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Evolutionary origins of Antarctic microbiota: invasion, selection and endemism

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Abstract: Increasing interest in the ecological roles, conservation and biotechnological potential of Antarctic microbiota has focused attention on their biodiversity and evolutionary origins. Antarctic microbial ecosystems provide useful models for general questions in evolutionary ecology given the relative isolation of the South Polar Region, the severe biological constraints imposed by the polar environment, and the absence of higher plants and animals in some Antarctic habitats. Sealed environments such as Lake Vostok and the overlying East Antarctic ice sheet provide unique, natural culture collections for studying microorganisms that have been isolated from the global gene pool over timescales of evolutionary significance. Most Antarctic environments, however, continue to receive microbial propagules from outside the region, as indicated by spore trap data, the microflora found in Antarctic snow and ice, the colonising taxa at geothermal sites, and the high frequency of apparently cosmopolitan species in most habitats. Differences in environmental stability and selection pressure among environments are likely to influence the degree of adaptive radiation and microbial endemism. The latter seems greater in the Southern Ocean by comparison with non-marine ecosystems of Antarctica, although there is some evidence of endemic species in highly specialised niches on the continent such as in the endolithic habitat and saline lakes. Analytical techniques such as 16S rDNA sequencing and DNA–DNA hybridisation are beginning to provide new insights into the genetic affinities and biodiversity of Antarctic microbiota, and are leading to a more rigorous evaluation of microbial endemism.

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Introduction

Microbes such as bacteria, fungi, micro-algae and protozoa play key roles within the biosphere as the primary colonizers of new habitats, contributors of biomass and energy at the base of food webs, recycling agents for essential macro- and micro-nutrients, and as pathogens and symbionts. In some ecosystems, microorganisms influence the photosynthetic–respiratory balance, and the availability of oxygen, CO_2 and other gases. In the deep evolutionary past, ancient microorganisms contributed the precursor cells and organelles that eventually led to multicellular eukaryotes. These earliest microbes also set the biogeochemical stage for the evolution of more complex life forms.

Despite the many essential roles played by microorganisms, we still understand relatively little about the genetic affinities and evolutionary ecology of most microbial taxa. Even the fundamental concept of what constitutes a species is a subject of ongoing discussion and debate amongst microbiologists (Castenholz 1992, Franzmann 1996). With the advent of molecular techniques, however, these uncertainties are now being addressed at an accelerated pace and we are beginning to witness major advances in understanding of microbial phylogeny, biodiversity and evolution.

Antarctica offers some unique opportunities for research on microbial evolution. As elsewhere, microbial communities are typically the dominant biomass component of Antarctic ecosystems and they control most of the biological flux of carbon, nutrients and energy (Wynn-Williams 1996). Unlike elsewhere (including the Arctic), this vast region has been relatively isolated from the rest of the world since the separation of Antarctica from Gondwanaland and the formation of the Polar Front > 10 million years ago. A currently debated issue in microbial ecology is to what extent a local population of microorganisms can genetically diverge from the rest of the global gene pool. If 'microbial endemism' (i.e. genotypes of bacteria, protists or other microorganisms specific to a geographical region) is at all possible, then Antarctica should be amongst the first places to look for such organisms and to examine the evolutionary processes that can give rise to microbial speciation.

A number of Antarctic microbial ecosystems are of special value to research in evolutionary ecology. Some Antarctic habitats have remained sealed for hundreds of thousands of years or longer, and pose unique opportunities for exploring microbial evolution in the absence of gene flow from outside biota. Many Antarctic environments contain food webs that are reduced in complexity by comparison with latitudes elsewhere, and these provide excellent systems for better understanding microbial processes in general, and for studying interactions of evolutionary significance in the absence of any confounding effects associated with higher plants or animals. The study of the microorganisms that survive and even thrive

in extreme Antarctic environments (extremophiles) is providing new insights into the biological mechanisms of adaptation and tolerance and is of special interest in biotechnology; for example, the use of psychrophiles in industrial processes (Russell 1998) and the application of eurythermal polar cyanobacteria for wastewater treatment in cold climates (Tang *et al.* 1997a).

There is a pressing need to understand Antarctic microbial ecosystems before they may be irreversibly damaged by human activities. Antarctic microbial communities are often unusual and intrinsically interesting because they have been subject to long periods of isolation with relatively low levels of disturbance; for example the living stromatolites on the bottom of the McMurdo Dry Valley lakes and the ancient endolithic communities living inside Antarctic rocks. From the late 1950s onwards, all of these habitats and communities have been subject to the threat of major disturbance and loss by human activities in Antarctica (e.g. coastal ecosystems in maritime Antarctica, Fraser & Patterson 1997; the McMurdo Dry Valleys, Vincent 1996, Wharton & Doran 1999; the Larsemann Hills, Ellis-Evans *et al.* 1997; Lake Vostok under the East Antarctic ice sheet, Vincent 1999) as well as by anthropogenic changes in the global environment. Any assessment of the state of the Antarctic environment and its response to human impacts must consider effects at the microbial level, some of which may have broader ecosystem-wide and global implications (e.g. the biological CO_2 pump in the Southern Ocean). An improved understanding of microbial biogeography and the evolutionary origins of Antarctic microbiota will be an essential step towards harnessing the genetic resources of this region for human needs, and towards ensuring the long term integrity and protection of Antarctic ecosystems.

This review first asks the questions: what are the pathways of microbial gene flow from the rest of the world into Antarctica and how efficient are these pathways relative to local dispersion. It then considers the strategies for microbial success in Antarctica, and how these might influence evolutionary processes within the polar environment. The final section of this review evaluates the question: are there microbial taxa that are endemic to Antarctica? This question is central to the evolutionary ecology of Antarctic microbes and is a primary theme for current and future research in polar microbiology.

