

Chapter 3

Fungal Diversity in Antarctic Soils

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Abstract Fungi have contributed to Antarctic ecosystems for >200 million years as, from the fossil record, it has been shown that fungi were present in Antarctica since at least the Triassic Period. Fungi have been reported from a wide variety of soils and substrates in far-ranging geographical locations and diverse habitats in Antarctica; the first reports being from as early as the beginning of the twentieth century. In Antarctic studies, non-lichenized fungi have generally been considered separately from lichenized forms and the list of non-lichenized fungi reported from Antarctic regions (including the sub-Antarctic) is extensive at +1,000 species. Fungi are notorious contaminants especially around sites of human activity, and it is crucial to acknowledge the difficulty of discerning transient/introduced versus indigenous and endemic fungi, and to understand their respective contributions to terrestrial biodiversity. To identify fungi, rigorous decontamination procedures on substrates are used along with conventional culturing methodologies and molecular technologies. This chapter focuses mainly on studies concerning terrestrial non-lichenized fungi published since 1993 and highlights specific taxonomic groups that are most important to Antarctic soil ecosystems.

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3.1 Introduction

Research on Antarctic fungi has occurred since the late 19th/early 20th century (Bommer and Rousseau 1905; Brown 1906) and much of the published work on soil microbiology was reviewed in a comprehensive way by Vishniac (1993). The list of non-lichenized fungi reported from Antarctic regions (continental as well as sub-Antarctic islands) is currently freely available for reference online through the British Antarctic Survey (Bridge et al. 2009). Given the number and variety of non-lichenized Antarctic fungal species recorded so far in their extensive review, Bridge and Spooner (2012) suggested that “fungi may be the most diverse biota in the Antarctic”. The present review attempts to build upon Vishniac (1993) by focusing on studies published since 1993 and highlighting regional investigations and specific taxonomic groups that are thought to be most important to Antarctic soil ecosystems. The sub-Antarctic Islands are generally not considered in this chapter as those ecosystems are influenced by a more temperate climate. Fungi in cryptoendolithic communities are covered in another chapter in this book (Chap. 9) as well as further detail on fungi found in ornithogenic soils (Chap. 6), and the potential effects of climate change on Antarctic fungal communities (Chap. 13).

3.1.1 Methods for Identification and Detection

Prior to the advent of the polymerase chain reaction (PCR) and more readily available sequencing technologies in the 1980s and 1990s, taxonomic identification of fungal isolates was primarily based on morphological characteristics. This by itself has proven problematic for many fungal clades based on the somewhat subjective nature of these assessments and the high degree of required mycological expertise. It has proven particularly difficult in the case of Antarctic fungi, which in some cases are thought to have lost or reduced morphological defining features (de Hoog et al. 2005) and also rarely produce sexual fruiting structures (Connell et al. 2010; Onofri et al. 2007). In the second decade of the 21st century, identification of fungal isolates is almost entirely based on molecular sequence comparisons. Although this is advantageous in that isolate phylogeny can be compared more objectively between different research groups, it is becoming increasingly clear that identification is dependent on, in some cases, non-curved public databases of dubious reliability (Bidartondo et al. 2008) and the paucity of sequences in general.

Culturing-based studies constituted the bulk of earlier Antarctic mycological investigations. The main advantage of these techniques is that they can be readily adapted to quantify abundances via serial dilutions and a library of isolates can be compiled for further study. The rather glaring disadvantage is that it is estimated only a small percentage of microbial organisms are capable of growing in known cultural media and a substantial bias towards fast growing and frequently

sporulating fungi can occur, as plating techniques preferentially count spores over hyphae (Vishniac 1996). Additionally, differing results dependent on the use of selective versus non-selective media and differences in time of year sampled illustrate that a “diversity of methods results in a greater diversity of species being detected” (Wyn-Williams 1996). Techniques that permit isolation of fungal deoxyribonucleic acid (DNA) from total environmental DNA, such as denaturing gel gradient electrophoresis (DGGE) (Arenz et al. 2006; Yergeau et al. 2007a), and direct cloning of DNA fragments have been used to gain a more comprehensive view of Antarctic fungal communities (Bridge and Newsham 2009; Lawley et al. 2004; Jumpponen et al. 2003) with the caveat that the detected organisms may not represent viable organisms. Metagenomic techniques such as pyrosequencing and illumina sequencing and functional genomic studies allow for more comprehensive studies of microbial community composition, abundance, and functionality (Yergeau et al. 2012; Teixeira et al. 2010) yet, to date, studies targeting Antarctic fungi have been few. Though molecular studies have greatly improved community inventories, they are prone to potential PCR and primer bias (Lawley et al. 2004). Truly comprehensive studies of fungal communities should employ both traditional culturing-based studies and molecular techniques in a complementary process.

