH	NGS; polyphasic approach (*C. scottianum*)	Sabbe et al. (2004), Taton et al. (2006), Namsaraev et al. (2010), Pessi et al. (2016, 2018)
	Microchaete	Endolithic and soil biofilms	MDV	Morphology	Friedmann et al. (1988)
	Nodularia	Chasmoendolithic, hypolithic and soil biofilms; aquatic biofilms (including mats)	JRI; MA; MDV, VH, VL	Morphology	Broady (1981, 1986), Jungblut et al. (2005), Brinkmann et al. (2007), Vincent (2007) and Komárek et al. (2015)
	Nostoc	Chasmoendolithic, cryoconite, epilithic, hypolithic and permafrost biofilms; benthic mats	AI; BI; DM; ED; LH; MA; MDV; MR, PT (also in Arctic); SO; VH; VL	Morphology; 16S−23S ITS sequencing; NGS; polyphasic approach (*Nostoc* sp., *N. commune*)	Broady (1981, 1986, 1989a), Thompson (1989), Ryan et al. (1989), Taton et al. (2003); Mueller & Pollard (2004); Pandey et al. (2004), Jungblut et al. (2005), Biondi et al. (2008), Büdel et al. (2008), Martineau et al. (2013), Micheli et al. (2014), Segawa et al. (2017), Pessi et al. (2018), Faluaburu et al. (2019) and Sohm et al. (2020)
	Petalonema	Lake benthic mats	BI; LH;, MA; MDV; VH	Polyphasic approach (*P. involvens*)	Taton et al. (2006)

Table 1 continued

Operational unit[a]	Genus	Ecotype	Sampling site[b]	Method of analysis	References
	Scytonema	Epilithic, hypolithic and soil biofilms; lake benthic mats	DM; MA; VL	Morphology	Broady ([1986](), [1989a]()), Ryan et al. ([1989]()), Thompson ([1989]()), Cavacini ([2001]()) and Cockell & Stokes ([2006]())
	Tolypothrix	Chasmoendolithic, hypolithic and soil biofilms; benthic mats	AI; MA; VH	Morphology	Broady ([1979](), [1986](), [1989b]()), Mataloni et al. ([2000]()), Taton et al. ([2006]()) and Brinkmann et al. ([2007]())
Subsection V	*Fisherella*	Ground biofilms	JRI	Morphology; NGS	Broady ([1996]()), Nienow & Friedmann ([1993]()), Brinkmann et al. ([2007]()) and Namsaraev et al. ([2010]())
	Stigonema	Chasmoendolithic, epilithic and soil biofilms; aquatic biofilms	ED; MA; SO	Morphology	Broady ([1989b]()) and Pandey et al. ([2004]())

[a]According to the bacteriological system (see Rippka et al., [1979](); Castenholz, [2001]())

[b]*AI* Alexander Island, *AP* Antarctica Peninsula, *BI* Bølingen Islands, *DM* Dronning Maud Land, *ED* Edward VII Peninsula (Princess Elizabeth Land), *JRI* James Ross Island, *KGI* King George Island, *LH* Larsemann Hills Oasis (Princess Elizabeth Land), *MA* Maritime Antarctic, *MDV* McMurdo Dry Valleys (Victoria Land), *MH* Mount Howe (Ross Glacier, Transantarctic Mountains, Victoria Land), *MR* Mawson Rock (Mac Robertson Land), *PT* Pyramid Trough, *SO* Schirmacher Oasis (Queen Maud Land), *SSI* South Shetland Islands, *TV* Taylor Valley (Transantarctic Mountains, Victoria Land), *VH* Vestfold Hills Oasis (Princess Elizabeth Land)

Bioactive compounds producers

A number of *Leptolyngbya* and *Phormidium* strains isolated from Adelaide Island (Marguerite Bay) were shown to produce cyanotoxins, e.g. microcystins and cylindrospermopsin, which may participate in adverse symbiotic relationships (Kleinteich et al., 2014). Generally, polar cyanobacteria have been considered the promising agents of biotechnology (Singh et al., 2005; Cornet et al., 2018). Indeed, 90% of the strains isolated from Antarctic microbial mats were found to produce antibacterial, antifungal and antitumor compounds (Biondi et al., 2008). In particular, cell extracts of *Leptolyngbya antarctica*, *Nostoc* spp., *P. murrayi*, *P. priestleyi*, and *Pseudophormidium* spp. inhibited multidrug resistant *E. coli*, as well as *Enterobacter aerogenes*, *Mycobacterium tuberculosis*, *Pseudomonas aeruginosa*, *Salmonella typhi* and *Staphylococcus aureus*; in addition, these cyanobacteria produced antifungal compounds towards *Aspergillus fumigatus* and *Cryptococcus neoformans* (Núñez-Montero & Barrientos, 2018).

Cosmopolitan and endemic species

Early floristic observations concluded that Antarctic terrestrial cyanobacteria belonged to cosmopolitan taxa (Broady et al., 1984). Later surveys of morphological and molecular traits (McKnight et al., 1998; Komárek & Anagnostidis, 1999; Taton et al., 2003; Casamatta et al., 2005; Singh et al., 2008; Jungblut et al., 2010; Martineau et al., 2013; Komárek, 2014; Rigonato et al., 2016; Pessi et al., 2018) indicated, on

Cyanobacteria are the only known prokaryotes able of oxygenic photosynthesis (often associated with 'aerobic' diazotrophy). Due to such metabolic self-dependence and an ability to adapt to nearly any type of environment, cyanobacteria could be suspected to penetrate nearly everywhere that is strikingly exemplified by Antarctic niches.

far-red light shifted Chl *d* or Chl *f* producing species *Acaryochlris marina* and *Halomicronema hongdechloris* are known to adapt to niches poor in white light (Averina et al., 2019). Based on the 16S rRNA gene sequencing data, similar cyanobacteria were detected in Antarctic biofilms including microbial mats (Jungblut et al., 2016; Pessi et al., 2016; Koo et al., 2017).

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one hand, the presence of sure cosmopolitan species (*Aphanocapsa* cf. *holastica*, *A.* cf. *hyalina*, *Arthronema* spp., *Calothrix* spp., *Coleodesmium* spp., *Geitlerinema deflexum*, *Hassallia discoidea* (*Tolypothrix discoidea*), *Hydrocoryne* cf. *spongiosa* Schwabe, *L. frigida*, *Microcoleus* spp., *Nostoc* spp., *Oscillatoria* spp., *Phormidium* spp., *Pseudanabaena* spp., *Schizothrix* spp., *Tolypothrix* spp. and *Wilmottia murrayi*), and, on the other hand, the presence of potential endemic species (*Aliterella antarctica*, *Chamaesiphon arctowskii*, *C. austro-polonicus*, *M. antarcticus*, *Nodularia* cf. *harveyana* Thuret, *P. pseudopriestleyi* and *O. subproboscidea*).

