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EXPERIMENTAL ARTICLES

Distribution of Bacteriochlorophyll between the Pigment–Protein Complexes of the Sulfur Photosynthetic Bacterium *Allochromatium minutissimum* Depending on Light Intensity at Different Temperatures

A. A. Solov'ev[1] and Yu. E. Erokhin

Institute of Basic Biological Problems, Russian Academy of Sciences, ul. Institutskaya 2, Pushchino, Moscow oblast, 142290 Russia

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Abstract—Variation of the distribution of bacteriochlorophyll *a* (BChl *a*) between external antenna (LH2) and core complexes (LH1 + RC) of the photosynthetic membrane of the sulfur bacterium *Allochromatium minutissimum* was studied at light intensities of 5 and 90 Wt/m^2 in the temperature range of 12–43°C. The increase of light intensity was shown to result in a 1.5- to 2-times increase of a photosynthetic unit (PSU). PSU sizes pass through a maximum depending on growth temperature, and the increase of light intensity (5 and 90 Wt/m^2) results in a shift of the maximal PSU size to higher temperatures (15 and 20°C, respectively). In the narrow temperature interval of ~14–17°C, the ratio of light intensity to PSU size is typical of phototrophs: lower light intensity corresponds to larger PSU size. The pattern of PSU size change depending on light intensity was shown to differ at extreme growth temperatures (12°C and over 35°C). The comparison of *Alc. minutissimum* PSU size with the data on *Rhodobacter capsulatus* and *Rhodopseudomonas palustris* by measuring the effective optical absorption cross-section for the reaction of photoinhibition of respiration shows a two to four times greater size of light-harvesting antenna for *Alc. minutissimum*, which seems to correspond to the maximum possible limit for purple bacteria.

Key words: Allochromatium minutissimum, bacterial photosynthesis, purple sulfur bacteria, photosynthetic unit.

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Since the middle of the last century, it has been thought that in photosynthetic bacteria, specific bacteriochlorophyll (BChl) content (BChl per unit cell mass) is inversely related to light intensity in anaerobic cultures and to oxygen tension in aerobic cultures. In anaerobic culture, the cells synthesize BChl in an amount that provides for maintenance of absorbed light energy at a more or less constant level, in spite of changes in incident light intensity [1]. Purple bacteria are able to adapt to light conditions due to variations of antenna size. In cells with low BChl *a* content, the ratio of intensity of the 875-nm band to the 800 or 850-nm ones is higher than in the cells with high BChl *a* content, because the content of core complexes (LH1 + RC) in the membrane of chromatophores weakly depends on growth conditions, in contrast to the content of peripheral antenna (LH2). This means that the size of a photosynthetic unit (PSU) decreases with increasing light intensity. The term "photosynthetic unit" implies a reaction center (RC) with associated BChl of the light-harvesting antenna complexes; PSU size is defined as the total number of BChl molecules in the membrane of chromatophores per one RC as in [2]. This problem has been studied in most detail for the strains of *Rhodobacter sphaeroides* [2]. At a transfer from moderately bright to very weak illumination, the content of LH1 + RC ensemble per cell mass unit in these strains may increase 2.5 times, whereas total BChl increases 25 times, reaching 300 molecules of antenna BChl *a* per one RC. It has been revealed that some species demonstrate adaptation properties typical of *Rb. sphaeroides* (*Rhodospirillum molischianum, Rhodocyclus gelatinosus, Rhodobacter capsulatus*); other species, on the contrary, do not show any pronounced changes in their absorption spectra in response to changed illumination (*Rhodomicrobium vannielii, Ectothiorhodospira halophila*) [3].

We have studied the BChl *a* distribution between the pigment complexes of the photosynthetic membrane of the strictly anaerobic sulfur purple bacterium *Allochromatium minutissimum* at different light intensities and

[1] Corresponding author; e-mail: alex_l_I@mail.ru

different temperatures. Temperature, along with light intensity, oxygen tension, and composition and concentration of substrates, is known to be the most powerful factor affecting morphogenesis and structure of the photosynthetic apparatus [4]. For example, in purple bacteria *Rhodopseudomonas acidophila* strain 7750 and *Allochromatium vinosum* strain D, the type of synthesized LH2-complex (B800-820 or B800-850) is controlled by temperature, and the higher temperature promotes biosynthesis of a more long-wave complex [5]. Previously, it has been shown that in *Alc. minutissimum* during the transfer from high to low light intensity the content of BChl *a* per cell mass unit remained practically unchanged, while the content of RC increased 1.5-fold [6].