3.1.2 Cosmopolitan Versus Endemic

A question, which has arisen frequently among Antarctic researchers, is how do we define “native” fungi versus temporary transients? Fungal vectoring can occur over long distances due to atmospheric circulation, birds and animals, and fungi are notorious contaminants especially around sites of human activity. Many species of fungi have great dispersal potential as confirmed, for the Antarctic Peninsula related to specific weather events, by spore trap data (Marshall 1996). In addition, the ability of many fungi to remain in a viable yet dormant spore stage for long periods of time complicates the issue. The practical implication of these concerns is that detection of a particular fungal species in soil or other substrate is often not considered definitive evidence that the species has a true ecological role to play in Antarctica. The presence of “cosmopolitan” species such as *Alternaria*, *Penicillium*, *Aspergillus*, *Cladosporium*, and others are particularly problematic due to their wide dispersal potential and ubiquitous association with human structures and material (Ruisi et al. 2007). Rigorous sterile procedures must be used when sampling to avoid contamination by the sampler. Fungi generally found to be restricted to areas of human activities strongly suggest human introduction (Azmi and Seppelt 1998).

Vincent (2000) postulated that Antarctica would be among the first place to look for microbial endemism, “if microbial endemism (i.e. genotypes of bacteria, protists or other microorganisms specific to a geographical region) is at all possible”, given the separation of Antarctica from Gondwanaland >10 million years

ago, presence of highly specialized niches, differences in environmental stability, and environmental selection pressure for specific adaptive strategies. However, Bridge and Spooner (2012) concluded that “The great majority of non-lichenized fungi so far described from the Antarctic are cosmopolitan species that also occur elsewhere, and there is relatively little evidence for either local co-evolution or significant numbers of endemic species”. Somewhat ironically, it may actually be easier to establish endemism rather than indigenism because a species simply has to be found in Antarctica and nowhere else in the world. Putative endemic status can then be assumed, provided the fungal species is not subsequently found elsewhere in an active role in a non-Antarctic location. Novel fungal species that have been described from Antarctic locations are listed in the attached Appendix.

Establishment of indigenous status (presence AND activity in Antarctica but also in non-Antarctic sites) is actually more problematic as it involves establishing metabolic activity or adaptation. Several criteria (Vishniac 1996) have been proposed to establish indigenous status, as follows:

1. *Visible growth in situ*. This is particularly problematic for Antarctic fungi, which very rarely form macroscopic fruiting structures. An exception is shown in Fig. 3.1, a fruiting body of *Galerina autumnalis*. Mushrooms and other macroscopic fruiting bodies of fungi are not common in Antarctica but they can be found infrequently on the Peninsula.
2. *Occurrence correlations with appropriate environmental variables such as organic matter*. Examples are frequently isolated species from highly specialized substrata, such as the keratinophilic *Geomyces pannorum*, which Vishniac (1996) described as “probably indigenous”.
3. *Growth preference of temperatures below 15 °C (psychrophile) and ability to survive freeze thawing*. This may be difficult to determine for reasons discussed in the next section but finding Antarctic isolates with lower temperature preferences than related non-Antarctic strains is at least some evidence of local adaptation.

3.1.3 Temperature Requirements

Most fungi isolated from Antarctic material are cold tolerant rather than true psychrophiles. Cold tolerance, e.g. psychrotrophic, involves capability of growth at around 0 °C (Gerday et al. 1997) but an optimum temperature for growth in the mesophilic range, above 15 °C (Robinson 2001; Vincent 2000). *Hydropisphaera peziza* and *Theobolus microsporus* are psychrotolerant strains of mesophiles isolated from Antarctic soils and adapted to grow at temperatures as low as 1 °C (Azmi and Seppelt 1997). Using the definitions of Morita (1975) and Gounot (1986), true psychrophiles would display maximum growth below 15 °C. It has been speculated that the paucity of true psychrophiles is due to Antarctic soils being dramatically affected by solar warming, and thus, native fungi must be

