

GLACIAL PERIODS ON EARLY EARTH AND IMPLICATIONS FOR THE EVOLUTION OF LIFE

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1. Introduction

Modern-day thermophiles and their habitats such as hydrothermal vents, surface hot springs and other high temperature environments are often viewed as analogs for Precambrian microbial ecosystems. The prebiotic Earth is thought to have been extremely hot, with the origin of life delayed by several hundred million years of cooling to temperatures that allowed the stable formation of biomolecules and ultimately cells (Schwartzman 1999, and references therein). Similarly, from analysis of 16S rDNA phylogenies, the tree of life is often considered to be rooted in high temperature (hyperthermophilic) microbes (Woese 1987). There is new geological evidence, however, that the early Earth may have cooled much more rapidly from its original Hadean state than was previously surmised (Valley et al. 2002). Molecular arguments concerning the hyperthermal roots of life now seem less certain (Doolittle 1999, Brochier and Philippe 2002). Furthermore, there is mounting support for the view that the Precambrian biosphere experienced extreme low temperature conditions at several intervals during the Paleo- and Neoproterozoic, and perhaps even during the earliest steps in the emergence and evolution of life (Nisbet and Fowler 1999).

The timing, duration and extent of cooling during the Precambrian are subjects of considerable discussion and debate, and views range from localized glacial activity to complete freeze-up of the ocean surface. Extreme cold has largely been considered as a negative factor that would cause severe inhibition of Precambrian biological processes, eventually leading to a widespread loss of species and perhaps even the total extinction of surface life (Williams et al. 1998). On the other hand, little attention has been given to the success and biodiversity of microbial communities that thrive in a variety of extreme cold environments in the modern-day polar regions and which indicate the potential for growth, survival and evolution despite prolonged subzero temperatures.

In the present article, we first briefly summarize the geological, geochemical and modeling evidence for freeze-up episodes during the Precambrian and the various scenarios that have been surmised from this evidence. We then examine the diverse range of microbial cryo-ecosystems that occur today in ice-bound and other extreme cold environments and that could provide analogs of low temperature systems on early

Earth. We place special emphasis on ice shelf ecosystems in the Arctic and Antarctic, a focus of our current research, and conclude by examining some of the evolutionary implications of extreme cold in the microbial habitats of the early Earth.

2. Earth's Earliest Freeze-up

Traditionally, the Precambrian has been thought of as a period characterized by prolonged extreme high temperatures at the surface of the planet and in the overlying atmosphere. During Earth's accretion phase, 4.56-4.45 Ga (10^9 years) before the present, there was sufficient heat from meteoritic impacts, collision with a Mars-size body, the formation of the metallic core, and high radioactivity, to melt the entire planet (Valley et al. 2002). Depending on the magnitude of ongoing bombardment by meteorites and the nature of the atmosphere, these hyperthermal, non-aqueous conditions may have persisted up until 3.6-3.8 Ga before the present, the date of the earliest known water-laid sediments. However, ancient zircon crystals (zirconium silicate, a component of granitic rocks that forms in the presence of water) have recently been discovered, and their analysis suggests that the early Earth may have cooled much more rapidly (Wilde et al. 2001). These crystals have been dated at 4.404 Ga and their isotopic signatures ($\delta^{18}\text{O}$) imply surface temperatures below 200 °C that would allow the existence of oceans at that time, some 500 Ma earlier than in previous models (Valley et al. 2002).

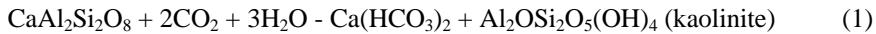
Could this early ocean have eventually cooled to freezing at or before the emergence of life? Some calculations suggest that freezing could have occurred even during the accretion phase of early Earth. Mukhin and Pimenov (2002) conclude that there would have been very high rates of convective cooling of surface impact craters, and that the early growing Earth could never have supported a steam atmosphere. Low partial pressures of CO₂ and H₂O in the overlying atmosphere would result in minimal greenhouse warming, and 90% of the Earth's surface would be below the freezing point of water. In this scenario, prebiotic Earth would be characterized by impact crater hot spots amidst a vast expanse of cold traps, conditions that could have favored the preservation and accumulation of organic molecule precursors formed during impact events (Mukhin et al. 1989).

Although the first scenarios of the origin of life invoked high temperature photochemical reactions, it is now known that biomolecules are highly unstable when subjected to prolonged heating (Levy and Miller 1998, Bada and Lazcano 2002) and it is unlikely that an RNA world could have persisted in hot water environments (Moulton et al. 2000). On the other hand, nucleic acids are preserved for long periods of time in the cold; for example, intact DNA has been extracted from ancient glacial ice (reviewed in Priscu and Christner 2003) while decomposition rates are rapid under warmer conditions. Even the ice-formation process itself could have favored early steps in the emergence of life. Freeze-up causes a concentration of solutes that can result in polymerization and the formation of biomolecule-like entities including oligonucleotides (Kanavarioti et al. 2001). This is analogous to the solute-concentrating processes that occur in clays, aerosols and evaporating water that can similarly lead to the synthesis of organic polymers.

The radiative output from the sun has gradually increased over Earth's history and was some 25% lower in the early Precambrian relative to today. Sagan and Mullen (1972) concluded that such a low incident radiative flux would result in a complete freeze-up of the Earth's oceans, yet noted the evidence of liquid water conditions in the Precambrian. This 'early faint sun paradox' is resolved by assuming that the concentration of greenhouse gases, especially CO₂ and CH₄, were massively higher relative to today.

There is debate, however, as to whether the initial high CO₂ concentrations could be maintained in the atmosphere of early Earth, particularly in the presence of liquid water that would dissolve the gas to form carbonates (Mukhin and Pimenov 2002). An atmosphere instead dominated by carbon monoxide, perhaps over a frozen Earth, appears to be more compatible with current notions of prebiotic synthesis and the origin of life (Miyakawa et al. 2002).

