

*Review Article***Bacterial Biodiversity, Cold Adaptation and Biotechnological Importance of Bacteria Occurring in Antarctica**S SHIVAJI^{1,2,*}, G S N REDDY¹ and M K CHATTOPADHYAY¹¹CSIR-Centre for Cellular and Molecular Biology, Uppal Road, Hyderabad 500 007, India²Prof. Brien Holden Eye Research Centre, L V Prasad Eye Institute, Banjara Hills, Hyderabad 500 034, India

(Received on 20 May 2016; Accepted on 24 November 2016)

Antarctica is the coldest, iciest, windiest and driest continent and defines the limits of temperature at which life forms can survive and divide. These cold loving microorganisms are known as psychrophiles and are present in all the unique habitats of Antarctica including permafrost and ice. Their distribution and abundance varies from habitat to habitat and several new genera and species have been discovered in the icy continent. They have several strategies by which they survive and divide at low temperature such as the ability to catalyze reactions and continue metabolism with cold-tolerant enzymes; ability to maintain optimum membrane fluidity at low temperature; occurrence of specific genes required for survival at low temperatures; presence of antifreeze-activity etc.. Enzymes from psychrophilic bacteria have been found to be useful for several purposes ranging from recombinant DNA technology to food processing. The ability of cold-tolerant organisms to degrade petroleum products and other environmental pollutants highlight them as potential candidates for bioremediation in extreme cold environments. The recently reported genome sequences of a number of novel cold-tolerant isolates are likely to provide some more insights into the mechanism of bacterial cryotolerance.

Keywords: Non-Cultivable Diversity; Cultivable Diversity; Novel Species; Cold Adaptation; Antarctica

Introduction

About 85% of the Earth's biosphere is permanently exposed to temperatures below 5°C and these cold habitats span from the Arctic to the Antarctic, from high-mountains such as Himalayas to the deep ocean and also includes frozen soils (permafrost), glaciers and ice sheets, polar sea ice and snow (Deming and Eicken, 2007). A major fraction of this low temperature environment is represented by the deep sea which constitutes 71% of the Earth's area. Other cold environments include cold water lakes, cold soils (especially subsoils), cold deserts, and caves. All these permanently cold environments have been successfully colonized by a class of microorganisms known as psychrophiles (grow from subzero to 30°C) (Morita, 1975; Helmke and Weyland, 2004; Laucks *et al.*, 2005). Among all the cold habitats, Antarctica is unique in that it is the coldest, driest, windiest and

iciest (with ice covered at an average thickness of 1.9 Km) of all known habitats covering approximately 5.4 million square miles in area and is thus considered as one of the most extreme habitats of the world (Vincent, 1988; Claridge and Campbell, 1977; Campbell and Claridge, 2000; Smith *et al.*, 1992). Despite the harsh climatic conditions, along with other life forms (such as mites, ticks, seals, penguins, mosses, lichens, bacteria, yeasts, algae etc) (<http://www.globalclassroom.org/antarct6.html>), psychrophilic bacteria dominate the continent and aid in nutrient recycling (Stokes and Redmond, 1966; Herbert and Bell, 1977; Tanner and Herbert, 1981; Delille and Legarde, 1974; Tanner, 1985; Voytek and Ward, 1995; Chessa *et al.*, 2000; Kelly *et al.*, 1978; Cavanagh *et al.*, 1996; Denner *et al.*, 2001; Cavicchioli and Thomas, 2000). Ekelof (1908 a and b) initiated studies on microbiology of the soil and air in Antarctica which was confirmed by Pirie (1904),

*Author for Correspondence: E-mail: shivas@ccmb.res.in; shivas@lvpei.org

Gazert (1912), Tsiklinsky (1908) and McLean (1918 a and b). Later the emphasis was to enumerate and identify unique microorganisms from the continent of Antarctica (Boyd, 1962; Boyd and Boyd, 1962; Friedmann, 1980; Margni and Castrelos, 1963, 1965; Marshall and Ohye, 1966; Meyer *et al.*, 1962; Pfiser and Burkholder, 1965; Tsyganov, 1970). However with the advent of culture independent identification of microorganisms based on 16S rRNA gene metagenomics a greater diversity of microbes from various habitats of Antarctica was discovered. Browsing the NCBI (<http://ncbi.nlm.nih.gov>) database for 16S rRNA gene sequences indicated that about 6000 16S rRNA gene sequences of bacteria from Antarctica have been deposited in the database. Of these close to 210 sequences corresponded to the novel species so far described from Antarctica (Shivaji and Reddy, 2009; Chattopadhyay *et al.*, 2014; Reddy *et al.*, 2016).

Diversity of Antarctica as Studied by Non-cultivable Methods

Antarctic bacterial diversity has been studied by both cultivable and non-cultivable methods (using 16S rRNA gene sequence and certain other functional genes) from various habitats including soil, cyanobacterial mats, water, sediments, sub-glacial out flow, crypto-endolithic sand stones, anoxic meromictic sediments, sediment core, ephemeral streams, ice core, geothermal vents, ornithogenic soil, penguins, sponges and intestinal microbiota of Antarctic fish (for reviews see Reddy *et al.*, 2016; Shivaji and Reddy, 2009; Chattopadhyay *et al.*, 2014; Bottos *et al.*, 2014). The bacterial abundance from the above habitats of Antarctica ranged from 0.2×10^2 to 0.6×10^{12} cells/gram (Carpenter *et al.*, 2000; Priscu *et al.*, 1999; Karl *et al.*, 1999; Delille and Gleizon, 2003), 0.2×10^2 to 10^7 cells/ml (Takii *et al.*, 1986; Franzmann *et al.*, 1990; Lo Giudice *et al.*, 2012) and 8×10^6 to 2.4×10^7 cells/gram (Lanoil *et al.*, 2009; Stibal *et al.*, 2012) and 10^5 to 10^{10} cells/gm (Ramsay and Stannard, 1986; Aislabie *et al.*, 2009) for ice, water, sediment and soil, respectively. Antarctic soils are highly heterogeneous and the diversity varied with respect to soil type. For instance, Antarctic Peninsula soils were dominated by Proteobacteria (47.0%), where as in West Antarctic soils and Transantarctic mountain soils Actinobacteria and Bacteroidetes (42.0% and 31% respectively) (Bottos *et al.*, 2014) were dominant and

in the Victoria Land soils Actinobacteria was dominant. Interestingly members of *Deinococcus-Thermus* are the third most dominating community (18.0%) in Transantarctic Mountain soils indicating that the bacterial communities across Antarctic soils vary significantly with geography, climate, soil physicochemical parameters and local biological influences. Further, unaffiliated clones associated with rare and unique taxa such as *Verrucomicrobia* and *Gemmatimonadetes* were also identified from Antarctic soils from Schirmacher Oasis (Shivaji *et al.*, 2004). In addition to above phylotypes Antarctic peninsula soils, west Antarctic soils and east Antarctic soils contain several unknown phylotypes (Shivaji *et al.*, 2004; Aislabie *et al.*, 2006; Yergeau *et al.*, 2007 a, b; Niederberger *et al.*, 2008; Aislabie *et al.*, 2009; Lee *et al.*, 2012; Tiao *et al.*, 2012; Bajerski and Wagner, 2013; Aislabie *et al.*, 2013).

Limited diversity studies on Antarctic sediments from Bratina island (Sjoling and Cowan, 2003), Ardley island (Li *et al.*, 2006), meromictic marine basin, Vestfold hills (Bowman *et al.*, 2000), Wright Glacier (Stibal *et al.*, 2012) revealed the dominance of phylotypes belonging to *Proteobacteria*, *Cytophaga-Flavobacterium-Bacteroides*, *Spirochaetaceae*, *Actinobacteria*, *Acidobacteria*, *Gemmatimonadetes*, *Firmicutes*, *Prochlorococcus*, *Cyanobacteria*, *Deltaproteobacteria* (specially the unique groups of *Desulfosarcina*, *Syntrophus* and *Geobacter/Pelobacter/Desulphuromonas* group), order Chlamydiales (Parachlamydiaceae), *Planctomycetes* and members of *Spirochaetales*. Carr *et al.* (2013) identified a total of fifty bacterial phyla from marine sediments beneath the Ross Ice Shelf and the predominant taxa reported were *Actinobacteria* (6.0%), *Bacteroidetes* (46.0%), *Chloroflexi* (25.0%), *Firmicutes* (14.0%), and the subphyla Beta- (20.0%), Delta- (25.0%) and Gamma-*Proteobacteria* (8.0%). The Betaproteobacteria were represented by only two genera *Thiobacillus* and *Teptidiphilum* and there was unusually high proportion of *Chloroflexi* group. Bowman *et al.* (2000) demonstrated that anoxic marine sediments contained more than 200 distinct phylotypes with close to 31.0% belonging to the low G+C Gram-positives. Interestingly while studying the vertical distribution of bacterial phyla in fresh water sediment in which *Proteobacteria*, *Bacteroidetes*, *Actinobacteria* and *Firmicutes* were dominant. Shivaji *et al.* (2011)

identified a few clones belonging to *Caldiserica* group, a thermophilic candidate phylum from Antarctica.

Aquatic microbial diversity of Antarctica is limited as only 0.4% of the total ice area of Antarctica (12.3 9 106 km²) is seasonally ice free (Wilkins *et al.*, 2013). Within this ice-free 50,850 Sq. Km area of Antarctica, the majority of bacteria belong to the phyla Proteobacteria representing 47.6% (*Alphaproteobacteria* [71.5%], *Betaproteobacteria* [18.8%], *Deltaproteobacteria* [2.0%] and *Gammaproteobacteria* [7.7%]) with dominating genera being *Rhodobacter* and *Sphingomonas* (Huang *et al.*, (2013). Besides, *Bacteroidetes* (15.1%), *Actinobacteria* (14.8%), *Chloroflexi* (10.2%), *Acidobacteria* (6.7%), *Firmicutes* (3.6%), *Gemmatimonadetes* (1.3%) and *Verrucomicrobia* (0.2%) are minor components, while *Deinococcus-Thermus*, *Nitrospira*, *Planctomycetes*, and *Fusobacteria* were also present. The most common genera are *Sphingomonas*, *Caulobacter*, *Brevundimonas*, *Janthinobacterium*, *Duganella*, *Polaromonas*, *Variovorax*, *Rhodoferrax*, *Flavobacterium*, *Pedobacter*, *Prevotella*, *Hymenobacter* and *Arcicella* (Wilkins *et al.*, 2013). In general, shift in diversity was observed with depth of sediment wherein the predominance of *Bacteroidetes*, *Betaproteobacteria* and *Actinobacteria* in the surface are replaced by *Gammaproteobacteria* with depth (Archer *et al.*, 2014). This is attributed to the tolerance to oxygen requirement of various members of the genera belonging to *Gammaproteobacteria*. The above observation was further supported by Kim *et al.*, (2014) wherein deep waters contained a high proportion of unclassified *Bacteria* (10–20%) along with Proteobacteria. Interestingly, the surface water contained two major clades representing *Polaribacter* (20 to 64%) and uncultivated *Oceanospirillaceae* (7 to 34%) while *Pelagibacter* increased in abundance with depth (7 to 42%) (Kim *et al.*, 2014). Response of bacterial community to hydrocarbon contamination also revealed a change in phylotypes profile. *Alphaproteobacteria*, *Gammaproteobacteria*, the *Cytophaga-Flavobacterium-Bacteroidetes* were major communities but genera *Psychrobacter*, *Arcobacter*, *Formosa algae*, *Polaribacter*, *Ulvibacter* and *Tenacibaculum* were

detected only in hydrocarbon contaminated water and the abundance of *Sulfitobacter* group was high in sea water and decreased drastically by almost 9 folds in contaminated seawater (Prabakaran *et al.*, 2007). The variation in marine and fresh water aquatic systems was evident in Antarctica. The fresh water ecosystems are dominated by groups such as *Flavobacterium*, *Pseudomonas* and *Polaromonas* (Michaud *et al.*, 2012) while *Sulfitobacter*, *Thalassospira*, members of *Roseobacter*, *Gelidibacter*, *Polaribacter*, *Psychroflexus*, *Psychromonas* and *Pseudoalteromonas* were restricted to marine waters (Prabakaran *et al.*, 2007; Guibert *et al.*, 2012; Lo Giudice *et al.*, 2012).

Sea ice, in general, is a dynamic, porous matrix that harbors a network of brine pores and channels that harbor active (Junge *et al.*, 2004; Søgaard, 2010) and diverse (Brown and Bowman, 2001; Brinkmeyer *et al.*, 2003; Maas *et al.*, 2012) bacterial communities. The ice-associated community contains photosynthetic, chemoautotrophic and heterotrophic bacteria beside Archaea and several other eukaryotes. Approximately 36%, 25% and 25% were contributed by *Gammaproteobacteria*, *Alphaproteobacteria* and *Cytophaga-Flavobacterium* group while members of *Actinobacteria* were very rarely present. Among the *Gammaproteobacteria* species of the genera *Colwellia* and *Glaciacola* were the most abundant and *Marinobacter* spp. were rare. The *Alphaproteobacteria* were dominated by members of the *Roseobacter* lineage while CF group was centered on *Polaribacter* group (Bowman *et al.*, 1997; Gosink *et al.*, 1998; Brown and Bowman, 2001; Junge *et al.*, 2002; Brinkmeyer *et al.*, 2003; Kuhn *et al.*, 2014; Lanoil *et al.*, 2009). Besides, the occurrence of communities such as *Shewanella*, *Marinobacter*, *Planococcus*, *Alteromonas*, *Pseudoalteromonas*, *Psychrobacter*, *Halomonas*, *Pseudomonas*, *Hyphomonas*, *Sphingomonas*, *Arthrobacter*, *Planococcus*, and *Halobacillus* were also reported (Bowman *et al.*, 1997). The temporal community analyses indicated a shift in community wherein *Paenisporosarcina* was reduced by 5 folds while *Bacillus* increased by 4 folds. In addition, *Acenetobacter* and *Cohnella* replaced *Paenibacillus* and *Jeotgalibacillus* in a span of two years (Doyle *et al.*, 2013).

Diversity of Antarctica as Studied by Using Functional Genes

Besides the routine 16S rRNA based diversity, functional gene based diversity was also explored from Antarctic habitats and the genes used were basically targeted to look for the sulfate-reducing bacteria (SRB), photosynthetic bacteria, hydrocarbon degrading bacteria, chitinase and ketosynthase producing communities. Targeting the gene *dsrA* (dissimilatory sulfite reductase), diverse group of sulfate-reducing bacteria was detected in Antarctic habitats (Karr et al., 2005). Recently, Watanabe et al. (2013) detected phylotypes, based on *aprA* (adenosine-5'-phosphosulfate reductase alpha subunit) belonging to the genera *Thiocapsa*, *Sulfuricella*, *Desulfobacterium*, *Desulfofaba* and *Desulfotomaculum* from Antarctic fresh water lakes. While more than 70% of sulfur transformation in subglacial lake sediments was contributed by two genera *Sideroxydans* and *Thiobacillus* (Purcell et al., 2014). Further, the involvement of *Marinobacter*, *Roseovarius* and *Psychroflexus* in marine-derived hypersaline lake in the Vestfold Hills, Antarctica, that has the highest concentration of dimethylsulfide (DMS) in a natural body of water was reported (Yau et al., 2013). The above studies indicated the dominance and involvement of *Alphaproteobacteria* and *Betaproteobacteria* in sulfate reduction and also aerobic anoxygenic photosynthesis in Antarctic habitats. In addition, based on Polycyclic aromatic hydrocarbon ring-hydroxylating dioxygenase (PAH-RHD) gene, diverse groups belonging to Proteobacteria, Actinobacteria, Verrucomicrobia, Bacteroidetes, Firmicutes, Chloroflexi, Gemmatimonadetes, Cyanobacteria, Chlorobium, and Acidobacteria were reported from Antarctic soils and sediments. Among these the genera *Terrabacter*, *Mycobacterium*, *Diaphorobacter* belonging to Gram-positives and *Sphingomonas* and *Burkholderia* of Gram-negatives were predominant (Muangchinda et al., 2014). While 14 distinct phylotypes representing the genera *Rhodococcus*, *Mycobacterium*, *Nocardioides*, *Terrabacter* and *Bacillus* were identified from Antarctic sediments based on PAH-dioxygenases (Marcos et al., 2009). Diversity studies based on alkane monooxygenases (Alk) genes from a sediment sample indicated the predominance of unique genes that are differentially distributed between the two sites,

the Admiralty Bay and King George Island of Peninsula Antarctica. The gene sequences identified the genera *Silicibacter*, *Gordonia*, *Prauserella*, *Nocardioides*, *Rhodococcus*, *Nocardia farcinica*, *Pseudomonas*, *Acidisphaera* and *Alcanivorax* (Kuhn et al., 2009). Besides, differential response of bacterial communities to hydrocarbon contamination was studied by Prabakaran et al. (2007). Studies based on chitinase genes (*chi67*, *chi69*, *chiA*, *chiB*, *chiF*) revealed the occurrence of *Janthinobacterium*, *Stenotrophomonas*, *Cytophaga*, *Streptomyces* and *Norcardiopsis* as the abundant genera from a 1600 year old sediment obtained from Ardley Island, Antarctica (Xiao et al., 2005). The phylogenetic analysis based on ketosynthase (KS) identified *Proteobacteria*, *Firmicutes*, *Planctomycetes*, *Cyanobacteria*, *Actinobacteria*, some uncultured symbiotic bacteria and five independent clades. Most of the identified KS showed below 80% identities at the AA level to their closest match revealing the great diversity and novelty of ketosynthase genes in Antarctic sediments (Zhao et al., 2008). Based on gene *pufM* (a gene coding for photosynthetic pigment-binding protein) 33 unique phylotypes related to *Rubrivivax*, *Acidiphilum*, *Rhodofera* and *Roseateles* were detected from Antarctic sediments (Karr et al., 2003; Stibal et al., 2012). While studying the diversity of *psbA* gene from Lake Bonney, unique phylotypes of genera *Nannochloropsis*, *Ochromonas* and *Isochrysis* were identified (Kong et al., 2014). The *amoA* based diversity studies indicated the dominance of only two genera, the *Nitrospira* and *Nitrosomonas*, as the ammonium oxidizing community in Antarctic habitats (Magalhães et al., 2014).

