Chapter 5
Rock-Inhabiting Fungi in Antarctica: New Frontiers of the Edge of Life

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5.1 Introduction

Adverse conditions in several places on the Antarctic continent are life-limiting factors (Ruisi et al. 2007). However, microorganisms can colonise the cracks and cavities in different types of rocks in Antarctica. Within such microhabitats, temperature, light, and available water result in a micro-climate favourable for colonisation by specific microorganisms (Gorbushina 2007). However, the rock surface is considered an inhospitable environment because of extreme temperature conditions, rapid changes in water activity and high ultraviolet (UV) radiation found in the region (Staley et al. 1982). Despite extreme conditions, distinct microbial communities are found inside rocks (called endolithic organisms) and on their surface (called epilithic organisms) (Warscheid and Braams 2000).

The microbial community in rocks usually comprises cyanobacteria, chemoorganotrophic bacteria, lichenised fungi (lichens), and non-lichenised fungi (Gorbushina 2007). Fungi are easily dispersed and settle on and colonise different substrates in different environmental conditions. The fungal community in rocks is formed by taxa sharing common macro- and micro-morphological characteristics

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but having different phylogenetic origins, which are called melanised fungi and micro-colonial fungi (MCF) (de Hoog and Grube 2008), represented by endemic (Onofri et al. 1999; Øvstedal and Lewis Smith 2001; Selbmann et al. 2005) and cosmopolite species (Gonçalves et al. 2017).

Rock-inhabiting fungi use various strategies to withstand extreme conditions and establish themselves successfully in this microhabitat. Mycosporines found in some fungi isolates from different rocks (Ruisi et al. 2007) function as photoprotectors and are associated with the survival, restricted growth and longevity of these fungi (Gorbushina et al. 2003). Meristematic growth and the presence of melanin in some species minimise the exposure of the colony surface to solar radiation and protect them against UV radiation (Gorbushina 2007). The thick melanised wall in many of these fungi is presumably a stable and highly effective protective barrier against UV radiation (Sterflinger et al. 2012). In contrast, endolithic fungi found inside rocks are protected from UV radiation by the habitat in which they are isolated (Gorbushina 2007).

Biological communities in rocks can survive extreme changes in planetary surface conditions to maintain viability for up to 100 years in the absence of liquid water, energy, and nutrient sources to induce cellular damage or death and to survive direct exposure to high doses of solar energy and cosmic radiation on the rock surface (Gorbushina et al. 2002). In this context, melanised fungi associated with rocks represent unique eukaryotes that can be used as study models for astrobiology, since they inhabit ecosystems exposed to high UV radiation and extreme temperatures, with scarce availability of water and nutrients.

Earlier studies have characterised a community of endolithic fungi associated with rocks from extreme environments such as deserts (Sterflinger et al. 2012; Gonçalves et al. 2015) and historical monuments exposed to high incidences of UV radiation and having low availability of water and nutrients (Sterflinger 2010b; Ruibal et al. 2008). In contrast, few studies have characterised the fungal diversity in rocks of the Antarctic continent, even though these environments represent a promising source of extremophilic fungi and eukaryotic models to study the limits of life and its applications in astrobiology (Onofri et al. 2004). Recent studies on the in vitro pathogenic potential of fungi obtained from Antarctic rock samples have highlighted the importance of conducting further investigations to identify possible pathogens that may pose a risk for humans by widespread dispersion owing to climatic changes on our planet (Gonçalves et al. 2017; Alves et al. 2019).

5.2 Rocks as Fungal Micro-Habitats

Rocks are naturally occurring solid materials composed of varying proportions of one or more minerals, which, in turn, are crystalline solids with a defined chemical composition and may include organic remains (Plummer and McGeary 1996). Rocks can be classified into three types: igneous, metamorphic, and sedimentary. The corresponding rock-forming environments are also classified similarly.

Igneous rocks are formed by the cooling and consolidation of magma (or melt). Magma is a molten material whose chemical composition depends on whether it is formed on the mantle or the crust of the planet. The density of magma is lesser than that of the surrounding solid material (country rocks), and its temperature and chemical composition influence its viscosity. While moving, magma can get lodged inside the fractures of the lithosphere or extrude on its surface, becoming lava in the latter case. In both cases, magma can form different types of rocks. When magma cools internally, it forms intrusive or plutonic igneous rocks, which have a higher mineral growth time (e.g. granites and gabbros). Plutonic rocks are varied, and their shape depends on their relationship with country rocks, commonly forming dikes, sills and batholiths. When magma extrudes on the surface, it cools faster, forming extrusive or volcanic igneous rocks (e.g. basalts and andesites).

When exposed, rocks may get weathered on contact with surface environmental conditions. Weathering is the set of physical and chemical processes that lead to the disaggregation (mechanical fragmentation) and decomposition (geochemical alteration) of rocks (Fig. 5.1). The main chemical weathering agents are liquid solutions, which may be acid rain (H_2CO_3) or organic acids released by organisms that colonise the rock surface. The minerals originally present in the rock interact with these weathering solutions to form new minerals, which are more adapted to the surface conditions. A leaching solution containing the most soluble chemical elements is also formed. The weathering of rocks results in the formation of soils that constitute a terrestrial layer (pedosphere), which is a product of the interaction between the lithosphere, biosphere, atmosphere and hydrosphere.

The action of agents such as water, wind, ice and gravity can lead to soil erosion. These agents also carry the eroded materials (sediments) and deposit them near or far from the source area. In the places where they are deposited, sediments consolidate by forming cements or because of the pressure exerted by the weight of the sedimentary package between the grains. This process is called diagenesis and results in the formation of sedimentary rocks or clastic sedimentary rocks (e.g.

Fig. 5.1 Examples of rocks in Keller Peninsula, King George Island, and South Shetland Archipelago, Antarctica, subjected to physical (**a**) and chemical (**b**) weathering in Antarctica. A rock fragment disaggregated by cryoclasts, which consists of breakage promoted by the increase in water volume through the cycles of freezing and thawing. (**b**) Reddish portions indicate the oxidation and remobilisation of iron in sulphide-enriched rocks. (Photos Credits: FS Oliveira)

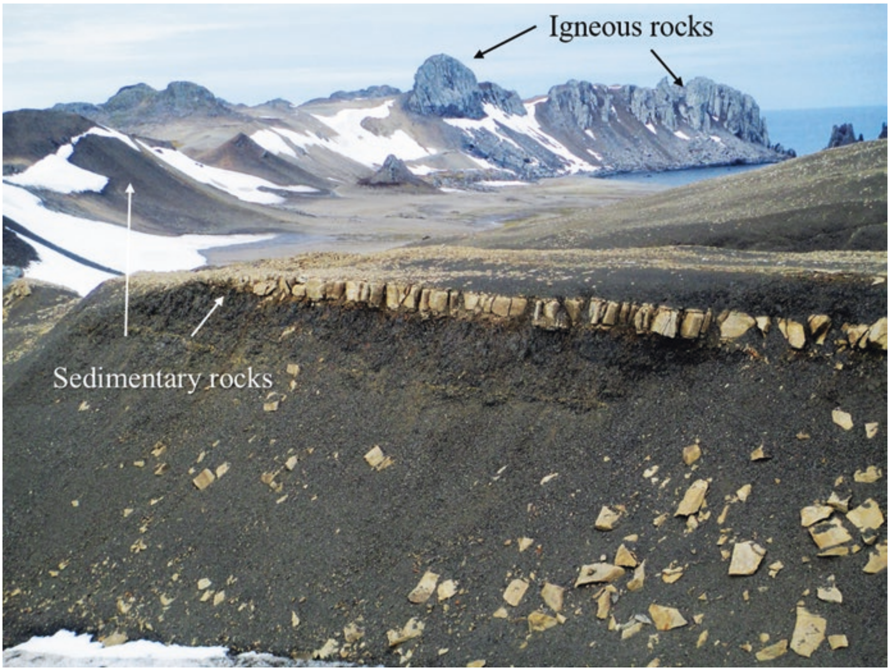

Fig. 5.2 Upper Jurassic-Lower Cretaceous sedimentary rocks and igneous intrusive rocks of Antarctic Peninsula Magmatic Arc in the President Head Peninsula, Snow Island, Antarctica. (Photos Credits: FS Oliveira)

sandstones, argillites, conglomerates and gaps). Chemical sedimentary rocks, such as some limestones, are formed by the precipitation of chemical compounds dissolved in water. The evolutionary history of several sedimentary rock-forming environments can be reconstituted by studying the features of these rocks, which usually have strata and layers produced by sedimentation processes (Fig. 5.2).

