Most photosynthetic LH1 antenna complexes undergo dissociation into B820 subunits, suggesting their universal character as structural modules. However, dissociation into subunits seems to occur reversibly only in the absence of carotenoids and the subunits were never found to bind carotenoids. The interactions of carotenoids with B820 have been studied in a newly developed reconstitution assay of the LH1 antenna from *Rhodospirillum rubrum* (Fiedor, L., Akahane, J., and Koyama, Y. (2004) Biochemistry 43, 16487–16496). These model studies show that B820 subunits strongly interact with carotenoids and spontaneously form stable LH1-like complexes with substoichiometric carotenoid content. This is the first experimental evidence that B820 may occur as a short-lived intermediate in the assembly of LH1 in vivo. The resulting complex of B820 subunits with carotenoid, termed iB873, is homogeneous, according to ion exchange chromatography and reproducible pigment composition. The iB873-bound carotenoid is as efficient in energy transfer to bacteriochlorophyll as the one in native antenna. To our knowledge, iB873 is the first complex binding functional carotenoid, with the spectral and biochemical properties intermediate between that of B820 and the fully assembled LH1.

The progress in biochemical (1–3), spectroscopic (4–8), and structural characterization (9–16) of purple bacterial light-harvesting complexes has greatly advanced our understanding of photosynthesis. These intramembranous antenna complexes are oligomers of small, heterodimeric proteins carrying BCHls and Crt. In peripheral light-harvesting complexes, LH2, LH3, or Crt-B820 associates are present in too low a concentration to be observed. Crt-B820 subunits bind Crt (2, 26), and no Crt-to-B820 energy transfer has been observed in *in vitro* studies (27). This indicates that Crt either somehow destabilize the B820 subcomplex, or they strongly promote its aggregation to the extent that Crt-B820 associates are present in too low a concentration to be observed.

We have studied the effects of carotenoids on B820 subunits via LH1 reconstitution in a newly developed model system (27) and provide evidence for the latter case, i.e. that Crt strongly interact with the subunits and enhance their aggregation. We also report on the trapping, for the first time, of a stable LH1-like complex of substoichiometric Crt content, which is a potential intermediate of LH1 assembly.

**EXPERIMENTAL PROCEDURES**

**Reagents and Solvents**—Acetone, benzene, methanol, and tetrahydrofuran, all of analytical grade, were purchased from Merck and used as supplied. LDAO (30% aqueous solution) was obtained from Fluka and *β*-n-acylglucopyranoside (*β*-OG) was from Calbiochem.

**Carotenoids**—Lycopene (Lyc) was extracted from tomato concentrate and purified by column chromatography on alumina, followed by repeated crystallization from a mixture of tetrahydrofuran and *n*-hexane (28). Rhodopin (Rhd) and anhydrohodovibrin (Anv) were extracted from the cells of *Allochromatium vinosum* (D). Both pigments were purified by column chromatography on alumina and then recrystal-
lized; Rhd from n-hexane, and Anv from a mixture of tetrahydrofuran and n-hexane (29). Spirilloxanthin (Spx) was extracted from wet cells of *Rhodospirillum rubrum* strain S1, and purified by low pressure column chromatography on Ca(OH)₂, using an acetone/benzene mixture for elution, and purified by recrystallization in n-hexane (30).

**B820 Isolation**—Carotenoids were removed from freeze-dried chromatophores by extraction with benzene, as previously described (27). A 50-mg portion of the resulting powder of benzene-extracted chromatophores was suspended, using a small homogenizer (Potter type), in 2.5 ml of Tris-Cl buffer (20 mM, pH 7.8), containing NaCl (10 mM) and sodium ascorbate (1 mM). The suspension was solubilized by a stepwise addition of 200-μl portions of 20% aqueous β-OG (w/v). This treatment was followed by absorption spectroscopy in the 700–900-nm region, and continued until no further changes were observed near 870 nm (final β-OG concentration ~3.4%). The solubilized fraction of the chromatophores was collected as a dark blue supernatant by centrifugation (6000 × g, 45 min, 4 °C) and was loaded onto a small column (4 cm × 0.5 cm) of DEAE-Sepharose (Fast Flow, Amersham Biosciences), pre-equilibrated in 1% β-OG (10 mM NaCl/20 mM Tris-Cl buffer, pH 7.8). The column was washed with 2–3 ml of the same eluent, and then a NaCl gradient (10–100 mM) was applied. The fraction eluting with 45 mM NaCl (4–5 ml) was discarded, and pure B820 was eluted with 75–85 mM NaCl (~7 ml) as a dark red fraction, with a yield of 70–80% with respect to the initial amount of detergent-solubilized chromatophores. Under these conditions, the RC remained bound to the column. The fraction of purified B820 was kept at ~30 °C in the dark. The polypeptide composition of the isolated B820 subunits was analyzed by Tricine SDS-PAGE (31).