Diversity of Antarctica as Studied by Cultivable Methods

The cultivable bacterial diversity was explored extensively from various habitats such as soil (Miwa, 1975; Yi and Chun, 2006; Ruckert, 1985; Shivaji et al., 1988; 1989a; 1989b; 1991; Wery et al., 2003; Bozal et al., 2007), water (Lo Giudice et al., 2012; Michaud et al., 2012; Soller et al., 2000; Labrenz et al., 2000; Cristóbal et al., 2011), algal mats (Reddy et al., 2000; 2002; 2003a; 2003b; 2004; Van Trappen et al., 2002; Spring et al., 2003; Peeters et al., 2011), ice (Shivaji et al., 2004; Antibus et al., 2012; Bowman et al., 1998) and sediments (Shivaji et al., 2011; Yu et al., 2011) and reviewed by Shivaji and Reddy (2009) and

Chattopadhyay *et al.* (2014) from Antarctica. Among the habitats, water, soil and mats are more diverse compared to ice and sediments as evident from the absence and abundance of various communities. In all the habitats the most dominating communities are *Proteobacteria*, *Cytophaga-Flavobacterium-Bacterioidetes*, *Actinobacteria* and *Firmicutes* and communities belonging to *Deinococcus-thermus* and *Spirochaetes* are restricted, interestingly, only to soil (Hirsch *et al.*, 2004; Antibus *et al.*, 2012; Franzmann & Dobson, 1992; Chattopadhyay *et al.*, 2014). Among the *Proteobacteria*, Gammaproteobacteria leads in abundance in soil (3%) and water (0.6%) while members of Epsilonproteobacteria were absent (Reddy *et al.*, 2016).

Relative percentage occurrence of cultivable bacteria from Antarctica indicated that the soils are dominated by *Firmicutes* (35%), *Actinobacteria* (25%) and *Proteobacteria* (18%), water is inhabited by *Proteobacteria* (42%), *Cytophaga-Flavobacterium-Bacterioidetes* (31%) and *Actinobacteria* (23%), algal mats are rich in *Proteobacteria* (40%), *Firmicutes* (28%) and *Cytophaga-Flavobacterium-Bacterioidetes* (24%), ice is abundant in *Proteobacteria* (48%), *Cytophaga-Flavobacterium-Bacterioidetes* (21%) and *Firmicutes* (19%) and finally the sediments communities are composed of *Proteobacteria* (50%) and *Actinobacteria* (29%) (Reddy *et al.*, 2016). The above statistics clearly indicate that *Proteobacteria* is ubiquitously present in all the Antarctic habitats. Close to 500 cultivable bacteria isolated from Antarctica represent the above major groups of *Proteobacteria*, *Cytophaga-Flavobacterium-Bacterioidetes*, *Actinobacteria* and *Firmicutes* represented by 172 genera (38 novel genera) and 209 novel species.

Novel Species From Antarctica

Till date close to 209 bacterial species have been described based on polyphasic taxonomy (except, *Desulfovibrio* of *Deltaproteobacteria*, *Hymenobacter* species of CFB group and a few species of *Carnobacterium* and *Clostridium* of *Firmicutes*), from various habitats of Antarctica and these novel species belonged to the phyla *Alphaproteobacteria*, *Betaproteobacteria*, *Gammaproteobacteria*, *Deltaproteobacteria*,

Epsilonproteobacteria, *CFB*, *Firmicutes*, *Actinobacter* and *Deinococcus-Thermus*. The relative frequency of the above isolates at the phyla level is shown in Fig. 1 and Table 1 (Bottos *et al.*, 2014; Chattopadhyay *et al.*, 2014; Reddy *et al.*, 2016). The most common feature of the novel species of Antarctica is their psychrophilic growth wherein they grow from zero or subzero temperatures to 30°C but not beyond. However, a few species like *Alicyclobacillus pohliae* (42-60°C) (Imperio *et al.*, 2008), *Aneurinibacillus terranovensis* (20-55°C), (Allan *et al.*, 2005), *Anoxybacillus amylolyticus* (45-65°C) (Poli *et al.*, 2006), *Bacillus fumrioli* (25-55°C) (Logan *et al.*, 2000), *Brevibacillus levickii* (15-55°C) (Allan *et al.*, 2005), *Paenibacillus cineris* (8-50°C) and *Paenibacillus cookie* (15-50°C) (Logan *et al.*, 2004) are moderately thermophilic and interestingly all these species were isolated from soil. The physiological characteristics with respect to the extracellular enzymes indicate approximately 79% of novel species secrete the enzyme phosphatase followed by protease (48.7%), lipase (48.5%), amylase (42%), β -glactosidase (32%) and urease (20%) (Fig. 2). Further, 68% of novel species described so far

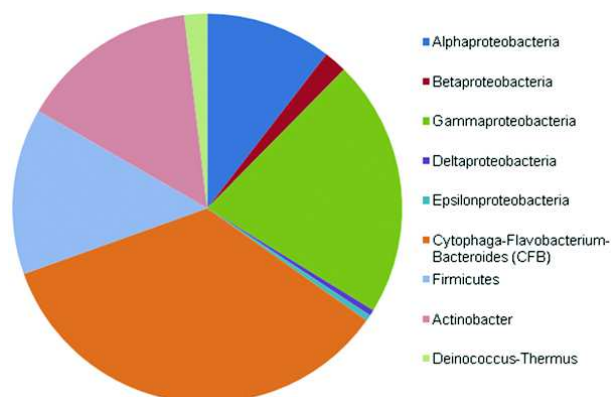


Fig. 1: Relative percentage of novel species described from various habitats of Antarctica

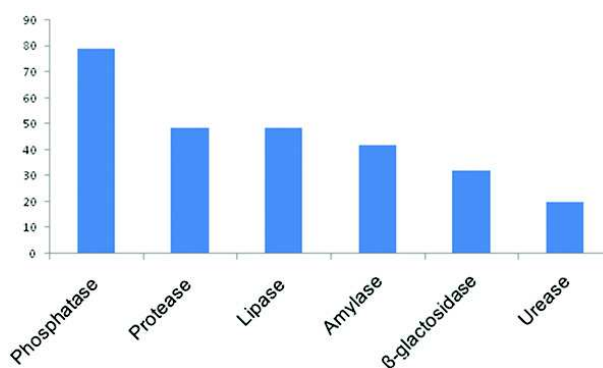


Fig. 2: Production of extracellular enzymes by novel species from Antarctica

Table 1: Important characteristics of novel bacterial species from Antarctica

S.No.	Name of the species	A	C	L	P	U	BG	Ph	Pi	FA	MK	DA	G+C	Ca	O	H	Lipids	16S rRNA gene Acc. No	
Alphaproteobacteria																			
1	1 <i>Antarctobacter heliothermus</i> *	-	-	-	+	ND	ND	ND	BY	18:1	Q10	ND	62.3	+	+	water	PG, PC	Y11552	
2	2 <i>Constrictibacter antarcticus</i> *	ND	ND	+	ND	ND	ND	+	-	18:1	Q10	ND	69.8	+	-	Rock	ND	AB510913	
3	3 <i>Loktanella fryxellensis</i> *	-	ND	-	-	-	+	+	PG	18:1ω7c	ND	ND	66	+	+	Mats	ND	AJ582225	
4	4 <i>Loktanella salsilacus</i>	-	ND	-	-	-	+	+	Biege	18:1ω7c	ND	ND	60	+	+	Mats	ND	AJ440997	
5	5 <i>Loktanella vestfoldensis</i>	-	ND	+	-	+	+	+	Pink	18:1ω7c	ND	ND	63	+	+	Mats	ND	AJ582226	
6	6 <i>Polymorphobacter multimanifer</i> *	ND	ND	-	-	-	-	+	Br	17:1ù6c	Q10	ND	68	+	+	Rock	PG, PE, SPL	AB649056	
7	7 <i>Pseudorhodobacter antarcticus</i>	-	ND	+	-	-	-	+	Pink	18:1ω7c	Q10	ND	57.1	+	+	Sediment	PG, PC	FJ196030	
8	8 <i>Pseudorhodobacter collinsensis</i>	-	+	-	+	+	+	+	Cream	18:1ω7c	Q10	ND	61	+	+	Ice cap	PC, PE, PG	KM978076	
9	9 <i>Pseudorhodobacter psychrotolerans</i>	-	ND	-	+	-	+	+	Cream	18:1ω7c	Q10	ND	60.1	+	+	Soil	PC, PG, UL	KT163920	
10	10 <i>Puniceibacterium antarcticum</i> *	-	ND	-	-	-	-	+	PR	18:1ω7c	ND	ND	60.7	+	+	Water	PC, PE, PG	KP136797	
11	11 <i>Rhodoligotrophos appendicifer</i> *	ND	ND	-	-	-	-	-	Red	16:0	Q9	ND	61.1	+	+	Water	PE, PG	AB617575	
12	12 <i>Robiginitomaculum antarcticum</i> *	ND	ND	+	-	-	+	+	Rusty	18:1ω7c	Q10	ND	60.3	+	-	Water	ND	EF495229	
13	13 <i>Roseibaca ekhonensis</i> *	-	ND	-	-	ND	ND	ND	Red	18:1ω7c	Q10	ND	61	+	+	Water	PC, PE, PG, DPG	AJ605746	
14	14 <i>Roseicitreum antarcticum</i> *	-	ND	-	-	+	+	ND	Pink	18:1ω7c	Q10	ND	63.3	+	+	Sediment	PC, PE, PG	FJ196006	
15	15 <i>Roseisalinus antarcticus</i> *	-	ND	-	-	ND	ND	ND	Rose	18:1ω7c	Q10	mDap	67	+	+	Water	ND	AJ605747	
16	16 <i>Roseovarius antarcticus</i>	-	ND	-	-	-	-	+	PY	18:1ω7c	Q10	ND	61	+	+	Bone	PC, PE, PG, DPG	KM347966	
17	17 <i>Roseovarius tolerans</i> *	-	ND	+	-	ND	ND	ND	Red	18:1	Q10	ND	64	+	+	Water	PC, PE, PG, DPG	Y11551	
18	18 <i>Sphingomonas aerolata</i>	-	ND	-	-	ND	+	+	O	18:1ω7c	Q10	ND	65.4	+	+	Water	PC, PE, PG, DPG, SPL	AJ429240	
19	19 <i>Sphingomonas aurantiaca</i>	-	ND	-	-	ND	+	+	O	18:1ω7c	Q10	ND	65	+	+	Water	PC, PE, PG, DPG, SPL	AJ429236	

20	20	<i>Sphingomonas faeni</i>	-	ND	-	-	ND	+	+	O	18:1ù7c	Q10	ND	63	+	+	Water	PC, PE, PG, DPG, SPL	AJ429239
21	21	<i>Staleyia guttiformis*</i>	-	ND	ND	-	ND	ND	ND	-	18:1ù7c	Q10	ND	56	-	+	Water	PC, PE, PG	Y16427
22	22	<i>Sulfitobacter brevis</i>	-	ND	ND	-	ND	ND	ND	-	18:1ù7c	Q10	ND	58	-	+	Water	PC, PE,D PG	Y16425
23	23	<i>Thalassospira lohafexi</i>	-	ND	-	+	-	-	+	-	18:1ù7c	Q10	ND	53	+	+	Water	PE, PG	GU584152
Betaproteobacteria																			
24	1	<i>Actimicrobium antarcticum* 2/4</i>	ND	ND	+	-	-	-	+	-	16:1ù7c	Q8	ND	65.9	+	+	Water	PE, PG, UL	HQ699437
25	2	<i>Herbaspirillum psychrotolerans</i>	+	ND	ND	+	+	ND	ND	-	16:1ù7c	Q8	ND	62.5	+	-	Soil	PE, PG, DPG	JN390675
26	3	<i>Polaromonas vacuolata*</i>	-	ND	+	-	+	ND	ND	-	16:1ù7c	ND	ND	52	+	+	Water	ND	U14585
27	4	<i>Rhodoferax antarcticus</i>	-	ND	ND	ND	ND	ND	ND	Peach	ND	ND	ND	61.5			Mat	ND	AF084947
Gammaproteobacteria																			
28	1	<i>Alteromonas stellipolaris</i>	+	ND	+	+	-	+	++	Br	16:0	ND	ND	45	+	+	Water	ND	AJ295715
29	2	<i>Glaciecola Polaris</i>	+	ND	+	-	-	+	+	-	16:0	ND	ND	44	+	+	Water	ND	AJ293820
30	3	<i>Granulosicoccus antarcticus**</i>	-	ND	+	+	-	+	-	-	16:1ù7c	Q8	ND	58	+	+	Water	ND	EF495228
31	4	<i>Granulosicoccus marinus</i>	-	-	+	+	-	+	+	-	18:1ù7c	Q8	ND	61	+	+	Water	ND	KF146345
32	5	<i>Hahella Antarctica</i>	ND	ND	-	-	-	-	+	Cr	16:1ù7c	Q9	ND	56.4	+	-	Water	ND	EF495227
33	6	<i>Halomonas alkaliantarctica</i>	-	ND	ND	-	-	ND	ND	-	18:1	Q9	ND	55	-	+	Water	PE, PG, DPG	AJ564880
34	7	<i>Halomonas glaciei</i>	-	ND	-	-	-	ND	-	-	18:1	Q8	ND	-	+	+	Water	ND	AJ431369
35	8	<i>Lysobacter oligotrophicus</i>	+	-	+	+	ND	+	ND	DB	i15:0	Q8	ND	66	+	+	Water	PE, PG, DPG	AB694977
36	9	<i>Marinobacter antarcticus</i>	-	ND	+	-	-	-	+	Br	16:1ù7c	ND	ND	55.8	+	+	Water	PE, PG, DPG	FJ196022
37	10	<i>Marinobacter guinea</i>	-	ND	+	-	-	-	+	-	16:1ù7c	Q9	ND	57.1	+	+	Sediment	ND	AM503093
38	11	<i>Marinobacter maritimus</i>	-	ND	+	-	+	-	+	Cr	18:1ù7c	Q9	ND	58	+	+	Water	ND	AJ704395
39	12	<i>Marinomonas Polaris</i>	-	ND	-	-	ND	+	+	-	18:1ù7c	ND	ND	41.2	+	-	Water	PE, PG	AJ833000
40	13	<i>Marinomonas ushuaiensis</i>	+	ND	-	-	-	ND	+	-	18:1ù7c	ND	ND	43.6	+	-	Water	ND	AJ627909
41	14	<i>Methylosphaera hansonii*</i>	ND	ND	ND	ND	-	ND	-	Y	16:1ù7c	ND	ND	46	+	+	Sediment	ND	U67929
42	15	<i>Neptunomonas Antarctica</i>	-	ND	-	-	-	-	+	-	16:1ù7c	Q8	ND	46	+	+	Sediment	ND	FJ713802
43	16	<i>Oleispira lenta</i>	-	ND	+	-	-	-	+	-	16:1ù7c	ND	ND	43	-	+	Water	ND	EU980447
44	17	<i>Oleispira antarctica*</i>	-	ND	+	-	-	ND	ND	-	16:1ù7c	ND	ND	42	+	+	Water	ND	AJ426420
45	18	<i>Pseudoalteromonas antarctica</i>	-	ND	+	+	-	-	+	-	16:1ù7c	ND	ND	42	+	+	Mud	ND	X98336

