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Pigment-Protein Complexes of Purple Photosynthetic Bacteria: An Overview

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A minireview of antenna and reaction center pigment-protein complexes of purple bacteria is presented. Advances in our knowledge of their structure and composition during the past 3 yr are emphasized and some new thoughts are introduced.

Key words: photochemical reaction center, chlorophyll protein, carotenoid, photosynthesis, light-harvesting, membrane protein

The photosynthetic pigments in bacteria are located in and on the photosynthetic membrane. In general these pigments do not exist "free," but rather are noncovalently bound to protein, forming two functionally and spectrally distinct classes of pigment-protein complexes: the photochemical reaction center and the light-harvesting complexes [1]. The majority of the pigment is present in the latter which acts as an antenna to absorb incident radiation and transfer it to the reaction center where the primary photochemical event occurs and in which only a few percent of the total pigment is located. The combination of these two types of complex form the bulk of the bacterial photosynthetic unit. By using suitable surfactants and standard protein purification techniques, it is possible to solubilize the photosynthetic membranes and independently purify and characterize the reaction center and the antenna complexes [1–3].

PHOTOCHEMICAL REACTION CENTERS

Unlike higher plants and algae, photosynthetic bacteria have only one photosystem. This has simplified the purification of the reaction center which can be obtained, completely free of antenna pigments and other extraneous material, from most purple bacteria and from one green filamentous bacterium, Chloroflexus aurantiacus (see

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[1.3] for a summary). The green sulfur photosynthetic bacteria have not yet yielded their reaction centers to isolation [4].

The most fully characterized reaction center is that of Rhodopseudomonas sphaeroides [5], in particular that of a carotenoidless mutant (R-26) of this species. It has a unit containing four molecules of bacteriochlorophyll *a*(BChl*a*), two molecules of bacteriopheophytin *a* (BPheo *a*), one molecule of carotenoid (absent in reaction centers isolated from carotenoidless mutants), one or two molecules of ubiquinone (UQ_{10}), and one atom of ferrous iron ([6,7], see also [3]). These components are noncovalently bound to three polypeptides of absolute molecular weights, 28, 32, and 36 kilodaltons (KD) [8] termed L, M, and H, respectively [3]. The reaction center unit contains one copy of each polypeptide [9]. This unit is not the simplest photochemically active particle that can be obtained. Treatment of it with chaotropic agents removes the H polypeptide [5] but not the pigment molecules nor the activity. The resulting LM-pigment complex has, however, reduced stability to detergents. Thus all of the reaction center pigments are associated with the L or the M subunit or both, and polypeptide H is colorless. The quinone(s) has been located on the M subunit [5,10], but the primary photochemical donor's (P870) precise location has not yet been determined in spite of much effort. The absorption spectrum and the assignment of absorption bands to chromophores present is depicted for Rps sphaeroides reaction centers in Figure 1A.

For studies of the structure and function of reaction centers considerable benefit is gained by adopting a comparative biochemical and biophysical approach. It is then possible to assess those features which are of general significance. To this end we have compared the composition of three distinct reaction center types in Table I. Data are given on the Rps sphaeroides reaction center and those isolated from a photosynthetic bacterium containing BChl *b*, Rps viridis [11], and a green filamentous bacterium, Chloroflexus aurantiacus [12]. The last organism contains BChl *a* and *c* and is thought [cf 12] to be related to an evolutionary precursor of green sulfur and purple sulfur and nonsulfur bacteria, in part because it has a photochemical reaction center and a minor portion of its antenna that are very like those of purple bacteria and a major part of its antenna that is like that of the green bacteria [4]. The absorption spectra of the three reaction centers (Fig. 1) emphasize most of the major differences between any one reaction center and the other two (Table I). Thus, the Rps viridis component has spectral forms absorbing further into the near infrared and more separated spectrally than those in the other two; this reflects the presence of BChl and BPheo *b* rather than BChl and BPheo *a*. Also, the presence of *c*-type cytochromes in the Rps viridis component but not in the others is indicated by the 420-nm band. Cytochromes are also present in reaction center preparations from another BChl *b*-containing organism (Thiocapsa pfennigii) and from a few BChl *a*-containing organisms (eg, Chromatium vinosum) [11]. The Chloroflexus reaction center contains more BPheo *a* (A_{760}), and less BChl *a* (A_{805}) than the Rps sphaeroides component (Table I, cf also Fig. 1A,C). This difference will be of use in delineating the mechanism of electron transfer during the primary photochemical event (see below).

