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Polar Actinomycetes and Their Secondary Metabolites

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Abstract
In the past decades, extreme environments have become a popular hot spot for scientists and researchers to find novel microorganisms and natural products with biological potential. Actinomycetes are Gram-positive bacteria. It is one of the most important microorganisms that produce various useful secondary metabolites. The novel species of actinomycetes from 2006–2018 were enormously discovered (2,085 species). Among those novel actinomycetes, 64 novel species were isolated from the Arctic, subarctic, and Antarctic regions (an approximate 3 % of novel actinomycetes since 2006). Over 60 % of polar actinomycetes were isolated from soil, followed by sea sediment, and rock. Ten species of actinomycetes were reported to have the ability to produce potential natural products. Most of compounds show antimicrobial activity.
Keywords: polar regions, Arctic, subarctic, Antarctic, actinomycetes, natural product

1. Polar Regions

The polar regions of the Earth include the regions surrounding geographical poles; the North and the South Poles. The polar regions are covered by ice and snow; floating pack ice (sea ice) in the North Pole and the Antarctic ice sheet in the South Pole.

1.1 Arctic

The Arctic is the region surrounding the North Pole, which includes the Arctic Ocean, adjacent seas, parts of Alaska (United States), Finland, Greenland (Kingdom of Denmark), Iceland, Northern Canada (Canada), Norway, Russia and Sweden. The Arctic region consists of an ocean with seasonally varying snow and ice cover, surrounded by land with treeless permafrost in the most part. Plants of the Arctic regions include mosses, lichens, dwarf shrubs and grasses which all grow relatively close to the ground, forming tundra. The climate in the Arctic region is extremely cold with average temperature range from around −34 °C to 0 °C in January, −10 °C to 10 °C in July, and winter temperature can drop below −50 °C over large parts of the Arctic. The Arctic is also being considered as a liquid-water-lacking, strong winds, low nutrient environment and high levels of UV radiation all the year round (Tian *et al*., 2017). Polar organisms have developed a vast array of biochemical and physiological adaptations to cope with the extreme conditions in the Arctic.

1.2 Subarctic

The subarctic is a region in the Northern Hemisphere immediately south of the true Arctic and covering much of Alaska, Canada, Iceland, the north of Scandinavia, Siberia, and the Shetland Islands. Generally, subarctic regions fall between 50 °N and 70 °N latitude, depending on local climates. The areas extend from Alaska to Newfoundland in North America and from northern Scandinavia to Siberia in Eurasia. Moreover, the northern island of Hokkaido (Japan) also has subarctic climate while the southern islands of Japan (known as the Nansei Shoto) locate in the sub-tropical zone. The subarctic climate is usually very cold in long winter, and cool to mild in short summer. The winter season extends over 8 months, which is always below freezing point, whereas the average temperature of summer season (extending 1–3 months) is at least 10 °C. The annual precipitation of this area is quite low because of extremely low temperature, amounting to no more than 380 mm to 500 mm over the year. Therefore, vegetation in regions with subarctic climates is generally of low diversity, mostly limited to conifers.

1.3 Antarctic

The Antarctic is the region surrounding the South Pole. It is covered by ice as high as 98 % of the continent without tundra, trees or forests. The average of ice cap of the South Pole is about 6,700 feet (2,000 m) in thickness. The South Pole was found in 1911 by Roald Amundsen. The Antarctic is surrounded by oceans. The temperature along the coast can reach to 10 °C in summer and drop to below −40 °C in winter. However, the temperature can rise to about −30 °C in summer but fall to below −80°C in winter over the highest parts of the interior. The lowest recorded temperature on the Earth's surface was −89.2 °C at Vostok station on July 21, 1983. Because of bad climate, most of people who live in Antarctic are only scientists and technicians engaged in research, no indigenous communities. Antarctic is a polar desert and is the driest continent on the Earth. The annual precipitation is approximately 200–500 mm. The Antarctic Peninsula receives about 900 mm of precipitation a year. Antarctic precipitation mainly falls as snow. Therefore, Antarctic plants are mainly mosses and lichens e.g. the endemic *Schistidium antarctici*, which is the dominant moss species in the area.

