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Formation of Bacteriochlorophyll Form B820 in Light Harvesting 2 Complexes from Purple Sulfur Bacteria Treated with Dioxane

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Abstract—Treatment of some sulfur bacteria (*Allochromatium minutissimum*, *Thiorhodospira sibirica*, and *Ectothiorhodospira halovacuolata* WN22) with dioxane results in formation of the bacteriochlorophyll form B820 in the light harvesting complex LH2. This form characterized by absorption maximum at 820 nm has the same absorption spectrum as B820 subcomplex from LH1 complex. Appearance of the B820 form was accompanied by a sharp decrease in absorption in the carotenoid region. This phenomenon observed in all LH2 complexes investigated may be attributed to formation of colorless carotenoid aggregates. This is very similar to the previously reported dissociation of the LH1 complex with carotenoids into B820 subcomplexes. Although the B820 form corresponded the bacteriochlorophyll dimer, its circular dichroism spectrum showed that pigment molecules in this dimer exhibit different interaction than those in the B820 subcomplex. The dioxane treatment of LH2 complexes isolated from *Rhodopseudomonas palustris* bacteria grown under normal or low intensity illumination did not result in formation of such dimers. It is suggested that bacteriochlorophyll B820 formation is related to unique structure of LH2 complexes from the sulfur bacteria.

Key words: photosynthetic bacteria, LH2 complexes, bacteriochlorophyll B820, dimers, dioxane, spectroscopy, electrophoresis

The photosynthetic apparatus of purple bacteria includes two types of light harvesting complexes. According to their position in the membrane with respect to reaction center they are classified as peripheral (LH2) and pericentral or core (LH1) complexes. These complexes are one of the most studied components of photosynthetic membranes [1-4]. The light harvesting complexes consist of two types (α and β) of low molecular weight polypeptides (<10 kD), bacteriochlorophyll, and carotenoids. Analysis of crystals of both complexes revealed their spatial organization. Polypeptides are orientated perpendicularly to the membrane; this results in formation of two rings comprising 8-9 and 15-16 polypeptide pairs in LH2 and LH1 complexes, respectively. Hydrophilic ends faced to both sides of the membrane interact with each other. Molecules of bacteriochlorophyll are located closer to periplasm between α-helices of the polypeptides. In LH2 and LH1 complexes, bacteriochlorophyll molecules absorb at 820-855 and 870-890 nm, respectively. The number of bacteriochlorophyll molecules corresponds to total number of α and β polypeptides in an individual complex. Carotenoids represent the second pigment component, which is also located between polypeptides in both complexes at stoichiometric ratio one carotinoid molecule per two polypeptides. Carotenoids are positioned in parallel to α-helix of polypeptides. One end of carotenoid molecule interacts with bacteriochlorophyll, whereas the other end is exposed to the cytoplasmic side of the membrane. LH2 complex contains additional bacteriochlorophyll (absorbance band at 800 nm) and carotenoid molecules located at the outer surface closer to the cytoplasm.

Most LH2 complexes can undergo conformational changes in the presence of nonionic detergents or solvents. These changes include shift of the long wavelength band of absorbance spectrum to the blue region by 20-35 nm. However, these changes do not involve bacteriochlorophyll molecules absorbing at 800 nm. Changes in the absorption spectrum of LH2 complex reflect altered

Abbreviations: DPA) diphenylamine; *Alc.*) *Allochromatium*; *Ect.*) *Ectothiorhodospira*; *Rps.*) *Rhodopseudomonas*; *Rsp.*) *Rhodospirillum*; *Rvi.*) *Rubrivivax*; *Trs.*) *Thiorhodospira*.

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interactions between corresponding bacteriochlorophyll molecules induced by changes in protein–protein interactions between hydrophilic polypeptide ends in the LH2 complex [5-12]. In LH1 complex, such changes have not been found. In LH1 complex, the shift of 880 nm absorbance band to 820 nm was caused by octyl glucoside-induced dissociation of carotenoidless complex into subunits (subcomplexes). Absorption spectra of such subcomplexes contain one band in the near infrared (IR) region with maximum at 820 nm. It is suggested that this band belongs to bacteriochlorophyll dimer, whereas the subcomplex consists of one or two pairs of α and β polypeptides [13-17].