46	19	<i>Pseudoalteromonas prydzensis</i>	+	ND	+	+	+	-	+	-	16:1ω7c	ND	ND	39	+	+	Ice	ND	U85855
47	20	<i>Pseudomonas antarctica</i>	-	-	+	-	+	-	+	-	18:1	ND	ND	61	+	+	Mat	ND	AJ537601
48	21	<i>Pseudomonas deceptionensis</i>	-	ND	-	-	+	-	-	-	16:1	ND	ND	53.8	+	+	Sediment	PE, PG, DPG	GU936597
49	22	<i>Pseudomonas extremaustralis</i>	-	ND	ND	-	-	-	ND	-	16:1ω7c	ND	ND	ND	+	+	Water	ND	AF405328
50	23	<i>Pseudomonas guinea</i>	-	ND	+	-	-	-	+	-	16:0	ND	ND	58.5	+	+	Soil	ND	AM491810
51	24	<i>Pseudomonas meridiana</i>	-	-	+	-	+	-	-	-	16:0	ND	ND	63	+	+	Mat	ND	AJ537602
52	25	<i>Pseudomonas prosekii</i>	-	-	-	+	-	ND	ND	-	ND	ND	ND	ND	+	+	Soil	ND	JN814372
53	26	<i>Pseudomonas proteolytica</i>	-	-	+	+	-	-	-	-	18:1	ND	ND	58	+	+	Mat	ND	AJ537603
54	27	<i>Psychrobacter adeliensis</i>	-	-	-	+	-	-	-	-	18:1ω9c	ND	ND	45	+	+	Water	ND	AJ539105
55	28	<i>Psychrobacter aquaticus</i>	-	-	+	-	+	-	+	-	16:1	Q8	ND	43.6	+	+	Mat	PE, PG, DPG	AJ584833
56	29	<i>Psychrobacter fozi</i>	-	ND	-	-	+	ND	+	-	18:1ω9c	ND	ND	44	+	+	Sediment	ND	AJ430827
57	30	<i>Psychrobacter frigidicola</i>	-	ND	-	-	-	-	-	-	18:1ω9c	ND	ND	42	+	+	Water	ND	AJ609556
58	31	<i>Psychrobacter luti</i>	-	ND	+	-	-	ND	+	-	18:1ω9c	ND	ND	45	+	+	Soil	ND	AJ430828
59	32	<i>Psychrobacter nivimaris</i>	-	ND	+	-	ND	ND	ND	-	18:1ω9c	ND	ND	42	+	+	Org.Mate	ND	AJ313425
60	33	<i>Psychrobacter proteolyticus</i>	-	ND	+	+	+	-	+	-	18:1ω9c	ND	ND	43.6	+	+	Water	ND	AJ272303
61	34	<i>Psychrobacter salsus</i>	-	ND	-	-	-	-	-	-	18:1ω9c	ND	ND	44	+	+	Water	ND	AJ539104
62	35	<i>Psychrobacter urativorans</i>	-	ND	-	-	+	-	-	-	18:1ω9c	ND	ND	46	+	+	Water	ND	AJ609555
63	36	<i>Psychrobacter vallis</i>	-	-	+	-	-	-	+	-	18:1ω9c	Q8	ND	46	+	+	Mat	PE, PG, DPG	AJ584832
64	37	<i>Psychromonas antarcticus*</i>	-	ND	ND	+	ND	ND	ND	-	16:1ω7c	Q8	ND	43	+	+	Soil	ND	Y14697
65	38	<i>Psychromonas kaikoa</i>	-	ND	ND	+	ND	ND	ND	-	16:1ω7c	Q8	ND	44	+	+	Sediment	PE, PG, DPG	AB052160
66	39	<i>Saccharospirillum impatiens*+</i>	ND	-	+	ND	ND	ND	-	-	18:1	Q8	mDap	55	+	+	Water	PE, PG, DPG	AJ315983
67	40	<i>Shewanella livingstonensis</i>	-	ND	+	+	-	+	+	-	16:1ω7c	MK7	ND	41	+	+	Water	PE, PG, DPG	AJ300834
68	41	<i>Shewanella frigidimarina</i>	-	ND	+	+	-	-	+	-	16:1ω7c	ND	ND	43	+	+	Ice	ND	U85903
69	42	<i>Shewanella gelidimarina</i>	-	ND	+	+	-	-	+	-	16:1ω7c	ND	ND	48	+	+	Ice	ND	U85907
70	43	<i>Shewanella vesiculosa</i>	-	ND	+	+	-	+	+	-	16:1ω7c	Q7	ND	42	+	+	Sediment	ND	AM980877
71	44	<i>Zhongshania antarctica*</i>	-	ND	-	-	-	-	ND	-	17:1ω8c	ND	ND	52.5	+	+	Ice	ND	FJ889619
72	45	<i>Zhongshania guokunii</i>	-	ND	-	-	-	-	ND	-	17:1ω8c	ND	ND	51.8	+	+	Water	ND	FJ889678
Deltaproteobacteria																			
73	1	<i>Desulfovibrio lacusfryxellense</i>	Not well characterized													Water	DQ767889		

Epsilonproteobacteria																		
74	1	<i>Campylobacter subantarcticus</i>														ird	AM933371	
CFB																		
75	1	<i>Aequorivita antarctica</i>	+	ND	+	-	-	ND	ND	ND	i15:0	ND	ND	ND	+	-	Sea water ND	AY027802
76	2	<i>Aequorivita capsosiphonis</i>	-	-	-	+	-	-	+	YO	I15:0	ND	ND	37	+	-	Algae ND	EU290153
77	3	<i>Aequorivita crocea</i>	-	ND	+	+	-	-	+	Y	Ai15:0	ND	ND	34	+	-	Sea water ND	AY027806
78	4	<i>Aequorivita lipolytica*</i>	-	ND	-	+	+	-	+	Y	Ai15:0	ND	ND	36	+	-	Sea water ND	AY027805
79	5	<i>Aequorivita sublithincola</i>	-	ND	-	-	+	-	+	O	Ai15:0	ND	ND	37	+	-	Sea water ND	AF170749
80	6	<i>Algibacter psychrophilus</i>	+	-	-	-	-	-	-	Y	17:0 2OH MK6	ND	ND	33.5	+	+	Sediment PE	KJ475138
81	7	<i>Algoriphagus antarcticus</i>	+	ND	-	-	-	-	+	O	Ai15:1ù10c	ND	ND	39	+	+	Mats ND	AJ577141
82	8	<i>Antarcticimonas flava*</i>	+	ND	+	+	-	+	+	Y	16:1ω7c MK6	ND	ND	37.3	+	-	Water PE, UL	EF554365
83	9	<i>Bizionia algorithergicola</i>	-	ND	-	+	-	-	+	Y	Ai15:1ω10c	ND	ND	34	+	+	Ice ND	AY694003
84	10	<i>Bizionia argentinensis</i>	-	ND	+	+	-	-	+	Y	Ai15:0 3OH	ND	ND	45	+	+	Ice ND	EU021217
85	11	<i>Bizionia gelidisalsuginis</i>	-	ND	+	+	-	-	+	Y	Ai15:0 3OH	ND	ND	39	+	+	Ice ND	AY694004
86	12	<i>Bizionia myxarmorum</i>	-	ND	+	+	-	-	+	Y	Ai15:0 3OH	ND	ND	43	+	+	Ice ND	AY694002
87	13	<i>Bizionia saleffrena</i>	-	ND	+	+	-	-	+	Y	Ai15:0 3OH	ND	ND	40	+	+	Ice ND	AY694005
88	14	<i>Cellulophaga algicola</i>	+	ND	+	+	-	+	-	YO	16:1ω7c	ND	ND	38	+	-	Ice ND	CP002453
89	15	<i>Chryseobacterium frigidisoli+</i>	ND	ND	+	-	ND	ND	Y	I15:0 2OH MK6	ND	ND	33.7	+	+	Soil ND	JN390676	
90	16	<i>Flavobacterium antarcticum</i>	-	-	+	+	-	-	+	Y	I15:0 MK6	ND	ND	38	+	+	Soil ND	AY581113
91	17	<i>Flavobacterium collinsense</i>	-	-	+	+	-	+	+	Y	I15:0	ND	ND	36.2	+	+	Soil PE, UL	KM288594
92	18	<i>Flavobacterium degerlachei</i>	+	-	-	-	-	-	+	Y	I15:0 2OH	ND	ND	34.2	+	+	Mat ND	AJ557886
93	19	<i>Flavobacterium faecale</i>	+	ND	ND	-	+	+	ND	Y	15:0 MK6	ND	ND	37	+	+	Sediment ND	KF214259
94	20	<i>Flavobacterium frigidarium</i>	-	-	+	+	+	+	ND	Y	16:1ω7c	ND	ND	35	+	+	Sediment ND	AF162266
95	21	<i>Flavobacterium frigidimaris+</i>	-	-	-	+	ND	+	ND	Flexi	16:0 MK6	ND	ND	34	+	-	Sediment ND	AB183888
96	22	<i>Flavobacterium frigoris</i>	-	-	+	-	-	-	++	OR	I15:0 2OH	ND	ND	35	+	+	Mats ND	AJ557887
97	23	<i>Flavobacterium fryxellicola</i>	-	-	+	-	-	-	++	YO	I15:0	ND	ND	36	+	+	Water ND	AJ811961
98	24	<i>Flavobacterium gelidilacus</i>	+	ND	-	+	-	-	++	YO	I15:0	ND	ND	32	+	+	Water ND	AJ440996
99	25	<i>Flavobacterium gillisiae</i>	+	-	+	-	-	-	ND	O	16:1ω7c	ND	ND	32	+	-	Sea ice ND	U85889
100	26	<i>Flavobacterium gondwanense</i>	+	ND	+	-	+	+	+	O	A15:0 MK6	ND	ND	39	+	+	Water ND	M92278
101	27	<i>Flavobacterium hibernum</i>	+	-	+	+	-	+	ND	Y	I15:0 MK6	ND	ND	34	+	-	Water ND	L39067
102	28	<i>Flavobacterium micromati</i>	-	ND	-	-	-	-	++	OR	I15:0 2OH	ND	ND	33	+	+	Mats ND	AJ557888

103	29	<i>Flavobacterium psychrolimnae</i>	+	-	-	-	-	++	Y	I15:0 2OH	ND	ND	34.5	+	+	Water	ND	AJ585428	
104	30	<i>Flavobacterium segetis</i>	+	-	+	-	+	+	O	16:1ω7c	MK6	ND	41	+	+	Soil	ND	AY581115	
105	31	<i>Flavobacterium salegens</i>	+	ND	+	+	-	+	Y	16:1ω7c	MK6	ND	41	+	+	Water	ND	M92279	
106	32	<i>Flavobacterium tegetincola</i>	-	-	+	-	-	ND	Y	16:1ω7c	ND	ND	32	+	-	Mud pool	ND	U85887	
107	33	<i>Flavobacterium weaverense</i>	+	-	+	-	+	+	Y	16:1ω7c	MK6	ND	37	+	+	Soil	ND	AY581114	
108	34	<i>Gelidibacter algens</i> *	+	ND	+	+	-	+	Y	A15:0	ND	ND	38	+	-	Sea ice	ND	U62914	
109	35	<i>Gelidibacter gilvus</i>	-	ND	+	-	-	+	Y	A15:0	ND	ND	39	+	-	Sea ice	ND	AF001369	
110	36	<i>Gelidibacter salicanalis</i>	-	ND	-	+	+	+	Y	a15:1ω10c	ND	ND	42	+	-	Sea ice	ND	AY694009	
111	37	<i>Gillisia hiemivivida</i>	+	ND	+	+	+	+	Y	A15:0	ND	ND	34	+	+	Ice core	ND	AY694006	
112	38	<i>Gillisia illustrilutea</i>	-	ND	-	-	-	-	Y	a15:1ω10c	ND	ND	32	+	+	Ice core	ND	AY694008	
113	39	<i>Gillisia limnaea</i> *	-	ND	-	+	-	+	Y	17:0 2OH	ND	ND	38	+	+	Mats	ND	AJ440991	
114	40	<i>Gillisia sandarakina</i>	+	ND	+	+	-	+	O	i16:0	ND	ND	36	+	+	Ice core	ND	AY694007	
115	41	<i>Hymenobacter algicola</i>	Not well characterized							RP	16:1ω7c	ND	ND	ND	-	+	Gl. water	ND	EU155009
116	42	<i>Hymenobacter antarcticus</i>								RP	16:1ω7c	ND	ND	ND	-	+	Gl. Water	ND	EU155012
117	43	<i>Hymenobacter elongates</i>								RP	I17:1	ND	ND	ND	-	+	Gl. Water	ND	GQ454797
118	44	<i>Hymenobacter fastidiosus</i>								RP	16:1ω7c	ND	ND	ND	-	+	Gl. Water	ND	EU155015
119	45	<i>Hymenobacter glaciei</i>								RP	16:1ω7c	ND	ND	ND	-	+	Gl. water	ND	GQ454806
120	46	<i>Hymenobacter roseosalivarius</i> *	+	-	+	+	-	ND	+	RP	16:1ω7c	MK7	ND	56	+	+	Soil	PE	Y18833
121	47	<i>Kordia Antarctica</i>	+	-	-	-	-	+	Y	16:1ω9c	MK6	ND	35	-	-	Sea water	PE, UL	JX456458	
122	48	<i>Lacinutrix copepodicola</i> *	-	ND	+	+	-	+	Y	I15:0	MK6	ND	32	+	+	Sea ice	PE	AY694001	
123	49	<i>Lacinutrix jangbogonensis</i>	-	ND	+	+	-	+	Y	I15:0	MK6	ND	37	+	+	Sea ice	PE	KF977035	
124	50	<i>Leeuwenhoekiella aequorea</i>	+	-	+	+	-	+	Y	17:1ω9c	MK6	ND	36	+	+	Sea ice	ND	AJ278780	
125	51	<i>Leeuwenhoekiella polynya</i> +	-	-	+	-	+	+	Y	I17:0 2 OH	MK6	ND	39	+	+	Water	PE, UL	KM101107	
126	52	<i>Lewinella Antarctica</i>	+	-	-	+	-	+	O	16:1ω7c	MK7	ND	50	+	-	Water	ND	EF554367	
127	53	<i>Maribacter antarcticus</i>	+	ND	+	-	-	+	O	I15:0	MK6	ND	37	+	+	Algae	PE	EU512921	
128	54	<i>Muricauda Antarctica</i>	-	ND	-	+	-	+	Br	I17:0 3OH	MK6	ND	45	+	+	Sea water	PE	JN166984	
129	55	<i>Nonlabens antarcticus</i>	-	-	-	+	-	+	O	Ai15:0	MK6	ND	38	+	+	Gl. core	PE	DQ660393	
130	56	<i>Pedobacter ardleyensis</i>	+	ND	-	-	-	+	Red	I15:0	MK7	ND	40	+	+	Soil	PE, Sphingo lipid	KJ631640.	
131	57	<i>Polaribacter filamentus</i>	+	-	ND	+	-	ND	Soh	I15:0 2OH	ND	ND	32	+	-	Sea water	ND	U73726	
132	58	<i>Polaribacter franzmannii</i>	+	-	ND	+	-	ND	O	I15:0 3OH	ND	ND	32	+	+	Sea ice	ND	U14586	