Schwartzman (1999) argues that the overall constraint on the emergence and evolution of life has been the rate of weathering reactions, specifically the reaction of CO₂ with silicates in the Earth's crust, for example for plagioclase, a common mineral in basalt:



He suggests that the consumption of atmospheric CO₂ by these reactions would have accelerated once biological communities emerged. In particular, the soils produced in developing terrestrial ecosystems would cause accelerated weathering by trapping pore water within a matrix that has a large specific surface area for chemical reactions. The resultant drop in atmospheric CO₂ and associated cooling could in turn have gradually set the stage for the evolution of less thermotolerant life-forms. However, the early emergence and development of ecosystems based on heat-loving prokaryotes now seems less certain.

Several biological lines of evidence have been used to argue the hyperthermal origins of life. The earliest apparent fossils resemble modern day cyanobacteria, such as oscillatoriains that occur in hot springs (Schopf and Klein 1992). However, oscillatoriains are also widely distributed in extreme cold environments, and in many parts of the north and south polar regions they are the ecosystem dominants (Vincent 2000). Deeply rooted Bacteria and Archaea were thought to be largely thermophiles and consistent with hot surface conditions on the Archaean Earth (Woese 1987). However, Archaea are now known to contain many extreme cold water representatives, for example in Antarctic surface waters (Massana et al. 1998) as well as throughout the frigid deep ocean. Recent studies on the latter suggest that these cold water Archaea (Crenarchaeota) may have a total population size of 10²⁸ cells, making them one of the ocean's most abundant cell types (Karner et al. 2001).

A hyperthermophilic root for the tree of life based on molecular clock analyses of 16S rDNA is often cited by researchers working on high-temperature environments such as geothermal soils (Huber et al. 2000) and deep subsurface rocks (Pedersen 1997), however these calculations now seem questionable. This type of analysis assumes linear evolution and hierarchical branching, and the method is flawed if there are deeply branching relationships (Gribaldo and Philippe 2002). Lateral gene transfer is increasingly viewed as a major feature of prokaryotic evolution, with strong evidence of transfer between distantly related organisms, even between the bacterial and archaeal

domains (Nelson et al. 1999). This common pattern of genetic exchange throws doubt on past interpretations of the ribosomal DNA tree (Doolittle 1999, Wolf et al. 2002). Phylogenies based on other genes do not support a 'hot start' to life and there is evidence that thermophily arose relatively late in evolutionary time. Studies of the GC content of rRNA in different organisms suggest a mesophilic common ancestor (Galtier et al. 1999). Analyses of the thermal stability and structure of biomolecules also seem more consistent with a 'cold start' hypothesis (Forterre 2002). Furthermore, new records and a re-analysis of the rDNA database suggests that a non-thermophilic group, the Planctomycetes, were the earliest bacteria to emerge (Brochier and Philippe 2002).

If the early Earth did indeed experience widespread glaciation there would need to be some mechanism to allow eventual thawing and open water conditions. One suggestion is that periodic bombardments could provide such energy (Bada et al. 1994). Small impacts could have pierced any surface crusts of ice over the oceans leading to the venting of greenhouse gases into the atmosphere and accelerated warming. Larger impacts could result in sufficient energy to cause complete melting. Bada et al. (1994) calculate that impacts of bolides greater than 100 km diameter would release enough thermal energy to melt 300 m of ice cover on a frozen ocean.

3. Glaciations during the Paleoproterozoic

The earliest geological evidence of widespread glaciation on Precambrian Earth is from rocks of the Paleoproterozoic era that are dated at about 2.4 Ga before the present (Fig. 1). Glacially derived sediments of this age occur in the Transvaal Supergroup of southern Africa, and paleomagnetic studies indicate that they formed within the tropics at a paleolatitude of 11 ± 6 degrees. These beds are interspersed with volcanic flows and are overlaid by a 100 m thick layer of banded iron formations. Further above is a 45 m stratum of manganese-rich carbonate (the Kalahari Manganese Field, the world's largest land-based reserve of Mn), overlaid by dolomite.

Kirschvink et al. (2000) have interpreted the Transvaal sequence as indicating that the global climate experienced a rapid and massive set of changes during the Paleoproterozoic. Specifically, they argue that global cooling caused run-away albedo conditions in which extreme cooling led to a complete freeze-up of the surface oceans, a so-called 'snowball Earth' event ('une Terre boule de neige', Kirschvink 2002) that persisted for tens of millions of years. By this scenario, the prolonged ice cover and cessation of thermohaline circulation prevented the re-oxygenation of the bottom waters of the ocean, leading to anoxia and accumulation of reduced iron (Fe II) and manganese (Mn II). Eventual warming caused by the gradual atmospheric accumulation of CO₂ from volcanoes allowed the melting of ice, and triggered a cyanobacterial bloom and photosynthetic oxygen production that in turn caused the massive precipitation of oxidized iron (Fe III), then manganese (Mn IV). Kirschvink et al. (2000) suggest that the resultant drop in trace metal availability may have resulted in competition for these elements and a divergence in the use of Fe or Mn by the enzyme superoxide dismutase. Their phylogenetic analysis of the amino acid sequences of this enzyme showed that such divergence may have taken place well after the initial separation of the Bacteria and Archaea lineages, perhaps consistent with a snowball Earth scenario.

4. Glaciations during the Neoproterozoic

Several lines of evidence indicate that extreme cooling also occurred towards the end of the Precambrian resulting in a series of snowball Earth events between 0.6 and 0.8 Ga before the present. Glaciogenic rocks from the Neoproterozoic are found today on most continents, indicative of widespread glaciation at that time. Paleomagnetic analysis of some of these rocks show that they have low paleolatitudes, suggesting that glacial conditions extended all the way to the tropics where the continental landmasses were centered (Hoffman and Schrag 2002). The break up of the supercontinent Rodinia at that time has been suggested as a potential mechanism favoring global cooling. Such a break up could have accelerated rock weathering, the consumption of atmospheric CO₂, by reactions such as Eq. 1., and may also have increased the availability of habitat for CO₂-fixing stromatolites in shallow seas (Hoffman et al. 1998). The localization of landmasses in the tropics would have also raised planetary albedo, further enhancing the tendency towards global glaciation (Kirschvink 1992).