Pathways of invasion

The invasion processes for Antarctic microbes are more varied than for larger biota, and include atmospheric circulation, ocean currents, birds, fish, marine mammals and human vectors. These transport processes can operate over long distances to allow gene flow from outside the Antarctic Region, and they also provide pathways for the redistribution of microorganisms within Antarctica. These dispersal mechanisms may be especially important during periods of climate change, when new microbial habitats become widely available for recolonization from local refugia such as nunataks, epishelf lakes, cryoconite holes and ice shelf ecosystems, or from source populations outside the Antarctic Region.

Long range transport by the wind

Four lines of evidence show that there is a physical coupling and transfer of microbiota between the rest of the world and Antarctica via atmospheric circulation processes. First, from the early 20th century onwards, researchers have shown that snow in the maritime Antarctic Region contains pollen from South American plants (Fritsch 1912 cited in Marshall 1996a), and spore trap data has confirmed the intermittent arrival of such pollen via the wind (see below). Second, the Antarctic ice sheet contains many species of microbiota that have not been found as living cells within present-day Antarctic habitats and that appear to have been blown in from outside the Antarctic Region. Third, geothermal habitats in Antarctica, specifically the fumeroles at the top of actively volcanic mountains in the Ross Sea sector, are separated by large distances yet contain assemblages of microbial species that resemble not only each other, but also geothermal assemblages in the temperate zone (Broady 1996). Finally, the non-marine habitats of Antarctica contain many cosmopolitan species of fungi, micro-algae, bacteria and protozoa (Vincent 1988) suggesting frequent aerial exchange with the rest of the world. Few of these Antarctic microbes, however, have been examined using molecular techniques and their genetic relatedness to populations elsewhere remains to be confirmed.

The aerial transport of microbiota into Antarctica may not be a continuous process, but may depend on specific weather events. On maritime Signy Island, the concentration of airborne pollen and spores rose by a factor of 20 during a period of strong winds between Tierra del Fuego and Antarctica (Marshall 1996a). Microscopic analysis of this material showed that it contained large concentrations of pollen of southern beech (*Nothofagus* spp.) and of South American gymnosperms (*Podocarpus* spp.) as well as spores of fungi that are well distributed throughout the temperate zones (*Tetraploa* and *Sporormiella*). From an analysis of synoptic weather charts, Marshall (1996a) concluded that weather patterns favouring this magnitude of dispersal into the maritime Antarctic Region could have occurred 18 times over the preceding 12 years. This level of connectivity between the maritime Antarctic Region and temperate latitudes as found in the South Orkney Islands is likely to be high relative to the continental Antarctic Region that is separated by a much greater distance from its neighbouring land masses.

As might be expected from its degree of isolation and the reduced importance or absence of terrestrial vegetation, the aerobiology of Antarctica differs substantially from that at other latitudes, including the Arctic. In a 13.5-month study of airborne fungal spores at sites on Signy Island, Marshall (1997) found that *Cladosporium* spores, the most abundant spores in the air in most parts of the world, were second in

numerical importance to chlaymdospores, which are typically a minor component elsewhere. The mean concentration of *Cladosporium* spores was 0.0184 m^{-3}, while temperate latitude counts are often in the range 10^3 to 10^4 m^{-3}. Fungal hyphae occurred in the air in peak concentrations at the time of arrival of other material from South America, indicating the importance of intermittent transport from lower latitudes for some microbial species.

Lake Vostok and its overlying ice sheet (78.5°S, 106.8°E, Fig. 1) provide a set of globally important environments for evaluating the processes of microbial immigration and evolution. This site lies in the heart of the Antarctic continent where the ice sheet acts as a giant catch basin for propagules blowing in from the rest of the world. The microbiological analysis of deep ice cores from Vostok has revealed the presence of many viable species including an actinomycete not found elsewhere to date *Nocardiopsis antarcticus* (Abyzov 1993). The microbiota in the upper portion of the core (last 3000 yr, Fig. 1) also include culturable yeasts, fungal mycelia and bacteria, dominated by nonsporulating forms such as *Pseudomonas* spp. Further down in the core at an age of about 10 000 yr the microbial assemblage shifts to dominance by spore-forming bacteria, and yeasts are no longer detectable by culture assays (Abyzov 1993). At the very bottom of the core (3.6 km depth, > 400 000 yr old) the ice is derived from the underlying column of liquid water (Jouzel *et al.* 1999). A variety of staining and biochemical assays have shown that this lake ice, like the overlying glacier ice, contains viable bacteria (Karl *et al.* 1999). 16S rDNA analysis has shown that this bottom assemblage is dominated by the genera *Actinomyces*, *Acidovorax*, *Comomonas* and the *Afipia* subgroup that is most commonly associated with root nodules (Priscu *et al.* 1999). The temperate latitude affinities of these organisms suggest that Antarctica has long been open to microbial colonisation by long range transport processes, although the difficult question of ice contamination during the coring at Vostok and subsequent sample-handling has yet to be fully resolved.

The presence of an active microbial community in Lake Vostok is still a matter for speculation, but the ancient nature of this environment (the water residence time is estimated as 1 million years) and its other distinctive properties (Vincent 1999), combined with the presence of nutrients, organic carbon and bacteria (Priscu *et al.* 1999, Karl *et al.* 1999), suggest that it is likely to contain an active community and at the very least an unusual subset of the world's microflora. The bottom sediments of Lake Vostok pre-date even the ancient water column and its living and fossil microbiota will be of special interest in the context of microbial evolution.

