Microbiology, Vol. 71, No. 5, 2002, pp. 601–607. Translated from Mikrobiologiya, Vol. 71, No. 5, 2002, pp. 697–704.

EXPERIMENTAL ARTICLES

The Absorption and Fluorescence Spectra of the Cyanobacterial Phycobionts of Cryptoendolithic Lichens in the High-Polar Regions of Antarctica

L. G. Erokhina, A. V. Shatilovich, O. P. Kaminskaya, and D. A. Gilichinskii

Institute of Fundamental Problems of Biology, Russian Academy of Sciences, Pushchino, Moscow oblast, 142290 Russia

Institute of Physicochemical and Biological Problems of Soil Science, Russian Academy of Sciences, Pushchino, Moscow oblast, 142290 Russia

Received May 8, 2001

Abstract—The algologically pure cultures of the green–brown cyanobacterium *Chroococcidiopsis* sp. and three cyanobacteria of the genus *Gloeocapsa*, the blue–green *Gloeocapsa* sp.$_1$, the brown *Gloeocapsa* sp.$_2$, and the red–orange *Gloeocapsa* sp.$_3$, were isolated from sandstones and rock fissures in the high-polar regions of Antarctica. These cyanobacteria are the most widespread phycobionts of cryptoendolithic lichens in these regions. The comparative analysis of the absorption and the second-derivative absorption spectra of the cyanobacteria revealed considerable differences in the content of chlorophyll *a* and in the content and composition of carotenoids and phycobiliproteins. In addition to phycocyanin, allophycocyanin, and allophycocyanin B, which were present in all of the cyanobacteria studied, *Gloeocapsa* sp.$_2$ also contained phycoerythrocyanin and *Gloeocapsa* sp.$_3$ phycoerythrocyanin and *C*-phycoerythrin (the latter pigment is typical of nitrogen-fixing cyanobacteria). The fluorescence spectra of *Gloeocapsa* sp.$_2$ and *Gloeocapsa* sp.$_3$ considerably differed from the fluorescence spectra of the other cyanobacteria as well. The data obtained suggest that various zones of the lichens may be dominated either by photoheterotrophic or photoautotrophic cyanobacterial phycobionts, which differ in the content and composition of photosynthetic pigments.

Key words: high-latitude regions of Antarctica, cyanobacterial phycobionts of cryptoendolithic lichens, pigments, absorption spectra, second-derivative absorption spectra, low-temperature fluorescence spectra.

The ecologically unique cryptoendolithic lichens of the dry high-polar high-mountain regions of Antarctica are the only representatives of flora in these harsh environments. Nienow and Freedmann described 5 types of cryptoendolithic lichen communities, three of which contained cyanobacteria as phycobionts [1]. One of these three lichens, named by the authors "*red-Gloeocapsa*," was found to contain six species of the cyanobacterial genus *Gloeocapsa* as well as the cyanobacteria *Eucapsis* sp. and *Anabaena* sp.$_2$, as phycobionts. A second lichen, named "*Hormatonema–Gloeocapsa*," contained *Hormatonema* sp., 7 species of the genus *Gloeocapsa*, and three species of the genera *Anabaena*, *Aphanocapsa*, and *Lyngbya*. The third lichen, "*Chroococcidiopsis* community," contained the only cyanobacterial phycobiont *Chroococcidiopsis* sp. As can be seen from these data, the major cyanobacterial phycobionts of the lichens belong to the genus *Gloeocapsa*. The phycobionts of this genus differed in color: three were blue–green, two were green–yellow–brown, and three were reddish tinted pink, purple, and bright red. The cells and the colonies of *Chroococcidiopsis* sp. were either blue–green or yellowish [1].

The aim of the present work was to isolate cyanobacterial phycobionts from the cryptoendolithic lichens of the high-polar regions of Antarctica and to study the content and composition of photosynthetic pigments in these cyanobacteria based on their absorption spectra, second-derivative absorption spectra, and low-temperature fluorescence spectra.

