ISSN 0026-2617, Microbiology, 2011, Vol. 80, No. 1, pp. 125–131. © Pleiades Publishing, Ltd., 2011.
Original Russian Text © M.S. Chuvochina, I.A. Alekhina, P. Normand, J.-R. Petit, S.A. Bulat, 2011, published in Mikrobiologiya, 2011, Vol. 80, No. 1, pp. 129 – 135.

EXPERIMENTAL ARTICLES

Three Events of Saharan Dust Deposition on the Mont Blanc Glacier Associated with Different Snow-Colonizing Bacterial Phylotypes

M. S. Chuvochina[1, a, b], I. A. Alekhina[a, b], P. Normand[c], J.-R. Petit[b], and S. A. Bulat[1, a, b]

[a] *St. Petersburg Nuclear Physics Institute, Russian Academy of Sciences, Gatchina, 188300 Russia*
[b] *Division of Molecular and Radiation Biophysics, Laboratory of Glaciology and Geophysics, CNRS, BP 96, 38402 Saint Martin, d'Héres Cedex Grenoble, France*
[c] *Division of Microbial Ecology, Lyon University 1, Lyon, 69622 Villeurbanne cedex, France*

Received March 1, 2010

Abstract—A preliminary study has demonstrated that the structure and species composition of microbial communities associated with events of dust deposition from the Sahara Desert to the Mont Blanc glacier varied considerably between samples originating from different time periods. Even for depositions within a single month, the dominant microbial phylotypes and candidates to colonize the snow pack were different. It is therefore highly probable that the structure and species composition of microbial communities will be different between any events of the kind. Apparently, the phenomenon does not correlate with the time the dust stays in the snow cover and consequently with the probable development of microorganisms in situ (three months, one month, and one week). The reasons for the variation may be the differences in conditions in the epicenter of a specific North African dust storm, as well as the history of the dust transport in the atmosphere. The candidates for joining the snow biome of Mont Blanc turned out to be different for three dust events (DEs) and belong to different, mostly minor, phylotypes related to *Crossiella cryophilus* (*Actinobacteria*), *Devosia limi* (α-*Proteobacteria*), *Deinococcus claudionis* (*Deinococcus-Thermus*), *Anabaena* sp. (*Cyanobacteria*), and *Hymenobacter soli* (*Bacteroidetes*). Since all these phylotypes have been previously isolated from soil samples of the Antarctic and Arctic, Arctic snow and ice, and the Alpine belt soils and sedimentary rocks of the glacier bed, they were tentatively ascribed to the group of snow pack colonizers.

Keywords: soil dust, dust deposition, snow, colonization, microorganisms, 16S rRNA, opportunistic pathogens, autotrophs, oligotrophs, psychrotrophs, astrobiology.

DOI: 10.1134/S0026261711010061

Methods of molecular biology employing genetic markers as 16S rRNA and functional genes [1, 2] allowed for discovery of an incomparably wider microbial diversity in comparison to traditional culturing methods. The sensitivity of molecular techniques makes it possible to work with samples containing as little as 1 cells/ml, for example, with the snow from the Vostok Antarctic station area [3]. Work with samples of such low biomass (as snow [3]) generates problems considerably different from those arising while working with samples of high biomass, such as soil. The major problem in the analysis of soil microbial diversity in samples containing up to 10^9 cell/g [4] is to underestimate it, while in snow, sample contaminations create a serious problem for singling out the true members of the microbial community.

Until recently, algae, e.g., members of the genera *Chlamydomonas* and *Chloromonas*, were the most studied components of the snow microbial communities [5], while bacterial diversity lacked attention. The total bacterial population in highland snow cover is presently known to vary between 3×10^3 [6] to 8.4×10^4 cells/ml [7] and proliferation in snow apparently affects only the numbers of certain phylotypes. High cell concentrations (up to 2.3×10^5 cells/ml [7]) may be due to sedimentation of abiogenic (mineral) particles (dust) onto the snow or their condensation during the snow melting period. For example, studies of snow in the vicinity of the Tateyama mountain chain in Japan revealed a single psychrophilic and two psychrotrophic bacterial species. Seasonal variations in bacterial numbers were confirmed by real-time PCR measurements of bacterial biomass [7]. This research demonstrated the correlation between the concentration of mineral particles from the atmosphere and bacterial biomass in the surface snow layer [7]. Later, Chinese researchers discovered a similar correlation during the study of the core of the eastern Rongbuk glacier on Mt. Everest in the Himalayas at 6518 m above sea level [8]. The concentration of culturable bacteria precipitated on the glacier during the premonsoon season, which coincided with the episodes of continental dust transport from northwestern China, was consid-