Based on the NCBI GenBank data, 33% of cyanobacterial OTUs obtained from Antarctic biotopes represent cosmopolitan taxa, while 67% of OTUs specifically belong to 'the cold biosphere' (Pessi et al., 2018). In particular, 5.4% of the OTUs were related to polar phylotypes; 6.3% grouped with Alpine, Andes, and Himalayan territories; 37.5% were potentially endemic, and 17.9% were definitely endemic (Pessi et al., 2018).

The question is further aggravated because some cyanobacteria are hard to identify (even at the genus level), and thus some of them have probably been misidentified (Strunecký et al., 2013). For instance, morphologically conspicuous *Phormidium* spp. strains could be erroneously attributed to other genera (Quesada & Vincent, 2012). Data obtained with easily available genetic tools, in particular 16S rRNA gene sequencing, indicated that a significant subset of cyanobacteria found in Antarctica was globally distributed (Namsaraev et al., 2010; Pessi et al., 2018). Additional criteria used for making distinction between the cosmopolitan and endemic species are necessary, for example 16S–23S ITS sequencing, multilocus sequencing, and high-depth metagenomic data (Whitaker et al., 2003; Comte et al. 2007; Jungblut et al., 2010; Quesada & Vincent, 2012). Nevertheless, many authors have reported high similarity between cyanobacteria from Antarctica, Arctic, high mountains, and cold deserts (Jungblut et al., 2005, 2010; Vincent & Quesada, 2012b; Jadoon et al., 2013; Kleinteich et al., 2014; Chrismas et al., 2015). For instance, *Gloeocapsa alpina*, *L. antarctica* and *Phormidesmis priestleyi* are widely distributed in polar and alpine environments (Comte et al., 2007; Lionard et al., 2012; Martineau et al., 2013; Palinska et al., 2017; Pessi et al., 2018).

There are two explanations for the presence of cosmopolitan taxa in Antarctica: they colonized the continent either before or after last glacial maximum (approximately 18,000 years ago). In fact, Antarctica, like other planetary regions, is open to the dispersal of diaspores (especially via anthropogenic activity), and external input of cyanobacteria is unavoidable. However, this process has little inluence on the intrinsic, relatively stable diversity of Antarctic cyanobacteria. Many Antarctic habitats (lakes, glacial creeks, seepages, wet soils, etc.) support annual microbial communities with specific features (taxonomic content, major representatives, succession, and zonal distribution), and these communities are dissimilar from those in their native regions (Komárek & Komárek, 2010).

Moreover, potentially endemic microorganisms are suggested to inhabit spatially isolated niches, particularly those with extreme environments (Jadoon et al., 2013; Lacap-Bugler et al., 2017). Because Antarctica underwent extremely long spatial isolation, and multiextreme ecotopes are common there, this continent is a good place to search for endemic species (Ribeiro et al., 2018). Despite reasonable skepticism, morphological and/or molecular analyses create the opportunities to find cyanobacteria that are exclusively associated with the Antarctic continent (Ellis-Evans, 1996; Bowman et al., 2000; Nadeau et al., 2001; de la Torre et al., 2003; Taton et al., 2003; Casamatta et al., 2005; Jungblut et al., 2005; Taton et al., 2006; Komárek & Komárek, 2010; Namsaraev et al., 2010; Chong et al., 2013; Jadoon et al., 2013; Chrismas et al., 2015; Pessi et al., 2018). Anyway, the old problem 'everything is (not) everywhere' (see Ribeiro et al., 2018; Spathatis et al., 2019) is far from being solved, and Antarctic cyanobacteria are among the touchstones.

A comparison of Antarctic and Arctic cyanobacteria

Antarctica has more severe climatic conditions than Arctic due to its higher location above sea level and the smaller contribution of warm currents to its climate. Nevertheless, high Arctic ice shelves are generally similar to the McMurdo Ice Shelf (Antarctica) in terms of their ecogeographic and climatic properties (Pointing et al., 2015).

The 16S rRNA gene fragments sequences of some high Arctic cyanobacteria were found to be 49.9% similar to those of Antarctic cyanobacteria (including those previously interpreted as endemic) as well as to those of Alpine cyanobacteria (Jungblut et al., 2010). In particular, one of the high Arctic sequences was 99.8% similar to that of *L. antarctica* isolated from the Larsemann Hills. More than 68% of the matching polar sequences corresponded to perennially cold terrestrial ecosystems, while the rest of the sequences corresponded to relatively warmer environments. These data suggest the distribution of low-temperature phylotypes throughout 'the cold biosphere' (Jungblut et al., 2010). Moreover, cold biosphere phylotypes were not restricted to a particular lineage or taxon (Laybourn-Parry & Pearce, 2007; Pessi et al., 2018; Kublanovskaya et al., 2019). For example, *A. hyalina*, *G. alpina*, *L. frigida*, *M. autumnale* (*P. autumnale*), *O. sancta* and *Nostoc* spp. comprise commonly encountered species in both poles regions. The corresponding 16S rRNA sequences were 94–99% mutually similar (Strunecký et al., 2013), and their matches were found in the Himalayan Mountains (Vincent, 2007) indicating a potentially global distribution in cold areas (Palinska et al., 2017). The 16S–23S rRNA ITS sequences of cryoconite cyanobacteria from Antarctica (King George Island and James Ross Island), Arctic (Alaska and Greenland) and Asia (the Himalayan, Pamir, Then-Shan, and Qilian Mountains) were grouped in 20 OTUs, six of which accounted for 88% of the sequences from glaciers of various locations (from both poles to central Asia) suggesting cosmopolitan species (Segawa et al., 2017).

Antarctic and Arctic cyanobacterial mats are often associated with lake sediments and meltwater ponds bottoms; alternatively, they are exposed to air. They are distinguished by their visual appearance and community structure: mats with hardly visible accumulation of microbial biomass; 'matlets' composed of loose flocs of olive-brown aggregates; and mats up to 10 mm thick covered by a thin (100 nm) orange surface layer (Mueller & Vincent, 2006). The most abundant photosynthetic organisms in all these Antarctic and high Arctic microbial mats are represented by *Leptolyngbya*, *Oscillatoria* and *Phormidium* which have thin filaments, as well as by green and 'chromophyte' eukaryotic microalgae (Mueller & Vincent, 2006; Quesada & Vincent, 2012).

