ISSN 0026-2617, Microbiology, 2015, Vol. 84, No. 2, pp. 125–129. © Pleiades Publishing, Ltd., 2015.

REVIEWS

Ecological Niches of Antarctic Phototrophic Communities during Global Glaciation

Z. B. Namsaraev[a, b, 1]

[a] *NRC "Kurchatov Institute", pl. Akademika Kurchatova 1, Moscow, 123182 Russia*

[b] *Winogradsky Institute of Microbiology, Russian Academy of Sciences, pr. 60-letiya Oktyabrya 7, k. 2, Moscow, 117312 Russia*

Received June 9, 2014

Abstract—According to paleontological data, large-scale, global glaciations occurred repeatedly over the history of Earth. Such glaciations unavoidably resulted in a sharp decrease in the number of habitats suitable for development of phototrophic microorganisms, which mostly require sunlight. Molecular data indicate that some groups of Antarctic phototrophic microorganisms emerged before formation of the Antarctic ice sheet (30–45 Ma) and probably survived the subsequent glaciation maxima. Analysis of the data on the present-day occurrence of phototrophs in Antarctica revealed the presence of liquid water in a habitat to be the key factor for survival of phototrophic communities. At negative air temperatures, this requirement may be met either in warmer microniches (0 to 30°C and higher) or in brines with freezing temperatures below zero (to −52°C). Development of phototrophic communities in such habitats may indicate the theoretical possibility of existence of the niches favoring growth of phototrophic microorganisms during Precambrian global glaciations. This possibility should be considered in paleontological reconstructions of development of life on Earth.

Keywords: Antarctica, phototrophic microorganisms, ecological niche, glaciations

DOI: 10.1134/S0026261715020083

Paleontological data suggest numerous large-scale glaciations in the history of Earth, which were probably global and spread to the tropical areas [1]. Glaciations were found to coincide with large-scale rearrangements in the biosphere. Thus, a series of Huronian glaciations coincided with oxygenation of the atmosphere, while a series of lower Proterozoic glaciations coincided with a decrease in diversity of stromatolite cyanobacterial communities and an increase in eukaryotic diversity, indicating the role of these events in the evolution of life.

Reliable data on the scale of Precambrian glaciations required for detailed reconstruction are absent. Scarce information is available even on the best-studied Neoproterozoic glaciations. Different estimates of sea ice occurrence and thickness at low latitudes vary considerably. The estimated sea ice thickness in the tropical zone varies from over 1 km, which prevents existence of photosynthesis-based life in the ocean [2], to less than 10 m, which makes it possible for photosynthetic organisms to develop under ice [3]. Various hypotheses exist concerning ice occurrence in the oceans, from complete ice cover over the oceans, including their equatorial area, to existence at ~20°–40° latitude [4]. The estimated ice covering of the dry land also varies from complete glaciation (snowball Earth) to a 5°–10° ice-free equatorial zone [5–7].

Global glaciations result in a drastic decrease in the number of habitats supporting development of phototrophic microorganisms. These organisms usually occur within the photic zone, i.e., to the depth not exceeding 200 m in lakes and sea (depending on the trophic status of a water body), up to ~ 1 cm in rocks (depending on the content of transparent quartz granules), up to 3–5 cm in sand, and to 10 m in ice (depending on its purity). Glaciations should have affected most strongly the populations of oxygenic phototrophic microorganisms (cyanobacteria, microalgae, etc.). Except for some microalgae capable of heterotrophic growth in the dark and probably some marine cyanobacteria incapable of photosynthesis, they require sunlight for development. These two groups of organisms are of special importance, since they carry out oxygenic photosynthesis, are among the major producers in diverse ecosystems, and exhibit massive development after large-scale glaciations [8]. In theory, most groups of anoxygenic phototrophic bacteria (APB) are less sensitive to the absence of sunlight, since they are capable of prolonged heterotrophic development in the dark. Moreover, some groups of purple bacteria at the bottom of the ocean may probably utilize the infrared radiation of geothermal phenomena for phototrophic growth. Green bac-

[1] Corresponding author; e-mail: zorigto@gmail.com

teria and heliobacteria are incapable of prolonged survival in the dark [9].