Ocean circulation

Most of the marine microbiota of Antarctica show a circumpolar distribution indicating the importance of the Antarctic Circumpolar Current and Antarctic Coastal Current in broad scale dispersal processes throughout the region. Most of the

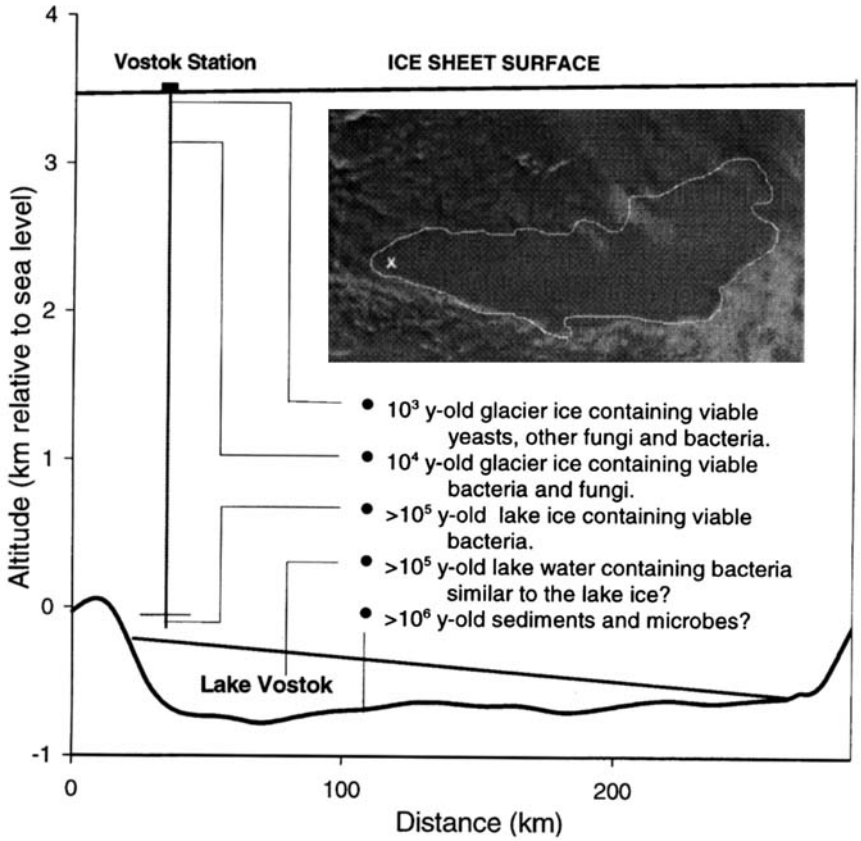

Fig 1. Lake Vostok in East Antarctica as a microbial resource for studies in evolutionary ecology. The vertical line under Vostok Station shows the position and extent of the current borehole. The lake has a maximum depth of 800 m of liquid water and is overlaid by 3600 m of ice. The vast extent of the lake (14 000 km^2) is indicated by the smooth surface of the ice sheet floating on the lake (insert: RADARSAT image of Lake Vostok, reproduced by permission of the Canadian Space Agency). Modified from Vincent (1999).

marine diatoms, for example, are found in most sectors of the Southern Ocean and include many cosmopolitan species (Medlin & Priddle 1990), suggesting ongoing exchange with the world ocean.

Molecular techniques are increasingly being applied to address the question of bacterial distribution in the Southern Ocean. For example, in a recent molecular study of the *Archaea*, these prokaryotes were found at all sampling sites in the seas around Antarctica. In the Ross Sea and Antarctic Peninsula regions the highest population densities of *Archaea* were in the depth range 150–500 m, suggesting that circumpolar deep water is an important conduit for the dispersal of microbiota around Antarctica as well for their export out of Antarctica to the rest of the world via transport in the deep sea and mixing across the Polar Front (Murray *et al.* 1999).

Birds, fish and mammals

Many Antarctic birds and mammals are migratory and pass across the Polar Front. Some fish species that normally reside north of the Polar Front are also found from time to time at more southerly latitudes, leading to the conclusion that the frontal zones "are not impervious barriers but may be penetrated by pelagic fish that are trapped in eddies" (Kock 1992, p. 34). Certain bird species, notably the Arctic tern and the skua, range as far north as the Arctic. All of these animals are likely to bring with them microorganisms from outside the Antarctic Region. Washings of the feathers of Antarctic birds have shown that they contain a wide range of viable microbes. For example, cultures from washings of the tail feathers from an Arctic tern yielded the cyanobacteria *Schizothrix calcicola* (Ag.) Gom. and *Nostoc commune* Vauch, the green alga *Chlorella vulgaris* Beijer, a *Bodo*-like protozoan and two additional heterotrophic nanoflagellates (Schlichting *et al.* 1978).

Human vectors

The increasing human presence in Antarctica has accelerated the rate of transfer of microbiota into the South Polar Region from the rest of the world. Cameron (1972) was among the first to draw attention to this effect by noting that after he had opened a can of food rations that was contaminated by *Penicillium*, the fungus became dispersed over the local soils at his remote campsite on Mount Howe (87°S) and was then detected in the next sample collection. A variety of micro-algae and cyanobacteria have been isolated from fruits and vegetables imported into Antarctica (Broady & Smith 1994). There is also concern that human activities may cause the transfer of infectious diseases in Antarctic wildlife. For example, Chilean scientists have detected antibodies to *Brucella* in seals in the vicinity of Cape Shirreff, Livingston Island, in the South Shetland Islands, and studies near Australia's Mawson station, Mac.Robertson Land, suggested that Adélie and emperor penguins at some locations had been exposed to Infectious Bursal Disease Virus. These microbial pathogens may act as a new biological selection pressure on some Antarctic animal populations.

