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EXPERIMENTAL ARTICLES

Some Factors Controlling the Biosynthesis of Chlorosome Antenna Bacteriochlorophylls in Green Filamentous Anoxygenic Phototrophic Bacteria of the Family *Oscillochloridaceae*

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Abstract—We determined the concentrations of bacteriochlorophylls (BChl) in the light-harvesting antennae of *Oscillochloris trichoides* (of the family *Oscillochloridaceae* belonging to green filamentous mesophilic bacteria) cultivated either with gabaculine, an inhibitor of the C-5 pathway of BChl biosynthesis in a number of bacteria, or at various illumination intensities,. We determined the BChl *c* : BChl *a* molar ratios in intact cells, in chlorosome–membrane complexes, and in isolated chlorosomes. We revealed that BChl *c* synthesis in *Osc. trichoides* was more gabaculine-sensitive than BChl *a* synthesis. Accordingly, an increase in gabaculine concentrations in the medium resulted in a decrease in the BChl *c* : BChl *a* ratio in the tested samples. We suggest that BChl synthesis in *Osc. trichoides* proceeds via the C-5 pathway, similar to representatives of other families of green bacteria (*Chlorobium limicola* and *Chloroflexus aurantiacus*). We demonstrated that the BChl *c* : BChl *a* ratio in the chlorosomes varied from 55 : 1 to 110 : 1, depending on light intensity. This ratio is, therefore, closer to that of *Chlorobiaceae*, and it significantly exceeds the BChl *c* : BChl *a* ratio in *Chloroflexaceae*.

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The capacity of phototrophic bacteria to use light energy is primarily due to the presence of specific pigments. Their composition is constant within specific taxonomic groups of photosynthetic bacteria. However, the contents of individual pigments vary depending both on the species involved and on the cultivation conditions. The bulk of light-harvesting pigments (including various types of bacteriochlorophylls (BChl) and carotenoids) in the cells of green filamentous and green sulfur bacteria is located within chlorosomes, unique antennal structures that are attached to the inner surface of the membrane, but are not membrane components per se. Chlorosomes are ellipsoids (100–200 × 70–100 × 10–20 nm) that are surrounded by a monolayer lipid–protein envelope. They consist of quasilinear BChl aggregates. The dipole moments of their Q_y-transitions are oriented along the longer chlorosome axis [1].

BChl *c*, BChl *d*, and BChl *e*, whose absorption spectra differ insignificantly, are the main chlorophyll pigments of green bacteria. All the chlorosomes also contain low amounts of BChl *a* that accounts for about 1% of the total weight of chlorosome BChl, which is involved in transferring excitation energy from BChl *c* to membrane antenna BChl *a* and subsequently to the photochemical reaction centers [2, 3]. The presence of these pigments allows green bacteria to use light with a wavelength of up to 840 nm. Carotenoids, auxiliary photosynthetic pigments, absorb light of the blue-green part of the spectrum (in the 400–500 nm range), supplying light energy to the main light-harvesting pigments.

The chlorosomes of green photosynthetic bacteria are the biggest light-harvesting antennae found in nature up to now. They enable cell growth at extremely low light intensities that occur, e. g., in the ocean at significant depths. Actually, the BChl organizational pattern in chlorosomes is based on pigment–pigment, and not pigment–protein interactions, in contrast to other photosynthetic antennal systems [4]. The issue concerning the nature (and the functional role) of substances performing structural functions in the chlorosomes has not been resolved up to now.

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Another distinctive feature of chlorosomes is the presence of several different homologues of one BChl species [2, 3]. In contrast, light-harvesting systems based on pigment–protein complexes lack such a type of pigment heterogeneity. Presumably, this pigment variability may be due to the unique arrangement of pigments in chlorosomes. The distribution of homologues of chlorosome BChl in green sulfur bacteria was shown to depend on light intensity during cultivation. For instance, decreased light intensity results in an increase in the degree of alkylation of the BChl chlorine ring, with a concomitant red shift in the absorption spectrum of the antenna system. These spectral changes are believed to be caused by the formation of BChl aggregates with relatively more hydrophobic side chains and absorption in the longer-wave region of the spectrum [5, 6].