[1] Corresponding author; e-mail: chuvochina@omrb.pnpi.spb.ru, sergey.bulat@ujf-grenoble.fr

erably higher than that before and after the monsoon. Therefore, it was concluded that microbiological record of the glacier core might be used to interpret the changes in atmospheric circulation, thus providing important information for the analysis of climatic changes on Earth [8]. Subsequent works determined that microbial diversity, rather than microbial numbers, correlated with the concentrations of atmospheric dust [9, 10]. Different bacterial species were isolated and cultured from glacier cores at varying depths, reflecting different ecological and climatic changes. The structure of bacterial communities during the similar climate events was different which is ascribed to the effects of different climate cycles and sources of bacterial origin [9, 10].

The Sahara Desert is known to be the largest source of soil dust aerosols in the atmosphere [11]. African soil dust was shown to contain viable microorganisms, including plant, animal, and human pathogens, even after long-term transport in the atmosphere [12, 13]. The biogeochemical effect of soil dust transport has been studied mainly for the cases of increased primary production in aquatic ecosystems [14, 15]. Besides inorganic nitrogen, phosphorus, and iron, dust contains organic carbon [16], which may serve as a substrate and energy source for growth of heterotrophic microorganisms.

Analysis of cores of the Mont Blanc glacier (French Alps) during the last 30 years has demonstrated that increased calcium content in ice was most probably associated with regular soil dust transport from northern Africa [17]. Being deposited on a glacier surface, the dust may act as both a transporting vehicle and a source of nutrients and energy for microorganisms. Therefore, the snow cover microbiota of mountain glaciers is assumed to be formed mostly by allochthonous microflora carried by dust transport.

The goal of the present work was a comparative study of the diversity of microbial communities having been formed in the snow cover of the Mont Blanc glacier as a result of three Saharan soil dust deposition events (dust storms) by means of bacterial 16S rRNA gene sequencing. The events differed by date of deposition as well as the duration of the dust's stay inside the snow. The aims of the study also included description of the species composition of microbial communities in each of the events and evaluation of the members contribution to the formation of the snow microbiome under conditions of low temperature of the Mont Blanc glacier at a height of 4250 m.

MATERIALS AND METHODS

The subjects of the study were microbial communities formed in the snow cover of the Mont Blanc glacier as result of three events of Saharan soil dust deposition (dust storms or dust events, DE).

Collection of surface snow containing discrete dust layers was carried out in September 2006 and May to June 2008 in the area of Col du Dome at the height of 4250 m above sea level. Usually, the spring–summer period in northern Africa is characterized by a high frequency of dust storms with subsequent effects detectable at considerable distances from the source. Samples of snow containing soil dust layers deposited on the glacier surface as a result of dust storms in Sahara desert in June 2006 (SDm06/2006), May 2008 (SDm05/2008), and June 2008 (SDm06/2008) were collected. The time periods of dust deposition in snow were three months, one month, and one week, respectively. SDm stands for the atmospheric transport of Saharan desert dust onto the Mont Blanc glacier (Saharan Dust on Mont Blanc) as a result of a dust storm.

Physicochemical conditions in the surface layer of snow on the Mont Blanc glacier are characterized by negative temperature (–11°C [18]), which is, however, considered sufficient for life (today, the temperature of –20°C is suggested to be the lowest threshold where microbial proliferation is still possible [19]). Average seasonal accumulation of the glacier at collection sites varied from 0.5 to 2.4 m water equivalent/year [20]. This probably decreases significantly the time the microorganisms are exposed to ultraviolet radiation when deposited on the open surface. Initially, the environment (snow cover) is oligotrophic; however, episodic transport of soil dust from the Sahara Desert characteristic of the place regularly enriches the snow with inorganic minerals and organic components [16, 17].

Snow samples were melted under clean conditions (purity class 10000, laminar class 100) of the Laboratory of Environmental Glaciology and Geophysics (CNRS-UJF, Grenoble, France). The material was then concentrated 111 (MB-SD2), 121 (MB5), and 176 times (MB-SD) using Centricon YM-3 filtrating columns (3 kDa, Millipore).