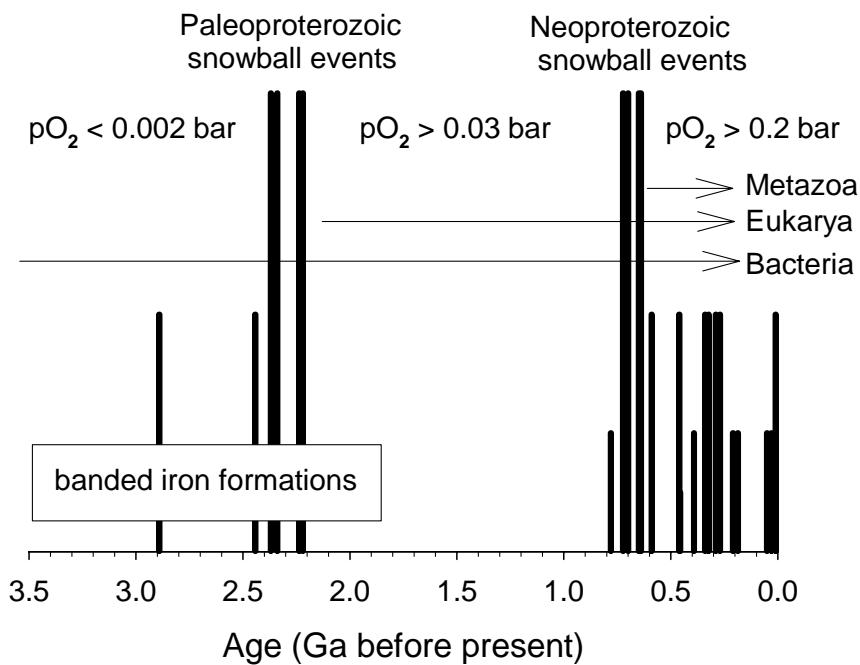


Figure 1. Glacial events during the last 3.5 Ga (vertical bars). Banded iron formations occurred continuously up to 1.86 Ma before the present, and also occur in Neoproterozoic glaciogenic rock formations. Modified from Hoffman and Schrag (2002).

A detailed analysis of the C-isotopic geochemistry of Neoproterozoic sequences seems consistent with snowball Earth events. The sequences show an unprecedented decrease in $\delta^{13}\text{C}$, followed by a slow return to normal levels (Hoffman et al. 1998). As the Earth got colder, the $\delta^{13}\text{C}$ of the oceans, and subsequently carbonate rocks, would drop due to a reduction in primary productivity. During the ensuing glaciation, the atmosphere and ocean would take on an isotopic signal similar to CO_2 from volcanic outgassing (Hoffman et al. 1998). Since carbonate production was curtailed by the global glaciations, the stratigraphic record includes lengthy gaps during these epochs. Also during this time, the ice cover would reduce the exposure of rock to silicate-weathering and would interrupt the hydrological cycle, allowing little precipitation. These reduced losses would cause volcano-derived CO_2 to gradually build up in the atmosphere, ultimately culminating in a strong greenhouse effect and rapid melting and break-up of the sea ice. After ocean-atmosphere communication was restored, the carbonates would take on a slightly more positive signal as atmospheric carbon was hydrated and precipitated, followed by a gradual, yet slight decrease due to Rayleigh distillation effects (Hoffman et al. 1998). It is also speculated that the drop in the carbonate $\delta^{13}\text{C}$ signature immediately prior to global freeze-up could have been the result of slow leakage of methane produced in anoxic oceanic basins (Schrag et al. 2002).

The Neoproterozoic glaciogenic sequences are overlain by thick caps of carbonate, specifically meters to tens of meters of dolostone and limestone. These are thought to represent the rain-out and subsequent carbonate precipitation of inorganic carbon that had built up in the atmosphere and ocean (Hoffman et al. 1998). These cap rocks are usually found above sequences showing glacial disturbance and are geographically widespread implying a global-scale process. The rocks indicate rapid depositional processes and severe perturbation of the global carbon cycle (Hoffman et al. 1998).

The analysis of banded iron formations, deposits of Fe(III) and chert, provides further evidence of large-scale freeze-up. These deposits are common in the stratigraphic record of early Earth, disappear after 1.86 Ga before the present and then reappear only within the Neoproterozoic glacial deposits (Fig. 1). This reappearance in the record after a 1.5 Ga absence is consistent with stagnation of the ocean and anoxia beneath the thick sea ice of a Neoproterozoic snowball Earth. The accumulation of reduced iron in the absence of reduced sulfur, and the subsequent precipitation of Fe(III) by oxygenic photosynthesis would have occurred during the ice-melt phase (Kirschvink 1992).

A variety of modeling analyses lend some support to the Neoproterozoic snowball Earth hypothesis. Application of a simple energy budget model shows the precarious balance between the two endpoints of complete global freeze-up and an ice-free Earth, and also illustrates the hysteresis in CO_2 conditions that control the planetary shift between these two disparate conditions (Fig. 2). The results of a GCM simulation using a 50 m slab ocean shows that under late Precambrian conditions of a 6% reduced solar constant, sea-ice and subfreezing temperatures occur from the poles to the Equator once atmospheric CO_2 concentrations fall below a threshold of 1700 ppm, (Jenkins and Smith 1999). Further calculations incorporating the latent heat of freezing suggest that the resultant ice could be relatively thin in the tropics and would allow some penetration of sunlight for photosynthesis into the seawaters beneath (McKay 2000). More recent modeling analyses based on equatorial temperatures of -30 °C and a spectral model for sunlight absorption suggest equilibrium ice thicknesses of the order of 1 km; however,

under conditions of slightly warmer surface temperatures and low albedo (for example associated with the transport of sediment to ice shelf surfaces in shallow seas; see Section 6.1, below) the simulated ice thickness is less than 1 m (Warren et al. 2002).