Metamorphic rocks are formed from the transformation of igneous and sedimentary rocks (Fig. 5.3). They can be created under conditions of high pressure and temperature in the interior of the planet. When a rock is tectonically positioned at a depth between 3 and 20 km, the pressure and the temperature conditions unsettle the original rock and transform its original minerals into new ones, whereas recrystallisation transforms its size and habit. Consequently, new texture and mineral assemblies are created. These transformations are called regional metamorphism, and represent one metamorphism type.

Igneous, metamorphic and sedimentary rocks can be transformed into one another. The spatial scale on which these transformations are manifested is global (called the rock cycle), and they are usually related to the lithosphere dynamics and the behaviour of the continental and oceanic plates. Correspondingly, the time scale also varies from millions to billions of years, and hence, processes that occur over a very long temporal scale, as opposed to those occurring over a shorter time scale

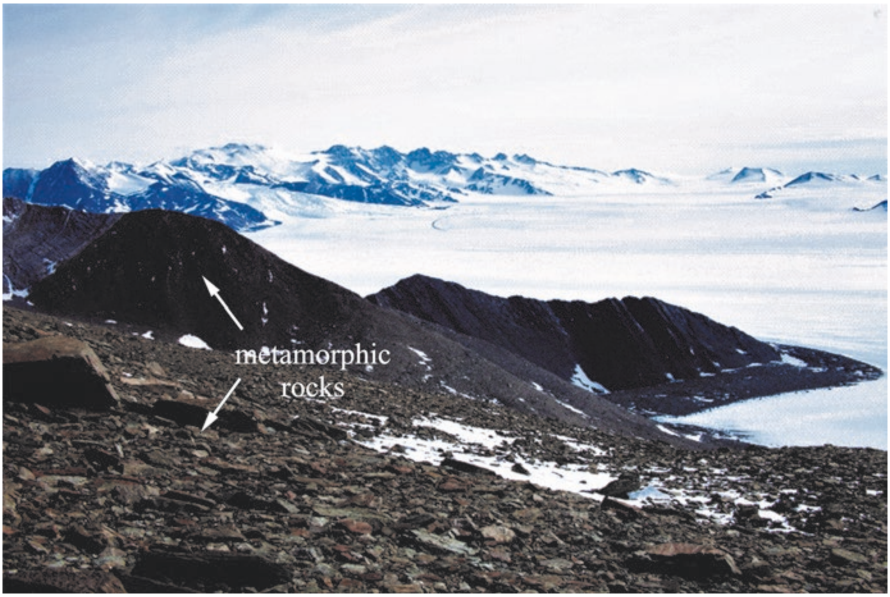

Fig. 5.3 Metamorphic rocks (phyllites and quartzites) from the Ellsworth Mountains, continental Antarctica. (Photos Credits: FS Oliveira)

(e.g. biological processes), are considered when studying the geological history of the planet. Nonetheless, rocks and geological events are strongly related to biotic systems and can influence the evolution of life. More importantly, they provide the habitat for various organisms.

For microorganisms, rocks may represent distinct microhabitats depending on the nature of the colonisation (Burford et al. 2003a). The characteristics of the rocks, their position in the landscape and the environmental conditions influence the type of organism inhabiting the rock and the form of microbial colonisation. Thus, understanding the fungal colonisation in rocks helps in understanding the interaction between the extrinsic and intrinsic factors of rocks. The extrinsic factors include the environmental aspects (climate, solar radiation, position in the landscape, wind and others) and biological aspects (types of colonising organisms and their adaptive capacity) (Gadd 2007). The intrinsic factors are related to the physical and chemical properties of rocks, in particular, their compositional, textural and structural aspects.

The compositional aspects are related to rock mineralogy and, consequently, the chemical composition of rocks (Wolfaardt et al. 1994; Rogers et al. 1998). The mineral composition of rocks can influence several microbial processes, such as energy generation, nutrient acquisition, cell adhesion and biofilm formation (Gadd et al. 2005; Gadd 2007). Rocks are composed of distinct mineral assemblies based on their forming environment. Some minerals may be rich in elements such as Fe, Mg, Ca, K, P, S and C, while others in Si and Al. Depending on the nutritional requirements of organisms, rocks containing certain minerals may be more suitable habitats than others (Gleeson et al. 2006). Additionally, minerals are weathered on rock surfaces in a distinctive way, with some being more resistant than others (such as quartz). Consequently, microbial access to mineral nutrients is related to the degree of resistance to weathering that the minerals exhibit and to the capacity of the organism to promote this access, considering that some microorganisms play an important role as agents of bioweathering, as discussed later.

The textural aspects include mineral organisations and their physical properties. Rock-forming environments favour specific types of mineral assemblies that may influence microbiological communities. Igneous rocks, for example, when extruded, have thicker, randomly arranged minerals with more closer inter-grain contacts. In contrast, in metamorphic and sedimentary rocks, minerals are organised in specific textures, which can vary from very oriented mineral foliation (schistosity) to compositional bands (separated felsic and mafic minerals) and stratified planes. Some of these organisations may facilitate the penetration and/or storage of water, making the rock more humid, influencing rock temperature, or representing segregation between specific types of minerals, as observed in the case of dark and light bands in metamorphic rocks (Fig. 5.4). In addition, the minerals can be thick or thin, which

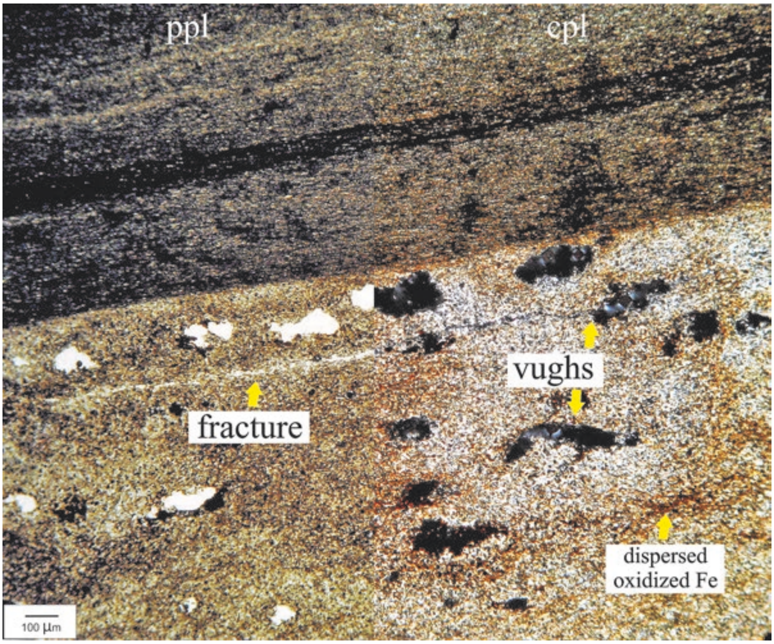

Fig. 5.4 Photomicrographs obtained through petrographic microscopy in polar polarised light (PPL) and crossed polarised light (CPL) of a sericitic phyllite from the Ellsworth Mountains, continental Antarctica, with alternation of dark and light bands. The lighter bands are more fractured than the dark bands, which may be related to the differential expansion of the rock. In addition, the light band has dissolution cavities, sometimes filled, and zones with dispersed oxidised iron, suggesting that they have undergone chemical weathering more efficiently. (Photos Credits: FS Oliveira)

can directly affect rock porosity and the degree of mineral alteration. Thus, not only mineral composition but also their physical and physicochemical properties such as microtopography, surface charge and hydrophobicity may influence microbial colonisation (Fredrickson et al. 1995; Bennett et al. 1996; Gadd 2007).