Thus, formation of bacteriochlorophyll B820 was not found in LH2 complexes. However, modeling of bacteriochlorophyll dimers in LH2 complexes based on circular clusters of these pigments revealed that such hypothetical dimers should absorb at 820 nm [18]. Studying formation of air-droplet films of LH2 complexes from sulfur bacteria in the presence of solvents, we found that films formed in the presence of dioxane are characterized by appearance of an absorption band at 820 nm. This band is very similar to the absorbance spectrum of subcomplex B820. In this study, we have investigated the possibility and conditions favoring dioxane-induced formation of bacteriochlorophyll B820 in LH2 complexes from various bacteria.

MATERIALS AND METHODS

Cells of *Alc. minutissimum*, *Trs. sibirica*, and *Ect. halovacuolata* WN22 were grown under white light (intensity of 2000 lx) and temperature of 25°C as described earlier [7, 11, 17, 19]. Cells of *Rps. palustris* strain AB were grown at low (300 lx) or normal (2000 lx) intensity as described [6]. For inhibition of carotenoid biosynthesis, the cultivation medium was supplemented with diphenylamine (12 mg/liter), which was re-crystallized from ethanol [7, 17, 19]. Samples isolated from cells grown in the presence of diphenylamine (DPA) were defined as DPA-objects. Chromatophores were isolated after cell sonication using differential centrifugation as described [17, 19]. Procedure of polyacrylamide gel electrophoresis of isolated complexes was described earlier [5]. Subcomplex B820 was isolated from DPA assembly LH1-RC of *Ect. sibirica* by electrophoresis in the presence of octyl glucoside as described [19]. LH2 complex was treated with dioxane in a spectrophotometric cuvette. Absorption spectra were registered using a UV-160 spectrophotometer (Shimadzu, Japan); circular dichroism spectra were registered using a Mark V dichrograph (Jobin-Yvon, France). For preparation of spectra for printing, they were digitized using a Graph2Digit 0.52b (designed by V. Plisko; plsoft.narod.ru) in "negative" mode with step 2 (1 nm = 2 pixels) and also Photoshop, Excel, and Origin software as described [17, 19].

The following reagents were used in this study: dodecyl maltoside (Anatrace, USA); Tris and lithium dodecyl sulfate (Sigma, USA). Dioxane (chemically pure grade) and also reagents for electrophoresis and bacteria cultivation were purchased from Russian suppliers.

RESULTS AND DISCUSSION

The effect of dioxane was investigated using LH2 complexes from three species of purple sulfur bacteria. Usually LH2 complexes from photosynthetic bacteria are characterized by two homogenous absorbance bands in the near IR region at 800 and 850 nm [1, 8-10, 20]. Complexes used in this study slightly differed in their spectral characteristics. LH2 complex from *Alc. minutissimum* had a heterogeneous absorption band at 800 nm, which consisted of two components absorbing at 796 and 802 nm [10, 11]. LH2 complex from *Trs. sibirica* had three absorbance bands, at 800, 830, and 850 nm. Several indirect data suggest its homogeneity [21-23]; however, this does not exclude its possible heterogeneity. LH2 complex from *Ect. halovacuolata* WN22 contained carotenoids of spirilloxanthin biosynthesis, but its spectral properties were similar to LH2 complexes from okenone-containing bacteria (Makhneva et al., unpublished observation). Its absorbance spectrum was characterized by a maximum at 830 nm and shoulder at 793 nm. In contrast to all known complexes, it contained a small amount of monomer bacteriochlorophyll (absorbance band at 770 nm). Other parameters of these complexes (polypeptide composition, supramolecular organization, etc.) were similar to those described in the literature [1, 20]. For comparison, we used LH2 complexes isolated from cells of non-sulfur bacteria *Rps. palustris* strain AB cultivated in light of low and normal intensity [6]. The absorption spectrum of the complex isolated from this bacterium was similar to the well-studied complexes isolated from non-sulfur bacteria. The absorption spectrum of this complex isolated from cells cultivated at normal intensity (2000 lx) was characterized by the presence of two bands with maxima at 803 and 858 nm (ratio 858/803 was 1.1). Reduction of light intensity of cell illumination to 300 lx resulted in blue shift of the long-wavelength band by 8 nm and the decrease of its intensity (ratio 850/802 was 0.55) in absorbance spectrum of this complex.