MATERIALS AND METHODS

Rock samples with distinct algal zones of lichens, violet–green in color, were collected from the Beacon permafrost sandstones and from rock fissions in the high-polar regions of Antarctica. The samples were ground aseptically and placed in petri dishes with mineral BG-11 medium [2]. The dishes were incubated for 60 days either at 8°C under illumination with the white light from luminescent lamps at an intensity of 400–600 lx or at 20°C under 15 000-lx illumination. The cyanobacterial cells and colonies grown under these conditions did not differ in size and color, although the number of colonies was greater in the second case. Some sandstone samples gave rise to green, brown, and red–orange cyanobacterial colonies, which might rep-

0026-2617/02/7105-0601$27.00 © 2002 MAIK "Nauka / Interperiodica"

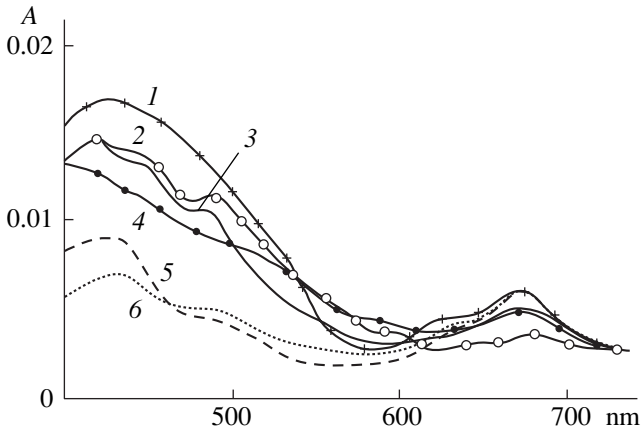

Fig. 1. The absorption spectra of (*1*) *Gloeocapsa* sp.$_1$, (*2*) *Gloeocapsa* sp.$_3$, (*3*) *Gloeocapsa* sp.$_2$, (*4*) *Chroococcidiopsis* sp., (*5*) *Gl. alpicola*, and (*6*) *Chr. thermalis.*

resent different species of the genus *Gloeocapsa* [1, 3]. These cyanobacteria were designated *Gloeocapsa* sp.$_1$, *Gloeocapsa* sp.$_2$, and *Gloeocapsa* sp.$_3$, respectively. Some samples from rock fissures gave rise to green–brown colonies of the cyanobacterium *Chroococcidiopsis* sp. To obtain cyanobacteria in algologically pure cultures, colonies grown in enrichment cultures were transferred to the liquid BG-11 medium and incubated at 20°C at 15 000-lx illumination in an atmosphere containing 2% CO_2 for 30 days. The laboratory cyanobacterial cultures *Gloeocapsa alpicola* CALU 743 and *Chroococcidiopsis thermalis* CALU 758 grown under the same conditions were also investigated for the sake of comparison.

The low-temperature fluorescence spectra of cyanobacteria were recorded at the liquid nitrogen temperature (–196°C) using a Hitachi 850 spectrophotometer (Japan). The optical density of the samples in this case did not exceed 0.1–0.2 optical units.

The absorption and the second-derivative absorption spectra of cyanobacteria were recorded at room temperature using a Shimadzu UV-1601 PC spectrophotometer (Japan). For this purpose, cell suspensions were dried in a flow of compressed air to give films about 0.5 mm in thickness. The content of chlorophyll *a* was estimated from the ratio of cell absorbance at 680 nm (the maximum of the major absorption peak of chlorophyll *a*) to cell absorbance at 730 nm. The relative content of the other photosynthetic pigments in cyanobacterial cells was estimated with reference to the content of chlorophyll *a* [4]. All the spectra were recorded in triplicate. Since the difference between such spectra did not exceed 10%, the figures show typical spectra.

RESULTS

Figure 1 shows the absorption spectra of the new isolates *Gloeocapsa* sp.$_1$, *Gloeocapsa* sp.$_2$, *Gloeocapsa* sp.$_3$, and *Chroococcidiopsis* sp. and the laboratory cyanobacterial cultures *Gl. alpicola* CALU 743 and *Chr. thermalis* CALU 758. According to the spectral data available in the literature [5], the absorption peaks at 680 and 620 nm belong to chlorophyll *a* and phycocyanin, respectively. Absorption in the region 450–500 nm was due to carotenoids. The broad band at 400–440 nm, which resulted from the overlapping of two peaks of chlorophyll *a* (at 418 and 438 nm), was observed only in the spectra of *Gl. alpicola* and *Chr. thermalis.*