Apart from these differences, the various reaction centers show considerable similarity. All reaction centers studied so far have the same pigment/primary donor ratio, contain quinones [3], and, when prepared from wild-type strains of purple bacteria, carotenoids [3]; note, however, the absence of carotenoids (bands in the 400–500-nm region) in the Chloroflexus complex (Fig. 1C). The carotenoid protects the reaction center pigments from destruction by photodynamic action occurring via

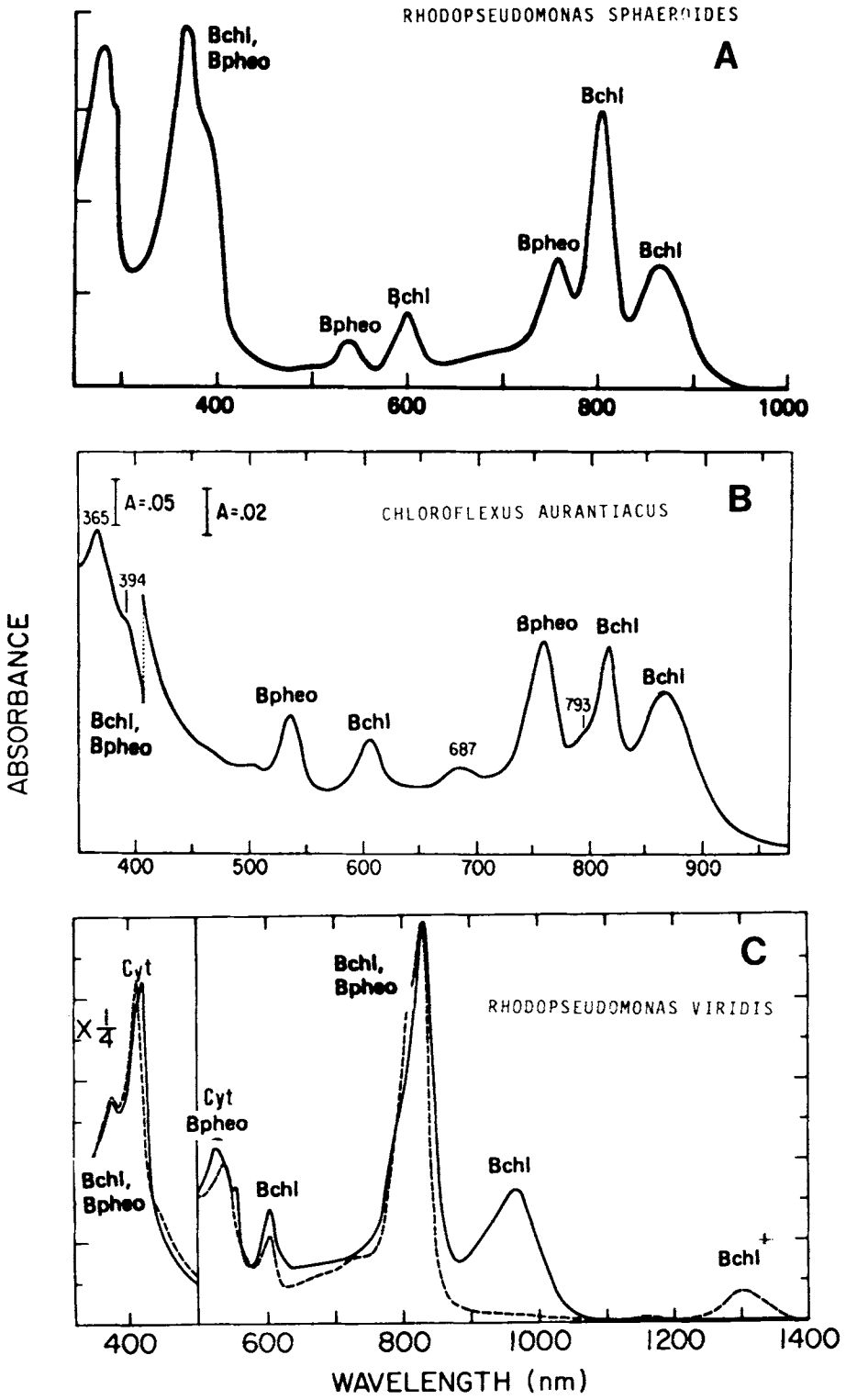

Fig. 1. Absorption spectra at room temperature of photochemical reaction centers isolated from Rps sphaeroides, a BChl *a*-containing bacterium (A); Chloroflexus aurantiacus, a green filamentous bacterium (B); Rps viridis, a BChl *b*-containing bacterium (C).

TABLE I. A Comparison of the Composition of Some Isolated Photochemical Reaction Centers

Species	Rps sphaeroides [3,5,8]	Rps viridis [11]	Chloroflexus aurantiacus [12]
Pigment content per P870 or P960 molecule	4 molecules BChl *a* 2 molecules BPheo *a* 2 molecules UQ_{10} 1 molecule carotenoid	4 molecules BChl *b* 2 molecules BPheo *b* 1 molecule UQ_{10} 1 molecule MQ_7 1 molecule carotenoid	3 molecules BChl *a* 3 molecules BPheo *a* No carotenoid
Subunit composition No. per P870 or P960 (and names)	3 (L, M, and H)	4 (L, M, H, and two *c* type cytochrome(s)[a])	2 (L and M?)
Apparent size of subunits from SDS-PAGE (from amino acid analyses)	H—28 (36) KD M—24 (32) KD L—21 (28) KD	H—35 KD M—28 KD L—24 KD cytochrome—38KD	M—30 KD L—28 KD

[a]4–5 hemes per P960 [11].

the triplet state of the chlorophyll present [7]. The polypeptides composing the reaction center have similar sizes to each other and to those in the reaction centers of other organisms (Table I), ie, they all lie between 25 and 40 KD. The molecular sizes have been obtained by sodium dodecyl sulfate-polyacrylamide gel electrophoresis (SDS-PAGE) in all cases; it is noteworthy for studies on all chlorophyll-proteins that for one organism (Rps sphaeroides) their true sizes have been found, by amino acid analysis, to be some 30% greater than their apparent molecular weights determined by SDS-PAGE [8]. There are apparently only two polypeptides in Chloroflexus reaction centers [51], but whether they are equivalent to L and M or M and H or are not equivalent to those in purple bacterial reaction centers remains