

Chapter 3

Cold-Adapted Yeasts in Arctic Habitats

Polona Zalar and Nina Gunde-Cimerman

Abstract The Arctic area is a polar region at the northernmost part of the Earth, north of the Arctic Circle (66° 33'N). It is a region of an ice-covered Arctic ocean, surrounded by treeless permafrost. The climate within the Circle is extremely cold, and much of the area is permanently covered with ice. Unlike in the temperate zones, where filamentous fungi prevail, extremophilic yeasts are particularly well adapted to these conditions and thus thrive in different polar environments. The range of Arctic environments inhabited by yeasts includes glacial ice with brine networks and inclusions, subglacial environments, soil, permafrost, Arctic sea and sea ice. Yeast isolates from cryoconite holes and cryptoendolithic environments are rare. The physiological activity of yeasts has been demonstrated at temperatures below -20°C . Studies of the abundance, distribution and taxonomy of Arctic yeasts are very much limited in comparison with the studies of the Antarctic yeasts. Interestingly, the dominant yeasts in the Arctic are also of basidiomycetous affinity and belong to the same genera that occur frequently in the Antarctic soils and polar offshore sea waters. These are different species of the genera *Aureobasidium*, *Candida*, *Debaryomyces*, *Metschnikowia*, *Pichia*, *Protomyces*, *Bensingtonia*, *Bulleromyces*, *Cryptococcus*, *Cystofilobasidium*, *Filobasidium*, *Leucosporidiella*, *Malassezia*, *Kondoa*, *Mastigobasidium*, *Mrakia*, *Mrakiella*, *Rhodospiridium*, *Rhodotorula*, *Sporidiobolus*, *Sporobolomyces*, *Trichosporon* and *Udeiomyces*. Amongst these, the polyphyletic genera *Cryptococcus* and *Rhodotorula* appear to be the predominant and are also represented by the highest numbers of species. Classical culture-based methods, molecular techniques and more recently also metagenomic analyses have revealed the existence of yet unknown species, genera and even new phylogenetic lineages.

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3.1 Introduction

The Arctic area is a polar region located at the northernmost part of the Earth, north of the Arctic Circle (66° 33'N). It is a region of an ice-covered Arctic ocean, surrounded by treeless permafrost. Geographically, it is spread over Greenland, parts of Iceland, Alaska and Norway (Svalbard; Fig. 3.1a), Sweden, Finland, Canada and Russia. The climate within the Circle is very cold, and much of the area is permanently covered with ice. In the mid-winter months, the temperatures can reach -50°C in the higher latitudes. In the summer months, sunlight melts the seas and the topsoil. The average temperature of the warmest month (July) does not exceed 10°C .

The main stress factors that influence microbial and therefore also fungal biodiversity in extremely cold polar areas are the low temperature, closely related to desiccation and low water availability (low A_w) due to freezing, the relatively high concentrations of ions and the generally low levels of nutrients in the liquid water and sometimes high UV irradiation and hypoxia. It appears that unlike in the temperate zones, where filamentous fungi prevail, yeasts are particularly well adapted to these conditions and thus thrive in different polar environments.

In spite of hard conditions and logistic problems, the initial studies on the presence of yeasts in the Earth's polar areas started more than a century ago with a study on Antarctic fungi performed in the early 1870s (Bridge et al. 2013). Thirty-seven research stations were established in the Arctic region, which prompted the research even in the most remote places (Fig. 3.1b). Initial studies of yeasts in polar areas were culture-based and concentrated primarily on the scarce vegetation, wooden remains, soil and permafrost, followed by studies of the aerosphere and rock-inhabiting yeast-like fungi. More recent studies have focused on water-based environments, such as sea water, glacial melt-water, snow, glacial and lake

Fig. 3.1 Arctic landscapes.
a Glaciers in Kongsfjorden, (Spitsbergen, Svalbard);
b Ablation zone of a glacier, icebergs on the sea surface;
c characteristic buildings of Ny-Ålesund settlement (78° 55' N, 11° 56' E, Spitsbergen, Svalbard), where research stations maintained by several countries are located



ice. The methods used for yeast detection have been time appropriate, from the classical early microscopical visualisation to molecular DNA-based techniques (Fell et al. 2006), which have been complemented lately by metagenomic studies (Simon et al. 2009; Kennedy et al. 2010; Ziolkowski et al. 2013), in which fungi were most often assessed only as a part of the overall analysis, mainly concentrated on the prokaryotic diversity.

Detailed taxonomic analyses based on physiological profiles and relevant molecular markers have allowed the description of numerous novel yeast species originating predominantly from the Antarctic (Montes et al. 1999; Scorzetti et al. 2000; Thomas-Hall and Watson 2002; Thomas-Hall et al. 2002; Vishniac 2002;

Libkind et al. 2005; Xin and Zhou 2007; Thomas-Hall et al. 2010), but also from other cold environments (Margesin et al. 2007; Margesin and Fell 2008; de García et al. 2010a, b; Thomas-Hall et al. 2010; Vishniac and Takashima 2010). Both in Arctic and Antarctic regions, basidiomycetous yeasts prevail (Branda et al. 2010). The majority of data on the occurrence of yeasts in the Arctic region can be retrieved as scattered reports (Gilichinsky et al. 2007; Frisvad 2008; Ludley and Robinson 2008; Libkind et al. 2009; Ozerskaya et al. 2009; Branda et al. 2010), or as information in public fungal databases, such as the CBS Fungal Biodiversity Centre or the American Type Culture Collection (ATCC), which can also serve as valuable sources for data on yeasts from cold regions. An overview of the public services collections preserving cold-adapted yeasts isolated from worldwide cold habitats is reported in Chap. 2.

The species with the broadest adaptive potential and the widest distributions across various polar niches are in particular different species of the genera *Bulleromyces*, *Cryptococcus*, *Cystofilobasidium*, *Dioszegia*, *Erythrobasidium*, *Filobasidium*, *Guehomyces*, *Leucosporidiella*, *Leucosporidium*, *Malassezia*, *Kondoa* (unpublished, from the Arctic), *Mastigobasidium*, *Mrakia*, *Mrakiella*, *Rhodospiridium*, *Rhodotorula*, *Sporidiobolus*, *Sporobolomyces*, *Trichosporon* and *Udeomyces*. Among these, *Cryptococcus* and *Rhodotorula*, which are both of polyphyletic origins that occur in several phylogenetic lineages of the Agaricomycotina, appear to be the predominant genera and are also represented by the highest numbers of species (Branda et al. 2010; Bellemain et al. 2013).