The content of chlorophyll *a*, estimated from the height of the peak at 680 nm, was minimal in *Gloeocapsa* sp.$_3$ and *Chroococcidiopsis* sp. cells and maximal in *Gloeocapsa* sp.$_1$ and *Gloeocapsa* sp.$_2$ cells (Fig. 1). In the two latter species, the content of chlorophyll *a* was comparable with that of *Gl. alpicola* and *Chr. thermalis.* The isolates also differed in the relative content of carotenoids. Namely, the ratio of absorbance at 490 nm, which is due to the total carotenoids, to the absorbance of chlorophyll *a* at 680 nm was equal to 4.0 for *Gloeocapsa* sp.$_3$, 3.0 for *Gloeocapsa* sp.$_2$, 2.2 for *Gloeocapsa* sp.$_1$, 1.7 for *Chroococcidiopsis* sp., 0.8 for *Gl. alpicola*, and 0.6 for *Chr. thermalis.* Accordingly, the relative content of carotenoids decreased in the order: *Gloeocapsa* sp.$_3$ > *Gloeocapsa* sp.$_2$ > *Chroococcidiopsis* sp. > *Gloeocapsa* sp.$_1$ > *Chr. thermalis* > *Gl. alpicola*. *Gl. alpicola*. The relative content of phycocyanin, estimated from the ratio of absorbance at 620 nm to the absorbance of chlorophyll *Chr. thermalis* at 680 nm, was maximal in *Gl. alpicola* and *Chr. thermalis* and minimal in *Gloeocapsa* sp.$_3$ cells. In general, the phycocyanin content of the cyanobacteria decreased in the order (figures in the parentheses indicate the ratio of the absorbance of phycocyanin to that of chlorophyll *a*): *Gl. alpicola* (0.9) = *Chr. thermalis* (0.9) > *Gloeocapsa* sp.$_1$ (0.8) = *Gloeocapsa* sp.$_2$ (0.8) > *Chroococcidiopsis* sp. (0.7) >> *Gloeocapsa* sp.$_3$ (0.25). Thus, there was a correlation between the contents of chlorophyll *a* and phycocyanin in the cyanobacteria studied.

The second-derivative absorption spectra of the cyanobacteria showed distinct peaks of chlorophyll *a* at 415–420 and 430–438 nm in the blue spectral region and at 681–682 and 715–720 nm in the red spectral region (Fig. 2 and the table), which agrees with the data of Bekasova *et al.* [5]. The situation with carotenoids was more complex. The second-derivative absorption spectra of *Gl. alpicola*, *Chr. thermalis*, *Gloeocapsa* sp.$_1$, and *Chroococcidiopsis* sp. exhibited two peaks of carotenoids, at 488 and 515–525 nm. The respective spectrum of *Gloeocapsa* sp.$_2$ had six peaks, at 460, 488, 500, 525, 532, and 540 nm. The heights of the major peaks (at 488 and 525 nm) of this cyanobacterium were comparable with those of the cyanobacteria *Gloeocapsa* sp.$_1$, *Chroococcidiopsis* sp., *Gl. alpicola*, and *Chr. thermalis.* The second-derivative spectrum of *Gloeocapsa* sp.$_3$ had seven peaks, at 444, 450, 488, 500 (shoulder), 515, 522, and 530 nm. The height of the peak at 488 nm of this cyanobacterium was twofold