Environmental adaptations of Antarctic cyanobacteria

The environmental adaptations and stress responses of Antarctic cyanobacteria have not been extensively studied on model strains. Among the rare exceptions are the *P. priestleyi* BC1401 cold and osmotic stress tolerance mechanisms (Chrismas et al., 2016). In this strain, intrinsic stress genes (and complementary genes broadly occurring among bacteria) were similar to those in cyanobacteria inhabiting 'the cold biosphere' (Antarctica, Arctic, Alps, etc.). In particular, exopolysaccharide (EPS) production by *P. priestleyi* BC1401 greatly contributed to survival in cold environments, and this adaptive mechanism was shown to be usual for cyanobacteria (Chrismas et al., 2016).

Low temperature

Antarctic cyanobacteria employ various mechanisms for adapting to cold environments as cold as $-60°C$. In particular, they were shown to contain a SigB-type sigma factor that acted as master regulator for different stress responses (Varin et al., 2012; Pointing et al., 2014). In the cold, the molecular chaperones DnaJ and DnaK were induced, and they ensured native conformation of regulatory proteins DnaA, GyrA and RecA which influence DNA topology (Varin et al., 2012). At RNA level, low temperatures induce RNA-binding proteins and cold shock proteins which act as translation-supporting molecular chaperones (Los & Murata, 1999). Additionally, RNA helicases were activated, and they eliminated anomalies in the RNA secondary structure. For example, *Anabaena* sp. PCC 7120 was shown to possess the RNA helicase gene *ctrB* and *ctrC*; the former was expressed during various stresses, while the latter was induced only in response to low temperature (Chamot et al., 1999). Regarding the structure-functional cell architecture, low temperatures decrease membrane fluidity, reduce enzyme activity, provoke atypical folding or denaturation of proteins, and initiate intracellular ice crystallization (D'Amico et al., 2006). To adapt their membranes to low temperature (homeoviscous adaptation strategy) cyanobacteria accumulate polyunsaturated fatty acids and short chain fatty acids as well as decrease the amount of branched and ring-containing fatty acids (D'Amico et al., 2006; Zakhia et al., 2008). In particular, acyl desaturases replace C16:0 and

C18:0 fatty acids with their C16:1- and C18:1-derivatives (Chintalapati et al., 2004). The decrease in membrane fluidity in *Synechocystis* sp. PCC 6803 was shown to activate the membranous signal receptor Hik which participates in the two-component signal system *Hik33* (Hik protein phosphorylates response regulator Rer1, the latter induces transcription of the *desB* desaturase gene). Additionally, the Rer1 protein triggers the synthesis of other proteins involved in the cold shock response, while correct protein folding is influenced by molecular chaperones of the Clp family (Los & Murata, 1999). In the case of *Synecchococcus* sp. PCC 7942, the number of ClpP1 proteins increased tenfold upon 1 day of culturing in the cold (Porankiewicz et al., 2002).

Antarctic psychrotolerant and psychrophilic cyanobacteria

According to their optimum growth, cyanobacteria are subdivided into psychrophiles, which can grow at approximately 0°C (opt., about + 10°C); mesophiles (opt., approximately + 20°C) and thermophiles (opt., approximately + 40°C).

The term 'psychrophilic' was initially applied to the bacteria capable of growing at 0°C. However, some species develop close to 0°C, although they optimally grow at + 20–30°C. Paradoxically, according to their optimal growth temperature, most of the assumed psychrophiles are in fact mesophiles. Unlike these, true psychrophiles have a lower limit of approximately 0°C, an optimum of approximately + 15°C, and an upper limit of approximately + 20°C; however, the strict positions of these thresholds are debatable. Bacteria that grow at low temperature but occur above the +20°C upper limit are referred to as psychrotrophic or psychrotolerant (Cavicchioli, 2016). The former term is common in food industry, while the latter term is used in the environmental ecology literature. In other words, psychrotolerant bacteria usually develop at temperatures approaching 0°C, while they grow optimally from + 20°C to + 25°C, with an upper limit as high as + 40°C. In contrast, psychrophyles grow even in temperatures below zero, although their optimal growth temperature is + 15°C, and their upper limit is below + 20°C (Russell, 2009).

Most of cultured Antarctic cyanobacteria are considered psychrotolerant because they optimally grow at temperatures above those found in the local environment (Roos & Vincent, 1998; Singh & Elster, 2007; Vincent, 2007; Zakhia et al., 2008). For instance, approximately 70% of filamentous strains isolated from microbial mats grew poorly at + 5°C, while their upper limit was above + 20°C. Notably, a study encompassing 27 isolates of mat forming cyanobacteria from Antarctica, Arctic and sub-Arctic had growth optima from + 15 to + 35°C (Tang et al., 1997). However, some Antarctic psychrotolerant filamentous cyanobacteria showed a negligible growth at +48°C (Castenholz & Schneider, 1993).

According to a phylogenetic reconstruction of filamentous cyanobacteria, the psychrotolerant phenotype originated repeatedly, and contemporary Antarctic extremophiles are related to strains from middle latitudes (Nadeau et al., 2001). Only a few Antarctic cyanobacteria are truly psychrophilic (Fritsen & Priscu, 1998). An example is *Microcoleus autumnalis* (opt., below + 15°C), which is most abundant in cold ecosystems worldwide (Chrismas et al., 2015). Filamentous strains isolated from McMurdo Ice Shelf were also considered psychrophilic (opt., + 8°C; max., + 24°C) as well as *Oscillatoria* sp. Ant-G16, *P. autumnale* Ant-Lunch and *P. autumnale* Ant-Orange (opt., from + 8 to + 12°C) (Nadeau & Castenholz, 2000). Notwithstanding slow growth, psychrophilic strains successfully colonized the cryosphere (Vincent, 2007; Vincent & Quesada, 2012b).

Water phase transition and osmotic stress

Water phase transitions strongly influence Antarctic microbiota. Unlike benthic cyanobacteria, which are submerged in liquid water (and for which phase transitions are not especially stress provoking), the inhabitants of ponds or springs that freeze through suffer from osmotic stress (Singh & Elster, 2007). Intracellular ice crystals may cause mechanical microdamages; to prevent these damages, various protective mechanisms are put into action. In other words, cyanobacteria employ various strategies that compensate for osmotic and the mechanical shock created by freezing. For instance, cyanobacteria synthesize water-absorbing EPSs, which hamper ice crystal formation (Vincent, 2007; Chrismas et al., 2016). Cyanobacteria that produce microbial mats at the McMurdo Ice Shelf often secrete ample amounts of

EPSs, which prevent ice nucleation at the cell surface (de los Rios et al., 2004; Zakhia et al., 2008).