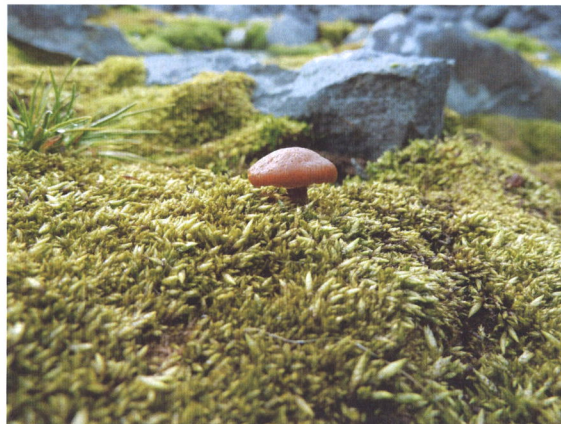


Fig. 3.1 Fruiting body of *Galerina autumnalis* (Syn = *Galerina marginata*) growing from moss on Anslers Island, Antarctica. Photo courtesy of Carolyn Lipke, Palmer Station, National Science Foundation

adapted to accommodate wide temperature swings. Thirty-five isolates from soil samples taken from a range of locations in Victoria Land between 72°30'S and 77°52'S, including hot soil samples from Mt Melbourne, gave 31 psychrotolerants, two psychrophiles, and one thermotolerant mesophile, demonstrating that within a defined locality, there exists considerable diversity (Zucconi et al. 1996). Robinson (2001) reviewed the subject of fungal adaptations to cold environments, which included abbreviated life cycles, lower saturation of phospholipid membranes, cryoprotectants and anti-freeze proteins, and enzymes that had greater activity at lower temperatures. Lower temperature preferences can also partly be explained by the work of Xiao et al. (2010), demonstrating anti-freeze protein activity in Antarctic fungal isolates, which also were demonstrated to be psychrophiles. Antarctic psychrophilic fungi have been isolated from cryptoendolithic communities (Selbmann et al. 2005; Weinstein et al. 2000) and glacial ice (Turchetti et al. 2011) as well as soils. Psychrophilic yeasts, designated “obvious indigenes”, were isolated from soils and in areas associated with melt streams with visible moss and lichen growth (Vishniac 1996). Xiao et al. (2010) reported a psychrophilic ascomycete species, *Antarctomyces psychrotrophicus*, isolated from the soils of the maritime and continental areas of Antarctica, suggesting a wide distribution of this fungal species in Antarctica.

3.1.4 Limiting Soil Factors

Antarctic soils are a challenging environment for many microorganisms; in addition to being frequently very cold (but subject to wide temperature swings in the Austral Summer) they tend to be highly oligotrophic, relatively saline, and very dry with limited water-holding capacity. Wyn-Williams (1996) described the fundamental importance of microorganisms, including microfungi, to the functioning of Antarctic ecosystems in the absence of macroscopic terrestrial animals. Vishniac (1996) speculated that as fungi are biodegraders and abundant on organic substrata, they have "analogous functions to cyanobacteria in the stabilization and amelioration of the soil structure". Arenz and Blanchette (2011) demonstrated, using 245 soil samples from 18 different locations throughout the Antarctic continent, that fungal abundance was more positively correlated with the percentage of total carbon than any other soil edaphic characteristics; soil moisture was also positively correlated with fungal abundance, while pH and conductivity (salinity) were negatively correlated. Organic carbon in soil is most likely due to input from primary producers whether they be from autochthonous or allochthonous sources, and so fungal abundances and diversity are likely to be strongly influenced by the presence of these organisms in the environment. In the Arenz and Blanchette (2011) study, it was not uncommon for soil samples to yield no culturable fungal organisms, especially from the sites with limited carbon. A related study using introduced sterile wood samples buried in the soil for 2 or 4 years found that the immediately surrounding soil could support significantly higher fungal abundances (1–2 orders of magnitude) than more distant background soils (Arenz and Blanchette 2011). The results of these studies indicated that the oligotrophic nature of most Antarctic soils is the primary factor limiting fungal presence and abundance. Soil characteristics such as nitrogen, pH, salinity, and moisture and climatic factors (temperatures and light regimes) are likely affecting fungi more indirectly through their direct influence on primary producer presence. This trend was also noted by Yergeau et al. (2007a) with soil microbial abundances (fungi and bacteria) significantly associated with location/plant-cover interactions and vegetation-related edaphic characteristics.