Total DNA was isolated from the samples using a PowerSoil DNA Isolation Kit (MoBio, United States) and was subsequently used in amplification reactions with a pair of universal primers (338Fb and com2) against the variable region v3-v5 of bacterial 16s rRNA genes as previously described in [21, 22]. To control the contamination with allochthonous DNA, blank DNA extraction and negative PCR samples (without sample addition) were introduced. The amplicons (~590 bp) were cloned into TOP10 cells using a TOPO TA Cloning Kit for Sequencing (Invitrogen, United States). The clones were analyzed by restriction with three endonucleases *Alu*I, *Hpa*II, and *Hae*III (Fermentas, Lithuania). Clones with similar restriction product profiles in agarose gel were combined into a single ribotype (ribo-phylotype), and one to three representatives of each ribotype were sequenced in LGC Genomics (formerly AGOWA) GmbH (Berlin, Germany). Nucleotide sequence alignment, comparison, and identification were performed using the CLUSTALW2 (http://www.ebi.ac.uk/Tools/clustalw2/index.html)

software package and the BLAST algorithm of the GenBank database (http://blast.ncbi.nlm.nih.gov/Blast.cgi). The nucleotide sequences demonstrating over 97.5% similarity and the same list of closely related sequences in the database were joined into a single phylotype. The phylotypes were compared with the home library of contaminants (the sequences revealed in different control reactions [21]), and only those lacking in the library considering the sequencing error (1%) were conserved for further study [21]. The phylotypes matching (over 97.5% similarity) those of human origin (e.g., the members of the human skin microbiome in GenBank) were marked as human-associated (HA). Phylogenetic reconstruction was performed by the maximum parsimony method using the MEGA4 software package. Thirty-two nucleotide sequences of the revealed phylotypes were deposited in the GenBank database under accession numbers HM104591–HM104622.

To verify the relation between dust deposition events and the atmospheric transport from Sahara, reverse trajectories of air mass movement were reconstructed using the HYSPLIT model (NOAA ARL Website, www.arl.noaa.gov/ready.php, GDAS meteorological data) for time periods corresponding to the dust storms in 2006 and 2008.

RESULTS AND DISCUSSION

Reversed trajectories of atmospheric masses (Fig. 1) pointing out the potential regions of dust events show that the layers of soil dust discovered in snow are connected to atmospheric transport from the Sahara. The sites where air current trajectories approach the relief line suggest that soil dust from the Sahara Desert during dust storms or along the air mass movement was possibly captured.

To create clone libraries of samples SDm06/2006, SDm05/2008, and SDm06/2008, 40, 38, and 38 clones were studied, respectively, providing over 74% coverage (according to Good's formula $(1 - n/N) \times 100$, where n represents the number of singlet phylotypes in the library and N, the number of clones analyzed). These clones were grouped by ribotyping. Nucleotide sequences were determined for the groups' representatives. Clones for the libraries of SDm06/2006, SDm05/2008, and SDm06/2008 were grouped into 12, 19, and 15 phylotypes, respectively, according to the similarity of their nucleotide sequences. Contaminant status tests in most cases revealed individual phylotypes-clones SDm06/2006 (one phylotype corresponding to one clone) and SDm05/2008 (one phylotype corresponding to one clone). Only SDm06/2008 made an exception, with three phylotypes corresponding to 11 (28.9%) clones in total, indicating the importance of use of contaminant libraries. Eventually, the number of phylotypes having passed the laboratory contamination control for the libraries of sample SDm05/2006, SDm05/2008, and SDm06/2008 was 11, 18, and 12 respectively.

In the course of identification, two to four HA phylotypes were also revealed in each library, which is of interest to clinical microbiologists studying opportunistic pathogens and pathogenic microorganisms. For example, in a number of north African regions, dust storms are known to cause local meningococcal infection outbreaks [23]. However, since the aim of the present study was to find potential colonizers of the snow cover, HA phylotypes were excluded from further investigation.

Thus, the final number of phylotypes having passed contamination control and unrelated to the human microbiome was 8, 14, and 10 for the libraries of SDm05/2006, SDm05/2008, and SDm06/2008 respectively. One phylotype was common for SDm05/2008 and SDm06/2008 (two clones in each case) and was identified as *Sphingomonas kaistensis* with 96.4% similarity of nucleotide sequences.

The selected 32 (or 31 taking into account the single common phylotype) phylotypes belonged to six taxonomic groups, namely, the *Actinobacteria* (13 phylotypes), α-*Proteobacteria* (9), *Deinococcus–Thermus* (2), *Firmicutes* (4), *Cyanobacteria* (1), and *Bacteroidetes* (3). Four phylotypes of the *Actinobacteria*, two phylotypes of *Deinococcus-Thermus*, and one phylotype of each of *Cyanobacteria, Bacteroidetes*, and *Firmicutes* were dominant (comprising three or more clones), while the *Actinobacteria* and *Deinococcus-Thermus* turned out to be leaders by phylotype number. All four dominant phylotypes of *Actinobacteria* were revealed in the two DEs of 2008 separated by only a summer month, while both dominant *Deinococcus-Thermus* phylotypes and all three dominant phylotypes of *Cyanobacteria, Bacteroidetes*, and *Firmicutes* were present only in the DE of 2006, which also occurred in the summer period, two years earlier. A dendrogram of all phylotypes demonstrates these results (Fig. 2). This tendency also turned out to be true for minor (by clone number) phylotypes. Thus, libraries of DE of 2006 and 2008 did not overlap in their bacterial community composition with the exception of the *Firmicutes* group where both *Bacillus* phylotypes originating from DE SDm05/2006 and SDm05/2008 turned out to be closely related.