2. Polar Environment and Biodiversity

The polar regions are the coldest places on the Earth (−88 to 15 °C). The sun is barely seen during the winter. On the other hand, in the summer, this area receive 24 hours of pure sunshine. There are two main polar regions on the Earth, which are the Arctic and the Antarctic. The polar regions are dominated by cold conditions and the presence of glacier ice, snow, and water. There are some differential between the Arctic and the Antarctic area. The Arctic, which found at the North Pole, is a frozen ocean surrounded by continental landmasses and open oceans, whereas Antarctica is a frozen continent, found at the South Pole, and surrounded merely by oceans. The region encircling the North Pole is called the Arctic Circle at 66° 33’ North. The arctic region sits inside the Arctic Circle and the subarctic region lies just below it between 50°–70° North. The daily temperature of Arctic region is lower than 10 °C. The climate of both polar regions consists of long cold winters and short cool summers.

The Arctic is not as cold as the Antarctic. Plant life in the Arctic is characterized largely by what grows on the tundra while plant life in the Antarctic is much less plentiful because only 1 % of the continent is ice free. Both regions have plenty of animal encounters on offer but the wildlife in Antarctica and the Arctic is very different. For example, polar bear, walrus, Arctic fox and musk ox are in the Arctic only or Penguins are only found in the southern hemisphere. However, some animals is found in both the north and south polar e.g. seals and whales. There are many researches about the microbial diversity of polar environments, which indicated that both Arctic and Antarctic continents are fertile ground for new bioactive compounds, genes, proteins, microorganisms and other products. The new bioactive compounds were discovered from bacteria, fungi, and actinomycetes such as a novel diketopiperazine were isolated from Antarctic psychrophilic bacterium; *Pseudoalteromonas haloplanktis* TAC125, *Penicillium crustosum* PRB-2; Antarctic deep-sea derived fungus produces two highly oxygenated polyketides, a new sulphur-containing natural alkaloid named microbiaeratin from *Microbiospora aerate* IMBAS-11A; actinomycetes isolated from the Antarctic Livingston Island (Tian *et al*., 2017), and so on.

3. Polar Actinomycetes

The polar regions have caught the attentions of scientists and researchers as research fields for discovery of new natural products and new organisms, including actinomycetes. Actinomycetes, Gram-positive bacteria with filamentous and branching growth pattern, are the large group of microorganism amongst prokaryotic domain. They play an important role in environments as major decomposers in soil ecosystems (Sylvia *et al*., 2005). Moreover, they are also an important source of secondary metabolites with medical benefits, high commercial value. In 2006–2018, vast novel actinomycetes (2,085 species) were discovered from various habitats. Among those actinomycetes, 64 novel actinomycetes (3.069 %) were isolated from polar regions (Table 1).

3.1 Arctic Actinomycetes

The Arctic actinomycetes habitats have been described from various sources, for instance, sea ice (Brinkmeyer *et al*., 2003), seafloor basalt (Lysnes *et al*., 2004), permafrost soil (Hansen *et al*., 2007), meltwater, snow (Larose *et al*., 2010), snowpack (Larose *et al*., 2013), and so on.

The past studies revealed the vast diversity of actinobacterial communities across the Arctic region. According to Finster *et al*. (2009) study, a closely related non-filamentous actinomycete, *Demequina lutea* sp. nov., was isolated from a permafrost soil collected from the Arctic region. Another, the studies of Katayama *et al*. (2009, 2010), irregular rod-shaped bacteria, *Glaciibacter superstes* sp. nov. and *Tomitella biformata* gen. nov., sp. nov., were isolated from a permafrost ice wedge in Alaska. Next, the study of Bajerski *et al*. (2011), a psychrotolerant bacterium, *Cryobacterium arcticum* sp. nov., was isolated from a soil sample collected from Store Koldewey, north-east Greenland in the Arctic. The other, the study of Zhang *et al*. (2014), microorganisms were isolated from the Arctic sampling marine sediments. From phylogenetic analysis, a total of 10 isolates were found to belong to known genera of the *Actinobacteria* including *Actinotalea*, *Arthrobacter*, *Brachybacterium*, *Brevibacterium*, *Kocuria*, *Kytococcus*, *Microbacterium*, *Micrococcus*, *Mycobacterium*, and *Pseudonocardia*. However, novel species of the genus *Streptomyces* was rarely reported so far from the Arctic region. Only one strain was recently reported. The novel *Streptomyces* sp. lately reported by Zhang *et al*. (2016), *Streptomyces arcticus* sp. nov., was isolated from a frozen soil sample collected from a glacier front in the Arctic.