Structural aspects include rock features such as humidity, temperature variation and gaseous flow that influence their behaviour. Rock porosity, presence of fractures, surface roughness and the actual colour of the rock are the main features. The pores (inter-grain spaces) and fractures (grain fragmentation in linear features) are conductors of water and gas, creating microhabitats suitable for certain microorganisms. Depending on the type of rock, the porosity will be higher or lower, and there may be distinctions between the proportion of macropores and micropores. Highly porous rocks – such as thick sedimentary rocks (psamtics) – are more efficient in water infiltration, which in turn depends on pore size and connectivity: larger pores transport water more efficiently and smaller pores retain it. Some petrogenetic processes such as magmatic cooling form less porous rocks as the growth of the minerals in such rocks generates closed suture planes with well-defined grain contacts. However, the situation changes based on how this cooling occurs. In extrusive igneous rocks, faster cooling can generate fractures that compensate for the loss of volume in the liquid-solid transformation. Likewise, depending on the volatile content in the magma, the rock can be enriched with vesicle-like pores. Intrusive igneous rocks can also contain many fractures because these rocks are formed at great depths, and their presence on the surface indicates that the overlying material has been eroded. In this process, the rocky body tends to undergo decompression, which leads to the formation of fractures (also known as relief joints).

The colour of the rocks and their surface roughness are related to aspects such as temperature (absorption and propagation of heat) and surface moisture. The rock colour depends on the minerals present and their state of weathering. Darker or greenish rocks are typically enriched with mafic minerals, usually of iron-magnesium composition. Lighter rocks are composed of felsic minerals, usually quartz-feldspars. When weathered, iron-rich minerals become oxidised, which attributes a reddish to yellowish coloration to the rocks. Darker rocks tend to retain more heat and, therefore, are more easily heated. The dilation between dark and light minerals is distinct and can generate micro-fractures in the contacts between them. If the rock is composed of thick minerals, it will typically exhibit a more irregular exposed surface. This surface roughness directly influences water retention, facilitating colonisation by biofilms.

5.3 Geological Overview of Antarctica and the South Shetland Islands

The geological framework of the Antarctic continent comprises a set of tectonic landscapes, as reflected in the chemical and petrological characteristics of its rocks and sediments. Generally, in the active convergent margins, there are common plutonic and volcanic associations as well as their metamorphic counterparts. The tholeiitic, calc-alkaline to alkaline chemical signature is a common characteristic of its rocks and is normally observed in their associated sediments. Divergent constructive margins such as mid-ocean ridges and back-arc basins mainly have a tholeiitic signature in their volcanic rocks. Within plate sceneries, the magmatism is normally associated with hot spots, having an alkaline to tholeiitic signature (Wilson 2007).

Several authors consider the term platform to be synonymous to craton, describing a tectonic stable part of the continent (Suess 1885; Kober 1921), normally with the oldest crust and rocks of the continent. Cratons are derived from a continuum set of tectonic processes in time and in different areas (from plate margin, within plate) (Condie 2013) and possess a great diversity of rocks with variable chemistry signatures, similar to an airplane black box.

Like other continents in the world, Antarctica possesses a set of tectonic sceneries with a Precambrian platform – the East Antarctic Shield and a Phanerozoic (post 540 My) mobile belt, and West Antarctica (including the Antarctic Peninsula). Both were sutured during the Ross Orogeny in the Cambro-Ordovician times (c. 540–480 My) (Fig. 5.5a).

The East Antarctic Shield is the oldest and biggest part of Antarctica, comprising a set of smaller Archaean cratonic cores (older than 2.5 Ga) surrounded by relatively younger Proterozoic mobile belts (2.5 Ga–540 My) and established in their current

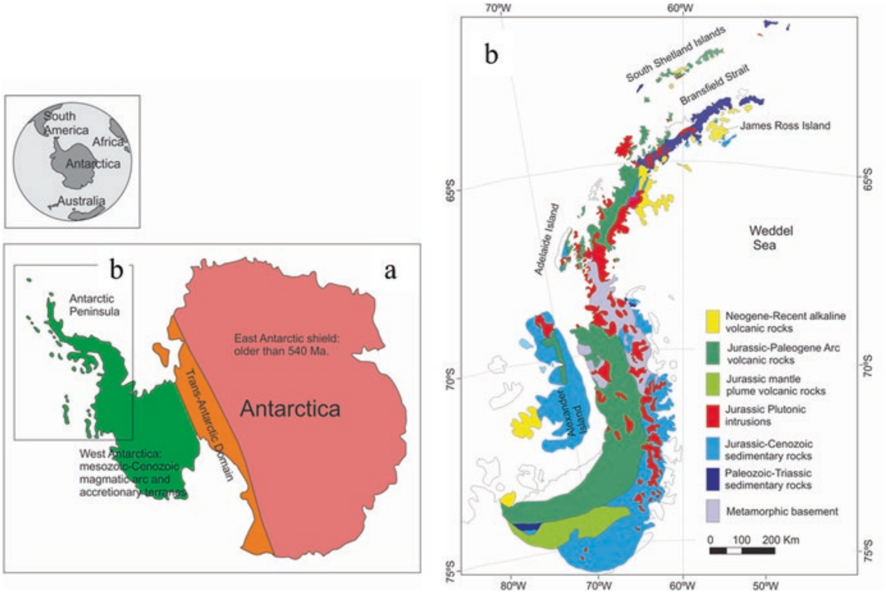

Fig. 5.5 (**a**) Tectonic domains in Antarctica. (Modified from Harley (2009)) and (**b**) geological sketch of the Antarctic Peninsula and South Shetlands Islands. (Modified from Burton-Johnson and Riley (2015))

configuration during the Pan-African Orogeny (c.700–500 My) (Vaughan et al. 2005; Fütterer et al. 2006).

The West Antarctic Shield is composed of five distinct terrenes: the Antarctic Peninsula, Thurston Island, Marie Bird Land, the Ellsworth-Whitmore Mountains (the southern region adjoining the Transantarctic Mountains) and the Haag Nunatak (Storey et al. 1988). Some of these terrenes were accreted in the western Pacific margin of Gondwanaland during the Ross Orogen (c. 540–480 My) (Ellsworth-Whitmore Mountains and Haag Nunatak), coeval with the East and West Gondwana collisional event (Tessensohn et al. 1999; Hervé et al. 2006). The other terrenes were structured in an orogenic belt during Mesozoic times (Birkenmajer 2001; Hervé et al. 2006). The limits and sutures between them are marked by strike-slip zones, further separated by rifts during the Gondwana breakup (Storey et al. 1998; Hervé et al. 2006).

The Antarctic Peninsular configuration can be associated with domains that represent the amalgamation of terrenes of different ages and compositions (Vaughan and Storey 2000), although most of them are parautochthonous. They are associated with turbiditic sequences in an accretionary wedge (the Trinity Peninsula Group and Le May Group) (Birkenmajer 2001; Hervé et al. 2006); low-grade metamorphic complex with turbiditic properties (the Scotia Complex) (Birkenmajer 1994); Jurassic calc-alkaline intrusive rocks, Antarctic Peninsula Batholith (Hervé et al. 2006) or Andean Intrusive Suite (Hawkes 1962; Barton 1961); and Jurassic to Lower Cretaceous basaltic and andesitic lava complex (the Antarctic Peninsula Volcanic Group (Gledhill et al. 1982) (Fig. 5.5b).