Although the vast majority of phylotypes exhibited high sequence similarity (including environmental clones, that is uncultured clones of unknown taxonomy known only by DNA) to GenBank sequences, they may be divided into three groups according to their similarity to known taxa: over 95% similarity (genus level), 19 phylotypes; 90–95% similarity, 10 phylotypes; and less than 90% similarity (phylum/class, unknown phylotypes), 3 phylotypes. Phylotype distribution among the groups was significantly different in the three DE. While in both DE of 2008, most of the phylotypes were identified at the level of genus and species, in the DE of 2006 this was true for

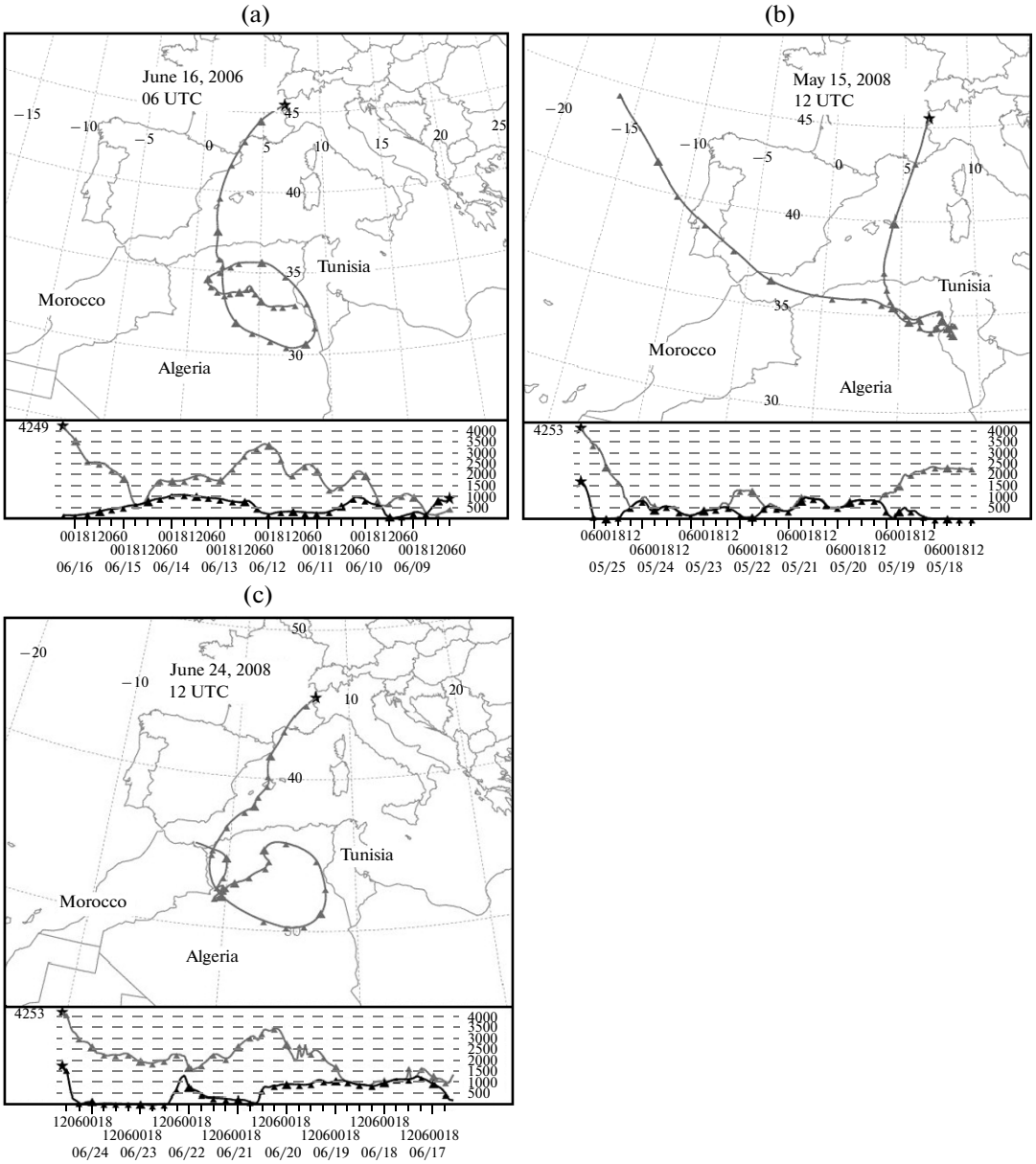

Fig. 1. Examples of eight-day reverse trajectories of air masses having reached the site of snow collection at Col du Dome at the height of 4250 m above sea level (marked with a black star). The graphs below the maps plot the history of atmospheric transport (gray line) toward the relief (black line) with height above sea level indications. SDm06/2006 (a), SDm05/2008 (b), SDm06/2008 (c).