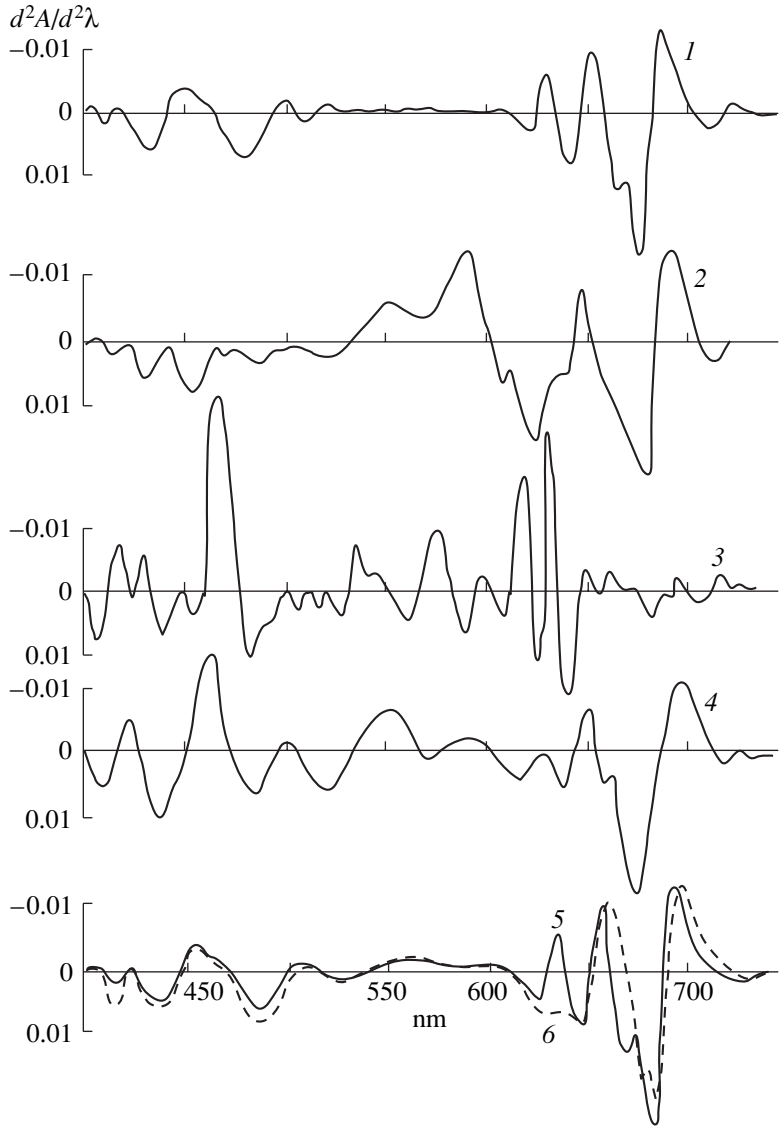

Fig. 2. The second-derivative absorption spectra of (*1*) *Gloeocapsa* sp.$_1$, (*2*) *Gloeocapsa* sp.$_2$, (*3*) *Gloeocapsa* sp.$_3$, (*4*) *Chroococcidiopsis* sp., (*5*) *Gl. alpicola*, and (*6*) *Chr. thermalis.*

higher than that of the other cyanobacteria. Therefore, the phycobionts under study greatly differed in the content and the composition of carotenoids.

The second-derivative spectra of all of the cyanobacteria had peaks typical of phycocyanin (620–625 nm), allophycocyanin (635–645 nm), and allophycocyanin B (660–665 nm), in agreement with the data of Bekasova *et al.* [5]. In addition, the spectrum of *Gloeocapsa* sp.$_2$ contained the phycoerythrocyanin peak at 615 nm and that of *Gloeocapsa* sp.$_3$ contained the peaks of phycoerythrocyanin (615 nm) and *C*-phycoerythrin (570 and 585 nm).

Figure 3 shows the fluorescence spectra of the cyanobacteria at different wavelengths of the excitation light. In agreement with the data of Bekasova *et al.* [5], the fluorescence spectra of *Gl. alpicola, Chr. thermalis, Chroococcidiopsis* sp., and *Gloeocapsa* sp.$_1$ largely depended on the excitation wavelength. When the fluorescence of the cyanobacteria was excited with a light wavelength corresponding to the Soret band of their absorption spectra (436 nm), the fluorescence spectra exhibited the major long-wavelength peak of chlorophyll *a* at 715–728 nm and two short-wavelength peaks of this pigment of about equal intensity at 686 and 696 nm, as well as the peak of allophycocyanin at 660 nm and a shoulder at 656 nm belonging to phycocyanin (Fig. 3a). Unlike the fluorescence spectrum of *Chroococcidiopsis* sp. (excitation at 436 nm), the spectrum of *Gloeocapsa* sp.$_1$ had the major long-wavelength peak of chlorophyll *a* at 715 nm and a shoulder at 725 nm. The intensities of the short-wavelength peaks of chlorophyll *a* at 686 and 696 nm were higher than that of the 715-nm peak. This can be explained by an increased

Positions (in nm) of the absorption peaks of chlorophyll *a* (Chl), carotenoids (Car), *C*-phycoerythrin (*C*-PE), phycoerythrocyanin (PEC), phycocyanin (PC), allophycocyanin (APC), and allophycocyanin B (APC B) in the second-derivative absorption spectra of cyanobacteria