Antarctica is a good actualistic model for determination of the types of habitats where phototrophic bacteria could have survived global glaciations. The Antarctic ice sheet is up to 4 km thick and annual average temperatures in central Antarctica are −50°C and lower, while the size of the ice sheet in summer exceeds 4000 km. In spite of its severe climate, the Antarctic continent possesses a relatively considerable diversity of phototrophic microorganisms and lower plants (cyanobacteria, microalgae, lichens, and mosses). The only two species of vascular plants found on this continent occur only in the Antarctic Peninsula, i.e., in the area with the mildest climate [10]. In most Antarctic ecosystems, phototrophic microorganisms are the main primary producers, which make this continent a good model of Precambrian conditions, when microorganisms dominated on Earth.

MOUNTAIN PEAKS ABOVE THE ICE SHEET SURFACE

The maximal height of Antarctic mountains is 4897 m (Vinson Massif, western Antarctica). A number of Antarctic mountains rise several meters to over 4 km above the surrounding ice sheet. Modern reconstructions of the volume of the Antarctic ice sheet, as well as analysis of the ice cores indicate that during the last glacial maximum (26 ka ago), the ice sheet was up to ~1400 m thicker (depending on the site) than at present [11]. Thus, during the last glacial maximum most Antarctic mountains had considerable elevation above the glacier surface, and ice-free zones were to exist in these sites.

According to its climatic parameters, Antarctica is a cold desert with insignificant precipitation over most of the continent (up to ~350 mm per year). Development of terrestrial microbial communities in Antarctica depends, as a rule, on the presence of liquid water in a given habitat [12]. Ice and snow thawing is the main source of liquid water. The major habitats for Antarctic phototrophic microorganisms are therefore the northern mountain slopes heated by sunlight, seepage sites of subterranean water, ephemeral flows and springs, and surface or subglacial lakes. Microbial crusts up to several cm thick developing on rock and soil surface at such habitats consist of lichens, microalgae, and filamentous cyanobacteria (lithophytic and edaphic communities). At the depth of up to ~1 cm below the rock surface, endolithic communities develop, in which unicellular cyanobacteria usually predominate [13].

At most of the Antarctic territory, in spite of the permanent negative air temperature, dark rock and soil surfaces are heated to positive temperatures, causing snow thawing. Our observations in the Sør Rondane Mountains (eastern Antarctica) elevating ~1200 m above sea level revealed that rock surfaces heated to 25°C, while air temperature at 2 m height was −2°C. Positive temperatures of the upper soil layer (up to 12.6°C at the air temperature −7.5°C) were reported even for the southernmost ice-free sites (Howe nunatak and La Gorce Mountains, 300 km from the South pole). At these sites, phototrophic communities developed, predominated by lichens (*Lecidea cancriformis* and *Carbonea vorticosa*), cyanobacteria (*Phormidium autumnale, Leptolyngbya fragilis,* and *Hammatoidea normanni*) and green microalgae (*Desmococcus cf. olivaceus*) [14]. For comparison, the average air temperature at the Amundsen-Scott station (South Pole) is −29 to −81°C (temperature range from −12 to −117°C).

We analyzed molecular diversity of cyanobacteria in Antarctic terrestrial communities of the Sør Rondane Mountains and carried out bioinformatic analysis of cyanobacterial diversity throughout the continent [15, 16]. Antarctic cyanobacteria were shown to exhibit high diversity. The communities contained all the major morphological groups: unicellular, filamentous, and heterocystous cyanobacteria. Most of the operational taxonomic units (OTU) do not have cultured representatives (57% or 24 out of 42). Among the groups with cultured representatives, cyanobacterial genera *Phormidium, Leptolyngbya,* and *Nostoc* were most common. The genera *Coleodesmium, Cyanothece, Geitlerinema, Acaryochloris, Anabaena, Fischerella*, and *Limnothrix* were represented by single OTUs. Geographical analysis of cyanobacterial occurrence revealed the possibility of a "high cyanobacterial diversity zone" between 70° and 80° S. Cyanobacterial diversity decreased drastically to the north and south of this zone. This finding is in disagreement with the traditional view of diversity decreasing in the Polar Regions. This zone may exist due to higher tolerance of cyanobacteria to low temperatures and decreased competition of cyanobacteria with mosses and lichens for light, water, and biogenic elements.