only one out of eight phylotypes. Importantly, in the latter library two interesting [24] dominant phylotypes of *Deinococcus* of the second group were obtained, demonstrating 94% similarity (by sequences) with the closest taxa known (*Deinococcus xinjiangensis* and *Deinococcus claudionis*). However, all attempts to isolate them in pure cultures to study their morphological and physiological responses to extreme environmental factors of the Mont Blanc habitat failed (Ph. Normand, data not shown). Two dominant phylotypes of the third group of unidentified taxonomic position were found in the 2006 DE and one in June 2008 (indicated in Fig. 2). This is an additional indication of the differences between the three DE in the structure of microbial communities.

Although a cluster of phylotypes, including three dominant ones, related to the genus *Geodermatophilus* of *Actinobacteria* (Fig. 2), which includes UV-resistant organisms of arid soils [25], prevailed in the two libraries of 2008 DE, subsequent study excluded them from the group of potential snow colonizers. Conversely, it was possible to describe as a colonizer one of the minor phylotypes from the same cluster (96.6% similarity to *Crossiella cryophilis*) of the DE of May 2008 (Fig. 2), which exhibited high similarity to bacteria detected

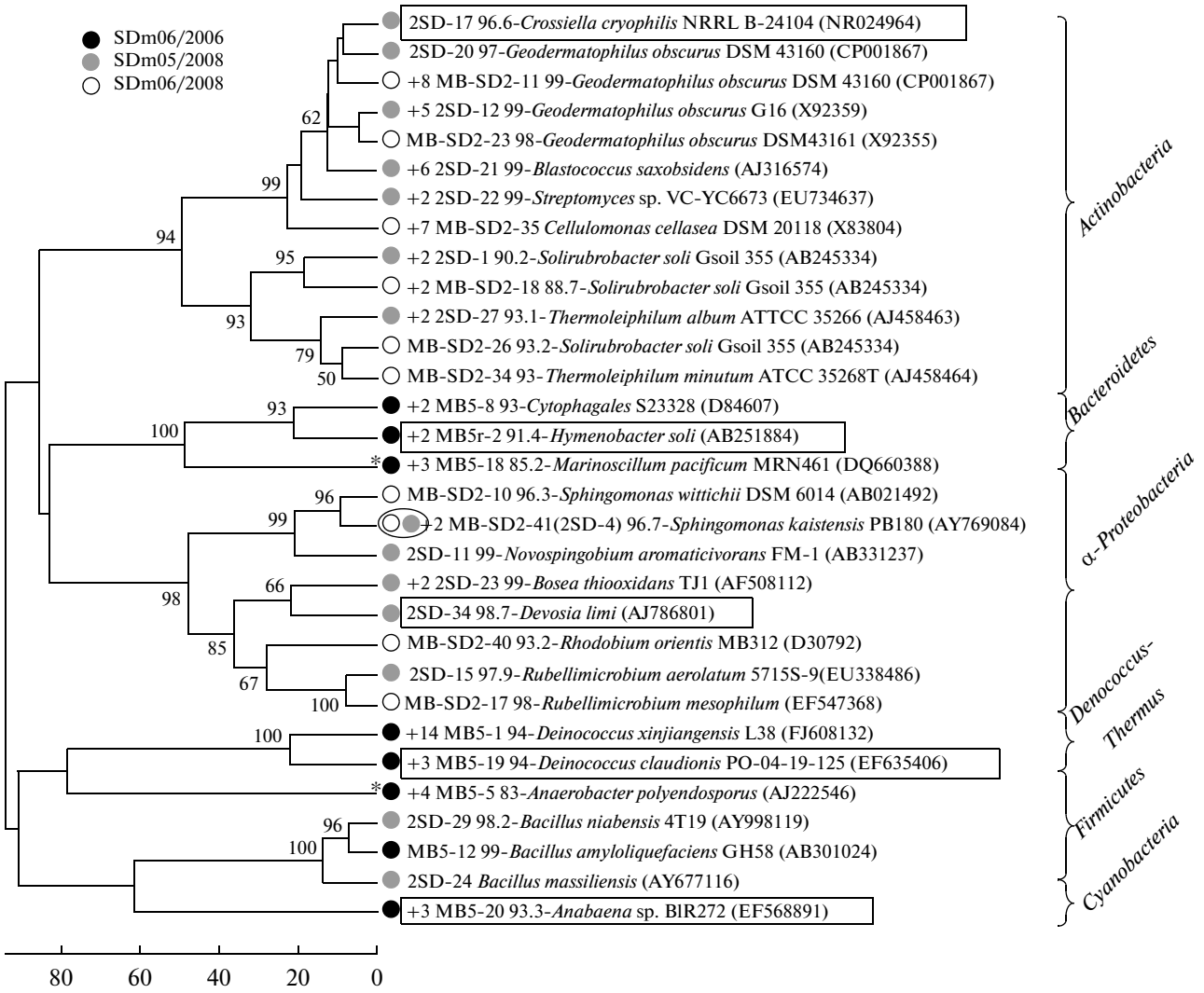

Fig. 2. Phylogenetic tree constructed on the basis of nucleotide sequences of bacterial 16S rRNA genes determined in three DEs on the Mont Blanc peak (maximum parsimony method for 513 nucleotide bases, 237 nucleotide bases being phylogenetically informative). Statistical support of branching order (bootstrap values of 50% and higher) is presented for analysis of 500 alternative trees. The frames indicate the possible snow cover colonizer phylotypes. The phylotypes of unidentified taxonomy are marked with a star. An ellipse indicates the only common phylotype for two dust events. The scale indicates the minimum number of phylogenetically significant nucleotide replacements required to achieve the topology of the tree.

earlier in cold habitats [26]. Within the α-*Proteobacteria* phylum, another minor phylotype (98.7% similarity to *Devosia limi*) of the DE of May 2008 was recognized as a snow colonizer candidate [27].