Cyanobacterium	*C*-PE	PEC	PC	APC	APC B	Car	Chl
Gloeocapsa sp.$_1$			622	640	660	488 515	418 438
							681 720
Gloeocapsa sp.$_2$		615	625	640	660	460 488	418 435
						500 525	682 720
						532 540	
Gloeocapsa sp.$_3$	570 585	615	622	645	662	444 460	415 432
						488	682 720
						sh. 500	
						515 522	
						530	
Chroococcidiopsis sp.			625	640	662	488 525	415 438
							682 720
Gl. alpicola			625	635	sh. 665	488 525	415 438
							681 715
Chr. thermalis			620		665	488 525	415 439
							681 720

Note: "sh." stands for "shoulder."

contribution of phycobiliproteins to the fluorescence of cyanobacterial cells in this spectral region [5]. This suggestion is confirmed by the presence of the fluorescence peaks of phycocyanin at 656 nm and of allophycocyanin at 663 nm, as well as by the presence of the shoulder at 675 nm, caused by the fluorescence of allophycocyanin B.

When the fluorescence of the laboratory cyanobacteria *Gl. alpicola* and *Chr. thermalis* and the phycobiont *Chroococcidiopsis* sp. was excited by illumination at 550 nm, the intensity of the major fluorescence maximum at 725–728 nm considerably decreased (Fig. 3b), whereas small peaks at 715 and 725 nm appeared [5]. The intensities of the latter peaks in the fluorescence

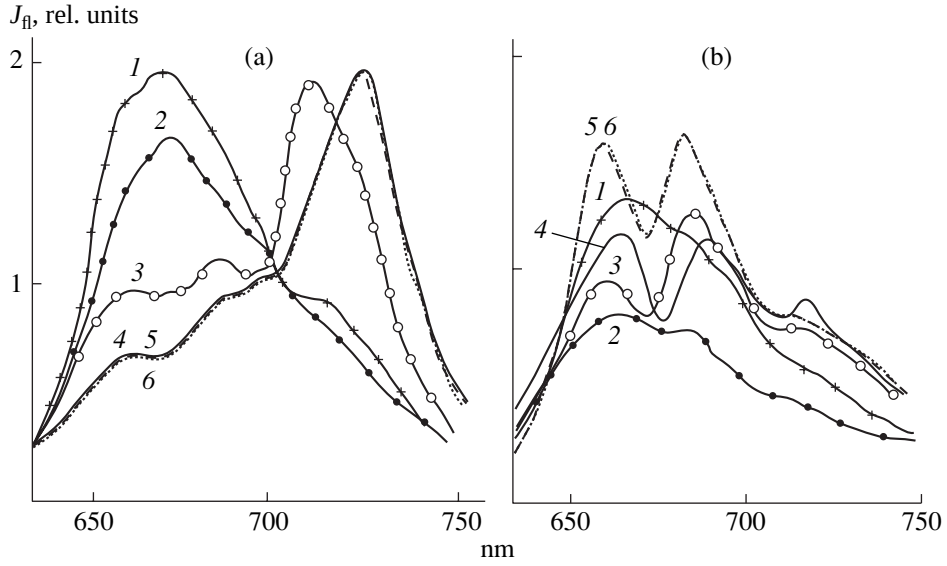

Fig. 3. The low-temperature fluorescence spectra of (*1*) *Gloeocapsa* sp.$_2$, (*2*) *Gloeocapsa* sp.$_3$, (*3*) *Gloeocapsa* sp.$_1$, (*4*) *Chroococcidiopsis* sp., (*5*) *Gl. alpicola*, and (*6*) *Chr. thermalis* excited at (a) 436 and (b) 550 nm.

spectrum of *Chroococcidiopsis* sp. were higher than in the spectra of *Gl. alpicola* and *Chr. thermalis*. The excitation at 550 nm led to an increased fluorescence of *Gl. alpicola*, *Chr. thermalis*, *Chroococcidiopsis* sp., and *Gloeocapsa* sp.$_1$ in the region of the short-wavelength fluorescence peaks of chlorophyll *a* (at 686 and 696 nm) and the fluorescence peak of allophycocyanin at 660 nm, in agreement with the observations made for other cyanobacteria [5]. Conversely, the intensity of these fluorescence peaks in the phycobionts *Chroococcidiopsis* sp. and, especially, *Gloeocapsa* sp.$_1$ were considerably lower under the excitation at 550 nm than at 436 nm.