Local dispersal

Once established within Antarctica, microorganisms can be redistributed by a variety of dispersal mechanisms. Cyanobacterial mats in streambeds, soils and at the edge of lakes and ponds can survive freeze-up and desiccation (Hawes *et al.* 1992), and in this dry state they are readily dispersed by the wind. Cyanobacteria-like particles have been observed in the clouds over the Ross Ice Shelf where they appear to act as biogenic nuclei for water droplet formation (Saxena 1982), and it has been suggested that a major origin of these particles may be the 1500 km^2 region of microbial mat communities on the McMurdo Ice Shelf (Vincent 1988). In the remote La Gorce Mountains at 86.5°S, 45% of all soil samples examined by Broady & Weinstein (1998) contained cyanobacterial sheath material that seemed to be derived from local mats of *Leptolyngbya fragilis* (Gom.) Anag. Spore trap data at Signy Island has shown that most collections had high concentrations of locally derived propagules (particularly lichen soredia; Marshall 1996b) and local taxa of algae and cyanobacteria were cultured from this material (Marshall & Chalmers 1997). These observations suggest the dominance of local dispersal over long range transport for microbial colonisation processes. Similarly, the circumpolar distribution of most microbiota in the Southern Ocean and the distinctive communities relative to more northerly latitudes (e.g. diatoms, Medlin & Priddle 1990) indicates the effectiveness of ocean currents in dispersing these organisms throughout the region.

Establishment and selection

Once a microbial propagule arrives at a potential habitat site via either long range or local dispersal processes, the Antarctic environment is likely to exert a strong selection pressure. Microorganisms in general exhibit one of three strategies for successful growth, reproduction and survival (Fig. 2):

1) specialists that occupy narrow niches and have a competitive advantage relative other colonising species, for example by having high-affinity nutrient transport systems that allow growth at low substrate concentrations, or fast growth rates that allow them to withstand greater losses by predation and other removal processes,

2) generalists that grow suboptimally but survive because of their tolerance to environmental extremes, and

3) generalists that occupy broad niches with periods (or patches) of optimal and suboptimal growth and acclimation. There are examples of each within the Antarctic Region, although certain species may exhibit different strategies in different niche dimensions (Vincent

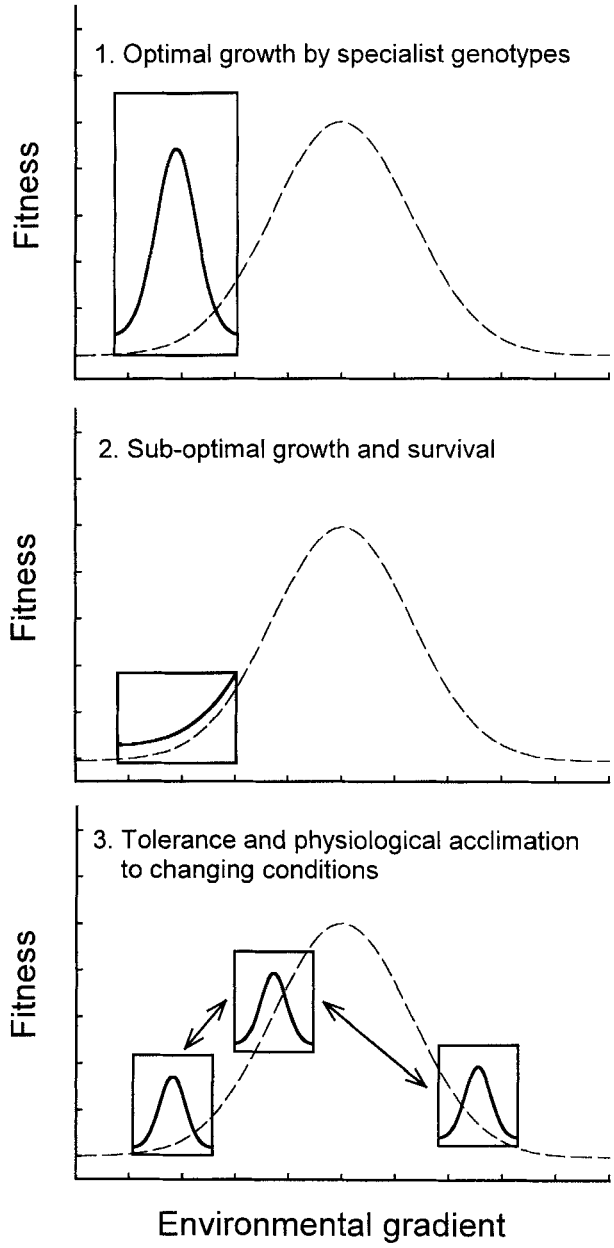

Fig. 2. Three potential niche strategies for microbial survival and growth in the Antarctic Region. The boxes show fitness (for example, as measured by growth or nutrient uptake rate) over the ambient environmental range for polar microbes relative to a generalised curve for temperate latitude microbiota (dashed line). The boxes show the fitness of Antarctic species over their ambient environmental range. Type 1 strategists have the highest level of goodness-of-fit to their environment with optimal growth within or near the ambient range and much greater fitness to the polar habitat than temperate latitude species. Type 2 strategists tolerate the Antarctic environment but show maximum growth rates well outside the Antarctic range, towards the environmental optima for temperate latitude species. Type 3 strategists exist under variable conditions and show short-term acclimation to fluctuations in the Antarctic environment. Modified from Vincent & Quesada (1997).

& Quesada 1997). Each strategy has different implications for the evolution of Antarctic biomolecules and biota.

Genetic adaptation towards optimal growth under extreme environmental conditions (a type 1 strategy) is illustrated by some Antarctic microorganisms with respect to temperature. There are psychrophilic species in aquatic, terrestrial and ice-bound habitats that have optimal growth at or below, sometimes well below, 15°C (Vincent 1988). These low temperature preferences are the result of proteins and lipids that perform optimally in the cold. For example, an α-amylase has been purified from an Antarctic strain of the bacterium *Alteromonas haloplanctis* that shares only a 66% sequence similarity with the same enzyme from a mesophilic source. The Antarctic enzyme has an apparent optimum temperature for activity that is more than 30 degrees lower than the mesophilic α-amylase and has a number of unusual structural properties that may account for its high catalytic efficiency at low temperatures (Russell 1998). The evolutionary questions of interest are whether such an enzyme has evolved within Antarctica, and how far it differs in amino acid sequence, three-dimensional structure and biophysical properties relative to α-amylases in other cold environments throughout the world.