We started our study by selection of acting concentration of dioxane. Since subcomplex B820 was usually isolated from carotenoidless membranes or LH1-RC assemblies [13-17], DPA complex LH2 from *Alc. minutissimum* was employed as the initial research object (Fig. 1). Addition of dioxane at final concentration 10-30% caused immediate conformational change in this complex characterized by blue shift (by ~30 nm) of the long wavelength absorbance band (Fig. 1a, spectra *2-4*).

Increase in duration of treatment up to 60 min caused partial destruction of the complex and appearance of the oxidation products of bacteriochlorophyll with the absorption maximum at 685 nm (Fig. 1b, spectra *2-4*). Treatment of LH2 complex with 40% dioxane resulted in immediate conformational change with simultaneous partial complex destruction characterized by appearance of the absorbance band typical for monomer bacteriochlorophyll (Fig. 1a, spectrum *5*). Increase in treatment time did not result in appearance of products of bacteriochlorophyll degradation as was observed at lower dioxane concentrations, and only B820 form was present on the absorption spectrum of the sample (Fig. 1b, spectrum *5*). Comparison of absorption spectra of LH2 complex before and after the treatment with 40% dioxane suggests that the major proportion of this complex obviously destroyed to colorless products of bacteriochlorophyll degradation. Rapid degradation of DPA complex LH2 from *Alc. minutissimum* induced by dioxane may be attributed to high lability of the complex structure after carotenoid removal. Addition of high dioxane concentration (40%) to LH2 complex did not result in immediate appearance of significant quantities of monomer bacteriochlorophyll typical for pigment extraction with acetone–methanol mixture [6, 7, 10].

This step of our study demonstrated that bacteriochlorophyll B820 appears in LH2 complex only in the presence of 40% dioxane. These results are consistent with our previous data on conformational changes in normal LH2 complex from *Alc. minutissimum* [10, 11, 24]. In those studies, we investigated effects of lower dioxane concentrations (20-30%) and only blue shift of long-wavelength absorption band without appearance of degradation products or appearance of band with absorption maximum about 820 nm was registered. So in subsequent experiments we studied only the effect of 40% dioxane on LH2 complexes from various bacteria (Fig. 2).

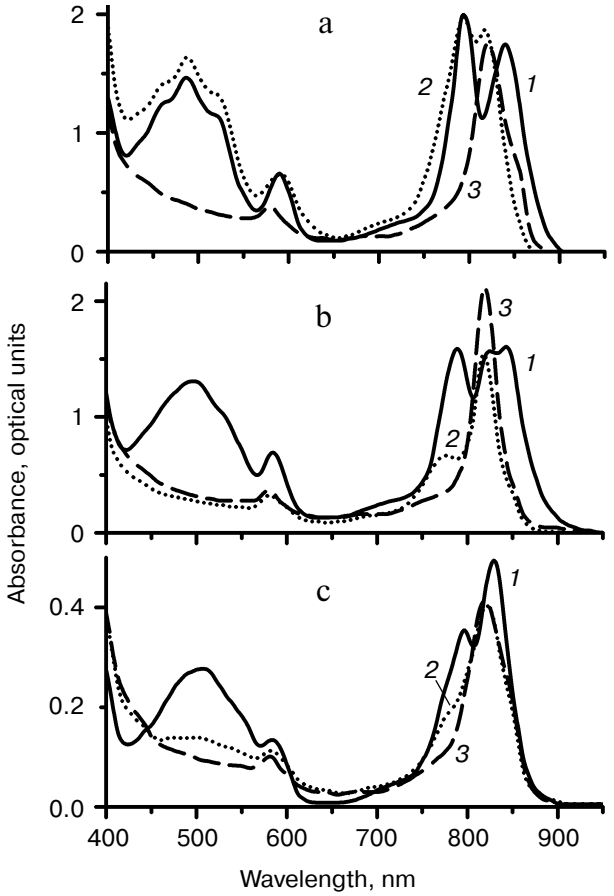

Fig. 2. Effect of dioxane on absorption spectrum of LH2 complexes from *Alc. minutissimum* (a), *Trs. sibirica* (b), and *Ect. halovacuolata* WN22 (c): *1*) initial spectrum; *2*) spectrum after addition of 40% dioxane; *3*) spectrum after 20 min incubation with 40% dioxane.