133	59	<i>Polaribacter irgensii</i> *	+	-	-	+	-	-	+	O	I15:0 3OH MK6 ND	31	+	+	Sea water PE	M61002		
134	60	<i>Polaribacter sejongensis</i>	+	ND	+	+	-	+	+	Y	I15:0 3OH MK6 ND	30	+	+	Soil PE	HQ853596		
135	61	<i>Pricia antarctica</i> *	-	ND	-	-	-	-	+	Y	I15:0G MK6 ND	44	+	+	Sediment PE	FJ889677		
136	62	<i>Psychroflexus lacisalsi</i>	+	ND	-	+	ND	-	+	O	A15:0 MK6 ND	35	+	+	Lake water ND	AB381940		
137	63	<i>Psychroflexus torques</i>	+	ND	+	+	-	-	+	O	A15:0 MK6 ND	33	+	+	Sea ice ND	U85881		
138	64	<i>Psychroserpens burtonensis</i> *	-	ND	+	+	-	-	+	YO	15:1 ω 10c ND ND	29	+	-	Lake Water ND	U62913		
139	65	<i>Psychroserpens jangbogonensis</i>	+	ND	-	-	-	-	+	Y	20:4 ω 6c MK6 ND	32.7	+	+	Sediment PE	KJ475160		
140	66	<i>Salegentibacter salegens</i> *	+	ND	+	+	ND	+	+	Y	I15:0 MK6 ND	38	+	+	Water ND	M92279		
141	67	<i>Sejonia antarctica</i> *	+	-	+	+	-	-	+	Y	17:1 ω 9c MK6 ND	34	+	+	Soil ND	AY553293		
142	68	<i>Sejonia jeonii</i>	-	-	-	+	+	-	+	Y	A15:0 MK6 ND	36	+	+	Moss ND	AY553294		
143	69	<i>Sejonia marina</i>	+	ND	+	+	-	-	+	Y	A15:0 MK6 ND	35	+	-	Sea water ND	EF554366		
144	70	<i>Subsaxibacter broadyi</i>	-	ND	+	+	-	-	+	Y	A15:0 ND ND	35	+	+	Cyano ND	AY693999		
145	71	<i>Subsaximicrobium saxinquilinus</i>	+	ND	+	+	-	-	+	O	I16:0 3OH ND ND	39	+	+	Cyano ND	AY693998		
146	72	<i>Subsaximicrobium wynnwilliamsii</i> *	+	ND	+	+	+	-	+	O	A15:0 ND ND	40	+	+	Cyano ND	AY693997		
147	73	<i>Ulvibacter antarcticus</i>	+	-	-	+	-	-	+	Y	I17:0 3OH MK6 ND	37	+	+	Sea water ND	EF554364		
Firmicutes 30																		
148	1	<i>Alicyclobacillus pohliae</i>	ND	ND	ND	ND	ND	ND	ND	ND	ND	55	-	-	Soil ND	AJ564766		
149	2	<i>Aneurinibacillus terranovensis</i>	+	ND	-	+	-	-	ND	ND	ND	44.6	+		Soil ND	AJ715385		
150	3	<i>Anoxybacillus amylolyticus</i>	+	ND	-	-	-	ND	ND	-	I15:0 MK7 ND	43.5	+	-	Soil ND	AJ618979		
151	4	<i>Bacillus fumarioli</i>	-	ND	-	+	-	-	ND	BC	I15:0 ND ND	40.7			Soil ND	AJ250056		
152	5	<i>Brevibacillus levickii</i>	+	ND	-	+	-	-	ND	ND	ND	50.3	+		Soil ND	AJ715378		
153	6	<i>Carnobacterium alterfunditum</i>	Not well characterized									16:0	ND	ND	ND	ND	L08623	
154	7	<i>Carnobacterium funditum</i>										16:0	ND	ND	34		ND	S86170
155	8	<i>Carnobacterium iners</i>										16:0	ND	mDap	34		Mats ND	HE583595
156	9	<i>Clostridium bowmanii</i>										16:1 ω 9c	ND	ND	32		ND	AJ506119
157	10	<i>Clostridium frigoris</i>										16:1 ω 9c	ND	ND	32		ND	AJ506116
158	11	<i>Clostridium lacusfryxellense</i>										16:1 ω 9c	ND	ND	32		ND	AJ506118
159	12	<i>Clostridium psychrophilum</i>										16:1 ω 9c	ND	ND	31.8		ND	AJ297443

160	13	<i>Clostridium schirmacherense</i>								15:0	ND	ND	24				ND	AM114453	
161	14	<i>Clostridium vincentii</i>								16:0	ND	ND	33				ND	X97432	
162	15	<i>Exiguobacterium antarcticum</i>	+	-	+	-	+	+	O	16:0	MK7	ND	48.5	+	+	Soil	PG, DPG, PS, PI, PE, UL	DQ019164	
163	16	<i>Exiguobacterium soli</i>	+	-	+	-	+	+	Y	15:0	MK7	ND	47	+		Soil	PG, DPG, PS, PI	AY864633	
164	17	<i>Exiguobacterium undae</i>	+	-	+	-	+	+	O	16:0	MK7	ND	48	+	+	Soil	PG, DPG, PS, PI, PE, UL	DQ019165	
165	18	<i>Jeotgalicoccus pinnipedialis</i>	ND	ND	ND	+	ND	-	-	15:0	MK7	ND	38.6	+	+		PG, DPG, PI	AJ251530	
166	19	<i>Paenibacillus antarcticus</i>	+	ND	+	-	+	-	ND	a15:0	ND	ND	40.7	+	+	Sediment	ND	AJ605292	
167	20	<i>Paenibacillus. cineris</i>	ND	ND	ND	-	-	+	ND	a15:0	ND	ND	51.5	+	+	Soil	ND	AJ575658	
168	21	<i>Paenibacillus cookie</i>	ND	ND	ND	-	-	+	ND	Y	a15:0	ND	51.6	+	+	Soil	ND	AJ250317	
169	22	<i>Paenibacillus darwinianus</i>	+	ND	-	-	ND	ND	ND	a15:0	MK7	ND	55.6	+	-	Soil	PG, DPG, PE	KF264455	
170	23	<i>Paenibacillus wyntsi</i>	+	ND	ND	-	-	+	ND	a15:0	ND	ND	44.6			Soil		AJ633647	
171	24	<i>Planococcus antarcticus</i>	-	ND	+	+	-	+	-	O	a15:0	MK7,8	ND	41.5	+	-	Mat	PG, DPG, PE	AJ314745
172	25	<i>Planococcus maitriensis</i>	-	ND	-	+	-	+	-	O	a15:0	MK7,8	ND	39	+	+	Mat	ND	AF500007
173	26	<i>Planococcus mmeekinii</i>	-	ND	-	+	ND	ND	ND	O	a15:0	MK7,8	ND	35	+	-	Brine	ND	AF041791
174	27	<i>Planococcus psychrophilus</i>	-	ND	+	+	-	+	-	O	a15:0	MK7,8	ND	44.5	+		Mat	PG, DPG, PE	AJ314746
175	28	<i>Psychrosinus fermentans</i>	Not well characterized							+	+	W				ater	ND	DQ767881	
176	29	<i>Sporosarcina Antarctica</i>	-	ND	-	-	-	+	LY	a15:0	MK7	ND	39.2	+	+	Soil	ND	EF154512	
177	30	<i>Sporosarcina macmurdoensis</i>	+	ND	-	+	-	-	+	a15:0	MK7	ND	44	+	-	Mat	ND	AJ514408	
178	Actinobacteria 6/31																		
179	1	<i>Arthrobacter antarcticus</i>	+	ND	-	-	+	-	+	Y	a15:0	MK8	Lys-Glu 68	+	+	Sediment	DPG, PE	AM931709	
180	2	<i>Arthrobacter ardleyensis</i>	-	-	+	+	ND	ND	ND	Y	a15:0	MK8	Lys-Ala-Glu 59.5	+	-	Sediment	ND	AJ551163	
181	3	<i>Arthrobacter cryotolerans</i>	-	ND	ND	+	-	-	+	-	a15:0	MK9H ₂	Lys-Glu 64.5	+	-	Soil	PG	GQ406812	
182	4	<i>Arthrobacter flavus</i>	+	ND	-	-	-	ND	ND	Y	a15:0	MK9H ₂	Lys-Thr-Ala ₃ 65	+	-	Mat	PE, PG, DPG	AB537168	
183	5	<i>Arthrobacter gangotriensis</i>	-	ND	-	+	+	-	+	Y	a15:0	MK8	Lys-Glu 66	+	+	Soil	ND	AJ606061	
184	6	<i>Arthrobacter kerguelensis</i>	-	ND	-	?	+	-	+	Y	a15:0	MK8	Lys-Glu 58	+	+	Sea water	ND	AJ606062	
185	7	<i>Arthrobacter livingstonensis</i>	-	ND	ND	-	+	ND	ND	W	a15:0	MK9H ₂	Lys-Thr-Ala 64.7	+	-	Soil	PG	GQ406811	
186	8	<i>Arthrobacter psychrochitini-philus</i>	+	+	+	-	-	ND	ND	Y	a15:0	MK9H ₂	Lys-Glu 58.5	+	-	Penguin	ND	AB588633	
187	9	<i>Arthrobacter roseus</i>	-	ND	-	+	-	-	+	R	a15:0	MK9H ₂	Lys-Thr-Ala ₃ 69	+	-	Mat	PE, PG, DPG	AJ278870	
188	10	<i>Barrientosiimonas humi*</i>	-	-	-	+	-	ND	ND	PY	a17:0	MK8H ₄	Lys-Ser-Asp 68.4	+	-	Soil	PE, PG, DPG, UL	JF346171	

189	11	<i>Curtobacterium psychrophilum</i> *	+	ND	ND	-	ND	ND	ND	-	a15:0	MK10	Dab	65	+	-Soil	PG, DPG, UL	D45058	
190	12	<i>Friedmanniella antarctica</i> *	+	ND	+	-	+	ND	ND	O	a15:0	9H4	Lys-Gly	73	+	-Sand stone	PG, DPG, PI, UL	Z78206	
191	13	<i>Friedmanniella lacustris</i>	-	ND	ND	+	-	ND	ND	O	a15:0	9H4	mDap	73	+	Water	ND	AJ132943	
192	14	<i>Kocuria Polar</i>	+	ND	+	-	-	-	-	O	a15:0	7H2	Lys-Ala ₃	72.5	+	+Mat	PG, DPG, PI	AJ278868	
193	15	<i>Leifsonia antarctica</i>	-	ND	-	+	-	+	+	Y	a15:0	MK10	Dab	-	+	Sediment	PG, DPG, PE	AM931710	
194	16	<i>Leifsonia aurea</i>	-	ND	-	-	-	+	-	Y	a15:0	MK11	Dab	64	+	Mat	ND	AJ438586	
195	17	<i>Leifsonia psychrotolerans</i>	+	ND	-	-	-	ND	ND	Y	a15:0	MK10	Dab	64.5	+	Soil	PG, DPG	GQ406810	
196	18	<i>Leifsonia rubra</i>	-	ND	-	-	-	+	-	R	a15:0	MK11	Dab	66	+	Mat	ND	AJ438585	
197	19	<i>Marisediminicola antarctica</i> *	-	ND	-	-	-	+	-	Y	a15:0	MK10	Orn	67	+	Sediment	PG, DPG	GQ496083	
198	20	<i>Micrococcus antarcticus</i>	+	ND	-	-	-	ND	ND	Y	a15:0	MK8	Lys	64.4	+	Soil	ND	EF154512	
199	21	<i>Micromonospora endolithica</i>	+	-	+	+	ND	ND	ND	Orange	I16:0	MK10	mDap	70	+	Sand stone	PE, PI, DPG	AJ560635	
200	22	<i>Modestobacter multiseptatus</i> *	+	ND	-	-	-	ND	+	Pink	18:0	MK9H2	mDap	69.9	+	Soil	PE, PG, DPG, PI	Y18646	
201	23	<i>Nesterenkonia lacusekhoensis</i>	-	ND	-	-	ND	ND	ND	Y	a15:0	MK7	Lys	66.1	+	Water	PC, PG, DPG	AJ290397	
202	24	<i>Nocardioides antarcticus</i>	-	ND	+	+	-	-	+	Cream	i16:0	MK8H4	mDap	66.7	+	Sediment	PG, DPG, UL3	KM347967	
203	25	<i>Nocardioides aquaticus</i>	+	ND	ND	+	ND	ND	ND	-	I16:1	MK8H4	mDap	69	+	Water	ND	X94145	
204	26	<i>Nocardiopsis fildesensis</i>	-	ND	-	-	-	ND	ND	-	i16:0	MK9H4	mDap	76.8	+	Soil	PC, PG, PME	FJ853144	
205	27	<i>Pseudonocardia antarctica</i>	+	ND	-	+	+	+	+	Brown	I16:0	MK8H4	mDap	71	+	Moraine	PC, PE, PI, PG, DPG	AJ576010	
206	28	<i>Rhodoglobus vestalii</i> *	ND	ND	ND	-	-	+	+	Red	a15:0	MK12	Orn	62	+	Water	ND	AJ459101	
207	29	<i>Sanguibacter antarcticus</i>	-	ND	-	-	-	-	-	Y	a15:0	MK9H4	ND	69.5	+	Sea Sand	ND	EF211071	
208	30	<i>Streptomyces fildesensis</i>	-	ND	+	ND	-	ND	-	YG	I16:0	MK9H6	mDap	70	+	Soil	PE, PI, DPG, PME	DQ408297	
209	31	<i>Streptomyces hypolithicus</i>	-	-	ND	+	-	ND	ND	-	ND	ND	mDap	ND	ND	ND	Quartz	ND	EU196762
Deinococcus Thermus																			
210	1	<i>Deinococcus antarcticus</i>	+	ND	+	+	ND	+	+	Pink	18:1ω7c	MK8	L-Orn	63.1	+	Soil	ND	KC494323	
211	2	<i>Deinococcus frigens</i>	+	ND	ND	+	-	+	ND	P-O	16:1ω9c	MK8	L-Orn	65.5	+	Soil	ND	AJ585981	
212	3	<i>Deinococcus saxicola</i>	+	ND	ND	+	-	-	ND	P-R	16:1ω9c	MK8	L-Orn	54.4	+	Soil	ND	AJ585984	
213	4	<i>Deinococcus marmoris</i>	-	-	ND	+	-	+	ND	P-R	16:1ω9c	MK8	L-Orn	62.8	+	Soil	ND	AJ585986	

*, Genus; **, Family; A, amylase; C, cellulase; L, lipase; P, protease; U, urease; BG, Beta-galactosidase; Ph, phosphatase; Ca, catalase; O, oxidase; Pig, pigment (o, orange; y, yellow; r, red; cr, cream; w, white); MK, quinine type; FA, Fatty acid methyl ester major; DA, diamino acid in peptidoglycan; GC, G+C content of the DNA; H, habitat (S, soil; Sd, sediment; Wf, fresh water; Ws, sea water; I, ice). ND = not determined; '+' = Present, '-' = Absent

are pigmented, indicating that pigmentation is a common phenomenon in Antarctic bacteria. Pigment is known to be involved in stress adaptation to low temperatures (Jaganadham *et al.*, 1996; Jaganadham *et al.*, 2000; Chattopadhyay *et al.*, 1997).

Alphaproteobacteria contributed 10.5% of total novel species isolated so far and the 23 novel species belonged to 16 genera of which 12 were novel genera described from Antarctic habitats (Table 1). Six of the novel species contained Bacterial chlorophyll (Liu *et al.*, 2014; Labrenz *et al.*, 1999; Labrenz *et al.*, 2000; Labrenz *et al.*, 2005; Labrenz *et al.*, 2009; Yu *et al.*, 2011) and could exhibit photoautotrophic type of growth. Majority of the species produced Alkaline phosphatase and β -galactosidase but none of them secreted amylase while only 3 and 5 species exhibited the activity for protease and lipase, indicating that this group is responsible for the availability of phosphate in Antarctic habitats. The presence of pigment is a common phenomenon in all except in case of *Constrictibacter antarcticus* (Yamada *et al.*, 2011). All the species contained their respective generic characteristics and the major fatty acid was C_{18:1} ω 7c and the respiratory quinone was Q10.