An ice sheet model has also been run using estimates of the Neoproterozoic climate regime and the results imply a band of open water in the tropics during snowball Earth events (Hyde et al. 2000). This 'slushball Earth' model is consistent with some observations but has been criticized as having an unrealistic distribution of continental landmasses; furthermore, the incomplete freeze-up that it predicts would not allow the ocean-wide anoxia that has been invoked to explain the mineral sequences (Hoffman and Schrag 2002).

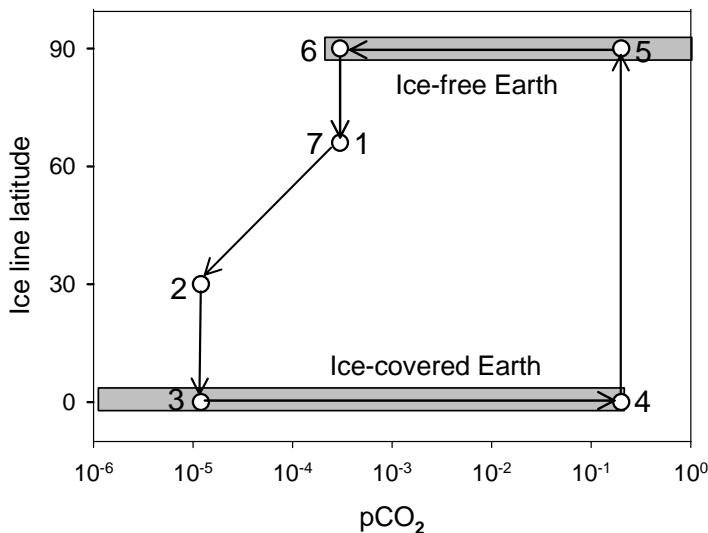


Figure 2. The postulated snowball Earth cycle. A decrease in $p\text{CO}_2$ from current values (1) results in ice expansion to lower latitudes (2) and a run-away albedo effect, ultimately causing a complete freeze-up to the Equator (3). A massive increase in $p\text{CO}_2$, for example via prolonged volcanic activity, would be required to melt the thick ice cover (4). Temperatures then rise to extreme values that preclude ice even at the highest latitudes (5); only after prolonged CO_2 drawdown (6) would cooling allow polar ice to the extent observed today (7). Based on Fig. 6 in Hoffman and Schrag (2002).

An alternative explanation of glaciogenic deposits at tropical latitudes is that the obliquity of the Earth (the tilt of the Earth's axis of rotation relative to its orbital plane) shifted to a large angle (Williams et al. 1998). With an obliquity greater than 54° , mean annual temperatures would be lower at the equator than at the poles and glaciation would be more likely at lower latitudes. Williams (1993) argued that an abrupt decrease in obliquity after 600 Ma resulted in an amelioration of climate that set the stage for the rise of metazoans. The obliquity model, however, has little direct support and seems inconsistent with several aspects of the geological record (Hoffman and Schrag 2002).

The snowball Earth hypothesis has stimulated intense debate in the Earth sciences community and there is currently no consensus about the extent of Neoproterozoic glaciation. Although complete freeze-up appears to reconcile several disparate types of

data including the carbonate stratigraphy, the $\delta^{13}\text{C}$ isotopic record, glaciogenic rock sequences and the banded iron formations, there are an increasing number of results that do not seem concordant. These include sedimentological data from northern Norway (Arnaud and Eyles 2002), stratigraphic analysis of Neoproterozoic glacial deposits in Oman (Leather et al. 2002), new analyses of the carbon and strontium isotopic records (Kennedy et al. 2001), evidence of glacial sediment deposition from free-floating icebergs (Condon et al. 2002), and modeling simulations of the Neoproterozoic climate and ocean with different land mass configurations (Poulsen et al. 2002).

One of the persistent challenges to the snowball Earth hypothesis is the argument that global freeze-up would result in the extinction of all living organisms, while the fossil record implies a continuity of life (Hoffman and Schrag 2002). Open water environments such as polynyas, flaws and tidecracks provide rich environments for diverse life-forms in today's polar regions. For example, more than 250 protist taxa have been identified in the North Water polynya between Ellesmere Island and Greenland (Lovejoy et al. 2002). Openings of this sort would clearly allow marine life to continue despite extensive glaciation, and would also allow anoxia elsewhere. Relatively thin ice cover in the tropics would similarly allow photosynthetic activity and complex food webs in seawaters beneath (McKay 2000), although other modeling scenarios imply that the ice could be too thick to allow such photosynthesis (Warren et al. 2002).

Earth scientists appear to be accepting the point of view that prokaryotes thrive in many extreme cold environments today on Earth, but still seem unaware 'that such environments can also harbor much more sophisticated organisms including eukaryotic algae and multicellular animals (metazoans). These modern-day cryo-ecosystems occur throughout alpine and polar regions, and can also be found in the cold temperate zones.

5. Modern-day Cryo-ecosystems

Micro-organisms are known to survive and even flourish in a wide range of present-day ice environments. Most bacteria and many eukaryotes are able to maintain prolonged dormancy under conditions of complete freeze-up, and in fact many microbes are routinely stored in liquid nitrogen (-196 °C). Conditions during the freezing process are critically important. Severe physical damage can be caused by ice crystal formation and there are osmotic and other chemical stresses caused by the freeze-concentration of solutes. Additionally, the mechanical stresses imposed during rethawing can result in cellular damage and mortality (Vincent 1988). However, many organisms have cellular and biochemical strategies that allow them to mitigate and withstand these effects. Such organisms are capable of rapid recovery after thawing and may also maintain substantial enzymatic and other biochemical activities at near-freezing temperatures (Deming and Huston 2000, Rothschild and Mancinelli 2001).