Even the Antarctic α-amylase, however, has an optimum temperature for activity that is well above that of the ambient seawater, suggesting that there has been insufficient time for full evolutionary adaptation to the Antarctic environment. In fact, microbial psychrophily seems much less prevalent throughout the Polar Regions than might be expected, even in perennially cold environments such as seawater and ice (table 10.1 in Vincent 1988). The common occurrence of psychrotrophs (microorganisms that grow at 5°C or less but have a temperature optimum for growth above 15°C) in Antarctica implies that the selection pressure for optimal growth in the cold is relatively weak by comparison with other constraints imposed by the environment. It might also suggest that biological interactions (competition, predation) selecting for rapid growth are less important for some Antarctic communities than the ability to tolerate the severe physical and chemical conditions (Vincent & James 1996).

Another extreme polar condition imposed on phototrophic organisms is the low irradiance experienced in some environments, even during the period of maximum incident radiation, for example in permanently ice-covered lakes and the micro-habitats below (sublithic) or within (endolithic) rocks. Studies on a strain of *Chlamydomonas subcaudata* Wille, a phytoplankton dominant in a McMurdo Dry Valley lake, have shown that it has various genetic adaptations towards optimal growth under extreme shade, including changes in its cellular ratio of the two photosystems (Morgan *et al.* 1998). It will be of great interest to examine the molecular affinities of this strain with chlamydomonads from elsewhere, including analogous environments in the Arctic (e.g. permanently ice-covered Lake A on Ellesmere Island).

Lateral gene transfer, that is the horizontal transfer of

genetic material between taxa, may have played a role in the development of specialised genotypes in Antarctica, as elsewhere. The eukaryotic cell is believed to have resulted from multiple gene transfers of this type, and phylogenetic schema for microbial evolution are increasingly having to incorporate networks of untreelike links between disparate branches (Doolittle 1999). These genetic processes are also likely in Antarctica, particularly in environments with high concentrations of diverse taxa such as sea ice and ice-mat consortia (e.g. Vincent *et al.* 2000a).

Many Antarctic microbes show a more limited biochemical and biophysical tuning to their ambient environment, with optimal growth conditions outside the environmental range of their habitats (type 2 strategy). For example, psychrotrophic bacteria and micro-algae are widely distributed in the frigid marine, terrestrial and freshwater environments of Antarctica (Vincent 1988). Even these organisms, however, show some adaptive fit towards their environment. For example, mat-forming cyanobacteria are often the biomass dominants in Antarctic lakes and streams; growth assays of 27 high latitude strains showed that they were all psychrotrophic but with a mean temperature optimum for growth significantly below that for strains from temperate latitudes (Tang *et al.* 1997b). Similarly, psychrotrophic bacteria from Antarctic lake sediments showed evidence of low temperature adaptation at the level of membrane transport (Nedwell & Rutter 1994), with considerable variation between strains in terms of ability to acclimate to the cold, for example through changes in membrane fatty acid composition (Fukunaga & Russell 1990). These observations imply an environmental selection for adaptive genotypes, and the potential for evolutionary divergence from temperate latitude microbiota. The greatest selection pressure on many Antarctic microorganisms may be the ability to survive seasonal extremes in the polar environment, such as freeze-up, desiccation and winter darkness. It will be particularly interesting to compare the proteins and genes that control this survival ability between related microbial groups in alpine, Arctic, and Antarctic habitats, and to determine whether distinct strategies have evolved in the South Polar environment.

In many Antarctic habitats, microorganisms have to contend with major variations in certain properties of their environment over the course of the year, and a type 3 strategy is therefore required with respect to these niche dimensions. For example, polar cyanobacteria are capable of major adjustments in their light-harvesting ability in response to the large seasonal changes in their ambient irradiance (Vincent *et al.* 2000b). Psychrotrophic bacteria from lake sediments have been shown to be capable of shifting their nutrient uptake parameters in response to temperature, and the speed of adjustment can influence the outcome of competitive interactions between species (Rutter & Nedwell 1994). Variable Antarctic environments, for example polar desert soils, moss habitats and ephemeral ponds, may select for generalist microorganisms, and these seem more likely to be cosmopolitan species that can grow in many parts of the world (e.g., the cyanobacterium *Nostoc commune* Vauch) rather than organisms that have evolved in Antarctica in response to specific conditions. In contrast, the more stable, perennially cold environments such as the Southern Ocean, would seem to be more conducive to the evolution of specialist genotypes, and this is reflected in the greater representation of Antarctic psychrophiles in sea ice and seawater and relative to non-marine habitats (table 10.1 in Vincent 1988).

Endemism

Given that Antarctica is open to invasion from elsewhere within the world, is it likely that microbiota could evolve within this region to eventually become new species, or are new arrivals and gene transfer from lower latitudes constantly displacing these nascent endemic microbes? There is a general maxim that has been long accepted by bacteriologists, that "everything is everywhere, but the environment selects" (Baas-Becking 1934 cited in Staley & Gosink 1999). Some protozoologists share a similar view, that "species are probably ubiquitous, although many may persist locally for long periods in a cryptic state – as 'potential' rather than 'active' biodiversity" (Findlay 1998). Such a view would suggest that the opportunities for microbial endemism are rather limited. In support of this view, many cosmopolitan species are found throughout Antarctica. For example, morphological analysis of heterotrophic protist communities from several marine and freshwater sites around Antarctica yielded 35 taxa, of which 34 had been previously reported from geographic locations elsewhere (Tong *et al.* 1997).