**Isolation of Native LH1 Antenna**—LH1 was obtained from chromatophores of *R. rubrum* S1 by a modification of the method of Picorel et al. (32), as described elsewhere (27).

**Formation of B880**—A sample of purified B820 in 1% β-OG (1 ml, A₂₈₀ = 9.4, equivalent to 0.11 μmol of BChla) was incubated, while being stirred at room temperature, with increasing amounts of Rhd or Anv. It was observed in 0.018-μmol portions as concentrated (0.033 mM) solution in acetone, to a final amount of 0.096 μmol of Crt and a final acetone concentration of ~20% (v/v). The absorption spectrum of the mixture was measured 5 min after each addition.

**Formation of Substoichiometric Complexes**—To a stirred sample of the purified B820 in 1% β-OG (1 ml, A₂₈₀ = 9.4) at room temperature a highly concentrated solution (0.2–0.4 mM) of Crt in organic solvent was added in small portions. Usually, 0.025–0.05 μmol of Crt were added per 0.11 μmol of BChla, in several 20–25-μl portions as an acetone solution (20 mM, pH 7.8) or 3-μl portions of benzene solution (total 0.5 ml). After removing the excess solvent in a stream of nitrogen (clear solution), the absorption spectrum of the reconstitution mixture was recorded. The sample was then diluted 3-fold with Tris-Cl buffer (20 mM, pH 7.8) and placed in the dark at 4 °C. Usually, after 48–72 h, a dark red precipitate formed, which was collected by a low speed centrifugation (10,000 × g, 5 min, 4 °C).

The precipitate formed with Spx was gently dissolved in a small volume of the Tris buffer, containing 0.8% β-OG and loaded onto a small column (3.5 × 0.5 cm) of DEAE-Sepharose (Fast Flow), pre-equilibrated in the same buffer. The dark red band remaining bound to the column was eluted by a NaCl gradient (50–110 mM) in the presence of 0.8% β-OG. A blue band containing B820 eluted at 70–80 mM NaCl, and a single band of a dark red fraction eluted at 110 mM NaCl. The dark red fraction (termed iB873) was re-chromatographed using the same method, then diluted to 0.7% β-OG, and stored at ~30 °C in the dark.

**Conversion of iB873 into B880**—The isolated fraction of iB873 in 0.7% β-OG (1 ml, A₂₈₀ = 4.3) was treated while being stirred with portions of Rhod (0.0042, 0.084, 0.0126, and 0.0168 μmol) in acetone, at room temperature. 10 min after adding each portion the absorption spectrum of the solution was measured. The precipitate of iB873 was re-dissolved with a Cary 50 spectrophotometer (Varian) in 1-mm quartz cells, and steady-state emission and excitation spectra (corrected) on a Spex Fluorog 1680 spectrofluorimeter (Johin-Yvon), equipped with 0.22 mm double monochromators, using rectangular quartz cells (2 × 10 mm). The absorption and fluorescence measurements were done at room temperature. The circular dichroism (CD) measurements were done with a J-710 (JASCO) spectropolarimeter in 5-mm quartz cells at 15 °C.

**RESULTS**

**B820 Isolation**—B820 subunits of the LH1 antenna from wild-type *R. rubrum* were isolated by a controlled solubilization of benzene-extracted chromatophores in detergent. The carotenoid-depleted chromatophores were titrated with β-OG and monitored by NIR absorption spectroscopy. A complete dissociation of the B870 form was achieved at ~3.4% β-OG. After removing the insoluble residue by centrifugation, the resulting solubilized fraction of B820 subunits (Fig. 1) was separated from the RC and free pigment (BChl) by ion exchange chromatography on DEAE-Sepharose in the presence of 1% β-OG. The same method was found applicable to purify the B820 subunits from chromatophores from a Crt-less G9 strain of *R. rubrum* (not shown).