Most Antarctic terrestrial cyanobacteria (79% or 33 out of 42 OTUs) were cosmopolites and have been revealed at sites outside Antarctica. Their occurrence in Antarctica may be due to their resistance to freezing or by local heating of rock surfaces (up to 25–30°C at northern slopes in summer).

Up to 21% of Antarctic cyanobacteria were potentially endemic. Investigation of enrichment cultures of potentially endemic Antarctic cyanobacteria of the *Cyanothece aeruginosa* group revealed that it was psychrophilic and adapted to existence at low temperatures. Available data are insufficient for the explanation of the origin of highly endemic groups of Antarctic cyanobacteria. Assuming 1% per 50 Ma as the rate of the 16S rRNA gene "molecular clock," these groups of cyanobacteria were formed over 150 Ma ago [17]. In the late Jurassic period Antarctic climate was probably moderately warm, comparable to the modern climate of Southern Europe.

Based on the 18S rRNA "molecular clock," the majority of Antarctic microalgae have estimated ages between 17 and 84 Ma and probably diverged from their closest relatives around the time of the opening of Drake Passage (30–45 Ma), while some lineages with longer branch lengths have estimated ages that precede the break-up of Gondwana (65–100 Ma ago) [18].

ICE AND SNOW SURFACE LAYER

Existence of phototrophic microorganisms in the photic zone of ice or snow also depends on the presence of liquid water. Three major types of phototrophic communities may be identified: cryoconites (in ice), lakes on the glacial shelf surface, and the so-called snow algae developing on the snow surface.

Cryoconites are formed when sand or stones occur upon the ice surface. Their occurrence is usually limited to several km from ice-free areas. Under sunlight, stones and sand become heated, melt the ice, and form a cryoconite hole. A stone below the ice surface is still heated by sunrays due to ice transparency. Submersion of the stone stops at a certain depth (usually not exceeding 1 m). Depending on climatic conditions, the water in a cryoconite hole may be permanently covered with ice or remain open for most of the summer season. Water temperature in cryoconites is usually from 0.1 to 1°C; at the same time, the ambient air temperature may be as low as –25°C. A phototrophic community consisting of cyanobacteria (*Cyanothece aeruginosa, Tolypothrix, Phormidium*, and *Leptolyngbya*) and microalgae develops on the surface of the sand in cryoconites [16].

The lakes at the surface of shelf glaciers (floating or partially lying on the sea bottom) appear in summer. Their salinity may vary from fresh, low-mineral to seawater (~35 g/L). In some lakes, thick (up to several cm) mats are formed mostly by filamentous cyanobacteria of the genera *Phormidium, Oscillatoria,* and *Lyngbya,* as well as by heterocystous cyanobacteria of the genera *Nostoc, Nodularia*, and *Anabaena* [20].

Another type of phototrophic communities is represented by snow algae, communities of microalgae developing on the snow surface. They are usually found at the edges of the glacial sheet and are often responsible for red coloration of snow (red snow, watermelon snow). Since snow algae have not been reported in the central regions of Antarctica, thawing at the glacier surface is one of prerequisites for their development. Similar to cryoconites, the temperature of liquid water at a glacier surface is 0.1 to 1°C. Green algae predominate in these communities: *Chlamydomonas nivalis* and *Chloromonas rubroleosa* [21].