The accretionary wedge-related units, intrusive batholitic series, and low-grade metamorphic complex have their counterparts in the Patagonian and Fuegan segments of the Andes (Hervé et al. 2006), representing the continuity of the orogenic process in Mesozoic times, before the Gondwana breakup (Dalziel 1984; Trouw et al. 1997). In this context, the Trinity Peninsula Group was deposited during the Permian-Triassic, in the fore-arc region, as a turbiditic association of pelites and wackes with associated pillows and hyaloclastite, metamorphosed in prehnite-pumpellyite facies (Hyden and Tanner 1981; Hervé et al. 2006).

During the Middle to Upper Jurassic, lacustrine and alluvial beds of Mount Flora Formation were deposited in the back-arc region over the eroded Trinity Peninsula Group. Simultaneously, the crustal units were intruded by the calc-alkaline intermediate to acid magmatism (Andean Intrusive Suite) and its volcanic counterparts (Birkenmajer 2001).

In the Cretaceous to Palaeogene times, the subduction process evolved, and the magmatic arc was shifted to the west, beginning the formation of the South Shetland arc. During the Oligocene, this migration induced an extensional regime into the lithosphere, between the older magmatic arc (Antarctic Peninsula) and the newer arc, opening the Brasfield rift (Birkenmajer 1992, 1994). In general, the magmatism ages in this orogenic zone became newer from south to north, evidencing a migration of the subduction zone (Birkenmajer 1992, 1994). Thus, the geological record of the more southern Snow and Smith Islands to the tip of Robert Island and

Greenwich Island, further to the north, show that magmatism and Jurassic-Cretaceous sedimentary units are more closely related to the Antarctic Peninsula, whereas on King George Island, the Palaeogenic record shows the same (Smellie et al. 1984; Birkenmajer 1994).

The tectonic scenery of the Bransfield retro-arc and the counter clockwise rotation of the continent during the Cenozoic induced subsea and terrestrial volcanism and created a structural framework in the South Shetland Islands that was dominated by tectonostratigraphic compartments limited by directional and transcurrent faults. The chemical signature of the magmatism is predominantly calc-alkaline to tholeiitic (Birkenmajer 1994, 2001). In King George Island, for example, Tectonic structuring is determined from chemical signatures of blocks separated by faults. Here, formal lithostratigraphic units are individualised (Barton 1965; Birkenmajer 1980; Smellie et al. 1984; Birkenmajer 2001), some of which are possibly synchronous but with no clear genetic and temporal relationships.

Thus, the rich geological history of Antarctica ensured the presence of a diverse lithology that includes all types of rocks in the Antarctic continent (Fig. 5.6) and the

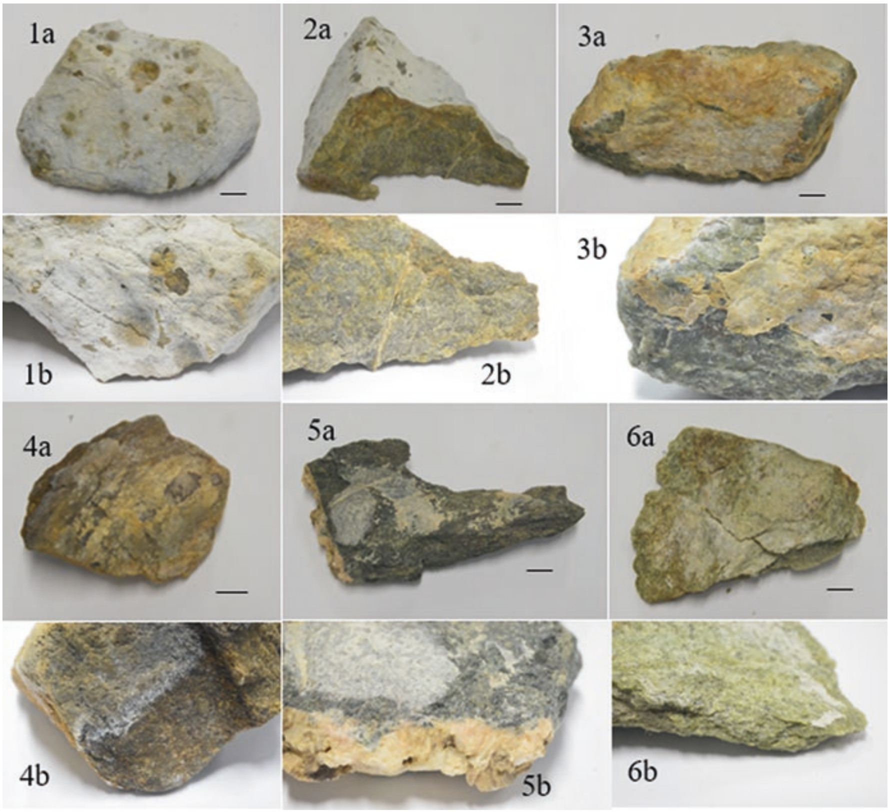

Fig. 5.6 Rocks from the Ellsworth Mountains of Continental Antarctica sources of epilithic and endolithic fungi. (Photos Credits: LH Rosa)

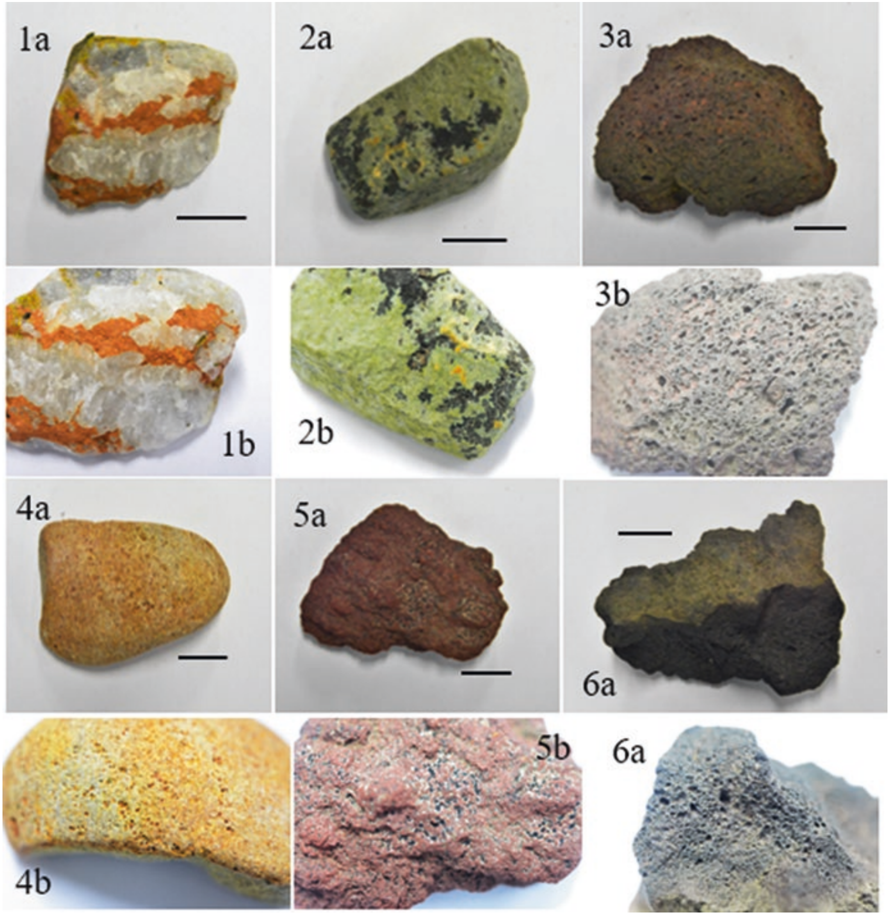

Fig. 5.7 Rocks from the Antarctic Peninsula as sources of epilithic and endolithic fungi. (Photos Credits: LH Rosa)

Antarctic Peninsula (Fig. 5.7). With the development of the polar cap from the Eocene, most of these rocks were covered by thick ice sheets. Nevertheless, in the ice-free areas, where thawing during the summer exposes the surface, it is possible to observe a diversified geology, which includes igneous, metamorphic and sedimentary rocks. These areas, specifically in the South Shetlands Archipelago, the Ellsworth Mountains and the Antarctic Peninsula, rock samples were collected to study fungal diversity (Gonçalves et al. 2017).

