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Psychrophilic and psychotolerant mycelial fungi

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ABSTRACT

A major portion of the earth's surface is cold and inhabited by a broad diversity of microbes capable of survival and growth at low temperatures. Among these, psycrophilic and psychrotolerant filamentous fungi have a pivotal position because of their role in the ecology of cold environments. In this review, an attempt has been made to summarize the developments in understanding the diversity of filamentous fungi, their adaptations and potential biotechnological applications.

Keywords: Mycelial fungi, psychrophilic fungi, psychrotolerent fungi, psychrotrophs, cryoprotectant, cold-active enzymes

INTRODUCTION

Temperature is one of the most significant factors that affect growth of living organisms in any environment. It influences microbial growth indirectly by affecting water availability and directly by influencing the composition of biomolecules of the living cells (Poindexter, 2009). The Earth is basically a cold planet as about 85 % of the biosphere is permanently exposed to low temperatures (below 5 °C) [Margesin *et al.*, 2007]. In such harsh conditions of cold environment, various structural and functional adaptations are required for successful survival and colonization (Bej and Mojib, 2010; Gostincar *et al.*, 2010). Although there are several reviews on thermophilic fungi (Satyanarayana *et al.*, 1992; Johri *et al.*, 1999; Maheshwari *et al.*, 2000; Ghazifard *et al.*, 2001), there are very few reports on psychrophilic fungi. The main focus of this review is on the terminology used to define the microbes in cold environments, the ecological niches occupied by psychrophilic and psychrotolerant mycelial fungi, their survival strategies or adaptations and their potential applications.

TERMINOLOGY USED FOR MICROBES IN COLD ENVIRONMENT

The first report on the ability of microorganisms to grow at 0 °C was by Forster (1887), who isolated some bacteria from cold natural sources. Thereafter, Schmidt-Nielson (1902) isolated some cold-loving bacteria and yeasts, and proposed the term 'psychrophile' for the microbes with the ability to grow at 0 °C. Later, Stokes (1963) described 'obligate psychrophiles' as microbes unable to grow at room temperatures between 20 - 25 °C. Deverall (1968) defined psychrophilic fungi as those having growth optima less than or near 10 °C, assuming 10 °C to be the growth minima for most fungi. The debate on defining cold inhabiting microbes according to their growth temperature continued. Eddy (1960) introduced the term 'psychrotroph' for microbes which are able to grow at temperatures 5 °C or lower. Since then biologists have described microbes thriving in cold niches by various terms like thermophobic, psychrobe, glaciale, rhigophile, cryophile and facultative psychrophile. The definitions proposed by Morita (1975) to describe microbes growing in the cold habitats, based on their cardinal growth temperatures, are widely accepted. He defined psychrophiles as organisms with temperature optima of ~15 °C or lower, while maximal and minimal growth temperatures are 20 °C and ≤ 0 °C, respectively. On the other hand, psychrotrophs/psychrotolerants are microbes with the ability to grow at low temperatures but having optimal and maximal growth temperature above 15 °C and 20 °C, respectively (growth temperature can be as high as 40 °C). Thus psychrophiles are cold-loving, while psychrotrophs are cold-tolerant microorganisms. Morita's definitions of psychrophily are applied to bacteria, but the same concept has been adopted for fungi (Watson *et al.*, 1978; Robinson, 2001). In higher organisms, another term commonly used is cryophiles (cold/ freeze loving organisms). The term cryosphere, first proposed by Dobrowolski (Barry *et al.*, 2011), refers collectively to the portions of Earth's surface having water in the frozen state like glaciers, snow cover, icebergs and permafrost. Very recently, Hoshino and Matsumoto (2012) proposed a term 'cryophilic fungi' to describe those which spend a part or whole life cycle in the cryosphere. Their proposal was based on the fact that fungi normally have different cells in their life cycle, and hence, their temperature dependence differs with respect to the stage of the life cycle (vegetative or reproductive) and is completely different from that of bacteria which have simple life cycles and propagate mainly by cell division. For example, the snow mould *Pythium iwayamai* is psychrotolerant based on thermal dependence of mycelial growth (18 - 20 °C), but the zoospore release and oospore germination require temperatures of < 15 °C, indicating the fungus to be a psychrophile (Hoshino and Matsumoto, 2012).