Unlike *Alphaproteobacteria*, only very few species of *Betaproteobacteria* were isolated and the reason could be the inadequate information on conducive media conditions. So far four novel species belonging to 4 different genera were reported out of which 2 were novel genera. The genus *Polaromonas vacuolata* (Irgens *et al.*, 1996) possessed intracellular gas vesicles. The genus *Rhodoferrax antarcticus* contained bacteriochlorophyll (Madigan *et al.*, 2000). All the species possessed their respective generic characteristics and the major fatty acid and respiratory quinone was C_{16:1} ω 7c and Q8 respectively.

Species belonging to *Betaproteobacteria* were the second largest group explored from Antarctic habitats. So far close to 44 novel species belonging to 18 genera were described of which 6 were novel genera. The genera *Oleispira* (Yakimov *et al.*, 2003) and *Methylosphaera* (Bowman *et al.*, 1997) were endemic to Antarctica. Further, novel family, *Granulosicoccaceae*, was reported from Antarctic water (Lee *et al.*, 2007). Majority of species produce phosphatase (70%) and lipase (64%) while enzymes protease (37.5%), urease (23.7%), β -galactosidase

(22%) and amylase (16.7%) are produced by less than 50% of the novel species (Table 1). Some of the novel species were interesting wherein *Pseudomonas prydzensis* produces chitinase (Bowman *et al.*, 1998), *Oleispira antarctica* can degrade hydrocarbons (Yakimov *et al.*, 2003), cells of species *Saccharospirillum* are microaerophilic (Labrenz *et al.*, 2003), *Methylosphaera hansonii* is a methanotroph (Bowman *et al.*, 1997) and *Alteromonas stellipolaris* produces buds (Van Trappen *et al.*, 2004).

CFB group of bacteria dominated various habitats of Antarctica (Bottos *et al.*, 2014) and constitute 35% of novel species from Antarctica. Interestingly all the novel species isolated were pigmented and yellow pigmented bacteria were the most common. So far 73 novel species belonging to CFB group were described and they belonged to 27 genera out of which 12 were novel genera. In addition, species belonging to the genera *Antarcticimonas*, *Pricia*, *Sejongia* and *Subsaximicrobium* were endemic to Antarctica. Among all the bacterial phyla from Antarctica, CFB group plays an important role in nutrient recycling as they produce phosphatase (91.5%), protease (64.7%), lipase (57.6%), amylase (58.8%), β -galactosidase (30.3%) and urease (15.4%). Species of the genus *Polaribacter* exhibited filamentous morphology while members of *Gelidibacter*, *Psychroflexus* and *Subsaximicrobium* exhibited gliding motility compared to other members of the phylum. Further, *Flavobacterium frigidimaris*, *F. gillisiae* and *F. gondwanense* were found to be rich in chitinase production. The yellow pigment found in majority of the species of CFB group is a carotenoid pigment and pigment involvement in low temperature adaptation was well established (Jaganadham *et al.*, 2000). The occurrence of pigment could be an important characteristic for the dominance of CFB members in Antarctic habitats compared to other group.

Novel species belonging to Firmicutes or Low G+C Gram-positive group contributed 13.8% (29 species) to the total unique species from Antarctica and 12 genera were the most common. The most common habit was soil but cyanobacterial mats also contained members of this group. Though most of the species were psychrophilic, this group also contained few moderately thermophilic species,

Alicyclobacillus pohliae (42-60°C) (Imperio *et al.*, 2008), *Aneurinibacillus terranovensis* (20-55°C), (Allan *et al.*, 2005), *Anoxybacillus amylolyticus* (45-65°C) (Poli *et al.*, 2006), *Bacillus fumrioli* (25-55°C) (Logan *et al.*, 2000), *Brevibacillus levickii* (15-55°C) (Allan *et al.*, 2005), *Paenibacillus cineris* (8-50°C) and *Paenibacillus cookie* (15-50°C) (Logan *et al.*, 2004). Some members of this group were unique wherein *Anoxybacillus amylolyticus* produce significant quantities of EPS and amylase (Poli *et al.*, 2006), *Carnobacterium* species produces lactic acid (Franzmann *et al.*, 1991) and *Clostridium schirmacherense* secretes proteases (Alam *et al.*, 2006). Further, members of *Exiguobacterium* possess a variety of phospholipids in their cell wall wherein they contained PE, PG, PI, PS, DPG in addition to some unknown lipids (Frühling *et al.*, 2002; Chaturvedi *et al.*, 2008).

Close to 31 novel species representing 16 genera of *Actinobacteria* were reported from various habitats of Antarctica (Table 1). Out of the 16 genera, six novel genera were described of which three genera *Barrientosimonas* (Lee *et al.*, 2013), *Marisediminicola* (Li *et al.*, 2010) and *Rhodoglobus* (Sheridan *et al.*, 2003) were endemic to Antarctica. Some of the novel species are unique wherein *Arthrobacter cryotolerans* (Ganzert *et al.*, 2011) produces H₂S, *Arthrobacter psychrochitiniphilus* (Wang *et al.*, 2009) secretes cold active extracellular chitinase and *Sanguibacter antarcticus* (Hong *et al.*, 2008) makes melanin. Interestingly, extracellular restriction endonuclease activity was detected in *Modestobacter multiseptatus* (Mevs *et al.*, 2000). Majority of *Actinobacterial* species from Antarctica were pigmented indicating the role of the pigment in their survival at low temperatures. Some of the species possess unique lipids in their cell wall wherein PME (phosphatidyl methylethanolamine) and PMI (2,6,10,15,19-pentamethylcosane) are synthesized by *Nocardiopsis fildesensis* (Xu *et al.*, 2014) and *Streptomyces fildesensis* (Li *et al.*, 2011) respectively. Among all the species *Leifsonia rubra* (0 to 18) (Reddy *et al.*, 2003b) and *Rhodoglobus vestalii* (-2 to 21) (Sheridan *et al.*, 2003) are unique in having the true psychrophilic growth temperature.

The coldest and driest environmental conditions persisting in Antarctica also supported the inhabitation of desiccation and radiation resistant bacterial

communities such as *Deinococcus*. So far, four novel species of the genus *Deinococcus* were explored and they are radiation resistant. All the species were psychrophilic and are capable of growing from 9 to 18°C while *Deinococcus antarcticus* is a mesophile with a growth temperature range of 20 to 40°C. All the novel species are pink to red colored with L-ornithine as the cell wall diamino acid. All the species possessed unique and unidentified lipids belonging to phosphoglycolipids, glycolipids, phospholipids and lipids. These exceptional lipids can be explored for the further industrial applications and may also have a role in desiccation and radiation tolerance.

Some Unique Features of Bacteria from Extreme Environments

A majority of bacterial isolates from Antarctica shared many common features with respect to growth wherein the maximum growth temperature was below 30°C with very few exceptions such as *Alicyclobacillus pohliae*, *Aneurinibacillus terranovensis*, *Anoxybacillus amylolyticus*, *Bacillus thermantarcticus* and *Brevibacillus levickii* (Lama *et al.*, 1996; Allan *et al.*, 2005; Poli *et al.*, 2006; Imperio *et al.*, 2008). Earlier studies also revealed that the G+C content of 16S rRNA gene correlated with the growth temperature in prokaryotes. An elongation of helix 17 was observed in five out of eight true psychrophilic species of the genus *Rhodoglobus* (An *et al.*, 2010) and *Leifsonia rubra* (Reddy *et al.*, 2003b) whose growth temperature was below 20°C. Occurrence of 16S rDNA operons with psychrotolerant signatures, the transitions from C and G to T and A, higher uracil content and G:U mismatches from mesophilic to psychrotolerant, was reported in the strains of *Bacillus* (Prüss *et al.*, 1999; Lauro *et al.*, 2007). Further swollen sporangia were observed in psychrophilic strains of the genus *Bacillus* compared to their nearest mesophilic counterparts (Reddy *et al.*, 2008; Abd El-Rahman *et al.*, 2002; Larkin and Stokes, 1967; Priest *et al.*, 1988). Recently, Reddy *et al.*, (2015) identified occurrence of an additional aromatic amino acid, proline, in the CspA protein of *Kocuria polaris* and assisting in adaptation to low temperature.

Cold Adaptation of Antarctica Bacteria

Various survival mechanisms at extreme low temperatures have been reported in Antarctica

bacteria and reviewed earlier (Finegold, 1986; Ray et al., 1998; Shivaji et al., 2007; Shivaji and Prakash, 2010; Singh et al., 2014; Chattopadhyay et al., 2014). Differential phosphorylation of lipopolysaccharides (low phosphorylation at low temperature) occurs in *Pseudomonas syringae*, an Antarctic psychrophilic bacterium, to modulate the permeability of outer membrane (Ray et al., 1994a). In addition, a temperature dependent phosphorylation and dephosphorylation was also demonstrated in *Pseudomonas syringae* wherein a 65 kDa protein was found to be phosphorylated at low temperature while the 30 kDa protein gets phosphorylated at high temperatures (Ray et al., 1994b). Further, several cold active enzymes have been studied in Antarctic bacteria and demonstrated the higher catalytic activity at low temperatures (Ray et al., 1992). Several extracellular enzymes have been characterized from Antarctic bacteria which include a protease (Ray et al., 1992), ribonuclease (Reddy et al., 1994), alkaline phosphatase (Chattopadhyay et al., 1995; Rina et al., 2000), subtilisin (Davail et al., 1994), beta-lactamase (Feller et al., 1997), citrate synthase (Russell et al., 1998), RNA polymerase (Uma et al., 1999), DNA ligase (Georgette et al., 2000), β -galactosidase (Hoyoux et al., 2001) and lipase (de Pascale et al., 2008; Ali et al., 2013). All above enzyme were catalytically active at low temperature and were heat-labile. The flexibility in activity at low temperature for enzymes from Antarctic bacteria were due to their unique structural features wherein the enzymes exhibited fewer residues of proline or arginine, decrease in hydrophobic residues and disulfide bonds and increase in polar amino acids (Gerday et al., 2000; Metpally and Reddy 2009; D'Amico et al., 2002).

The survival of Antarctic bacteria was also due to the homeoviscous adaptation of membrane fluidity. At low temperatures the membrane fluidity was maintained by changing the fatty acid composition wherein the unsaturated fatty acids, short chained and branched fatty acids are synthesized in response to low temperature (Chintalapati et al., 2004). Further, the cold inducible desaturases that convert saturated fatty acids to unsaturated fatty acids were also responsible (Chintalapati et al., 2006; Chintalapati et al., 2007) for adaptation of Antarctic bacteria. In addition, the role of *cis-trans* isomerase was also implicated in maintaining the membrane fluidity in Antarctic bacteria (Kiran et al., 2005). Further, the

increased syntheses of polar carotenoids were observed in maintaining the homeoviscous status of the membranes (Jagannadham et al., 1991; Jagannadham et al., 1996; Chattopadhyay et al., 1997).

Besides several genes and promoters involved in cold adaptation of Antarctic bacteria were explored. An amino acyltransferase (Sundareswaran et al., 2010), trmE coding for GTPase (Singh et al., 2009), hutU operon (Janiyani and Ray, 2002), rpoS (Jovicic et al., 2008), RecBCD (Pavankumar et al., 2010) gene were known to be up regulated during the cold growth. In addition several cold inducible promoters responsible for regulation of genes at low temperature were identified (Duilio et al., 2004).

Our group has recently reported the genome sequence of a number of psychrophiles from different cold habitats like Antarctica (Sreenivas et al., 2014; Reddy et al., 2013; Kumar et al., 2013 a), Arctic (Shivaji et al., 2013a; 2013b; Kumar et al., 2013 b), Himalayan glaciers (Reddy et al., 2014) and Stratosphere (Shivaji et al., 2012). A comparative genome analysis of Csps in the psychrophilic *Sphingobacterium antarcticum*, *Oceanisphaera arctica* and *Exiguobacterium indicum* indicated that CspA was present in all of them, Csp C, D, E and G were present in at least one of the 3 isolates whereas Csp B and I were absent (unpublished). The implications of this observation with respect to cold adaptation warrant further studies. Comparative genome analysis of psychrophiles besides providing information on the role of specific genes in cold adaptation would promise insight into the adaptive response of bacteria to other stressors (viz high salt, high and low pH).

Biotechnological Potential of Antarctica Bacteria

Cold-active and/or thermolabile enzymes obtained from cold-tolerant organisms are of immense biotechnological importance. A thermolabile phosphatase, from an Antarctic bacterium has been used for restriction enzyme digestion, dephosphorylation, enzyme inactivation, and ligation or end-labelling. In addition cold-active proteases are suitable for food processing and in leather industries and are also useful in laundries for removal of stains. Cold-adapted bacteria are capable of degrading hydrocarbons (Margesin and Schinner, 2001; Powell

et al., 2006; Shukor *et al.*, 2009; Timmis *et al.*, 2010) but some hydrocarbons like asphalt are recalcitrant in nature and resist microbial degradation (Kimes *et al.*, 2014). Microorganisms having the capacity to degrade PCBs have also been isolated from both the Arctic and Antarctic regions (Master and Mohan 1998; De Dominico *et al.*, 2004). Several strains are also known to produce lipases useful in lipase-mediated biodiesel production (Moreno and Rojo, 2014).

References

- Abd El-Rahman H A, Fritze D, Spröer C and Claus D (2002) Two novel psychrotolerant species, *Bacillus psychrotolerans* sp. nov. and *Bacillus psychrodurans* sp. nov., which contain ornithine in their cell walls *Int J Syst Evol Microbiol* **52** 2127-2133
- Aislabie J M, Chhour K L, Saul D J, Miyauchi S, Ayton J, Paetzold R F and Balks M R (2006) Dominant bacteria in soils of Marble Point and Wright Valley, Victoria Land, Antarctica *Soil Biol Biochem* **38** 3041-3056
- Aislabie J, Jordan S, Ayton J, Klassen J L, Barker G M and Turner S (2009) Bacterial diversity associated with ornithogenic soil of the Ross Sea region, Antarctica *Can J Microbiol* **55** 21-36
- Aislabie J M, Lau A, Dsouza M, Shepherd C, Rhodes P and Turner S J (2013) Bacterial composition of soils of the Lake Wellman area, Darwin Mountains, Antarctica *Extremophiles* **17** 775-786
- Alam S I, Dixit A, Reddy G S, Dube S, Palit M, Shivaji S and Singh L (2006) *Clostridium schirmacherense* sp. nov., an obligately anaerobic, proteolytic, psychrophilic bacterium isolated from lake sediment of Schirmacher Oasis, Antarctica *Int J Syst Evol Microbiol* **56** 715-20
- Ali M S, Ganasen M, Rahman R N, Chor A L, Salleh A B and Basri M (2013) Cold-adapted RTX lipase from Antarctic *Pseudomonas* sp. strain AMS8: isolation, molecular modeling and heterologous expression *Protein J* **32** 317-25
- Allan R N, Lebbe L, Heyrman J, De Vos P, Buchanan C J and Logan N A (2005) *Brevibacillus levickii* sp. nov. and *Aneurinibacillus terranovensensis* sp. nov., two novel thermoacidophiles isolated from geothermal soils of northern Victoria Land, Antarctica *Int J Syst Evol Microbiol* **55** 1039-1050

Conclusion

Microorganisms are a bioresource and the workhorses of biotechnology. Further extremophiles like the ones that survive under freezing temperatures are all the more important due to their ability to carry out biological processes under extreme freezing temperatures. This review focuses on the bacterial biodiversity of different habitats of Antarctica and explores their capability to survive under freezing condition and highlights their biotechnological potential.