Psychrotolerant bacteria are capable of synthesizing extracellular ice-binding proteins (IBPs), as well as antifreeze proteins, which reduce the water freezing temperature (Raymond et al., 2007). In particular, Antarctic bacteria isolated from the sea, a shelf, polar lake ice and frozen soil were resistant to phase transitions because they contained IBPs that hampered ice crystal growth and prevented water recrystallization (Raymond et al., 2007). Thus, Antarctic cyanobacteria are not fatally threatened by freeze–thaw cycles (Sabacká & Elster, 2006; Vincent, 2007).

Antarctic water pools freeze yearly; in late autumn, microbial mats are submerged in fresh water, while in winter the salinity increases several-fold. To escape osmotic stress, cyanobacteria synthesize compatible solutes, such as sucrose, trehalose, glucosyl-glycerol and glycine betain which not only prevent plasmolysis, but also reduce the freezing point of the cytoplasm (Raymond & Fritsen, 2000; Zakhia et al., 2008).

Bright light and high UV radiation

During prolonged periods of light, microbial communities are influenced by high solar radiation, particularly by harmful 325–425 nm UV radiation (Tanabe et al., 2010).

Among the most deteriorative consequences of the exposure to bright light are reactive oxygen species (ROS), in particular singlet oxygen and superoxide anion-radical. In the case of cyanobacteria, the remedy for these damaging molecules comes from ROS protective enzymes (superoxide dismutase, in the first instance) and from carotenoids that perform excited state quenching via heat dissipation (Vincent & Quesada, 2012a). Due to the high carotenoid content, cyanobacterial plankton and microbial mats in Antarctic shoal water are often red or dark olive colored (see Fig. 2c–g). Previous studies have shown that carotenoids are selectively accumulated by cyanobacteria that occupy the surface water layer, while those in deeper horizons develop a green or blue-green color due to high Chl *a* (or both Chl *a* and phycocyanin) content (Quesada & Vincent, 1999, 2007).

To protect their DNA from UV radiation, cyanobacteria have been shown to reduce the production of potent endogenous photosensitizers (Chl *a* and phycobiliproteins) and to accumulate counter-photodamage substances (carotenoids, gloeocapsin, scytonemin and mycosporin) (Proteau et al., 1993) as well as to intensify their DNA repair processes (Vincent, 2007; Zakhia et al., 2008). For example, high scytonemin content caused cyanobacteria to turn black (Proteau et al., 1993; Stal, 2012; Vincent & Quesada, 2012b) (see also Figs. 2a and 3d).

Some cultured Antarctic cyanobacteria were found to respond to large variations in ambient irradiance (including UV) through shifts in pigment content (Quesada & Vincent, 1999).

Roos and Vincent (1998) reported the combined detrimental influence of UV and cold on pigments, growth and photosynthesis in mats formed by the Antarctic cyanobacterium *P. murrayi*. These data suggested that psychrotrophic cyanobacteria could be especially prone to UV damage. Unexpectedly, *P. murrayi* increased its growth under UV irradiation possibly due to the stimulation of the repair processess. The rate of these processes could depend on biosynthetic capacity or on the direct involvement of temperature in the damage–repair balance.

Antarctic cyanobacteria ecotypes

Cyanobacteria occupy a variety of Antarctic niches, including snow, ice, streams, lakes, sea water and soil. Additionally, they are found in cryoconites, and hypolithic and endolithic mineral-associated microbial assemblages (Quesada & Vincent, 1999; Gilichinsky et al., 2007; Vincent, 2007; Cameron et al., 2012; Pointing et al., 2014). Biofilms represent most abundant ecotype, while other ecotypes (except a planktonic ecotype) incorporate biofilms as their essential form, although they are usually distinguished according to the substrate they inhabit.

Planktonic ecotype

The first study of Antarctic plankton performed with lake water from the McMurdo Dry Valleys and Signi Island reported the genera *Synechococcus* and *Synechocystis* (Goldmann et al., 1967). These and other unicellular cyanobacteria characterized by an advantageous cell surface area-to-volume ratio were shown to dominate the freshwater plankton and to produce dense populations even with a shortage of biogenic elements (Hawes, 1990; Vincent, 2007; Vincent &
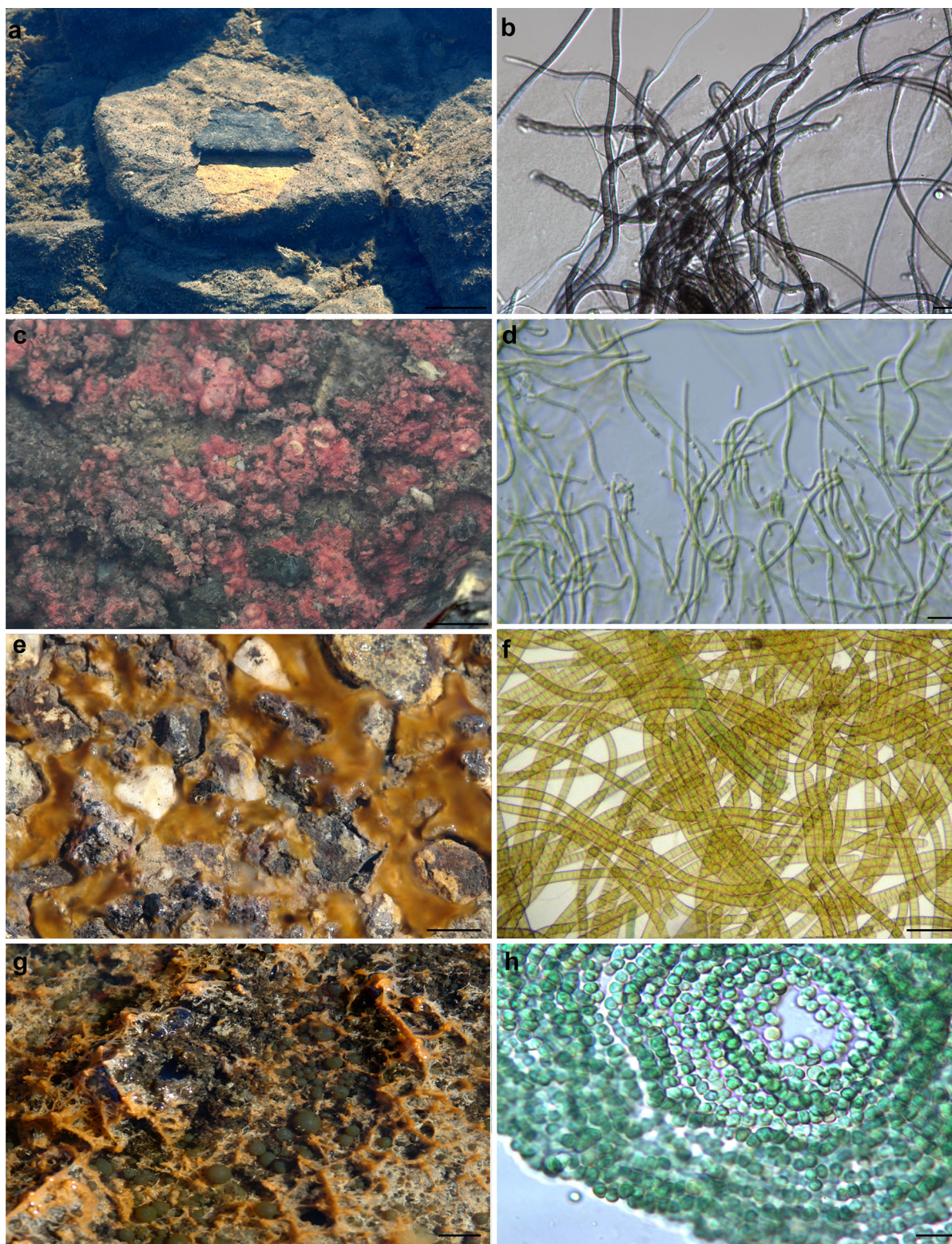
◄**Fig. 2** Cyanobacterial communities in Schirmacher Oasis. Black lamellar biofilm at the bottom of a small pond (**a**)—produced by *Leptolyngbya* sp. and *Phormidesmis* sp. (**b**). Red tuberous biofilm at the stream bottom (**c**)—produced by *Leptolyngbya* sp. (**d**). Dark-olive globular colonies on the surface of maroon biofilm at the stream bottom (**e**)—produced by *Oscillatoria sancta* (**f**). Dark-olive globular colonies at microbial mat surface (**g**)—produced by *Nostoc sphaericum* (**h**). Scale bars: 1 cm (**a**, **c**, **e** and **g**) and 50 μm (**b**, **d**, **f** and **h**). Original photographs of Russian Antarctic Expedition-2018 material