HABITATS OF PSYCHROPHILIC FUNGI

Psychrophiles have an important position in Earth's ecosystem as the average temperature of Earth is 15°C and a large portion of our ecosystem (> 80%) is permanently cold with temperatures < 5 °C. The cold microbial niches span from high mountains to the deep ocean, from the Antarctic to the Arctic. Approximately 71% of Earth is covered by oceans with > 90% at cold temperatures. Of the remaining land surface, 35% is covered by snow, 24% by permafrost and 10% by glaciers, while sea ice amounts to 13% of the Earth's surface (Margesin and Miteva, 2011). Other cold environments include cold soils (mainly subsoils), cold water lakes, cold deserts, and caves. In spite of the huge area, the research done on psychrophiles is very limited as compared to thermophiles. Some of the cold ecological niches along with their fungal diversity are discussed below.

1. **Atmosphere:** Viable fungi have been found in air samples collected from near the earth's surface up to the stratosphere. Their survival under such conditions is affected by their ability to resist starvation, freezing, desiccation and radiation. The cells may enter the atmosphere as aerosols, remaining airborne for varying periods of time before being deposited again as precipitation. In the tropospheric cloud water, diverse fungi and bacteria have been found in the range of 10^3-10^5 ml^{-1} (Margesin and Miteva, 2011). These microbes seem to play an important role in atmospheric processes like formation of clouds, ice and snow (Morris *et al*., 2008).

2. **Snow:** It is a major component of the cryosphere, covering seasonally or permanently up to 35 % of the earth's land surface (mainly in the Northern Hemisphere). Abundance of microbes in this ecosystem varies with respect to the height and latitude with total numbers in the range of 10^3-10^5 ml^{-1} of melted snow (Margesin and Miteva, 2011). In the regions covered with snow, psychrophilic fungi with temperature optima below 10 °C are predominant (Leeuwen *et al*., 2012).

3. **Glaciers:** They are considered the harshest environments due to subfreezing temperatures ranging between -56 and -10 °C, low nutrient and water availability and high pressure. Nevertheless, microbiological studies detected a variable diversity, including psychrophilic fungi; the source appears to be the deposited terrestrial dust and marine surface aerosols. Several fungal isolates have been detected in ancient ice samples of Antartica, Tibet and Greenland (Margesin and Miteva, 2011).

4. **Cold lakes:** These are represented by various polar (Arctic and Antarctic) and alpine mountain lakes exhibiting broad geographical and environmental diversity (Vincent *et al*., 2008). In the Arctic, there are more lakes (1432) as compared to in the Antarctic (174) [Ryanzhin *et al*., 2010]. The source of the ice microbial communities includes soil, atmosphere and others.

5. **Oceans:** The deep sea defined as the lowest layer of ocean, which is below the thermocline, is characterized by extreme cold environments (< 5 °C) along with low nutrition, darkness and high hydrostatic pressure. Fungi are rare in such habitats but those present are polyextremophiles as they have to adapt to various extreme conditions (Hoshino and Matsumoto, 2012). A study to understand the fungal diversity in various deep sea samples around the world (11 samples collected from 4,000 - 15,000 m depths) by 18S ribotyping revealed only 32 kinds of organisms with only four putative filamentous fungal types, the remaining being yeasts (Bass *et al*., 2007).

6. **Cold soils:** These include the polar soils and alpine soils. In the Arctic soils, apart from low temperatures, low moisture, low nutrients and repeat freeze-thaw cycles are other limiting factors. A significant effect of vegetation was seen on the fungal communities in the Alaskan soils, where Tussock soils containing high quantities of recalcitrants were dominated by *Ascomycetes*, while shrub soils with higher amount of bioavailable carbon were having more of *Zygomycetes* (Wallenstein *et al*., 2007). The Antarctic soils differ from Arctic as they are colder, drier and alkaline with low nutrients and with lower numbers and diversity of viable fungi (Vishniac, 1996).