- An S Y, Xiao T and Yokota A (2010) Reclassification of *Leifsonia aurea* to the genus *Rhodoglobus* as *Rhodoglobus aureus* comb. nov., and emended description of *Rhodoglobus vestalii* Sheridan *et al.* 2003 *J Gen Appl Microbiol* **56** 53-5
- Antibus D E, Leff L G, Hall B L, Baeseman J L and Blackwood C B (2012) Cultivable bacteria from ancient algal mats from the McMurdo Dry Valleys, Antarctica *Extremophiles* **16** 105-114
- Archer S D, McDonald I R, Herbold C W and Cary S C (2014) Characterisation of bacterioplankton communities in the meltwater ponds of Bratina Island, Victoria Land, Antarctica *FEMS Microbiol Ecol* **89** 451-464
- Bajerski F and Wagner D (2013) Bacterial succession in Antarctic soils of two glacier forefields on Larsemann Hills, East Antarctica *FEMS Microbiol Ecol* **85** 128-142
- Bottos E M, Woo A C, Zawar-Reza P, Pointing S B and Cary S C (2014) Airborne bacterial populations above desert soils of the McMurdo Dry Valleys, Antarctica *Microb Ecol* **67** 120-128
- Bowman J P, McCammon S A, Brown M V, Nichols D S and McMeekin T A (1997) Diversity and association of psychrophilic bacteria in Antarctic sea ice *Appl Environ Microbiol* **63** 3068-3078
- Bowman J P, Gosink J J, McCammon S A, Lewis T E, Nichols D S, Nichols P D, Skerratt J H, Staley J T and McMeekin T A (1998) *Colwellia demingiae* sp. nov., *Colwellia hornerae* sp. nov., *Colwellia rossensis* sp. nov. and *Colwellia psychrotropica* sp. nov.: psychrophilic Antarctic species with the ability to synthesize docosahexanoic acid (22:6 omega 3) *Int J Syst Bacteriol* **48** 1171-1180
- Bowman J P, Rea S M, McCammon S A and McMeekin T A (2000) Diversity and community structure within anoxic sediment from marine salinity meromictic lakes and a coastal meromictic marine basin, Vestfold Hills, Eastern Antarctica *Environ Microbiol* **2** 227-237

- Boyd W L (1962) Comparison of soil bacteria and their metabolic activities in Arctic and Antarctic regions *Polar Rec* **11** 319
- Boyd W L and Boyd J W (1962) Presence of *Azotobacter* species in polar regions *J Bacteriol* **85** 1121-1123
- Bozal N, Montes M J and Mercadé E (2007) *Pseudomonas guinea* sp. nov., a novel psychrotolerant bacterium from an Antarctic environment *Int J Syst Evol Microbiol* **57** 2609-2612
- Brinkmeyer R, Knittel K, Jürgens J, Weyland H, Amann R and Helmke E (2003) Diversity and structure of bacterial communities in Arctic versus Antarctic pack ice *Appl Environ Microbiol* **69** 6610-6619
- Brown M V and Bowman J P (2001) A molecular phylogenetic survey of sea-ice microbial communities (SIMCO) *FEMS Microbiol Ecol* **35** 267-275
- Campbell I B and Claridge G G C (2000) In: Antarctic Ecosystems: Models for Wider Understanding, W. Davidson, C. Howard-Williams and P. Broady (eds.)
- Carpenter E J, Lin S and Capone D G (2000) Bacterial activity in South Pole snow *Appl Environ Microbiol* **66** 4514-4517
- Carr S A, Vogel S W, Dunbar R B, Brandes J, Spear J R, Levy R, Naish T R, Powell R D, Wakeham S G and Mandernack K W (2013) Bacterial abundance and composition in marine sediments beneath the Ross Ice Shelf, Antarctica *Geobiology* **11** 377-395
- Cavanagh J, Austin J J and Sanderson K (1996) Novel *Psychrobacter* species from Antarctic ornithogenic soils *Int J Syst Bacteriol* **46** 841-848
- Cavicchioli R and Thomas T (2000) Extremophiles. In: Encyclopedia of Microbiology. Second Edition (J. Lederberg, Ed.), Vol 2, p 317-337, Academic Press, San Diego
- Chaturvedi P, Prabahaar V, Manorama R, Pindi P K, Bhadra B, Begum Z and Shivaji S (2008) *Exiguobacterium soli* sp. nov., a psychrophilic bacterium from the McMurdo Dry Valleys, Antarctica *Int J Syst Evol Microbiol* **58** 2447-53
- Chattopadhyay M K, Uma Devi K, Gopishankar Y and Shivaji S (1995) Thermolabile alkaline phosphatase from *Sphingobacterium antarcticus*, a psychrotrophic bacterium from Antarctica *Polar Biol* **15** 215-219
- Chattopadhyay M K, Jagannadham M V, Vairamani M and Shivaji S (1997) Carotenoid pigments of an antarctic psychrotrophic bacterium *Micrococcus roseus*: temperature dependent biosynthesis, structure, and interaction with synthetic membranes *Biochem Biophys Res Commun* **239** 85-90
- Chattopadhyay M K, Reddy, G S N and Shivaji S (2014) Psychrophilic bacteria: Biodiversity, Molecular basis of cold adaptation and biotechnological implications *Curr Biotech* **3** 100-116
- Chessa J P, Petrescu I, Bentahir M, Van Beeumen J and Gerday C (2000) Purification, physico-chemical characterization and sequence of a heat labile alkaline metalloprotease isolated from a psychrophilic *Pseudomonas* species *Biochim Biophys Acta* **1479** 265-274
- Chintalapati S, Kiran M D and Shivaji S (2004) Role of membrane lipid fatty acids in cold adaptation *Cell Mol Biol (Noisy-le-grand)* **50** 631-42
- Chintalapati S, Prakash J S, Gupta P, Ohtani S, Suzuki I, Sakamoto T, Murata N and Shivaji S (2006) A novel Delta9 acyl-lipid desaturase, DesC2, from cyanobacteria acts on fatty acids esterified to the sn-2 position of glycerolipids *Biochem J* **398** 207-14
- Chintalapati S, Prakash J S, Singh A K, Ohtani S, Suzuki I, Murata N and Shivaji S (2007) Desaturase genes in a psychrotolerant *Nostoc* sp. are constitutively expressed at low temperature *Biochem Biophys Res Commun* **362** 81-7
- Claridge G G C and Campbell I B (1977) The salts in Antarctic soils, their distribution and relationship to soil processes *Soil Sci* **123** 377-384
- Cristóbal H A, López M A, Kothe E and Abate C M (2011) Diversity of protease-producing marine bacteria from sub-antarctic environments *J Basic Microbiol* **51** 590-600
- D'Amico S, Claverie P, Collins T, Georgette D, Gratia E, Hoyoux A, Meuwis M A, Feller G and Gerday C (2002) Molecular basis of cold adaptation. *Philos Trans R Soc Lond B Biol Sci* **357** 917-25
- Davaill S, Feller G, Narinx E and Gerday C (1994) Cold adaptation of proteins. Purification, characterization, and sequence of the heat-labile subtilisin from the antarctic psychrophile *Bacillus* TA41 *J Biol Chem* **269** 17448-53
- Delille D and Lagarde E (1974) Contribution a l'etude ecologique des Milieux subantarctiques *V Rev Inst Pasteur Lyon* **7** 149-165
- Deming J W and Eicken H (2007) Life in ice. In: Baross, J. and W. Sullivan (eds.) Planets and life – The emerging science of astrobiology, Cambridge University Press, Cambridge, p 292-312
- De Domenico M, Lo Giudice A, Michaud L, Saitta M and Bruni V (2004) Diesel oil and PCB- degrading psychrotrophic bacteria isolated from Antarctic seawaters (Terra Nova Bay, Ross Sea) *Polar Research* **23** 141-146
- Delille D and Gleizon F (2003) Distribution of enteric bacteria in

- Antarctic seawater surrounding the Port-aux-Français permanent station (Kerguelen Island) *Mar Pollut Bull* **46** 1179-1183
- Denner E B M, Mark B, Busse H J, Turkiewicz M and Lubitz W (2001) *Psychrobacter proteolyticus* sp. nov., a psychrotrophic, halotolerant bacterium isolated from the Antarctic Krill *Euphausia superba* Dana, Excreting a cold-adapted metalloprotease *Syst Appl Microbiol* **24** 44-53
- de Pascale D, Cusano A M, Autore F, Parrilli E, di Prisco G, Marino G and Tutino M L (2008) The cold-active Lip1 lipase from the Antarctic bacterium *Pseudoalteromonas haloplanktis* TAC125 is a member of a new bacterial lipolytic enzyme family *Extremophiles* **12** 311-23
- Doyle S M, Montross S N, Skidmore M L and Christner B C (2013) Characterizing microbial diversity and the potential for metabolic function at -15°C in the Basal ice of Taylor glacier, Antarctica *Biology (Basel)* **2** 1034-1053
- Duilio A, Madonna S, Tutino M L, Pirozzi M, Sanna G and Marino G (2004) Promoters from a cold-adapted bacterium: definition of a consensus motif and molecular characterization of UP regulative elements *Extremophiles* **8** 125-32
- Ekelof E (1908a) Bakteriologische studien während der Schwedischen Sudpolar expedition 1901-1903. In: Wissenschaftliche Ergebnisse der Schwedischen sudpolar Expedition 1901-1903. O. Nordenskjöld (ed.) Lithogr. Inst.Generalstabs, Stockholm.210
- Ekelof E (1908b) Studien über den Bakteriengehalt der Luft und des Erdbodens der antarktischen Gegenden, ausgeführt während der schwedischen sudpolar expedition 1901-1903. *ZHyg Infekt* **56** 344-370
- Feller G, Zekhnini Z, Lamotte-Brasseur J and Gerday C (1997) Enzymes from cold-adapted microorganisms. The class C beta-lactamase from the Antarctic psychrophile *Psychrobacter immobilis* A5 *Eur J Biochem* **244** 186-91
- Finegold L (1986) Molecular aspects of adaptation to extreme cold environments *Adv Space Res* **6** 257-64
- Frühling A, Schumann P, Hippe H, Sträubler B and Stackebrandt E (2002) *Exiguobacterium undae* sp. nov. and *Exiguobacterium antarcticum* sp. nov *Int J Syst Evol Microbiol* **52** 1171-6
- Franzmann P D, Deprez P P, McGuire A J, McMeekin T A and Burton H R (1990) The Heterotrophic, Bacterial Microbiota of Burton Lake, Antarctica *Polar Biol* **10** 261-264
- Franzmann P D, Höpfl P, Weiss N and Tindall B J (1991) Psychrotrophic, lactic acid-producing bacteria from anoxic waters in Ace Lake, Antarctica; *Carnobacterium funditum* sp. nov. and *Carnobacterium alterfunditum* sp. nov *Arch Microbiol* **156** 255-62
- Franzmann P D and Dobson S J (1992) Cell wall-less, free-living spirochetes in Antarctica *FEMS Microbiol Lett* **76** 289-292
- Friedman E I (1980) Endolithic microbial life in hot and cold deserts *Orig Life* **10** 223-235
- Ganzert L, Bajerski F, Mangelsdorf K, Lipski A and Wagner D (2011) *Arthrobacter livingstonensis* sp. nov. and *Arthrobacter cryotolerans* sp. nov., salt-tolerant and psychrotolerant species from Antarctic soil *Int J Syst Evol Microbiol* **61** 979-84
- Gazert H (1912) Untersuchungen über Meeresbakterien und deren Einfluss auf den Stoffwechsel im Meer. Deutsche Südpolar expedition. 1901-1903 Berlin, **7** 268-296
- Georlette D, Jónsson Z O, Van Petegem F, Chessa J, Van Beeumen J, Hübscher U and Gerday C (2000) A DNA ligase from the psychrophile *Pseudoalteromonas haloplanktis* gives insights into the adaptation of proteins to low temperatures *Eur J Biochem* **267** 3502-12
- Gerday C, Aittaleb M, Bentahir M, Chessa J P, Claverie P, Collins T, D'Amico S, Dumont J, Garsoux G, Georlette D, Hoyoux A, Lonhienne T, Meuwis M A and Feller G (2000) Cold-adapted enzymes: from fundamentals to biotechnology *Trends Biotechnol* **18** 103-7
- Gosink J J, Woese C R and Staley J T (1998) *Polaribacter* gen. nov., with three new species, *P. irgensii* sp. nov., *P. franzmannii* sp. nov., and *P. filamentus* sp. nov., gas vacuolate polar marine bacteria of the Cytophaga-Flavobacterium-Bacteroides group and reclassification of *Flectobacillus glomeratus* as *Polaribacter glomeratus* comb. nov *Int J Syst Bacteriol* **48** 223-235
- Guibert L M, Loviso C L, Marcos M S, Commendatore M G, Dionisi H M and Lozada M (2012) Alkane biodegradation genes from chronically polluted subantarctic coastal sediments and their shifts in response to oil exposure *Microb Ecol* **64** 605-616
- Helmke E and Weyland H (2004) Psychrophilic versus psychrotolerant bacteria-occurrence and significance in polar and temperate marine habitats *Cell Mol Biol* **50** 553-561
- Herbert R A and Bell C R (1977) Growth characteristics of an obligately psychrophilic *Vibrio* sp *Arch Microbiol* **113** 215-20
- Hirsch P, Mevs U, Kroppenstedt R M, Schumann P and Stackebrandt E (2004) Cryptoendolithic actinomycetes from Antarctic sandstone rock samples: *Micromonospora endolithica* sp. nov. and two isolates related to

- Micromonospora coerulea* Jensen 1932 *Syst Appl Microbiol* **27** 166-174
- Hong S G, Lee Y K, Yim J H, Chun J and Lee H K (2008) *Sanguibacter antarcticus* sp. nov., isolated from Antarctic sea sand *Int J Syst Evol Microbiol* **58** 50-2
- Hoyoux A, Jennes I, Dubois P, Genicot S, Dubail F, François J M, Baise E, Feller G and Gerday C (2001) Cold-adapted beta-galactosidase from the Antarctic psychrophile *Pseudoalteromonas haloplanktis* *Appl Environ Microbiol* **67** 1529-35
- Huang Y, Zhang J and Zhu L (2013) Evaluation of the application potential of bentonites in phenanthrene bioremediation by characterizing the biofilm community *Bioresour Technol* **134** 17-23
- Imperio T, Viti C and Marri L (2008) *Alicyclobacillus pohliae* sp. nov., a thermophilic, endospore-forming bacterium isolated from geothermal soil of the north-west slope of Mount Melbourne (Antarctica) *Int J Syst Evol Microbiol* **58** 221-225
- Irgens R L, Gosink J J and Staley J T (1996) *Polaromonas vacuolata* gen. nov., sp. nov., a psychrophilic, marine, gas vacuolate bacterium from Antarctica *Int J Syst Bacteriol* **46** 822-6
- Jagannadham M V, Rao V J and Shivaji S (1991) The major carotenoid pigment of a psychrotrophic *Micrococcus roseus* strain: purification, structure, and interaction with synthetic membranes *J Bacteriol* **173** 7911-7
- Jagannadham M V, Chattopadhyay M K and Shivaji S (1996) The major carotenoid pigment of a psychrotrophic *Micrococcus roseus* strain: fluorescence properties of the pigment and its binding to membranes *Biochem Biophys Res Commun* **220** 724-8
- Jagannadham M V, Chattopadhyay M K, Subbalakshmi C, Vairamani M, Narayanan K, Rao C M and Shivaji S (2000) Carotenoids of an Antarctic psychrotolerant bacterium, *Sphingobacterium antarcticus*, and a mesophilic bacterium, *Sphingobacterium multivorum*. *Arch Microbiol* **173** 418-24
- Janiyani K L and Ray M K (2002) Cloning, sequencing, and expression of the cold-inducible hutU gene from the antarctic psychrotrophic bacterium *Pseudomonas syringae* *Appl Environ Microbiol* **68** 1-10
- Jovcic B, Bertani I, Venturi V, Topisirovic L and Kojic M (2008) 5' Untranslated region of the *Pseudomonas putida* WCS358 stationary phase sigma factor rpoSmRNA is involved in RpoS translational regulation *J Microbiol* **46** 56-61
- Junge K, Imhoff F, Staley T and Deming J W (2002) Phylogenetic diversity of numerically important Arctic sea-ice bacteria cultured at subzero temperature *Microb Ecol* **43** 315-328
- Junge K, Eicken H and Deming J W (2004) Bacterial activity at -2 to -20°C in Arctic wintertime sea ice *Appl Environ Microbiol* **70** 550-557
- Karl D M, Bird D F, Björkman K, Houlihan T, Shackelford R and Tupas L (1999) Microorganisms in the accreted ice of Lake Vostok, Antarctica *Science* **286** 2144-2147
- Karr E A, Sattley W M, Jung D O, Madigan M T and Achenbach L A (2003) Remarkable diversity of phototrophic purple bacteria in a permanently frozen Antarctic lake *Appl Environ Microbiol* **69** 4910-4914
- Karr E A, Sattley W M, Rice M R, Jung D O, Madigan M T and Achenbach L A (2005) Diversity and distribution of sulfate-reducing bacteria in permanently frozen Lake Fryxell, McMurdo Dry Valleys, Antarctica *Appl Environ Microbiol* **71** 6353-6359
- Kelly M D, Lukaschewsky S and Anderson C G (1978) Bacterial flora of Antarctic krill and some of their enzymatic properties *J Food Sci* **43** 1196-1197
- Kim J G, Park S J, Quan Z X, Jung M Y, Cha I T, Kim S J, Kim K H, Yang E J, Kim Y N, Lee S H and Rhee S K (2014) Unveiling abundance and distribution of planktonic Bacteria and Archaea in a polynya in Amundsen Sea, Antarctica *Environ Microbiol* **16** 566-578
- Kimes N E, Callaghan A V, Suflita J M and Morris P J (2014) Microbial transformation of the Deepwater Horizon oil spill-past, present, and future perspectives *Front Microbiol* **5** 603
- Kiran M D, Annapoorni S, Suzuki I, Murata N and Shivaji S (2005) Cis-trans isomerase gene in psychrophilic *Pseudomonas syringae* is constitutively expressed during growth and under conditions of temperature and solvent stress *Extremophiles* **9** 117-25
- Kong W, Li W, Romancova I, Prášil O and Morgan-Kiss R M (2014) An integrated study of photochemical function and expression of a key photochemical gene (psbA) in photosynthetic communities of Lake Bonney (McMurdo Dry Valleys, Antarctica) *FEMS Microbiol Ecol* **89** 293-302
- Kuhn E, Bellicanta G S and Pellizari V H (2009) New *alk* genes detected in Antarctic marine sediments *Environ Microbiol* **11** 669-673
- Kuhn E, Ichimura A S, Peng V, Fritsen C H, Trubl G, Doran P T and Murray A E (2014) Brine assemblages of ultra small microbial cells within the ice cover of Lake Vida, Antarctica *Appl Environ Microbiol* **80** 3687-3698

