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REVIEW

Photosynthetic Units of Phototrophic Organisms

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Abstract—Photoautotrophic organisms play a key role in the biosphere of the Earth, converting solar energy of the 350-1000 nm range into biochemically available form. In contemporary aquatic and terrestrial ecosystems, the dominating groups are the oxygen evolving cyanobacteria, algae, and higher plants. Anoxygenic phototrophic microorganisms occupy mainly ecological niches with extreme environmental conditions. Despite diverse evolution of all these taxonomic groups, their photosynthetic apparatus has a similar molecular design and identical principles of operation. This review covers recent data about features of the structural and functional organization of pigment–protein complexes of the basic types of photosynthetic units in prokaryotes and eukaryotes. A correspondence between the optical properties of various photosynthetic units and the natural light conditions is discussed.

Key words: chlorophyll, bacteriochlorophyll, reaction center, pigment–protein complexes, light-harvesting antenna, photosynthetic unit

THE CONCEPT OF PHOTOSYNTHETIC UNIT

In the beginning of XX century, action spectrum measurements by K. A. Timirjazev and other investigators showed a key role of chlorophyll (Chl) in photosynthesis. Later the concept of photosynthetic unit (PSU) took on special significance. For the first time, this concept was theoretically formulated by Gaffron and Wohl [1] based on the data of Emerson and Arnold [2] for photosynthetic rate under pulse illumination. It was found that the maximal yield of O_2 in the green alga *Chlorella* is attained under illumination by short (<10 μsec) saturating light flashes with dark intervals >20 msec; however, this yield does not exceed one molecule O_2 per ~2500 Chl molecules. This implies that the majority of Chl molecules transfer the absorbed energy to a reaction center (RC), where the photochemical reaction takes place.

The Emerson–Arnold PSU size derived from Chl/O_2 ratio was long used as the basic parameter in quantitative estimations of adaptive or developmental changes of the pigment apparatus of photosynthesis. However, as this parameter does not contain information on the allocation of Chl to later discovered two photosystems (PSI and PSII) [3], the term "PSU size" is now applied only to the number of pigment molecules that furnish energy directly to one particular photochemical reaction [4-6]. It is necessary to distinguish this quantity of the functional PSU size from a quantity, used sometimes under the same name, of a stoichiometric ratio of the total Chl content in sample to content of reaction centers of either of the two photosystems [7, 8]. In this connection, it is wrong to accept a broad interpretation of the term PSU used in some publications [9] that equate it to an assembly of the two photosystem complexes and intersystem electron transport chain. Such model is incompatible with the data about lateral heterogeneity of distribution of the two photosystem complexes in thylakoid membranes and variable stoichiometry of the two RC types in different species during adaptation and development [10-12]. Therefore, only the idea of PSU as the assembly of a certain RC associated with its light harvesting antennae has real meaning. In the case of dense packing of pigment–protein complexes within the membrane, there is the possibility to share the antenna by several RC that results in averaging of the functional PSU size. This review deals with recent data on the PSU design in the main taxonomic groups of phototrophs.

Abbreviations: Chl) chlorophyll; BChl) bacteriochlorophyll; Phe) pheophytin; BPh) bacteriopheophytin; RC) reaction center; PSI (II)) photosystem I (II); PSU) photosynthetic unit; LH1) the core light-harvesting complex of purple bacteria; LH2) the peripheral light-harvesting complex of purple bacteria; LHC) light-harvesting complex of algae and higher plants.

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TWO TYPES OF PHOTOSYNTHETIC REACTION CENTERS

Ability for phototrophy is found among many groups of bacteria [13], whose evolution originated all known types of photosynthetic RC [14-16]. According to the molecular biology of protein subunits [17], two main types of RC complexes include at least five different subtypes (table). These two types of RC are distinguished by the terminal electron acceptor in the electron transport chain. Type-I RC (or FeS-type) complexes from heliobacteria, green sulfur bacteria, and PSI of oxyphototrophs (hereinafter used for all O_2 evolving organisms) contain low potential iron-sulfur clusters as the terminal electron acceptor. Type-II RC complexes from green filamentous bacteria, purple bacteria, and PSII of oxyphototrophs contain quinone as the terminal electron acceptor. Besides, these types of RC differ in intermediate electron acceptor, which is Chl or its derivatives in all type-I RC complexes [18, 19] and (bacterio)pheophytin in type-II RC complexes [14].

Another distinctive feature of different RCs is their spatial relation with the proximal antenna system. PSI and related photosystems from heliobacteria and green sulfur bacteria are dimers of protein subunits PsaA/PsaB, $(PshA)_2$, and $(PscA)_2$, respectively, which bind not only six (bacterio)chlorophylls participating in the electron transfer chain, but also ~20-100 pigment molecules of the core antenna. Heterodimers of the type-II RC protein subunits from green filamentous bacteria and purple bacteria (L/M) and PSII (D1/D2) contain only six chlorin molecules participating in phototransfer of electrons (D1/D2 complex contains two additional Chl *a* molecules participating in transfer of excitation energy). Only PSII complexes include a core antenna, but its pigments are bound to separate protein subunits, CP43 and CP47 (table).

Along with general similarity, there are also considerable differences in the primary and secondary protein

Known types of photosynthetic reaction centers (RC) and composition of their light-harvesting antenna complexes

Taxonomic group	Proteins of RC complex	Primary electron donor of RC	Antenna proteins of RC	Supplementary antenna complexes of PSU (number of pigment molecules per RC)
		Type I reaction centers		
Heliobacteria	$(PshA)_2$	P798 (2 BChl *g′*)	$(PshA)_2$ (2 Chl *a* + 34 BChl *g*)	none
Green sulfur bacteria	$(PscA)_2$	P840 (2 BChl *a′*)	$(PshA)_2$ (4 Chl *a* + 16 BChl *a*)	chlorosomes (⩽2000 BChl *c*,*d*,*e*,*a*); 2 FMO (42 BChl *a*)
Oxyphototrophs	PsaA/PsaB	P700 (Chl *a*/Chl *a′*)	PsaA/PsaB (⩾90 Chl *a*,*b*)	phycobilisomes (250-1400 chromophores); IsiA, Pcb, or LHC *a*/*b*/*c*/carotenoids (100-500 molecules)
Oxyphototrophs, *Acaryochloris marina*	PsaA/PsaB	P740 (Chl *d*/Chl *d′*)	PsaA/PsaB (⩾90 Chl *d*)	phycobilins (⩽24 chromophores)
		Type II reaction centers		
Green filamentous bacteria	L/M (3 Bchl *a* + 3 BPh *a*)	P865 (2 BChl *a*)	none	chlorosomes (⩽800 BChl *c*,*d*,*e*,*a*); LH808-866 (36 BChl *a*)
Purple bacteria	L/M (4 Bchl *a* + 2 BPh *a*)	P870 (2 BChl *a*)	none	LH1 (32 BChl *a*), LH2 (27-32 BChl *a*)
Purple bacteria, *Rhodopseudomonas viridis*	L/M (4 Bchl *b* + 2 BPh *b*)	P980 (2 BChl *b*)	none	LH1 (32 BChl *b*)
Purple bacteria, *Acidiphilium rubrum*	L/M (4 Zn-BChl *a* + + 2 BPh *a*)	P850 (2 Zn-BChl *a*)	none	LH1 (32 Zn-BChl *a*)
Oxyphototrophs	D1/D2 (6 Chl *a* + 2 Phe *a*)	P680 (2 Chl *a*)	CP43/CP47 (13 + 16 Chl *a*,*d*)	phycobilisomes (250-1400 chromophores); Pcb or LHC *a*/*b*/*c*/carotenoids (100-500 molecules)

structure, relative orientation, and distances between individual cofactors within each particular RC complex. The variety of chemical and optical properties of the special pigment pair of the primary electron donor in various RCs should be noted, especially in purple bacteria. In particular, several BChl *b*-containing purple bacteria are known. The acidophilic purple bacterium *Acidiphilium rubrum* contains BChl *a*, whose central metal Mg is substituted with Zn [20, 21]. Recently, a BChl *a*-containing strain of a purple sulfur bacterium was isolated, which has unusually long wavelength of Q_y absorption band at 963 nm and the bleaching band of primary electron donor at 925 nm [22]. Thus, there are now known at least eight types of the primary donors of RC differing in the chemical character of the pigments (table); each special pair of type-I RC obligatorily includes the 13^2-epimer of (bacterio)chlorophyll [23].

Various groups of anoxygenic photosynthetic bacteria contain only one type of RC complex, evolutionarily related either to PSI or PSII. All known O_2-evolving phototrophs, i.e., prokaryotic cyanobacteria, prochlorophytes and *Acaryochloris marina*, and eukaryotic algae and higher plants, contain two functionally coupled PSI and PSII. General similarities of structure of the antenna complexes [24] and of function of the two RC types are evidence of their familiar relationship and origin from a common molecular ancestor [14-16]. Some recent data from phylogenetic analysis of apoproteins [15] indicated that type-I RC is the earlier. However, a phylogenetic tree based on the analysis of evolution of Mg-tetrapyrrole biosynthesis genes [16] shows that all photosynthetic lineages descended from a purple bacterium-like ancestor with type-II RC. The evolution of direct ancestors of O_2-evolving PSII is the most mysterious [25, 26].

Light harvesting complexes of photosynthetic organisms are characterized by a much wider variety of structure. There are reasons to believe that their evolution proceeded rather independently from RC complexes, and, in oxyphototrophs, it further continued after endosymbiotic insertion into eukaryotic cells of a cyanobacterial ancestor containing conservative cores of two photosystem [27, 28].