The absorption spectrum of the B820 fraction is shown in Fig. 1. The high value of the A₂₈₀/A₃₇₀ ratio (2.33), exceeding that of other preparations (33), and the absence of shoulders near 690 nm (chlorin oxidation product) and 770 nm (free BChla) are indicative of the purity of the preparation. The quality of the B820 fraction was confirmed by SDS-PAGE, which showed only two low molecular mass polypeptides at apparent molecular weights between 6 and 10 kDa (not shown). The integrity of the isolated B820 subunits was further confirmed by their ability to reassociate to B870. Lowering the detergent concentration to 0.5%, at room temperature, caused an immediate association of B820 to a species with the Q₅ transition located at 870 nm (Fig. 1).

**Interactions of Carotenoids with B820 Subunits**—Crt was introduced into the B820 system by adding aliquots of concentrated solutions in organic solvents, while keeping all other parameters constant, including in particular the β-OG concentration (1%). As described in previous LH1 reconstitution studies (27, 34), acetone (miscible with water) was found appropriate as a carrier for most Crt, allowing the performance of a saturating titration experiment.

The absorption spectra recorded during the titration of B820 subunits with Crt are shown in Fig. 2. The addition of Crt (in acetone) to the B820 subunits in 1% β-OG resulted in a gradual red shift of the BChla Q₅ transition to 880–881 nm, and the appearance of Crt absorption bands in the 420–580 nm region. The Crt absorption bands are also red-shifted with respect to the control acetone solutions (Fig. 2 and Table 1) or in 1% β-OG without LH1 proteins (not shown).
of 5.5 μm, at which point the BChl:Crt ratio is 2:1.2. Acetone alone (not shown) and additional portions of Crt (and acetone) had practically no further effect on the Q<sub>y</sub> transition. Very similar spectral shifts and effects on the B820 subunits were observed with Anv (not shown).

Formation of an Intermediate of LH1 Complex—The spectra obtained during titration do not show isosbestic points (Fig. 2), which indicates the formation of intermediates. Spectral deconvolution indicated a species with a Q<sub>y</sub>-band of BChl absorbing at 870–872 nm and red-shifted Crt absorption bands, but these intermediates were generally present only as mixtures with B820 and the final B880 complex (not shown). A chance observation, however, was intriguing; complexes with these spectral characteristics precipitate from the solution after the detergent concentration is lowered to 0.33% and chilled to 4 °C. The precipitates were collected by low speed centrifugation, suspended again in the Tris buffer without detergent, and their absorption spectra were measured. Table 1 lists their main absorption maxima, compared with the absorption maxima of Crts in control acetone solutions and their maxima in LH1 complexes reconstituted with the same Crts (27).

Most of these complexes rapidly deteriorated when solubilized with β-OG (0.8%). However, in the case of Spx, the solubilized precipitate was stable enough to be purified by repeated ion exchange chromatography in the presence of 0.8% β-OG. It was termed iB873 because of: (i) its intermediate BChl (Q<sub>y</sub> at 873 nm) and Crt absorption maxima, between those of B820 and B880 (Fig. 3 and Table 1), (ii) its intermediate Crt content, and (iii) the possibility to further convert it to B880 (see below).

Properties of iB873—The absorption spectrum of iB873 resembles that of native LH1 (Fig. 3), but with the following differences: (i) the BChl Q<sub>y</sub> transition is slightly broader, and its maximum is blue-shifted to 873 nm; (ii) there is a prominent absorption decrease in the Crt region, which clearly indicates a reduced Crt-to-BChl ratio in this species (see below); (iii) Spx absorption transitions are blue-shifted by 5–11 nm with respect to the corresponding absorption transitions in the native LH1 (see also Table 1).

The CD spectra of the two complexes, recorded in the range between 350 and 600 nm, show more distinct differences (Fig. 3, inset). Native LH1 shows a broad negative band in the carotenoid region (400–580 nm), located between two positive bands, which are due to the BChla Soret and Q<sub>x</sub> transitions. This CD spectrum resembles the reported spectrum of photosynthetic membranes from the same bacterium (34, 35). iB873 shows instead a broad and well-structured positive band in the carotenoid region, whose peaks coincide with the absorption bands. There is also a sign inversion of the Soret-band CD, while the Q<sub>x</sub> region remained unchanged.