3.2 Fungi in the Fossil Record and Glacial Ice

Fungi have been present in Antarctica since at least the Permian period with many examples of diverse fossil fungi being found from the Triassic and Jurassic Periods, as demonstrated by paleomycological and paleoecological investigations (Harper et al. 2012; Stubblefield and Taylor 1983; Taylor and Osborne 1996; Taylor and White 1989). The fossil record from Antarctica suggests the potential relationships that existed were similar to those among the major groups of extant fungi including endogonaceous mycorrhizal associations and wood-decaying

fungi, which are widespread today throughout the world (Stubblefield and Taylor 1983; Taylor and White 1989). The presence of fungi in silicified gymnosperm woods (Fig. 3.2) and in peat deposits has provided an important source of information on how these fungi functioned as major decomposers of organic matter, including lignin, for over 200 million years (Kidston and Lang 1921; Stubblefield and Taylor 1983; White and Taylor 1989). Taylor and White (1989) introduced the hypothesis that some of these fungi were likely terrestrial saprophytes, degrading organic materials, and evolving on shorelines and in swamps, where organic materials accumulated prior to the evolution of land plants. Other studies indicated that some fossil fungi were tree parasites and colonized living trees where they exhibited interactions with tyloses and other tree defenses (Harper et al. 2012) or caused wood degradation (Stubblefield and Taylor 1983). The finding of white pocket rot in *Araucarioxylon* and *Vertebraria*, from the Triassic and Permian periods, respectively, demonstrates that fungi with the ability to selectively degrade lignin occurred early in the evolution of fungi and remarkably, had very similar decay patterns to modern day fungi that produce white pocket rots in living trees (Blanchette 1991). Recent molecular clock analyses of 31 fungal genomes representing a wide range of wood-decay basidiomycetes suggest that the ability to degrade lignin corresponds to the end of the Carboniferous period (Floudas et al. 2012). The fossil record from Antarctica appears to hold some of the first evidence of these wood-destroying fungi and their effects on wood.

Fungi have also been found in glacial ice, with fungal spores and hyphae often remarkably well preserved. Taylor et al. (1997) and Ma et al. (2000) described detection and characterization of fungi trapped in glacial ice from Greenland, and the oldest glacial ice from which viable organisms have been recovered was 750,000 years old from Western China (Christner et al. 2003). This work has been extended to fungal recovery in Antarctic ice ranging in age from less than 500 to approximately 200,000 years old, demonstrating that most of the fungi recovered were similar to contemporary fungi, and revealing a higher number of ascomycetes than basidiomycetes (Patel 2006). Additional research that focuses on the ancient fungi trapped in ice is needed to further advance our knowledge on the biology, ecology, and diversity of non-lichenized fungi existing in Antarctica.

3.3 Specific Taxa and Genera

Onofri et al. (2004) reported that in Antarctica, 0.6 % of the known fungal species were water moulds (Kingdom Chromista) and 99.4 % were composed of true fungi including yeasts (unicellular organisms) and filamentous fungi from the phyla Chytridiomycota, Zygomycota, Ascomycota, and Basidiomycota. In general, the fungal communities of Antarctic soils are dominated by filamentous ascomycetes with basidiomycete yeasts also a strong component, particularly in the Dry Valleys (Arenz and Blanchette 2011; Connell et al. 2008). Filamentous basidiomycetes have been very rarely isolated (Ludley and Robinson 2008) and even their



Fig. 3.2 Transverse section of silicified *Araucarioxylon*, an ancient gymnosperm, from the Fremouw Peak locality in the Beardmore Glacier area, Antarctica with a white pocket rot caused by a wood-decay fungus. This fossil wood is from the Triassic period and demonstrates the presence of fungi interacting with trees in Antarctica >200 million years ago. Diameter of the fossil wood shown is approximately 7 cm. Photograph by the authors, fossil wood from Thomas Taylor, University of Kansas