PHOTOSYNTHETIC UNITS OF ANOXYPHOTOTROPHS

The most simply arranged photosynthetic unit of heliobacteria (Fig. 1a) [24] is the inseparable complex of RC and core antenna—homodimer $(PshA)_2$, which contains at least 34 BChl *g* molecules including special pair BChl *g*′ (P798) and two molecules of 8′-OH-Chl *a* [18]. The PSUs of all other groups of phototrophs contain one or more complementary light harvesting complexes (LH(C)). These antenna complexes can be classified in the groups of intramembrane (LH1, LH2, LHC Chl *a*,

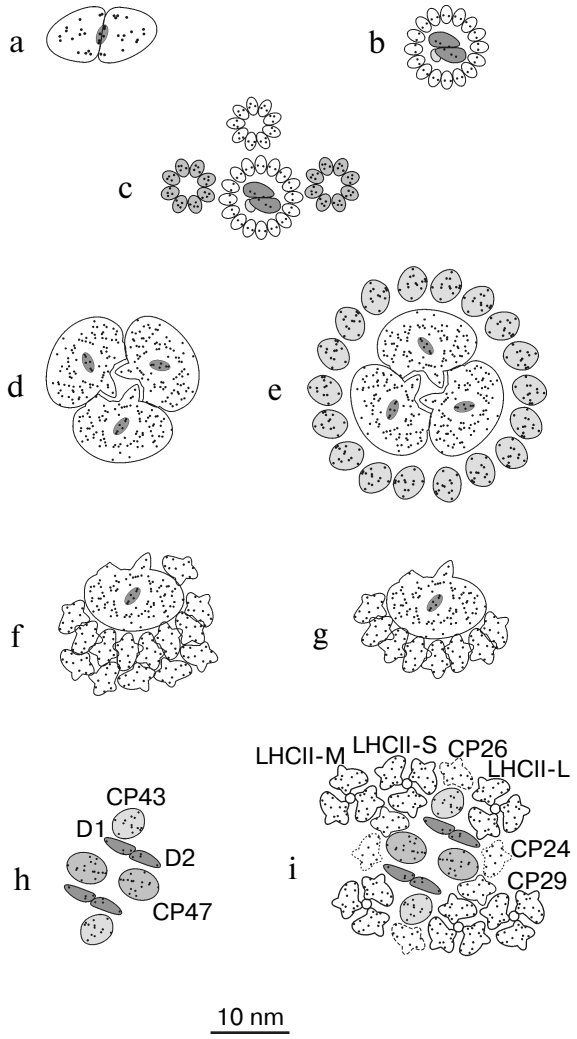

Fig. 1. Photosynthetic units with intramembrane pigment–protein complexes. Top view projections of the complexes in the membrane plane are shown according to known data of X-ray crystal analysis and electron microscopy of isolated particles or by homology with related complexes (see appropriate references in text). Points mark positions of Mg atoms (or their substitutes) in individual chlorin molecules. The reaction center domains are colored gray. Contours of the complexes are proportional to the protein molecule sizes (bar is 10 nm). Reconstructions of probable organization of PSUs: a) $(PshA)_2$ core complex from heliobacteria; b) L/M–LH1 core complex from the purple bacterium *Rhodospirillum rubrum*; c) supercomplex L/M–LH1–$(LH2_{B800})_2$–$LH2_{B800\text{-}850}$ from the purple bacterium *Rhodopseudomonas palustris* grown under low light; d) prokaryotic PSI (trimer of core complex, which contains PsaA/PsaB and small subunits); e) PSI from *Prochlorococcus* sp. (trimer of core and 18 Pcb); f) PSI from the green alga *Chlamydomonas reinhardtii* (core and LHCI oligomer, which consists of 14 Lhca subunits); g) PSI from higher plants (core and LHCI oligomer, which consists of 8 Lhca subunits); h) prokaryotic PSII (dimer of core, which consists of D1/D2/CP43/CP47 subunits); i) α-unit of PSII from higher plants (dimer of a supercomplex, which contains core, CP24, CP26, CP29, and three trimers of LHCII).

a/*b*, *a*/*c*) and extramembrane (chlorosomes, phycobilisomes) complexes.

The first group includes pigments–protein complexes whose structure and mode of interaction with pigments are highly similar to the RC proteins. Usually they consist of subunits, which are dimers or trimers, sometimes monomers, of polypeptides spanning one or several times across the photosynthetic membrane. (Bacterio)chlorophylls are noncovalently bound to protein by ligands of Mg^{2+}, mainly via His residues.

In photosynthetic units of purple bacteria (Fig. 1, b and c), the role of proximal "core" antenna of RC (L/M) complex is carried out by a surrounding ring of LH1. In many purple bacteria, the latter is termed B875 according to its Q_y absorption band, but in some BChl *a*-containing species the band of LH1 is at 909, 918, or 963 nm [22], whereas in BChl *b*-containing species that is at 1020 nm. Peripheral antenna also consists of LH2 ring complexes [29], which have several variants with different spectral properties and pigment composition (B800-850, B800-820, or B800), depending on species and growth conditions [30-32]. Application of biochemical and molecular biological methods in combination with site directed mutagenesis has established that the LH1 and LH2 complexes are designed according to the same modular principle [33, 34]. Each complex is an oligomer of a basic subunit, which consists of a pair of small hydrophobic polypeptides (α and β) binding 1-2 BChls. Novoderezhkin and Razjivin were the first to predict and experimentally prove [35-38] that the antenna complexes of purple bacteria are arranged in circular structures of BChl molecules with delocalized excitons.

Electron diffraction studies on LH1 crystals from *Rhodospirillum rubrum* have shown that this complex is a 16-meric ring [39] binding 32 BChls. Recently, scanning of native membranes of *Rhodopseudomonas viridis* by atomic force microscopy directly showed that the L- and M-subunits of RC are surrounded by a closed ellipsoid of 16 subunits of LH1 and contact with the latter at the short ellipsis axis. Thus the structural data well correspond to the model of a proximal antenna, which consists of at least 16-meric LH1 ring complex for the complete surrounding of RC of purple bacteria.

Nevertheless, this model collides with some data. The ratio RC/LH1 in cells of purple bacteria is considered to be fixed. However, functional and biochemical estimations of the PSU antenna size in several species, containing only RC/LH1 complexes, showed from 24 to 30 BChl molecules [22, 41, 42]. The apparent contradiction with data on a 16-meric structure of the LH1 ring can be explained by a loss of BChl in some subunits or by the presence in cells of the complexes with non-closed rings. Particularly, findings have been reported [43, 44] that indicate the possible existence in $LH2^-$ mutant of *Rhodobacter sphaeroides* of non-closed rings of 12 subunits of LH1, and formation of supercomplexes of two RC complexes surrounded by these structures in association with one complex of cytochromes bc_1. Another model suggests the existence of enclosed rings of the LH1–RC core complexes but being also connected in pairs through cytochrome bc_1 [45]. It is assumed that such structure of LH1–RC can depend on the presence of a protein PufX, which is inserted into the LH1 ring and provides a gate for the diffusion transfer of ubiquinone [29, 46]. A question however remains open about universality of such PSU organization in purple bacteria, as the protein PufX was not found in *Rhodospirillum rubrum* and *Rhodopseudomonas viridis*. Moreover, some authors challenge the validity of the hypothesis about the existence of the RC–cyt bc_1 supercomplexes [47].

At present, there are X-ray structural data for a few crystal complexes of peripheral antenna LH2 from purple bacteria, B800-850 [48] and B800-820 [31] of *Rps. acidophila* and B800-850 of *Rsp. molischianum* [49]. LH2 complexes are usually nanomers of α/β subunits forming two rings of 27 BChls (9 molecules B800 and 18 molecules B850) [29, 48]. However, in some species of purple bacteria, LH2 is formed by an octamer of subunits binding 24 BChls [30, 32, 49], and the complex B800 from the low light-grown cells of *Rhodopseudomonas palustris* contains 32 BChl *a*, as each of the two polypeptides bind two pigment molecules [32]. Synthesis of the complementary light harvesting antenna LH2 in different species of purple bacteria depends on the growth light conditions and results in increase in the PSU sizes by at least 2-4 times [41]. In low light-grown cells of *Rhodopseudomonas palustris*, nanomeric B800-850 complexes are mainly replaced by octameric B800 complexes [32] (they are sometimes termed LH3). This can lead to heterogeneity of the PSU population in the species with respect to composition of the antenna complexes. Figure 1c shows a possible model of PSU structure in *Rhodopseudomonas palustris* based on data from [32, 41]. The maximal effective sizes of PSUs of purple bacteria, apparently, do not exceed 200 BChl molecules, when the LH2/LH1 ratio in cells reaches 6, which corresponds to the complete surrounding of LH1/RC by the peripheral antenna complexes.

Giant extramembrane light harvesting complexes of chlorosomes serve as complementary peripheral antenna for type-I RC of green sulfur bacteria and type-II RC of green filamentous bacteria [50-53]. Chlorosomes are located on the inner surface of the cytoplasmic membrane as ellipsoid bodies with dimensions of 100-200 × 30-100 × 15-30 nm depending on species and growth conditions [54, 55]. A monolayer protein-lipid envelope of chlorosomes encloses 10-30 cylindrical subunits, which are longitudinally ordered in 1-3 layers and have a diameter of 5.2 nm in green filamentous bacteria and 10 nm in green sulfur bacteria [56]. These water-soluble subunits consist of self-assembled pigment aggregates of BChl *c*, *d*, or *e* and their mixtures with absorption maxi-

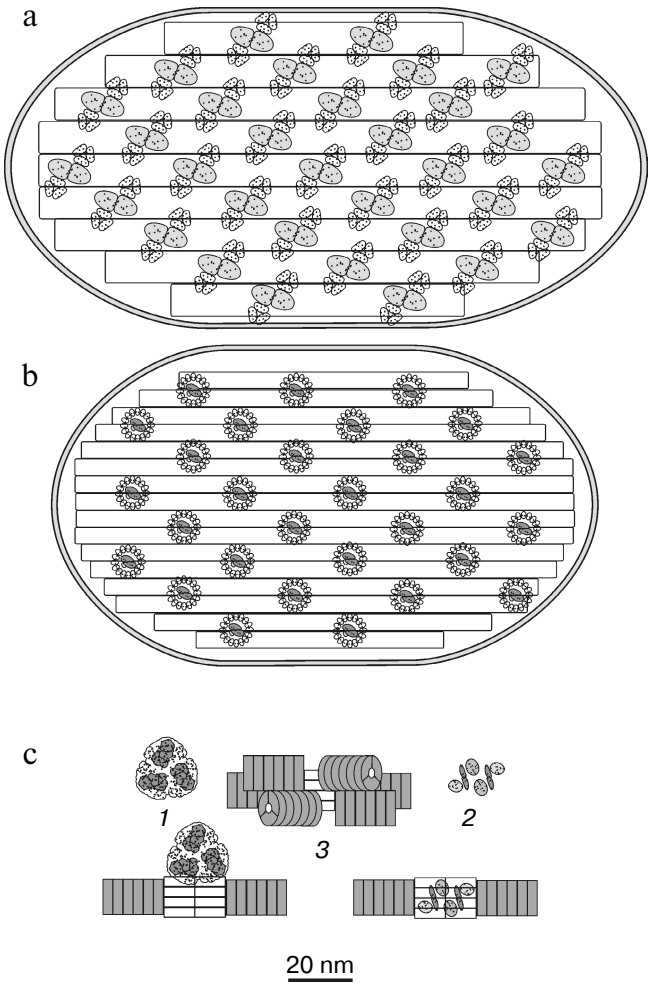

Fig. 2. Reconstruction of probable organization of photosynthetic units with extramembrane light harvesting complexes. Projections of sections of these complexes at the level of lower rows of pigment-containing cylindrical subunits are imposed on projections of intramembrane complexes and shown from top view in the membrane plane. Points mark positions of Mg atoms (or their substitutes) in individual chlorin molecules of intramembrane pigment–protein complexes. Images of all complexes are on the same scale (the bar is 20 nm): a) association of chlorosome with the complexes of $(PscA)_2$ core and two FMO trimers in green sulfur bacteria; b) association of chlorosome with complexes of L/M–LH808-866 in green filamentous bacteria; c) association of phycobilisomes (*3*) (above, general view of the whole complex; below, only two core cylinders connected to membrane and two peripheral cylinders) with PSI trimers (*1*) and PSII dimers (*2*) in cyanobacteria. The loose association of PSI with phycobilisomes is caused by the presence of protruding extrinsic subunits PsaC/PsaD/PsaE (gray areas).