to be established [12]. The first choice seems most likely in light of the simplest *active* unit of purple bacteria reaction centers containing only the L and M polypeptides. The L, M, and H subunits are intrinsic membrane proteins with a substantial nonpolar residue content [9]. Considerable experimental effort has been expended trying to sequence the reaction center polypeptides from Rps sphaeroides [8]. The sequences are still only known for the first 30 or so residues of each of the polypeptides. However, the DNA sequencing of the structural genes for the reaction center polypeptides is now underway in G. Feher's laboratory in La Jolla, California, and in other laboratories; these results are eagerly awaited.

The general mechanism for reaction center function has mainly arisen from studies on isolated reaction centers, particularly the Rps sphaeroides and Rps viridis reaction centers [5,13–15]. Thus it is thought that when the reaction center is excited (usually by energy transfer from the antenna system in vivo) a pair of BChl *a* molecules (P870 in BChl *a*-containing organisms and P960 in BChl *b*-containing organisms) is raised to the first excited singlet state, P^*. Over the next 200 psec a series of electron-transfer events leads to a stable separation of charge with an electron from P^* ultimately residing on a quinone [13]. Initially the electron is thought to be transferred from P^* to one of the two BChl *a* molecules that do not form P870 (or P960), and it then migrates by way of one or both [11] BPheo *a* molecules to one of the two UQ_{10} molecules [13]. This chain of pigmented electron acceptors, which

rapidly transfers the electron, seems to be an essential feature of reaction center function in both bacteria and plants [14], and appears to be the mechanism whereby wasteful back reactions (ie, charge recombination events, $P^+ A^- \rightarrow PA$) are minimized. Thus of the six porphyrin-chromophore molecules in the reaction center, two BChl molecules function as the primary electron donor, and two perhaps more, of the four remaining BChl and BPheo molecules function as early electron acceptors. The Fe^{2+} in isolated reaction centers does not seem to participate in electron transfer [8]. A very similar assemblage of electron carriers also apparently participates in the primary event of photosystem II in plants [15].