- Kumar P A, Sreenivas A, Aditya Singh and Shivaji S (2013a) Draft genome sequence of *Winogradskyella psychrotolerans* RS-3T, isolated from the marine transect of Kongsfjorden, Ny-Ålesund, Svalbard, Arctic *Genome Announc* **1** e00630-13
- Kumar P A, Aditya Singh, Sreenivas A, Begum Z, Reddy G S N and Shivaji S (2013b) Draft genome sequence of *Leifsoniarubra* CMS 76R T, isolated from a cyanobacterial mat sample from a pond in Wright Valley, McMurdo, Antarctica *Genome Announc* **1** e00633-13
- Labrenz M, Collins M D, Lawson P A, Tindall B J, Schumann P and Hirsch P (1999) *Roseovarius tolerans* gen. nov., sp. nov., a budding bacterium with variable bacteriochlorophyll a production from hypersaline Ekho Lake *Int J Syst Bacteriol* **49** 137-47
- Labrenz M, Tindall B J, Lawson P A, Collins M D, Schumann P and Hirsch P (2000) *Staleyia guttiformis* gen. nov., sp. nov. and *Sulfitobacter brevis* sp. nov., alpha-3-Proteobacteria from hypersaline, heliothermal and meromictic Antarctic Ekho Lake *Int J Syst Evol Microbiol* **50** 303-313
- Labrenz M, Lawson P A, Tindall B J, Collins M D and Hirsch P (2003) *Saccharospirillum impatiens* gen. nov., sp. nov., a novel gamma-Proteobacterium isolated from hypersaline Ekho Lake (East Antarctica) *Int J Syst Evol Microbiol* **53** 653-60
- Labrenz M, Lawson P A, Tindall B J, Collins M D and Hirsch P (2005) *Roseisalinus antarcticus* gen. nov., sp. nov., a novel aerobic bacteriochlorophyll a-producing alpha-proteobacterium isolated from hypersaline Ekho Lake, Antarctica *Int J Syst Evol Microbiol* **55** 41-7
- Labrenz M, Lawson P A, Tindall B J and Hirsch P (2009) *Roseibaca ekhonensis* gen. nov., sp. nov., an alkalitolerant and aerobic bacteriochlorophyll a-producing alphaproteobacterium from hypersaline Ekho Lake *Int J Syst Evol Microbiol* **59** 1935-40
- Lama L, Nicolaus B, Calandrelli V, Esposito E and Gambacorta A (1996) Xylanase produced by *Bacillus thermoantarcticus*, a new thermophilic bacillus *Enzyme Eng* **XIII** 284-286
- Lanoil B, Skidmore M, Priscu J C, Han S, Foo W, Vogel S W, Tulaczyk S and Engelhardt H (2009) Bacteria beneath the West Antarctic ice sheet *Environ Microbiol* **11** 609-615
- Larkin J M and Stokes J L (1967) Taxonomy of psychrophilic strains of *Bacillus* *J Bacteriol* **94** 889-895
- Laucks M L, Sengupta A, Junge K, Davis E J and Swan-son B D (2005) Comparison of psychro-active Arctic marine bacteria and common mesophilic bacteria using surface-enhanced Raman spectroscopy *Appl Spectr* **10** 1222-1228
- Lauro F M, Chastain R A, Blankenship L E, Yayanos A A and Bartlett D H (2007) The unique 16S rRNA genes of piezophiles reflect both phylogeny and adaptation *Appl Environ Microbiol* **73** 838-845
- Lee K, Lee H K, Choi T H, Kim K M and Cho J C (2007) *Granulosicoccaceae* fam. nov., to include *Granulosicoccus antarcticus* gen. nov., sp. nov., a non-phototrophic, obligately aerobic chemoheterotroph in the order Chromatiales, isolated from Antarctic seawater *J Microbiol Biotechnol* **17** 1483-1490
- Lee C K, Barbier B A, Bottos E M, McDonald I R and Cary S C (2012) The Inter-Valley Soil Comparative Survey: the ecology of Dry Valley edaphic microbial communities *ISME J* **6** 1046-1057
- Lee L H, Cheah Y K, Sidik S M, Xie Q Y, Tang Y L, Lin H P, Mutalib N S and Hong K (2013) *Barrientosiimonas humi* gen. nov., sp. nov., an actinobacterium of the family *Dermacoccaceae* *Int J Syst Evol Microbiol* **63** 241-8
- Li H R, Yu Y, Luo W and Zeng Y X (2010) *Marisediminicola antarctica* gen. nov., sp. nov., an actinobacterium isolated from the Antarctic *Int J Syst Evol Microbiol* **60** 2535-9
- Li S, Xiao X, Yin X and Wang F (2006) Bacterial community along a historic lake sediment core of Ardley island west Antarctica *Extremophile* **10** 461-467
- Li J, Tian X P, Zhu T J, Yang L L and Li W J (2011) *Streptomyces fildesensis* sp. nov., a novel streptomycete isolated from Antarctic soil. *Antonie Van Leeuwenhoek* **100** 537-43
- Liu C, Zhang X Y, Su H N, Zhou M Y, Chen B, Li H, Chen X L, Zhao D L, Zhou B C, Shi M, Zhang Y Z (2014) *Puniceibacterium antarcticum* gen. nov., sp. nov., isolated from seawater *Int J Syst Evol Microbiol* **64** 1566-72
- Logan N A, Lebbe L, Hoste B, Goris J, Forsyth G, Heyndrickx M, Murray B L, Syme N, Wynn-Williams D D and De Vos P (2000) Aerobic endospore-forming bacteria from geothermal environments in northern Victoria Land, Antarctica, and Candlemas Island, South Sandwich archipelago, with the proposal of *Bacillus fumarioli* sp. nov *Int J Syst Evol Microbiol* **50** 1741-53
- Logan N A, De Clerck E, Lebbe L, Verhelst A, Goris J, Forsyth G, Rodríguez-Díaz M, Heyndrickx M and De Vos P (2004) *Paenibacillus cineris* sp. nov. and *Paenibacillus cookii* sp. nov., from Antarctic volcanic soils and a gelatin-processing plant *Int J Syst Evol Microbiol* **54** 1071-6
- Lo Giudice A, Caruso C, Mangano S, Bruni V, De Domenico M and Michaud L (2012) Marine bacterioplankton diversity and community composition in an antarctic coastal environment *Microb Ecol* **63** 210-223
- Maas E W, Simpson A M, Martin A, Thompson S, Koh E Y,

- Davy S K, Ryan K G and O'Toole R F (2012) Phylogenetic analyses of bacteria in sea ice at Cape Hallett, Antarctica *N Z J Mar Freshw Res* **46** 3-12
- Madigan M T, Jung D O, Woese C R and Achenbach L A (2000) *Rhodoferrax antarcticus* sp. nov., a moderately psychrophilic purple nonsulfur bacterium isolated from an Antarctic microbial mat *Arch Microbiol* **173** 269-77
- Magalhães C M, Machado A, Frank-Fahle B, Lee C K and Cary S C (2014) The ecological dichotomy of ammonia-oxidizing archaea and bacteria in the hyper-arid soils of the Antarctic Dry Valleys *Front Microbiol* **5** 515
- Marcos M S, Lozada M and Dionisi H M (2009) Aromatic hydrocarbon degradation genes from chronically polluted Subantarctic marine sediments *Lett Appl Microbiol* **49** 602-608
- Margesin R and Schinner F (2001) Biodegradation and bioremediation of hydrocarbons in extreme environments *Appl Microbiol Biotechnol* **56** 650-663
- Margini R A and Castrelos O D (1963) *Exámenes bacteriológicos de aire, rieve y suelo de carbo primaruera y Estacion científica Ellsworth Inst Antarcti Argent Publ* **76** 1-15
- Margini R A and Castrelos O D (1965) Las bacterias del Antartico y su relacion con la epoca del ano contrib *Inst Antart Argent* **141** 1-19
- Marshall B J and Ohye D F (1966) *Bacillus macquariensis* sp. nov., a psychrotrophic bacterium from sub-antarctic soil *J Gen Microbiol* **44** 41-6
- Master E R and Mohn W W (1998) Psychrotolerant bacteria Isolated from Arctic Soil that degrade polychlorinated biphenyls at low temperatures *Appl Environ Microbiol* **64** 4823-4829
- McLean A L (1918a) Bacteria of ice and snow in Antarctica *Nature* **102** 35-39
- McLean A L (1918b) Bacteriological and other researches Australian Antarctic Expedition 1911-1914 *Scient Rep* **7** 1-128
- Metpally R P and Reddy B V (2009) Comparative proteome analysis of psychrophilic versus mesophilic bacterial species: Insights into the molecular basis of cold adaptation of proteins *BMC Genomics* **10** 11
- Mevs U, Stackebrandt E, Schumann P, Gallikowski C A and Hirsch P (2000) *Modestobacter multiseptatus* gen. nov., sp. nov., a budding actinomycete from soils of the Asgard Range (Transantarctic Mountains) *Int J Syst Evol Microbiol* **50** 337-46
- Meyer G H, Morrow M B, Wyss O, Berg T E and Littlepage J L (1962) Antarctica: The microbiology of an unfrozen saline pond *Science* **138** 1103-4
- Michaud L, Caruso C, Mangano S, Interdonato F, Bruni V and Lo Giudice A (2012) Predominance of *Flavobacterium*, *Pseudomonas*, and *Polaromonas* within the prokaryotic community of freshwater shallow lakes in the northern Victoria Land, East Antarctica *FEMS Microbiol Ecol* **82** 391-404
- Miwa T (1975) Clostridia in soil of the Antarctica *Jpn J Med Sci Biol* **28** 201-213
- Moreno R and Rojo F (2014) Features of pseudomonads growing at low temperatures: another facet of their versatility *Environ Microbiol Rep* **6** 417-426
- Morita R Y (1975) Psychrophilic Bacteria *Bacteriol Rev* **39** 144-167
- Muangchinda C, Chavanich S, Viyakarn V, Watanabe K, Imura S, Vangnai A S and Pinyakong O (2014) Abundance and diversity of functional genes involved in the degradation of aromatic hydrocarbons in Antarctic soils and sediments around Syowa Station *Environ Sci Pollut Res* **22** 4725-4735
- Niederberger T D, McDonald I R, Hacker A L, Soo R M, Barrett J E, Wall D H and Cary S C (2008) Microbial community composition in soils of Northern Victoria Land, Antarctica *Environ Microbiol* **10** 1713-1724
- Pavankumar T L, Sinha A K and Ray M K (2010) All three subunits of RecBCD enzyme are essential for DNA repair and low-temperature growth in the Antarctic *Pseudomonas syringae* Lz4W *PLoS One* **5** e9412
- Peeters K, Hodgson D A, Convey P and Willems A (2011) Culturable diversity of heterotrophic bacteria in Forlidas Pond (Pensacola Mountains) and Lundström Lake (Shackleton Range), Antarctica *Microb Ecol* **62** 399-413
- Pfiser R M and Burkholder P R (1965) Numerical taxonomy of some bacteria isolated from Antarctic and tropical sea waters *J Bacteriol* **90** 863-872
- Pirie J H H (1904) First Antarctic voyage of the Scotia *J Bacteriol Scottish Geog Mag* **20** 129-132
- Poli A, Esposito E, Lama L, Orlando P, Nicolaus G, de Appolonia F, Gambacorta A and Nicolaus B (2006) *Anoxybacillus amylolyticus* sp. nov., a thermophilic amylase producing bacterium isolated from Mount Rittmann (Antarctica) *Syst Appl Microbiol* **29** 300-307
- Powell S M, Ferguson S H, Bowman J P and Snape I (2006) Using real-time PCR to assess changes in the hydrocarbon-degrading microbial community in Antarctic soil during bioremediation *Microb Ecol* **52** 523-532
- Prabakaran S R, Manorama R, Delille D and Shivaji S (2007)