Energy Transfer—The emission spectra of native LH1 and iB873 (Fig. 4) were obtained by exciting the complexes at wavelengths corresponding to the maxima of the Crt 0→1 transition, i.e. at 513 nm and 506 nm, respectively, where absorption by BChla in LH1 is minimal (Fig. 1). The emission spectra have very similar shapes; but the emission maximum of iB873 is blue-shifted (5–6 nm) as compared with LH1, which reflects its blue-shifted Q<sub>y</sub> absorption band.

In both complexes the Crt is functionally coupled to BChl: the excitation maxima in the Crt region reproduce well the characteristic positions of the Spx absorption maxima in the two complexes, but their relative intensities reflect the reduced Crt content of iB873 (see below).

Conversion into B880—The effects of adding a concentrated solution of Rhd in acetone to purified iB873 (obtained with Spx) are shown in Fig. 5. With more Rhd present, the absorption in the Crt region increases, and at the same time the Q<sub>x</sub> transition narrows and shifts to 882 nm. These changes indicate that iB873 retains the ability to bind more Crt.

Pigment Stoichiometry in iB873—The Crt:BChl ratios of LH1 and iB873 were analyzed by an exhaustive pigment extraction into organic solvents. The absorption spectra of the combined extracts, normalized to the intensity of the BChla Q<sub>y</sub> transition, are shown in Fig. 6. As judged from the absence of a chlorin peak near 690 nm, the extraction method is quick and mild enough not to cause oxidation BChla to chlorins (36).

A comparison of the relative intensities of the Crt (at 496 nm) and BChl (at 770 nm) absorption bands shows that the Crt content in iB873 is only 40% of that in the native antenna. Assuming a molar ratio BChla to Crt of 2:1 in the latter (32), this ratio is as high as 5:1 in the iB873 associate.

DISCUSSION

Interactions of B820 Subunits with Crts—B820 is, at least in vitro, an intermediate in the assembly of carotenoid-less LH1 (B870) from its components, viz. BChl and the α and β polypeptides. Irrespective of its preparation, it seems always devoid of carotenoids, even if derived from carotenoid-containing bacteria (2, 26). Its aggregation states and reassociation to B870 have been studied in considerable detail. Depending on the detergent:protein ratio, dimers (22, 23), and higher aggregates (37) have been observed as intermediates during the B870 formation, which showed relatively small red shifts of the Q<sub>y</sub> transitions (845–850 nm). However, no such intermediates have been observed in the few LH1 reconstitution studies, carried out in the presence of Crts (3, 27, 34). Complexes of systematically decreasing sizes, which may be considered as intermediates, have been observed in controlled dissociation of LH1 from *Rhodobacter sphaeroides* (38).

The formation of a Crt-containing B880 complex by solely adding Crt to B820, without changing the detergent concentration, provides clear evidence for interactions between B820 and Crts. The gradual red shift of the main absorption band in the product and the absence of isosbestic points indicated that this transformation is a multistep process. All Crts applied in the present study (Sp, Anv, Lyc, and Rhd) caused similar effects, irrespective of their rather varied structures, indicating that these interactions are not restricted to a specific type of Crt. There is always a significant red shift of the BChla Q<sub>x</sub> transition, indicating that Crt-B820 interactions cause a considerable change in the aggregation state of the subunits. There is
Main absorption maxima of carotenoids in acetone solution, and intermediate complexes (iB873) formed by treatment of B820 subunits with substoichiometric amounts of these carotenoids (see “Experimental Procedures” for details), compared with the corresponding maxima in native LH1 from S1 *R. rubrum* and in reconstituted LH1 complexes.

| Crt in acetone | Intermediate complex iB873 | Reconstituted LH1<sup>a</sup> |
|----------------|---------------------------|-----------------------------|
| Lyc            | 504 473 446 510 483 454 457 871 519 486 457 880 | 519 486 457 880             |
| Anh            | 516 485 526 504 473 454 871 536 503 484 883  | 536 503 484 883             |
| Spx            | 526 493 542 505 473 457 870 549 513 484 883  | 549 513 484 883             |
| Spx (isolated iB873) | 543 506 475 873          |                             |

<sup>a</sup> Data taken from Ref. 27.

**TABLE I**

Main absorption maxima of different carotenoids and intermediate complexes (iB873)

**Intermediate of LH1 Antenna**

Also a red shift of Crt absorptions, which is another, independent, indicator of the Crt-subunit interactions (27).