5.4 Geological Adaptations Facilitating Hospitable Rock Habitats

The mineral constituents of rocks are weathered by physical (mechanical), chemical and biological processes; each process acts according to the environment and its conditions (Ferris et al. 1987; Banfield et al. 1999; Vaughan et al. 2002). Rocks undergo bio-weathering to form mineral soil through diagenesis or mineral dissolution (Ehrlich 1996; 1998) by the action of microorganisms (May 2003; Gadd et al. 2005, 2006) such as bacteria, fungi and algae (Ehrlich 2002; Burford et al. 2003b; Gleeson et al. 2005, 2006), which excrete chemical agents such as inorganic acids (sulphuric and nitric acids), organic (citric, oxalic and gluconic acids) and binder products such as siderophores (Greek *sideros* = iron, *phores* = transporter) to aid in the process of bio-weathering. Additionally, reactive mineral constituents of rocks (Fe, Mn, S^{2-} or $SO4^{2-}$) undergo oxidation or reduction to assist this phenomenon. Microbial bio-weathering acts on all igneous and sedimentary rocks, including siliceous rocks (silica, silicates and aluminosilicates) and calcareous rocks (Ehrlich 1996, 1998).

The surface of exposed rocks presents environmental constraints such as temperature and humidity fluctuations, intense solar radiation and lack of nutrients that influence the colonisation, growth and development of microorganisms (Gorbushina 2007), making the rocks one of the most inhospitable habitats for microbial life (Staley et al. 1982). The temperature on the surface of the rocks varies greatly (ranging from −45 to +60 °C). Similarly, the availability of water also varies as rock surfaces might go through long periods of almost total desiccation or torrential desert rains may result in the formation of water films on them. Rock surfaces are also exposed to relatively low doses of cosmic radiation at night and extremely high infrared and ultraviolet (UV) radiation on summer days. Sudden rains can cause the availability of nutrients and energy sources to range from zero to abundant on the surface of rocks (Gorbushina 2007).

Black MCF, black yeasts, lichenised fungi, and cyanobacteria are among the most stress-tolerant organisms living on Earth (de Hoog and Grube 2008). They exhibit adaptations to tolerate multiple stresses and are characterised as polytolerant to environments with multiple and variable stress parameters (Gorbushina 2007). Microorganisms ensure their survival and success through community growth (Costerton and Stoodley 2003). Biofilms formed on rocks consist of algae, cyanobacteria, heterotrophic bacteria, lichenised and non-lichenised fungi, as well as free-living organisms (such as MCF), and microscopic animals (such as mites and insects) (Gorbushina and Petersen 2000; Gorbushina 2007).

5.5 Subaerial Biofilms in Rocks

The lithosphere, an area of interaction between a solid substrate and the atmosphere, is an ancient terrestrial and inhospitable niche that first housed microbial associations when biofilms were the only life-forms on Earth (Gorbushina 2007). Microbial biofilms are represented by heterogeneous matrices of microorganisms concentrated in one interface (usually solid–liquid) and typically surrounded by an extracellular polymer substance (Rosenberg 1989; Hall-Stoodley et al. 2004).

These microbial communities are fossil records, mainly from hydrothermal environments. Supposed filaments in a biofilm, dating back 3.2 billion years, were found in rocks obtained from the bottom of the sea at Pilbara Craton in Australia. Additionally, microcolonies were also identified in a biofilm dating back 3.3–3.4 billion years, found in the formation of Kornberg in South Africa (Westall et al. 2001). These data confirm that the complex organisation, specialisation and functioning of these microbial communities have evolved over the years, and they have been able to establish themselves in various extreme environments such as in ice, hot springs and on rock surfaces (Chertov et al. 2004).

Subaerial biofilms (SABs) are microbial communities that develop on a solid mineral surface exposed to the atmosphere and are mainly composed of algae, bacteria, cyanobacteria, and fungi (Gorbushina 2007). Owing to the considerable environmental adversities that rocks present, colonies of free microorganisms rarely form on this substrate; instead, the formation of SABs in rocks guarantees the survival and success of these organisms. SBA formation follows the topographic profile of the substrate, which can include cracks, pores, mineral grains and cementing material (Gorbushina 2007). Bioreceptivity is the potential that the rock surface presents for colonisation by one or more groups of living organisms without causing bio-weathering (Guillitte 1995) and is directly dependent on petrographic parameters such as mineral composition, porosity and permeability of the rock material, which help to define the microbial community of SABs (Warscheid and Braams 2000). SAB microorganisms are classified according to the shape that they establish on the surface of the rock as epilithic (microorganisms that grow on the rock surface) of the rock and cryptoendolithic (microorganisms that penetrate a few millimetres inside the rock) (Warscheid and Braams 2000).

SABs are initially formed by photoautotrophic microorganisms (algae and cyanobacteria), which use sunlight and CO_2 from the atmosphere as a source of carbon and energy (Gorbushina 2007). Heterotrophic microorganisms (most bacteria and all fungi) require some organic source for their growth, which is provided by the metabolism of phototrophic organisms or the deposition of particles in the atmosphere (Suihko et al. 2007). All these organisms are embedded in arrays of extracellular polymeric substances (EPS) (Characklis and Marshall 1990) that describe SABs (Fig. 5.8a) and its interactions (Fig. 5.8b). The chemical composition of EPS is heterogeneous: more than 99% water, heteropolysaccharides, uronic acids, a few proteins (Konhauser 2007), and nucleic acids (Tolker-Nielsen 2006). EPS function as barriers against toxic metal ions that trap scarce nutrients, prevent bacteriophage and amoeba infections, prevent desiccation (Singleton 2005), provide the microorganisms in the biofilm with carbon and energy sources, and protect the microorganisms from high temperatures and freezing (Konhauser 2007). EPS also aid in the distribution of water in the biofilm during periods of rain and the distribution of the reserve water during periods of drought. Furthermore, it also plays a fundamental role in the maintenance of cell viability and the access to atmospheric water vapour (Gorbushina 2007).