The goal of the present work was to study BChl *a* distribution between the LH2 complex and the LH1 + RC ensemble under the effect of two factors, temperature and light intensity, during growth of the photosynthetic bacterium *Allochromatium minutissimum.* Three independent methods were used: (a) measurement of the ratio of BChl *a* in the LH2-complex and in the LH1 + RC ensemble by absorption spectra of acetone–methanol extracts at 770 nm; (b) measurement of the ratio of "total" BChl *a* at 590 nm directly in the absorption spectra of the same objects; and (c) evaluation of PSU size by measuring the effective optical cross-section for the reaction of photoinhibition of respiration [7, 8]. Each of these methods has its plusses and minuses (see Materials and Methods), but their results are in qualitative agreement.

MATERIALS AND METHODS

Bacterium *Allochromatium minutissimum* from the Collection of Microorganisms of Moscow State University was grown under continuous illumination in modified Larsen's medium [9] containing 0.2% sodium acetate and 0.05% sodium sulfide. Under these conditions, biomass growth is observed in the temperature range of 12 to 43°C at normal (close to physiological) light intensity, 90 Wt/m^2, and in the range of 12 to 35°C at a lower light intensity, 5 Wt/m^2. Cell mass was harvested in the beginning of the stationary phase.

Chromatophores were isolated according to [10] by centrifugation after sonication of the cells in an UZG 13-0,1/22 module ultrasound generator at 22 kHz and resuspended in 0.05 M Tris–HCl buffer, pH 8.0.

LH2 complexes and LH1 + RC ensembles were isolated by preparative electrophoresis in 7% polyacrylamide gel with Triton X-100 [10]. Chromatophores were solubilized for 2 h at 4°C at the detergent concentration of 3.3%. The complexes were eluted by grinding and soaking of gels under stirring for 24 h at 4°C in 0.01 M Tris–HCl buffer, pH 8.0, with the addition of 0.1% Triton X-100. The completeness of elution was controlled by gel washing with minor portions of detergent-containing buffer on a paper filter to a colorless state.

BChl *a* was extracted from the eluates with an acetone–methanol mixture (7 : 2) at 4°C in the dark, as in [1]. Denatured proteins were separated by centrifugation. Spectrophotometric detection of BChl *a* at 770 nm was performed as quickly as possible because of its relative instability in organic solvents, particularly in the light.

Absorption spectra in solutions and gels were measured with an UV-160 Shimadzu spectrophotometer (Japan). For registration of the spectra of the complexes directly in gels, the respective zones were excised from the columns. Pure gels, of the same thickness as the complex-containing ones, were placed into the control cuvette to compensate for light scattering. The spectra were digitized using a portable E-24 module (L-Card) with PowerGraph software (InterOptika-S).

Decomposition of the optical absorption spectra of the LH1 + RC ensemble into Lorentzian-shaped subbands was performed using a built-in PFM block of the OriginPro 7.5 software, which made it possible to estimate the contents of "total" BChl *a* by the absorption band of 590 nm.

PSU size was functionally assessed by the method based on the measurement of optical cross-sections for the reaction of photoinhibition of respiration under pulse excitation of reaction centers in intact cells [7, 8].

RESULTS AND DISCUSSION

The main results of this research are presented in the table and in Figure 1. PSU size ($N_{BChl\,a}$) was determined by the molar ratio of total BChl *a* to RC as in [2]. PSU size was assessed on the basis of pigment composition of the LH1 + RC ensemble from *Rhodospirillum rubrum* (36 molecules of BChl *a*) [11], keeping in mind that LH1 are present in the membrane in the stoichiometric ratio 1 : 1 with RC [3, 12].