A special group of yeasts, extremely adapted to different types of extreme environments (Selbmann et al. 2008; Zalar et al. 2008), are melanised, black, yeast-like fungi (Onofri et al. 1999). These study organisms can inhabit environments as different and extreme as Antarctic rocks (Selbmann et al. 2005; Gorbushina 2007) and Arctic glacial ice with high salt concentrations (Butinar et al. 2011). The black yeasts can colonise environments on Earth that resemble most environments on the planet Mars, and have therefore been used as the closest eukaryotic models for exobiological speculations. Their astonishing viability after freezing and thawing, as well as after UV exposure, and their tolerance to osmotic imbalances have shown their uncommon ability to survive under harsh external pressures (Selbmann et al. 2005; Onofri et al. 2008).

In comparison with the studies of the Antarctic yeasts, the studies of the Arctic yeasts with respect to their abundance, distribution and taxonomy are very much limited. Taxonomic characterisations have shown that the dominant yeasts in the Arctic are also of basidiomycetous affinity and belong to the same genera that occur frequently in the Antarctic soils and polar offshore sea waters (Jones 1976; Abyzov 1993; Abyzov et al. 2004; Onofri et al. 2004; Vishniac 2006). The species of the genera *Cryptococcus*, *Cystofilobasidium*, *Rhodospiridium*, *Trichosporon* and *Rhodotorula* are predominant yeasts in the various habitats of the Arctic (Starmer et al. 2005; Raspor and Zupan 2006; Butinar et al. 2007, 2011; Vishniac and Takashima 2010; de García et al. 2012). The distribution of the discovered Arctic yeasts ranges from circumpolar to endemic and cosmopolitan species. Whereas some yeasts that are endemic to the Arctic region show psychrophilic

behaviour (Margesin and Fell 2008; de García et al. 2012), the majority are psychrotolerant and globally distributed. The global warming phenomena, resulting in the accelerated melting of polar ice, facilitate their transportation via global water systems (Grabińska-Loniewska et al. 2007) and air currents. Some Arctic yeasts were previously known only from human proximity; as inhabitants of freezers, cold storage rooms, refrigerated and even frozen food. In Table 3.1 to the best of our knowledge, all known yeast species from diverse Arctic environments are listed.

Many recovered Arctic yeast species represent reservoirs of rare or still unknown microbial species, and therefore also of novel biological processes. Although most investigations of yeasts in the Arctic have been limited to their biodiversity, an increasing number of studies have been oriented towards extra-cellular enzymatic activities of yeasts, antifreeze proteins, the biosynthesis of secondary metabolites and bioremediation at low temperatures (Margesin 2009; Simon et al. 2009; Pathan et al. 2010; Lee et al. 2012), providing us with a better understanding of the complexity of these processes at 'the edge of life' (Robinson 2001; Ruissi et al. 2007; Xiao et al. 2010). Recently, adaptations to cold and consequentially low water activity at the molecular level have also received more attention, expanding the realm of extremophilic model organisms from prokaryotes to yeasts (Gostinčar et al. 2008; Turk et al. 2011).

3.2 Yeasts on Arctic Vegetation, in Soil and Permafrost

Limiting factors for microbial growth and activity in the Arctic soils are extremely low temperatures, cycles of freezing and thawing, low annual precipitation and low nutrient content (Margesin and Miteva 2011). Annual soil temperatures recorded at 10 cm depth can range between -27 and 14 °C in the High Arctic, and between -7 and 11 °C in the Low Arctic (Timling and Taylor 2012). Because of non uniform snow distribution, wide temperature differences can be recorded in the underlying soil. A considerable microbial activity occurs in the region between the snow packs and above permafrost region, even at the temperatures below freezing point (Sturm et al. 2005). The activity is prompted during the short growing season, lasting up to 6 weeks in the High Arctic up to 4 months in the Low Arctic, when the upper 30–60 cm of soil is thawing, which can result in anaerobic condition due to the underlying permafrost preventing drainage. On the other hand, freezing can cause desiccation and salt accumulation in salt crusts. Due to diverse cryogenic processes, Arctic soils are shaped into extremely heterogeneous environment, with pH values ranging from 4 to 9, and relatively variable amount of carbon (Timling and Taylor 2012).

Yeasts have been reported in connection with the subarctic vegetation and soil. Mainly, basidiomycetous yeasts have been isolated from soil and adjacent berries, flowers, vegetation of the littoral zone, forest trees and grasses, while ascomycetous yeasts have been recovered more in connection with vegetation (Babjeva and

Table 3.1 Ascomycetous and basidiomycetous yeasts reported from different Arctic habitats. Letters indicate references, listed in the legend

	Plants	Soil	Glaciers, subglacial habitats	Permafrost	Sea water, sea ice	Others
Ascomycota						
<i>Aureobasidium pullulans</i>	a	a	f	e, j	j	
<i>Candida apicola</i>	a					
<i>Pichia kudriavzevii</i> (formerly <i>Candida krusei</i>)	a					
<i>Candida molischiana</i> (anamorph of <i>Kuraishia molischiana</i>)	a					
<i>Candida norvegica</i>		g				
<i>Candida parapsilosis</i>					m	
<i>Candida pseudointermedia</i>	a					
<i>Candida quercitrusa</i>	a					
<i>Candida sake</i>	a					
<i>Candida santamariae</i>	a					
<i>Debaryomyces hansenii</i>	a			e*	m	
<i>Debaryomyces marinus</i>					m	
<i>Metschnikowia bicuspidata</i>					m	
<i>Metschnikowia pulcherrima</i>	a					
<i>Metschnikowia reukauffii</i>	a					
<i>Metschnikowia zobellii</i>					m	
<i>Meyerozyna guilliermondii</i> (formerly <i>Pichia guilliermondii</i>)				e*	m	
<i>Scheffersomyces spartinae</i> (formerly <i>Pichia spartinae</i>)	a				m	
<i>Protomyces inouyei</i>					m	
Basidiomycota						
<i>Bensingtonia yamatoana</i>		g*				
<i>Bulleromyces albus</i>			h			
<i>Cryptococcus adeliensis</i>			h			
<i>Cryptococcus aerius</i>		g				

(continued)

Table 3.1 (continued)