The fluorescence spectra of the phycobionts *Gloeocapsa* sp.$_2$ and *Gloeocapsa* sp.$_3$ considerably differed from those of *Gl. alpicola*, *Chr. thermalis*, *Chroococcidiopsis* sp., and *Gloeocapsa* sp.$_1$ (Fig. 3). The fluorescence spectrum of *Gloeocapsa* sp.$_2$ (excitation at 436 nm) had a small peak at 715 nm and a shoulder at 725 nm, belonging to chlorophyll *a*. The short-wavelength peaks of chlorophyll *a* at 686 and 696 nm were present as shoulders. At the same time, the fluorescence of allophycocyanin at 670 nm and of allophycocyanin B at 675 nm (shoulder) considerably increased. The shoulder at 663 nm, which is due to the fluorescence of phycocyanin, somewhat shifted because of the intense fluorescence of allophycocyanin. In the fluorescence spectrum of *Gloeocapsa* sp.$_3$, the long-wavelength maximum of chlorophyll *a* was indistinct and looked like a shoulder located at 720 nm. The short-wavelength fluorescence maxima of chlorophyll *a* in this phycobiont manifested themselves as shoulders at 686 and 696 nm on the longer-wavelength side of the intense fluorescence band of the total phycobiliproteins, with the major fluorescence peak of allophycocyanin B centered at 675 nm. As can be seen from Fig. 3a, the fluorescence spectra of *Gloeocapsa* sp.$_2$ and *Gloeocapsa* sp.$_3$ excited with the 436-nm light were similar, although the intensity of the fluorescence of the latter phycobiont was lower than that of the former phycobiont.

Excitation at 550 nm gave similar results (the fluorescence spectra of these two phycobionts were similar but differ in the intensity). The fluorescence spectra of both *Gloeocapsa* sp.$_2$ and *Gloeocapsa* sp.$_3$ had a shoulder of chlorophyll *a* at 720–725 nm and the indistinct peaks of this pigment at 686 and 696 nm. The broad fluorescence band centered at 675 nm was due to allophycocyanin B. Thus, unlike the fluorescence spectra of *Gl. alpicola*, *Chr. thermalis*, *Chroococcidiopsis* sp., and *Gloeocapsa* sp.$_1$, the fluorescence spectra of *Gloeocapsa* sp.$_2$ and particularly *Gloeocapsa* sp.$_3$ virtually did not depend on the wavelength of the excitation light. The analysis of the fluorescence spectra of the phycobionts showed that the higher the content of chlorophyll *a* in cyanobacterial cells, the more intense the long-wavelength fluorescence maxima of this pigment in response to excitation in the spectral region of the Soret band (436 nm) and in the region of the maximum absorption of phycobiliproteins (550 nm). The fluorescence spectra (excited both at 436 and 550 nm) of the phycobiont *Gloeocapsa* sp.$_2$, which contains phycoerythrocyanin in addition to phycocyanin, and *Gloeocapsa* sp.$_3$, which contains phycoerythrocyanin and *C*-phycoerythrin in addition to phycocyanin, exhibited the presence of the broad fluorescence band centered at 675 nm, which belongs to allophycocyanin B (the final acceptor of excitation energy in phycobilisomes), and the shoulders at 686 and 696 nm, which belong to chlorophyll *a*.

DISCUSSION

The relationships between mycobionts and cyanobacterial phycobionts in the cryptoendolithic lichens of the ecologically extreme high-polar regions of Antarctica remain poorly understood [1]. Of interest is the fact that these lichens contain several cyanobacterial phycobionts of the genus *Gloeocapsa*, differing in color.