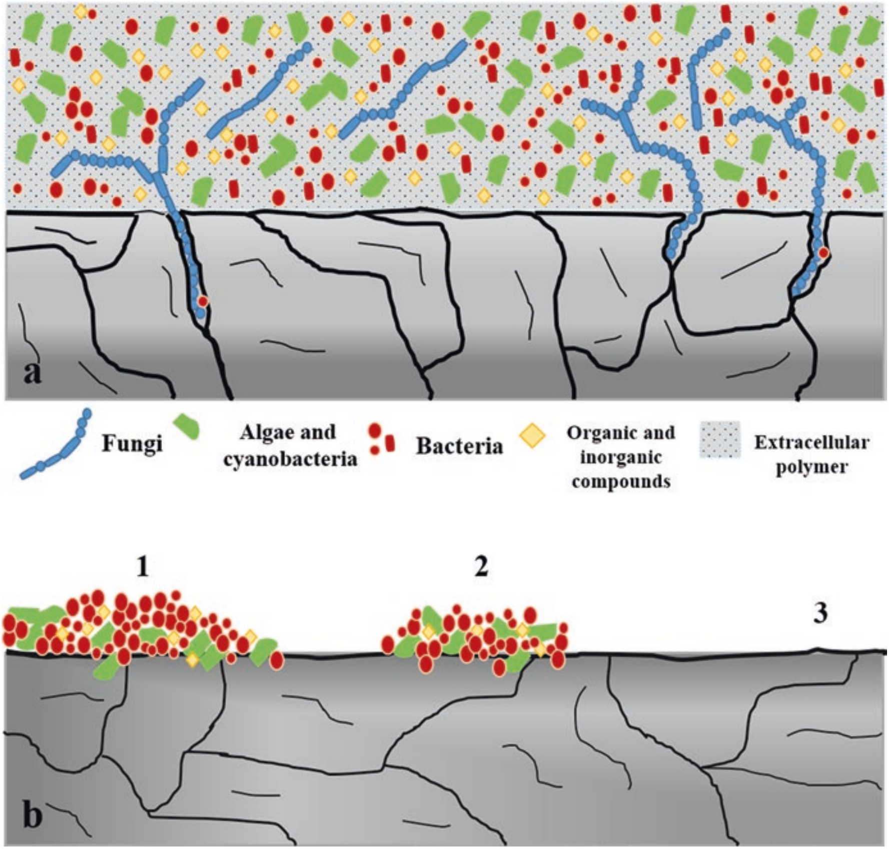

Fig. 5.8 Schematic representation of subaerial biofilms (SABs) and interactions. (**a**) Different microorganisms embedded in an EPS matrix, forming a small microbial ecosystem. (**b**) SABs form between the lithosphere and atmosphere, and the interactions observed at their interface are as follows: (**1**) between the organisms composing the SAB, (**2**) between the biofilm and atmosphere, and (**3**) between the atmosphere and substrate. (Adapted from Gorbushina (2007))

5.6 Fungi-Inhabiting Rocks

Fungi inhabit rocks as free forms or as biofilms by symbiotic associations with photobionts through the process of lichenisation (lichenised fungi, also known as lichens) (Gorbushina 2007). Fungi present on the rock surface contribute to its bioweathering, playing a role in the formation of the soils and, consequently, in the supply of soluble nutrients to the microbial community in this substrate (Burford et al. 2003a).

Fungi-inhabiting rocks can be classified as follows: epilithic fungi, which colonise the rock surface and grow as lichens or in biofilms; endolithic fungi, which grow in pre-existing cracks and crevices of the rocks and are visible on the rock surface; and cryptoendolithic fungi that grow a free life forms in cavities and pores formed by their mechanical action (Gorbushina 2007). Under extreme conditions restricting life (such as temperature extremes and water and nutrient shortages), fungi actively penetrate the rock and are not visible from the substrate surface (Gorbushina 2007). Fungi-inhabiting rocks can also be classified into two taxonomically and ecologically distinct groups: (i) soil *Hyphomycetes* of epiphytic origin (de Leo et al. 1996) and melanised micro-colonies, with the latter forming compact micro-colonies, and (ii) *Ascomycetes* of the orders *Chaetothyriales*, *Dothideales* and *Capnodiales* (Staley et al. 1982; Gorbushina et al. 1993; Diakumaku et al. 1995; Wollenzien et al. 1995; Sterflinger et al. 1999).

Mycelial growth and the ability of some fungal species to grow dimorphically, i.e. to change their filamentous growth to yeast-like growth, contribute to their predominance in BSA (Gorbushina and Panina 1992; Gorbushina et al. 1993; Wollenzien et al. 1995). The mycelial growth facilitates the penetration and utilization of the nutrients of the rock, while the microcolonial growth or cells similar to the one of a yeast, is adopted in case of nutritional scarcity or environmental stress (Gorbushina 2007).

Black MCF form a polyphyletic group that is found in rocks in the free-living form (Staley et al. 1982; Ruibal et al. 2008). MCF exhibit a meristematic growth pattern, which provides an optimum surface/volume ratio (Wollenzien et al. 1995), decreases water loss and minimises colony contact surface on exposure to sun and other chemical and physical stresses (Sterflinger 2010a). MCF have an in situ and in vitro growth rate of 1–5 mm per month, expend little energy with dispersion and sporulation (Gorbushina 2003; Gorbushina et al. 2003) and can reproduce by isodiametric division (Sterflinger 2006). Owing to their considerable morphological plasticity, they can explore different substrates ranging from saline to acidic (Ruibal et al. 2005, 2008; Plemenitaš and Gunde-Cimerman 2005; Selbmann et al. 2005, 2008, 2014a; Egidi et al. 2014; Isola et al. 2016). MCF are distributed worldwide, and in addition to colonising exposed rock surfaces, they have been isolated from Mediterranean monuments (Urzì et al. 1991; Wollenzien et al. 1995; Ruibal et al. 2005, 2008; Isola et al. 2016), Antarctic rocks (Selbmann et al. 2015a, b), and solar panels (Martin-Sanchez et al. 2018). In addition to morphological adaptations, MCF have distinct cellular characteristics: cells are mainly composed of complex lipids, the presence of pigments and a dense cell wall (Selbmann et al. 2008), as detailed in Table 5.1.

Table 5.1 Special cellular characteristics of micro-colonial fungi (MCF) according to Selbmann et al. (2008)

Cell composition	Cell wall	Pigments
Mono-, di- and triacylglycerols	Chitin	Melanins
Phosphatidylcholine	Melanin	Carotenoids (colourless and brown–red)
Phosphatidylethanolamines	Polysaccharides	
Sterols, sterol ethers		
Phosphatidylethanolamines and free fatty acids		

MCF-inhabiting rocks synthesise the pigment melanin in their cell walls (Gorbushina et al. 1993; Diakumaku et al. 1995), which protects the fungus from UV radiation and gives it mechanical strength to penetrate the cracks of the rocks (Gorbushina 2007). Dadachova and Casadevall (2008) reported that melanised fungi can produce adenosine triphosphate (ATP) by a mechanism called 'radiotropism'. Based on the resistance and adaptability exhibited by melanised fungi in environments with high ionising radiation, the authors concluded that the radiation could alter the electrochemical properties of melanin to enable the pigment to function in energy transduction and, consequently, increase the growth of melanised fungi. Thus, MCF are considered interesting organisms for studies on adaptation to severe conditions (Kogej et al. 2006). Likewise, rocks are interesting targets for research on survival-related characteristics in hostile environments (Gorbushina et al. 2003).

5.7 Fungal Diversity and Distribution in Antarctic Rocks

The fungal communities in rocks of extreme environments such as hot deserts (Gonçalves et al. 2015), historical monuments (Sterflinger 2010b) and rock formations exposed to UV radiation (Ruibal et al. 2008) have been studied for some years. The earliest studies were mainly conducted on cyanobacteria and algae present in rocks in the 1970s and 1980s by Friedmann (1977, 1982) and Friedmann and Ocampo (1976). Friedmann et al. (1987) monitored the climatic conditions to which the cryptoendolithic community was exposed in the Ross Desert in Antarctica. However, considering the territorial expanse of the Antarctic continent, the knowledge about the fungal community-inhabiting rocks in different ecosystems remains limited.

Studies about fungal diversity isolated from Antarctic rocks involve the observation of these microorganisms in the substrate itself, through cultivation techniques or culture-independent techniques. Table 5.2 includes some of the fungal taxa observed in rock samples collected from different sites in the Antarctic continent and peninsula. However, the attempt to cultivate fungi from rock samples collected from northern Victoria Land was not successful (Onofri et al. 1999). Small portions of rocks were inoculated onto plates containing malt extract culture media and incubated at 10 °C and 30 °C; however, the rapid growth of psychrophilic and psychrotolerant fungi prevented the development/growth of pure cultures. For this reason, the description of the new genus *Friedmanniomyces* and the species *Friedmanniomyces endolithicus* was based on the morphological characteristics observed in the natural substrate.