As for the 2006 DE, three phylotypes were selected as snow colonization candidates, two major ones (94% similarity to *Deinococcus claudionis* and 93.3% similarity to *Anabaena* sp.) [24, 28] and a minor one (91.4% similarity to *Hymenobacter soli*) [29] of the phyla *Deinococcus-Thermus, Cyanobacteria*, and *Bacteroidetes*, respectively. All the related taxa were isolated from soil samples in the Antarctic and Arctic, Arctic snow and ice, and from soils of the alpine belt and glacier bed sediments. However, to confirm that the phylotypes belong to the "snowy" biome, studies of the time-dependent and seasonal biomass variations are required.

Thus, a preliminary study has demonstrated that the structure and species composition of microbial communities associated with episodic dust transport from the Sahara Desert to the Mont Blanc glacier varied significantly depending on time periods of transport. Even for dust transport events occurring within one month from each other, the dominant phylotypes and candidates for colonization were different. It may be expected that, in the case of other events of the kind, the structure and species composition will be different. The duration of deposition of dust (and consequently microorganisms) in the snow (three months, one month, and one week) is hardly related to this

phenomenon, although it could be the subject of an independent study. Even a three-month interval does not seem to be enough to collect the "snowy" phylotypes, since it might be too short for accumulation of sufficient biomass. Assuming bacteria proliferating in the parietal water layers of soil capillaries in perpetually frozen soil even at −10°C, the minimum cell doubling time may be 20 days [30]. The Mont Blanc "snowy" biome candidates revealed were different for all three DE and belonged to both dominant and minor phylotypes. The reason for the difference may be both the conditions in the dust storm epicenter in northern Africa and the history of a specific dust transport event in the atmosphere. Studies on amplification of full-size bacterial 16S rRNA genes as indirect indicators of live intact "snowy" biota may contribute to a more complete vision of microbial diversity and ways of snow microbiota formation in high-altitude glaciers.

ACKNOWLEDGMENTS

The authors are grateful to the staff of the Laboratory of Environmental Glaciology and Geophysics (LGGE-CNRS, Grenoble, France) M. Debre, B. Jourda, and E. Le Mer for their assistance in snow sample collection.

The work was supported by a grant of the Russian Foundation for Basic Research (project no. 10-04-01223 (S.A. Bulat)) and ANR 07-Blan-0223-Lac Vostok (J.-R. Petit).