We succeeded in isolating four *Gloeocapsa* species, which were blue–green, brown, green–brown, and red–orange colored. These cyanobacterial species differed in the composition and the content of various photosynthetic pigments not only each other, but also from the free-living laboratory cyanobacterial cultures *Gl. alpicola* and *Chr. thermalis*. In addition to chlorophyll *a* and carotenoids, all of the cyanobacteria studied contained the phycobiliproteins phycocyanin, allophycocyanin, and allophycocyanin B, which are indispensable components of phycobilisomes and are synthesized constitutively even in the dark under heterotrophic conditions. It is known that the content of phycocyanin, one of the major component of phycobilisomes (the light-harvesting antennas of cyanobacteria), strongly correlates with the content of chlorophyll *a* and depends on the cultivation conditions, particularly on the presence of appropriate nutrients in the medium [6]. Chlorophyll *a* and phycocyanin are primarily present in the cyanobacterial phycobionts of the lichens whose fungal hyphae rapidly grow in rock fissures, characterized by low insolation but a 5- to 7-fold increased illumination in the red spectral region due to sunlight scattering [1]. This must favor the synthesis of chlorophyll *a* and phycocyanin in cyanobacterial phycobionts [7], which turn blue–green or green–brown when the synthesis of these photosynthetic pigments is intensified. Cyanobacteria with the intense synthesis of photosynthetic pigments (in the case at hand, these are *Gloeocapsa* sp.$_1$ and likely *Chroococcidiopsis* sp.) must possess active photosynthesis. Such cyanobacteria must prevail in the zone of intense growth of the fungal hyphae of a lichen, where phycobionts provide actively growing mycobionts with the products of photosynthesis. In turn, mycobionts provide cyanobacterial phycobionts with their metabolites, thereby maintaining the high growth rate of the lichen cyanobacteria [1, 8, 9]. It can be suggested that cyanobacteria tinted green implement the photoheterotrophic or heterotrophic

type of metabolism. It should be noted in this regard that photoautotrophic cyanobacteria may possess the phototrophic or mixotrophic type of metabolism in symbiotic communities with fungi [8].

The brown phycobiont *Gloeocapsa* sp.$_2$ and the red–orange phycobiont *Gloeocapsa* sp.$_3$ synthesize phycoerythrocyanin, whereas *Gloeocapsa* sp.$_3$ synthesizes phycoerythrocyanin and *C*-phycoerythrin. Unlike the synthesis of the other phycobiliproteins, the synthesis of *C*-phycoerythrin is induced by light. Under intense illumination, this phycobiliprotein can be synthesized in amounts exceeding the demand of the photosynthetic apparatus for this pigment [10]. The excess *C*-phycoerythrin may serve as a storage protein, as follows from the fact that it is actively synthesized and accumulated in nitrogen-fixing cyanobacteria [6, 11]. These cyanobacteria may use light not only for photosynthesis, but also for nitrogen fixation. The alga-enriched zones of cryptoendolithic lichens located close to the dark-pigmented core of their thallus, which absorbs red light, are thereby illuminated by the complement blue–green light [1]. Such an illumination promotes the synthesis of *C*-phycoerythrin [7, 12]; therefore, nitrogen-fixing cyanobacterial phycobionts may dominate in these zones or in the peripheral regions of the lichen thallus, where the flux of metabolites from heterotrophic mycobionts is low [8]. Friedmann and Kibler [13] suggested that the cryptoendolithic lichens of the high-polar regions of Antarctica contain nitrogen-fixing cyanobacterial phycobionts, which may enrich the surface layers of the lichens with organic substances.

An analysis of the absorption and the second-derivative absorption spectra of the red–orange *C*-phycoerythrocyanin-containing cyanobacteria showed the presence of increased amounts of various carotenoids but decreased amounts of chlorophyll *a* and phycocyanin. Carotenoids, which possess photoprotective properties [14], promote the adaptation of photosynthesizing organisms to environments characterized by low temperatures and excess illumination. The intense synthesis of carotenoids in phycobionts slows down the synthesis of the major photosynthetic pigments and thereby diminishes the photodestructive action of intense illumination on the photosynthetic apparatus of the algae [15]. This implies that red–orange cyanobacteria must be best adapted to extreme environments characterized by intense insolation and low temperatures and must dominate in the superficial or peripheral zones of lichens.

The low fluorescence of red–orange cyanobacteria can be explained by the relatively low content of chlorophyll *a* in these phycobionts. This agrees with the data available in the literature on the chromatic and achromatic adaptation of photosynthetic apparatus under excess illumination [15]. Our observations and those of Bekasova *et al.* [5, 16] showed that the presence of *C*-phycoerythrin and phycoerythrocyanin in phycobionts affects their fluorescence spectra. The spectral changes may reflect the different states of photosystems 1 and 2, whose activity is limited by the dark regulatory reactions of the photosynthetic apparatus, in the phycobionts that live in extreme environments.

Thus, the study of the spectral characteristics of the cyanobacterial phycobionts of cryptoendolithic lichens inhabiting the high-polar regions of Antarctica showed that these phycobionts possess either photoheterotrophic or photoautotrophic type of metabolism and differ in the content and composition of photosynthetic pigments. These differences can be related to specificities in the nutrition of the lichen symbionts and changes in the intensity and the spectral composition of photoillumination in different zones of the lichens in the course of their growth. These problems needs further investigation.