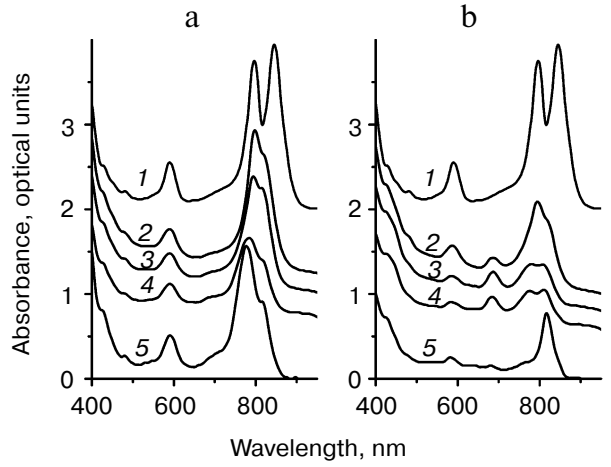

Fig. 1. Effect of dioxane on absorption spectrum of DPA complex LH2 from *Alc. minutissimum*. Spectra identification: *1*) LH2 complex before dioxane addition; *2-5*) LH2 complex after treatment with 10% (*2*), 20% (*3*), 30% (*4*), and 40% (*5*) dioxane. Spectra were recorded immediately after addition (a) or after 60 min incubation (b) with dioxane.

Treatment of LH2 complex from *Alc. minutissimum* with 40% dioxane caused initial conformational change (shift of the long-wavelength band to 818 nm). Preincubation with dioxane for 20 min resulted in disappearance of absorbance bands of LH2 complex in the near IR-region and appearance of an intense band with maximum at 820 nm (Fig. 2a and table). Such treatment also caused a decrease and shift to 582 nm of the absorption band of the Q_x transition of bacteriochlorophyll and disappearance of carotenoid absorbance bands. Dioxane caused similar effects on LH2 complexes from *Trs. sibirica* (Fig. 2b and table) and *Ect. halovacuolata* WN22 (Fig. 2c and table). There was the only one exception: conformational changes were not registered in these complexes and the absorption band of B820 form appeared immediately after dioxane addition. Maximums of carotenoid absor-

Bacteriochlorophyll absorption maximums in LH2 complexes from various bacteria before and after treatment with dioxane

	Alc. minutissimum		*Trs. sibirica*	*Ect. halovacuolata*	*Rps. palustris*	
	LH2	LH2 DPA	LH2	LH2	LH2 normal light	LH2 low intensity light
Control	843	848	846		858	850
			827	827		
	797	797	791	796	803	802
	591	590	586	584	589	586
+40% dioxane	(853)*			(850)	(815, 840)	(815, 845)
	819	820	821	820	805	813
	581	582	581	582	583	582

Note: In parentheses minor absorption bands revealed as shoulders on spectra are given.

bance disappeared simultaneously with appearance of B820 form (Fig. 2, b and c, spectra *2* and *3*). LH2 complexes from *Rps. palustris* (Fig. 3 and table) had distinct behavior. They (as well as complexes from *Alc. minutissimum*) underwent initial conformational transition (characterized by blue shift of the long-wavelength band by 20-28 nm) followed by a decrease in carotenoid absorbance typical for all studied complexes from sulfur bacteria (Fig. 2). However, subsequently, absorption bands of LH2 complexes from *Rps. palustris* insignificantly shifted and after treatment with dioxane for 30-60 min their spectra resembled the spectra of partially degraded complexes (Fig. 3, a, b, and inset; and table).