Quesada, 2012a). Unicellular picocyanobacteria are also the most abundant photosynthetic microorganisms among the East Antarctica saline lake plankton. In striking contrast to their success in low and middle latitude lakes, picocyanobacteria are generally absent or sparse in polar seas except for the regions that receive advective inputs from more favorable environments (Vincent & Quesada, 2012a). Most of filamentous planktonic cyanobacteria belong to *Nostoc* and related genera (Pandey et al., 2004).

Biofilm ecotype

In the traditional sense of the word, biofilms represent thin (from several μm to a few mm thick) lamellae or small (up to several mm in diameter) globules which are formed by microbial associations embedded in a polymeric matrix they synthesize in contact with solid substrates (Costerton et al., 1995; Rossi & De Philippis, 2015). Additionally, floc biofilms are produced in plankton or floating metaphyton (Kublanovskaya et al., 2020). In addition to underwater biofilms, biofilms are found on soil, ground or rock surfaces. Antarctic biofilms are preferentially produced by filamentous cyanobacteria of the genera *Leptolyngbya*, *Microcoleus*, *Oscillatoria* and *Phormidium* (Ellis-Evans, 1996; Singh & Elster, 2007; Suman et al., 2010; Vincent & Quesada, 2012a; Sumner et al., 2016). In turn, biofilm-producing unicellular cyanobacteria belong to the genera *Gloeocapsa* and *Microcystis* (Pandey et al., 2004; Jungblut et al., 2005; Taton et al. 2006; Pearce et al., 2012; Pessi et al., 2016). Another unicellular genus, *Chamaesiphon*, was present in the lake biofilms of the Schirmacher Oasis (Pandey et al., 2004); corresponding tags were also detected in lake and stream biofilms of Hope Bay (Tell

et al., 1995; Izaguirre & Pizarro, 2000; Bonaventura et al., 2006).

Biofilms with different forms, colors and surface textures produced by filamentous cyanobacteria in the Schirmacher Oasis are demonstrated in Fig. 2.

Microbial mat ecotype

Microbial mats are massive (up to one meter thick), durable, often stratified and sometimes mineralized biofilms. Their consistency varies from gelatinous to hard; texture, from smooth or velvety to mammillate; outline, from prostrate lamellae to pinnacles or cones (Stahl et al., 2013).

Cyanobacterial mats are common in Antarctic lakes as well as in small water reservoirs, streams, and melt snow canals (Ellis-Evans, 1996; Suman et al., 2010; Sumner et al., 2016). They sporadically cover the bottom surface, as exemplified by flat mats in Lake Vanda (Victoria Land) or conical mats in Lake Untersee (Sumner et al., 2016; Koo et al., 2017). Epilithon mats in streams and small pools produced by seasonal ice and snow melt are mainly represented by the filamentous genera *Leptolyngbya*, *Oscillatoria* and *Phormidium* (Izaguirre & Pizarro, 2000; de los Rios et al., 2004). The fibrous consistency of most Antarctic microbial mats is due to these cyanobacteria (Singh & Elster, 2007; Chrismas et al., 2015; Pessi et al., 2016; Koo et al., 2017). Metagenomic data obtained from conical stratified mats in Lake Untersee showed that cyanobacteria of the genera *Leptolyngbya*, *Phormidium*, *Pseudanabaena* and *Tychonema* comprised up to 90% of the NGS library tags in the upper water layers (Koo et al., 2017; Weisleitner et al., 2019). These cyanobacteria were accompanied by the genera *Calothrix* and *Nodularia* as well as with *Nostoc* spp. which is considered a primary source of fixed nitrogen in Antarctic lakes (de los Rios et al., 2004; Komárek & Komárek, 2010; Vincent & Quesada, 2012a; Prieto-Barajas et al., 2018). Unicellular mat-forming Antarctic cyanobacteria belong to the genera *Chamaesiphon*, *Chroococcus*, *Gloeocapsa* and *Synechococcus* (Izaguirre & Pizarro, 2000; Taton et al., 2003; de los Rios et al., 2004; Wood et al., 2008; Vincent & Quesada, 2012a).