Counter to the view of limited endemism are the observations that the Antarctic Region is more isolated than other parts of the world, that its aerobiology differs from elsewhere, that local dispersal processes favouring local species are more efficient than long range dispersal, and that there has been environmental selection for specific adaptive strategies over a period of several million years. It is also likely that classic taxonomic criteria do not provide an accurate guide to the extent of genetic and physiological divergence.

Franzmann (1996) undertook the first detailed molecular analysis of Antarctic microbiota to address the question of prokaryotic divergence in the South Polar Region. Ten Antarctic bacteria (mostly from saline lakes in the Vestfold Hills) were compared in terms of their growth–temperature characteristics and their 16S rDNA sequences relative to the most closely related bacteria available in culture from temperate latitudes. The Antarctic species all had lower temperature optima for growth (by 7–24°C), and the median sequence dissimilarity relative to the temperate strains was 4.5%. Assuming an evolutionary rate of 1% divergence in 16S rDNA 25 million yr^{-1} (Moran *et al.* 1993, cited in Franzmann 1996), this would equate to phylogenetic divergence of the Antarctic taxa from those in temperate latitudes beginning > 100 million yrs BP, well before the isolation and cooling of

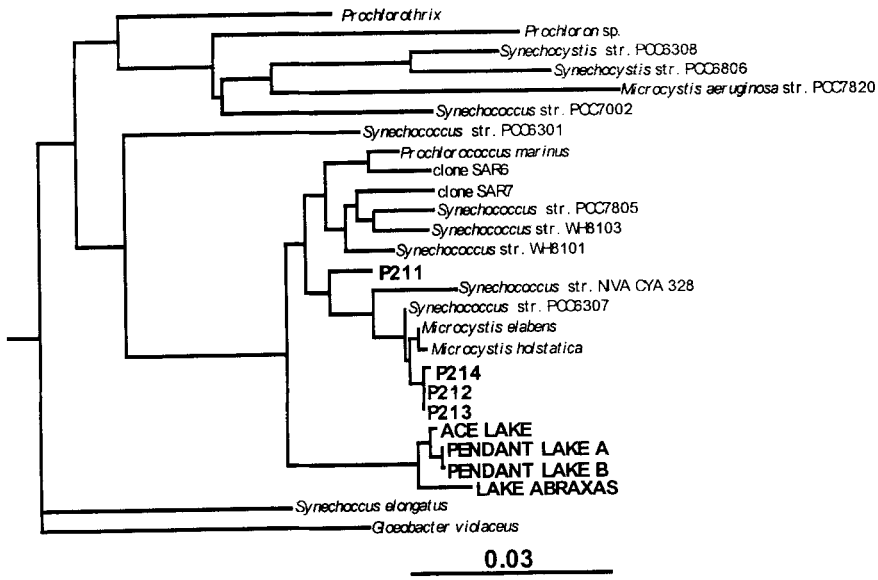

Fig. 3. 16S rDNA phylogenetic tree for cyanobacteria showing the position of *Synechococcus*-like isolates from lakes and ponds in the Arctic (P211, P212, P213 and P214) and Antarctica (ACE, PENDANT A/B and ABRAXAS). Further details are given in Vincent *et al.* (2000b).

Antarctica. These results imply that Antarctica contains an unusual subset of prokaryotes that are poorly represented at lower latitudes. However, Franzmann *et al.* (1997) note the incompleteness of the database, and that the branching patterns may change substantially as more microorganisms are discovered and sequenced within and outside Antarctica. For example, the 4.5% dissimilarity value might reflect the possibility that more closely related strains from temperate regions have yet to be sequenced.

Analytical techniques such as pigment analysis and ribosomal-RNA gene sequencing (rDNA) are also beginning to provide new insights into the genetic diversity and evolutionary relationships of Antarctic phototrophs. For example, an analysis of high latitude picocyanobacteria showed that there were considerable differences between Arctic and Antarctic strains (Vincent *et al.* 2000b). Three *Synechococcus* isolates from saline lakes in the Vestfold Hills, East Antarctica, were closely related (96% similar) to *Prochlorococcus marinus,* but formed a distinct cluster relative to all other known picocyanobacteria (Fig. 3). Sequences of isolates from a much broader range of habitats are required to assess the evolutionary divergence of Arctic and Antarctic cyanobacteria, and this approach would be usefully applied to other groups of microphototrophs such as diatoms and phytoflagellates.

Many new species of bacteria, micro-algae, fungi and protozoa have been described from Antarctica and have not been recorded elsewhere in the world (examples in Table I and Figs 4 & 5), suggesting that the level of endemism could be considerable. Similarly, the application of 16S rDNA analysis to Antarctic bacteria implies the presence of not only unusual species, but also novel taxa at the genus, family, and even higher levels (Bowman *et al.* 2000). However, several caveats need to be kept in mind in interpreting these results.