**Formation of iB873**—Native LH1 contains 1 Crt per 2 BChl LH1 (32), and red shifts induced by the addition of Crt to isolated B820 also saturate at this level. The formation of a new type of complex, iB873, has been observed when Crts were added to B820 in substoichiometric amounts. While complexes of this type were spectroscopically detectable with all Crts studied (Table I), iB873 formed with Spx is sufficiently stable and can be handled and chromatographed in detergent at room temperature. It could be isolated using ion exchange chromatography, and its spectral properties determined. It is homogeneous according to the chromatography and reproducible pigment composition. To our knowledge, this is the first complex binding functional Crt with absorption properties intermediate...
between that of B820 and fully assembled LH1, formed by B820 subunits and Crts. The \( \text{Spx:BChla} \) ratio in the \( \alpha \beta \)-iB873 complex is only 40% of that in native LH1, where the carotenoid content is 2 BChls to 1 Crt viz. 1 Crt per protomer (32). At the \( \beta \)-OG concentration used (1%), the Crt-free B820 is known to exist as a monomer carrying 2 BChls, even though it is known to dimerize at higher detergent concentrations (22). Assuming that in iB873, integer numbers of Crt and the subunits form an associate, a Crt:BChl ratio of 0.4 implies that in iB873, on average, 5 \( \alpha \beta \)-heterodimers should bind two Spx molecules.

Emission and CD measurements clearly indicate a close interaction of Crt with the other components, BChla and the polypeptides, within iB873. Following the excitation of the complex into the Spx absorption at 506 nm, a typical LH1 fluorescence is observed in the NIR region. The position of the emission band maximum at 900 nm confirms the energy transfer from Spx to the iB873 BChls, and implies close contacts of Crt molecules with the BChl complement. Characteristically, for Spx (13 conjugated \( \pi \)–\( \pi \) bonds) in LH1 antennas (39), the Crt-to-B873 energy transfer in iB873 is not particularly effective (~30%); yet it is clearly visible in the excitation spectrum. However, taking into account the reduced Crt content in iB873, the Spx-to-BChla energy transfer efficiency in this complex is quite similar to that of the native LH1 (34, 39).

In native (B)Chl-Crt-proteins, Crts give rise to strong and characteristic CD signals. This optical activity is even seen with achiral Crt, and therefore it must result from interactions with the chiral environment. Strong CD signals are also seen in iB873, but they differ from those of Crt in native LH1 not only by their sign, but also by the structure and positions of the maxima. In many Crt-BChl proteins (e.g. LH1 and LH2 complexes), there is a conspicuous non-coincidence of absorption and CD bands (35), the reason for which remains unclear. Excitonic interactions among Crts could produce such shifts, but the occurrence of direct Crt-Crt interactions has hitherto been demonstrated conclusively only in a single case, the peridinin-chlorophyll \( \beta \)-open \( OG \) molecules from dinoflagellates (40, 41). No such shifts have been observed with iB873: its CD spectrum shows reasonably well defined maxima in the Crt region between 400 and 570 nm, whose positions coincide with band progression in the absorption. This indicates the monomeric character of Crt in iB873, with no significant intercarotenoid interactions. Such interactions in iB873 are also unlikely from a Poisson analysis of the occupancies of the Crt binding sites in this complex, which were modeled assuming that the Crt molecules distribute randomly (non-cooperative binding). A simulation of a 40% saturation of Crt in iB873 (assuming one Crt binding site per protomer) reveals that as much as 93% of the bound Crt molecules are likely not to have another Crt in their vicinity, but rather an empty Crt binding site. Hence, almost all Crt molecules retain a monomeric character and, as shown by the efficient energy transfer, they must be strongly coupled to BChls. If no further rearrangements take place during the conversion of iB873 to B880, the inversion of the CD signal of Spx in the native LH1 antenna from \( R. \ rubrum \) as well as the non-coincidence of CD and absorption maxima, are indications of Crt-Crt interactions rather than of Crt-BChla interactions in LH1.