	Plants	Soil	Glaciers, subglacial habitats	Permafrost	Sea water, sea ice	Others
<i>Cryptococcus albidosimilis</i>	a		h			
<i>Cryptococcus albidus</i>		g	f, h			
<i>Cryptococcus antarcticus</i>		g				d(DFS)
<i>Cryptococcus aquaticus</i>		g				
<i>Cryptococcus carescens</i>			n, h			
<i>Cryptococcus flavus</i>	a					
<i>Cryptococcus fonscae</i>			n			
<i>Cryptococcus gastricus</i>	a					k(S)* o(CH)
<i>Cryptococcus gibescens</i>			h			
<i>Cryptococcus heimaeyensis</i>		c				
<i>Cryptococcus heveanensis</i>	a					
<i>Cryptococcus humicola</i>			f			
<i>Dioszegia hungarica</i> (formerly <i>Cryptococcus hungaricus</i>)	a					
<i>Cryptococcus laurentii</i>	a	a	h	e*		
<i>Cryptococcus liquefaciens</i>		g	h			
<i>Cryptococcus luteolus</i>	a					
<i>Cryptococcus macerans</i>			h			d(DFS)
<i>Cryptococcus magnus</i>	a		h			
<i>Cryptococcus oeirensis</i>			h			
<i>Cryptococcus podzolicus</i>		a				
<i>Cryptococcus psychrotolerans</i>			n			
<i>Cryptococcus saitoi</i>			h			
<i>Cryptococcus skinnerii</i>	a					
<i>Cryptococcus tephrensis</i>		c				
<i>Cryptococcus terricola</i>	a	a, g				k(S)*

(continued)

Table 3.1 (continued)

	Plants	Soil	Glaciers, subglacial habitats	Permafrost	Sea water, sea ice	Others
<i>Cryptococcus victorinae</i>		g	n, h	e*		
<i>Cryptococcus walticus</i>		g				
<i>Cystoflobasidium capitatum</i> (formerly <i>Cystoflobasidium lari-marini</i>)	a	a				d(DFS)
<i>Cystoflobasidium inimo-miniatum</i>	a	a				
<i>Filobasidium uniguttulatum</i>			h			
<i>Leucosporidiella fragaria</i>			h			
<i>Leucosporidiella creatinivora</i>		g				
<i>Leucosporidium scottii</i>	a	g*				
<i>Leucosporidium antarcticum</i>	a	a				
<i>Mrakia frigida</i>		g				
<i>Mrakia gelida</i>						k(S)*
<i>Mrakia psychrophyla</i>						k(S)*
<i>Mrakiella cryoconiti</i>						j(CR)
<i>Rhodospiridium diobovatum</i>			h			
<i>Rhodospiridium kratochvilovae</i>		g				
<i>Rhodotorula arctica</i>		l				
<i>Rhodotorula aurantiaca</i>	a					
<i>Rhodotorula buffonii</i>	a			b		
<i>Leucosporidiella creatinivora</i> (formerly <i>Rhodotorula creatinivora</i>)						
<i>Rhodotorula fujianensis</i> (anamorph of <i>Curvibasidium cygneicollum</i>)	a					k(S)*
<i>Rhodotorula glacialis</i>	a					
<i>Rhodotorula hylophila</i>	a					
<i>Rhodotorula laryngis</i>			f, h			
<i>Rhodotorula minuta</i>	a		h			
<i>Rhodotorula mucilaginosae</i>	a		f, h			

(continued)

Table 3.1 (continued)

	Plants	Soil	Glaciers, subglacial habitats	Permafrost	Sea water, sea ice	Others
<i>Leucosporidiella muscorum</i> (formerly <i>Rhodotorula muscorum</i>)	a			b		k(S)*
<i>Leucosporidiella yakutica</i> (formerly <i>Rhodotorula yakutica</i>)						
<i>Sporidiobolus salmonicolor</i> (teleomorph of <i>Sporobolomyces salmonicolor</i>)	a	f				
<i>Sporobolomyces roseus</i> (anamorph of <i>Sporidiobolus metaroseus</i>)	a					
<i>Trichosporon cutaneum</i>	a					
<i>Trichosporon mucoides</i>		h				
<i>Guehomyces pullulans</i> (formerly <i>Trichosporon pullulans</i>)	a	b				

S sediments; CH cryoconite holes; DFS diverse frozen samples
*nearest phylogenetic neighbour, related to
a Babjeva and Reshetova (1998), b Golubev (1998), c Vishniac (2002), d Birgisson et al. (2003), e Gilichinsky et al. (2005), f Starmer et al. (2005), g Vishniac (2006), h Butinar et al. (2007), i Margesin and Fell (2008), j Zalar et al. (2008), k Pathan et al. (2010), l Vishniac and Takashima (2010), m Butinar et al. (2011), n de García et al. (2012), o Singh and Singh (2012)

Reshetova 1998). The multivariant analysis of soil samples collected all over the globe over the latitudinal gradient has shown the temperature among other factors (precipitation, electrical conductivity, pH, vegetation types) as the major factor for yeast distribution. The success of the soil-inhabiting polyphyletic genus *Cryptococcus* is mainly attributed to their capsules, which enable them to grow in mineral soil types distributed all over the globe (Vishniac 2006). A list of yeast species inhabiting polar soils of Arctic is reported in Table 3.1.

Permafrost, ground that is comprised of soil, sediment or rock, and includes ice and organic material, which remains at or below 0 °C for at least two consecutive years, presents even harsher conditions for microbial activity. Permafrost is a strictly thermal phenomenon and does not depend on the composition of the ground. Permafrost in polar regions covers more than 25 % of the land surface and significant parts of the coastal sea shelves (Wagner 2008). Together with seasonally frozen soils, permafrost represents a large part (approximately 50 %) of the terrestrial Earth (Panikov 2009). Permafrost reaches depths of 600–800 m in the Eurasian tundra and a depth of 1,450 m in the Antarctic deserts (Steven et al. 2006). Usually, it is divided into three temperature-depth layers. The surface, active layer is influenced by air temperature fluctuations, with a thickness from a few cm to 10 m and temperatures fluctuating from +15 to –35 °C. The second layer is composed of perennially frozen permafrost sediments, with a thickness from 10 to 20 m and temperatures from 0 to –15 °C. The third and deepest layer is composed of stable permafrost sediments, with temperatures from –5 to –10 °C (Wagner 2008). In the active layer and in the middle layer of permafrost, intensive physicochemical processes take place, strongly influencing microbial diversity, whereas in the deeper permafrost sediments, the conditions can remain stable for long periods of time, limiting the microbial processes (Wagner 2008). Thermal conditions influence the formation of different cryogenic structures, such as ‘ice wedges’ (a crack in the ground formed by a narrow or thin piece of ice), connected with the atmosphere, unfrozen layers of ground in permafrost, called ‘taliks’, and lenses of brine in permafrost, called ‘cryopegs’.