Earlier we already observed a decrease in carotenoid absorbance that was similar to that of observed in this study (Figs. 2 and 3); this decrease was due to dissociation of LH1 complex into B820 subcomplexes induced by octyl glucoside in specially prepared membranes of *Rsp. rubrum* containing carotenoids [25, 26]. In these reports, the decrease in carotenoid absorbance was attributed to formation of their colorless aggregates. Later we found that similar aggregates can be formed *in vivo* during inhibition of carotenoid biosynthesis [27]. Colorless aggregates of spirilloxanthin (absorbance bands at 300 and 370 nm) with molecular mass exceeding 600 kD were also isolated from *Rvi. gelatinosus* mutant lacking tetraheme-

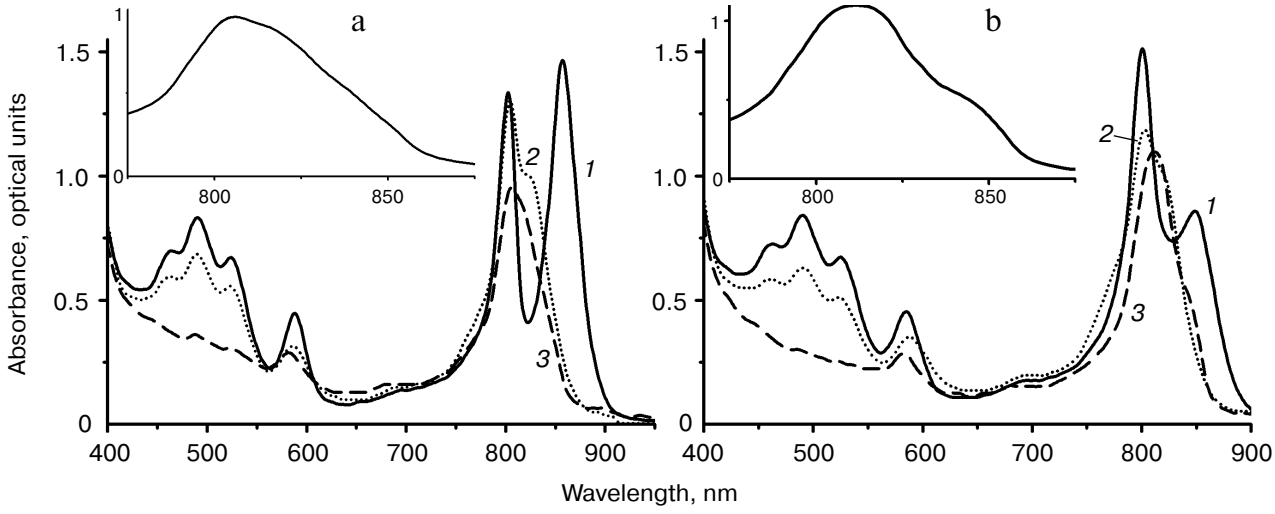

Fig. 3. Effect of 40% dioxane on absorption spectra of control LH2 complexes from *Rps. palustris* strain AB cells grown at light intensity of 2000 (a) and 300 lx (b): *1*) control; *2*) after addition of dioxane; *3*) after incubation for 60 (a) or 30 min (b) with dioxane. The inset (a and b) shows a magnified part of spectrum *3*.

cytochrome after membrane treatment with lauryl dimethylamine oxide (LDAO) [28]. It is possible that dioxane releases carotenoids from binding sites in LH2 complexes, and the released carotenoids also aggregate with formation of colorless aggregates. Thus, appearance of B820 form during treatment of LH2 complex with 40% dioxane is very similar to dissociation of LH1 complex containing carotenoids into B820 subcomplexes [25, 26].

The absorption band of B820 form may also be heterogeneous. In LH2 complexes from *Alc. minutissimum* (Fig. 2a, spectrum *3*; and table) and *Ect. halovacuolata* WN22 (Fig. 2c, spectrum *3*; and table) the absorption band had a small shoulder at 840-860 nm, which was never detected in subcomplexes B820 [13, 17]. These subcomplexes may contain small quantities of monomer bacteriochlorophyll as contaminants (due to insufficient purification) [14, 15]. Nevertheless, treatment of some LH2 complexes with 40% dioxane resulted in formation of B820 form; absorption spectra of this form were nearly identical to the absorption spectrum of classical subcomplex B820 (Fig. 4). The only difference was in the absorbance band corresponding to the Q_x transition of bacteriochlorophyll in "dioxane" complexes (Fig. 4, spectra *1* and *3*); this band was shifted to the blue region by ~10 nm compared with subcomplex B820 (Fig. 4, spectrum *2*; and table). Good evidence exists that treatment of LH2 complexes with dioxane results in bacteriochlorophyll dimerization. However, in the dimers (B820 form) bacteriochlorophyll molecules interact in a different manner than in B820 subcomplexes. This suggestion is supported by circular dichroism (CD) spectra (Fig. 5). Both spectra are characterized by almost symmetrical negative and positive absorbance bands. However, the short-wavelength band in the CD spectrum of B820 subcomplex is positive, whereas in B820 form from LH2 complex this band is negative; the same was found in corresponding long-wavelength absorption bands. It should also be noted that the absorption bands of the CD spectrum of B820 form are shifted into the red region by 35-40 nm compared with B820 subcomplex [14, 15, 18]. These results also do not coincide to the calculated data of the CD spectrum for the dimer of LH2 complex, which would be similar to the spectrum of B820 complex [18].