The structural organization of BChl in the chlorosome has not yet been elucidated. Until recently, it was assumed that pigments form cylindrical structures with a diameter of 5–10 nm, arranged parallel to the longer chlorosome axis. This model was based on electron microscopic studies using freeze-fractured cells [7]. A more recent work presents a new model envisaging lamellar organization of BChl aggregates in *Chlorobium tepidum* chlorosomes with a period of 20 Å [8], based on cryoelectron microscopy and x-ray scattering data.

Chlorosome BChl biosynthesis in the two well-known families of green bacteria, *Chlorobiaceae* and *Chloroflexaceae*, is subject to regulation by both physiological (light intensity, oxygen concentration in the medium, etc.) [9, 10] and non-physiological factors, including anesthetic gases (e. g., acetylene) [11] and gabaculine, a derivative of aminobenzoic acid [9].

We presented earlier the results of our comparative study of the spectral properties of light-harvesting pigments of the chlorosome and membrane antennae of the filamentous mesophilic anoxygenic bacterium *Osc. trichoides* DG-6 [12–14], a representative of *Oscillochloridaceae*, the recently discovered family of green bacteria [15], and these pigments in the species of two other families of green bacteria.

The goal of this work was to perform a comparative analysis of BChl composition in intact cells, chlorosome–membrane complexes (CMC), and chlorosomes of *Osc. trichoides* cells cultivated with gabaculine, an inhibitor of the C-5 pathway of BChl biosynthesis, as well as an investigation at various light intensities.

MATERIALS AND METHODS

This study was conducted with *Osc. trichoides* DG-6, the type strain of the species *Osc. trichoides* (327 KM MGU) [15]. The cultures were grown, as described earlier, under anaerobic conditions at 30°C on a modified DGN medium with constant stirring at a light intensity of 200–1000 W/m^2 (using luminescent lamps) [12]. In some experiments, the cultures were grown with gabaculine, a specific inhibitor of BChl biosynthesis in a number of bacterial species [16].

Chlorosome–membrane complexes (CMC) were isolated in 10 mM Tris–HCl buffer (pH 8.0) in the presence of 10 mM sodium ascorbate (pH 7.0) as described earlier [12]. The resulting CMC were mixed with 87% glycerol (v/v) and stored at –70°C.

Chlorosomes were isolated from *Osc. trichoides* in a continuous sucrose gradient in the presence of 10 mM sodium ascorbate and 2 M sodium thiocyanate as described earlier [13].

Absorption spectra were recorded at room temperature with a Hitachi-557 spectrophotometer (Japan), and the errors associated with these measurements did not exceed 3%.

The BChl *c* : BChl *a* molar ratio was determined by the method of Feick et al. [17]. Samples were extracted for 20 min in the dark at 4°C with a 25-fold volume of an acetone–methanol mixture (7 : 2, v/v). The absorption of transparent supernatants was measured at their long-wave maximums, i.e., at 769 nm and 663 nm for BChl *a* and BChl *c*, respectively. Calculations were based on molar extinction coefficients, ε, of 68.6 and 74 mM^{-1} cm^{-1} for BChl *a* and BChl *c*, respectively.

Protein concentrations in cell suspensions were determined colorimetrically by the Lowry method [18].

All the results presented below are the means of the data obtained in 4–5 independent experiments.

RESULTS AND DISCUSSION

Effect of gabaculine on bacteriochlorophyll synthesis in *Osc. trichoides* cells. We investigated the influence of gabaculine, or 3-amino-2,3-dihydrobenzoic acid, on BChl biosynthesis in *Osc. trichoides* cells. Gabaculine is a specific inhibitor of the biosynthesis of 5-aminolevulinic acid (5-ALA), the main BChl precursor in most phototrophic organisms [16]. *Osc. trichoides* was cultivated for 72 h at gabaculine concentrations of 0.5 to 2.5 μM at a light intensity of 200 W/m^2. Cultivation under these conditions, with up to 2.5 μM gabaculine in the medium, only insignificantly influenced the total protein content in bacterial cells (the protein concentration remained within the range of 0.23–0.24 mg/ml of cell suspension).