Different types of permafrost habitats are characterised by extremely low temperatures, freeze–thaw cycles, low water and nutrient availability, and low gas permeability (Morozova et al. 2007; Wagner 2008; Panikov 2009). For many years, permafrost was considered a depository of ancient microbial life, but the recently discovered intensive winter gas fluxes of methane and carbon dioxide from the tundra to the atmosphere have led to an intensified search for organisms able to metabolise below the freezing point. Now we know that the total microbial biomass in permafrost is comparable to that of the communities of temperate soil ecosystems (Wagner 2008; Wagner et al. 2005). Microbial communities in permafrost are represented by dormant propagules of mesophilic cosmopolitan species that have been deposited from the surrounding areas by wind and animals, but also by active indigenous culturable or non-culturable species of Archaea, Bacteria and Eukarya, particularly fungi (Ruisi et al. 2007; Panikov 2009). It has been demonstrated that yeast species not only survive under permafrost conditions, but also can sustain an active metabolism (Rivkina et al. 2004; Wagner 2008). It

appears that yeasts are more resistant to hostile permafrost environments and show more vigorous growth in frozen habitats than bacteria (Steven et al. 2006). Depending on the depth and age of the samples, the numbers of culturable yeasts can vary from 10 to almost 100,000 CFU g⁻¹ material. The peaks of fungal populations in permafrost are microfocal and, importantly, they show a parallel decrease in species numbers (Ozerskaya et al. 2008).

Permafrosts in Arctic and Antarctic areas differ considerably. Permafrost in the Antarctic regions is typically dry, with low intertidal water, while the Arctic permafrost is, in contrast, impregnated with ice. During the thaw, the underlying permafrost can prevent drainage of soils, leading to temporary anoxic conditions, while subsequent freezing can lead to desiccation and an increased salinity, especially in the High Arctic, where salt crusts can form on the soil surface due to the high rates of evaporation. The Arctic soils are shaped also by cryogenic processes, such as repeated freeze–thaw cycles, cryoturbation, frost heaving, thermal cracking, and the formation of needle ice and ice lenses. As a result, the Arctic soils are extremely heterogeneous at small scales. Soil pH values can vary between 4 and 9, nutrient contents (N, P, K) are generally low, while carbon can vary substantially (Timling and Taylor 2012).

Fungal diversity in the Arctic permafrost has been studied mainly over the last decade. The first studies concentrated on the longevity of frozen cells, while in later studies mainly biodiversity was investigated. Since DNA may be preserved in permafrost soils either as an intracellular DNA within the intact, cryopreserved cells, or as an extracellular DNA adsorbed to sediment particles, the recent studies also include DNA metabarcoding (Bellemain et al. 2013).

Viable yeasts and fungi have been isolated from Siberian permafrost sediments that have remained in a frozen state for up to 3 million years, although they were preserved in considerably lower numbers than the prokaryotic cells (Golubev 1998; Faizutdinova et al. 2005). Upon thawing, these microorganisms were able to resume their metabolic activities (Takano et al. 2004). In some permafrost regions, yeasts represented an important, or even the major (up to 100 %), part of all of the fungi isolated, and 20–25 % of the total aerobic heterotrophs (Vorobyova et al. 1997; Steven et al. 2006). Researchers have even managed to isolate yeasts below freezing point on solid media (cellulose powder or plastic film) with ethanol as the sole carbon source without using artificial antifreezes. Enrichment from soil and permafrost obtained on such frozen solid media contained mainly fungi, and further purification resulted in an isolation of basidiomycetous yeasts of the genera *Mrakia* and *Leucosporidium*, as well as of ascomycetous fungi of the genus *Geomyces* (Panikov and Sizova 2007).

Most of the yeasts isolated from the Arctic permafrost were cosmopolitan mesophilic species, which are easily dispersed via air, water and animals (Samson et al. 2002). These yeasts might represent a recent contamination of the permafrost, and this thus makes the identification of the indigenous species more difficult (Lydolph et al. 2005; Ruisi et al. 2007). However, it has been shown that permafrost contains a considerable taxonomic diversity with significant numbers of new taxa (Golubev 1998; Vishniac and Takashima 2010). The taxonomic diversity

and ecological diversity of the ancient fungal communities of the Arctic permafrost fungi were assessed by combining next generation sequencing and metabarcoding of the DNA, preserved in permafrost. Twenty-six sediment samples from two localities in Siberia dated 16,000–32,000 radiocarbon years were analysed for fungal ITS. Among the operational taxonomic units (OTUs), there were sequences that belonged to almost all of the known yeast groups, and the following genera were detected: (1) *Malassezia*, a lipophilous basidiomycete yeast genus and (2) *Cryptococcus*, *Mrakiella* and *Rhodotorula*, putative psychrophilic fungi, which might represent a modern DNA from metabolically active individuals. Saccharomycetales were not identified to the genus level (Bellemain et al. 2013).

In culture, the most frequently isolated yeasts from these permafrost sediments belong to the genera *Cryptococcus*, *Rhodotorula* and *Saccharomyces*. By the use of standard culture techniques, yeast species of the genera *Bulleromyces*, *Candida*, *Clavispora*, *Debaryomyces*, *Dioszegia*, *Guehomyces*, *Leucosporidium*, *Mrakia*, *Pichia*, *Pseudozyma*, *Rhodospiridium*, *Sporidiobolus*, *Sporobolomyces*, *Tilletiopsis*, *Torulaspora*, *Trichosporon* and *Leucosporidium* have also been found in permafrost (Vishniac 1993; Thomas-Hall and Watson 2002; Vishniac 2006; Margesin et al. 2007; Xin and Zhou 2007).