The ultimate aim of research on reaction centers is to obtain their three-dimensional (3-D) structure and relative orientation in the membrane with respect to other components [16]. Until recently, models for the organization of the photosynthetic participants have had to come from indirect experimental techniques, such as photoselection [17,18], linear dichroism [19–21], or neutron diffraction [22], due to the lack of availability of crystals for x-ray studies. The 2-D ordered array in the Rps viridis membrane has proved useful for observing the arrangement of the reaction center and antenna components [23]. While such information is, and will continue to be, of great value, it will not yield the fine structural detail needed. Three-dimensional crystallization of a photochemical reaction center is required for such purposes, and this has only recently been accomplished for the first time [24]. The crystals are large and tetragonal (space group P4,2,2) and diffract clearly to beyond 2.5 Å. It should, therefore, only be a matter of time before the complete structure of one reaction center is available. This is an extremely exciting prospect. If, indeed, the complete set of reaction center pigments can be visualized, and each ascribed to one of the six chromophore molecules present in the reaction center, we will have an understanding of the mechanism of the primary photochemical reaction and a molecular explanation of spectral forms of the pigments in the detail researchers have been seeking for many years; however, much additional study of the function of each chromophore is needed not only to make full use of the crystallographic data but also to aid in assigning each of the chromophore molecules, found in the 3-D structure, to the spectral forms present in the isolated reaction centers.

THE LIGHT-HARVESTING PIGMENT-PROTEIN COMPLEXES

In the past few years there has been a major increase in information available on both the structure and the function of the light-harvesting complexes of photosynthetic bacteria (see [1,2,25] for reviews). In the case of the purple bacteria it is now possible to highlight several features of the antenna complexes which seem to be of general significance.

Previously, based upon structural and functional data on a few purified complexes, we proposed [1,2,25] that antenna complexes from purple bacteria were of two distinct classes. In all purple bacteria there is one type of antenna complex which appears to be intimately associated with the reaction centers that apparently occurs in a fixed stoichiometry relative to the reaction center [26]. The B890-protein from Rhodospirillum rubrum [27] or B875-protein from Rps sphaeroides [28] are examples of this class of antenna complexes. The prefix B indicates bulk (ie, antenna) pigment absorbing maximally in the near infrared (IR) at the wavelength(s) given. Many species of purple bacteria contain a second type of antenna complexes [1,2]. This

TABLE II. Comparison of the Major Antenna Caroteno-Chlorophyll-Proteins in Purple Bacteria*

	B890-protein class		B800-850-protein class		
			B800-850-protein		
Antenna type	B890-protein	B875-protein	Type I	Type II	B800-820-protein
Examples of bacteria containing antenna type	Rsp. rubrum C. vinosum Rps. acidophila ? Rps. viridis	Rps. palustris Rps. capsulata Rps. sphaeroides Rps. gelatinosa	Rps. acidophila 7750 and 7050 (high light grown)	C. vinosum Rps. acidophila 7050 (low-light grown)	
BChl *a*: carotenoid	2:1	2:2	3:1	3:1	3:1
No. of polypeptides in isolated complex	2	2	2 or 3	2	2
No. of amino acid residues in polypeptides	52 and 54	52–58 and 47–48	54–60 and 52	~50–65	~50–65
Intensity of CD spectrum of long wavelength band[a]	Strong	Weak	Strong	Strong	Strong

*The quantitative data are based on analysis of complexes isolated from only a few of the species given as examples.
[a]All spectra indicate BChl dimer present in the band.

type, of which the B800-850-proteins from Rps sphaeroides or Rps capsulata [29,30] are examples, is present in variable amounts with respect to the reaction center [1,26]. It is thought that by varying the amount of the B800-850-protein, bacteria modulate the size of their photosynthetic unit in response to environmental conditions such as changes in incident light intensity [25,26].