The results of the biochemical study on the effect of gabaculine on BChl *c* and BChl *a* biosynthesis in *Osc. trichoides* cells are shown in Fig. 1. The initial BChl *c* and BChl *a* concentrations in cultures grown without the inhibitor were 117 and 4.7 nmol/mg of protein, respectively. Cultivation in the presence of 0.25 to 2.5 μM gabaculine resulted in a considerable decrease in the BChl *c* content of the sample, which dropped to 23.3 nmol/mg of protein at 2.5 μM gabaculine, i.e., decreased fivefold relative to the initial BChl *c* concentration in inhibitor-free cultures. The BChl *a* content

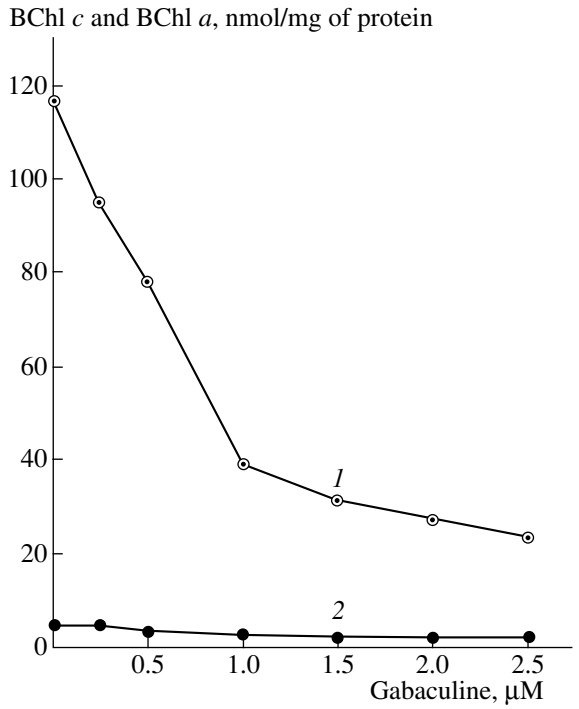

Fig. 1. Fig. 1. Inhibition of BChl *c* (*1*) and BChl *a* (*2*) biosynthesis by gabaculine in *Osc. trichoides* cells. Light intensity during the cultivation was 200 W/m^2, and the cultivation time, 72 h.

decreased, at 2.5 μM gabaculine, to 1.9 nmol/mg of protein, which is ca. 2.5 times below the BChl *a* content in inhibitor-untreated cultures. Hence, BChl *c* synthesis in *Osc. trichoides* is more sensitive to gabaculine than BChl *a* synthesis.

Figure 2 presents the absorption spectra of four *Osc. trichoides* cultures grown without gabaculine and with 1.0, 1.5, and 2.5 μM of gabaculine in the medium. From the data of Fig. 1 it is evident that the differences in the BChl *a* content of the cells grown with 1.0, 1.5, and 2.5 μM gabaculine were insignificant. This enabled us to normalize the recorded absorption spectra according to the absorption maximum of the membrane BChl *a* (852 nm). An analysis of the absorption spectra presented in Fig. 2 revealed that an increase in the inhibitor concentration in the medium resulted in a decrease in the chlorosome BChl *c* content (manifesting itself as a gradual decrease in the maximum absorption value in the BChl *c* band).

It was shown earlier that in the green phototrophic bacteria *Chl. limicola* and *Cfx. aurantiacus* gabaculine also had a stronger inhibitory effect on BChl *c* biosynthesis than on BChl *a* biosynthesis [9, 16]. BChl formation in these organisms proceeds via the C-5 pathway that involves the formation of 5-ALA, the main BChl precursor, from glutamate [19]. It was revealed that the inhibition of tetrapyrrole synthesis by gabaculine (in plants, algae, some purple bacteria, and the green bacteria mentioned above) is due to the suppression of glutamate-1-semialdehyde aminotransferase, the terminal enzyme in the reaction sequence of the C-5 pathway that results in converting glutamate into δ-aminolevulinate, the tetrapyrrole precursor [16]. Hence, the results obtained suggest that chlorosome BChl biosynthesis in *Osc. trichoides* DG-6 proceeds via the C-5 pathway, similar to *Chl. limicola* and *Cfx. aurantiacus.*

The BChl *c* : BChl *a* molar ratios both in intact cells and in the chlorosome–membrane complexes (CMC) isolated from them drastically decreased with an