ZONES OF HYDROTHERMAL ACTIVITY

Antarctica is a volcanically active continent with numerous manifestations of hydrothermal activity both below the glacial sheet and on the ground surface. Numerous sites of fumaroles and heated soils are known in the vicinity of the active volcano Mount Erebus and on Deception Island (close to the Antarctic Peninsula). Phototrophic microbial communities develop at the surfaces of soil and hydrotherm bottom sediments. The wide range of temperatures allows for development of different types of communities, including mesophilic and thermophilic. In thermophilic communities, typical thermophilic cyanobacteria *Mastigocladus laminosus* and *Fischerella muscicola*, growing at 60–70°C, were found. Molecular analysis of the cyanobacteria from Mount Erebus revealed their high similarity to the members of these taxa retrieved from other regions. Since the distance to the closest hydrothermal area (New Zealand) is ~4000 km, detection of these organisms may be an indication of intercontinental transfer of thermophilic bacteria [16].

LAKES

Salinity of Antarctic lakes varies within a broad range, from freshwater ones, resulting from ice melting, to hypersaline. In Antarctica, low temperature and freezing result in formation of some of the highest-salinity lakes on Earth, such as Don Juan Pond with ~480 g/L mineralization. Predominance of $CaCl_2$ (413 g/L) and NaCl (29 g/L) in this lake results in the brine not freezing till about –52°C, which is the lowest calculated temperature for aquatic solutions [22]. A cyanobacterial mat with predominance of cyanobacteria *Oscillatoria* sp. and the presence of green microalgae morphologically resembling *Chlorella* sp. and *Dunaliella* sp. was observed at the lake surface close to the shore [23]. Existence of microbial life in this lake is of interest for astrobiology, since the ice-covered ocean on Europa (a satellite of Jupiter) may be close in composition to the Don Juan Pond brine.

At lower salinity, phototrophic communities with high diversity of cyanobacteria, microalgae, and anoxygenic phototrophic bacteria develop in Antarctic lakes [24]. Cyanobacteria, belonging mostly to the genera *Leptolyngbya* and *Phormidium*, often form mats at the bottom, which sometimes occur at depths of ~100 m. Mats with conical protrusions were observed in Lake Untersee (eastern Antarctica), which is permanently covered by ice ~3 m thick. These structures may be a modern model for formation of *Conophyton*-type stromatolites [25]. The bottom sediments of Antarctic lakes, including microbial mats, may reach considerable thickness due to low rates of organic matter decomposition and burial by sedimentary materials. Investigation of the sediment samples 50–4530 years old from a lake in Skarvsnes, Lützow Holm Bay (east Antarctica) revealed the preservation of cyanobacterial structures on millennial timescales. Apart from polysaccharide sheaths, some pigments, as well as thylakoids were preserved [26].

CONCLUSION

Analysis of Antarctic phototrophic communities of various types shows their ability to thrive within a broad range of ambient conditions utilizing various survival mechanisms. At the cellular level, these mechanisms include synthesis of intracellular cryoprotectors preventing formation of ice crystals inside the cells, formation of thick extracellular sheaths, transition to a metabolically inactive state at temperatures below a certain level and rapid activation under favorable conditions, etc. Combined application of these mechanisms enables the microorganisms to retain some activity at temperatures reaching –10 to –15°C [27]. Importantly, these mechanisms may occur in some microorganisms from moderate zones. This is confirmed by the detection of cyanobacterial taxa of cosmopolite occurrence in Antarctica [16].

The presence of liquid water in a habitat is the major factor at the community level [12]. At negative air temperatures, this condition could be met in brines freezing at subzero temperatures (as low as –52°C for calcium chloride solutions of Don Juan Pond) or in microniches with the temperatures from 0 to 30°C and higher. Such microniches may occur at the mountain peaks rising above the surface of the continental ice sheet, on ice surface several km from the peaks, at the edges of the ice sheet, in hydrothermal areas, and in terrestrial lakes with low thickness of ice. Combined action of these factors determines the conditions for existence of modern Antarctic phototrophic communities. Detection of phototrophic communities in Antarctic habitats may indicate that ecological niches favorable for development of phototrophic microorganisms could theoretically exist on land surface during Precambrian global glaciations. This should be considered in paleontological reconstructions of the conditions required for development of life on Earth during glaciation maxima [28]. The spectrum of ecological conditions in these environments favors development of various microbial groups, from thermophiles to psychrophiles. Molecular clock data indicate that many groups of Antarctic phototrophic microorganisms emerged prior to the beginning of formation of the Antarctic ice sheet (30–45 Ma ago) and successfully survived the subsequent glaciation maxima.