While the functional distinction between the two classes of antenna complex remains valid, it appears, from more recent biochemical analyses of a wider range of purple bacterial light-harvesting complexes, that structurally each of those two classes has at least two subdivisions (Table II). The reasoning behind this elaboration will be discussed at length below.

The B800-850 Antenna Complexes

The B800-850 antenna complex from Rps sphaeroides occurs in the photosynthetic membrane as a multimer of a minimum unit [cf. 29] consisting of three molecules of BChl *a*, one molecule of carotenoid, and one copy of each of two polypeptides [27,31,32]. These polypeptides have low molecular weights (< 10,000 KD) [32,33], are as hydrophobic as the L and M polypeptides of the reaction center (indeed they are soluble in 1:1 (v/v) chloroform:methanol!), and have been sequenced (see below). No one has yet succeeded in isolating this minimum unit in a pigmented form. The smallest isolated pigmented complex has a $M_r \geqslant 100{,}000$, which is much

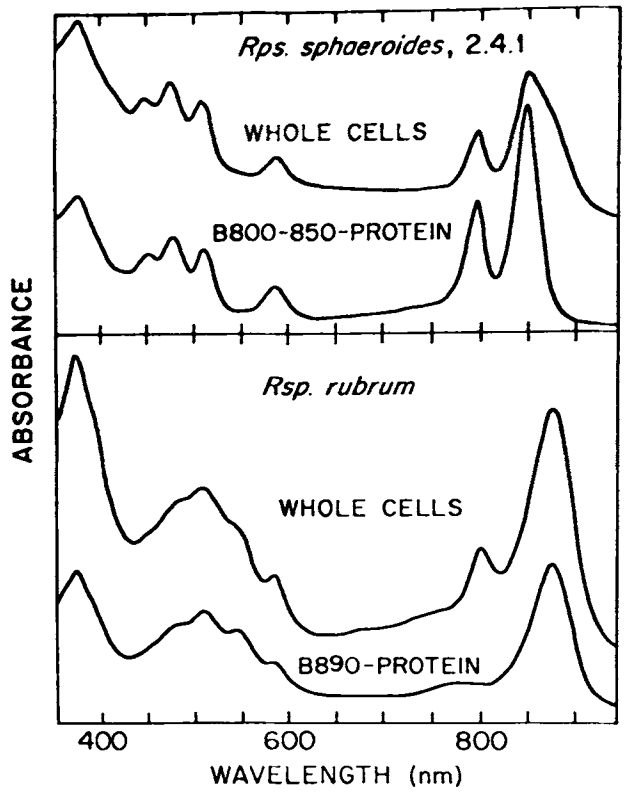

Fig. 2. Absorption spectra at room temperature of two purple bacteria and antenna caroteno-BChl *a*-proteins isolated from them. Rsp rubrum S1 contains a single antenna complex, the B890-protein shown in the lower portion of the figure. The 800-nm peak and the 760-nm shoulder in its whole cell spectrum are contributed by the absorbance of BChl and BPheo in the reaction center (cf. Fig. 1).

greater than that of the proposed building block [see 29]. The absorption spectrum of the B800-850-protein complex is given in Figure 2. Two of the BChl *a* molecules contribute the 850-nm absorption band, while the third is responsible for the 800-nm absorption [27,31]. It is the carotenoid in this complex, and not that in the B890 or B875 complex,that is responsible for the observed electrochromic carotenoid band shift during ongoing photosynthesis [34]. There is a partial revertant of the blue-green mutant Rps sphaeroides R-26, R-26.1, which contains an altered B800-850-protein in which the 800-nm-absorbing BChl *a* molecule is absent [35]. Amino acid sequence studies are under way comparing this to the wild-type complex to see whether, by difference, the binding site for the 800 nm BChl *a* can be identified from sequence data [36].