ACKNOWLEDGMENTS

We are grateful to L.T. Serebryakova for growing the cyanobacteria *Gl. alpicola* CALU 743 and *Chr. thermalis* CALU 758.

This work was supported by grant no. 01-04-48752 from the Russian Foundation for Basic Research.

REFERENCES

1. Nienow, J.A. and Friedmann, E.I., Terrestrial Lithophytic (Rock) Communities, *Antarctic Microbiology*, Friedmann, E.I., Ed., New York: Wiley-Liss, 1993.
2. Stanier, R., Kunisawa, R., and Mandel, M., Purification and Properties of Unicellular Blue–Green Algae (Order *Chroococcales*), *Bacteriol. Rev.*, 1971, vol. 35, no. 1, pp. 171–175.
3. Muzafarov, A.M., Ergashev, A.E., and Khalilov, S., *Opredelitel' sinezelenykh vodoroslei Srednei Azii* (Manual of the Blue–Green Algae of Middle Asia), Tashkent: FAN, 1987, vol. 1.
4. Erokhina, L.G., Vishnivetskaya, T.A., and Gilichinskii, D.A., The Content and Composition of Phycobilisome Pigments in Cells of Ancient Viable Cyanobacteria from Arctic Permafrost, *Mikrobiologiya*, 1998, vol. 67, no. 6, pp. 821–826.
5. Bekasova, O.D., Sineshchekov, V.A., and Sineshchekov, A.V., The Investigation of the Excitation Energy Transfer from Phycobilisomes to Chlorophyll in *Nostoc muscorum* by Derivative and Selective Fluorimetry, *Biofizika*, 1988, vol. 33, no. 1, pp. 71–76.
6. Erokhina, L.G., Accumulation of Phycobiliproteins in Free-living Nitrogen-fixing Cyanobacteria Grown on Various Nitrogen Sources, *Fiziol. Rast.* (Moscow), 1990, vol. 37, no. 6, pp. 1138–1145.
7. Bennet, A. and Bogorad, L., Complementary Chromatic Adaptation in a Filamentous Blue–Green Alga, *J. Cell Biol.*, 1973, vol. 58, no. 2, pp. 419–427.
8. Golubkova, N.S., Components of Lichens and Their Interactions, *Zhizn' Rast.*, 1976, vol. 3, pp. 380–385.

9. Friedmann, E.I., Endolithic Microorganisms in the Antarctic Cold Desert, *Science*, 1982, vol. 215, pp. 1045–1053.

10. Wyman, M., Gregory, R., and Carr, N., Novel Role for Phycoerythrin in a Marine Cyanobacterium *Synechococcus* Strain DC-2, *Science*, 1985, vol. 230, pp. 819–822.

11. Erokhina, L.G., Spectral Characteristics of Nitrogen-fixing Cyanobacteria, *Fiziol. Rast.* (Moscow), 1988, vol. 35, no. 5, pp. 994–1000.

12. Erokhina, L.G., Spectral Effects of the Chromatic Adaptation of Nitrogen-fixing Cyanobacteria Grown on Various Nitrogen Sources, *Mikrobiologiya*, 1992, vol. 61, no. 6, pp. 690–697.

13. Friedmann, E.I. and Kibler, A.P., Nitrogen Economy of Endolithic Microbial Communities in Hot and Cold Deserts, *Microb. Ecol.*, 1980, no. 6, pp. 95–108.

14. Koroleva, O.Ya., Cold Adaptation of the Photosynthetic Apparatus of the Arctic Species *Oxyria digyna*, *Fiziol. Rast.* (Moscow), 1996, vol. 43, no. 3, pp. 367–373.

15. Litvin, F.F. and Zvalinskii, V.I., The Dependence of Photosynthesis on the Intensity and Wavelength of Light and the Problem of Chromatic and Nonchromatic Adaptation, *Fiziol. Rast.* (Moscow), 1991, vol. 38, no. 4, pp. 629–640.

16. Gulyaev, B.A., Teten'kin, V.L., and Bekasova, O.D., Pigment Orientation and Energy Migration in Blue–Green Algae and Isolated Phycobilisomes, *Izv. Akad. Nauk SSSR, Ser. Biol.*, 1981, no. 2, pp. 188–200.