Relevance to the Assembly of LH1 Antenna—Both the spontaneous formation of iB873 upon addition of Crt to B820 and its stability, may be relevant for understanding the assembly of the bacterial core antenna. iB873 has the characteristics of an intermediate species according to several criteria: (i) an intermediate position of its \( Q_Y \) transition between those of B820 and B880, (ii) an intermediate Crt content, and (iii) the conversion to B880 when more Crt is applied. This would be the first observation of an intermediate in the assembly of an LH1 antenna in the presence of Crt. According to the position of its \( Q_Y \) transition it should be termed B873. Since this term has been traditionally applied to the Crt-less counterpart of complete LH1 antenna absorbing at the same position (e.g. from \( R. \ rubrum \), Ref. 19), and in order to emphasize the intermediate character of the newly found species and its ability to bind Crts, we chose to name it iB873.

The substoichiometric pigment ratio in iB873 suggests that it may not have the structure of a complete ring as in the native antenna (16 \( \alpha \beta \) heterodimers), but could well be a smaller sized associate of several B820 subunits with few Crt molecules; beginning with five \( \alpha \beta \) heterodimers carrying two Crt molecules: \( \text{Crt}_2 \times \text{B820}_5 \) (see above). There may exist a series of intermediates of various stoichiometries and sizes, which appear during the process of the core antenna formation, but there is no evidence for such heterogeneity from the absorption, fluorescence, and CD spectra.

Stable iB873 may therefore represent a hitherto elusive intermediate stage of LH1 formation, which could be trapped due to a combination of stabilizing effects exerted on the subunits by the detergent and by Crt. The stabilization effect of \( \beta \)-OG on the B820 subunits themselves has been well established, as this detergent is most commonly used in their isolation (2). It is possible that, in analogy to the detergent molecules found in the crystal structures of LH2 and RH (42–44), \( \beta \)-OG molecules specifically occupy Crt binding sites on the subunits, and thus provide interactions that stabilize the complex. In another detergent, LDAO, in which the cooperative effects of Crts on the formation of LH1 complexes have recently been investigated, no such intermediates were observed (27).

The stabilization effect of Crts on pigment-protein complexes appears to have several origins. Traditionally, the hydrophobic interactions of Crts with the amino acid side chains were considered the most important ones (2, 21). However, recent theoretical calculations point out that also intermolecular \( \pi \)–\( \pi \) stacking interactions between Crts and aromatic amino acid side chains have to be taken into account as a stabilizing factor (45). Recently, the forces which stabilize B820 subunits were characterized as originating to a large extent from hydrophobic interactions between N-terminal extensions of the \( \alpha \) and \( \beta \) polypeptides at the membrane interface (2, 23). As pointed out by these authors and also shown in the present study, this stabilizing energy cannot be large, as the B820 subunits retain the ability to interact and bind free Crts. By this binding, Crts then strongly promote further association of the subunits to form larger aggregates. Two modes may be envisioned for the binding of Crts to B820 subunits: 1) Crt molecules bind between the hydrophobic surfaces (the \( \alpha \)-helical stretches of the \( \alpha \) and \( \beta \) polypeptides) of adjacent B820 subunits, thus “cementing” the entire structure; as in other photosynthetic complexes (9, 10, 40, 42), here the interactions of Crt with the long chain alcohol residue of BChl may also play some role; and/or 2) interactions of Crt molecules with \( \alpha \)-helical stretches may cause some rearrangement (and exposure?) of their N-terminal regions, which then enforce intersubunit interactions. In addition to the stabilizing effects of Crts in LH1 complexes discussed above, the increased stability of iB873 formed with Spx in particular may be caused by specific interactions (e.g. hydrogen bonds) of the methoxy side groups of the Crt with the polar residues of the \( \alpha \) and \( \beta \) polypeptides.

In conclusion, the Crt-less B820 subunits are able to interact with different Crts. These interactions promote aggregation of the subunits to complexes, which spectroscopically resemble the native LH1 antenna, and at least one intermediate in the process has been identified. This suggests that B820 subunits
may occur as short-lived intermediates in the assembly of LH1 antenna also in vivo.