3.2 Subarctic Actinomycetes

The subarctic actinomycetes inhabit a diversity of environments. Many novel actinomycetes were isolated from various sources of subarctic terrestrial environments, for instance, hay meadow soil (Kim *et al*., 2010, 2012a, 2013; Zucchi *et al*., 2012, 2013; Santhanam *et al*., 2013), forest soil (Tamura *et al*., 2010; Ozdemir-Kocak *et al*., 2014, 2017), lake side soil (Ara *et al*., 2011b, 2012b), rock surface (Carlsohn *et al*., 2007b, 2008), etc. The actinomycetes were also isolated from other environments, such as sea sediments (Jiang *et al*., 2009; Hamada *et al*., 2013a, 2013b), rainwater (Hwang *et al*., 2015), or the living organisms like lichens (Yamamura *et al*., 2011; Hamada, *et al*., 2012), and marine sea squirts (Bjerga *et al*., 2014).

3.3 Antarctic Actinomycetes

The Antarctic actinomycetes have been isolated from diverse habitats, such as soils (Moncheva *et al*., 2002; Pan *et al*., 2013; Encheva-Malinova *et al*., 2014), marine sediments (Deng *et al*., 2015), sandstones (de la Torre *et al*., 2003; Hirsch *et al*., 2004), sea water (Gupta *et al*., 2004), penguin guano (Wang *et al*., 2009), and so on. Many studies reveal that Streptomycetes possess dominant actinomycete in soil habitat (Moncheva *et al*., 2002; Pan *et al*., 2013; Encheva-Malinova *et al*., 2014). The study of Encheva-Malinova *et al*. (2014) reported that Streptomycetes are not only an abundant group of soil microorganisms in the Antarctica but also have a good potential in producing biologically active substances against phytopathogenic bacteria. In addition, Pan *et al*. (2013) reported that the Antarctic environments are rich sources of novel species and rare genera of actinomycetes with the ability to produce bioactive compounds.

Table 1. The novel polar actinobacteria discovered between 2006–2018

Strain	Polar	Region	Isolation technique			Reference
			Pretreatment procedure	Media	Incubation temperature and time	
Cryobacterium arcticum	Arctic	North-east Greenland	–	Nutrient agar	16 °C	Bajerski *et al*., 2011
Demequina lutea	Arctic	Spitsbergen, northern Norway	–	R2A agar	15 °C	Finster *et al*., 2009
Glaciibacter superstes	Arctic	Alaska, USA	The ice wedge was surface sterilized by immersing in 70% ethanol and burning to remove ethanol or contaminated surface ice.	Luria broth, LBG, R2B, 100-fold-diluted LB and LBG, Hickey-Tresner revised medium with antibiotics, minimal medium, minimal medium plus glucose, MME-1, and MME-2	15 °C, 3 months in the dark	Katayama *et al*., 2009
Streptomyces arcticus	Arctic	Foreland of a glacier in the High Arctic, Arctic	–	Mineral agar 1 Gause medium	28 °C, 14–21 days	Zhang *et al*., 2016
Tomitella biformata	Arctic	Alaska, USA	The ice wedge was surface sterilized by immersing in 70% ethanol and burning to remove ethanol or contaminated surface ice.	Luria broth, LBG, R2B, 100-fold-diluted LB and LBG, Hickey-Tresner revised medium with antibiotics, minimal medium, minimal medium plus glucose, MME-1, and MME-2	15 °C, 3 months in the dark	Katayama *et al*., 2010
Actinomadura xylanilytica	Subarctic	Northum-berland, UK	Pre-heated soil suspension (55 °C, 20 min)	Starch-casein agar with cycloheximide and nystatin	28 °C, 21 days	Zucchi *et al*., 2013

Table 1. The novel polar actinobacteria discovered between 2006–2018 (*Continued*)