The analogous B800-850-protein of Rps capsulata (M_r = 170,000) has been studied with equal intensity to the Rps sphaeroides complex [eg, 37–39]. It is essentially the same as the Rps sphaeroides component except that an additional, colorless M_r = 14,000 polypeptide is present in the isolated Rps capsulata complex

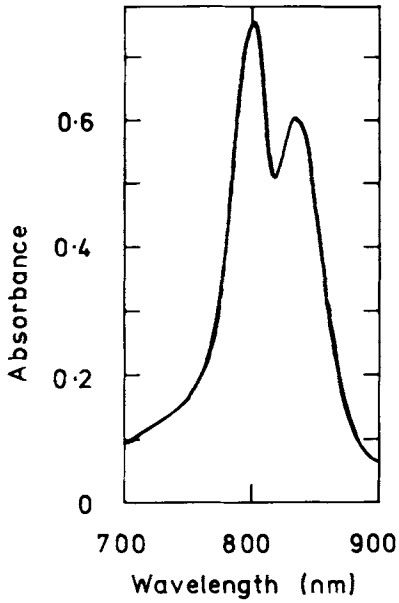

Fig. 3. Near-infrared absorption of the B800-850-protein of Rps Acidophila 7050 grown under low light intensity.

[37]. The carotenoid molecule and one of the three BChl *a* molecules are associated with the smaller of the apoproteins, and the other two BChl are with the larger in this complex [38]. In the B800-850-proteins of both organisms the pigment-pigment distance is 10–14 Å [40].

We have termed the two B800-850 antenna complexes above type I B800-850-protein (Table II). This subtype is characterized by its 850-nm absorption band being about 1.5 times as intense as the 800-nm band (Fig. 2). Alternatively, some species of purple bacteria contain a B800-850 antenna complex in which the 850-nm absorption band is of equal or lower intensity than the 800 nm band (Fig. 3), eg, the complexes isolated from Chromatium vinosum [41] and Rps acidophila strain 7050, when grown at low light intensities [42]. We designate these B800-850 antenna complexes as type II complexes. The best-characerized example of which is the complex isolated from Rps acidophila 7050 [42]. It contains two different low molecular weight polypeptides, three molecules of BChl *a* and one molecule of carotenoid (per pair of these polypeptides). That is, it has the same composition as the Rps sphaeroides complex, but unlike the type I B800-850 complexes, type II from both Rps acidophila and C vinosum shows more spectral variability: the position of the 850-nm absorption maximum can vary between 835 and 855 nm, depending upon such factors as detergent concentration, pH, etc [1,2,41,42]; and the exact position alters the relative heights of the 800 and 850 nm peaks. It is also noteworthy that, so far, whenever the type II B800-850 antenna complex occurs in a bacterium, there is also a B800-820 antenna complex [41,42]. Their biochemical interrelationship is not yet clearly defined, but in Rps acidophila, they appear to have a very similar

polypeptide composition and in C vinosum the holocomplexes have very similar sizes and identical pigment contents [41].

The B890-Protein Complex

The B890 antenna complex of Rsp rubrum is the most fully characterized of this class [2,33,43–45]. Its absorption spectrum is depicted in Figure 2. The minimum unit of the B890-protein complex consists of two molecules of BChl *a* and one molecule of carotenoid (usually spirilloxanthin) bound to two low molecular weight, hydrophobic polypeptides [2,44,47]. These two polypeptides have been sequenced for Rsp rubrum and they consist of 52 and 54 amino acids [43,44]. The 890-nm absorption band shows an intense circular dichroism (CD) spectrum, typical of a BChl dimer [27]. The corresponding antenna complexes from C vinosum [2,41] and Rps acidophila [42] seem to have these same characteristics.

In contrast the analogous light-harvesting complex (B875-protein) from all other species studied so far, such as Rps sphaeroides, is rather different (Table II). It contains two molecules of BChl *a* and *two* molecules of carotenoid per pair of polypeptide [28]; has its near IR maximum at shorter wavelengths than the B890 complex; and this 875-nm absorption band, unlike the 890 nm band of the analogous complex in Rsp rubrum, shows only a weak CD spectrum. These differences make us now segregate the B890 antenna complexes into two subclasses: B890-protein complex and B875-protein complexes.