REFERENCES

1. Amann, R.I., Ludwig, W., and Schleifer, K.H., Phylogenetic Identification and in situ Detection of Individual Microbial Cells Without Cultivation, *Microbiol. Rev.,* 1995, vol. 59, pp. 143–169.
2. Zézé, A., Mutch, L.A., and Young, J.P.W., Direct Amplification of *nodD* from Community DNA Reveals the Genetic Diversity of *Rhizobium leguminosarum* in Soil, *Environ. Microbiol.,* 2001, vol. 3, pp. 363–370.
3. Bulat, S.A., Alekhina, I.A., Lipenkov, V.Ya., Lukin, V.V., Marie, D., and Petit, Zh.R., Cell Concentrations of Microorganisms in Glacial and Lake Ice of the Vostok Ice Core, East Antarctica, *Mikrobiologiya,* 2009, vol. 78, no. 6, pp. 850–852 [*Microbiology* (Engl. Transl.), vol. 78, no. 6, pp. 808–810].
4. Whitman, W.B., Coleman, D.C., and Wiebe, W.J., Prokaryotes: The Unseen Majority, *Proc. Natl. Acad. Sci. USA*, 1998, vol. 95, pp. 6578–6583.
5. Thomas, W.H. and Duval, B., Snow Algae: Snow Albedo Changes, Algal-Bacterial Interrelationships, and Ultraviolet Radiation Effects, *Arctic Alpine Res.*, 1995, vol. 27, no. 4, pp. 389–399.
6. Bauer, H., Kasper-Giebl, A., Löflund, M., Giebl, H., Hitenberger, R., Zibuschka, F., and Puxbaum, H., The Contribution of Bacteria and Fungal Spores to the Organic Carbon Content of Cloud Water, Precipitation and Aerosols, *Atmos. Res.,* 2002, vol. 64, pp. 109–119.
7. Segawa, T., Miyamoto, K., Ushida, K., Agata, K., Okada, N., and Kohshima, S., Seasonal Change in Bacterial Flora and Biomass in Mountain Snow from the Tateyama Mountains, Japan, Analyzed by 16S rRNA Gene Sequencing and Real-Time PCR, *Appl. Environ. Microbiol.*, 2005, vol. 71, no. 1, pp. 123–130.
8. Zhang, S. and Hou, S., Ma, X., Qin, D., and Chen, T., Culturable Bacteria in Himalayan Ice in Response to Atmospheric Circulation, *Biogeosciences,* 2007, vol. 4, pp. 1–9.
9. Zhang, S., Hou, S., Wu, Y., and Qin, D., Bacteria in Himalayan Glacial Ice and Its Relationship to Dust, *Biogeosciences,* 2008, vol. 5, no. 6, pp. 1741–1750.
10. Zhang, X.F., Yao, T.D., Tian, L.D., Xu, S.J., and An, L.Z., Phylogenetic and Physiological Diversity of Bacteria Isolated from Puruogangri Ice Core, *Microb. Ecol.,* 2008, vol. 55, pp. 476–488.
11. Moulin, C., Lambert, C.E., Dulac, F., and Dayan, U., Control of Atmospheric Export of Dust from North Africa by the North Atlantic Oscillation, *Nature,* 1997, vol. 387, no. 6634, pp. 691–694.
12. Griffin, D.W., Garrison, V.H., Herman, J.R., and Shinn, E.A., African Desert Dust in the Caribbean Atmosphere: Microbiology and Public Health, *Aerobiologia,* 2001, vol. 17, pp. 203–213.
13. Prospero, J.M., Blades, E., Mathison, G., and Naidu, R., Interhemispheric Transport of Viable Fungi and Bacteria from Africa to the Caribbean with Soil Dust, *Aerobiologia,* 2005, vol. 21, pp. 1–19.
14. Bonnet, S., Guieu, C., Chiaverini, J., Ras, J., and Stock, A., Effect of Atmospheric Nutrients on the Autotrophic Communities in a Low Nutrient, Low Chlorophyll System, *Limnol. Oceanogr.,* 2005, vol. 50, pp. 1810–1819.
15. Pulido-Villena, E., Morales-Baquero, R., and Reche, I., Evidence of an Atmospheric Forcing of Bacterioplankton and Phytoplankton Dynamics in a High Mountain Lake, *Aquat. Sci.,* 2008, vol. 70, pp. 1–9.
16. Eglinton, T.I., Eglinton, G., Dupont, L., Sholkovitz, E.R., Montlucon, D., and Reddy, C.M., Composition, Age, and Provenance of Organic Matter in NW African Dust over the Atlantic Ocean, *Geochem. Geophys. Geosyst.*, 2002, vol. 3, no. 8, p. 1050.
17. De Angelis, M. and Gaudichet, A., Saharan Dust Deposition over Mont Blanc (French Alps) During the Last 30 Years, *Tellus,* 1991, vol. 43B, pp. 61–75.
18. Vincent, C., Le Meur E., Six D., Possenti P., Lefebvre E., Funk M. Climate Warming Revealed by Englacial Temperatures at Col du Dome (4250 m, Mont Blanc Area), *Geophys. Rev. Lett.*, 2007, vol. 34, no. 16, p. L16502.
19. The MEPAG Special Regions—Science Analysis Group // Findings of the Mars Special Regions Science Analysis Group, *Astrobiology,* 2006, vol. 6, no. 5, pp. 677–732.
20. Preunkert, S., Wagenbach, D., Legrand, M., and Vincent, C., Col du Dome (Mt Blanc Massif, French Alps) Suitability for Ice-Core Studies in Relation with Past Atmospheric Chemistry Over Europe, *TELLUS,* 2000, vol. 52B, no. 3, pp. 993–1012.
21. Bulat, S.A., Alekhina, I.A., Blot, M., Petit, J.R., De Angelis, M., Wagenbach, D., Lipenkov, V.Ya., Vasilyeva, L.P., Wloch, D.M., Raynaud, D., and Lukin, V.V.,