For comparison, we have also investigated the effect of 40% dioxane on membranes and LH1-RC assembly (Fig. 6). Traces of B820 form was found only in LH1-RC assembly (Fig. 6b, spectrum *3*). It is possible that slightly different organization of LH1 complexes than LH2 com-

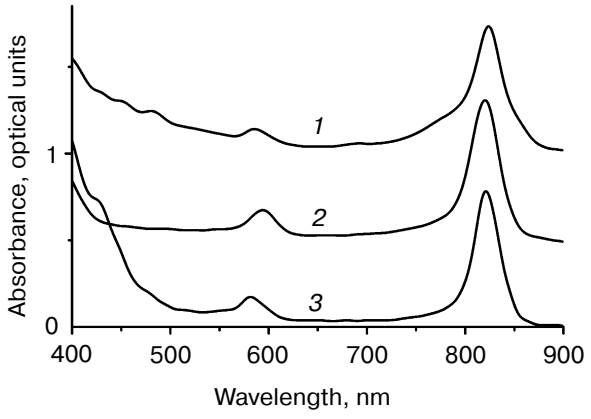

Fig. 4. Absorption spectra of LH2 from *Trs. sibirica* (*1*) and DPA complex LH2 from *Alc. minutissimum* (*3*) after treatment with 40% dioxane and absorption spectrum of classical B820 subcomplex (*2*) isolated after treatment of *Trs. sibirica* DPA assembly LH1-RC with 20% octyl glucoside.

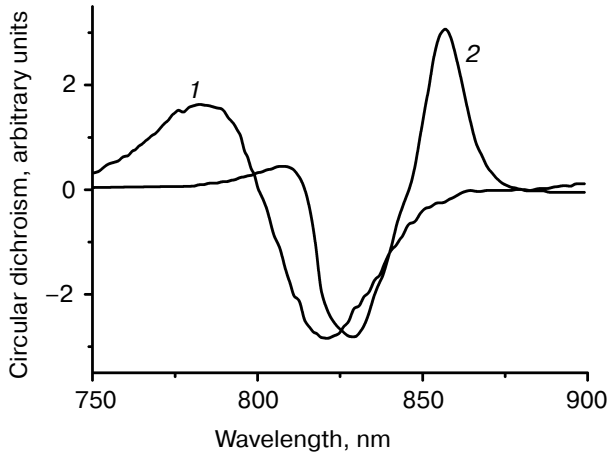

Fig. 5. Circular dichroism spectra of B820 subcomplex (*1*) and LH2 complex of *Trs. sibirica* treated with 40% dioxane (*2*).

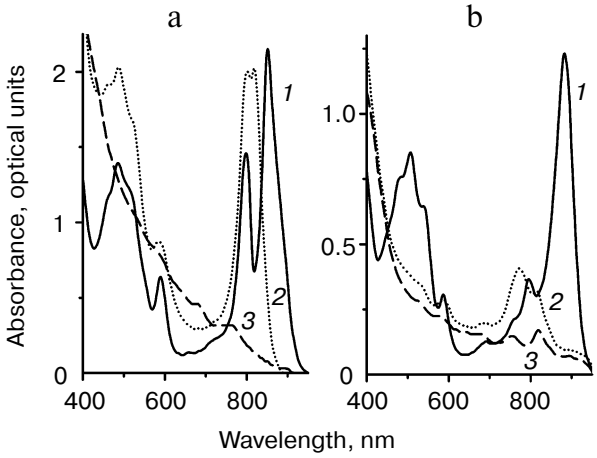

Fig. 6. Effect of 40% dioxane on the absorption spectrum of: a) control membranes from *Alc. minutissimum* ((*1*) initial spectrum, (*2*) after addition of dioxane, (*3*) after incubation with dioxane for 20 min); b) control LH1-RC assembly from *Trs. sibirica* ((*1*) initial spectrum, (*2*) after addition of dioxane, (*3*) after incubation with dioxane for 10 min).

plexes, presence of other factors in the whole membranes (intercomplex interactions, large quantities of lipids, etc.) are limiting factor(s) of its formation.