mum at 720-760 nm. In contrast to all others light harvesting complexes, these pigment aggregates do not contain protein and, depending on the diameter of subunits, are organized in bi- or mono-layer tubular macrocycles of chains of BChl molecules [57, 58]. The structure of BChl aggregates in the cylindrical subunits is still debated. In the opinion of some researchers, analysis of spectroscopic data indicates in favor of the model of a highly dense packing of pigments [57, 58], but studies of other authors give prove to the model of a low density packing of the cylindrical aggregates consisting of blocks which include six chains of 4-8 BChl molecules [46, 59, 60]. Depending on the accepted model, each chlorosome can contain from 3000 up to 200,000 molecules of BChl *c*, *d*, or *e* [18, 53, 59, 60]. In chlorosomes containing a mixture of BChl *c*+*d*, each pigment forms separate cylindrical subunits, and the BChl *d*-containing rods are arranged distally with respect to the baseplate of the chlorosome on the surface of the cytoplasmic membrane [61].

The baseplate of the chlorosome envelope is the site of a minor pigment BChl *a* with absorption maximum at 795 nm (a typical molar ratio BChl *c*/BChl *a*-795 is ~25 : 1 in green filamentous bacteria and (300-500) : 1 in green sulfur bacteria). There are findings [62, 63] that this BChl *a* is bound with a protein CsmA of the lipid envelope of chlorosome in equimolar ratio. It is assumed that the basal minor BChl *a*-795 antenna provides transfer of excitation energy from chlorosome to the intramembrane RC complexes. In green filamentous bacteria, this energy transfer is mediated through intramembrane B808-866 complexes, which surround type-II RC complexes, are structurally similar to LH1 and LH2, and probably represent oligomers of αβ-subunits binding 36-48 BChl *a* [53, 64]. In green sulfur bacteria, the chlorosome baseplate with basal antenna towers above on the Fenna–Mathews–Olson (FMO) protein complexes containing BChl *a* with absorption maximum at 808 nm. Two trimers of the FMO protein subunits, each binding seven BChl *a* molecules (in total 42 BChl *a*), are associated on the cytoplasmic side of the membrane with a type-I RC core complex, containing 16 molecules BChl *a* and four Chl a_{PD} [18, 65]. Each chlorosome serves as a collective light-harvesting antenna of tens of RCs (Fig. 2, a and b). In green filamentous bacteria, the chlorosome binds ~20 RCs, and each PSU of 52 BChl *a* (RC + B808-866) shares on average ~800 extra BChl *c* [53]. From reported data about pigment content in cells of the green sulfur bacterium *Chlorobium tepidum* (the weight ratio of BChl *c*/BChl *a*/Chl a_{PD} = 1760 : 44 : 4 [66]) it can be calculated that each PSU of 58 BChl *a* (6 FMO + RC core, containing also four Chl a_{PD} [18]) share on average up to ~2000 BChl *c*. Taking into account geometrical sizes, the chlorosome of green sulfur bacteria can serve about 30-40 RC (Fig. 2a).

PHOTOSYNTHETIC UNITS OF OXYPHOTOTROPHS

Dominating in the Earth's biosphere, O_2-evolving photosynthetic organisms are characterized by a significant genetic diversity including ten divisions in aqueous

ecosystems and six divisions of terrestrial plants. This diversity is also mirrored in the structure of photosynthetic apparatus, mainly, the light harvesting antenna complexes of PSUs. The most conservative part of each PSU is the core complexes of PSI and PSII. X-Ray crystal analysis of these complexes from the thermophilic cyanobacterium *Synechococcus elongatus* shows that each monomer of PSI trimer contains 96 Chl *a* (85 Chl in PsaA/PsaB and 11 Chl in small subunits PsaJ, K, L, M, X) [67] (Fig. 1d), and each monomer of PSII dimer contains 32 Chl *a* + 2 Phe *a* (6 Chl + 2 Phe in D1/D2, 14 Chl in CP47, and 12 Chl in CP43) [68]. Subsequent, more detailed analysis of the crystallographic data [69] revealed 16 Chl in CP47 and 13 Chl in CP43 (Fig. 1h), which confirms a previous functional estimation of 37 chlorin molecules in PSII core [70]. On the basis of information about location and relative orientation of all pigment molecules in the crystals of PSI and PSII complexes, models of the main pathways of excitation energy transfer from antennal chlorophyll to the reaction centers have been developed [69, 71].

For a long time it was generally accepted that Chl *a* is a sole light harvesting pigment of the core complexes of the two photosystems [72, 73]. However, it has been recently found that one of the main biomass photoproducers, nanoplanktonic prokaryotes of the genus *Prochlorococcus*, contain divinyl-Chl a_2 instead of Chl *a* in the cores of both photosystems [74, 75], and PSI contains up to 20% of Chl b_2 [76]. A recently discovered ascidian symbiont, the prokaryote *Acaryochlorois marina*, contains Chl *d* as the major light harvesting pigment of PSI and PSII [77-81]. Moreover, the gene of Chl *a* oxygenase [82] involved in Chl *b* synthesis in higher plants was expressed in the cells of the cyanobacterium *Synechocystis* 6803 [83-85] resulting in replacement of a significant part of Chl *a* by Chl *b* in PSI and PSII complexes, and in the PSII RC, Phe *a* was also replaced by Phe *b* [84, 85]. It was reported [83] that isolated PSI core complexes from the green alga *Chlamydomonas reinhardtii* can normally contain ~4% Chl *b*, but this requires additional verification. Nevertheless, all these findings are evidence of a low specificity of some Chl-binding sites in the core antenna complexes of the two photosystems.

It is noteworthy that there are at least 11 sites of Chl binding on several small transmembrane subunits, which are intimately associated with the PsaA/PsaB dimer of PSI of prokaryotes and eukaryotes [67, 86-89]. Eukaryotes have two additional subunits PsaH and PsaG, which presumably can bind Chl *a* [89]. The functional significance of the light harvesting characteristics of these subunits remains obscure. Probably, some of these subunits mediate transfer of excitation energy between monomers of PSI trimers of prokaryotes [90], as it is particularly known about a structural role of the protein PsaL in formation of these trimers. Similarly, in eukaryotes, the cluster of PsaH/L subunits can be a specific site of connection for a phospho-LHCII [91, 92], while PsaJ/F, PsaG, and PsaK mediate transfer of excitation energy from different peripheral LHCI subcomplexes [89] to monomeric PSI core.

Cyanobacteria and red algae employ as a light harvesting antenna phycobilisomes, giant extramembrane assemblies on the stromal side of thylakoids [93-95]. The main part of the phycobilisomes is formed by water-soluble proteins: phycoerythrins (absorption maxima at 495 and/or 565-575 nm), phycoerythrocyanin (575 nm), phycocyanins (615-640 nm), and allophycocyanins (650-655 nm). These proteins bind chromophores of covalently linked linear tetrapyrroles, phycocyanobilin, phycoerythrobilin, phycourobilin, and phycobiliviolin. Electron microscopy and X-ray analysis data [94, 96-99] show that each phycobiliprotein of cyanobacteria and red algae consists of toroidal $(\alpha\beta)_3$-subunits formed by trimers of α- and β-polypeptides. Face-to-face pairs of the trimers form hexamers of the same phycobiliprotein, which are able to stack in cylindrical aggregates of the same or mixed composition by means of the protein-specific linker polypeptides. Phycobilisomes are formed by these rod elements, which are designed as two substructures: 1) the core of a pyramidal bundle of three (two in the base + one on the top) rods of diameter of 9.5 nm, which consist of four trimers of allophycocyanin, each of ~3.5 nm thickness, and are situated on the membrane surface (in some species, the core consists of two basal rods or five rods including three on the top); 2) a fan of peripheral rods (typically 6, but sometimes 8 or 10), which are radially divergent from the core, have diameter of 11 nm and consist of 2-4 hexamers either of phycocyanin or the combination of phycocyanin and phycoerythrin (proximal and distal disks relative to the core, respectively). As αβ-monomers of different bilins contain 2-6 chromophores, their total number in cyanobacterial phycobilisomes varies within 250-1400 and in phycobilisomes of red algae can reach ~2500 [73, 94]. There are several morphological types of phycobilisomes, of which the most abundant are hemidiscoidal (diameter of 50-80 nm) and hemiellipsoidal (50-60 × 30-40 × 20-40 nm), which are mainly distinguished in that in the former the peripheral cylinders interact with the core separately, while in the latter they are arranged as close bundles. All known models of phycobilisome structure remain simplified and have geometrical problems in alignment of peripheral rods around the core rods of a smaller diameter. This problem is at least partly resolved by the discovery in the cyanobacterium *Thermosynechococcus vulcanus* of a minor fraction of concave $(\alpha\beta)_3$-subunits of phycocyanin-614, which can form contacts between the two substructures of phycobilisomes [100].

Efficient transfer of excitation energy within the peripheral rods occurs mainly toward the core due to ordered spatial distribution of the subunits with a long-wavelength shift of their absorption maxima from distal to

proximal hexamers [93, 94], as well as due to optimal orientation of chromophores within the hexamers [98]. The allophycocyanin core contains two of the long-wavelength chromophores, terminal energy emitters, which interact with intramembrane Chl complexes. One of these chromophores, allophycocyanin-B, is located in the core linker polypeptide ApcE, operating as an anchor of the phycobilisome for its association with thylakoid membrane and/or PSII.