New species of the non-lichenised fungus *Lichenothelia antarctica* was obtained from rocks in the Signy and Lynch Islands, Antarctica (Øvstedal and Lewis Smith 2001). The genus *Lichenothelia* has also been isolated from the stalk of lichenised fungi, and hence, members of this genus have been included in studies of lichenised fungi. Selbmann et al. (2005) isolated 20 meristematic fungi, identified as *Cryomyces*

Table 5.2 Distribution of fungi found in rocks collected from Continental Antarctica and the Antarctic Peninsula

Location	Taxon	References
Continental Antarctica		
Northern Victoria Land	*Friedmanniomyces endolithicus*	Onofri et al. (1999)
Different sites	*Lichenothelia antarctica*	Øvstedal and Lewis Smith (2001)
	Cryomyces antarcticus	Selbmann et al. (2005)
	Cryomyces minteri	
	Friedmanniomyces simplex	
	Friedmanniomyces endolithicus	
	Dothideales spp.	
McMurdo Dry Valleys	*Taphrina antarctica*	Selbmann et al. (2014b)
Ellsworth Mountain	*Acremonium* sp.	Gonçalves et al. (2017)
	Byssochlamys spectabilis	
	Cladosporium halotolerans	
	Cladosporium sp.	
	Debaryomyces hansenii	
	Rhodotorula mucilaginosa	
	Penicillium chrysogenum	
	Penicillium cf. *coffeae*	
	Penicillium citrinum	
	Penicillium tardochrysogenum	
Different sites	*Acarospora* sp.	Coleine et al. (2018)
	Acarosporaceae	
	Alternaria sp.	
	Aspergillus sp.	
	Aureobasidium pullulans	
	Buellia sp.	
	Cryomyces antarcticus	
	Cryptococcus sp.	
	Dothideales	
	Dothideomycetes	
	Eurotiomycetes	
	Friedmanniomyces endolithicus	
	Fusarium proliferatum	
	Lecanorales	
	Lecidea cancriformis	
	Lecidea laboriosa	
	Parmeliaceae	
	Penicillium sp.	
	Pezizales	
	Pleosporales	
	Saitoella coloradoensis	
	Sarcinomyces crustaceus	

(continued)

Table 5.2 (continued)

Location	Taxon	References
	Solicoccozyma aeria	
	Sporormiaceae	
	Verrucaria sp.	
Antarctica Peninsula		
Deception Island	*Eichleriella* sp.	Alves et al. (2019)
	Fusarium sp.	
	Lecanoromycetes sp.	
	Cladophialophora sp.	
	Pseudogymnoascus sp.	
	Rhodotorula mucilaginosa	
	Penicillium sp.	
	Penicillium sp.	
	Phaeosphaeria sp.	
	Protomyces inouyei	
	Pseudogymnoascus destructans	
	Thelebolus globosus	
Robert Island	*Antarctomyces pellizariae*	
	Candida sp.	
	Cladophialophora sp.	
	Cladosporium sp.	
	Cladosporium sp.	
	Cladosporium sp.	
	Curvularia sp.	
	Helotiaceae sp.	
	Protomyces inouyei	
	Vishniacozyma victoriae	
King George Island	*Acremonium* sp.	
	Cladosporium sp.	
Penguin Island	*Cyphellophora* sp.	
	Paracladophialophora sp.	
	Paracladophialophora sp.	
	Penicillium chrysogenum	
Livingston Island	*Paracylindrocarpon* sp.	
Nelson Island	*Glarea* sp.	
	Penicillium tardochrysogenum	

antarcticus, *Cryomyces minteri*, *Friedmanniomyces endolithicus*, *Friedmanniomyces simplex* (species endemic to Antarctica), and six unidentified isolates of the order *Dothideales*, from samples of sandstone, granite and soils from several Antarctic sites.

The isolates were identified by morphological and physiological techniques and sequencing of the internal transcribed spacer (ITS) region. With the exception of one isolate, all were characterised as psychrophiles capable of growing in a temperature range of 0–20 °C. The fungi had a thick melanised cell wall, produced exopolysaccharide and exhibited meristematic growth and were, therefore, considered well adapted to withstand the extreme conditions in cold deserts such as Antarctica. The cryptoendolithic community demonstrated a life cycle similar to those observed in algae and cyanobacteria, which is considered to be an important strategy for survival in hostile environments and may be further related to possible forms of life that could be found beyond Earth, such as on Mars, where the initial conditions resemble the cold deserts of Antarctica.

Two novel yeast isolates were obtained from Antarctic rock samples collected in northern and southern Victoria Land (from the Dry Valleys region). The yeasts were phylogenetically reclassified within the genus *Taphrina*, and owing to low sequence similarity with other yeasts, and species *Taphrina antarctica* (Selbmann et al. 2014b).

Gonçalves et al. (2017) studied the diversity of cultivable fungi in rocks collected from the Ellsworth Mountains region, located in the ice sheet of western Antarctica in the Heritage Range of the Antarctic continent. Unlike other studies, Gonçalves et al. (2017) obtained 71 isolates that were identified by morphological and molecular techniques as belonging to the genera *Acremonium*, *Byssochlamys*, *Cladosporium*, *Penicillium*, *Debaryomyces,* and *Rhodotorula*. The rock samples were subjected to mineral analysis and classified into quartzites or phyllites with cavities partially filled by secondary materials rich in iron or aluminium. These characteristics suggest that the rocks underwent biogeochemical modification, perhaps caused by fungal bio-weathering.

Using culture-independent techniques such as ITS region sequencing, Coleine et al. (2018) investigated the diversity and structure of the cryptoendolithic fungal community in sandstone samples obtained from along a gradient ranging from 1000 to 3300 m altitude. The predominant organisms were lichenised fungi and *Dothideomycetes*. The operative taxonomical units (OTU) included *Solicoccozyma aeria*, *Lecanorales*, *Acarosporaceae* spp., *Cryomyces antarcticus*, *Friedmanniomyces endolithicus*, *Basidiomycota* spp., *Buellia* sp., *Sporormiaceae* spp., *Fusarium proliferatum,* and *Penicillium* sp. Based on their results, Coleine et al. (2018) suggested that the studied fungal community was highly adapted but had limitations to environmental disturbances and was not influenced by abiotic factors.

Alves et al. (2019) investigated the diversity of cultivable fungi in rocks obtained from different islands (King George, Penguin, Nelson, Robert, Half Moon, Livingston, and Deception Islands) belonging to the South Shetlands Archipelago of in the Antarctic Peninsula. In their study, 386 isolates, identified through molecular biology techniques, were obtained: *Acremonium*, *Antarctomyces*, *Cladophialophora*, *Cladosporium*, *Curvularia*, *Cyphellophora*, *Eichleriella*, *Fusarium*, *Glarea*, *Lecanoromycetes*, *Paracladophialophora*, *Paracylindrocarpon*, *Penicillium*, *Phaeosphaeria*, *Protomyces*, *Pseudogymnoascus*, *Rhodotorula*, *Thelebolus*, and *Vishniacozyma*. In addition, 14 taxa (which included unusual genera or genera identified at high taxonomic hierarchical levels) showed low coverage and identities when compared to sequences of known species deposited in GenBank, indicating that these taxa may represent new species of Antarctic fungi. Broadly speaking, the diversity, richness and dominance of the fungal community observed in this study were high compared to other Antarctic habitats. The rock samples were also subjected to petrographic analysis and classified into seven types: basalts, andesites, granite, rhyolite, diorite, gaps and tufts. Andesites, basalts, rhyolites and breccias showed the highest fungal diversity and were also the most abundant rocks in the South Shetland Islands, which suggests an important interaction between biological colonisation and regional geology.