In addition to cyanobacterial contributions, microbial mat biomass and scaffolds are provided by Bacillariophyceae, Charophyceae and Chlorophyceae; other eukaryotic microalgae belonging to
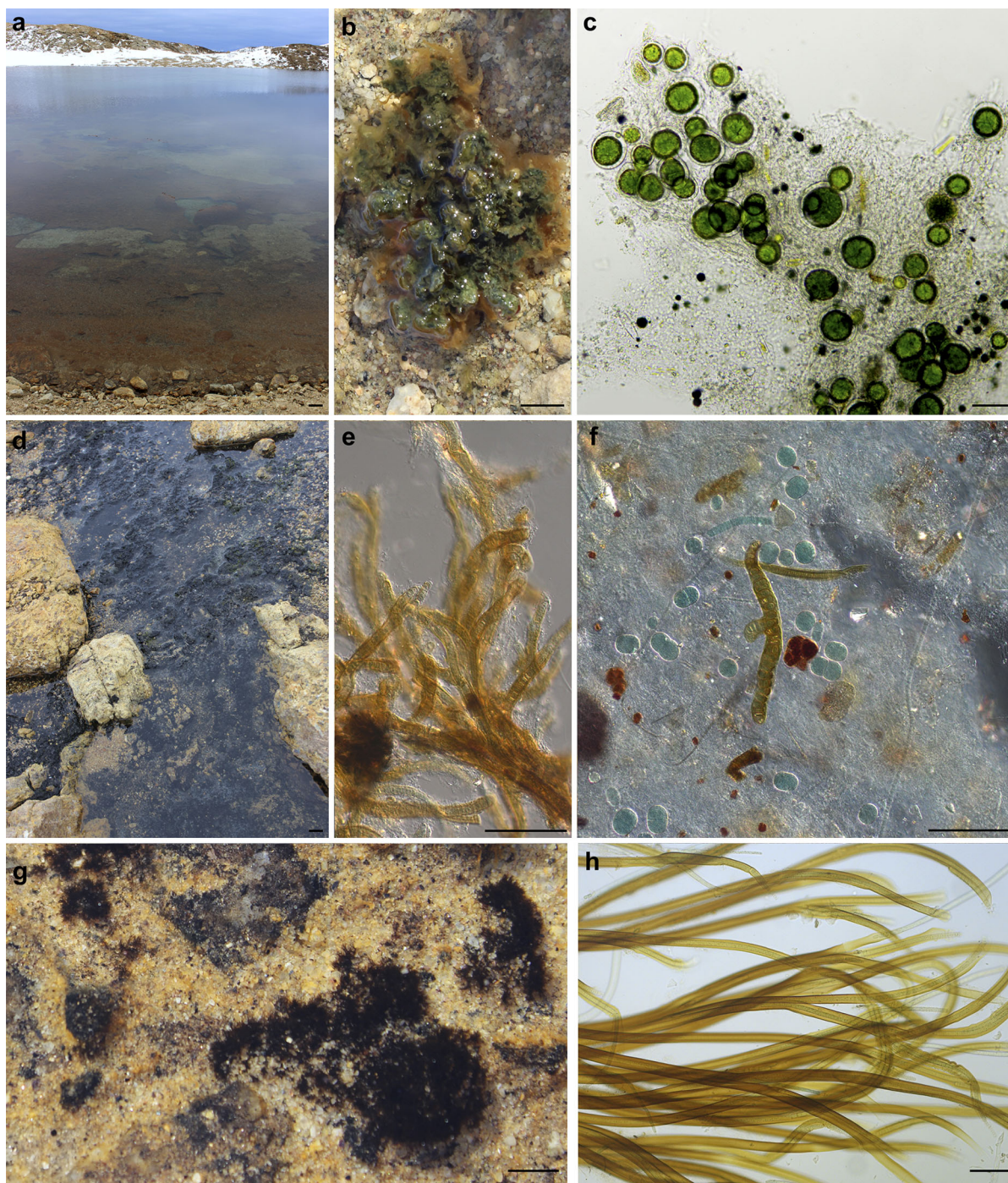
Fig. 3 Microbial communities from a water pool on Larsemann Hills. Brownish-green lamellar bottom mats from Lake Reid (**a**). Blue-green lower layer of Lake Reid microbial mat (**b**) produced by the cyanobacteria *Chlorogloea* sp. and *Leptolyngbya* sp., the chlorococcalean alga *Kentrosphaeria* sp., and the diatom *Pinnularia microstauron* (**c**). Black tuberous bottom mats in a shallow stream that falls into Skandrett Lake (**d**)—produced by the ctyanobacteria *Hassallia* sp. (**e**) and by *Gloeocapsa* sp., *Cyanothece* sp., *Leptolyngbya* sp., *Phormidium* sp. and *Stigonema* sp. (**f**). Bushy mats in the Discussion Lake littoral zone (**g**)—produced by the cyanobacterium *Coelodesmium* sp. (**h**). Scale bars: 10 cm (**a**, **d**), 1 cm (**b**, **g**) and 100 μm (**c**, **e**, **f** and **h**). Original photographs of Russian Antarctic Expedition-2018 material

the Cryptophyceae, Rhodophyceae, Synurophyceae, Tribophyceae and Xanthophyceae, as well as euglenoids, are less abundant (Bonaventura et al., 2006; Vincent & Quesada, 2012a). A recent study of benthic mats in the Larsemann Hills, Vestfold Hills and McMurdo Dry Valleys lakes revealed rich microbial diversity comprising 1,500 noncyanobacterial strains (a subset of nine lakes), 60 cyanobacterial strains (24 lakes), 230 microfungal strains (17 lakes), 91 eukaryotic microalgae strains (three lakes) and 50 protozoan strains (six lakes). In the case of noncyanobacteria, as many as 320 strains belonging to different physiological groups were isolated from a teaspoon-size sample (Hodgson, 2012).

Moist grounds around lakes and ponds were found to often support black or brown microbial mats of *Nostoc* spp. (Niederberger et al., 2012) or orange/red mats of *Phormidium* spp. (Vincent et al., 1993). Black mats could be entrained in lake ice and form aggregates that fix CO_2 and N_2, creating a self-sustaining microbial community (Paerl & Priscu, 1998). In stream ecosystems, different microbial mat types were observed for different channel parts: orange, red and green mats were typically found in the main stream channel, and black mats were found along wet stream banks (in the hyporheic zone) (Alger et al., 1997; McKnight et al., 1999, 2004). Orange, red and green microbial mats are dominated by non-nitrogen-fixing *Phormidium* spp., as well as by diatoms, while black mats are composed of nitrogen-fixing *Nostoc* spp. (Alger et al., 1997). Although microbial mats are not ubiquitous, they are common in shallow streams with stone beds produced via long-term freezing through of saturated porous alluvium (McKnight et al., 1998; Fountain et al., 1999). In addition to the wealth of data on microbial mat cyanobacteria, recent studies have also tended to focus on diatoms (e.g., Stanish et al. (2011), or on other bacteria associated with differently colored mats (Kohler et al., 2016; Van Horn et al., 2016).