Since the LH2 complex in *Alc. minutissimum* can be easily separated from the LH1 + RC ensemble [10], the measurement of BChl *a* content by means of its extraction with organic solvents from isolated complexes seems to be the most direct method. The data obtained are shown in the table.

It has been established empirically that decomposition of the spectrum of the LH1 + RC ensemble into Lorentz components in the wavelength range of 400–650 nm, including the region of absorption of carotinoids, though not perfect, still gives the absorption value of the 590-nm band of BChl *a* (Fig. 2). Its application results in satisfactory accordance with the estimates of BChl *a* ratio in LH2 complexes and LH1 + RC ensembles by extraction with the acetone–methanol mixture (table). The absorption value of BChl *a* at 590 nm in LH2 complex is taken in this case directly from the spectrum without decomposition into Lorentz components.

Application of the measurement of effective optical cross-section for the reaction of photoinhibition of res-

Distribution of BChl *a* in LH2 complexes and LH1 + RC ensembles of the purple bacterium *Allochromatium minutissimum*

Sample	PSU size			BChl a_{LH2} /BChl a_{LH1+RC}*	
	By respiration photoinhibition	By the ratio of BChl *a* absorption in acetone–methanol extracts from LH2 and LH1 + RC	By the ratio of BChl *a* absorption at 590 nm in LH2 and LH1 + RC		
12°C, 5 Wt/m^2	160	172 ± 10	207 ± 12	3.77 ± 0.28	4.74 ± 0.32
12°C, 90 Wt/m^2		176 ± 8	210 ± 5	3.88 ± 0.22	4.82 ± 0.15
15°C, 5 Wt/m^2	260	236 ± 9	231 ± 6	5.56 ± 0.25	5.41 ± 0.16
15°C, 90 Wt/m^2	195 ± 10	158 ± 10	201 ± 9	3.39 ± 0.28	4.59 ± 0.25
20°C, 5 Wt/m^2	125 ± 10	170 ± 8	171 ± 5	3.73 ± 0.22	3.74 ± 0.14
20°C, 90 Wt/m^2	245 ± 15	230 ± 9	240 ± 5	5.40 ± 0.25	5.67 ± 0.15
25°C, 5 Wt/m^2	100 ± 10	170 ± 9	180 ± 7	3.72 ± 0.25	3.99 ± 0.20
25°C, 90 Wt/m^2	210 ± 10	205 ± 11	202 ± 7	4.69 ± 0.30	4.60 ± 0.19
30°C, 5 Wt/m^2		160 ± 7	174 ± 1.5	3.44 ± 0.19	3.84 ± 0.04
30°C, 90 Wt/m^2		187 ± 5	190 ± 5	4.20 ± 0.14	4.29 ± 0.14
35°C, 5 Wt/m^2		140 ± 12	164 ± 10	2.89 ± 0.33	3.56 ± 0.27
35°C, 90 Wt/m^2		155 ± 11	177 ± 10	3.30 ± 0.31	3.91 ± 0.27
39°C, 90 Wt/m^2		139 ± 10	162 ± 11	2.86 ± 0.28	3.50 ± 0.32
41°C, 90 Wt/m^2		150 ± 12	188 ± 14	3.16 ± 0.33	4.21 ± 0.38
42°C, 90 Wt/m^2		149 ± 10	179 ± 10	3.14 ± 0.28	3.98 ± 0.27
43°C, 90 Wt/m^2		188 ± 11	200 ± 8	4.22 ± 0.31	4.57 ± 0.23

* Left column: the data on the ratio of BChl *a* in the complexes by acetone–methanol extracts; right column: by "total" BChl *a* in absorption spectra. The table gives the values of the mean ± standard deviation, $n = 5$.

piration in intact cells [7, 8] for assessment of PSU size was limited to only a small temperature interval (Fig. 1c) due to an abrupt increase of the signal-to-noise ratio of registration of this reaction at extreme temperatures. The estimates of PCU size obtained by this method are close to the results of two previous methods, which is particularly valuable because this measurement is based on the functional properties and interaction of LH2 complexes and LH1 + RC ensembles.