CONCLUDING REMARKS

In spite of subtle differences between the various antenna types described above, they all possess many similar properties. Thus all the antenna polypeptides (B890, B875, or B800-850) are small ($<$ 10 KD), occur in pairs, and are extremely hydrophobic (often being soluble in a mixture of chloroform and methanol). Secondly, the three or four pigment molecules are bound to two different polypeptides to form what is believed to be the minimum building block from which a supermolecular aggregate $\geqslant$ 100 KD is constructed in situ. H. Zuber and colleagues [33,36,44,46] have sequenced both polypeptides (termed by them LHP 1 and LHP 2) of the B890-protein of Rsp rubrum, the B875-proteins of Rps sphaeroides and the Rps gelatinosa, the B1015-protein of Rps viridis, and the B800-850-proteins of Rps sphaeroides and Rps gelatinosa. LHP 1 of the B800-850-protein of Rps capsulata has also been sequenced [45]. The data show each polypeptide has three domains: a polar N-terminus, a hydrophobic core of 20–23 residues which may be homologous in all the sequences obtained, and a polar C-terminus. This research group has proposed that the amino terminus protrudes into the cytoplasm, the carboxy terminus into the periplasm, and the hydrophobic core forms an α-helix which crosses the lipid bilayer and binds one, sometimes two, BChl molecule via a histidine ligand. Such a bipolar-transmembrane organization should prevent the BChl-protein molecules from "flip-flopping" in the membrane. So far the water-soluble BChl *a*-protein antenna complex from Prosthecochloris aestuarii [4] is the only antenna complex that has been crystallized. The three-dimensional structure of the complex has been determined by x-ray crystallography [47], and it is a trimeric structure. Each monomer polypeptide (M_r = 42,000) binds seven molecules of BChl *a* in a baglike structure composed largely of β-pleated sheets.

Advances in our knowledge of the purple bacterial complexes have come rapidly in the 1980s, but although we know the subunit composition of the antenna complexes and the amino acid sequence of their apoproteins, we must now learn more about the readily isolatable holocomplexes. We need to know their true molecular size and the number of copies of each of the polypeptides present in the isolated unit. Above all, we need to obtain the 3-D arrangement of the pigments and the proteins which requires crystallization of the holocomplex. Since the more complex photochemical reaction center has already been crystallized [24], it may not be too long before crystallization of these antenna pigment-proteins is accomplished. We also need to delineate the relative arrangement and amounts of the antenna complexes and the reaction center component in the chromatophore membrane [eg, 22,23]. Last but not least, we must further our understanding of the biosynthesis of the proteins and how the stoichiometry of polypeptides within and between complexes is controlled [cf. 48,49].

What relationship might these bacterial complexes have to the plant antenna and reaction center complexes? Less is known of the composition and the amino acid sequence of the plant antenna chlorophyll-proteins than of the bacterial complexes. However, one obvious difference is that the plant apoproteins are invariably much larger (M_r = 20,000–70,000). Thus, we should probably not expect any considerable phylogenetic identities (eg, sequence) between the antenna complexes, and perhaps the best we can hope for will be that lesser features will be common such as histidine's being a fifth ligand to chlorophyll in that pigment's binding to protein, and hydrophobic α-helices traversing the membrane and anchoring the antenna pigment-proteins to it. The baglike structure of the water-soluble green bacterial complex does not, at this stage, seem to be a common feature of antenna chlorophyll-proteins as originally anticipated. Interestingly, both the bacterial and the major antenna complex of green plants have the same orientation (N-terminus in the cytoplasm) with respect to the photosynthetic membrane [cf. 50]. The similarities in the mechanism of the primary event in the purple bacterial reaction center and in the photosystem II reaction center of plants (see above), could imply they were phylogenetically related. If so, we anticipate a relationship of the L and M polypeptides of the bacterial reaction center to the 43-KD and/or the 47-KD chlorophyll-proteins of Photosystem II. One might also expect the H subunit to have its equivalent component in the plant system, and its equivalence to the so-called herbicide-binding protein is being discussed and tested. Obviously, much more sequence data and the use of specific antibodies are required to advance such interrelationships any further

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