For a long time it was considered, that phycobilisomes are mainly, if not exclusively, antenna complexes of PSII [93, 94]. For explanation of the presence of the phycobilisome bands in PSI spectra, a model of spillover of excitation energy from PSII on contacting PSI has been suggested [101]. However, subsequent studies clearly showed the feasibility of effective direct transfer of excitation energy from phycobilisomes to PSI without any mediation of PSII [102-107]. The model of a random statistical interaction of phycobilisomes with each of two photosystems (Fig. 2c) is supported by the findings of a fast lateral diffusion of these giant supramolecular complexes along a surface of the thylakoid membrane [108, 109]. Every single phycobilisome is able to interact with the PSII core dimer [94, 95, 107] (in red algae, probably, with PSII tetramer [110]) or/and with two monomers or one trimer of PSI [107]. It should be noted that the molecular regulatory mechanism of interaction of phycobilisomes with two photosystems remains unknown [95, 111].

Phycobiliproteins also act as an extramembrane light-harvesting antenna without formation of phycobilisomes in species from three different groups of oxyphototrophs, namely Chl *b*-containing prokaryote *Prochlorococcus marinus*, Chl *d*-containing prokaryote *Acaryochloris marina*, and cryptophyte algae.

It was found that the deep-sea species *Prochlorococcus marinus* CCMP 1375 contains α- and β-subunits of a novel type of phycoerythrin [112, 113], which bind one and four chromophores, respectively, predominantly phycourobilin (absorption maximum at 495 nm). These biliproteins are associated with thylakoids [113] and apparently transfer excitation energy to Chl b_2 [114], but their content is low and their exact location is unknown. Phycobiliproteins of *Acaryochloris marina* form rods, which contain up to four hexamers of αβ-subunits of phycocyanin and include allophycocyanin as a minor terminal acceptor of energy [115]. Electron microscopic studies [116] have revealed that the phycobiliproteins form large clusters between thylakoid grana in the cell periphery, and action spectra of functional activity [81] indicate their participation in excitation energy transfer to both PSII and PSI.

Cryptophyte algae contain phycobiliproteins inside the lumenal space of thylakoids [93, 94], and each species contains only one of their type, either phycoerythrin-545 or phycocyanin-645. β-Subunits of the phycobiliproteins have a high degree of homology with the β-subunits of phycoerythrin from red algae and cyanobacteria and bind three modified bilin chromophores, whereas the shorter α-subunits are unrelated to other proteins and carry a single chromophore, mesobiliverdin or 15,16-dihydrobiliverdin [117, 118]. According to crystallographic data [118], the cryptophyte phycobiliproteins have the $(\alpha_1\beta)(\alpha_2\beta)$-heteromeric structure and are capable of excitation energy transfer to intramembrane light-harvesting complexes LHC *a/c*. However, the question about pathways of energy transfer to photosystems with participation of the phycobiliproteins in various species of cryptomonads still remains open.

It was long considered that prokaryotic oxyphototrophs have no intramembrane peripheral antenna complexes, unlike eukaryotic phototrophs. In the 1980s, this opinion was disproved by the findings of adaptive changes in cyanobacteria under iron-deficient conditions and by the discovery of prochlorophytes. In cyanobacteria, deficiency of Fe ions in the medium induces expression of the gene *isiA* encoding synthesis of a protein CP43′ with a high degree of homology to the PSII core protein CP43 [119, 120]. These proteins have a similar sequence forming six transmembrane helices and the main difference is that IsiA lacks a large hydrophilic loop on the lumenal side of thylakoids. Gulyaev et al. [121-123] were the first to report findings that implied effective transfer of excitation energy from IsiA complexes on both PSI and PSII. However, the direct measurements of the PSII function sizes by the light saturation curves of Chl fluorescence upon short light flashes [124] did not reveal a connection of IsiA with PSII. At the same time, electron microscopy studies [120, 125, 126] have shown that the Fe-deficient cyanobacteria contain supercomplexes of a ring of 18 IsiA around the PSI trimers, increasing the effective antenna sizes by 75%.

The discovery of light harvesting Chl *a/b* complexes in species of unrelated taxa of *Prochloron*, *Prochlorothrix*, and *Prochlorococcus* [74, 75] was at first misinterpreted as a sign of a missing intermediate branch in the evolution of phototrophs via endosymbiosis of a cyanobacterial ancestor with a eukaryote cell. However, it was soon found that the genes *pcb* encoding these proteins are unrelated with a superfamily of the genes *lhc* encoding the antenna LHC proteins of eukaryotes, but the Pcb proteins belong to a family related to IsiA, CP43, and CP47 [127-129]. Similar to IsiA–PSI supercomplexes in Fe-deficient cyanobacteria, it was recently shown that *Prochlorococcus* SS120 contains analogous Pcb–PSI supercomplexes of a ring of 18 Pcb (Chl *a*/Chl *b* ~ 1) around of PSI trimers [130] (Fig. 1e). It still remains obscure whether there are similar structures in *Prochloron* and *Prochlorothrix*, as the number of *pcb* genes considerably differs in various species, especially *Prochlorococcus* [128, 129]. Pigment composition of the Pcb complexes in different species of prochlorophytes also considerably differs in both chemi-

cal nature and the molar ratio of different Chl [74, 75]. In *Prochlorococcus*, the Pcb complexes contain divinyl-forms of Chl a_2 and Chl b_2, while in *Prochloron* and *Prochlorothrix* they contain usual monovinyl-forms of Chl *a* and Chl *b*. In different species of *Prochloron*, the antenna has been found to include a significant amount (3-15%) of divinyl-protochlorophyllide *a*, structurally related to Chl c_2 [131].

It was recently reported [132] that Chl *d*-containing prokaryote *Acaryochloris marina* also contains an intramembrane light harvesting Chl *d*/*a*–protein complex, which can be similar to the Pcb proteins. Collectively, these findings indicate an independent evolution of the biosynthesis pathways of apoproteins and pigments from the photosynthetic apparatus [28].

In terrestrial plants and green algae, the peripheral antenna of PSI and PSII consists of at least 10 different Chl *a*/*b*-proteins, which are encoded by a family of *lhc* genes from the nuclear genome, and, together with associated carotenoids, form seven separate pigment–protein complexes [72, 133]. This provides a considerable heterogeneity of the PSU sizes of two photosystems in different domains of thylakoid membranes [134].

LHCI complex of higher plants consists of four proteins Lhca1-4, which form subcomplexes LHCI-680A (Lhca3), LHCI-680B (Lhca2), and LHCI-730 (heterodimer Lhca1/Lhca4). According to the electron microscopy data [135], LHCI from higher plants is aligned only on one side of the monomeric PSI core complex, viz. on the same side where IsiA and Pcb complexes in the trimer from prokaryotes are located (Fig. 1g). On the basis of findings about chemical cross-linkage between neighboring subunits, a model of LHCI–PSI was proposed [89], in which two Lhca1/Lhca4 heterodimers contact with the PSI core near the interface of major subunits PsaA/B, where subunits PsaJ/F are also located, while homo- or heterodimers of Lhca2 and Lhca3 are associated with the sites of PsaG and PsaK. Electron microscopy image analysis of LHCI–PSI complexes from the green alga *Chlamydomonas reinhardtii* [92] has revealed the presence of ~6 extra subunits of LHCI, 3-4 of which form the second external layer, and 2-3 are asymmetrically joined from one side to subunit PsaH (Fig. 1f).

Available data about Chl content (6-12) and Chl *a*/*b* ratio (1.5-3) in Lhca1-4 and LHCI are contradictory [72, 89, 133], which may reflect a variable pigment/protein stoichiometry and a low specificity of the Chl binding sites. In this connection, it should be noted that Chl *b*-deficient mutants of plants (defective in the gene of Chl *a*-oxygenase) retain normal amounts of Lhca1-3 antenna protein, but do not synthesize Lhca4 [136, 137]. Reconstruction experiments with Lhca1/Lhca4 heterodimers [138] indicate a requirement for Chl *b* binding to specific sites on these subunits for their normal heterodimerization with appearance of a typical long-wavelength 730 nm fluorescence of the complex at 77K. Taking into account the number of 10 Chl molecules in every Lhca subunit [139], the LHCI antenna sizes of higher plants and *Chlamydomonas reinhardtii* can be 80 and ~140 Chl *a*+*b*, respectively. Functional measurements indicate that the effective LHCI antenna sizes in intact cells of the alga are still larger (~170 Chl) [5].

Chl *a*/*b*-proteins of PSII are coded by six genes *lhcb1-6* and form a hierarchical composite structure of its PSU [72, 133] (Fig. 1i). Complexes CP29 (Lhcb4), CP26 (Lhcb5), and CP24 (Lhcb6) constitute the proximal peripheral antenna of PSII core dimers [140], at which subunit CP29 closely contacts with D1 and CP47, while CP26 is associated with CP43 [141]. The proximal antenna also includes one LHCII trimeric complex, probably, $(Lhcb1)_2$/Lhcb3 [134], which is named S-LHCII [140, 142] as it strongly associated with subunits CP43, CP29, and CP26 of PSII dimer complexes. PSII supercomplexes can additionally include at specific sites trimers M-LHCII and L-LHCII [140] (moderately and loosely associated, respectively), which probably belong to the most abundant type Lhcb1/Lhcb2 [134]. On the basis of electron microscopy analysis of the PSII submembrane particles [140], the existence of tetrameric megacomplexes $(M\text{-}LHCII)_4$–$(S\text{-}LHCII)_4$–$(PSII\ core)_4$ in the grana domain of thylakoids is assumed to be plausible.

In estimation of the peripheral antenna size of PSII complexes, it is necessary to proceed from stoichiometric ratios of one monomer of CP29, CP26, and CP24 complexes and 1-4 LHCII trimers per PSII core monomer. At present, the detailed X-ray crystal structure is only known for LHCII complexes [143], which revealed 12 Chl binding sites (seven Chl *a* and five Chl *b*) per monomer. However, mild extraction methods gave isolated LHCII complexes containing a 13th molecule of loosely bound Chl *a* [144]. The other Chl *a*/*b*-complexes of PSII probably bind a smaller number of Chl molecules, from 8 to 10 [145]. Therefore, 1-4 LHCII (39-156 Chl) + CP29/CP26/CP24 (~28 Chl) can include 65-180 Chl. Studies of Chl *b*-deficient mutants of green plants and algae have shown that stability of all six Lhcb proteins depends on synthesis of the pigment [146], and Lhcb6 > Lhcb1 > Lhcb2, Lhcb3, Lhcb4 > Lhcb5 [136, 137]. A model of stepwise assembly of LHC in the chloroplast envelope is suggested [147], which postulates a particular role of Chl *b* and Chl *a*-oxygenase in the proper folding and stabilization of the polypeptide chain.