REFERENCES

1. Chumakov, N.M. and Sergeev, V.N., The problem of climate zonality in the late Precambrian. Climate and biospheric events, in *Klimat v epokhi krupnykh biosfernykh perestroek* (Climate during the Epochs of Major Biospheric Reorganizations), Moscow: Nauka, 2004, pp. 271–289.
2. Goodman, J.C. and Pierrehumbert, R.T., Glacial flow of floating marine ice in "Snowball Earth," *J. Geophys. Res.–Oceans*, 2003, vol. 108, p. 3308.
3. Warren, S., Brandt,R.E., and McKay, C.P., Snowball Earth: ice thickness on the tropical ocean, *J. Geophys. Res.*, 2002, vol.107, pp. 1–17.
4. Poulsen, C.J., Pierrehumbert, R.T., and Jacob, R.L., Impact of ocean dynamics on the simulation of the Neoproterozoic "Snowball Earth," *Geophys. Res. Lett.*, 2001, vol. 28, pp. 1575–1578.
5. Hyde, W.T., Crowley, T.J., Baum, S.K., and Peltier, W.R., Neoproterozoic "snowball Earth" simulations with a coupled climate/ice-sheet model, *Nature*, 2000, vol. 405, pp. 425–429.
6. Fairchild, I.F. and Kennedy, M.J., Neoproterozoic glaciation in the Earth System, *J. Geol. Soc. London*, 2007, vol. 164, pp. 895–921.
7. Macdonald, F.A., Schmitz, M.D., Crowley, J.L., Roots, C.F., Jones, D.S., Maloof, A.C., Strauss, J.V., Cohen, P.A., Johnston, D.T., and Schrag, D.P., Calibrating the Cryogenian, *Science*, 2010, vol. 327, pp. 1241–1243.
8. Olcott, A.N., Sessions, A.L., Corsetti, F.A., Kaufman, A.J., and de Oliviera, T.F., Biomarker evidence for photosynthesis during Neoproterozoic glaciations, *Science*, 2005, vol. 310, pp. 471–474.
9. The *Archaea* and the deeply branching and phototrophic *Bacteria*, in *Bergey's Manual of Systematic Bacteriology, 2nd ed.*, Boone, D.R., Castenholz, R.W., and Garrity, G.M., Eds., New York: Springer, 2001, vol. 1, pp. 601–623.
10. Convey, P., Gibson, J.A.E., Hillenbrand, C.-D., Hodgson, D.A., Pugh, P.J., Smellie, J.L., and Stevens, M.I., Antarctic terrestrial life—challenging the history of the frozen continent?, *Biol. Rev.*, 2008, vol. 83, pp. 103–117.
11. Ackert, J.R.P., Mukhopadhyay, S., Parizek, B.R., and Borns, H.W., Ice elevation near the West Antarctic ice sheet divide during the last glaciation, *Geophys. Res. Lett.*, 2007, vol. 34, p. L21506.
12. Kennedy, A.D., Water as a limiting factor in the Antarctic terrestrial environment: a biogeographical synthesis, *Arct. Alp. Res.,* 1993, vol. 25, pp. 308–315.
13. Broady, P.A., Diversity, distribution and dispersal of Antarctic terrestrial algae, *Biodivers. Conserv.*, 1996, vol. 5, pp. 1307–1335.
14. Broady, P.A. and Weinstein, R., Algae, lichens and fungi in La Gorce Mountains, Antarctica, *Antarctic Sci.*, 1998, vol. 10, pp. 376–385.
15. Fernández-Carazo, R., Namsaraev, Z., Mano, M.J., Ertz, D., and Wilmotte, A., Cyanobacterial diversity for an anthropogenic impact assessment in the Sør Rondane Mountains area (Antarctica), *Antarctic Sci.*, 2012, vol. 24, pp. 229–242.
16. Namsaraev, Z., Mano, M.J., Fernandez, R., and Wilmotte, A., Biogeography of terrestrial cyanobacteria from Antarctic ice-free areas, *Ann. Glaciol.*, 2011, vol. 51, pp. 171–177.
17. Ochman, H. and Wilson, A.C., Evolution in bacteria: evidence for a universal substitution rate in cellular genomes, *J. Mol. Evol.*, 1987, vol. 26, pp. 74–86.