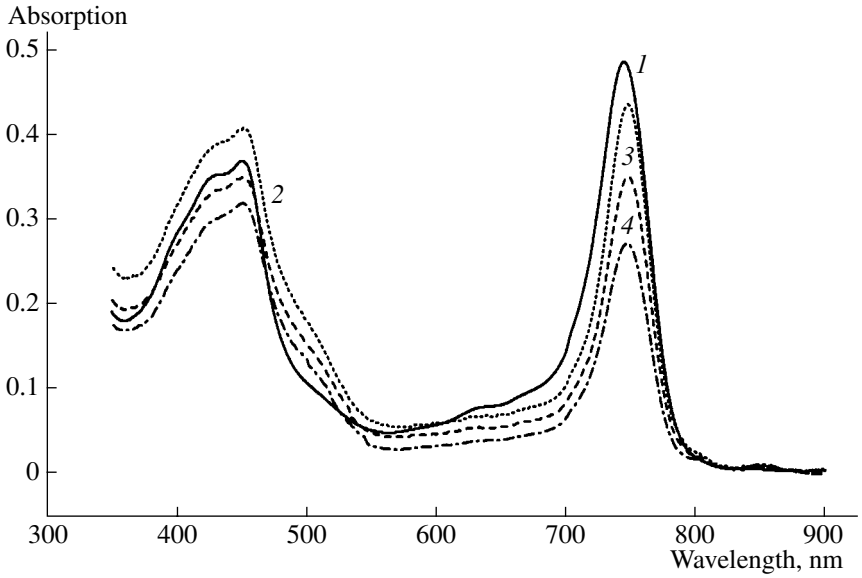

Fig. 2. Fig. 2. Absorption spectra of *Osc. trichoides* cells grown without gabaculine (*1*), with 1.0 μM (*2*), with 1.5 μM (*3*), and with 2.5 μM gabaculine (*4*). The spectra of gabaculine-treated cells were normalized based on the absorption maximum of the membrane BChl *a* (852 nm).

Table 1. Effect of gabaculine on BChl *c* : BChl *a* molar ratios in intact cells and in the chlorosome–membrane complexes isolated from them

Fraction	Gabaculine concentration in the medium (μM)	BChl *c* : BChl *a* molar ratio
Intact cells	0	23 : 1
	0.5	21 : 1
	1.0	16 : 1
	1.5	14 : 1
	2.0	13 : 1
	2.5	12 : 1
Chlorosome–membrane complexes	0	25 : 1
	1.0	17 : 1
	1.5	15 : 1
	2.5	13 : 1

Table 2. Effect of light intensity on BChl *c* : BChl *a* molar ratios in intact cells, in the chlorosome–membrane complexes, and in chlorosomes isolated from them

Fraction	Light intensity (W/m^2)	BChl *c* : BChl *a* molar ratio
Intact cells	200	23 : 1
	500	15 : 1
	1000	13 : 1
Chlorosome–membrane complexes	200	25 : 1
	500	17 : 1
	1000	14 : 1
Chlorosomes	200	100 : 1
	500	70 : 1
	1000	55 : 1

increase in inhibitor concentrations in the medium, due to the higher sensitivity of BChl *c* synthesis to gabaculine, compared to BChl *a* synthesis. The molar ratios changed from 23 : 1–25 : 1 without gabaculine to 12 : 1–13 : 1 with 2.5 μM gabaculine in the medium (in cells and CMC, respectively, see Table 1).

The BChl *c* : BChl *a* molar ratio was 52 : 1 in the chlorosomes isolated from cells grown with 2.5 μM gabaculine, while in the chlorosomes isolated from gabaculine-untreated cells this molar ratio was 100 : 1.

Effect of light intensity on the biosynthesis of light-harvesting antenna bacteriochlorophyll in *Osc. trichoides*. It was earlier shown by us that light intensity is the important factor controlling the size of the chlorosome antenna in the representatives of the new family *Oscillochloridaceae*, similar to two other families of green bacteria, *Chlorobiaceae* and *Chloroflexaceae* [13]. An increase in light intensity resulted in a decrease in the size of the BChl *c* chlorosome antenna of *Osc. trichoides*. Fig. 3a presents the room temperature absorption spectra of CMC isolated from *Osc. trichoides* cells that were grown at light intensities of 200, 500, and 1000 W/m^2. The absorption bands with maximums of 748–750 nm in the long-wavelength region of the spectra were caused by chlorosome BChl *c* absorption, whereas the 852 nm absorption band resulted from the contribution of the membrane BChl *a* [13]. From Fig. 3b it is evident that an increase in light intensity from 200 to 1000 W/m^2 caused a substantial (more than twofold) increase in the amplitude of the Q_y-band of membrane BChl *a*, whose magnitude is insignificant in the absorption spectrum of the cells grown at the lowest light intensity (200 W/m^2).