One member of the LHC protein family of PSII is CP22 (PsbS), whose precise location remains unknown, but it is probably close to PSII core complex. There are findings [148] on a key photoprotective role of this protein in ΔpH- and xanthophyll-dependent quenching of excitation (concerning the mechanism of this regulation see [149, 150]). Unlike the closely related Lhcb1-6 proteins, which have three transmembrane α-helices [143], the PsbS protein has four helices spanning the thylakoid

membrane. Helices I and III of PsbS and the Lhc family are similar, while helices II and IV of PsbS are similar to helix II of Lhc proteins. This implies that Lhc proteins descended from an ancestor similar to PsbS, which in turn has originated by duplication of a gene coding a two-helical protein [151]. Cyanobacteria possess the gene *hliA* coding a one-helix protein HLIP, whose synthesis is induced by stress caused by high intensities of light [152], and which has similarities to helices I and III of PsbS. Neither the PsbS nor HLIP proteins bind Chl, which supports a hypothesis about primary photoprotective instead of light harvesting functions of ancestors of the Lhc protein family (including PsbS) in evolution of oxyphototrophs [153, 154]. Similarly, in green plants and algae, stress upon high intensities of light, as well as illumination of etiolated seedlings induce rapid synthesis of a protein ELIP [155-157], which has three transmembrane α-helices with a high degree of homology to Chl *a/b*-proteins [153, 154], but binds mainly carotenoids (lutein) and Chl *a* in molar ratio of 2 : 1 (in contrast to the ratio of 1 : (3-4) in Lhc proteins).

The restricted volume of this brief review does not allow dwelling on dynamic aspects of the relationships between antenna complexes of the two photosystems and on their heterogeneity caused by segregation in different regions of thylakoid membranes [12, 70, 158]. Also, regulatory mechanisms of distribution of excitation energy between PSII and PSI with participation of cascade reactions of protein phosphorylation and lateral displacement of a mobile LHCII fraction along membrane [159] are beyond the scope of this review.

The photosynthetic apparatus of red algae has features of an intermediate between cyanobacteria and green plants. On one hand, it includes extramembrane light harvesting complexes of phycobilisomes and, on the other hand, contains an intramembrane Chl *a*–protein complex, which is functionally connected with PSI and is coded by nuclear genes *lhcaR1* and *lhcaR2* [160]. The LHC *a/a* proteins of red algae belong to the same family as LHC *a/b* and LHC *a/c* proteins, and contain eight common conservative sites of Chl *a* binding, as well as four zeaxanthin molecules, which are specific to these complexes but do not participate in transfer of excitation energy [161].

A combined group of chromophytes includes various classes of algae containing intramembrane light harvesting complexes of fucoxanthin–LHC *a/c*, which are characterized by a high molar ratio of carotenoids/Chl (~1 : 1) and wide ranges of the ratio of Chl *a/c* (from 1 up to 7) [72]. Fucoxanthin effectively transfers energy to Chl, and there are no biochemical differences between the Lhcf antenna proteins, associated with PSI and PSII [162]. In the prasinophycean alga *Mantoniella squamata*, the major light harvesting complex, prasinoxanthin–LHC *a/b/c*, has the ratio of these three Chl species ~9 : 6 : 1, and is not selective for interaction with PSI and PSII as well [163].

Regarding diversity of the structure of peripheral light harvesting antenna, dinoflagellate algae are unique possessing both the intramembrane peridinin–LHC *a/c* complexes related to other LHCs [164] and a unique water-soluble peridinin–Chl *a*-protein that has no close relationship to the latter. This protein belongs to a few antenna complexes with known crystallographic structure [165]. Each subunit of a trimer of the water-soluble protein binds eight peridinin molecules and two Chl *a*, providing effective intermolecular transfer of excitation energy [166, 167]. Thus, it is the sole known antenna complex whose light-harvesting function is mainly performed by carotenoids. It is suggested that aggregates of the water-soluble peridinin–Chl *a*-protein form an extramembrane antenna in dinoflagellates [73], but its relationships with the intramembrane complexes remain unknown.

In vitro reconstruction experiments on binding of pigment extracts from various species of algae with a recombinant apoprotein LhcaR1 from the red alga *Porphyridium cruentum* [161] have shown a complete functional interchangeability of Chl *a*, *b*, and *c* in the eight conservative sites of Chl binding on the three α-helices of polypeptide chain. The same interchangeability in proportions characteristic for the relevant native LHC was observed for carotenoids zeaxanthin, lutein, fucoxanthin, and peridinin, which implies the presence of many nonspecific binding sites of these pigments in the protein complex. These findings are convincing evidence of a "molecular opportunism" (using a figurative expression from [28]) in the evolution of the photosynthetic light harvesting systems and of relative independence of evolution of the pigments and proteins.

ADAPTATION OF PHOTOTROPHS TO NATURAL LIGHT CONDITIONS

The source of light energy for photosynthesis is solar radiation (the solar spectrum is presented on the web-site http://mesola.obspm.fr/solar_spect.), which is characterized by a significant variation in spectral composition and photon flux rate depending on many factors [168, 169]. The sunlight composition especially strongly changes passing through the water column (Fig. 3a). Pure water attenuates mainly the infrared spectral part of the photon flux [170], and calculations show that there is virtually no light >750 nm at depths >1 m, while at depths more than 10 and 100 m this threshold is shifted to 600 and 550 nm, respectively. The short-wavelength threshold of the spectral region of light transmission by pure water is also narrowed with depth, but this is especially sensitive to the scattering of energy by impurities in water, such as plankton cells and mineral particles [171]. Cells of photosynthetic organisms also attenuate and change the composition of transmitted sunlight according to their

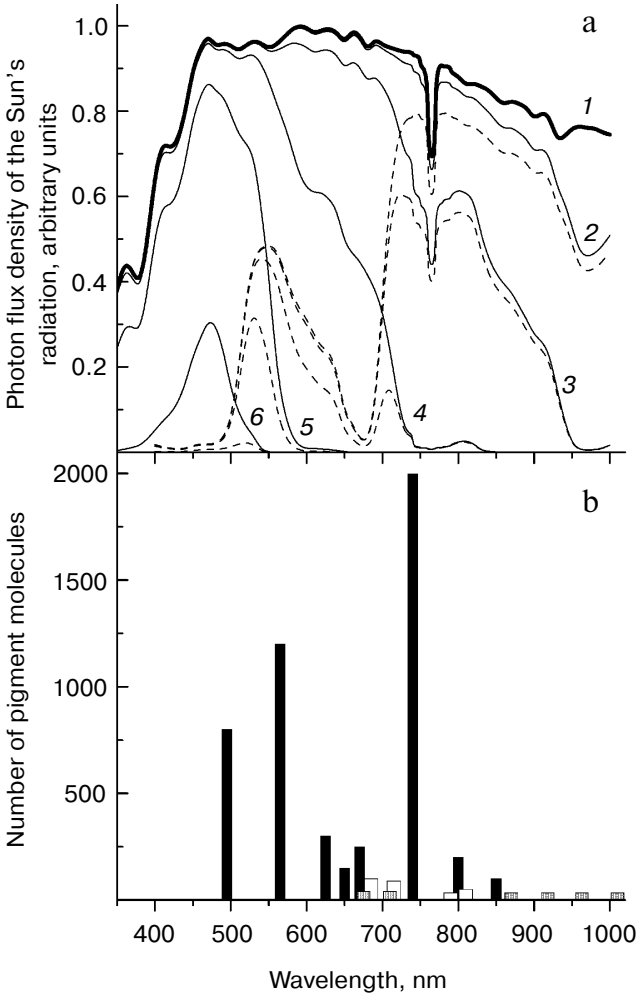

Fig. 3. Relationship between environmental light conditions and the pigment composition of photosynthetic units of various groups of phototrophic organisms. a) Spectral dependence of photon flux density of the Sun's radiation (latitude 90°) at the Earth's surface under dry and pure atmosphere (*1*), and on the pure water depth of 1 cm (*2*), 10 cm (*3*), 1 m (*4*), 10 m (*5*), and 100 m (*6*). The dashed lines show attenuation of this radiation by a suspension of *Chlorella*-like green alga with the absorbance of a column of 10 cells. b) Distribution of pigment–protein complexes of phototrophic organisms by the position of a long-wavelength maximum of absorbance and by pigment content per RC in a separate PSUs. White columns: PSI core complex (Chl *a* maximum at 680 nm), PSI from *Acaryochloris marina* (Chl *d*-710), RCs from heliobacteria (BChl *g*-790), and green sulfur bacteria (BChl *a*-810). Gray columns: PSII core complex (Chl *a*-675), PSII from *Acaryochloris marina* (Chl *d*-705 nm), LH1-RC from purple bacteria (BChl *a*-880, BChl *a*-918, BChl *a*-963, BChl *b*-1010). Black columns (maximal number of pigment molecules per RC): R-phycoerythrin-containing phycobilisomes from red algae (495 and 565 nm), C-phycocyanin-containing phycobilisomes from cyanobacteria (625 nm), LHC *a*/*b* complexes from algae and higher plants (Chl *b*-650 and Chl *a*-670), chlorosomes of green sulfur and filamentous bacteria (BChl *a*-740), LH2 complexes from purple bacteria (BChl *a*-800, BChl *a*-850).

absorbance spectrum (Fig. 3a, dashed lines). In the terrestrial environment, the leaf canopy similarly influences transmitted light [169].

Figure 3b shows in a generalized form the above described (see preceding paragraphs and the table) optical parameters of the pigment–protein complexes that constitute PSUs of the main taxonomic groups of phototrophic organisms. Comparison of these parameters, namely, the size of antenna and position of its long-wavelength absorption maximum with composition of solar radiation in the different water depths (Fig. 3a) indicates a divergence of various groups during adaptation to the environmental light conditions. Basically, it is suggested that a natural stratification of aqueous phototrophic communities exists according to the depth of inhabitancy [93, 172]. Particularly, the zone of effective photosynthesis apparently does not exceed a few cm for BChl *b*-containing purple bacteria, several tens of cm for heliobacteria and BChl *a*-containing purple bacteria, and less than 2 m for chlorosome-containing green bacteria. The expansion of oxyphototrophs to water depths up to 100-200 m occurred due to synthesis of the phycoerythrin-containing phycobilisomes and the antenna complexes binding Chl *b* and/or carotenoids.