5.8 Rock-Inhabiting Fungi and Astrobiology

The theory of panspermia suggests that simple life forms may have collided with Earth after a long period of permanence in space and developed, throughout evolution, the forms of life known today on the planet (Paulino-Lima and Lage 2009). Alternately, lithopanspermia – a theory complementary to panspermia – proposes the transfer and ejection of viable living material off the origin planet, resistance to the conditions of space and intact arrival of the biological material on the target planet (Onofri et al. 2012). Astrobiology addresses the possibility of extra-terrestrial life searching for remnants of processes and structures of biological origin outside Earth (Des Marais et al. 2008; Des Marais and Walter 1999; Gargaud et al. 2011).

The choice of physical, chemical, biological and environmental factors and living organisms as models for astrobiological studies is important because of the following factors: (i) the analogy between geological, biological, or environmental conditions helps to elucidate processes on Earth that can be extrapolated to other planets and validate and interpret information obtained by satellites and other space exploration equipment; (ii) these factors are necessary for testing astrobiological research instruments, field exploration procedures, and, furthermore, preparing astronauts for future space missions; and (iii) to evaluate the possibility of extra-terrestrial life by means of appropriate model microorganisms, it is essential to investigate how life persists and resists these conditions (Fairén et al. 2010; Martins et al. 2017). The motivation for studying astrobiology extends beyond technological development and knowledge about the solar system and galaxies. Astrobiology studies and conclusions are dependent on the development of several interrelated areas that constitute this scenario and are applicable to different sectors such as engineering, biotechnology, food and pharmaceutical industry, philosophy, politics, and economics (Paulino-Lima and Lage 2009).

Choosing a model living organism to elucidate the possibility of existence of extra-terrestrial life is crucial; in the last few decades, extremophilic microorganisms have been garnering interest as suitable model organisms, expanding the concept of limits for microbial growth (Antunes et al. 2011; Ferrer et al. 2012; Stock et al. 2012; Shtarkman et al. 2013). Prokaryotic organisms have already demonstrated an advantage for colonisation and establishment in extreme environments, but in recent years, studies have shown that besides colonising these environments, eukaryotes may show a greater degree of resistance than that exhibited by prokaryotes (Shtarkman et al. 2013; Horneck et al. 2016; Pacelli et al. 2017). MCF-inhabiting Antarctic rocks exhibit adaptations that enable them to establish in and explore hostile environments, making them potentially suitable eukaryotic models for astrobiology studies. The cold desert in the Dry Valleys of McMurdo, Antarctica, is the largest ice-free area of Antarctica, where the air temperature varies from −20 to −50 °C in winter and −15 to 15 °C in summer, whereas the temperatures tend to be higher on the soil surface. The area is also arid and receives high solar irradiation (Onofri et al. 2008). These conditions have been postulated to resemble the conditions prevailing on Mars (Onofri et al. 2004) and have been simulated to assess the ability of eukaryotic microorganisms to survive at the edge of life.

Cryomyces antarcticus, a cryophilic black MCF with optimal growth below 15 °C and endemic to the region, was isolated from rocks and soil in the deserts of McMurdo Dry Valleys in Antarctica (Selbmann et al. 2005). *Cryomyces antarcticus* is considered as the most extremophilic eukaryote known in the present day and shows resistance to solar radiation, radioactivity, desiccation and oligotrophic conditions, analogous to space and Mars (Onofri et al. 2004, 2008). Therefore, *C. antarcticus* and other species of black rock fungi have been used as eukaryotic models in astrobiological studies and experiments with gamma radiation (Onofri et al. 2004). *Cryomyces antarcticus* is considered as the best model organism for astrobiological studies. Several studies have been conducted to evaluate its phenotypic plasticity and survival in hostile conditions such as space exposures in the European Space Agency-European Technology Exposure Facility (ESA-EUTEF), Lichens and Fungi Experiment (LIFE) (Onofri et al. 2012, 2015) and Biology and Mars Experiment (BIOMEX) (de Vera et al. 2012), proving that its tolerance to extreme conditions extends from high and low temperatures, desiccation, and lack of nutrients to lethal doses of ionising and UV radiation (Onofri et al. 2008, 2012, 2015; Selbmann et al. 2011).

Some pioneering studies have sought to understand the relationship between fungi that inhabit extreme environments limiting life, confined in pristine regions of the planet, and their virulence potential in humans because little is known about the behaviour of these organisms and their response if they come in contact with human beings.

Approximately 5% of fungal species cause some type of disease in mammals (Kwon-Chung and Bennett 1992). Among the disease-causing fungi, some species of melanised fungi are considered opportunistic with significant clinical importance (de Hoog et al. 1994, 1998, 2000). Chromoblastomycosis, a disease which causes lesions on the skin, can be caused by species of the order *Chaetothyriales*, and it exhibits an invasive meristematic phase with muriform cells (Matsumoto et al. 1984). Muriform cells are also known as sclerotic bodies, fumagoid cells (name given to brownish fungal corpuscles), or Medlar cells and are polyhedric fungal elements with septation in two distinct planes, formed to aid adaptation to hostile conditions.

Concomitant to adaptation in extreme environments, virulence factors for humans, plants and animals have been found in unknown species of fungi in unexplored regions, such as Antarctica, promoting attention to the fungal community found in Antarctic rocks. Gonçalves et al. (2017) were the first to describe an opportunistic, in vitro pathogenic behaviour of fungal species isolated from the rocks of the continental Antarctic desert. According to their study, taxa that have one or more physiological characteristics with pathogenic profiles are phylogenetically close to opportunistic and/or mycotoxigenic pathogens and suggesting that these taxa may represent primitive eukaryotic organisms with genomes that can be used to study the evolutionary origins of opportunistic virulence in fungi.

From these results, new questions about the pathogenic potential of fungi isolated from Antarctic rocks were addressed by Alves et al. (2019) in their study, which found 159 taxa capable of growing at 37 °C, belonging to the genera *Penicillium*, *Fusarium*, and *Rhodotorula*. Physiological in vitro tests such as determination of haemolytic activity, protease and phospholipase production, temperature-induced dimorphism, spore diameter, ability to grow at different pH ranges and determination of minimal inhibitory concentration (MIC) of amphotericin B were performed on these isolates to understand and evaluate their pathogenic potential. *Penicillium chrysogenum* obtained from Antarctic rocks exhibited several physiological factors of pathogenicity and has been reported in other studies as an etiological agent of systemic diseases in immunocompromised patients (de Hoog et al. 2000).

5.9 Conclusions and Perspectives

Although extreme conditions on the Antarctic continent limit life, fungi often inhabit the surface and interior of different rocks in the region, either by symbiotic associations or as a free-living form. In these extreme ecosystems, the fungal community may contribute to the bio-weathering of the rocks, playing a role in soil formation and, consequently, in the supply of soluble nutrients to the microbial community in this substrate. Non-lichenised fungi found in the natural environment of the rocks tolerate different stresses through various adaptive strategies and successfully survive in this substrate. The microbial community in these ecosystems is generally composed of endemic taxa with very specific physiological characteristics. Recent studies have reported that cosmopolitan taxa may also be present in Antarctic rocks and form a community comprising epilithic, endolithic, and cryptoendolithic fungi. Understanding the composition of the fungal community in Antarctic rocks, their adaptations to the environmental conditions and the influence of abiotic factors on these microorganisms has considerable importance; currently, however, there are very few studies on the cryptoendolithic community of Antarctica. In this context, studies aiming to investigate the fungal diversity in Antarctic rocks through cultivation techniques and metagenomic approaches and studies related to environmental data such as rock composition and climatic measurements, as well as the physiological, biochemical, genetic, and evolutionary evaluation, are crucial to understand the dynamics of the fungal community in Antarctica.

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