In contrast, the alpine soils (high mountainous regions above forests) have seasonal fluctuations in temperatures causing regular freeze-thaw cycles, and have higher moisture, and thus, microbial communities show seasonal variation (Lipson, 2007). In the Himalayas and Rockies, *Chytridiomycota* was the dominant fungal phylum in the periglacial soils at high altitudes (Freeman *et al*., 2009). Conversely, the dry soils at high altitudes of 3000-5400 m in the Anapurna mountains of Nepal inhabit xerophilic and psychrophilic fungi like *Eurotium* and *Aspergillus* (Petrovic *et al*., 2000). A psychrophilic fungus *Mucor strictus* isolated from Alpine soil grows optimally at 10 °C (Schipper, 1967) (**Fig. 1**). In general, the diverse flora of Alpine and Arctic regions includes a variety of filamentous fungi in their rhizosoheric soils (Domsch *et al*., 1980). In one study, Sahay *et al*., (2013) isolated two psychrophilic fungal strains, identified as *Truncatella angustata* and *Psudogymnoascus* sp., exhibiting defective growth above 20 °C and capable of metabolizing starch, cellulose, casein; these can be potential source of biotechnologically important cold active enzymes.

7. **Permafrost:** It is defined as the land surface like soils and rock permanently exposed to very low temperatures, thus remaining frozen. It is one of the most extreme

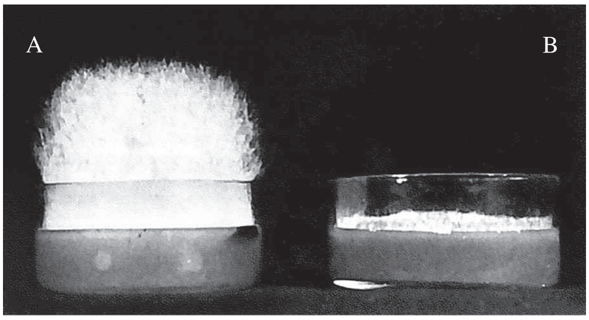

Fig. 1. *Mucor strictus*: (A) at 10 °C (B) at 20 °C (Adapted from Schipper *et al*., 1967).

environments covering > 20 % of the land surface on the earth. Several fungi have been isolated from permafrost cryopegs (Gilichinsky *et al*., 2005). The permafrost soils of the Arctic, Antarctic and mountains have also been reviewed (Margesin *et al.*, 2009); numerous filamentous fungi have been reported from permafrost soil (Margesin, 2008). They contain abundant biodiversity despite extreme low temperatures, low nutrition, darkness and constant exposure to gamma radiation; both culture-dependant and culture-independent methods have been employed to study their diversity. Filamentous fungi in permafrost range from 10 – 10^5 fungal colonies g^{-1} sample, with no apparent relationship between number and the depth or age of permafrost (Kochkina *et al*., 2001; Ozerskaya *et al*., 2009). A good diversity of *Ascomycetes* and *Basidiomycetes* was recorded in the Arctic permafrost, some common genera being *Penicillium*, *Aspergillus*, *Geomyces* and *Cladosporium* (Ozerskaya *et al*., 2009). Similarly in the Antarctic permafrost studies, there was low fungal density combined with high diversity. Various ascomycetous and basidiomycetous fungi were discovered dominated by *Penicillium* and *Cladosporium* sp., not detected by molecular methods (Kochkina *et al*., 2012). A common feature in sediments of permafrost is the presence of several types of sterile mycelium, which requires culture-independent techniques for identification.

8. Caves: The permanent temperature in many subterranean and glaciated caves is < 10 °C. Along with low temperatures, there is low nutrition, high moisture and darkness. Usually such caves are inhabited by psychrotrophs rather than psychrophiles, in fact they support oligotrophic and psychrotolerant fungi. Some reports on psychotrophic cave fungi include *Penicillium cavernicola* (Frisvad and Samson, 2004) and chicken sandwitch cave fungus *Microascus caviariformes* (Malloch and Hubart, 1987). The sudden appearance of a fatal fungal disease, White Nose Syndrome (WNS) caused by *Geomyces destructans*, in the cave dwelling bats of North America (Lorch *et al*., 2011) has led to an increased interest in the microflora of these cold habitats. Very recently, a world review was published on various fungi (molds, yeast and slime molds) reported from caves and cave-like habitats (Vanderwolf *et al*., 2013). The most commonly reported genera included *Geomyces*, *Aspergillus*, *Mucor*, *Penicillium*, *Trichoderma,* etc., a major proportion being of ascomycetous fungi; most of the cave fungi function as parasites or degraders.