The microbial biodiversity in cryopegs in permafrost originating from the Arctic Ocean regression in Siberia were studied by Gilichinsky et al. (2005). From the brine in cryopegs, aerobic and anaerobic, halotolerant and halophilic, psychrophilic and psychrotolerant bacteria, mycelial fungi and yeasts of the genera *Cryptococcus*, *Debaryomyces* and *Pichia* have been identified, as well as black yeast *Aureobasidium pullulans* var. *pullulans*. Activities were detected below 0 °C, and the isolated microbes were considered as survivors of 43,000 years at –10 °C (Gilichinsky et al. 2005).

3.3 Yeasts and Yeast-Like Fungi in/on Rocks

The Arctic region is rich in stony and rocky habitats. The rock represents a dwelling place as well as a substrate for endolithic microorganisms, including yeasts. The conditions on the surface of the rock are the harshest ones seen, and they can only be sustained by lichens (Friedmann 1982; Nienow and Friedmann 1993; Selbmann et al. 2005), assigned as epiliths. The interiors of the rock protect—to some extent—life from environmental extremes, which allows for the growth of different kinds of endolithic microorganisms (Friedmann and Koriem 1989; de los Ríos et al. 2003, 2005; McLoughlin et al. 2007). Non-lichenised, rock-inhabiting fungi in polar regions are cryptoendoliths that establish themselves under an abiotic crust on the successive layers of the rock surface. The darkly pigmented non-lichenised yeasts inhabit the black layer, and *Rhodotorula* and *Sporobolomyces*, together with hyaline filamentous fungi, inhabit the white layer (Burford et al. 2003).

Yeasts living within the rock are exposed to different kinds of stress factors, which can include a high UV irradiation, low temperatures, desiccation, repeated freeze-thawing and a lack of nutrients. The general response of the cryptoendolithic fungi to these conditions is a high level of simplification. They primarily grow as multicellular clumps and have the ability to shift to a simpler life cycle and meristematic growth, which also includes the loss of sexual, and in some fungi even asexual, reproduction (Selbmann et al. 2005). Through such simplification, they can conclude their life cycle in a shorter time, with less energy needed and hence at a lower metabolic cost (Ruisi et al. 2007).

While the Antarctic cryptoendolithic fungi, including yeasts, such as *Cryptococcus friedmannii* (Vishniac 1985), have been long investigated (Friedmann 1982; Onofri et al. 1999, 2004; Selbmann et al. 2005, 2008), studies on the Arctic cryptoendolithic fungi have been initiated only recently (Omelson et al. 2006, 2007; Selbmann 2013, personal communication). The studies performed on cryptoendoliths in the sandstone outcrops of the Canadian High Arctic have revealed the presence of black-pigmented yeast-like fungi (Omelson et al. 2006, 2007). Although these isolates have not been identified, it appears that the general microbial diversity in the Arctic rock is higher in comparison with similar habitats in Antarctica. The main reasons for this are probably the higher temperatures and moisture and to a lesser extent the lower pH and higher concentrations of iron, aluminium and silicon in the overlying surface (Omelson et al. 2007). The total time that is available for ideal metabolic activity within the cryptoendolithic environment in the Canadian High Arctic has been estimated as 2,500 h per year (Omelson et al. 2006), whereas for the Antarctic Dry Valleys it has been estimated as between 50 and 500 h per year (Omelson et al. 2006). These and other studies performed over the last few years have shown that the cryptoendolithic yeasts are much more widespread and common than previously thought. It appears that the conditions in the rocks are prohibitive enough to prevent the settlement and the growth of competitive cosmopolitan yeasts, yet they enable a slow growth of only the most specialised black yeasts. To our current knowledge, only the genera of black yeasts *Friedmanniomyces* and *Cryomyces* are endemic to Antarctica (Selbmann et al. 2005), whereas other recently described genera and species of black yeasts *Elasticomyces*, *Recurvomyces* and *Acidomyces* have also been found in diverse, geographically remote, mountainous regions, e.g. the Andes of Argentina and the Italian Alps (Selbmann et al. 2008). An in-depth review of the distribution of black yeasts in worldwide cold habitats is reported in Chap. 8.

The most recent study performed in a gypsum-based endolithic community in the polar desert of the Canadian High Arctic characterised the microbial community diversity, turnover and microbe–mineral interactions. Pyrotag sequencing of 16S/18S rRNA demonstrated the presence of a diverse community of phototrophic and heterotrophic bacteria, algae and fungi. The diversity observed by molecular techniques was confirmed by stable carbon isotope analysis of the lipids in viable microbial membranes, which indicated that the atmospheric carbon is assimilated into the microbial community biomass. Among fungi, the sequences of Hypocreales, Verrucariales, Chaetothyriales, Helotiales, Capnodiales, Erysiphales,

Lecanoreales and Dothideales were detected, which excludes true yeasts (Ziolkowski et al. 2013).

3.4 Yeasts in Sea Water and Sea Ice

Yeast communities in oceanic environments appear to be composed of ubiquitous and endemic species (Kohlmeyer and Kohlmeyer 1979). Typical ubiquitous marine yeasts are the ascomycetous yeast *Debaryomyces hansenii* and the basidiomycetous yeast genera *Cryptococcus* and *Rhodotorula*. Although the isolation frequency of yeasts falls with depth, ascomycetous yeasts (e.g. *Candida*, *Debaryomyces*, *Kluyveromyces*, *Pichia* and *Saccharomyces*) are more common in shallow waters, while yeasts belonging to the Basidiomycetes (*Cryptococcus*, *Rhodospiridium*, *Rhodotorula*, *Sporobolomyces*) are more common in deep waters. Mainly basidiomycetous yeasts have also been isolated from polar offshore sea waters (Jones 1976). The genera *Rhodotorula*, *Cryptococcus*, *Debaryomyces* and *Candida*, which predominate among yeasts isolated from the deep-sea waters, also prevail in cold polar areas and in the vicinity of sea ice (Butinar et al. 2011). In particular, *Rhodotorula* spp. yeasts show a strong ubiquity, since they were isolated from deep-sea vents, from a depth of 11,000 m (Gadanhó and Sampaio 2005), from deep-sea sediments (Nagahama et al. 2001), from coastal waters (Gadanhó et al. 2003; Gadanhó and Sampaio 2004), and from the Arctic ocean (Gunde-Cimerman et al. 2003). Recent data have shown that animals living in deep-sea hydrothermal vents are a new niche for colonisation by yeasts, which frequently occur either in the Arctic water-based environments or in the hypersaline environments (Kutty and Philip 2008; Burgaud et al. 2010). For example, the psychrophilic marine yeast *Leucosporidium scottii*, previously known as autochthonous in the oceanic regions close to Antarctica, was found recently in association with deep-sea hydrothermal animals. The authors hypothesised that this could be an evidence of global exchanges from polar environments to deep-sea vents (Burgaud et al. 2010). An overview of the occurrence of cold-adapted yeasts in the deep sea is reported in Chap. 7.