Mineralized cyanobacterial mats (contemporary stromatolites) often occurred underneath perennial ice (Wharton et al., 1983, 1993). Flattened stromatolites are observed in McMurdo Dry Valleys lakes (Parker et al., 1981), while those in Lake Joyce are column shaped (Mackey et al., 2015). Pinnacle-shaped and conical stratified microbial mats are common in Antarctic lakes (Sumner et al., 2016; Koo et al., 2017).

Antarctic microbial mats of different forms, colors and surface textures collectively produced by cyanobacteria and eukaryotic microalgae are demonstrated in Figs. 3 and 4.

Soil crust ecotype

Antarctic cyanobacteria can form biological soil crusts (BSCs) which cover bare ground in ice deserts which are essentially free of liquid water. These soil surface biofilms additionally incorporate green algae, lichens and mosses; EPS-producing filamentous cyanobacteria not only stabilize the entire assemblage, but also provide it with fixed nitrogen (Quesada & Vincent, 1999). BSC samples from two Sør Rondane Mountains ridge (Queen Maud Land) nunataks, i.e. hills or rocks protruding from ice cover, were shown to contain the filamentous genera *Leptolyngbya*, *Microcoleus* and *Phormidium*; at the Princess Elisabeth Station (Utsteinen Ridge), some unicellular genera were found (Pushkareva et al., 2018).

Soil ecotype

Antarctic soils vary from relatively fertile (in coastal regions) to extremely infertile (in continental deserts), and severe environments generally select for limited microbial diversity and simple food webs (Bottos et al., 2014). The Antarctic soil metagenome preferentially encompasses proteobacterial and actinobacterial phylotypes (Pearce et al., 2012). Soil cyanobacteria are represented by the genera *Anabaena*, *Leptolyngbya*, *Microcoleus*, *Microcystis*, *Oscillatoria*, *Phormidium*, *Nostoc* and *Synechococcus* (Taton et al., 2006; Pearce et al., 2012). Generally, the taxonomic content of terrestrial cyanobacteria has much in common with aquatic cyanobacteria (Gordon et al., 2000; Singh & Elster, 2007; Lopatina et al., 2016). A previous study found cyanobacteria in all permafrost samples; they started to grow in melt snow, but as soon as the meltwater flowed away, they were succeeded by eukaryotic microalgae (Gilichinsky et al., 2007).

Cryoconite and hypolithic ecotypes

Cryoconites are small despressions developed under wind-blown patches of mineral sediments or desiccated microbial mats; both types of solid substrates fall
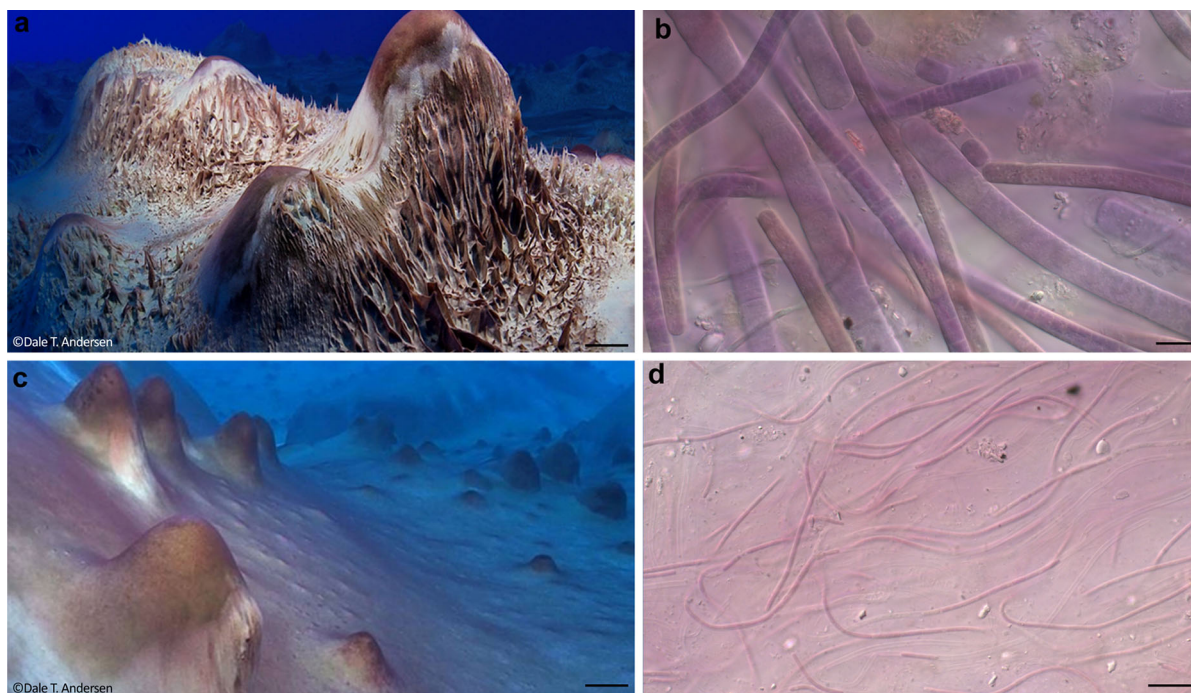
Fig. 4 Lake Untersee deep water microbial mats. Conical (**a**) and pinnacle-shaped (**c**) mats with the maroon top layer produced by the cyanobacteria *Oscillatoria* sp. and *Phormidium* sp. (**b**), and the lower layer produced by the cyanobacterium *Leptolyngbya* sp., with green patches containing the cyanobacterium *Geitlerinema* sp. and chlorococcalean algae (**d**). Scale bars: 15 cm (**a**, **c**) and 10 μm (**b**, **d**). Material of Chicago Tawani Foundation and NASA Exobiology & Astrobiology Program Expedition-2019, image courtesy Dale T. Andersen (**a**, **c**). Original photographs of the material sampled by SS in 2019 (**b**, **d**)

into the underlying ice because of advection heat input. The subsequent growth of biofilms in these depressions underlies the development of local ecosystems (Hodgson, 2012). Cryoconite cyanobacteria primarily belong to the filamentous genera *Leptolyngbya*, *Nostoc* and *Phormidium* (Cameron et al., 2012; Makhalanyane et al., 2015). Unicellular cyanobacteria of the genus *Chamaesiphon* were found in cryoconites on the Wright Valley Glacier (McMurdo Dry Valleys) and Canada Glacier (Queen Victoria Land) (Jungblut & Vincent, 2017; Sommers et al., 2019).