typically dominant role as wood-decay fungi in temperate ecosystems has been taken over by ascomycetes in Antarctica (Blanchette et al. 2004b). However, a few filamentous basidiomycetes have been reported including *Sistotrema brinkmannii* found in the Antarctic Dry Valleys (Hao et al. 2010) and *Fibulobasidium* and *Tremella* species on the Antarctic Peninsula (Arenz and Blanchette 2011). Zygomycetes are also isolated with some frequency although not typically as dominant components of fungal communities, with some possible exceptions (Lawley et al. 2004). Chytridiomycota are not frequently reported but were noted to be highly abundant representatives of clone libraries in a specific-site associated with frequent snowmelt (Bridge and Newsham 2009). As they were the dominant components of fungal biodiversity in similarly unvegetated but high elevation soils in Nepal and Colorado (Freeman et al. 2009), it may be that the relative paucity of chytrid isolations has been due to reliance on traditional culturing techniques, which bias against them. Using techniques more specifically designed to target them, Chytridiomycota were isolated from freshwater Antarctic lakes and ponds (Paterson 1973).

Bridge and Spooner (2012) list over 400 fungal genera that have been reported from Antarctic regions (including the sub-Antarctic). However, the list of fungal genera that are reported most frequently from the Antarctic Continent, Peninsula, and immediate surrounding islands can be condensed into a much shorter list.

Ascomycota–Filamentous: *Alternaria*, *Aspergillus*, *Cadophora*, *Cladosporium*, *Epicoccum*, *Geomyces*, *Paecilomyces*, *Penicillium*, *Phaeosphaeria*, *Phoma*, *Scolecobasidium*, and *Thelobolus*

Ascomycota–Yeasts: *Aureobasidium*, *Candida*, *Chaetomium*, *Debaryomyces*, and *Exophiala*

Basidiomycota–Yeasts: *Cryptococcus*, *Rhodoturla*, and *Mrakia*

Zygomycota: *Mortierella* and *Mucor*

3.4 Fungi on the Antarctic Peninsula

The Antarctic Peninsula has a warmer and more humid climate than the rest of continental Antarctica. This is of course partly due to the lower latitude of most of the Peninsula, but it also benefits from a prevailing and relatively warm ocean current impacting from the west. This effect is especially strong on the western coast of the Antarctic Peninsula, which has many more ice-free locations than the eastern coast and has been described as having a maritime climate. These relatively warm and humid conditions allow soils on the Peninsula to support more abundant and diverse fungal communities than other ice-free locations on the continent.

A recent culturing-based study revealed substantially greater fungal species richness in Peninsula soils (0.66 unique Operational Taxonomic Units [OTU] per soil sample) relative to the soils of the Ross Sea Region (0.28 unique OTUs per soil sample) although it must be acknowledged that the Peninsula survey drew from a greater number of sampling locations (Arenz and Blanchette 2011). However, Lawley et al. (2004) also found that maritime Peninsula sites had 3–4 times the fungal diversity than more southerly continental sites.

The Antarctic Peninsula is the only location on the continent that supports vascular plant life, and the two species present, *Deschampsia antarctica* and *Colobanthus quitensis*, are restricted to the Peninsula's northern tip and western coast. The presence of vascular plant life provides fungal niche opportunities unique on the continent. *Alternaria* and *Phaeosphaeria* spp., along with several unidentified ascomycete species, were isolated as endophytes of *D. antarctica* leaves (Rosa et al. 2009). Roots from both *C. quitensis* and *D. antarctica* were found to be colonized by so-called dark septate endophytes (DSE) on the Leonie Islands along the western coast of the Antarctic Peninsula (Upton et al. 2009), among other maritime and sub-Antarctic locations. These DSE isolates were found to be largely composed of fungi from the Helotiales order including the *Lep-todontidium*, *Rhizoscyphus*, *Tapesia*, and *Mollisia* genera (Upton et al. 2008).

Although the two species of native vascular plants are restricted to the sub-Antarctic and Antarctic Peninsula, non-vascular plants including mosses and liverworts are more widespread throughout the continent. Mycorrhizal-like infections from *Rhizoscyphussericae* have been noted in the Antarctic liverwort *Cephaloziella varians* (Williams et al. 1994; Upson et al. 2007). Another study on this liverwort noted more ambiguous associations with a number of ascomycete fungi, whose sequences were cloned from the "rhizoid environment" (Jumponnen et al. 2003). Fungi have also been isolated from mosses from locations including King George Island (Moller and Dreyfuss 1996) and fruiting bodies of Agaricales, including *Galerina* and *Omphalia* species, can be found associated with mosses on many of the South Shetland Islands and the Antarctic Peninsula (Fig. 3.1) (authors unpublished data; Guminska et al. 1994; Pegler et al. 1980; Putzke and Pereira 1996). Fungal predators of tardigrades and rotifers, *Lecophagus muscicola*, *L. longispora*, and *L. antarcticus*, are relevant although not strictly soil-inhabiting fungi and they were isolated from sediments and cyanobacterial mats (McInnis 2003). Understanding the ability of these fungi to adapt from one environment to another will assist in determining their ecosystem impact, as McInnis (2003) wrote "Such shallow freshwater sites may represent a physical extension of damp terrestrial habitats as, like the surrounding terrestrial catchments, they freeze solid for up to 9 months each year, and are less influenced by sedimentation and burial processes seen at deeper sites".