Strain	Polar	Region	Isolation technique			Reference
			Pretreatment procedure	Media	Incubation temperature and time	
Actinomycetospora rishiriensis	Subarctic	Rishiri Island, Hokkaido, Japan	–	Humic acid-vitamin agar with nalidixic acid and cycloheximide	30 °C, 2 weeks	Yamamura *et al.*, 2011
Actinophytocola burenkhanensis	Subarctic	Mongolia	Re-hydration centrifugation	Humic acid-vitamin agar with trimethoprim and nalidixic acid	28 °C, 3 weeks	Ara *et al.*, 2011a
Actinoplanes rishiriensis	Subarctic	Rishiri Island, Hokkaido, Japan	Air-dried at room temperature for 7 days, processed by re-hydration centrifugation	Humic acid-vitamin agar with nalidixic acid and cycloheximide	30 °C, 2 weeks	Yamamura *et al.*, 2012
Amycolatopsis saalfeldensis	Subarctic	Thuringia, Germany	–	Casein mineral agar with cycloheximide	28 °C, 4 weeks	Carlsohn *et al.*, 2007b
Angustibacter luteus	Subarctic	Rishiri Island, Hokkaido, Japan	–	Humic acid-vitamin agar with nalidixic acid and cycloheximide	–	Tamura *et al.*, 2010
Cryptosporangium mongoliense	Subarctic	Mongolia	Re-hydration centrifugation	Humic acid-vitamin agar with rimethoprim and nalidixic acid	28 °C, 3 weeks	Ara *et al.*, 2012a
Dactylosporangium luridum	Subarctic	Northumberland, UK	–	*Streptomyces* isolation medium with cycloheximide and oxytetracycline	–	Kim *et al.*, 2010
Dactylosporangium luteum	Subarctic	Northumberland, UK	–	*Streptomyces* isolation medium with cycloheximide and oxytetracycline	–	Kim *et al.*, 2010

Table 1. The novel polar actinobacteria discovered between 2006–2018 (*Continued*)

Strain	Polar	Region	Isolation technique			Reference
			Pretreatment procedure	Media	Incubation temperature and time	
Demequina flava	Subarctic	Rishiri Island, Hokkaido, Japan	–	NBRC medium 802 with NaCl, cycloheximide and nalidixic acid	30 °C, 1 week	Hamada *et al.*, 2013a
Demequina sediminicola	Subarctic	Rishiri Island, Hokkaido, Japan	–	NBRC medium 802 with NaCl, cycloheximide and nalidixic acid	30 °C, 1 week	Hamada *et al.*, 2013a
Fodinicola feengrottensis	Subarctic	Thuringia, Germany	–	Starch-casein agar with cycloheximide	28 °C, 4 weeks	Carlsohn *et al.*, 2008
Herbidospora mongoliensis	Subarctic	Khuvsgul province, Mongolia	–	Humic acid-vitamin agar with trimethoprim and nalidixic acid	28 °C, 3 weeks	Ara *et al.*, 2012b
Janibacter cremeus	Subarctic	Rishiri Island, Hokkaido, Japan	–	NBRC medium 802 with NaCl, cycloheximide and nalidixic acid	30 °C, 1 week	Hamada *et al.*, 2013b
Kribbella aluminosa	Subarctic	Thuringia, Germany	–	Water agar with Bacto 0.1 % peptone and 0.02 % yeast extract, mineral agar Gauze 1 or starch-casein agar. All of the media were supplemented with cycloheximide.	28 °C, 4 weeks	Carlsohn *et al.*, 2007a
Kribbella soli	Subarctic	Southwest Troparevsky Forest Park, Moscow, Russia	–	Tryptone-yeast extract-glucose agar with cycloheximide, nalidixic acid, and rifampicin	28 °C, 21 days	Ozdemir-Kocak *et al.*, 2017

Table 1. The novel polar actinobacteria discovered between 2006–2018 (*Continued*)

Strain	Polar	Region	Isolation technique			Reference
			Pretreatment procedure	Media	Incubation temperature and time	
Luteimicrobium album	Subarctic	Rishiri Island, Hokkaido, Japan	Air dried the lichen sample at room temperature for 7 days	Humic acid-vitamin agar with nalidixic acid and cycloheximide	30 °C, 2 weeks	Hamada, *et al.*, 2012
Luteimicrobium subarcticum	Subarctic	Rishiri Island, Hokkaido, Japan	–	Maltose-Bennett's medium	–	Hamada, *et al.*, 2010
Nocardia zapadnayensis	Subarctic	Zapadnaya Southwest Forest Park, Moscow, Russia	–	Glucose-yeast extract-malt extract medium with cycloheximide, nalidixic acid, and rifampicin	28 °C, 21 days	Ozdemir-Kocak *et al.*, 2016
Nonomuraea muscovyensis	Subarctic	Moscow, Russia	Air dried the sample at room temperature for 14 days in a 2 mm mesh sieve, and triturated using strength Ringer's solution (Merck) and shaken for 30 min on a tumble shaker. Suspensions were pre-warmed in a water bath (60 °C, 20 min)	Tryptone-yeast extract-glucose and vitamin agar, with cycloheximide, nalidixic acid, and rifampicin	28 °C, 21 days	Ozdemir-Kocak *et al.*, 2014
Promicromonospora flava	Subarctic	Germany	–	Baltic Sea water with nalidixic acid and nystatin	28 °C, 21 days	Jiang *et al.*, 2009