Thus, based on the data of Fig. 3, one can conclude that natural selection provided survival of the phototrophs with the best correspondence of the optical properties of their PSUs to the composition of solar radiation in their inhabitancy. In aqueous ecosystems, competition between photosynthetic organisms for light energy directed evolution of the peripheral antenna complexes of PSUs to capture accessible photons in the spectral regions of low light absorbance by competitors. These two factors favored high diversity of these complexes in aqueous oxyphototrophs in contrast to terrestrial plants. Core complexes of PSI and PSII in oxyphototrophs are more conservative, but the partial or complete substitution of Chl *a* in these complexes by Chl b_2 in *Prochlorococcus* [76] and by Chl *d* in *Acaryochloris* [79, 80] indicates that their composition can also change under the pressure of natural selection. Along with the phylogenetic light adaptation there are also more flexible ontogenetic mechanisms of tuning of PSU optical properties in response to light conditions. In some strains of purple bacteria, low light intensity induces synthesis of LH2 subunits with a short-wavelength shift of the main absorption band of Bchl *a* [32]. Some part of phycoerythrin-containing cyanobacteria develops a mechanism of chromatic adaptation [93, 94], which allows them to regulate spectral properties of phycobilisomes by means of changes of phycoerythrin/phycocyanin ratio.

A similar strategy of divergence by optical properties of pigments has been discovered in the widespread group of marine eubacteria, which contain several spectral variants adapted to different light conditions over the water depth, of proteorhodopsins [173, 174], related to a reti-

nal-containing protein bacteriorhodopsin from halophilic archaea [175]. These proteins operate as light-driven H^+-pumps across membranes, providing phototrophy without participation of PSU complexes.

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APPENDIX

After this review was written, evidences have come to light that subunits Pcb of the intramembrane Chl *a/b*-antenna in cells of Chl *b*-containing cyanobacteria *Prochloron didemni* (Bibby, T. S., Nield, J., Chen, M., Larkum, A. W. D., and Barber, J. (2003) *Proc. Natl. Acad. Sci. USA*, **100**, 9050-9054) and *Prochlorothrix hollandica* (Boichenko, V. A., Pinevich, A. V., and Stadnichuk, I. N., in preparation) form supercomplexes with PSII, contrary to *Prochlorococcus* sp., in which supercomplexes Pcb–PSI have been previously described [130]. Recently the first X-ray analysis of LHCI–PSI supercomplex from higher plants (Ben-Shem, A., Frolow, F., and Nelson, N. (2003) *Nature*, **426**, 630-635) has unexpectedly shown that there are only four LHCI subunits instead of eight (as in the reconstruction of Fig. 1). A similar supercomplex from the alga *Chlamydomonas* probably includes a larger number of the subunits (Kargul, J., Nield, J., and Barber, J. (2003) *J. Biol. Chem.*, **278**, 16135-16141). The latest studies of RC–LHI complexes from purple bacteria have revealed both new details of their structure and significant differences in various species. The complexes in *Rps. palustris* form incomplete circles of 15 subunits around one RC (Roszak et al. (2003) *Science*, **302**, 1969-1972), whereas open circles of such 12 subunits in *Rb. sphaeroides* surround RC dimers through the mediation of two subunits of protein PufX (Scheuring, S., et al. (2004) *J. Biol. Chem.*, **279**, 3620-3626).

REFERENCES

1. Gaffron, H., and Wohl, K. (1936) *Naturwissenschaften*, **24**, 81-90.
2. Emerson, R., and Arnold, W. (1932) *J. Gen. Physiol.*, **16**, 191-205.
3. Hill, R., and Bendall, F. (1960) *Nature*, **186**, 136-137.
4. Boichenko, V. A., and Litvin, F. F. (1986) *Doklady Akad. Nauk*, **286**, 733-737.
5. Boichenko, V. A., Ladygin, V. G., and Litvin, F. F. (1989) *Mol. Biol. (Moscow)*, **23**, 107-118.
6. Mauzerall, D., and Greenbaum, N. (1989) *Biochim. Biophys. Acta*, **974**, 119-140.
7. Bukhov, N. G., Chetverikov, A. G., Rozhkovskii, A. D., and Voskresenskaya, N. P. (1984) *Biofizika*, **29**, 289-293.
8. Bukhov, N. G., Rozhkovskii, A. D., Chetverikov, A. G., and Voskresenskaya, N. P. (1986) *Biofizika*, **31**, 99-104.
9. Zonneveld, C. (1997) *J. Theor. Biol.*, **186**, 381-388.
10. Andersson, B., and Anderson, J. M. (1980) *Biochim. Biophys. Acta*, **593**, 427-440.
11. Anderson, J. M., and Melis, A. (1983) *Proc. Natl. Acad. Sci. USA*, **80**, 745-749.
12. Melis, A. (1991) *Biochim. Biophys. Acta*, **1058**, 87-106.
13. Woese, C. R., Kandler, O., and Wheelis, M. L. (1990) *Proc. Natl. Acad. Sci. USA*, **87**, 4576-4579.
14. Blankenship, R. E. (1992) *Photosynth. Res.*, **33**, 91-111.
15. Baymann, F., Brugna, M., Mühlenhoff, U., and Nitschke, W. (2001) *Biochim. Biophys. Acta*, **1507**, 291-310.
16. Xiong, J., and Bauer, C. E. (2002) *Annu. Rev. Plant Physiol. Plant Mol. Biol.*, **53**, 503-521.
17. Schubert, W.-D., Klukas, O., Saenger, W., Witt, H. T., Fromme, P., and Krauss, N. (1998) *J. Mol. Biol.*, **280**, 297-314.
18. Neerken, S., and Amesz, J. (2001) *Biochim. Biophys. Acta*, **1507**, 278-290.
19. Hauska, G., Schoedl, T., Remigy, H., and Tsiotis, G. (2001) *Biochim. Biophys. Acta*, **1507**, 260-277.
20. Wakao, N., Yokoi, N., Isoyama, N., Hiraishi, A., Shimada, K., Kobayashi, M., Kise, H., Iwaki, M., Itoh, S., Takaichi, S., and Sakurai, Y. (1996) *Plant Cell Physiol.*, **37**, 889-893.
21. Mimuro, M., Kobayashi, M., Shimada, K., Uezono, K., and Nozawa, T. (2000) *Biochemistry*, **39**, 4020-4027.
22. Permentier, H. P., Neerken, S., Overmann, J., and Amesz, J. (2001) *Biochemistry*, **40**, 5573-5578.
23. Akiyama, M., Miyashita, H., Kise, H., Watanabe, T., Mimuro, M., Miyachi, S., and Kobayashi, M. (2002) *Photosynth. Res.*, **74**, 97-107.
24. Fyfe, P. K., Jones, M. R., and Heathcote, P. (2002) *FEBS Lett.*, **530**, 117-123.
25. Blankenship, R. E., and Hartman, H. (1998) *Trends Biochem. Sci.*, **23**, 94-97.
26. Dismukes, G. C., Klimov, V. V., Baranov, S. V., Kozlov, Y. N., DasGupta, J., and Tyryshkin, A. (2001) *Proc. Natl. Acad. Sci. USA*, **98**, 2170-2175.
27. Tomitani, A., Okada, K., Miyashita, H., Matthijs, H. C. P., Ohna, T., and Tanaka, A. (1999) *Nature*, **400**, 159-162.
28. Green, B. R. (2001) *Proc. Natl. Acad. Sci. USA*, **98**, 2119-2121.
29. Cogdell, R. J., Isaacs, N. W., Howard, T. D., McLuskey, K., Fraster, N. J., and Prince, S. M. (1999) *J. Bacteriol.*, **181**, 3869-3879.
30. Georgakopoulou, S., Frese, R. N., Johnson, E., Koolhaas, C., Cogdell, R. J., van Grondelle, R., and van der Zwan, G. (2002) *Biophys. J.*, **82**, 2184-2197.
31. McLuskey, K., Prince, S. M., Cogdell, R. J., and Isaacs, N. W. (2001) *Biochemistry*, **40**, 8783-8789.
32. Hartigan, N., Tharia, H. A., Sweeney, F., Lawless, A. M., and Papiz, M. Z. (2002) *Biophys. J.*, **82**, 963-977.
33. Zuber, H., and Cogdell, R. J. (1995) in *Anoxygenic Photosynthetic Bacteria* (Blankenship, R. E., Madigan, M. T., and Bauer, C. E., eds.) Kluwer Academic Publishers, Dordrecht, pp. 315-348.
34. Hunter, C. N. (1995) in *Anoxygenic Photosynthetic Bacteria* (Blankenship, R. E., Madigan, M. T., and Bauer, C. E., eds.) Kluwer Academic Publishers, Dordrecht, pp. 473-501.
35. Novoderezhkin, V. I., and Razjivin, A. P. (1993) *FEBS Lett.*, **330**, 5-7.
36. Novoderezhkin, V. I., and Razjivin, A. P. (1995) *Biophys. J.*, **68**, 1089-1100.