When seasonal temperatures drop and frozen seawater forms a semisolid matrix, seasonally transient sea ice is formed. It is constantly broken up and reshaped by the wind and the ocean currents, and it has a highly variable temperature, both temporally and spatially, with temperatures ranging from -1°C to as low as -50°C in winter. The seasonally transient sea ice is permeated by a network of channels and pores, filled with brine. These sea-ice brine channels remain liquid up to -35°C and can reach 20 % (w/v) NaCl concentration. Changes in the salinity and temperature are thus the dominant factors that influence the biological communities within the sea ice (Brown and Bowman 2001; Thomas and Dieckmann 2002). At very low external temperatures, most of the microbial biomass finds refuge in the central mass of the ice within brine pockets, whereas in spring, dense microbial communities can develop at the bottom of the

ice (Gosink et al. 1993). Although autotrophic algal communities are relatively well described, sea-ice-dwelling fungal communities have been less documented (Brown and Bowman 2001; Gunde-Cimerman et al. 2003, 2005). For example, when DNA was extracted from an Arctic sea-ice sample, some of the eukaryotic clones detected were described as fungal (Thomas and Dieckmann 2002). From Svalbard (Arctic), conventional culture-based methods with sea-ice samples have yielded up to 7,000 CFU fungi L⁻¹ (Gunde-Cimerman et al. 2003). Most (85 %) of the isolates were basidiomycetous yeasts, which were mainly represented by *Cryptococcus adeliensis* and *Rhodotorula mucilaginosa*. The neighbouring sea water contained *D. hansenii*, *D. maramus*, *Meyerozyma guilliermondii* (formerly *Pichia guilliermondii*), a novel species resembling *Candida galli* and *Metschnikowia bicuspidata*. Of all these, only *M. guilliermondii* was isolated exclusively from sea ice, while snow/ice in the fjord tidal zone included *Candida parapsilosis*, *D. hansenii*, *M. guilliermondii* and *Metschnikowia zobellii* (Butinar et al. 2011). All of these isolated strains were characterised as psychrotolerant and xero/halo-tolerant. When sea ice melts, the entrapped yeasts and other microbes are released into the oceans; however, up to our knowledge, no studies report on the dynamics of these processes. Only a few studies have reported on the occurrence of yeasts in the Arctic aquatic habitats and their global distribution, particularly in deep-sea waters.

3.5 Yeasts in Glaciers and Subglacial Environments

Glacial ice was long considered as an extremely stable and static environment. Ice-core analyses were used to document and date past climate changes, geological events and human activities. Isolation of viable microorganisms from ice cores has unravelled ancient, 'living microbial fossils' in the older layers, which originated from northern latitudes, and temperate as well as tropical regions (Abyzov 1993; Ma et al. 1999, 2000). Low numbers of filamentous fungi, but no yeasts, were isolated from 10,000–13,000-year-old Greenland ice (Ma et al. 1999, 2000). PCR amplification of fragments of the eukaryotic 18S rRNA genes that were extracted from 2,000-year-old to 4,000-year-old ice-core samples from north Greenland led to the identification of a diversity of fungi, plants, algae and protists (Price 2000). All of these findings of fungi in glacier ice cores have been interpreted as the result of coincidental aeolian deposits of spores or mycelium into the ice during its geological history.

Recent investigations have shown that ice in glaciers is a much more dynamic habitat than previously thought, on the microscale as well as at the level of geomorphology. Active microbes have been found in all types of glaciers, but their abundance and activity are greatest in polythermal and temperate types. Their presence is connected to the availability of water, which is in turn related to the heat budget and the distribution of drainage channels in the ice.

Four key glacial ecosystems have so far been identified: the proglacial environment, seasonally flooded by glacial melt-water; the glacier surface, i.e. the supraglacial system; the ice-bed interface, i.e. the subglacial system; and the englacial system, which exists *inside* glacial ice.

Ice in temperate glaciers is permeated by a continuous network of aqueous veins that are formed due to sea salts deposited as aerosols, as they are essentially insoluble in ice crystals. Due to the percolation of the salts from the top of the glacier to its bottom, salts can accumulate to relatively high concentrations in the bottom parts of glaciers (Price 2000). Although these liquid veins, located between the ice crystals in bulk polycrystalline ice, can have high ionic strength (Price 2000; Rohde and Price 2007), they contain living microorganisms of different physiological groups. To the authors' knowledge, the presence of yeasts within these veins has not been demonstrated yet. These microorganisms can serve as inocula when they reach the subglacial environment that contains more liquid water.

The heat budget of melting ice is controlled not only by physical phenomena such as solar radiation and air temperature, but also by quick seismic shifts (Ekstrom et al. 2003; Fahnestock 2003), which affect the formation of cryokarst phenomena and distribution of ice at the pressure melting point. Water in a glacier can thus exist on the surface of glaciers as channels, films, veins and pockets at grain interstices or boundaries and also as caves, interglacial lakes or moulins within the glaciers (Christner et al. 2000). If these waters reach the glacier bed and mix with the groundwater and glacial basal melt-water, rock and sediment, they create a dynamic subglacial environment.

Initially these environments were considered abiotic; however, large microbial communities dominated by aerobic, heterotrophic Betaproteobacteria were discovered in 2000 (Skidmore et al. 2000; Foght et al. 2004) and yeasts and other fungi in 2003 (Gunde-Cimerman et al. 2003, 2005; Sonjak et al. 2006; Butinar et al. 2007; Zalar et al. 2008). The yeast counts detected in the subglacial samples were two orders of magnitude greater when compared with those in supraglacial samples (with up to 4×10^6 CFU L⁻¹). Yeasts were primarily associated with the clear glacier ice, while filamentous fungi were detected with the highest counts in debris-rich subglacial ice (Butinar et al. 2007; Sonjak et al. 2006). In another study by Singh et al. (2013), the viable counts of yeast cells in ice-melted water from glacier samples were lower and ranged between 3×10^3 and 1×10^4 CFU L⁻¹.