Table 1. The novel polar actinobacteria discovered between 2006–2018 (*Continued*)

Strain	Polar	Region	Isolation technique			Reference
			Pretreatment procedure	Media	Incubation temperature and time	
Pseudonocardia khuvsgulensis	Subarctic	Khuvsgul province, Mongolia	Soil samples were dried at room temperature for 5–7 days and then inoculated using the rehydration-centrifugation.	Humic acid-vitamin agar with trimethoprim and nalidixic acid	28 °C, 3–4 weeks	Ara *et al.*, 2011b
Pseudonocardia mongoliensis	Subarctic	Khuvsgul province, Mongolia	Dried at room temperature for 5–7 days and then inoculated using the rehydration-centrifugation.	Humic acid-vitamin agar with trimethoprim and nalidixic acid	28 °C, 3–4 weeks	Ara *et al.*, 2011b
Pseudonocardia tetrahydrofuranoxydans	Subarctic	Germany	Enrichment	Mineral salts media with tetrahydrofuran	28 °C	Kämpfer *et al.*, 2006
Psychromicrobium silvestre	Subarctic	Italian Alps	Shaken the sample in sodium pyrophosphate for 15 min at 150 rpm	R2A agar with cycloheximide	20 °C	Schumann *et al.*, 2017
Rhodococcus aerolatus	Subarctic	Subarctic Bering Sea	–	Marine agar 2216	20 °C, 1 week	Hwang *et al.*, 2015
Rothia aerolata	Subarctic	North-Rhine-Westphalia, Germany	Enriched in NaCl/ phosphate buffer by cooling the bioaerosal suspension at 4 °C, 24 h	CHROMagar MRSA	37 °C, 48 hours	Kämpfer *et al.*, 2016

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Table 1. The novel polar actinobacteria discovered between 2006–2018 (*Continued*)

Strain	Polar	Region	Isolation technique			Reference
			Pretreatment procedure	Media	Incubation temperature and time	
Streptacidiphilus durhamensis	Subarctic	County Durham, England	–	Starch casein agar and gellan gum with cycloheximide and nystatin	28 °C, 4 weeks	Golinska *et al.*, 2013a
Streptacidiphilus hamsterleyensis	Subarctic	County Durham, England	–	Starch casein agar using either agar or gellan gum as gelling agents.	–	Golinska *et al.*, 2013b
Streptacidiphilus toruniensis	Subarctic	Torun Basin, Poland	–	Starch casein agar with cycloheximide and nystatin	28 °C, 4 weeks	Golinska *et al.*, 2016
Streptomyces brevispora	Subarctic	Northumberland, UK	Pre-heated soil suspension (55 °C, 20 min)	Starch casein agar with cycloheximide and nystatin	28 °C, 21 days	Zucchi *et al.*, 2012
Streptomyces chlorus	Subarctic	Northumberland, UK	–	Starch casein agar with cycloheximide and nystatin	28 °C, 21 days	Kim *et al.*, 2013
Streptomyces cinnabarigriseus	Subarctic	Kamchatka Peninsula, Russia	–	–	–	Landwehr *et al.*, 2018
Streptomyces cocklensis	Subarctic	Northumberland, UK	Pre-heated soil suspension (55 °C, 20 min)	Starch casein agar with cycloheximide and nystatin	28 °C, 21 days	Kim *et al.*, 2012b
Streptomyces erringtonii	Subarctic	Northumberland, UK	–	Starch casein agar with cycloheximide, nalidixic acid, and oxytetracycline	28 °C, 14 days	Santhanam *et al.*, 2013
Streptomyces herbaceus	Subarctic	Northumberland, UK	–	Starch casein agar with cycloheximide and nystatin	28 °C, 21 days	Kim *et al.*, 2012a
Streptomyces incanus	Subarctic	Northumberland, UK	–	Starch casein agar with cycloheximide and nystatin	28 °C, 21 days	Kim *et al.*, 2012a
Streptomyces kaempferi	Subarctic	Northumberland, UK	–	Starch casein agar with cycloheximide, nalidixic acid, and oxytetracycline	28 °C, 14 days	Santhanam *et al.*, 2013
Streptomyces laculatispora	Subarctic	Northumberland, UK	Pre-heated soil suspension (55 °C, 20 min)	Starch casein agar with cycloheximide and nystatin	28 °C, 21 days	Zucchi *et al.*, 2012
Streptomyces lunaelactis	Subarctic	Comblain-au-Pont, Belgium	Samples were freeze-dried and suspended in 0.25X strength Ringer's solution with 0.001 % Tween 80.	International *Streptomyces* Project media and starch nitrate medium with nalidixic acid and nystatin	17 °C, 1 month	Maciejewska *et al.*, 2015
Streptomyces pratens	Subarctic	Northumberland, UK	–	Starch casein agar with cycloheximide and nystatin	28 °C, 21 days	Kim *et al.*, 2012a
Streptomyces staurosporininus	Subarctic	Northumberland, UK	Pre-heated soil suspension (55 °C, 20 min)	Starch casein agar with cycloheximide and nystatin	28 °C, 21 days	Kim *et al.*, 2012c
Streptomyces viridis	Subarctic	Northumberland, UK	–	Starch casein agar with cycloheximide and nystatin	28 °C, 21 days	Kim *et al.*, 2013