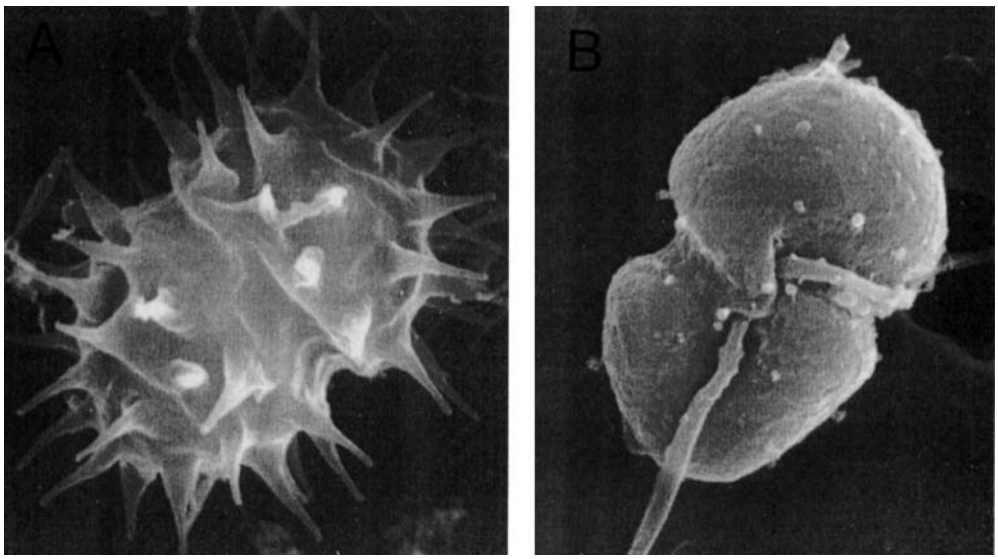

Fig. 4. The **a.** cyst and **b.** vegetative cell of *Polarella glacialis,* a sea-ice dinoflagellate genus and species that to date has only been recorded in Antarctica. The cysts are 12–17 μm long while the vegetative cells are 10–15 μm long. Reproduced from Montresor *et al.* (1999) by permission of the authors and the *Journal of Phycology.*

Table I. Candidates for microbial endemism: examples of species that have been described and only recorded from Antarctica.

Taxon	Habitat	Taxonomic reference
Bacteria		
Antarctobacter heliothermus*	solar-heated lake, Vestfold Hills	Labrenz *et al.* 1998
Clostridium vincentii	anoxic sediments, McMurdo Ice Shelf	Mountfort *et al.* 1997
Colwellia spp.	Antarctic sea ice	Bowman *et al.* 1998a
Flavobacterium gondwanense	saline lake, Vestfold Hills	Dobson *et al.* 1993
Gelidibacter algens*	East Antarctic sea ice	Bowman *et al.* 1997a
Halomonas subglaciescola	saline lake, Vestfold Hills	Franzmann *et al.* 1987
Methylosphaera hansonii*	saline lake, Vestfold Hills	Bowman *et al.* 1997b
Modestobacter multiseptatus*	soils, TransAntarctic Mountains	Mevs *et al.* 2000
Nocardiopsis antarcticus	East Antarctic Ice Sfheet	Abyzov 1993
Octadecobacter antarcticus	Antarctic sea ice	Gosink *et al.* 1997
Polaribacter spp.	Antarctic sea ice	Gosink *et al.* 1998
Polaromonas vacuolata*	Antarctic sea ice	Irgens *et al.* 1996
Pseudomonas antarctica	Ross Island	Obata *et al.* 1999
Psychroflexus gondwanense*	East Antarctic sea ice	Bowman *et al.* 1998b
Psychroflexus torquis*	East Antarctic sea ice	Bowman *et al.* 1998a
Psychromonas antarcticus*	anoxic sediments, McMurdo Ice Shelf	Mountfort *et al.* 1998
Psychroserpens burtonensis*	Antarctic saline lakes	Bowman *et al.* 1997a
Shewanella frigidimarina	sea ice, Prydz Bay	Bowman *et al.* 1997c
Shewanella gelidimarina	sea ice, Prydz Bay	Bowman *et al.* 1997
Sphingobacterium antarcticus	soils, Schirmacher Oasis	Shivaji *et al.* 1992
Fungi		
Cryptococcus antarcticus	McMurdo Dry Valley soils	Vishniac & Baharaeen 1982
Crytococcus vishniacii	McMurdo Dry Valley soils	Vishniac & Baharaeen 1982
Friedmanniomyces endolithicus*	Antarctic rocks	Onofri *et al.* 1999
Microalgae		
Eucampia antarctica	Southern Ocean	Hasle & Syvertsen 1996
Hemichloris antarctica*	McMurdo Dry Valley rocks	Tschermak-Woess & Friedmann 1984
Polarella glacialis*	McMurdo Sound	Montresor *et al.* 1999
Pseudopleurochloris antarctica*	Ross Sea pack ice	Andreoli *et al.* 1999
Koliella antarctica	Ross Sea	Andreoli *et al.* 1998
Pyramimonas gelidicola	East Antarctic sea ice and lakes	McFadden *et al.* 1982
Thalassiosira antarctica	marginal ice edge zone	Hasle & Syvertsen 1996
Thalassiothrix antarctica	Southern Ocean	Hasle & Syvertsen 1996
Protozoa		
Commation spp.	Southern Ocean	Thomasen & Larsen 1993
Euplotes antarcticus	sea ice, Weddell Sea	Fenchel & Lee 1972
Kiitoksia kaloista	freshwater lake	Tong *et al.* 1997
Notodendrodes antarctikos*	inshore Ross Sea sediments	De Laca *et al.* 1980
Spiroprorodon glacialis	sea ice, Weddell Sea	Fenchel & Lee 1972

*The asterisk indicates that the genus has not been recorded to date outside Antarctica.

Firstly, the molecular analysis of microbes is still in its infancy throughout the world and the database is expanding rapidly. Secondly, the Arctic lacks the large national and multinational research programs that operate in Antarctica, and any differences between the two regions may in part reflect undersampling in the North Polar Region, or the present lack of appropriate comparisons. For example, it will be interesting to determine the molecular affinities of closely related microalgae in the Southern Ocean and Arctic Ocean such as the diatoms *Thalassiosira antarctica* Comber and *T. antarctica* var. *borealis* Fryxell, Doucethe & Hubbard.