37. Novoderezhkin, V. I., and Razjivin, A. P. (1997) *Biofizika*, **42**, 164-168.
38. Danielius, R. V., Mineyev, A. P., and Razjivin, A. P. (1989) *FEBS Lett.*, **250**, 183-186.
39. Karrasch, S., Bullough, P. A., and Ghosh, R. (1995) *EMBO J.*, **14**, 631-638.
40. Scheuring, S., Seguin, J., Marco, S., Levy, D., Robert, B., and Rigaud, J. L. (2003) *Proc. Natl. Acad. Sci. USA*, **100**, 1690-1693.
41. Boichenko, V. A., and Makhneva, Z. K. (1994) *Biochemistry (Moscow)*, **59**, 885-890.
42. Francke, C., and Amesz, J. (1995) *Photosynth. Res.*, **46**, 347-352.
43. Westerhuis, W. H. J., Vos, M., van Grondelle, R., Amesz, J., and Niederman, R. A. (1998) *Biochim. Biophys. Acta*, **1366**, 317-329.
44. Jungas, C., Ranck, J.-L., Rigaud, J.-L., Joliot, P., and Vermeglio, A. (1999) *EMBO J.*, **18**, 534-542.
45. Frese, R. N., Olsen, J. D., Branvall, R., Westerhuis, W. H. J., Hunter, C. N., and van Grondelle, R. (2000) *Proc. Natl. Acad. Sci. USA*, **97**, 5197-5202.
46. Francia, F., Wang, J., Venturoli, G., Melandri, B. A., Barz, W. P., and Oesterhelt, D. (1999) *Biochemistry*, **38**, 6834-6845.
47. Crofts, A. R. (2000) *Trends Microbiol.*, **8**, 105-107.
48. McDermott, G., Prince, S. M., Freer, A. A., Hawthornthwaite-Lawless, A. M., Papiz, M. Z., Cogdell, R. J., and Isaacs, N. W. (1995) *Nature*, **374**, 517-521.
49. Koepke, J., Hu, X., Muenke, K., Schulten, K., and Michel, H. (1996) *Structure*, **4**, 581-597.
50. Blankenship, R. E., Olson, J. M., and Miller, M. (1995) in *Anoxygenic Photosynthetic Bacteria* (Blankenship, R. E., Madigan, M. T., and Bauer, C. E., eds.) Kluwer Academic Publishers, Dordrecht, pp. 399-435.
51. Oelze, J., and Golecki, J. R. (1995) in *Anoxygenic Photosynthetic Bacteria* (Blankenship, R. E., Madigan, M. T., and Bauer, C. E., eds.) Kluwer Academic Publishers, Dordrecht, pp. 259-278.
52. Olson, J. M. (1998) *Photochem. Photobiol.*, **67**, 61-75.
53. Schmidt, K. A., and Trissl, H.-W. (1998) *Photosynth. Res.*, **58**, 43-55.
54. Golecki, J. R., and Oelze, J. (1987) *Arch. Microbiol.*, **148**, 236-241.
55. Martinez-Planells, A., Arellano, J. B., Borrego, C. M., López-Iglesias, C., Gich, F., and Garcia-Gil, J. (2002) *Photosynth. Res.*, **71**, 83-90.
56. Fetisova, Z., Freiberg, A., Novoderezhkin, V., Taisova, A., and Timpmann, K. (1996) *FEBS Lett.*, **383**, 233-236.
57. Prokhorenko, V. I., Steensgaard, D. B., and Holzwarth, A. R. (2000) *Biophys. J.*, **79**, 2105-2120.
58. Van Rossum, B.-J., Steensgaard, D. B., Mulder, F. M., Boender, G. J., Schaffner, K., Holzwarth, A. R., and de Groot, H. J. (2001) *Biochemistry*, **40**, 1587-1595.
59. Yakovlev, A., Novoderezhkin, V., Taisova, A., and Fetisova, Z. (2002) *Photosynth. Res.*, **71**, 19-32.
60. Yakovlev, A. G., Taisova, A. S., and Fetisova, Z. G. (2002) *FEBS Lett.*, **512**, 129-132.
61. Steensgaard, D. B., van Walree, C. A., Permentier, H., Bańeras, L., Borrego, C. M., Garcia-Gil, J., Aartsma, T. J., Amesz, J., and Holzwarth, A. R. (2000) *Biochim. Biophys. Acta*, **1457**, 71-80.
62. Sakuragi, Y., Frigaard, N.-U., Shimada, K., and Matsuura, K. (1999) *Biochim. Biophys. Acta*, **1413**, 172-180.
63. Bryant, D. A., Vassilieva, E. V., Frigaard, N.-U., and Li, H. (2002) *Biochemistry*, **41**, 14403-14411.
64. Novoderezhkin, V., and Fetisova, Z. (1999) *Biophys. J.*, **77**, 424-430.
65. Rémigy, H.-W., Hauska, G., Müller, S. A., and Tsiotis, G. (2002) *Photosynth. Res.*, **71**, 91-98.
66. Frigaard, N.-U., Voigt, G., and Bryant, D. A. (2002) *J. Bacteriol.*, **184**, 3368-3376.
67. Jordan, P., Fromme, P., Witt, H. T., Klukas, O., Saenger, W., and Krauss, N. (2001) *Nature*, **411**, 909-917.
68. Zouni, A., Witt, H.-T., Kern, J., Fromme, P., Krauss, N., Saenger, W., and Orth, P. (2001) *Nature*, **409**, 739-743.
69. Vasil'ev, S., Orth, P., Zouni, A., Owens, T. G., and Bruce, D. (2001) *Proc. Natl. Acad. Sci. USA*, **98**, 8602-8607.
70. Boichenko, V. A. (1998) *Photosynth. Res.*, **58**, 163-174.
71. Byrdin, M., Jordan, P., Krauss, N., Fromme, P., Stehlik, D., and Schlodder, E. (2002) *Biophys. J.*, **83**, 433-457.
72. Green, B. R., and Durnford, D. G. (1996) *Annu. Rev. Plant Physiol. Plant Mol. Biol.*, **47**, 685-714.
73. Gantt, E. (1996) *Photosynth. Res.*, **48**, 47-53.
74. Post, A. F., and Bullerjahn, G. S. (1994) *FEMS Microbiol Rev.*, **13**, 393-413.
75. Partensky, F., Hess, W. R., and Vaulot, D. (1999) *Microbiol. Mol. Biol. Rev.*, **63**, 106-127.
76. Garczarek, L., van der Staay, G. W. M., Thomas, J. C., and Partensky, F. (1998) *Photosynth. Res.*, **56**, 131-141.
77. Miyashita, H., Ikemoto, H., Kurano, N., Adachi, K., Chihara, M., and Miyachi, S. (1996) *Nature*, **383**, 402.
78. Miyashita, H., Adachi, K., Kurano, N., Ikemoto, H., Chihara, M., and Miyachi, S. (1997) *Plant Cell Physiol.*, **38**, 274-281.
79. Hu, Q., Miyashita, H., Iwasaki, I., Kurano, N., Miyachi, S., Iwaki, M., and Itoh, S. (1998) *Proc. Natl. Acad. Sci. USA*, **95**, 13319-13323.
80. Hu, Q., Marquardt, J., Iwasaki, I., Miyashita, H., Kurano, N., Mörschel, E., and Miyachi, S. (1999) *Biochim. Biophys. Acta*, **1412**, 250-261.
81. Boichenko, V. A., Klimov, V. V., Miyashita, H., and Miyachi, S. (2000) *Photosynth. Res.*, **65**, 269-277.
82. Tanaka, A., Ito, H., Tanaka, R., Tanaka, N. K., Yoshida, K., and Okada, K. (1998) *Proc. Natl. Acad. Sci. USA*, **95**, 12719-12723.
83. Satoh, S., Ikeuchi, M., Mimuro, M., and Tanaka, A. (2001) *J. Biol. Chem.*, **276**, 4293-4297.
84. Xu, H., Vavilin, D., and Vermaas, W. (2001) *Proc. Natl. Acad. Sci. USA*, **98**, 14168-14173.
85. Vavilin, D., Xu, H., Lin, S., and Vermaas, W. (2003) *Biochemistry*, **42**, 1731-1746.
86. Fromme, P., Jordan, P., and Krauss, N. (2001) *Biochim. Biophys. Acta*, **1507**, 5-31.
87. Chitnis, P. R. (2001) *Annu. Rev. Plant Physiol. Plant Mol. Biol.*, **52**, 593-626.
88. Xu, W., Tang, H., Wang, Y., and Chitnis, P. R. (2001) *Biochim. Biophys. Acta*, **1507**, 32-40.
89. Scheller, H. V., Jensen, P. E., Haldrup, A., Lunde, C., and Knoetzel, J. (2001) *Biochim. Biophys. Acta*, **1507**, 41-60.
90. Karapetyan, N. V., Holzwarth, A. R., and Rögner, M. (1999) *FEBS Lett.*, **460**, 395-400.
91. Lunde, C., Jensen, P. E., Haldrup, A., Knoetzel, J., and Scheller, H. V. (2000) *Nature*, **408**, 613-615.
92. Germano, M., Yakushevska, A. E., Keegstra, W., van Gorkom, H. J., Dekker, J. P., and Boekema, E. J. (2002) *FEBS Lett.*, **525**, 121-125.