Table 1. The novel polar actinobacteria discovered between 2006–2018 (*Continued*)

Strain	Polar	Region	Isolation technique			Reference
			Pretreatment procedure	Media	Incubation temperature and time	
Williamsia faeni	Subarctic	Northumberland, UK	–	Gauze's medium 2 with cycloheximide, nalidixic acid, novobiocin, and nystatin	30 °C, 21 days	Jones *et al.*, 2010
Arthrobacter antarcticus	Antarctic	Southern Ocean off Antarctica	–	Nutrient agar	22 °C, 7 days	Pindi *et al.*, 2010
Arthrobacter livingstonensis	Antarctic	Livingston Island, Antarctica	Soil sample was mixed with 0.9% (w/v) NaCl and shaken at 4 °C, 20 min at 150 rpm.	Synthetic BRII agar	16 °C, 7–14 days	Ganzert *et al.*, 2011a
Arthrobacter psychrochitiniphilus	Antarctic	Adélie penguin guano, Antarctica	–	M9 agar with 1% (w/v) colloidal chitin	10 °C, 7–28 days	Wang *et al.*, 2009
Leifsonia psychrotolerans	Antarctic	Livingston Island, Antarctica	Mixed sample with 0.9% (w/v) NaCl and shaken for 20 min at 150 rpm.	Synthetic BRII agar	16 °C, 7–14 days	Ganzert *et al.*, 2011b
Marisediminicola antarctica	Antarctic	Chinese Antarctic Zhongshan Station, east Antarctica	Dried sample at 8 °C for 2 weeks, diluted with sterile seawater, vortexed and allowed to settle for 30 min	Gause Mineral agar 1 with cycloheximide, nystatin, and nalidixic acid	10 °C, 4 days	Li *et al.*, 2010
Nesterenkonia aurantiaca	Antarctic	Cape King, Antarctica	Mixed sample with growth medium A and enrichment growth medium B	Medium A agar	10 °C, 1 week	Finore *et al.*, 2016

Table 1. The novel polar actinobacteria discovered between 2006–2018 (*Continued*)

Strain	Polar	Region	Isolation technique			Reference
			Pretreatment procedure	Media	Incubation temperature and time	
Nocardioides antarcticus	Antarctic	King George Island, Antarctica	–	Marine broth and 2216 agar	4 °C, 1 month	Deng *et al.*, 2015
Nocardiopsis fildesensis	Antarctic	King George Island, Antarctica	–	Gause 1 agar	28 °C, 7 days	Xu *et al.*, 2014
Paeniglutamicibacter antarcticus	Antarctic	Southern Ocean off Antarctica	–	Nutrient agar	22 °C, 7 days	Pindi *et al.*, 2010 Busse, 2016
Paeniglutamicibacter cryotolerans	Antarctic	Livingston Island, Antarctica	Mixed with 0.9% (w/v) NaCl and shaken for 20 min at 150 rpm	Synthetic BRII agar	16 °C, 7–14 days	Ganzert *et al.*, 2011a Busse, 2016
Raineyella antarctica	Antarctic	Lake Zub, Antarctica	–	Synthetic medium with D-glucose (AM)	3 °C	Pikuta *et al.*, 2016
Sanguibacter antarcticus	Antarctic	King George Island, Antarctica	–	ZoBell agar supplemented with 0.4% colloidal chitin	20 °C	Hong *et al.*, 2008
Sanguibacter gelidistatuariae	Antarctic	Lake Podprudnoye, Antarctica	–	–	–	Pikuta *et al.*, 2017
Streptomyces fildesensis	Antarctic	King George Island, Antarctica	–	Inorganic salts starch agar	28 °C, 2 weeks	Li *et al.*, 2011
Streptomyces hypolithicus	Antarctic	Miers Valley, eastern Antarctica	–	Starch casein nitrate agar	22 °C, 21 days	Rose-Hill *et al.*, 2009