A third reason for caution in interpreting current species data is that the approaches adopted to date may be insufficient to resolve taxonomic similarities and differences of evolutionary significance. Staley & Gosink (1999) compared several bipolar pairs of sea ice bacterial species within the same genus by 16S rDNA and also by DNA–DNA hybridisation. They found that while the former approach confirmed the original diagnosis as separate species, the DNA–DNA re-association tests indicated a high percentage relatedness that would not justify this separation. They conclude that 16S rDNA sequences are too highly conserved to allow the identification of taxa that are endemic to one or both Polar Regions. These authors also observe that while all sea ice bacterial species examined to date are restricted to one or the other Polar Regions (i.e. no bipolar strains have been identified as yet), there is no evidence of geographic clustering. This absence of clades of species in the Arctic or Antarctic suggests a lack of adaptive radiation and endemism of the type found in other polar biota, for example Antarctic nothothenioid fish (Kock 1992). Staley & Gosink (1999) note, however, that additional work is required on a much

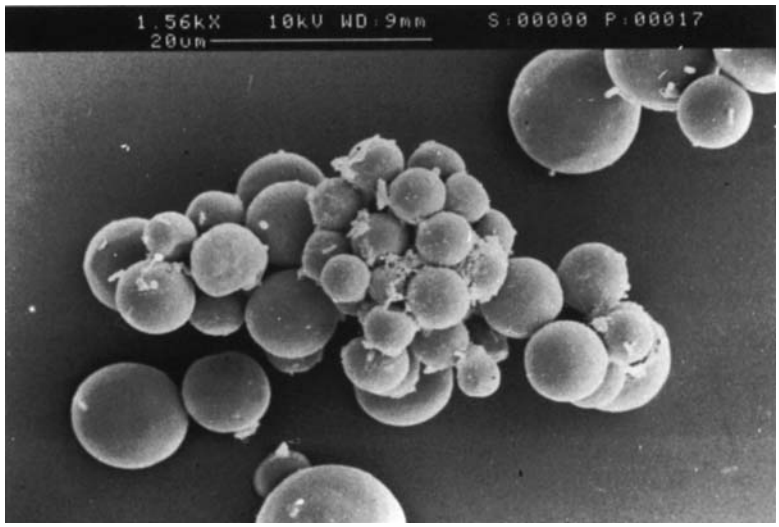

Fig. 5. Scanning electron micrograph of Pseudopleurochloris antarctic, a new algal genus and species from Antarctic pack ice. Reproduced by permission of Dr C. Andreoli. Details are given in Andreoli *et al.* (1999).

larger number of polar strains before this aspect can be fully evaluated.

Conclusions

Despite the pre-eminent importance of microbial communities in the Polar Regions, our understanding of their evolutionary characteristics is still at a rudimentary stage. The need for this information has been heightened by the increased level of human activities and impacts in Antarctica, and by the observation that the polar regions are currently subject to unprecedented rates of change caused by ozone depletion, rapid climate shifts and the long range transport of contaminants. Although the latter processes are operating at a global scale, many of the environmental impacts are amplified in the Polar Regions (Vincent & Hobbie 2000). Antarctic microbial communities are likely to be changing, but we still lack the fundamental knowledge to assess their current biodiversity and uniqueness, and the magnitude and implications of any change.

The study of Antarctic microbiota will continue to help develop general models in evolutionary ecology by offering isolated populations that have been subject to severe environmental pressures. Ancient microbial ecosystems such as Lake Vostok, cryptoendolithic communities and living stromatolites may be especially interesting in this regard given that they have been sequestered from the rest of the world for $> 10^3$ yr, potentially sufficient time for microbial evolution to operate.

Research on Antarctic microbiota may also provide insights into how microorganisms survived, adapted and diversified during critical periods in the evolution of life on Earth. A recent theory based on geological evidence indicates that the entire world ocean was frozen by runaway ice-albedo events during the Paleoproterozoic and Neoproterozoic, near the time of origin of the eukaryotic cell type and the adaptive radiation of metazoa (the Snowball Earth hypothesis). The extensive microbial mat communities on ice in Antarctica as well as the Arctic are dominated by similar organisms to those in the Proterozoic fossil record, and studies on these present-day analogues are showing how the mat-forming species can provide protected microhabitats for the survival, growth and evolution of less tolerant biota, including multicellular eukaryotes, during periods of extensive glaciation (Vincent *et al.* 2000a). These cryo-environments and a variety of other habitats such as cryoconite holes (Vincent 2000), ice-dammed fjords ("epishelf lakes", Bayly & Burton 1993), thick-ice covered lakes and nunataks may have played a role as refugia for microorganisms and other biota during periods of glacial advance in Antarctica, and thereby favoured the development of endemic species.

Polar microbial ecology is currently in an exciting phase of rapid development. New microbial habitats are being discovered and explored: e.g. lake ice, Priscu *et al.* 1998; shelf ice, Vincent *et al.* 2000a; remote mountains, Broady & Weinstein 1998; subglacial lake ice, Karl *et al.* 1999, Priscu *et al.* 1999; and symbiotic associations in krill, Kawaguchi & Toda 1997. Adaptive strategies of evolutionary significance are being newly identified: e.g. winter survival mechanisms in Antarctic protists, Laybourn-Parry *et al.* in press; shade adaptation in Antarctic phytoflagellates, Morgan *et al.* 1998; and UV survival strategies in Antarctic cyanobacteria, Quesada & Vincent 1997. There has been an explosive increase in the number of taxonomic descriptions of new microbial species (Table I). New molecular techniques are becoming available to address phylogenetic questions that in the past were simply intractable (e.g. Staley & Gosink 1999, Bowman *et al.* 2000). In the past, the focus has necessarily been on those species that can be brought into culture, perhaps biasing the sample collections towards culturable generalists rather than specialist Type 1 genotypes. The application of DNA techniques is now allowing a more complete census of the presence and absence of microbial taxa (e.g. Murray *et al.* 1999, Voytek *et al.* 1999). This accelerating pace of research on polar microbial

communities is likely to result in important new insights, not only about the genetic affinities of Arctic and Antarctic microbiota, but also about the evolutionary ecology of microorganisms throughout the biosphere.

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