93. Stadnichuk, I. N. (1991) *Advances of Science and Technology. Biological Chemistry* [in Russian], Vol. 46, VINITI, Moscow, pp. 1-172.
94. Sidler, W. (1994) in *The Molecular Biology of Cyanobacteria* (Bryant, D. A., ed.) Kluwer Academic Publishers, Dordrecht, pp. 139-216.
95. Bald, D., Kruip, J., and Rögner, M. (1996) *Photosynth. Res.*, **49**, 103-118.
96. Brejc, K., Ficner, R., Huber, R., and Steinbacher, S. (1995) *J. Mol. Biol.*, **249**, 424-440.
97. Chang, W., Jiang, T., Wan, Z., Zhang, J., Yang, Z., and Liang, D. (1996) *J. Mol. Biol.*, **262**, 721-731.
98. Stec, B., Troxler, R. F., and Teeter, M. M. (1999) *Biophys. J.*, **76**, 2912-2921.
99. Reuter, W., Wiegand, G., Huber, R., and Than, M. E. (1999) *Proc. Natl. Acad. Sci. USA*, **96**, 1363-1368.
100. Adir, N., and Lerner, N. (2003) *J. Biol. Chem.*, **278**, 25926-25932.
101. Biggins, J., and Bruce, D. (1989) *Photosynth. Res.*, **20**, 1-34.
102. Mullineaux, C. W. (1992) *Biochim. Biophys. Acta*, **1100**, 285-292.
103. Mullineaux, C. W. (1994) *Biochim. Biophys. Acta*, **1184**, 71-77.
104. Elanskaya, I. V., Allakhverdiev, S. I., Boichenko, V. A., Klimov, V. V., Demeter, S., Timofeev, K. N., and Shestakov, S. V. (1994) *Biochemistry (Moscow)*, **59**, 929-934.
105. Glazer, A. N., Gindt, Y. M., Chan, C. F., and Sauer, K. (1994) *Photosynth. Res.*, **40**, 167-173.
106. Ashby, M. K., and Mullineaux, K. W. (1999) *Photosynth. Res.*, **61**, 169-179.
107. Rakhimberdieva, M. G., Boichenko, V. A., Karapetyan, N. V., and Stadnichuk, I. N. (2001) *Biochemistry*, **40**, 15780-15788.
108. Mullineaux, C. W., Tobin, M. J., and Jones, G. R. (1997) *Nature*, **390**, 421-424.
109. Sarcina, M., Tobin, M. J., and Mullineaux, C. W. (2001) *J. Biol. Chem.*, **276**, 46830-46834.
110. Ley, A. C. (1984) *Plant Physiol.*, **74**, 451-454.
111. McConnell, M. D., Koop, R., Vasil'ev, S., and Bruce, D. (2002) *Plant Physiol.*, **130**, 1201-1212.
112. Hess, W. R., Partensky, F., van der Staay, G. W. M., Garcia-Fernandez, J. M., Börner, T., and Vaulot, D. (1996) *Proc. Natl. Acad. Sci. USA*, **93**, 11126-11130.
113. Hess, W. R., Steglich, C., Lichtlé, C., and Partensky, F. (1999) *Plant Mol. Biol.*, **40**, 507-521.
114. Lokstein, H., Steglich, C., and Hess, W. R. (1999) *Biochim. Biophys. Acta*, **1410**, 97-98.
115. Marquardt, J., Senger, H., Miyashita, H., Miyachi, S., and Mörschel, E. (1997) *FEBS Lett.*, **410**, 428-432.
116. Marquardt, J., Mörschel, E., Rhiel, E., and Westermann, M. (2000) *Arch. Microbiol.*, **174**, 181-188.
117. Wedemayer, G. J., Kidd, D. G., Wemmer, D. E., and Glazer, A. N. (1992) *J. Biol. Chem.*, **267**, 7315-7331.
118. Wilk, K. E., Harrop, S. J., Jankova, L., Edler, D., Keenan, G., Sharples, F., Hiller, R. G., and Curmi, P. M. G. (1999) *Proc. Natl. Acad. Sci. USA*, **96**, 8901-8906.
119. Burnap, R. L., Troyan, T., and Sherman, L. A. (1993) *Plant Physiol.*, **103**, 893-902.
120. Bibby, T. S., Nield, J., and Barber, J. (2001) *J. Biol. Chem.*, **276**, 43246-43252.
121. Golitsin, V. M., Tetenkin, V. L., and Gulyaev, B. A. (1995) *Biochemistry (Moscow)*, **60**, 611-616.
122. Tetenkin, V. L., Gulyaev, B. A., and Golitsin, V. M. (1997) *Biochemistry (Moscow)*, **62**, 523-529.
123. Tetenkin, V. L., Golitsin, V. M., and Gulyaev, B. A. (1998) *Biochemistry (Moscow)*, **63**, 584-591.
124. Falk, S., Samson, G., Bruce, D., Huner, N. P. A., and Laudenbach, D. E. (1995) *Photosynth. Res.*, **45**, 51-60.
125. Bibby, T. S., Nield, J., and Barber, J. (2001) *Nature*, **412**, 743-745.
126. Boekema, E. J., Hifney, A., Yakushevska, A. E., Piotrowski, M., Keegstra, W., Berry, S., Michel, K. P., Pistorius, E. K., and Kruip, J. (2001) *Nature*, **412**, 745-748.
127. Palenik, B., and Haselkorn, R. (1992) *Nature*, **355**, 265-267.
128. La Roche, J., van der Staay, G. W. M., Partensky, F., Ducret, A., Aebersold, R., Li, R., Golden, S. S., Hiller, R. G., Wrench, P. M., Larkum, A. W. D., and Green, B. R. (1996) *Proc. Natl. Acad. Sci. USA*, **93**, 15244-15248.
129. Garczarek, L., Hess, W. R., Holtzendorff, J., van der Staay, G. W. M., and Partensky, F. (2000) *Proc. Natl. Acad. Sci. USA*, **97**, 4098-4101.
130. Bibby, T. S., Nield, J., Partensky, F., and Barber, J. (2001) *Nature*, **413**, 590.
131. Helfrich, M., Ross, A., King, G. C., Turner, A. G., and Larkum, A. W. D. (1999) *Biochim. Biophys. Acta*, **1410**, 262-272.
132. Chen, M., Quinnell, R. G., and Larkum, A. W. D. (2002) *FEBS Lett.*, **514**, 149-152.
133. Jansson, S. (1994) *Biochim. Biophys. Acta*, **1184**, 1-19.
134. Jansson, S., Stefánsson, H., Nyström, U., Gustafsson, P., and Albertsson, P.-A. (1997) *Biochim. Biophys. Acta*, **1320**, 297-309.
135. Boekema, E. J., Jensen, P. E., Schlodder, E., van Breemen, J. F. L., van Roon, H., Scheller, V. H., and Dekker, J. P. (2001) *Biochemistry*, **40**, 1029-1036.
136. Bossmann, B., Knoetzel, J., and Jansson, S. (1997) *Photosynth. Res.*, **52**, 127-136.
137. Bossmann, B., Grimme, L. H., and Knoetzel, J. (1999) *Planta*, **207**, 551-558.
138. Schmid, V. H. R., Cammarata, K. V., Bruns, B. U., and Schmidt, G. W. (1997) *Proc. Natl. Acad. Sci. USA*, **94**, 7667-7672.
139. Croce, R., Morosinotto, T., Castelletti, S., Breton, J., and Bassi, R. (2002) *Biochim. Biophys. Acta*, **1556**, 29-40.
140. Boekema, E. J., van Roon, H., Galkoen, F., Bassi, R., and Dekker, J. P. (1999) *Biochemistry*, **38**, 2233-2239.
141. Yakushevska, A. E., Keegstra, W., Boekema, E. J., Dekker, J. P., Andersson, J., Jansson, S., Ruban, A. V., and Horton, P. (2003) *Biochemistry*, **42**, 608-613.
142. Boekema, E. J., van Roon, H., and Dekker, J. P. (1998) *FEBS Lett.*, **424**, 95-99.
143. Kühlbrandt, W., Wang, D. N., and Fujiyoshi, Y. (1994) *Nature*, **367**, 614-621.
144. Caffarri, S., Croce, R., Breton, J., and Bassi, R. (2001) *J. Biol. Chem.*, **276**, 35924-35933.
145. Das, S. K., and Frank, H. A. (2002) *Biochemistry*, **41**, 13087-13095.
146. Espineda, C. E., Linford, A. S., Devine, D., and Brusslan, J. A. (1999) *Proc. Natl. Acad. Sci. USA*, **96**, 10507-10511.
147. Hoober, J. K., and Eggink, L. L. (2001) *FEBS Lett.*, **489**, 1-3.

148. Li, X.-P., Björkman, O., Shih, C., Grossman, A. R., Rosenquist, M., Jansson, S., and Niyogi, K. K. (2000) *Nature*, **403**, 391-395.
149. Horton, P., Ruban, A. V., and Walters, R. G. (1996) *Annu. Rev. Plant Physiol. Plant Mol. Biol.*, **47**, 655-684.
150. Niyogi, K. K. (1999) *Annu. Rev. Plant Physiol. Plant Mol. Biol.*, **50**, 333-359.
151. Green, B. R., and Pichersky, E. (1994) *Photosynth. Res.*, **39**, 149-162.
152. Miroshnichenko-Dolganov, N. A., Bhaya, D., and Grossman, A. R. (1995) *Proc. Natl. Acad. Sci. USA*, **92**, 636-640.
153. Green, B. R., and Kühlbrandt, W. (1995) *Photosynth. Res.*, **44**, 139-148.
154. Montane, M. H., and Kloppstech, K. (2000) *Gene*, **258**, 1-8.
155. Adamska, I., Roobol-Bóza, M., Lindahl, M., and Andersson, B. (1999) *Eur. J. Biochem.*, **260**, 453-460.
156. Adamska, I., Kruse, E., and Kloppstech, K. (2001) *J. Biol. Chem.*, **276**, 8582-8587.
157. Krol, M., Spangfort, M. D., Huner, N. P. A., Oquist, G., Gustafsson, P., and Jansson, S. (1995) *Plant Physiol.*, **107**, 873-883.
158. Albertsson, P.-A. (1995) *Photosynth. Res.*, **46**, 141-149.
159. Allen, J. F. (1992) *Biochim. Biophys. Acta*, **1098**, 275-335.
160. Tan, S., Ducret, A., Aebersold, R., and Gantt, E. (1997) *Photosynth. Res.*, **53**, 129-140.
161. Grabowski, B., Cunningham, F. X., Jr., and Gantt, E. (2001) *Proc. Natl. Acad. Sci. USA*, **98**, 2911-2916.
162. De Martino, A., Douady, D., Quinet-Szely, M., Rousseau, B., Crépineau, F., Apt, K., and Caron, L. (2000) *Eur. J. Biochem.*, **267**, 5540-5549.
163. Goss, R., Wilhelm, C., and Garab, G. (2000) *Biochim. Biophys. Acta*, **1457**, 190-199.
164. Durnford, D. G., Deane, J. A., Tan, S., McFadden, G. I., Gantt, E., and Green, B. R. (1999) *J. Mol. Evol.*, **48**, 59-68.
165. Hofmann, E., Wrench, P. M., Sharples, F. P., Hiller, R. G., Welte, W., and Diederichs, K. (1996) *Science*, **272**, 1788-1791.
166. Damjanovic, A., Ritz, T., and Schulten, K. (2000) *Biophys. J.*, **79**, 1695-1705.
167. Krueger, B. P., Lampoura, S. S., van Stokkum, I. H. M., Papagiannakis, E., Salverda, J. M., Gradinaru, C. C., Rutkauskas, D., Hiller, R. G., and van Grondelle, R. (2001) *Biophys. J.*, **80**, 2843-2855.
168. Sharonov, V. V. (1945) *Tables for Calculations of Natural Illumination and Visibility* [in Russian], USSR Academy Press, Moscow.
169. Smith, H. (1982) *Ann. Rev. Plant Physiol.*, **33**, 481-518.
170. Grigorjev, I. S., and Mejlikhov, E. Z. (eds.) (1991) *Physical Units*, *Handbook* [in Russian], Energoatomizdat, Moscow, pp. 1191-1195.
171. Jerlov, N. G. (1976) *Marine Optics*, Elsevier, Amsterdam.
172. Litvin, F. F., and Zvalinskii, V. I. (1983) *Uspekhi Sovrem. Biol.*, **3**, 339-357.
173. Béja, O., Aravind, L., Koonin, E. V., Suzuki, M. T., Hadd, A., Nguyen, L. P., Jovanovich, S. B., Gates, C. M., Feldman, R. A., Spudich, J. L., Spudich, E. N., and DeLong, E. F. (2000) *Science*, **289**, 1902-1906.
174. Béja, O., Spudich, E. N., Spudich, J. L., Leclerc, M., and DeLong, E. F. (2001) *Nature*, **411**, 786-789.
175. Oesterhelt, D., and Stoeckenius, W. (1973) *Proc. Natl. Acad. Sci. USA*, **70**, 2853-2857.