4. Natural Products Produced by the Polar Actinomycetes

In the past decades, a vast amount of new biological natural products with various activities, for instance, anti-bacteria, anti-tumor, anti-virus and so on, have been isolated from polar organisms including microorganisms, lichen, moss, bryozoans, cnidarians, echinoderms, mollusks, sponges and tunicates (Tian *et al*., 2017). In addition, natural products from the polar actinomycetes have been reported in several review articles (Table 2).

4.1 Natural Products Produced by the Arctic Actinomycetes

In 2005, Macherla *et al*. reviewed the studies on three new pyrrolosesquiterpenes, glaciapyrroles A, B and C, which obtained from a *Streptomyces* sp. NPS008187 isolated from a marine sediment collected in Alaska near the Arctic. In the study of Shin *et al*. (2010), an angiogenesis inhibitor, Cyclo-(L-Pro-L-Met), was isolated from the Arctic seaweed-associated actinomycete, Nocardiopsis sp. 03N67. A novel phenazine derivative, N-(2-hydroxyphenyl)-2-phenazinamine (NHP), was obtained from a marine actinomycete *Nocardia dassonvillei* BM-17 isolated from a sediment sample collected in the Arctic Ocean (Gao *et al*., 2012). The compound showed significant antifungal activity against *Candida albicans*, and high cancer cell cytotoxicity against HepG2, A549, HCT-116 and COC1 cells. Nitrosporeusines A and B, unprecedented thioester-bearing alkaloids, were isolated from the Arctic *Streptomyces nitrosporeus* (Yang *et al*., 2013). Compounds showed inhibitory activity against the influenza WSN virus (H1N1) in Madin-Darby canine kidney (MDCK) cells. Two new benzoxazine secondary metabolites, arcticoside and C-1027 chromophore-V, were isolated from the Arctic *Streptomyces* sp., having ability in inhibiting *Candida albicans* isocritrate lyase enzyme. Furthermore, C-1027 chromophore-V compound exhibited significant cytotoxicity against breast carcinoma and colorectal carcinoma (Moon *et al*., 2014).

The Arctic actinomycete *Tomitella biformata* AHU1821^T, which isolated from an ice wedge in the Fox permafrost tunnel, Alaska, USA, was found to produce a resuscitation promoting factor (Rpf). In 2013, Puspita *et al*. identified *rpf* gene homologs in *Tomitella biformata* AHU 1821^T and bioactivities of Rpf. The result found that the protein was functional and could promote the growth of dividing in low-inoculum cultures and resuscitate non-dividing cells in spite of differences in sequences from previously studied Rpf. This Rpf was required at higher concentrations to promote its growth and to resuscitate itself from a non-dividing state than other studies.

4.2 Natural Products Produced by the Subarctic Actinomycetes

The marine actinomycete *Streptomyces lunaelactis* MM109^T, isolated from a moonmilk speleothem in the cave 'Grotte des Collemboles' located in the subarctic area (Comblain-au-Pont, Belgium), has furnished a ferroverdin A, an intracellular green-pigmented metabolite (Maciejewska *et al*., 2015). The green pigmentation of the isolate was observed when the strain was cultivated on ISP3 media. Ferroverdin A consisting of three p-vinylphenyl-3-nitroso-4-hydroxybenzoate ligands complexed with a ferrous ion ($C_{45}H_{30}N_3O_{12}Fe$) formerly extracted and characterized from *Streptomyces* sp. strain WK-5344 (ferroverdins B and C). All ferroverdins showed a dose-dependent inhibitory activity against human cholesteryl ester transfer protein (CETP) (Tabata *et al*., 1999; Tomoda *et al*., 1999).

4.3 Natural Products Produced by the Antarctic Actinomycetes

In 2008, Hong *et al.* isolated the Antarctic bacterium *Sanguibacter antarcticus* KOPRI 21702, which produces a cold-active extracellular chitinase; Chi21702. An extracellular chitinase with cold-active characteristics was purified by Park *et al*. in 2009 and was optimized in 2011 by Han *et al.* found that chitin and glycerol were selected as main carbon sources, for the ratio of complex nitrogen sources to carbon sources was determined to be 0.5. The most influent mineral components on enzyme production are NaCl, $Fe(C_6H_5O_7)$, and $MgCl_2$. The optimal conditions are 25 °C, pH 6.5, and above 30 % of air saturation. The optimized conditions increased enzyme production about 7.5 fold (90 U/L). Surprisingly, Chi21702 showed high activity even at low temperature close to the melting point of water (0 °C). Hence, the enzyme is suitable to produce N-Acetylglucosamine at or below room temperature that could be applied for a process at low temperature in industry.