- Predominance of *Roseobacter*, *Sulfitobacter*, *Glaciecola* and *Psychrobacter* in seawater collected off Ushuaia, Argentina, Sub-Antarctica *FEMS Microbiol Ecol* **59** 342-355
- Priest F G, Goodfellow M and Todd C (1988) A numerical classification of the genus *Bacillus* *J Gen Microbiol* **134** 1847-1882
- Priscu J C, Adams E E, Lyons W B, Voytek M A, Mogk D W, Brown R L, McKay C P, Takacs C D, Welch K A, Wolf C F, Kirshtein J D and Avci R (1999) Geomicrobiology of subglacial ice above Lake Vostok, Antarctica *Science* **286** 2141-2144
- Prüss B M, Francis K P, von Stetten F and Scherer S (1999) Correlation of 16S ribosomal DNA signature sequences with temperature-dependent growth rates of mesophilic and psychrotolerant strains of the *Bacillus cereus* Group *J Bacteriol* **181** 2624-2630
- Purcell A M, Mikucki J A, Achberger A M, Alekhina I A, Barbante C, Christner B C, Ghosh D, Michaud A B, Mitchell A C, Priscu J C, Scherer R, Skidmore M L and Vick-Majors T J, The Wissard Science Team (2014) Microbial sulfur transformations in sediments from Subglacial Lake Whillans *Front Microbiol* **5** 594
- Ramsay A J and Stannard R E (1986) Numbers and viability of bacteria in ornithogenic soils of Antarctica *Polar Biol* **5** 195-198
- Ray M K, Devi K U, Kumar G S and Shivaji S (1992) Extracellular protease from the antarctic yeast *Candida humicola* *Appl Environ Microbiol* **58** 1918-23
- Ray M K, Kumar G S and Shivaji S (1994a) Phosphorylation of lipopolysaccharides in the Antarctic psychrotroph *Pseudomonas syringae*: a possible role in temperature adaptation *J Bacteriol* **176** 4243-9
- Ray M K, Kumar G S and Shivaji S (1994b) Phosphorylation of lipopolysaccharides in the Antarctic psychrotroph *Pseudomonas syringae*: a possible role in temperature adaptation *J Bacteriol* **176** 4243-9
- Ray M K, Kumar G S, Janiyani K, Kannan K, Jagtap P, Basu M K and Shivaji S (1998) Adaptation to low temperature and regulation of gene expression in Antarctic psychrotrophic bacteria *J Biosci* **23** 423-435
- Reddy G S N, Rajagopalan G and Shivaji S (1994) Thermolabile ribonuclease from Antarctic psychrotrophic bacteria: detection of the enzyme in various bacteria and purification from *Pseudomonas fluorescens* *FEMS Microbiol Lett* **122** 211-216
- Reddy G S N, Agarwal R K, Matsumoto G I and Shivaji S (2000) *Arthrobacter flavus* sp. nov., a psychrotrophic bacterium isolated from a pond in Mc Murdo Dry Valley, Antarctica *Int J Syst Evol Microbiol* **50** 1553-1561
- Reddy G S N, Prakash J S, Matsumoto G I, Stackebrandt E and Shivaji S (2002) *Arthrobacter roseus* sp. nov., a psychrophilic bacterium isolated from an antarctic cyanobacterial mat sample. *Int J Syst Evol Microbiol* **52** 1017-21
- Reddy G S N, Matsumoto G I and Shivaji S (2003a) *Sporosarcina macmurdoensis* sp. nov. from a cyanobacterial mat samples from a pond in the McMurdo dry valley, Antarctica *Int J Syst Evol Microbiol* **53** 1363-1367
- Reddy G S N, Prakash J S S, Srinivas R, Matsumoto G I and Shivaji S (2003b) *Leifsonia rubra* sp. nov. and *Leifsonia aurea* sp. nov. psychrophiles from a Pond in Antarctica *Int J Syst Evol Microbiol* **53** 977-984
- Reddy G S N, Matsumoto G I, Shuman P, Stackebrandt E and Shivaji S (2004) Psychrophilic *Pseudomonas* from Antarctica: *Pseudomonas antarctica* sp. nov., *Pseudomonas meridiana* sp. nov. and *Pseudomonas proteolytica* sp. nov *Int J Syst Evol Microbiol* **54** 713-719
- Reddy G S N, Uttam A and Shivaji S (2008) *Bacillus cecembensis* sp. nov., a bacterium isolated from the Pindari glacier of the Himalayan mountain ranges, India *Int J Syst Evol Microbiol* **58** 2330-2335
- Reddy G S N, Ara S, Singh A, Kumar Pinnaka A and Shivaji S (2013) Draft genome sequence of *Psychrobacter aquaticus* CMS 56T, isolated from a cyanobacterial mat sample collected from water bodies in the McMurdo Dry Valley region of Antarctica *Genome Announc* **1** e00918-13
- Reddy G S N, Sreenivas A and Shivaji S (2014) Draft genome sequence *Cryobacterium roopkundensis* strain RuGI7, isolated from a soil sample in the vicinity of Roopkund Lake, Himalayas, India *Genome Announc* **2** e01206-14
- Reddy G S N, Sreenivas A and Shivaji S (2015) Draft genome of *Kocuria polaris* CMS 76or^T isolated from cyanobacterial mats, McMurdo Dry Valley, Antarctica: an insight into CspA family of proteins from *Kocuria polaris* CMS 76or^T *Arch Microbiol* **197** 1019-1026
- Reddy G S N, Chattopadhyay M K and Shivaji S (2016) Biodiversity, Adaptation and Biotechnological importance of bacteria occurring in cold climates. In. Biotechnology of Extremophiles: Advances and Challenges. Ed. Pabulo H. Rampelotto (in press).
- Rina M, Pozidis C, Mavromatis K, Tzanodaskalaki M, Kokkinidis M and Bouriotis V (2000) Alkaline phosphatase from the Antarctic strain TAB5. Properties and psychrophilic adaptations *Eur J Biochem* **267** 1230-8
- Ruckert G (1985) *Myxobacteria* from Antarctic soils *Biol Fert Soil* **1** 215-216

- Russell R J, Gerike U, Danson M J, Hough D W and Taylor G L (1998) Structural adaptations of the cold-active citrate synthase from an Antarctic bacterium *Structure* **6** 351-61
- Sheridan P P, Loveland-Curtze J, Miteva V I and Brenchley J E (2003) *Rhodoglobus vestalii* gen. nov., sp. nov., a novel psychrophilic organism isolated from an Antarctic Dry Valley lake *Int J Syst Evol Microbiol* **53** 985-94
- Shivaji S, Rao N S, Saisree L, Sheth V, Reddy G S N and Bhargava P M (1988) Isolation and identification of *Micrococcus roseus* and *Planococcus* sp. from Schirmacher Oasis, Antarctica *J Biosci* **113** 409-414
- Shivaji S, Rao N S, Saisree L, Sheth V, Reddy G S N and Bhargava P M (1989a) Isolation and identification of *Pseudomonas* sp. from Schirmacher Oasis, Antarctica *Appl Environ Microbiol* **55** 767-770
- Shivaji S, Rao N S, Saisree L, Reddy G S N, Seshu Kumar G and Bhargava P M (1989b) Isolates of *Arthrobacter* from the soils of Schirmacher Oasis, Antarctica *Polar Biol* **10** 225-229
- Shivaji S, Ray M K, Kumar G S, Reddy G S N, Saisree L and Wynn-Williams D D (1991) Identification of *Janthinobacterium lividum* from the soils of the Island of Scotia Ridge from Antarctic Peninsula *Polar Biol* **11** 267-272
- Shivaji S, Reddy G S N, Prasad R A, Kutty R and Ravenschlag K (2004) Bacterial diversity of a soil sample from Schirmacher Oasis, Antarctica *Cell Mol Biol* **50** 525-536
- Shivaji S, Kiran M D and Chintalapati S (2007) Perception and transduction of low temperature in bacteria. In: Physiology and biochemistry of extremophiles. Gerday C, Glansdor VN (Ed) ASM Press, Washington, 194-207
- Shivaji S and Reddy G S N (2009) Chapter 2. Bacterial biodiversity of Antarctica: conventional polyphasic and rRNA approaches. In: Polar Microbiology: The Ecology, Biodiversity and Bioremediation Potential of Microorganisms in Extremely Cold Environments; Bej A K, Aislabie J, Atlas R M, Eds. Taylor & Francis group
- Shivaji S and Prakash J S (2010) How do bacteria sense and respond to low temperature? *Arch Microbiol* **192** 85-95
- Shivaji S, Kumari K, Kishore K H, Pindi P K, Rao P S, Radha Srinivas T N, Asthana R and Ravindra R (2011) Vertical distribution of bacteria in a lake sediment from Antarctica by culture-independent and culture-dependent approaches *Res Microbiol* **162** 191-203
- Shivaji S, Ara S, Singh S K, Bandi S, Singh A and Pinnaka A K (2012) Draft genome sequence of *Bacillus Isronensis* strain B3W22, isolated from the upper atmosphere *J Bacteriol* **194** 6624-6625
- Shivaji S, Ara S, Singh A and Pinnaka A K (2013a) Draft genome sequence of *Cyclobacterium qasimii* M12-11B T, isolated from an Arctic marine sediment *Genome Announc* **1** e00642-13
- Shivaji S, Ara S, Prasad S, Manasa B P, Begum Z, Singh A and Pinnaka A K (2013b) Draft genome sequence of *Arcticibacter svalbardensis* MN12-7T, a member of the family Sphingobacteriaceae isolated from an Arctic soil sample *Genome Announc* **1** e00484-13
- Shukor M Y, Hassan N A, Jusoh A Z, Perumal N, Shamaan N A, MacCormack W P and Syed M A (2009) Isolation and characterization of a *Pseudomonas* diesel-degrading strain from Antarctica *J Environ Biol* **30** 1-6
- Singh A K, Pindi P K, Dube S, Sundareswaran V R and Shivaji S (2009) In the psychrophilic *Pseudomonas syringae*, trmE is important for low temperature growth *Appl Environ Microbiol* **75** 4419-4426
- Singh P, Singh SM and Dhakephalkar P (2014) Diversity, cold active enzymes and adaptation strategies of bacteria inhabiting glacier cryoconite holes of High Arctic *Extremophiles* **18** 229-242
- Sjöling S and Cowan DA (2003) High 16S rDNA bacterial diversity in glacial meltwater lake sediment, Bratina Island, Antarctica *Extremophiles* **7** 275-282
- Smith R C, Prezelin B B, Baker K S, Bidigare R R, Boucher N P, Coley T, Karentz D, MacIntyre S, Matlick H A, Menzies D, Ondrusek M, Wan Z and Waters K J (1992) Ozone depletion: ultraviolet radiation and phytoplankton biology in Antarctic waters *Science* **255** 952-959
- Søgaard D H, Kristensen M, Rysgaard S, Glud R N, Hansen P J and Hilligsøe K M (2010) Autotrophic and heterotrophic activity in Arctic first-year sea ice: Seasonal study from Malene Bight, SW Greenland *Mar Ecol Prog Ser* **419** 31-45
- Söller R, Hirsch P, Blohm D and Labrenz M (2000) Differentiation of newly described antarctic bacterial isolates related to *Roseobacter* species based on 16S-23S rDNA internal transcribed spacer sequences *Int J Syst Evol Microbiol* **50** 909-915
- Spring S, Merkhoffer B, Weiss N, Kroppenstedt R M, Hippe H and Stackebrandt E (2003) Characterization of novel psychrophilic clostridia from an Antarctic microbial mat: description of *Clostridium frigroris* sp. nov., *Clostridium lacusfryxellense* sp. nov., *Clostridium bowmanii* sp. nov., and *Clostridium psychrophilum* sp. nov., and reclassification of *Clostridium laramiense* as *Clostridium estertheticum* subsp. *laramiense* subsp. nov *Int J Syst Evol Microbiol* **53** 1019-1029

- Sreenivas A, Reddy G SN and Shivaji S (2014) Draft genome sequence of a psychrophilic bacterium *Sphingomonas antarcticum* 4BY, isolated from the soils of Schirmacher oasis, Antarctica *Genome Announc* **2** e00696-14
- Stibal M, Hasan F, Wadham J L, Sharp M J and Anesio A M (2012) Prokaryotic diversity in sediments beneath two polar glaciers with contrasting organic carbon substrates *Extremophiles* **16** 255-265
- Stokes J L and Reymond M L (1966) Quantitative ecology of psychrophilic microorganisms *Appl Microbiol* **14** 74-78
- Sundareswaran V R, Singh A K, Dube S and Shivaji S (2010) Aspartate aminotransferase is involved in cold adaptation in psychrophilic *Pseudomonas syringae* *Arch Microbiol* **192** 663-672
- Takii S, Kondal T, Hiraishi A, Matsumoto G I, Kawano T and Torii T (1986) Vertical distribution in and isolation of bacteria from Lake Vanda: an Antarctic lake *Hydrobiologia* **135** 15-21
- Tanner A C and Herbert R A (1981) Nutrient regeneration in Antarctic marine sediments *Kiel Meeresforsch Sanderh* **5** 390-395
- Tanner A C (1985) The role of bacteria in the cycling of nutrients within the maritime Antarctic environment. Antarctic Nutrient Cycles and Food Webs (ed. W R Siegfried, P R Condy and Laws R M), Springer Verlag, Berlin, Heidelberg, p 123-127
- Tiao G, Lee C K, McDonald I R, Cowan D A and Cary S C (2012) Rapid microbial response to the presence of an ancient relic in the Antarctic Dry Valleys *Nat Commun* **3** 660
- Timmis K N, McGenity T J, Meer J R and deLorenzo V (eds.) (2010) Handbook of hydrocarbon and lipid microbiology. Berlin; Heidelberg: Springer Verlag. doi: 10.1007/978-3-540-77587-4
- Tsiklinsky M (1908) La flore microbieene dans les regions due pole Sud. In: Expedition Antarctique Francais 1903-1905. **3** 1-33
- Tsyganov V A (1970) Detection and morphological cultural characteristics of *Actinomycetes* from the antarctic *Mikrobiologia* **39** 821-826
- Uma S, Jadhav R S, Kumar G S, Shivaji S and Ray M K (1999) A RNA polymerase with transcriptional activity at 0 degrees C from the Antarctic bacterium *Pseudomonas syringae* *FEBS Lett* **453** 313-7
- Van Trappen S, Mergaert J, Van Eygen S, Dawyndt P, Cnockaert M C and Swings J (2002) Diversity of 746 heterotrophic bacteria isolated from microbial mats from ten Antarctic lakes *Syst Appl Microbiol* **25** 603-610
- Van Trappen S, Tan T L, Yang J, Mergaert J and Swings J (2004) *Glaciecola polaris* sp. nov., a novel budding and prosthecate bacterium from the Arctic Ocean, and emended description of the genus *Glaciecola* *Int J Syst Evol Microbiol* **54** 1765-1771
- Vincent C F (1988) Microbial ecosystems of Antarctica. Cambridge: Cambridge University Press 303
- Voytek M A and Ward B B (1995) Detection of ammonium-oxidizing bacteria of the beta-subclass of the class Proteobacteria in aquatic samples with the PCR *Appl Environ Microbiol* **61** 1444-1450
- Wang F, Gai Y, Chen M and Xiao X (2009) *Arthrobacter psychrochitiniphilus* sp. nov., a psychrotrophic bacterium isolated from Antarctica *Int J Syst Evol Microbiol* **59** 2759-62
- Watanabe T, Kojima H, Takano Y and Fukui M (2013) Diversity of sulfur-cycle prokaryotes in freshwater lake sediments investigated using *aprA* as the functional marker gene *Syst Appl Microbiol* **36** 436-443
- Wery N, Gerike U, Sharman A, Chaudhuri J B, Hough D W and Danson M J (2003) Use of a packed-column bioreactor for isolation of diverse protease-producing bacteria from antarctic soil *Appl Environ Microbiol* **69** 1457-1464
- Wilkins D, Yau S, Williams T J, Allen M A, Brown M V, DeMaere M Z, Lauro F M and Cavicchioli R (2013) Key microbial drivers in Antarctic aquatic environments *FEMS Microbiol Rev* **37** 303-335
- Xiao X, Yin X, Lin J, Sun L, You Z, Wang P and Wang F (2005) Chitinase genes in lake sediments of Ardley Island, Antarctica *Appl Environ Microbiol* **71** 7904-7909
- Xu S, Yan L, Zhang X, Wang C, Feng G and Li J (2014) *Nocardiopsis fildesensis* sp. nov., an actinomycete isolated from soil *Int J Syst Evol Microbiol* **64** 174-9
- Yakimov M M, Giuliano L, Gentile G, Crisafi E, Chernikova T N, Abraham W R, Lünsdorf H, Timmis K N and Golyshin P N (2003) *Oleispira antarctica* gen. nov., sp. nov., a novel hydrocarbonoclastic marine bacterium isolated from Antarctic coastal sea water *Int J Syst Evol Microbiol* **53** 779-85
- Yamada K, Fukuda W, Kondo Y, Miyoshi Y, Atomi H and Imanaka T (2011) *Constrictibacter antarcticus* gen. nov., sp. nov., a cryptoendolithic micro-organism from Antarctic white rock *Int J Syst Evol Microbiol* **61** 1973-80
- Yau S, Lauro F M, Williams T J, Demaere M Z, Brown M V, Rich J, Gibson J A and Cavicchioli R (2013) Metagenomic insights into strategies of carbon conservation and unusual sulfur biogeochemistry in a hypersaline Antarctic lake *Int J Syst Evol Microbiol* **7** 1944-1961

- Yergeau E, Newsham K K, Pearce D A and Kowalchuk G A (2007a) Patterns of bacterial diversity across a range of Antarctic terrestrial habitats *Environ Microbiol* **9** 2670-2682
- Yergeau E, Bokhorst S, Huiskes A H, Boschker H T, Aerts R and Kowalchuk G A (2007b) Size and structure of bacterial, fungal and nematode communities along an Antarctic environmental gradient *FEMS Microbiol Ecol* **59** 436-451
- Yi H and Chun J (2006) *Flavobacterium weaverense* sp. nov. and *Flavobacterium segetis* sp. nov., novel psychrophiles isolated from the Antarctic *Int J Syst Evol Microbiol* **56** 1239-1244
- Yu Y, Li H R, Zeng Y X and Chen B (2011) Bacterial diversity and bioprospecting for cold-active hydrolytic enzymes from culturable bacteria associated with sediment from Nella Fjord, Eastern Antarctica *Mar Drugs* **9** 184-195
- Zhao J, Yang N and Zeng R (2008) Phylogenetic analysis of type I polyketide synthase and nonribosomal peptide synthetase genes in Antarctic sediment *Extremophiles* **12** 97-105.