The analysis of our measurements shows that decreased light intensity does not lead to an increase of PSU size in *Alc. minutissimum* at the optimal physiological temperatures. On the contrary, reduction of light intensity from 90 to 5 Wt/m^2 results in a 1.5–2-time decrease of PSU in this culture. Temperature has a significant effect on PSU size. As can be seen from Fig. 1, PSU sizes pass through a maximum depending on cell growth temperature, and at increasing light intensity (5 and 90 Wt/m^2) the maximum PSU size shifts to higher temperatures (15 and 20°C, respectively). In the narrow temperature range of ~14–17°C, the ratio between PSU size and light intensity typical of phototrophs is observed properly: larger PSU size corresponds to lower light intensity. Figure 1 also shows that the ability for changing PSU size depending on light intensity is

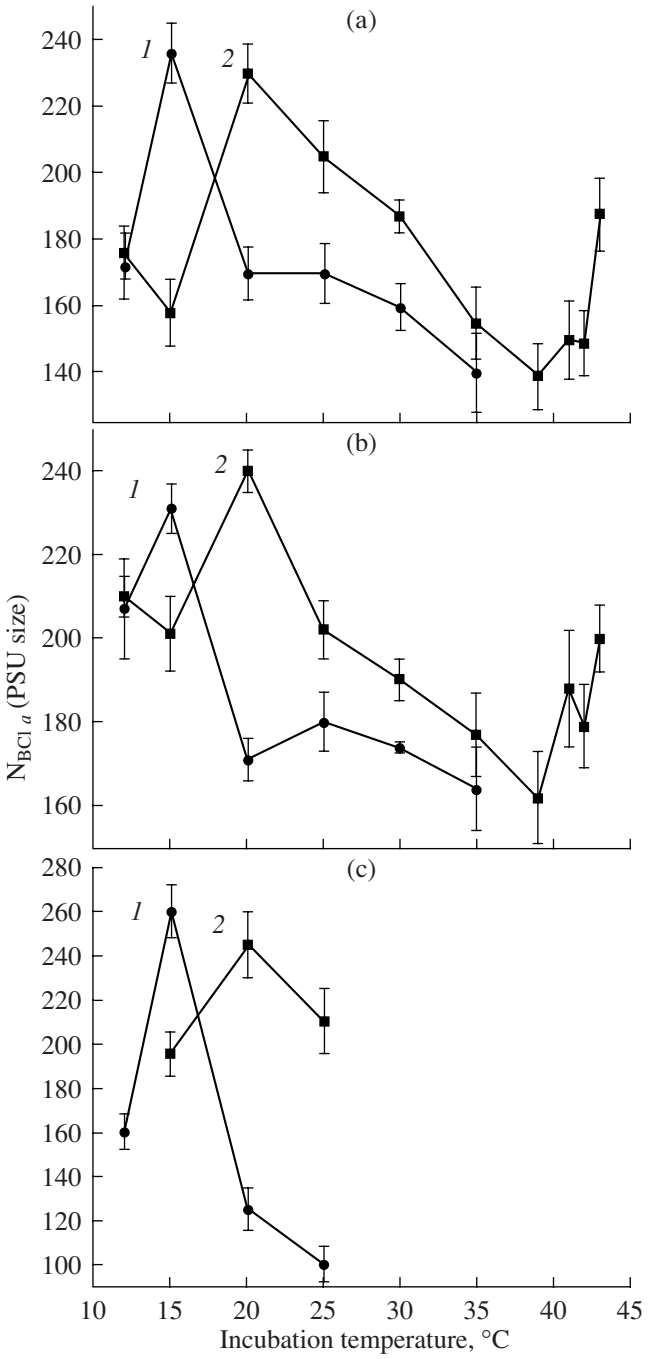

Fig. 1. Dependence of *Alc. minutissimum* PSU sizes on cell growth temperatures: by acetone–methanol extracts of BChl *a* from LH2 complexes and LH1 + RC ensembles (a); by the ratio of "total" BChl absoption at 590 nm in the spectra of the same objects (b); by measurement of the optic cross-section for the reaction of photoinhibition of respiration under pulse excitation of reaction centers in whole cells [7, 8] (c). Light intensity: 5 Wt/m^2 (*1*) and 90 Wt/m^2 (*2*).