Hypolithic cyanobacteria are widespread in Antarctic deserts where they occupy the underside of opaque quartz rocks in contact with soil (Cockell & Stokes, 2004). Their nitrogen fixation ensures the bioproductivity of all the ground microbiota (Cowan et al., 2011). The McMurdo Dry Valleys soil samples tested by high-throughput sequencing and the GeoChip microarray technique showed a relative prevalence of actinobacteria, while cyanobacteria dominated in

less diverse hypolithic communities (Wei et al., 2016). According to 16S rRNA gene sequencing and restriction fragment length polymorphism data, potentially endemic *Phormidium* spp. strains were most abundant among hypolithic cyanobacteria (Lacap-Bugler et al., 2017).

The hypolithic *Chroococcidiopsis* sp., *P. priestleyi* and *Nostoc* sp. that were dominant in Lake Untersee environs are shown in Fig. 5a.

Endolithic ecotype

Biofilm-forming endolithic microorganisms are subdivided into chasmoendolithes, which occupy stone fractures, cryptoendolithes, which inhabit stone pores or cavities, and euendolithes, which tunnel into stone bodies (Golubič & Schneider, 2003). Endolithic cyanobacteria usually colonize the upper (several mm thick) light-transparent layer of granite, gypsum, limestone and sandstone rocks. These cyanobacteria were initially considered rare; later, they were
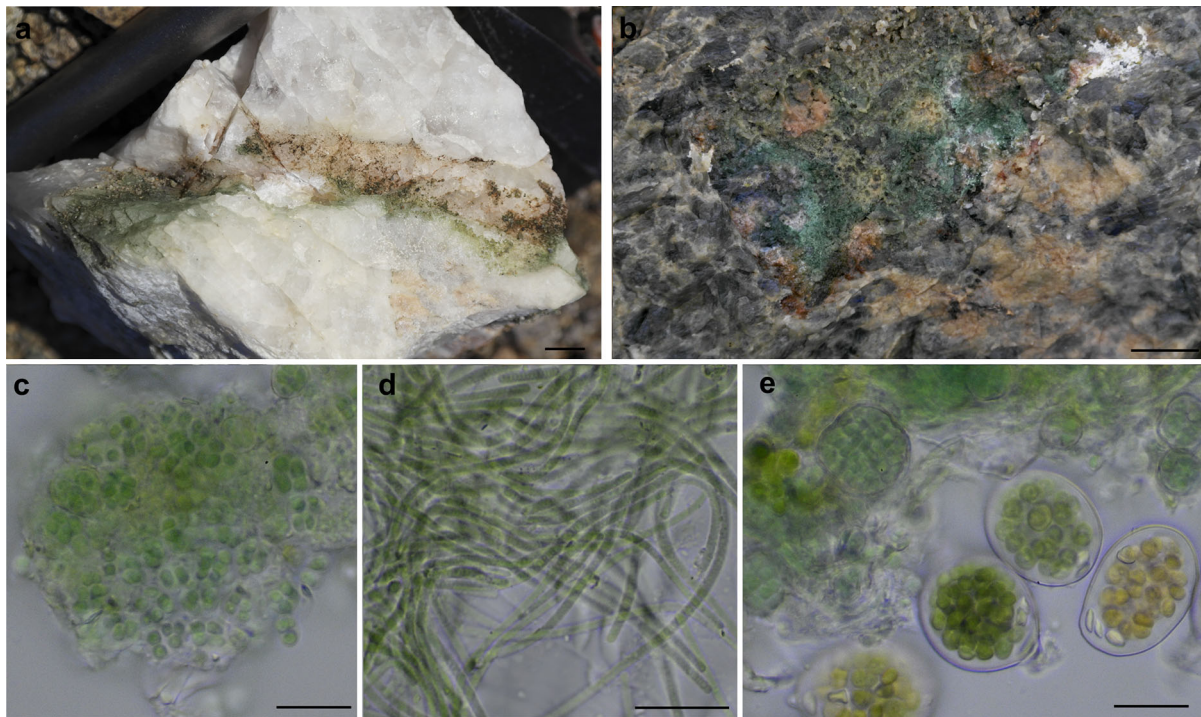
Fig. 5 Lake Untersee environs hypolithic (**a**) and chasmoendolithic (**b**) cyanobacteria, with the prevalence of *Chroococcidiopsis* sp. (**c**), *Phormidesmis priestleyi* (**d**) and *Nostoc* sp. (**e**). Scale bars: 1 cm (**a**, **b**) and 10 μm (**c**, **d** and **e**). Original photographs of Russian Antarctic Expedition-2018 material

recognized as being broadly distributed and the most abundant endolithic microorganisms (Hughes & Lawley, 2003) as well as principal primary producers in Antarctic deserts (Quesada & Vincent, 2012). Their coinhabitants belong to the main bacterial phyla as well as to some groups of archaea, eukaryotic microalgae, microfungi and lichens. The taxonomic structure of endolithic cyanobacteria is relatively uniform, thus, on Alexander Island (Alexander I Land), it was similar to that on Beacon Sandstone Heights (Queen Victoria Land) (Wynn-Williams et al., 1999). According an analysis of cultured strains and NGS data, the diversity of endolithic cyanobacteria in the McMurdo Dry Valleys depended on humidity, with the most abundant genera being *Leptolyngbya*, *Nodosilinea* and *Plectolyngbya* (Rego et al., 2018). The use of the GeoChip microarray technique revealed a variety of stress responses in the Antarctic chasmoendolithic community which encompasses archaea, cyanobacteria, anoxygenic photosynthetic bacteria, heterotrophic bacteria, and microfungi (Wei et al., 2015).

The chasmoendolithic *Chroococcidiopsis* sp., *P. priestleyi* and *Nostoc* sp. that were dominant in Lake Untersee environs are shown in Fig. 5b.

Conclusion

Research of the Antarctic microbiota is on the rise, and current achievements are impressive. However, especially with regard to cyanobacteria, many drawbacks and limitations remain. First, the diversity of Antarctic cyanobacteria has been studied from one perspective, with the researchers usually relying on morphological or metagenomic data; moreover, there is no consensus between bacteriologists and phycologists (due to the intricate interplay of morphological records, genomic data, and culturability restrictions, to say nothing of taxonomic obstacles). Second, although Antarctic cyanobacteria often produce biofilms (especially microbial mats), ecophysiological data on these symbiotic associations are fragmentary, and partner relationships are underexplored. Third, the specificity of 'the Antarctic cyanobacteria biosphere' is

understudied due to the unresolved problem of endemism in prokaryotes (Curren & Leong, 2020), particularly cyanobacteria (Ribeiro et al., 2018; Spathatis et al., 2019). Fourth, the strains of Antarctic cyanobacteria maintained in culture are not numerous and not very diverse. Looking into these issues is at the forefront of cyanobacteriology, which is supported by related biosciences and earth sciences.

Declarations

Conflict of interest The authors declare no conflict of interests.

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