Snow provides a habitat for many types of microbial communities in the polar regions (Vincent 1988) as well as at temperate latitudes (Jones et al. 2001). These communities are often dominated by eukaryotic algae that are rich in UV-protecting carotenoids (Hoham and Ling 2000). Their primary production can in turn support metazoan grazers such as tardigrades, collembolans and ice worms. The latter, unusual annelids that are phylogenetically related to leeches, are adapted to freeze-thaw transitions and complete

their life cycles despite temperatures that rarely rise above 0 °C (Shain et al. 2001). An unrelated group of 'ice worms' (polychaetes) has been discovered growing on methane hydrates in frigid deep waters of the ocean (Fisher et al. 2000), suggesting another kind of chemoautotrophic ecosystem, in addition to hydrothermal vents, that could potentially survive during major freeze-up events.

Observations by the explorer Nordenskiöld on the Greenland ice cap in the 19th century revealed that 'a brown polycellular alga' (mostly cyanobacteria but also eukaryotes) bound together the sediments in water-filled depressions in the ice; these communities in turn accelerated local melting and the further development of microbial mats (Vincent 2000). These so-called cryoconite communities occur widely on glaciers in the Arctic and Antarctica as well as in alpine environments elsewhere, and support micro-invertebrates such as nematodes, rotifers and tardigrades (Mueller et al. 2001).

Sea ice covers more than 25 million km² of the ocean surface each year and provides a dynamic, highly structured environment for microbial communities as well as an associated food web (Vincent 1988, and references therein). The biomass dominants in these microbial ecosystems are eukaryotic algae (mostly pennate diatoms) that live in the extensive brine channels between the elongate ice crystals. These environments are also the habitat for a variety of other microbial extremophiles including many new taxa of bacteria that have been isolated and characterized over the last decade (Staley and Gosink 1999, Thomas and Dieckmann 2002, Bowman 2003).

Freshwater ice lacks the brine channeling of sea ice and contains a much less developed microbial flora. Nonetheless, microbial consortia of cyanobacteria, microalgae and heterotrophic bacteria have been observed in the ice on a variety of polar and alpine lakes (Priscu and Fritsen 1998, Priscu and Christner 2003). An unusual type of cryo-environment has been recently described in the McMurdo Dry Valleys, a benthic layer of brine-ice slush (<-10 °C) overlain by 19 m of lake ice (Doran et al. 2002).

Several other extreme low temperature environments have been described in recent years including streams beneath glaciers (Skidmore et al. 2000), the junction between ice crystals in the Antarctic ice cap (Price 2000), ancient permafrost soils (Rivkina et al. 2000) and supercooled water in ice clouds (Sattler et al. 2001). These underscore the broad success of microbial communities in surviving freeze-up and near-freezing growth conditions. One environment in particular, the thick sea ice that occurs today as ice shelves in the polar regions, is of particular relevance to discussions about Precambrian glaciation. These Arctic and Antarctic ice shelves provide the habitat for several types of microbial mat community. The mats are dominated by prokaryotes, but also provide local refugia for the growth and development of more complex organisms including eukaryotic microalgae and microinvertebrates.

6. Ice Shelf Cryo-ecosystems

Thick perennial sea ice is likely to have been especially widespread during glacial periods on Earth, including global freeze-up events of the Precambrian. The microbial communities living in this type of environment today are thus of great interest as analogs for cryo-ecosystems of the past. Microbial studies have now been conducted on two landfast, thick-ice (10-80 m) systems: the McMurdo Ice Shelf in the Ross Sea sector of

Antarctica, and the Ward Hunt Ice Shelf in high Arctic Canada (Fig. 3). These environments are completely frozen throughout most of the year, but both contain rich biological communities dominated by cyanobacteria that resume photosynthesis and growth during the periods of meltwater generation each summer.

6.1. MCMURDO ICE SHELF

The McMurdo Ice Shelf is composed of 1200 km² of marine-derived ice at the western edge of the Ross Ice Shelf. The ablation zone consists of two types of environment (Howard-Williams et al. 1990). About 30% of its area is characterized by an undulating topography, covered by a layer of moraine and marine sediments 10 to 20 cm thick. This material is thought to be transported up from the seabed by anchor ice formation or from zones of ice grounding on the sea floor (Debenham 1920) and results in low surface albedo values that influence the equilibrium thickness of ice (see Section 4 above) as well as the local topography (Fig. 3). The ice shelf undulations range up to 20 m, with the hollows occupied by melt ponds ranging from 1- 30 000 m² in area. The remainder of the ice shelf surface is characterized by a flatter overall relief, but with turrets of ice up to 0.5 m tall. Sediment cover is patchy in this region and the ponds tend to be small and shallow. In late summer, flowing waters are common in this 'pinnacle ice' region, including fast-flowing rivers up to several km long. In some areas there are elongate, north-south oriented parallel ponds, with no visible outflows.

The meltwater ponds of the McMurdo Ice Shelf encompass a broad range of salinities that reflect the variable influence of the underlying sea during ice formation, and redissolution of salts during the production of melt waters. In a set of extensive transect surveys (Howard-Williams et al. 1990), pinnacle ice melt waters ranged from 57 to 4000 µS cm⁻¹, while the undulating ponds spanned a much wider range from fresh (130 µS cm⁻¹) to hypersaline (56 000 µS cm⁻¹). On parts of the ice shelf there are large deposits of mirabilite ($\text{Na}_2\text{SO}_4 \cdot 10\text{H}_2\text{O}$) which form salts beds up to 1 m thick. These are thought to be derived from trapped pockets of seawater brines during the basal freezing of the ice, with the brines or precipitated salts then transported to the surface via cracks in the ice, or via the ongoing process of basal freezing and surface ablation. The ice shelf thus supports microhabitats for halophilic as well as low salinity microbes.