Table 2 contains the results of studying the effect of light intensity on the BChl *c* : BChl *a* molar ratio in *Osc. trichoides* cells, in CMC isolated from them, and in chlorosomes. It was established that the BChl *c* : BChl *a* molar ratios in *Osc. trichoides* cells and CMC were 23–25 : 1, 15–17 : 1, and 13–14 : 1 in the cells grown at light intensities of 200, 500, and 1000 W/cm^2, respectively.

The BChl *c* : BChl *a* molar ratio was 100–110 : 1 in *Osc. trichoides* chlorosomes isolated from cells cultivated at a light intensity of 200 W/m^2, i.e., there were over 100 BChl *c* molecules per one BChl *a* molecule. Increasing the light intensity from 200 to 500 and 1000 W/m^2 during cultivation resulted in a decrease in the chlorosome BChl *c* : BChl *a* molar ratio to 70 : 1 and 55 : 1, respectively.

The BChl *c* : BChl *a* molar ratios in intact cells and isolated chlorosomes of the representatives of the families *Chlorobiaceae* and *Chloroflexaceae* were shown to vary depending on the light intensities applied [10, 17, 20, 21]. For instance, the BChl *c* : BChl *a* molar ratios were 0.9, 6.6, and 11.0 in the CMC of *Cfx. aurantiacus* grown at high, moderate, and low light intensities, respectively [17], while in the chlorosomes the ratios varied from 25 : 1 (the maximum BChl *c* : BChl *a* molar ratio for this species) at low light intensities [17] to 2 : 1 at high light intensities [22]. As for green sulfur bacteria that are adapted to growth at extremely low light intensities in nature, the influence of light on BChl *c* synthesis was much less pronounced than in the green filamentous bacterium *Cfx. aurantiacus*. BChl *c* : BChl *a* molar ratios of 90 : 1–100 : 1 are typical of chlorosomes of *Chl. limicola* grown at moderate or low light intensities [3, 13]. According to the data presented in the literature, cultivation of various *Chlorobium* species at high light intensities causes a twofold decrease in the chlorosome BChl *c* content, but does not significantly affect chlorosome BChl *a* synthesis [1, 5, 23, 24], resulting in a corresponding decrease in the chlorosome BChl *c* : BChl *a* molar ratios.

We have earlier demonstrated that quantitative changes in the chlorosome pigment composition, under the influ-