Traditionally, extreme psychrophiles have been isolated from the polar region samples **(Table 1.)**, but of late the interest in deep sea, permafrost and other sources has increased that has led to several new discoveries. For example, filamentous fungi have been reported from Antarctic lichens (Moller and Dreyfuss, 1996). Also in the alpine and polar regions, abundance of fungal symbionts of lichens have been discovered (Smith, 1984). Some psychrophilic fungi have also been found associated with dung for e.g. *Thelobolus* (Hoog *et al*., 2005). Some authors have suggested that the actual diversity of Antarctic fungi may be far greater than estimated presently (Bridge and Spooner, 2012). In fact, Godinho *et al.* (2013) reported marine macroalgae to shelter fungi (many of them rare or non-indiginious) in Antartica, whereby they were able to provide an interesting model of algal-fungal interactions under the extreme marine polar conditions, thus enhancing our knowledge of the Antarctic fungal communities. Simultaneously these also have served as a potential source of bioactive compounds like antifungals.

A group of fungi often found in cold environments is ‘snow moulds’, which refers to fungi and fungi-like microbes commonly occurring as pathogens of plants in cold areas like Arctic and Antarctic, mainly in regions

Table 1: Some filamentous fungi reported from Polar Regions (adapted from Robinson, 2001).

Region	Isolation site	Isolates	Reference
Arctic	Soil and litter	*Phialophora hoffmanni, Cladosporium cladosporioides, Geomyces pannorum*	Flanagan and Scarborough, 1974
	Soil, Devon Island, Canada	*Phoma herbarum*	Widden and Parkinson, 1978
	Barren soils, Franz Joseph land	54 isolates	Bergero *et al*., 1999
Antarctic	Soil, Signy island	14 taxa	Latter and Heal, 1971
	Signy island	Soil fungi	Bailey and Wynn-Williams, 1982
	Plant and soil, Subantarctic Macquarie island, Antarctic Casey Station	31 isolates	Kerry, 1990
	Soil and moss, Victoria Island	35 isolates	Zucconi *et al*., 1996
	Fellfield soils, Signy Island	*Humicola marvinii*	Weinstein *et al*., 1997
	Moss samples in continental Antarctica	*Verticillium lecanii*	Fenice *et al*., 1998
	Associated with marine endemic macroalgae	148 isolates	Godinho *et al*., 2013

covered most of the time by snow (Hoshino *et al*., 2009). Such infections are caused mainly by *Ascomycetes* (*Thyronectria antartica* var. *hyperantartica*), *Basidiomycetes* (*Typhula ishikariensis*) and *Oomycetes* (*Pythium*) [Tojo and Newsham, 2012].

SURVIVAL STRATEGIES OF PSYCHROPHILIC MYCELIAL FUNGI

Various extremophilic microbes are increasingly becoming the focus of scientific research in the last decade or so, ensuing discoveries of stress tolerance mechanisms (Gostincar *et al*., 2010). Psychrophilic microorganisms also confront various challenges in their cold habitats. The survival and proliferation of psychrophilic fungi in cold environments indicate that they have developed survival strategies to overcome barriers present in such conditions. Some of the major endurance challenges include reduced membrane fluidity, lower enzyme activities, reduced transcription and translation rates, altered mode of nutrient and waste product transport, altered cell division, cold induced protein denaturation, altered protein folding patterns, and cytoplasmic ice crystal formation (D'Amico *et al*., 2006). In fact the minimum growth temperature limits of psychrophiles are fixed by the physical properties of the aqueous solvent systems both inside and outside the cell, rather than by the properties of cellular macromolecules (Robinson, 2001). The structural and functional adaptations for the survival of prokaryotes at low temperatures have been better understood (Russell *et al.*, 1990; Bej and Mojib, 2010; Shivaji and Prakash, 2010) than those of the fungi. Robinson (2001) and very recently Maggi *et al.* (2013) have attempted to summarize various possible morphological and physiological adaptations for low temperature survival in fungi as discussed below:

1. **Cryoprotectant sugars:** Trehalose, the most widely distributed disaccharide in fungi (Thevelein, 1984), is an important storage compound in the vegetative cells and spores of fungi (Lewis and Smith, 1967), where it is found along with glycogen and sugar alcohols. It is a stress protectant in the cytosol (Cooke and Whipps, 1993), membrane stabilizer during dehydration (Goodrich *et al*., 1988) and recently discovered as a cryoprotectant. Several fungi like *Humicola marvinii*, *Mortierella elongata* and *Hebeloma* spp. have been shown to accumulate excess of trehalose, when incubated at low temperatures (Tibbett *et al*., 1998a; Weinstein *et al*., 2000).

2. **Polyols:** There may be an increase in the concentrations of glycerol and mannitol to maintain the cells' turgor pressure in response to low temperature mediated decline in external water pressure (Cooke and Whipps, 1993). Polyols are considered to act as 'physiological buffering agents' in fungi to provide suitable environment for enzyme activity (Jennings, 1984). A study comparing 2 strains of *Humicola* sp. provided suitable evidence for a potential cryoprotectant role of polyols (Weinstein *et al*., 1997).

3. **Lipids/fatty acids:** Evidence suggests that the membrane composition determines the ability of fungi to grow at different temperatures (Cooke and Whipps, 1993). For example, in different *Mucor* spp., an increase in unsaturated fatty acids (Dexter and Cooke, 1984a; b) as well as diversity in membrane phospholipids (Hammonds and Smith, 1986; Chintalpati *et al*., 2004) has been observed with decreasing incubation temperatures. In fact the comparison of the phospholipid composition in the membrane lipids of the same fungal species isolated from both Antarctic and temperate regions again validated the effect of low temperature on increase in membrane unsaturated fatty acids (like oleic acid, linoleic acid, linolenic acid etc.) [Maggi *et al*., 2013], and this adaptation was evident in ~ 80 % of the Antarctic fungal species.

4. **Antifreeze proteins (AFP):** These proteins help fungi to grow at low temperatures by preventing the formation of ice crystals, thus allowing them to survive through freeze-thaw cycles and keeping the substrates available for assimilation (Snider *et al*., 2000). Evidence comes from the isolates of *Typhula* sp. and snow mould fungi, showing antifreeze activity in all fractions (Snider *et al*., 2000).

5. **Cold active enzymes:** Various species of decomposers and mycorrhizal fungi from cold Arctic and Antarctic environments have been reported to produce enzymes active at moderately low temperatures (Weinstein *et al*., 1997; Tibbett *et al*., 1998a; b). In cold-adapted enzymes, flexibility appears to play a crucial role in catalysis, which allows the accommodation of the substrate at low temperature, at the same time permitting the movement of water and release of the product (Marx *et al*., 2007).

Exopolysaccharides (Selbmann *et al*., 2002), antioxidants (Ratner and Fikhte, 1982), mycosporines (Kogej *et al*., 2006) and glycogens (Gocheva *et al*., 2006) are a few other means to protect psychrophilic fungi from freeze-thaw cycles. In contrast to their mesophilic counterparts, Arctic strains of *Penicillium* have been observed to contain trehalose and protective enzyme such as catalase and superoxide dismutase (SOD) at lower temperatures, which have a role in protecting the microorganisms from reactive oxygen species as solubility of gases increases at low temperature (Montiel, 2000). *Geomyces pannorum*, a widely spread Antarctic strain, has been found to withstand extreme cold conditions by means of a strong but non-enzymatic oxidative response, mainly through the production of phenolics (Maggi *et al*., 2013). Psychrophilic species of *Mortierella* produce sterols and fatty acids which may have a protective role in its survival at low temperatures (Weete and Gandhi, 1999). A simple physiological adaptation to low temperatures like change in the distribution of viable cytoplasm within hyphae, might permit the mycelium to survive in freezing conditions (Addy *et al*., 1994). Similarly the production of RNA chaperones to suppress undesirable secondary RNA structure formation (Kwak *et al*., 2011) is another physiological adaptation in cold tolerant fungi. Low temperature tolerance by fungi is thus not controlled by one single physiological means, but is rather an overall cellular phenomenon (Russell, 1990). In contrast, the upper growth temperature limit can be due to the lack of activity of a single enzyme (Robinson, 2001).