Many of the meltwater ponds on the McMurdo Ice Shelf contain a benthic layer of microbial 'ice-mats' (Fig. 3, Vincent 1988, Hawes et al. 1993). In the pinnacle ice region, the mats form a loosely bound community of cyanobacterial filaments and diatoms amongst the thin layer of gravel and sediments on the ice. In the undulating ice ponds, however, the communities are composed of cohesive, mucilaginous biofilms up to 50 mm thick. These microbial mats are often brightly pigmented with a surface orange, pink or brown layer rich in photoprotective carotenoids overlying a blue-green layer enriched in light-harvesting pigments, especially phycocyanin and chlorophyll *a*. In some of the more saline habitats, these aerobic upper layers are underlain by thin film of purple sulfur bacteria and then a deeper, black anaerobic zone. The upper layers are dominated by cyanobacteria, typically oscillatorians, although in some ponds there are also high populations of *Nostoc commune* and *N. microscopicum*. Profiles of spectral irradiance through the mat have shown that the surface carotenoid-rich layer screens out UV and blue wavelengths and that the oscillatorians in the photosynthetically most

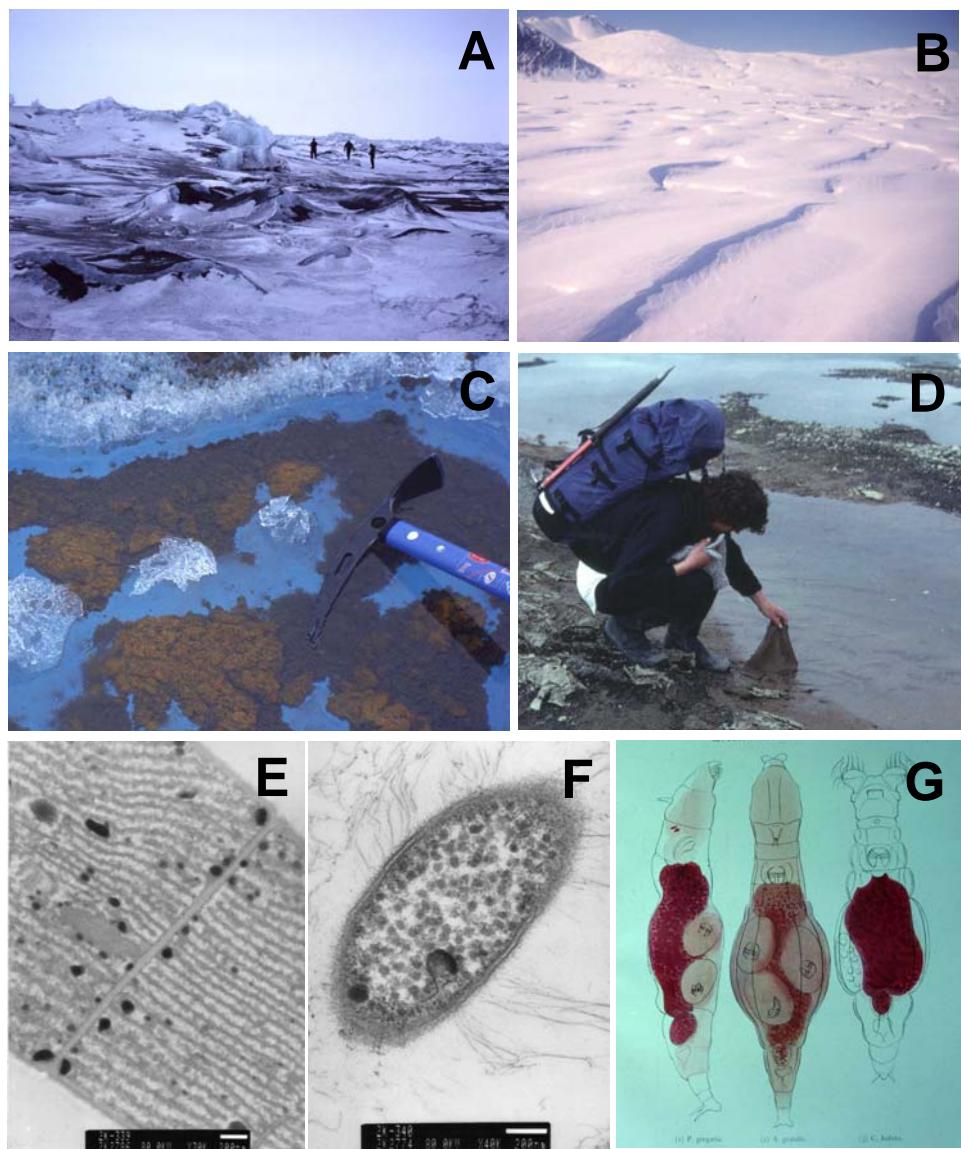


Figure 3. Ice shelf cryo-ecosystems. A. The McMurdo Ice Shelf, Antarctica, with marine sediments over the undulating, deep-frozen ice in late October. B. The undulating ice of the Ward Hunt Ice Shelf, Arctic Canada, with snow cover in early summer (June 1999). C. Microbial ice-mats in a meltwater pool on the Ward Hunt Ice Shelf. D. Microbial mats in a pond on the Koettlitz Glacier, at the edge of the McMurdo Ice Shelf. E, F. Transmission electron micrographs of a microbial mat from the McMurdo Ice Shelf showing thylakoid membranes of an oscillatorian, and a bacterium full of phage-like particles (Valérie Villeneuve et al., Centre d'Études Nordiques, Université Laval; unpublished); G. The rotifer *Philodina gregaria* rich in carotenoids derived from feeding on Antarctic cyanobacterial mats (Murray 1910).

active blue-green layer grow under highly shaded, orange-light conditions. Infrared radiation penetrates through the cyanobacterial layers to the deep stratum of photosynthetic sulfur bacteria below (Vincent et al. 1993).

There have been many ecophysiological studies on the both the intact mats of the McMurdo Ice Shelf as well as on taxa that have been isolated from these ice-mats and investigated in laboratory culture. All of the mats have proven to show nitrogenase activity, even those dominated by oscillatorians, but with some presence of the heterocystous genera *Nostoc*, *Anabaena* and *Nodularia*. These oscillatorian mats averaged a fixation rate that was estimated as $1 \text{ g m}^{-2} \text{ a}^{-1}$, which would account for about one third of the total nitrogen requirement of the mat community (Fernández-Valiente et al. 2001).