As the Antarctic Peninsula extends along a predominantly North-South gradient, it provides an opportunity to test hypotheses related to the ecological effects of latitude, which are often assumed to decrease in biodiversity as distance increases from the equator (Broady and Weinstein 1998). Lawley et al. (2004) tested this hypothesis on six Antarctic Peninsula sites across a range of latitude from 60°S to 72°S with isolates collected over a number of Antarctic field seasons, yet found no significant decrease in eukaryote diversity as latitude and environmental severity increased and that even the most southerly location (Alexander Island) had the highest diversity. Among the six sites studied, 13–38 % of recoverable sequences were from the fungal kingdom. Lawley et al. (2004) also showed limited overlap between the eukaryotic biota of the different study sites, indicating a high level of Antarctic site isolation and possibly endemism, with ascomycete, basidiomycete, and zygomycete sequences identified. In soils from Signey Island and Coal Nunatak, the zygosporic sequences dominated.

Yergeau et al. (2007b) utilized a microbial functional gene microarray to assess and compare the abundance of genes critical to microbial-mediated ecological processes between sites on the Antarctic Peninsula and the Falklands Islands and Signey Island. This study found that fungal genes were more highly detected than other sources of carbon decomposition genes at sites on the Antarctic Peninsula, supporting the widely held hypothesis that fungi are the dominant decomposers in these environments.

3.5 Fungi on Ross Island

The exposed soil environments of the Ross Sea Region extend roughly 1,000 km farther south than the central portion of the Antarctic Peninsula. Primary production in this area is largely dependent on scattered patches of moss and lichens, with no documented vascular plants. Ross Island soils are largely composed of volcanic scoria yet due to coastal proximity and marine influences have relatively higher amounts of organic matter deposition than Dry Valley soils much farther inland (Cowan and Ah Tow 2004). Ornithogenic soils around penguin colonies form important sources of carbon inputs to local ecosystems and the fungi associated with these environments are reviewed elsewhere in this book (Chap. 6).

Similar to the Antarctic Peninsula, Ross Island, off the coast of Victoria Land in McMurdo Sound, has significant human impact as it is home to New Zealand's Scott Base and also to the largest Antarctic settlement, the U.S.A. Antarctic Program's McMurdo Station, which hosts a population of some 1,000 researchers and support staff during the Austral Summer. Although changes in the Antarctic Treaty Systems during the 1980s and 1990s led to stricter rules in how Bases and Stations should dispose of their waste and otherwise interact with the environment, the potential for fungal introductions to the continent remains an ongoing concern. In addition to the documented transportation of fungal propagules and soil (Hughes et al. 2010), humans can also influence native fungal communities via the introduction of exotic materials to the continent. Arenz et al. (2010) demonstrated that introduced exotic substrates, which are relatively carbon rich, can initiate large changes in microbial communities in these otherwise oligotrophic soil systems.

Ross Island has had human impact for over a century since it was the base of operations for the early polar explorers, Robert F. Scott and Ernest Shackleton, who conducted the first scientific inquiries in the Antarctic continent and engaged in the "race for the pole" with Roald Amundsen. Many of their wooden structures and artefacts were left behind and are considered an important component of historic heritage from the "Heroic Era" of Antarctic Exploration, 1897–1914. Fungi that are likely indigenous to the local area have been found to be causing a number of serious deterioration issues on these structures and artefacts (Fig. 3.3) and have themselves been the subject of study (Blanchette et al. 2004b; Arenz et al. 2006, 2010; Held et al. 2005; Duncan et al. 2008, 2010; Blanchette et al. 2010; Farrell et al. 2011). These fungi, capable of causing degradation of the historic huts and artefacts, are similar to those present in the soils near the huts and in remote locations; the most frequently isolated genera were *Cadophora*, *Cladosporium*, and *Geomyces* (Arenz et al. 2006) with *Cadophora* also isolated from five out of eight petroleum-contaminated soil samples (Blanchette et al. 2004a) around a historic fuel depot at the Terra Nova Hut, Cape Evans. The latter findings are consistent with the findings of Aislabie et al. (2001) that *Phialophora* (reclassified subsequently as *Cadophora*) was the dominant species in oil-contaminated soil sites in the McMurdo Sound region. In addition, many of these same fungal genera have been found on historic artefacts and