Table 2. Natural products synthesized by the polar actinomycetes

Strain	Polar	Region	Natural product	Bioactivity	Reference
Nocardiopsis dassonvillei BM-17	Arctic	the Arctic Ocean, Norway	*N*-(2-hydroxyphenyl)-2-phenazinamine	Antifungal and anticytotoxic	Gao *et al.*, 2012
Nocardiopsis sp. 03N67	Arctic	–	*Cyclo*-(L-Pro-L-Met)	Anti-angiogenesis	Shin *et al.*, 2010
Tomitella biformata	Arctic	Alaska, USA	Resuscitation promoting factor (Rpf)	Promotes growth and resuscitates non-dividing cells	Puspita *et al.*, 2013
Streptomyces nitrosporeus	Arctic	–	Nitrosporeusines A and B	Antiviral	Yang *et al.*, 2013
Streptomyces sp.	Arctic	The East Siberian continental margin	Arcticoside	Enzyme inhibitory	Moon *et al.*, 2014
Streptomyces sp.	Arctic	The East Siberian continental margin	C-1027 chromophore-V	Enzyme inhibitory and cytotoxic	Moon *et al.*, 2014
Streptomyces sp. NPS008187	Arctic	Alaska, USA	Glaciapyrroles A, B and C	Unknown	Macherla *et al.*, 2005
Amycolatopsis saalfeldensis	Subarctic	Thuringia, Germany	Not shown	Strong inhibition of *Candida albicans*	Nimaichand *et al.*, 2015
Kribbella aluminosa	Subarctic	Thuringia, Germany	Not shown	Strongly inhibitory to *Staphylococcus aureus*, *Mycobacterium smegmatis*, and *C. albicans*, and moderately antagonistic to *Escherichia coli*	Nimaichand *et al.*, 2015
Streptacidiphilus durhamensis	Subarctic	County Durham, England	Bioactive silver nanoparticles [bio(AgNPs)]	Against clinical bacteria	Buszewki *et al.*, 2018
Streptomyces cinnabarigriseus	Subarctic	Kamchatka Peninsula, Russia	Cinnabaramides	Inhibitors of the human 20S proteasome	Landwehr *et al.*, 2018

Table 2. Natural products synthesized by the polar actinomycetes (*Continued*)

Strain	Polar	Region	Natural product	Bioactivity	Reference
Streptomyces cocklensis	Subarctic	Northumberland, UK	Dioxamycin	Antibiotic	Kim *et al.*, 2012b
Streptomyces lunaelactis	Subarctic	Comblain-au-Pont, Belgium	Ferroverdin A; Intracellular green-pigmented	Dose-dependent inhibitory activity against human cholesteryl ester transfer protein (CETP)	Maciejewska *et al.*, 2015; Tabata *et al.*, 1999; Tomoda *et al.*, 1999
Streptomyces staurosporininus	Subarctic	Northumberland, UK	Staurosporine	Cytotoxic, protein kinase inhibitor, antibiotic, antitumor, strong antihypertensive activity, induces apoptosis in human papillomavirus positive oral carcinoma cells, anti-parasitic, anti-oomycete,	Kim *et al.*, 2012c
Sanguibacter antarcticus	Antarctic	King George Island, Antarctica	Extracellular cold-active chitinase	Chitin-degrading enzyme	Han *et al.*, 2011
Streptomyces fildesensis	Antarctic	King George Island, Antarctica	LL-2,6-diaminopimelate	Antibiotic	Li *et al.*, 2011

5. Conclusion

Many actinomycetes are yet to be discovered. As a consequence, the extreme environments including polar regions have got lots of attention among scientists and researchers with the aims to discover novel microorganisms and beneficial natural productions. The previous studies revealed the vast diversity of actinobacterial communities across the Arctic, subarctic and Antarctic regions. There are many genera of actinomycetes inhabit polar regions, for instance, *Amycolatopsis*, *Demequina*, *Nocardiopsis*, *Pseudonocardia*, *Streptomyces*, and so on.

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