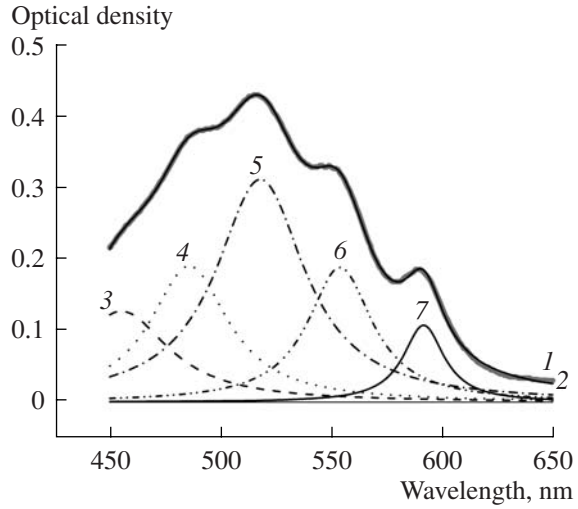

Fig. 2. Decomposition of the spectrum of optical absorption of the LH1 + RC ensemble from *Alc. minutissimum* chromatophores into Lorentzian-shaped subbands. Curves *3–7* are model subbands. Curve *2* is their envelope. Curve *1* is the experimental absorption spectrum of the LH1 + RC ensemble in gel. Model subband *7* is used as an absorption band of "total" BChl *a* in the LH1 + RC ensemble.

impaired at extreme temperatures, which may be due to the unbalance of biosynthesis of BChl *a*, proteins, lipids, etc. PSU size was shown to increase at 90 Wt/m^2 and at temperatures above 39°C up to 43°C. The total content of BChl *a* in the membrane gradually increases with rising temperature and abruptly drops at 43°C (Fig. 3). A similar picture was observed for *R. rubrum* and *Rb. sphaeroides* [13].

The ratio of the main components of LH1 + RC ensembles and the external antenna (BChl *a*, carotenoids, proteins) in the membrane is determined by a complex set of transcriptional, translational, and post-translational processes, as well as by regulation of other cellular biosynthetic processes. As a rule, high light intensities result in a general decrease of BChl *a* content and of the quantity of LH2 complexes in the anaerobic culture. This regulation proceeds during initiation of transcription and after transcription due to the differences in the rates of mRNA decomposition and modulation of the activity of the enzymes of pigment synthesis. For example, the lowered content of LH2 complexes in the cells of *Rb. capsulatus* grown anaerobically at a high light intensity is a result of a post-transcriptional regulatory process, because the stationary levels of mRNA for the proteins of LH2 complex in the culture grown at a high light intensity (140 Wt/m^2) are about four times higher than the levels at low intensity (2 Wt/m^2) [14]. Unusual behavior of *Alc. minutissumum*, when the total content of BChl *a* in the culture at increasing light intensity was almost unchanged [6] and the relative content of LH2 complexes increased, is probably associated with the fact that these LH2 complexes are represented by multiple (iso)forms of α and β-subunits [15]. It is known, for example, that the genome of *Rhodopseudomonas palustris* contains five antenna gene clusters encoding α and β-polypeptides of the LH2 complex, and the reg-

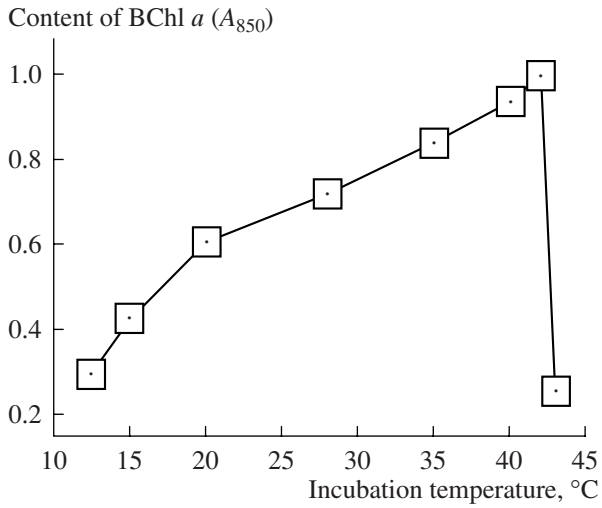

Fig. 3. Relative content of BChl *a* in chromatophores (by absorption band of 850 nm) from the cells of *Alc. minutissimum* grown under light intensity of 90 Wt/m^2 depending on growth temperature.