Fig. 3.3 Dark-pigmented fungi growing on a wooden crate from the historic Cape Evans hut built by Robert Scott in 1911. Many of the fungi found in soils of the Ross Sea region have been found colonizing wood and other organic materials brought to Antarctica by the early explorers. Photograph by the authors

structures on the Antarctic Peninsula suggesting a circumpolar distribution (Arenz and Blanchette 2009).

An air monitoring study conducted over 5 years, with summer and winter samplings, testing the interior and exterior areas of the historic huts, demonstrated that frequently isolated soil genera were producing significant aerial spores, with *Cladosporium cladosporioides*, *Pseudeurotium desertorum*, *Geomyces* species and *Antarctomyces psychrotrophicus* dominating the air environment of the huts with species of *Cadophora* and *Thelebolus* also isolated (Duncan et al. 2010). Due to the great diversity of *Cadophora* species found in the historic woods, their presence in soils, and dead moss thalli (Tosi et al. 2004), Blanchette et al. (2010) speculated that these *Cadophora* species are likely endemic to Antarctica and not introduced species. An ancestral link between the saprophytic *Cadophora* species currently being isolated from Antarctic soils and organic substrates and the fossilized terrestrial saprophytic fungi proposed by Taylor and White (1989) has been suggested (Farrell et al. 2011).

3.6 Fungi on the Antarctic Continent

Victoria Land (which includes the McMurdo Dry Valleys) represents some of the most extreme conditions on the planet, with very dry, cold, highly saline, and low organic content soils (Connell et al. 2008). Yeasts and a variety of fungi have been cultured (Connell et al. 2006, 2008; Vishniac 2006a, b) or detected in these soils, but filamentous fungal abundance was significantly lower in the more inland sites (Connell et al. 2006). Fell et al. (2000) observed an association between basidiomycete yeasts in soils of low moisture content and ascomycetes and zygomycetes in soils with higher water content.

From soils collected from locations in the Transantarctic Mountains (Mount Fleming and the Allan Hills) and Lake Fryxell Basin, Arenz et al. (2006) obtained DNA sequences via DGGE representative of both filamentous fungi and yeasts and similar genera to the soils of Ross Island. However, the only fungi detected using culturing methods by Arenz et al. (2006) from these same soil samples were yeasts such as *Cryptococcus antarcticus*, *C. friedmannii*, *C. vishniacii*, and *Candida parasilosis*. This suggested that the isolated filamentous fungal DNA sequence represented non-viable spores or hyphae. Broady and Weinstein (1998) reported both lichens and filamentous fungi from the La Gorce Mountains (86°30'S, 147°W), a small range in Queen Maud Mountains, which is approximately 350 km from the South Pole. This is the furthest south that mycelia-producing fungi have been reported from open soil environments; however, only four of the 80 collected soil samples yielded fungal isolates even after using a wide range of culturing temperatures. *Cryptococcus* species predominated in most soils, as found in a multivariate analysis of yeast isolates from soil samples on a latitudinal gradient (>77°S to >64°N), including isolates from the Ross Desert (Vishniac 2006b). In this study, the association of *Cryptococcus* yeast species with extreme Antarctic mineral soils was attributed to their polysaccharide capsules, which is thought to contribute significantly to xerotolerance. For almost all sample sites (having determined yeast abundance as well as species identification), 44 % of the distribution of predominant yeast species could be explained by combinations of temperature, precipitation, and electrical conductivity (salinity) (Vishniac 2006b).