Nitrogen fixation as well as other physiological processes continue over a broad range of salinities indicating substantial tolerance to the variable conditions during freeze-up and melting. For example, Hawes et al. (1999) found that photosynthesis and respiration by McMurdo Ice Shelf microbial mats continued at conductivities $> 20 \text{ mS cm}^{-1}$, and it was only at 80 mS cm^{-1} (almost 2x seawater) that respiration declined. The microbial mats are also tolerant of prolonged desiccation, particularly those dominated by *Nostoc* (Hawes et al. 1992). In terms of temperature responses, most of the cyanobacterial isolates from the ice shelf mats have proved to be psychrotolerant rather than psychrophilic (Tang et al. 1997), although with some exceptions (Nadeau and Castenholz 2000). Growth optima are above 15°C , well above the warmest ambient conditions of most of the ponds.

The cyanobacteria of the mats seem to be highly tolerant of ambient UV radiation and *in situ* screening of solar UVA and UVB radiation produced no enhancement of their physiological activities (Quesada et al. 2001). This pronounced UV-resistance is the result of four lines of defense against the damaging effects of bright solar radiation (Vincent and Quesada 1997): escape through migration (Nadeau et al. 1999); screening by UV-absorbing pigments; quenching of reactive oxygen species, for example by carotenoids (Roos and Vincent 1998); and damage-repair mechanisms.

A variety of interesting bacteria are now known to occur in the anoxic underlayers of these mats. This community is fuelled by autotrophically derived carbon from the overlying cyanobacteria. The carbon flux is primarily to CO_2 rather than to methane, and sulfate reduction is the main terminal anaerobic process (Mountfort et al. 1998). One isolate from below the cyanobacterial mat of a freshwater pond on the ice shelf, *Clostridium vincentii*, was found to be obligately anaerobic and psychrophilic. Optimal growth was at 12°C , which is high relative to marine psychrophiles (e.g., relative to bacteria from the Southern Ocean). This isolate survived freeze-thaw cycles and grew well under salinities up to 30 %. It utilized a variety of mono- and disaccharides for growth including the cyanobacterial cell wall constituent N-acetyl glucosamine (Mountfort et al. 1997). Another novel psychophile, *Psychromonas antarcticus*, was obtained from below the mat of a saline pond on the ice shelf. This isolate grew over the range $2 - 17^\circ\text{C}$ (optimal growth at 12°C), tolerated high salt concentrations (10-40 %), and like *C. vincentii*, fermented N-acetyl glucosamine (Mountfort et al. 1998).

Studies on below-mat sediments have shown that freeze-thaw cycles influence the balance between methanogenesis and sulfate reduction (Mountfort et al. 2003). In low salinity sediments from ponds on the McMurdo Ice Shelf, both of these processes declined after freezing, but the carbon flow from acetate to methane increased relative to

sulfate reduction. In sediments from high salinity ponds, sulfate production always dominated but became uncoupled from acetate oxidation after freezing.

Although these mat communities are dominated by photosynthetic and heterotrophic prokaryotes, they also contain a variety of other organisms. Virus-like particles have been detected throughout the mat profiles (up to 5×10^9 particles ml⁻¹ of interstitial water, Valérie Villeneuve et al., unpublished), and TEM analysis of the mats has indicated the presence of bacteriophage (Fig. 3). Various eukaryotic algae occur within the mats, particularly small diatoms and green algae. Other protists occur within the mats such as ciliates and flagellates, and several micro-invertebrates occur including nematodes and abundant populations of rotifers (Suren 1990, Fig. 3).

6.2. WARD HUNT ICE SHELF

The Ward Hunt Ice Shelf extends northwards from the coast of Ellesmere Island in the Canada high Arctic and is one of several remnants of a much larger ice shelf system that extended 500 km along the northern coastline at the beginning of the 20th century (Vincent et al. 2001). Its upper ice surface of about 450 km² is a parallel system of wave-like troughs and ridges (Fig. 3) that contain elongate meltwater lakes and streams, typically 10 m wide, up to 3 m deep and 5 - 20 km long. Cylindrical holes up to 40 cm wide and 30 cm deep occur at the base of some of the elongate lakes, and have a higher conductivity and pH than the rest of the lake water. Similar holes but of more variable width (1-70 cm) also occur as discrete meltwater-filled pools at higher elevations on the ice ridges. The meltwaters of the lakes and pools have mostly low conductivities, however like the McMurdo Ice Shelf there is evidence that the ice and meltwater solutes are derived from the sea. The ratio of potassium to chloride relative to the same ratio for seawater is often around 1.0 in both systems, while the same ratio for sulfate is much higher (up to 67) consistent with the redissolution of mirabilite precipitated during the freezing of seawater. In parts of the Ward Hunt Ice Shelf, the surface contains marine sediments as well as sponges, molluscs and benthic crustaceans, further attesting to the marine origins of this glacial system. Similar marine fossils are found over the surface of the McMurdo Ice Shelf.

As in Antarctica, microbial mats are a feature of the Ward Hunt Ice Shelf, and also the nearby Markham Ice Shelf. These occur over the marine sediments that are periodically submerged by melt waters as well as in the cylindrical depressions in the ridge ice and at the base of the elongate lakes. The mats consist of a 2-10 mm layer of sediment that is loosely bound together by oscillatorian cyanobacteria and sometimes highly pigmented by a thin surface layer of cyanobacteria and chlorophytes containing orange carotenoids (Fig. 3). In an initial survey, chlorophyll *a* concentrations in these mats ranged from 0.4 to 15.3 µg Chl *a* cm⁻² which overlaps with the McMurdo values (Howard-Williams et al. 1990). However, the mats cover a small area (less than 1 %) of the total Ward Hunt Ice Shelf and the standing stock of microbial biomass is thus much lower than on the Antarctic ice shelf.