Ecological mechanisms for survival of fungi at low temperatures may include cold-avoidance, whereby the spores which have survived over winter or dispersed from somewhere else through airspora, germinate only during spring and summer, thereby avoiding the extreme winter (Robinson, 2001). The presence of sterile mycelia (shortened life cycles) and dark septate hyphae (as melanin protects from drying and low temperature) seem to be other mechanisms for cold adaptation in these fungi (Robinson, 2001). Melanin production also protects the fungal mycelia and spores from UV-B light (Zucconi *et al*., 2002).

BIOTECHNOLOGICAL APPLICATIONS OF PSYCHROPHILIC AND PSYCHROTOLERANT FUNGI

Cold-adapted microorganisms can be exploited in bioremediation of polluted cold soils and wastewaters and as source of cold active enzymes with numerous applications in the fields of medicine, industry, cosmetics, detergents and molecular biology (Margesin and Feller, 2010) as described below:

1. Bioremediation and low-energy wastewater treatment: Psychrophiles are responsible for degradation of organic matter at low temperature and finds potential applications in numerous biotechnological processes requiring low temperatures (Duncan *et al*., 2008). Psychrophilic and psychrotolerant fungi are important in the decomposition cycles in cold ecosystems and contribute significant biomass in microbial community of the soil (Xin and Zhou, 2007; Margesin *et al*., 2007). The decomposer basidiomycetous fungi in the Arctic and Antartic ecosystems have been reviewed in detail and found to play important roles in biogeochemical cycles (Ludley and Robinson, 2008).

Fungi and bacteria capable of degrading high amounts of organic matter at low temperatures in less time represent a potential source of inocula for quicker wastewater treatment (Margesin and Feller, 2010). The application of filamentous fungi in the treatment of high-strength wastewater as a substrate is an innovative option. Fungal growth can convert the organic substances in wastewater into readily harvestable fungal biomass, which can further be processed as animal feed (Guest and Smith, 2002).

2. As source of valuable biomolecules: Filamentous fungi are frequently cultured in food industries as a source of valuable products including proteins and a variety of chemicals using comparatively inexpensive substrates such as starch and molasses (Barbesgaard *et al*., 1992). Some proteins and peptide from fungi have special properties. Hydrophobins, a unique class of low molecular weight fungal proteins have gained special attention (Linder *et al*., 2005). Hydrophobins are surface active hydrophobic molecules and can be easily purified by surfactant based two phase system (Joensu *et al*., 2010) and this property can be exploited to produce hydrophobin tagged protein expression for easy purification of the recombinant protein. Mycosporine-derived molecules may also be of biotechnological interest because of their UV-absorbance properties (Volkmann *et al*., 2003). Lipids from psychrophilic and psychrotolerant fungi may have a desirable high relative amount of polyunsaturated fatty acids (Weete and Gandhi 1999). A new compound has been isolated from the marine fungus, *Penicillium oxalicum* 0321F$_1$, which was identified by spectroscopic analysis as 2-(4-hydroxybenzoyl) quinazolin-4(3H)-one, and has been found moderately inhibitory to tobacco mosaic virus (TMV) and the gastric cancer cell line (SGC-7901) of humans, thus holding immense potential in therapy (Shena *et al*., 2013).