ulation of transcription of these operons may be different depending on light intensity. For example, all five operons are transcribed under high light intensity under anaerobic growth conditions, while only three of them are transcribed at low intensity [16]. Moreover, the LH2 complexes corresponding to these operons differ in the efficiency of energy transfer to the LH1 complex [17]. All the above creates necessary prerequisites for effective regulation in response to the changing illumination conditions, alternative to simple variation of the external antenna content in the membrane.

Comparison of effective optical cross-sections σ_{PSU} for the reaction of photoinhibition of respiration in the whole cells of *Alc. minutissimum* with the data obtained for *Rps. palustris* (Fig. 4) [8, 18] and *Rb. capsulatus* [18] shows a 2 to 4 times higher value for the light-harvesting antenna, which seems to be one of the largest in purple bacteria (Fig. 5) [3]. Previously, we have used the method of electrophoresis in polyacrylamide gel with application of mild detergents (sodium deoxycholate, CHAPS) to demonstrate the heterogeneity of LH2 complexes in the membrane of *Alc. minutissimus* chromatophores and suggested that some of the LH2 complexes are linked with the LH1 + RC ensemble and its dimer, while the rest form a free pool in the native membrane [19]. The latest experimental data obtained by the method of atomic force microscopy indeed demonstrate a strongly pronounced heterogeneity of lateral organization of the native photosynthetic membrane: membrane regions with the LH1 + RC ensembles encircled in eight rings of LH2 complexes were found, along with the zones of contacting LH1 + RC ensembles without LH2 complexes, as well as zones with dense hexagonal packing of the rings of LH2 complexes [20, 21]. Thus, the latest structural studies have shown that the term "photosynthetic unit" does not reflect the long-range ordering and formation of real ordered structures

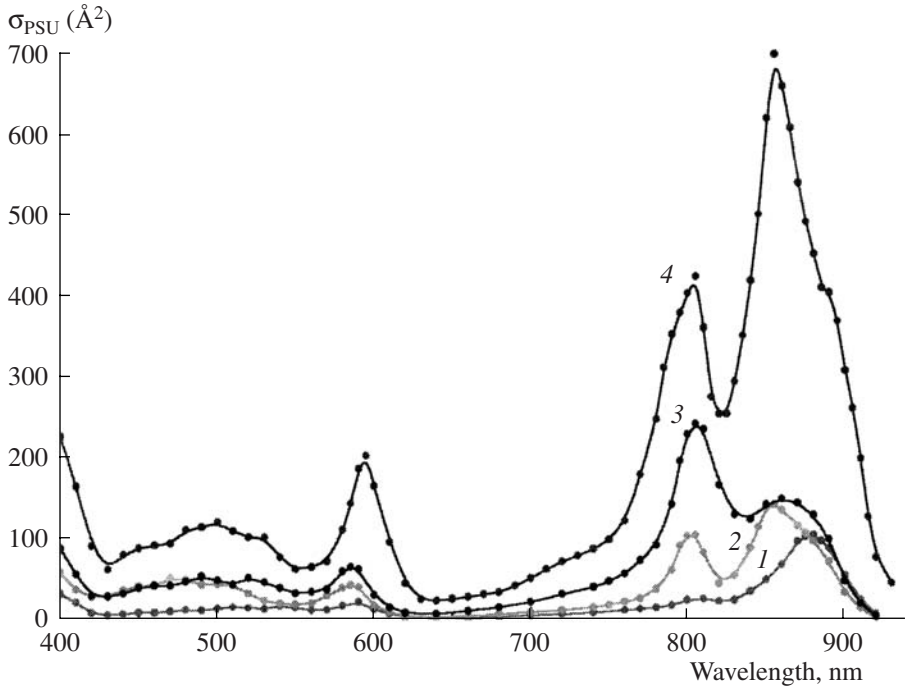

Fig. 4. The spectra of effective optical cross-section σ_{PSU} (Å^2) for the reaction of photoinhibition of respiration in the cells of *R. rubrum* (*1*), *Rps. palustris* grown at high (*2*) and low (*3*) light intensity and 30°C, and *Alc. minutissimum* (*4*) grown at a low light intensity at 15°C.