Thus, in the present study we have found that treatment of LH2 complexes isolated from some sulfur bacteria with 40% dioxane results in formation of B820 form of bacteriochlorophyll (dimers). The absorption spectrum of this form is similar to B820 subcomplex (part of LH1 complex). Perhaps, appearance of this form becomes possible due to structural arrangement of LH2 complexes, particularly, due to existence of a circular cluster of bacteriochlorophyll molecules in which pigment molecules interact with each other. Although this circular structure of pigment molecules is considered (from a physical viewpoint) as a whole unit [29], it is clear that dioxane alters this interaction and causes significant impairments in the structure of this complex. It seems unlikely that direct dissociation of bacteriochlorophyll cluster into dimers (as is observed during dissociation of LH1 cluster into B820 subcomplexes in the presence of octyl glucoside [13-16]) represents the subsequent stage of this process. Obviously, dioxane initiates unfolding of complex structure followed by formation of protein-bound monomeric bacteriochlorophyll with subsequent pigment dimerization. However, dioxane does not impair protein–pigment bonds, otherwise treatment with dioxane would result in pigment release and formation of a monomeric forms of bacteriochlorophyll. We did not observe this product. This suggests significant contribution of the circular cluster of bacteriochlorophyll in LH2 complexes into the studied process. Indirectly, this is supported by the absence of this pigment form in model systems. These systems were studied in detail by A. A. Krasnovsky [30-32]. It was shown that concentrated bacteriochlorophyll solutions in polar or non-polar solvents are characterized by absorption bands in the near IR region; these spectral bands were also found in corresponding forms of pigments *in vivo*. Evaporation of these solutions in vacuum resulted in formation of films with maximums at 800 and 860 nm. Additional treatment of these films with vapors of water or solvents caused shift of long-wavelength maximum to 900-920 nm. Study of aggregation of chlorophyll and its analogs in the systems dimethylformamide or acetonitrile–water [33] also did not reveal formation of pigment dimers. Finally, in micelles of various detergents [34] and also in systems solvent–water (Scheer H., personal communication) bacteriochlorophyll form absorbing at 820 nm was not detected. Results of our experiments demonstrate an important role of certain ratio dioxane–water in the dimer formation. However, model systems have not been studied in this work, and this represents a goal of subsequent investigations.

Differences in absorption spectra of bacteriochlorophyll dimers obtained during dioxane treatment of LH2 complexes from various bacteria may reflect individual features of organization of each particular complex. Evidently, all investigated LH2 complexes from sulfur bacteria *Alc. minutissimum*, *Trs. sibirica*, and *Ect. halovacuolata* WN22 differ in their structure from similar complexes from non-sulfur bacteria. Lack of B820 form after dioxane treatment of two types of LH2 complexes from *Rps. palustris* strain AB supports this suggestion.

It remains unclear what happens to bacteriochlorophyll monomers. In LH2 complexes from *Alc. minutissimum* and *Ect. halovacuolata* WN22 these molecules possibly contribute to appearance of additional bands (table) or rapidly degrade to colorless products.

Resultant bacteriochlorophyll dimers may represent promising models for studies of various aspects of pigment–pigment interactions in relatively simple systems, and also for development of theoretical models of conversion of circular clusters of bacteriochlorophyll into dimers. Coincidence of spectral characteristics of bacteriochlorophyll dimers (B820 form) from LH2 complexes and B820 subcomplexes suggests that subsequently it would be possible to develop an approach for isolation of corresponding subcomplexes from LH2 complexes and to study principles of assembly of these complexes *in vitro*, as has been demonstrated for LH1 complexes [13-17].

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