3. Source of cold-active enzymes: Cold-adapted enzymes serve as useful tools in biotechnology, finding applicability in detergents (proteases, amylases, lipases and cellulases), as additives in food industry (proteases, galactosidase, xylanases, lipase, pectinase, etc.), as additive in textile industry (cellulases in stone washing) and as tools in molecular biology (ligases, kinases, etc.) [Marx *et al*., 2007]. Psychrophilic fungi have the ability to produce many extracellular enzymes which aid them in nutrient uptake (Feller and Gerday, 2003; Fenice *et al*., 1997). For example, insect exoskeleton can be broken down by chitinolytic enzymes from *Verticillium lacanii* working at low temperature in Antarctica (Fenice *et al*., 1998). However, insect pathogenic fungi have rarely been reported from Antarctic environment (Bridge and Worland, 2004). Some fungi in Antarctica produce keratinases which helps in breaking down animal skin (Mercantini *et al*., 1993), for example, *Geomyces pannorum* (Krishnan *et al*., 2011). All these enzymes may have low temperature optima and are of course of great interest for the biotechnological industry (Margesin and Schinner, 1994; Bradner *et al*., 1999; Cavicchioli *et al*., 2002). Interestingly, some of the enzymes from cold-adapted fungi have mesophilic properties (Cairns *et al*., 1995). *Myrosclerotinia borealis* produces several polygalacturonases and bioactive polypeptides in the sclerotia (Takasawa *et al*., 1997; Newstead and Huner., 2005). Cold active lipases have been reported from *Geotrichum candidum* and *Pencillium roqueforti* isolated from frozen food samples (Alford and Pierce, 1996). *Aspergillus nidulans* has been reported to produce cold-active lipolytic enzymes (Mayordomo *et al*., 2000). A soluble acid invertase was extracted from the psychrophile *Monographella nivalis* grown on sucrose in submerged cultivation. In crude preparation, this enzyme was stable at pH 2 - 6 for 1 h at temperatures up to 47 °C (Cairns *et al*., 1995). An Antarctic filamentous fungus

Verticillium sp. P9 produces two extracellular tannin acyl hydrolases (TAH I and TAH II) [Burnecka *et al.*, 2007]. The tannases are used extensively in food, feed, beverage, brewing, pharmaceutical and chemical industries for synthesis of pyrogallol, gallic acid, propyl gallate, coffee-flavoured and instant tea soft drinks, clarification of fruit juices and beer (Boadi and Neufeld, 2001; Mahendran *et al*,. 2006). This enzyme is also useful in animal feed manufacture (Nuero and Reyes, 2002). Cid *et al.* (2013) screened sponge associated fungi from the Antartica for the isolation of cold active xylanases and they isolated a *Cladosporium* sp. that produced xylanase with highest activity at low temperatures.

4. In Medicine: Two new epipolythiodioxopiperazines, named chetracins B and C (1 and 2), and five new diketopiperazines, named chetracin D (4) and oidioperazines A-D (5, 10, 12, and 13), were isolated from the fungus *Oidiodendron truncatum* GW3-13, along with six known compounds (3, 6, 7, 8, 9, and 11) [Li *et al.*, 2012]. A novel psychrotolerent Greenland isolate *Penicillium jamesonlandense,* which grows optimally at 17–18 °C, produces a spectrum of secondary metabolites of high chemical diversity that includes kojic acid, griseofulvin, pseurotin, penicillic acid, tryptoquivalins, chrysogine and cycloaspeptide. Another novel psychrotolerant isolate from Rocky Mountains, Wyoming also produces kojic acid, asperfuran and cycloaspeptide (Frisvad *et al.*, 2006). Feng *et al.*, (2013) isolated three glycosides from a cold adapted *Mucor* sp. Among these, 1-hydroxy-3-methoxy-8-methyl-2-O-β-D-glucopyranosylnaphthaline exhibited cytotoxic activity against five tumour cells, namely A-549, HL-60, MCF-7, SMMC-7721, and SW480.