During a survey by Connell et al. (2010) of the culturable soil fungal populations in samples collected in Taylor Valley, 13 basidiomycetous yeast strains were isolated belonging to the *Dioszegia* clade of the Tremellales (Tremellomycetes, Agaricomycotina) but the isolates obtained did not correspond to any previously recognized species with two novel species described, *Dioszegia antarctica* and *Dioszegia cryoxerica*. The latter species typifies some of the aspects earlier cited when studying Antarctic mycology. Although the isolates were notable for producing true hyphae with clamp connections and haustoria, no sexual structures were observed. The two novel species can be considered obligate psychrophiles, since they failed to grow above 20 °C and grew best between 10 and 15 °C.

Pointing et al. (2009) reported the first culture-independent survey of multi-domain microbial biodiversity in the high inland McKelvey Valley, and found that

landscape-scales and stochastic moisture input had little impact on community structure but in this study, fungi were detected only in endolithic and chamosolithic communities. In a subsequent study of soil samples from McKelvey Valley, Rao et al. (2011) addressed fungal species richness, analyzing total and putative metabolically active assemblages, using environmental DNA and RNA (cDNA), respectively, plus cultivation with a variety of media and selection conditions. A highly restricted assemblage of just seven phylotypes that affiliated phylogenetically within two known genera, *Helicodendron* and *Zalerion* were revealed, with the latter dominating, and none of the commonly found moulds or mitospore genera observed by other Antarctic investigators were encountered, perhaps as this valley is relatively far inland. The *Helicodendron* species are part of a largely saprophytic family often found on submerged plant debris. *Zalerion* taxa are mostly known from descriptions of marine substrates (Hyde et al. 2000) and this may indicate that a degree of tolerance to saline conditions gave a selective advantage to these fungi in the valleys where soils are appreciably saline as a result of sublimative water loss (Doran et al. 2002), and they have strongly pigmented hyphae which appears important for ultraviolet protection.

Chan et al. 2013 extended the microbial biodiversity study using GeoChip 4, a microarray approach which identifies a broad range of metagenomic 'potential' with the most relevant focus on functional ecology. With this approach, they identified in McKelvey Valley both ascomycetes and basidiomycetes with the ability to catabolize complex aromatic compounds.

3.7 Conclusions

The list of fungi isolated from Antarctic soils continues to grow, and more importantly their functional role in the various ecosystems is becoming elucidated. Despite challenges inherent in determining fungal activity and endemism, it is increasingly clear that Antarctic fungi play an important role in decomposition and nutrient recycling and are crucial for soil ecosystem processes. Furthermore, based on the fungal genera that are most frequently identified, it is apparent that specific clades within the Kingdom Fungi differ widely in their ability to adapt to these relatively extreme environmental conditions. Climatic variability, abiotic soil characteristics, presence or absence of primary producers, as well as potential human impacts, all play key roles in determining the composition of fungal communities on the most southern continent. Despite significant advances made in understanding the nature and ecological role of Antarctic fungi, crucial questions remain unresolved. To what extent has gene and genotype flow from more temperate locations impacted the evolution of fungal species in Antarctica? What will be the ultimate effect of human introductions of fungal propagules and exotic substrates on indigenous fungi? And what will be the ultimate impact of predicted climate change on Antarctic microbial communities?

Appendix: Putative Antarctic Fungal Endemics

<i>Aposiodaria antarctica</i>	Stchigel et al. (2003)
<i>Thielavia antarctica</i>	Stchigel et al. (2003)
<i>Antarctomyces psychrotrophicus</i>	Stchigel et al. (2001)
<i>Cadophora</i> species H37	Blanchette et al. (2004b)
<i>Cadophora</i> species 4E71-1	Blanchette et al. (2004b)
<i>Cadophora</i> species NH1-2	Blanchette et al. (2004b)
<i>Cadophora</i> species 7R16	Blanchette et al. (2010)
<i>Cryptococcus antarcticus</i>	Vishniac and Baharaeen (1982)
<i>Cryptococcus friedmannii</i>	Vishniac (1985)
<i>Cryptococcus victoriae</i>	Montes et al. (1999)
<i>Cryptococcus vishniacii</i>	Vischniac and Hempling (1979)
<i>Coniobolus antarcticus</i>	Tosi et al. (2004)
<i>Dioszegia antarctica</i>	Connell et al. (2010)
<i>Dioszegia cryoxerica</i>	Connell et al. (2010)
<i>Friedmanniomyces endolithicus</i>	Onofri et al. (1999)
<i>Lecophagus antarcticus</i>	McInnis (2003)
<i>Mrakia psychrophila</i>	Xin and Zhou (2007)

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