According to the species diversity and the abundance, the majority of the species were assigned to the hymenomycetous yeasts (*Filobasidium*/*Cryptococcus albidus* taxa of the Tremellales). The stable core of the subglacial yeast communities was represented by *Cryptococcus liquefaciens*, *R. mucilaginosa*, *D. hansenii* and *M. guillermundii* (Butinar et al. 2007, 2011; de García et al. 2012), while in the study by Singh et al. (2013), *C. adeliensis*, *C. albidosimilis*, *C. saitoi*, *Rhodospiridium lusitaniae* and *R. mucilaginosa* prevailed.

Ascomycetous yeasts have been found in glaciers of the Southern and Northern Hemisphere only occasionally, the main reason probably being isolation media with water activity close to 1.0. When media with lowered water activity were

Fig. 3.2 Glacial ice with gypsum inclusions



used, a much higher number of ascomycetous yeasts were retrieved (Gunde-Cimerman et al. 2003). The dominant ascomycetous yeast species was *D. hansenii*, with different species of the genera *Candida*, *Metschnikowia* and *Pichia* (de García et al. 2010a). A surprising discovery was made in ice rich in gypsum precipitations (Fig. 3.2). Although such samples of ice contained some basidiomycetous yeasts, they were dominated by osmotolerant ascomycetous black yeast *A. pullulans*. This species is of great biotechnological importance due to its production of the extrapolymer polysaccharide pullulan, as well as numerous extracellular hydrolytic enzymes (Chi et al. 2009). Recently, *A. pullulans* has been described to comprise four varieties, of which three have been detected in polar environments. The most well known of these, *A. pullulans* var. *pullulans*, is a cosmopolitan taxon that has been found at both poles in glaciers (Zalar et al. 2008) and in Greenland ice sheets (Starmer et al. 2005). The *A. pullulans* var. *melanogenum* has been isolated mainly from oligotrophic watery habitats, such as melted glacial water from the Italian Alps (Branda et al. 2010), and melted subglacial water of the Arctic Svalbard glaciers (Zalar et al. 2008). The sequence data of five molecular markers have revealed an additional variety, named *A. pullulans* var. *subglaciale*, which has so far been isolated only from the subglacial ice of Svalbard glaciers and the immediate surroundings (Zalar et al. 2008). This variety probably represents an example of geographic isolation and initiation of speciation of this panglobal species (Gostinčar et al. 2010), indicating its high genetic variability. It appears likely that more varieties of *A. pullulans* will be discovered and described in polar environments in the future.

In the area of Svalbard (Arctic Archipelago), yeasts have also been isolated from ice and melt-water and from puddles in the vicinity of glaciers (Pathan et al. 2010; Butinar et al. 2011). The isolated yeasts were phylogenetically affiliated to *Cryptococcus gastricus*, *C. terricolus*, *Leucosporidiella muscorum* (formerly *Rhodotorula muscorum*), *Mrakia psychrophila*, *Mrakia gelida* and *Rhodotorula glacialis*. Strains belonging to the genera *Mrakia* and *Mrakiella* have been found in many cold climates throughout the world, such as Antarctica, Greenland,

Siberia, Alaska and Patagonia. *Mrakia* is the dominant yeast genus in Antarctic soil, representing 24 % of the yeast species. Since it is not able to grow at temperatures above 20 °C, it can be defined as an obligate psychrophile. There was a major overlap in the detected species diversity with yeasts detected in Italian Alpine glaciers (Turchetti et al. 2008; Branda et al. 2010; Thomas-Hall et al. 2010) and in Patagonian glaciers (de García et al. 2007). Three novel species—*Mrakia robertii*, *Mrakia blollopis* and a related anamorphic species *Mrakiella nic-combsii*—were isolated from Antarctica and the Italian Alps, as well as the novel genus *Glaciozyma* with two newly described species, namely *Glaciozyma martinii* and *Glaciozyma watsonii* and the reclassified *Leucosporidium antarcticum*, now *Glaciozyma antarctica* (Thomas-Hall et al. 2010). In the Italian Alpine glaciers, *Cr. gastricus* and *Rhodotorula psychrophenolica* (Branda et al. 2010) prevailed. Surprisingly, the opportunistic pathogenic black yeast *Exophiala dermatitidis* has been found in the supraglacial environment of an Italian glacier (Branda et al. 2010). A complete overview of the distribution of cold-adapted yeast species (including black yeasts) in worldwide cold habitats is reported in Chaps. 3, 4, 5, 6, 7 and 8.

3.6 Yeasts in Cryoconite Holes

Cryoconite holes are formed when solar-heated dark organic and inorganic wind-blown debris melts into the underlying ice. These melt-water-filled depressions in the surface ice are formed in the ablation zones of glaciers and ice sheets of the Arctic, Antarctic and Alpine regions, as a result of the low albedo of localised debris accumulations (Edwards et al. 2013). They consist mostly of both organic and inorganic matter, 90 % immersed in water, with the remaining space filled with air. The holes can range from less than 1 cm to 1 m in width. They seldom grow deeper than 60 cm, although they can coalesce into bigger holes or become interconnected by melt-water channels. The cryoconite holes in the Arctic seem to be more interconnected than the holes in the Antarctica, which is the most probable explanation for the difference in the community structures and dynamics between the two environments. As the solar radiation decreases, an ice cover can form on the water surface and grow downwards. With faster freezing rates, solutes can become trapped in brine pockets with salinities up to 10 % NaCl. These ponds can freeze only after reaching brine temperatures of −12 °C. In relation to the melt regime of the glacier surface, the cryoconite holes can last from several days to weeks, or to entire seasons. On some stable glaciers, they are thought to have remained for at least a 100 years, thus serving as biological refuges during periods of extreme cold (Mueller et al. 2001; Vincent et al. 2004).

The cryoconite holes provide niches within a permanently cold and hostile environment, assigned as ice-cold hot spots of microbial diversity (Edwards et al. 2013). The organic matter, also presenting the important driver in the process of cryoconite hole formation, mainly includes algae, cyanobacteria, bacteria, fungi

and rotifers, while the inorganic matter is a mixture of minerals and trace elements (Singh and Singh 2012). During the polar summer, photosynthesis by algae and cyanobacteria within the cryoconite hole can provide sufficient nutrients for complex community development.