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REFERENCES

1. Zuber, H., and Cogdell, R. J. (1995) in Anoxygenic Photosynthetic Bacteria (Blankenship, R. E., Madigan, M. T., and Bauer, C. E., eds) pp. 315–348, Kluwer Academic Publishers, Dordrecht
2. Loach, P. A., and Parkes-Loach, P. S. (1995) in Anoxygenic Photosynthetic Bacteria (Blankenship, R. E., Madigan, M. T., and Bauer, C. E., eds) pp. 437–471, Kluwer Academic Publishers, Dordrecht
3. Fiedor, L., Leupold, D., Truchner, K., Voigt, B., Hunter, C. N., Scherz, A., and Scheer, H. (2001) Biochemistry 40, 3737–3747
4. Sundström, V., and van Grondelle, R. (1995) in Anoxygenic Photosynthetic Bacteria (Blankenship, R. E., Madigan, M. T., and Bauer, C. E., eds) pp. 349–372, Kluwer Academic Publishers, Dordrecht
5. Sundström, V., Pullerits, T., and van Grondelle, R. (1999) J. Phys. Chem. B 103, 2327–2346
6. van Oijen, A. M., Ketelaars, M., Kohler, J., Aartsma, T. J., and Schmidt, J. (1999) Science 285, 400–402
7. van Amerongen, H., Vallum, L., and van Grondelle, R. (2000) Photosynthetic Excitons, World Scientific, Singapore
8. Fiedor, L., Scheer, H., Hunter, C. N., Tschirschwitz, F., Voigt, B., Ehler, J., Nibbering, E., Leupold, D., and Elsaesser, T. (2000) Chem. Phys. Lett. 319, 145–152
9. McDermott, G., Prince, S. M., Freer, A. A., Hawthornthwaite-Lawless, A. M., Papiz, M. Z., Cogdell, R. J., and Isaacs, N. W. (1996) Nature 374, 517–521
10. Koepke, J., Hu, X., Murenke, C., Schulzen, K., and Michel, H. (1996) Structure 4, 581–597
11. Roszak, A. W., Howard, T. D., Southall, J., Gardiner, A. T., Law, C. J., Isaacs, N. W., and Loach, P. A. (2003) EMBO J. 22, 11293–11297
12. Ben-Shem, A., Frolow, F., and Nelson, N. (2004) Science 302, 1632–1640
13. Liu, Z., Yan, H., Wang, K., Kuang, T., Jiping, Z., Gui, L., An, X., and Chang, W. (2004) Nature 428, 287–292
14. Ben-Shem, A., Frolow, F., and Nelson, N. (2003) Nature 426, 630–635
15. Liu, Z., Yan, H., Wang, K., Kuang, T., Jiping, Z., Gui, L., An, X., and Chang, W. (2004) Nature 428, 287–292
16. Kozik, K. N., Ivenson, T. M., Maglaiou, K., Barber, J., and Iwata, S. (2004) Science 303, 1831–1838
17. Bahatyrova, S., Frese, R. N., Siebert, C. A., Olsen, J. D., van der Werf, K. O., van Grondelle, R., Niedermann, R. A., Bullough, P. A., Otto, C., and Hunter, C. N. (2004) Nature 430, 1058–1062
18. Scheuring, S., Sturis, J. N., Prima, V., Bernadac, A., Levy, D., and Rigaud, J.-L. (2004) Proc. Natl. Acad. Sci. U. S. A. 101, 11293–11297
19. Karrasch, S., Bullough, P. A., and Ghosh, R. (1995) EMBO J. 14, 631–638
20. Miller, J. F., Hinchigeri, S. B., Parkes-Loach, P. S., Callahan, P. M., Sprinkle, J. R., Ricehono, J. R., and Loach, P. A. (1987) Biochemistry 26, 5055–5062
21. Ghosh, R., Hauser, H., and Bachofen, R. (1988) Biochemistry 27, 1004–1014
22. Chang, M. C., Callahan, P. M., Parkes-Loach, P. S., Cotton, T. M., and Loach, P. A. (1990) Biochemistry 29, 421–429
23. Sturis, J. N., and Robert, B. (1994) J. Mol. Biol. 238, 445–454
24. Vegh, A. P., and Robert, B. (2002) FEBS Lett. 529, 222–226
25. Aartsma, T. J., and Schmidt, J. (1999) Photosynthesis: From Light to Biosphere (Mathis, P., ed), pp. 919–922, Kluwer, Dordrecht
26. Prince, S. M., Howard, T. D., Myles, D. A. A., Wilkinson, C., Papiz, M. Z., Freer, A. A., Cogdell, R. J., and Isaacs, N. W. (2003) J. Mol. Biol. 326, 307–315
27. Wang, Y., and Hu, X. (2002) J. Am. Chem. Soc. 124, 8445–8451