18. De Wever, A., Leliaert, F., Verleyen, E., Vanormelingen, P., Van der Gucht, K., Hodgson, D.A., Sabbe, K., and Vyverman, W., Hidden levels of phylodiversity in Antarctic green algae: further evidence for the existence of glacial refugia, *Proc. Royal Soc. London Ser. B*, 2009, vol. 276, pp. 3591–3599.

19. Cameron, K.A., Hodson, A.J., and Osborn, A.M., Structure and diversity of bacterial, eukaryotic and archaeal communities in glacial cryoconite holes from the Arctic and the Antarctic, *FEMS Microbiol. Ecol.,* 2012, vol. 82, pp. 254–267.

20. Jungblut, A.D., Hawes, I., Mountfort, D., Hitzfeld, B., Dietrich, D.R., Burns, B.P., and Neilan, B.A., Diversity within cyanobacterial mat communities in variable salinity meltwater ponds of McMurdo Ice Shelf, Antarctica, *Environ, Microbiol.*, 2005, vol. 7, pp. 519–529.

21. Kawecka, B., Ecology of snow algae, *Polish Polar Res.*, 1986, vol. 7, pp. 407–415.

22. Marion, G.M., A theoretical evaluation of mineral stability in Don Juan Pond, Wright Valley, Victoria Land, *Antarctic Sci.*, 1997, vol. 9, pp. 92–99.

23. Siegel, B.Z., McMurty, G., Siegel, S.M., Chen, J., and Larock, P., Life in the calcium chloride environment of Don Juan Pond, Antarctica, *Nature*, 1979, vol. 280, pp. 828–829.

24. Taton, A., Grubisic, S., Balthasart, P., Hodgson, D.A., Laybourn-Parry, J., and Wilmotte, A., Biogeographical distribution and ecological ranges of benthic cyanobacteria in East Antarctic lakes, *FEMS Microbiol. Ecol.*, 2006, vol. 57, pp. 272–289.

25. Andersen, D.T., Sumner, D.Y., Hawes, I., Webster-Brown, J., and McKay, C.P., Discovery of large conical stromatolites in Lake Untersee, Antarctica, *Geobiology*, 2011, vol. 9, pp. 280–293.

26. Lepot, K., Compère, P., Gérard, E., Namsaraev, Z., Verleyen, E., Tavernier, I., Hodgson, D. A., Vyverman, W., Gilbert, B., Wilmotte, A., and Javaux, E.J., Organic and mineral imprints in fossil photosynthetic mats of an East Antarctic lake, *Geobiology*, 2014, vol. 12, pp. 424–450.

27. Elster, J. and Benson, E.E., Life in the polar terrestrial environment a focus on algae and cyanobacteria, in *Life in the Frozen State*, Fuller, B., Lane, N., and Benson, E.E., Eds., London: Taylor and Francis, 2004, pp. 111–149.

28. Namsaraev, Z.B., Antarctica as a model of survival of terrestrial phototrophic communities during Precambrian global glaciations, in *Vodorosli v evolutsii biosferi. Seriya: "Geo-biologicheskiye protsessi v proshlom"* (Algae in the Evolution of Biosphere. Series: "Geo-Biological Processes in the Past"), Rozhnov, S.V., Ed., Moscow: Paleontological Institute Russ. Acad. Sci., 2014, pp. 67–76.

Translated by P. Sigalevich