The dominant organisms are typically nitrogen-fixing, filamentous, mat-forming cyanobacteria. Light microscopy has also documented the presence of pollen grains, bacteria, algae, diatoms, occasional microinvertebrates, filamentous fungi and yeasts. The latter two groups drive the process of organic macromolecule degradation through cold-adapted enzyme secretion, thereby assisting in nutrient cycling (Singh and Singh 2012). Psychrotolerants prevail, while psychrophiles have been detected only rarely (Mueller et al. 2001; Vincent et al. 2004).

The best-known culturable components of the sampled cryoconite holes in Svalbard are the psychrophilic basidiomycete yeasts of the classes Tremellomycetes (*Mrakia* and *Cryptococcus*) and Microbotryomycetes (*Glaciozyma* and *Rhodotorula*), with several species known only from glacial habitats. These yeasts are often dominant in culture-based studies depending on the plating method used. For yeasts and filamentous fungi, the number of CFU g⁻¹ of the sediment sample was calculated to be about 7×10^3 to 1.4×10^4 and 4×10^3 to 1.2×10^4 , respectively. In the cryoconite holes at higher latitudes, more yeast species than fungi were recovered, while filamentous fungi were more abundant at the lowermost point (Singh and Singh 2012). However, the isolated species comprise only a minor component of the fungal communities, as assessed by a T-RFLP study of rRNA ITS amplicons (Edwards et al. 2013), since the most dominant T-RFLP peaks did not match any of the cultured isolates.

3.7 Conclusions

The extremely cold Arctic environment is inhabited by extremophilic yeasts that even today represent a largely unknown biodiversity. Classical culture-based methods, molecular techniques and more recently also metagenomic analyses (Simon et al. 2009; Kennedy et al. 2010; Bellemain et al. 2013) have revealed the existence of novel species and genera, and even novel phylogenetic lineages. Over the past decades, studies of yeasts were focused on the one hand on living fossils entrapped in the ice, providing us with an insight into the biological past, while on the other hand we discovered unexpectedly large metabolically active communities. The range of Arctic environments that are inhabited by yeasts and were previously considered abiotic or dominated exclusively by Bacteria has been expanded to include rocks, sea ice, microbial mats on sea-ice shelves, glacial brine networks and inclusions, subglacial environments, cryoconite holes and permafrost. The physiological activity of the yeasts has been demonstrated at temperatures below $-20\text{ }^{\circ}\text{C}$ (Rivkina et al. 2000; Deming 2002; Price and Sowers 2004). The adaptation of psychrophilic yeast species to cold environments is reflected in their structural and biochemical characteristics, e.g. the production of cold-adapted

enzymes, cryoprotectant wall carbohydrates, pigments, as well as higher amounts of polyunsaturated fatty acids in cytoplasmic membranes and a high amount of intracellular lipids (Thomas-Hall et al. 2010). The complex adaptation strategies of cold-adapted yeasts to low temperatures are reviewed in Chaps. 9, 10, 11, 12, 13, 14 and 15.

In spite of the adaptations studied at the cellular level, the ecological role of the yeasts in cold environments remains mainly unknown. Their heterotrophic metabolism and ability to degrade organic macromolecules through the secretion of extracellular hydrolytic cold-adapted enzymes suggest their potential auxiliary role as biogeochemical nutrient recyclers; however, more studies are needed to clarify complex connections between yeasts and other microbial communities, particularly in the cryosphere. Also, more focus should be given to the complex interplay of interactions amongst not only biological, but also chemical and physical factors. Particularly processes occurring at water–ice interfaces, e.g. solute concentration, pressure and the physical state of the water and ice, rather than the effect of temperature alone should be emphasised. For example in permafrost, 2–7 % of the water persists as briny liquid films and lenses (cryopegs) that form as a result of the salting out of soils as the *in situ* temperature drops and remains at about -10°C . Therefore, our understanding should not be limited only to psychrophilic and psychrotolerant yeasts, but should also include the eco-physiological group of yeasts, which live at the critical interface inherent to the phase change of (saline) water to ice.

It is well known that the polar environments are increasingly threatened by the global overheating; particularly the glaciers are retreating most rapidly. Since the glacier habitats (cryosphere) include some of the largest unexplored and extreme biospheres of Earth, this phenomenon determines the potential complete loss of an as yet unexplored reservoir of unknown microbial species. The influence of climate change on fungi is just beginning to be evaluated in the Arctic. Evidence from palaeobotanical studies and from contemporary warming experiments alike indicates that the Arctic soil fungal communities have responded to, and are likely to respond to, climate warming. The analyses of the DNA preserved in the ancient permafrost in northeastern Siberia have revealed that fungal communities changed in concert with plant communities after the last Ice Age. As the environment altered, the tundra became dominated by shrubs and trees, which expanded into the previous tundra steppe and fungal communities changed from yeast-like and parasitic fungi to communities with root-associated macrofungi (Timling and Taylor 2012). In this context, the isolation and *ex situ* conservation of the psychrophilic microorganisms can be seen as a means of avoiding their possible extinction. Yeasts inhabiting the Arctic environment efficiently spread via air, soil, water, marine animals, including those that inhabit deep sea vents (Burgaud et al. 2010), and polar birds (Dynowska et al. 2013), and seed their immediate environment, affecting the local geobiochemistry. It remains mainly unclear to what extent the air and water currents can transport the yeasts globally to temperate zones, where they can find refuge either in the refrigerated food or in other cold man-made environments. This is certainly an issue that is gaining importance with

the accelerated disappearance of the polar environments and the increased release of microbes in non-polar areas.

The importance of psychrophilic and psychrotolerant yeasts has also increased due to the mounting evidence that the biosphere has experienced several extremely low temperature periods, perhaps even during the earliest stages in the emergence and evolution of life. The Earth has been covered in ice four times through the Snowball Earth periods. These episodes ranged from 3 to 30 million years each (Bodisetsch et al. 2005). The entire world ocean was frozen near the time of origin of the eukaryotic cell and the adaptive radiation of Metazoa. It has been hypothesised that the endemic descendants of the primitive cold-adapted microorganisms can live today in rock, lakes, sediments and in subglacial ice. Since 'microbial endemism' is currently a much debated issue in microbial ecology, the polar regions and other extreme environments should be amongst the first places to be examined for the evolutionary processes that could give rise to microbial speciation (Vincent 2000; Gostinčar et al. 2010). Since yeasts have reaffirmed themselves as one of the ecologically most successful eukaryotic lineages, they represent important model organisms, which have developed little-investigated adaptive strategies that are crucial for successful survival in some of the harshest and most extreme environments on our planet.

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