DNA Signature of Thermophilic Bacteria from the Aged Accretion Ice of Lake Vostok, Antarctica: Implications for Searching for Life in Extreme Icy Environments, *Int. J. Astrobiol.*, 2004, vol. 3, no. 1, pp. 1–12.

22. Lavire, C., Normand, P., Alekhina, I.A., Bulat, S.A., Prieur, D., Birrien, J.L., Fournier, P., Hänni, C., and Petit, J.R., Presence of *Hydrogenophilus thermoluteolus* DNA in Accretion Ice in the Subglacial Lake Vostok, Antarctica, Assessed Using *rrs, cbb* and *hox, Environ. Microbiol.*, 2006, vol. 8, no. 12, pp. 2106–2114.

23. Polymenakou, P.N.V., Mandalakis, M., Stephanou, E.G., and Tselepides, A., Particle Size Distribution of Airborne Microorganisms and Pathogens During an Intense African Dust Event in the Eastern Mediterranean, *EHP,* 2008, vol. 116, no. 3, pp. 292–296.

24. Callegan, R.P., Nobre, M.F., McTernan, P.M., Battista, J.R., Navarro-Gonález, R., McKay, C.P., Costa, M.S., and Rainey, F.A., Description of Four Novel Psychrophilic, Ionizing Radiation-Sensitive *Deinococcus* Species from Alpine Environments, *Int. J. Syst. Evol. Microbiol.*, 2008, vol. 58, no. 5, pp. 1252–1258.

25. Kuhlman, K.R., Allenbach, L.B., Ball, C.L., Fusco, W.G., La Duc, M.T., Kuhlman, G.M., Anderson, R.C., Stuecker, T., Erickson, I.K., Benardini, J., and Crawford, R.L., Enumeration, Isolation, and Characterization of Ultraviolet (UV-C) Resistant Bacteria from Rock Varnish in the Whipple Mountains, California, *ICARUS,* 2005, vol. 174, no. 2, pp. 585–595.

26. Saul, D.J., Aislabie, J.M., Brown, C.E., Harris, L., and Foght, J.M., Hydrocarbon Contamination Changes the Bacterial Diversity of Soil from Around Scott Base, Antarctica, *FEMS Microbiol. Ecol.*, 2005, vol. 53, pp. 141–155.

27. Foght, J., Aislabie, J., Turner, S., Brown, C.E., Ryburn, J., Saul, D.J., and Lawson, W., Culturable Bacteria in Subglacial Sediments and Ice from Two Southern Hemisphere Glaciers, *Microb. Ecol.,* 2004, vol. 47, no. 4, pp. 329–340.

28. Pointing, S.B., Warren-Rhodes, K.A., Lacap, D.C., Rhodes, K.L., and McKay, C.P., Hypolithic Community Shifts Occur as a Result of Liquid Water Availability Along Environmental Gradients in China's Hot and Cold Hyperarid Deserts, *Environ. Microbiol.,* 2007, vol. 9, no. 2, pp. 414–424.

29. Larose, C., Berger, S., Ferrari, C., Navarro, E., Dommergue, A., Schneider, D., and Vogel, T.M., Microbial Sequences Retrieved from Environmental Samples from Seasonal Arctic Snow and Meltwater from Svalbard, Norway, *Extremophiles,* 2010, vol. 14, no. 2, pp. 205–212.

30. Rivkina, E.M., Friedmann, E.I., Mckay, C.P., and Gilichinsky, D.A., Metabolic Activity of Permafrost Bacteria below the Freezing Point, *Appl. Environ. Microbiol.*, 2000, vol. 66, no. 8, pp. 3230–3233.