5. Negative impact of psychrophilic fungi: The psychrophilic aquatic fungus *Leptomitus lacteus* known as paper mill fungus develops in winter as an abundant cotton-like mycelium in rivers receiving paper mill effluents. It causes serious pollution (Holzinger, 1987). The fungus of the genus *Typhula* known as snow mould is pathogenic to grass and winter cereals like wheat (Chang *et al.*, 2006). It remains in the vegetative state during winter and cannot grow at temperatures above 15 °C, and hence, remains dormant through the summer in a resting phase known as sclerotium. When the plants become covered with snow, the sclerotia germinate and the fungus grows. It is very common in areas with deep snow as the thick layer of snow efficiently insulates the infected plants from cold and the temperature at snow-plant interface remains around 0 °C during entire winter (Heimstra and Liston, 2011). A psychrophilic fungus was found to be involved in White Nose Syndrome (WNS) of Bats (*Myotis lucifugus*) which led to their massive deaths in hibernation sites around Albany, New York; this psychrophilic fungus was identified as *Geomyces destructans* as appeared identical to the pure cultures of *G. destructans* by direct microscopic examination (**Fig. 2**) and this was further established through sensitive molecular methods (Chaturvedi *et al.*, 2010). The psychrophilic fungus *Keratinomyces ceretanicus* is pathogenic for humans and animals (Punsola and Guarro, 1984).

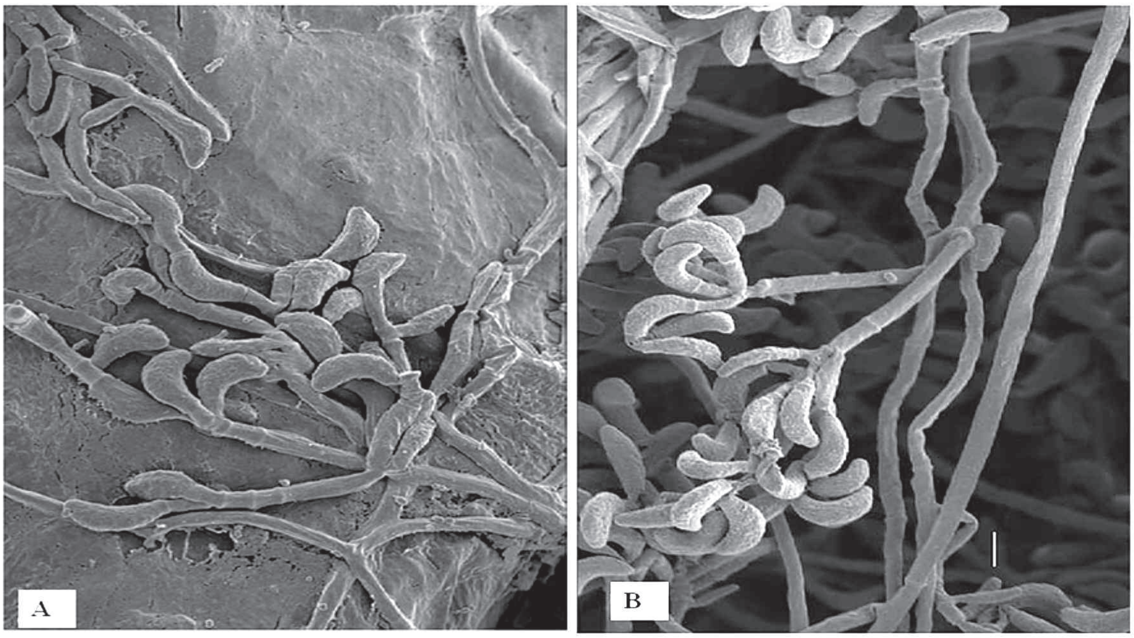

Fig. 2: *Geomyces destructans* present in bat tissues and the pure cultures were found similar (A) SEM micrograph prepared from bat tissue samples showing fungal hyphae and spores on the surface, (B) SEM micrograph prepared from *G. destructans* culture isolated from bat tissue samples collected from Williams Hotel Mine (adopted from Chaturvedi *et al.*, 2010).

Most of the biotechnological applications of psychrophiles are useful in conserving energy, and thus, helpful in saving the environment, thereby leading to the development of greener technologies.

CONCLUSIONS

The harsh cold environments all over the globe are inhabited by a great variety of psychrophilic as well as psychrotolerant fungi. These fungi are able to survive and grow in such extreme environments due to their specific physiological, biochemical as well as structural adaptations. The survival strategies have led to the evolution of novel biomolecules, which find applications in medicine and industry. Despite numerous investigations on the cold-loving moulds from varied habitats, this still remains a vastly unexplored area with immense biotechnological prospects.

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