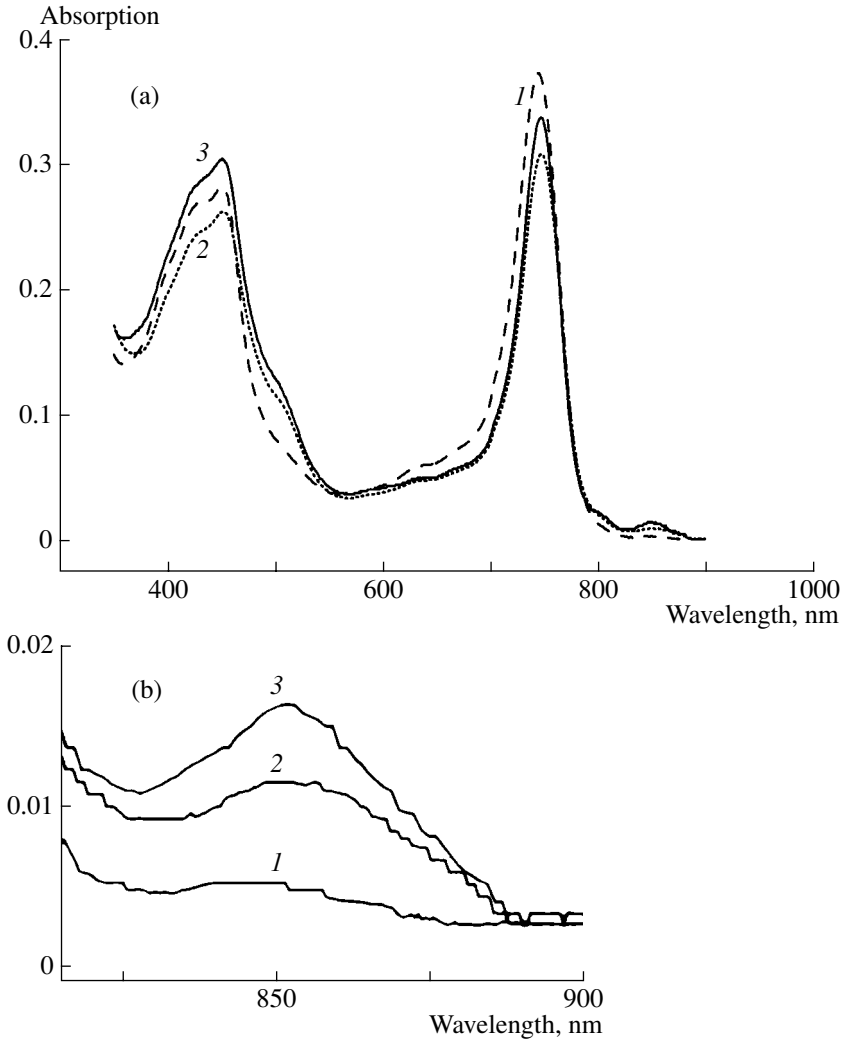

Fig. 3. (a) Absorption spectra of the chlorosome–membrane complexes isolated from *Osc. trichoides* cells grown at various light intensities; (b) Enlarged part of the absorption spectrum within the 810–900 nm range. *1*, *2*, and *3*, absorption spectra at light intensities of 200, 500, and 1 000 W/m^2.

ence of various factors that inhibit chlorosome BChl biosynthesis, are correlated with structural alterations in the chlorosomes. Electron microscopy of ultrathin sections of *Chl. aurantiacus* and *Chl. limicola* cells revealed that chlorosome height is the most labile parameter that significantly varies depending on light intensity and the presence/absence of the inhibitor gabaculine in the medium. This is also the crucial parameter in terms of efficient energy transfer from the peripheral light-harvesting antenna (chlorosomes) to reaction centers [20, 21]. Other researchers presented evidence that the BChl *c* content in the chlorosomes of the facultative anaerobic phototroph *Cfx. aurantiacus* may differ by a factor of ca. 35 (per cell dry weight), depending on the light intensity applied during cell cultivation. BChl synthesis is completely blocked under aerobic cultivation conditions [1]. The size of *Chl. vibrioforme* and *Chl. tepidum* chlorosomes may decrease tenfold as a result of inhibiting BChl *c* biosynthesis with acetylene, while no significant growth rate changes occur at saturating light intensities [5, 11]. Research on the development of chlorosomes in the green filamentous bacterium *Cfx. aurantiacus* after the transition from chemotrophic (aerobic, dark) to phototrophic (anaerobic, light) conditions revealed that chlorosomes were almost completely absent under chemotrophic conditions. Almost all the cells contained chlorosomes after about a day of cultivation under phototrophic conditions. The chlorosome volume increased up to the onset of the stationary growth phase [25]. In addition, it was shown that cells grown under chemotrophic conditions contained all the polypeptides usually present in chlorosome envelopes, suggesting that empty chlorosome sacs existed in chemotrophic cells, to be filled with BChl *c* under phototrophic conditions. These data are consistent with the results of the studies on the effect of acetylene (an inhibitor of chlorosome BChl) on the biosynthesis of chlorosome proteins in green sulfur bacterium *Chl. tepidum*, which displays no considerable qualitative and quantita-

tive changes in chlorosome proteins in spite of a drastic decrease in the chlorosome BChl *c* content [24].

The data obtained in this work indicate that the BChl *c* : BChl *a* molar ratios of *Osc. trichoides* chlorosomes are similar to those of the chlorosomes of the representatives of the *Chlorobiaceae* family and significantly exceed the values that are characteristic for *Chl. aurantiacus* chlorosomes. However, Keppen et al. [15] showed that β- and γ-carotenes, which are typical of the *Chloroflexaceae* family, were the main carotenoids of *Osc. trichoides* cells.

Thus, the size of the chlorosome antenna of all the three known families of green phototrophic bacteria (*Chlorobiaceae, Chloroflexaceae*, and *Oscillochloridaceae*) varies depending on cultivation conditions. Using physiological (light intensity, temperature, and oxygen availability) and non-physiological (anesthetic gases and gabaculine) factors enables us to obtain cultures with various sizes of chlorosomes that may significantly differ in their BChl *c* : BChl *a* molar ratios.

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