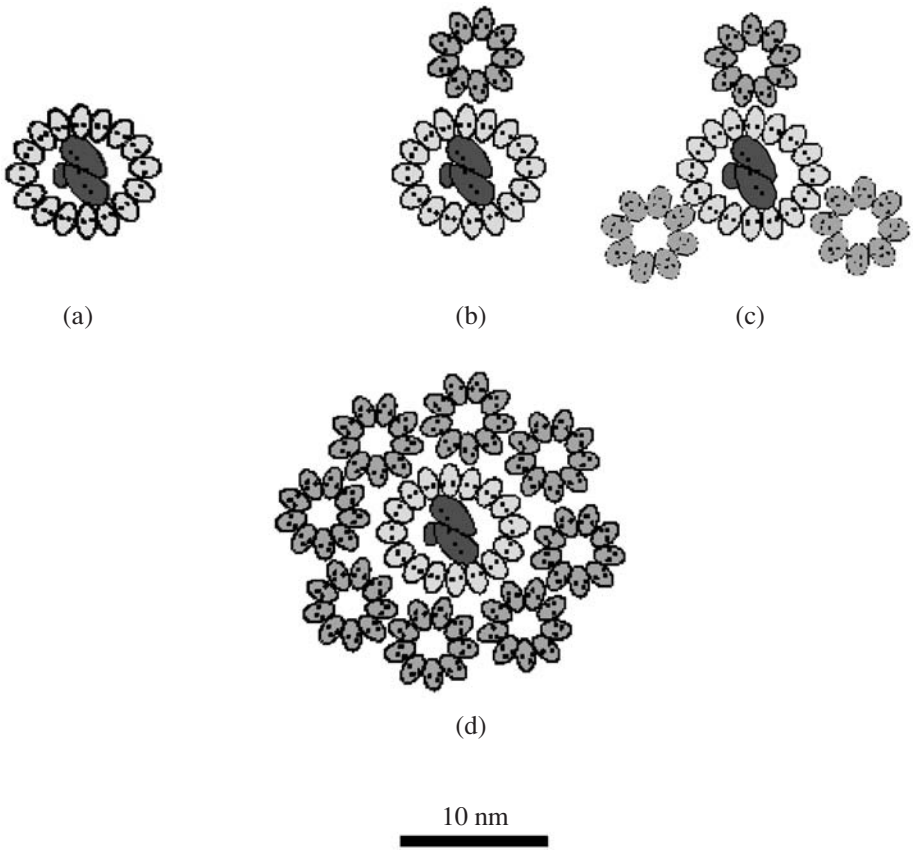

Fig. 5. Models of possible PSU organization in purple bacteria: LH1 + RC ensemble in *R. rubrum* ($N_{BChl\,a}$ = 36) (a); LH1 + RC + $LH2_{B800–850}$ ensemble of *Rps. palustris* grown at a high light intensity ($N_{BChl\,a}$ = 63) (b); LH1 + RC + $(LH2_{B800})_2$ + $LH2_{B800–850}$ ensemble of *Rps. palustris* grown at a low light intensity ($N_{BChl\,a}$ = 127) (c); and LH1 + RC + $(LH2_{B800–850})_8$ ensemble of *Alc. minutissimus* grown at a low light intensity and a temperature of 15°C ($N_{BChl\,a}$ = 252) (d). The contours of all complexes are proportional to the sizes of protein molecules (bar scale: 10 nm).

in the native membrane, but rather points to the functional interaction and relationship of the light-harvesting system and RC.

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