Nitrogen-fixing cyanobacteria appear to be sparse in the Ward Hunt communities, perhaps reflecting low phosphorus concentrations (and low N:P ratios) by comparison with those at McMurdo, and there is a high biomass of chlorophytes, in particular

Palmellopsis, *Chlorosarcinopsis*, *Pleurastrum*, *Chlamydomonas*, *Chlamydocapsa*, *Chlorella*, *Bracteococcus*, *Chlorococcum* and *Klebsormidium*. Like the McMurdo mats, these communities also contain abundant populations of small benthic and aerophilic diatoms. The most common diatom species is *Chamaepinnularia (Navicula) begeri*, with subdominance by species of *Nitzschia*, *Navicula*, *Luticola*, *Achnanthes* and *Pinnularia*. The diatom flora of the McMurdo mat is similarly dominated by the genera *Navicula*, *Nitzschia*, *Pinnularia* and *Achnanthes* (Howard-Williams et al. 1990). The microbial mats of the Ward Hunt Ice Shelf, like those in Antarctica also harbor a variety of other organisms including viruses, ciliates, flagellates, heterotrophic bacteria and microinvertebrates (Vincent et al. 2000). The latter group includes rotifers, tardigrades, nematodes and turbellaria (flatworms).

7. Evolutionary Implications

What would be the evolutionary consequences of one or more snowball Earth cycles as depicted in Figure 2? The initial phase of freeze-up (steps 1 to 3) would likely be accompanied by mass extinction and a reduction in genetic diversity. Thermophilic species would only survive in isolated refugia such as geothermal springs, volcanic vents and (for non-phototrophs) deep-sea hydrothermal systems. There would be increasing selection for cold-tolerant genotypes that could gradually adapt to decreased temperatures and freeze-up conditions. The strategies found today in the ice shelf ecosystems would seem well suited to such conditions, with psychrotrophic species adapted to prolonged freezing, intermittent thaw cycles and brief periods of slow growth during melt-out. As today, the microbial mats would allow a broad range of taxa to thrive under relatively protected conditions. The cyanobacterial UV-screens and quenching agents for reactive oxygen species would greatly reduce the impact of UV and bright PAR exposure, and the matrix of exopolymeric substances (EPS) produced by oscillatorians would protect all organisms within the fabric of the mat from freeze-thaw damage, as in annual sea-ice ecosystems (Krembs et al. 2003).

How long could such communities persist in the face of ongoing cooling (steps 3 to 4 in Fig. 2)? The global freeze-up scenarios to date have tended to focus on the low mean annual temperatures and the need for continuous liquid water conditions for the persistence of life. Kirschvink et al. (2000), in considering a hyperthermal ancestry for the three kingdoms of life, note that 'during a long snowball state, hydrothermal springs may have been one of the few places on Earth where liquid water was continuously maintained in the presence of sunlight'. However, the modern day ice shelf ecosystems experience only intermittent liquid water. Furthermore, high concentrations of solutes depress the freezing point of water to temperatures well below 0 °C, and in some Antarctic microbial mat environments (Ross Island ponds) the freeze-concentration of solutes results in liquid water conditions that persist well into winter despite air temperatures below - 40 °C (Schmidt et al. 1991). The presence of large quantities of marine derived salts and sediments on the modern day Ward Hunt and McMurdo ice shelves also suggests mechanisms that would tend to favor the persistence of microbial habitats. These solutes allow liquid water at low subzero temperatures, while black sediments derived from the sea floor enhance local radiative heating within or at the

surface of the ice. The low albedo due to sediments would also affect sea ice dynamics and thickness (Warren et al. 2002).

Microbial mats have long been considered ideal environments for evolutionary processes to operate, although the focus to date has been on hot water systems. The microbial consortia of such mats consist of highly concentrated populations from diverse functional groups in contact with each other. Physical and chemical interactions are likely to be particularly strong in such communities and could lead to mutualism, symbiosis, even eukaryogenesis. For example, Nisbet and Fowler (1999) suggest that eukaryotes could have formed by fusion of symbiotic partners living across the redox boundary in thermophilic mats. Ice-mats of the type that exist today and perhaps during Precambrian glaciations, have surface layers that are charged in oxygen because of its high solubility at low temperatures, and many also have anoxic bottom layers, thereby resulting in strong gradients in redox conditions and associated microbial community structure. Extracellular DNA would be relatively stable in these ice-cool conditions, perhaps further stabilized by the cyanobacterial EPS, increasing the opportunities for genetic transformation. As seen in today's mats, bacteriophage (Fig. 3) and virus-like particles are common, and transduction could thus also facilitate lateral gene transfer.

Under the most extreme cold of the snowball Earth scenario (step 3 in Fig. 2) near-surface liquid water environments could have been rare or non-existent. However, as seen in today's ice shelf environments, prolonged dormancy is an important feature of ice-mat ecology, and allows the communities to maintain a large, perennial biomass despite the prevalence of non-growth conditions in their surrounding habitat. The transition to hot-house conditions (step 4 to 5, Fig. 2) may have been the most severe constraint on microbial growth and survival. Such a regime would have largely extirpated truly psychrophilic species from surface environments, although the deep ocean would have offered a vast refuge for cold-loving chemotrophs. Phototrophic species such as cyanobacteria and eukaryotes with broad thermal tolerances, as seen in today's ice-mats, would have been especially successful. The final return to warm conditions could have been the trigger for accelerated evolution and genetic exchange from isolated refugia, and the emergence of diverse life forms as observed in the Cambrian fossil record (Hoffman and Schrag 2000).

For some evolutionary biologists and Earth scientists, only prokaryotes could have survived the global glaciations of the Proterozoic. Thus Cavalier-Smith (2002) postulates that 'there is no problem, as plastids evolved just after the Varangerian [final Neoproterozoic glaciation] snowball Earth melted. If this is true, only bacterial photosynthesizers need have survived the near global glaciations and eukaryotic algae could have originated and radiated immediately after the climate rewarmed, with animals following hard on their heels in the Vendian and Cambrian.' Yet as shown here, today's ice shelf ecosystems contain rich microbial mats that contain many eukaryotes including diatoms, flagellates, ciliates, colonial green algae, and also metazoa such as rotifers (Fig. 3) and flatworms. These organisms thrive despite prolonged freeze-up and dormancy, and offer insights into how complex life may have persisted and evolved, even during the glacial upheavals of the Precambrian.

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