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EXCITON INTERACTION AMONG CHLOROPHYLL MOLECULES IN BACTERIOCHLOROPHYLL *a* PROTEINS AND BACTERIOCHLOROPHYLL *a* REACTION CENTER COMPLEXES FROM GREEN BACTERIA*

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SUMMARY

Absorption and CD spectra of bacteriochlorophyll *a* proteins and bacteriochlorophyll *a* reaction center complexes from two strains of *Chlorobium limicola* were recorded at 77 °K. Visual inspection showed that the Q_y-band of chlorophyll in either protein was split into at least five components. Analysis of the spectra in terms of asymmetric Gaussian component pairs by means of computer program GAMET showed that six components are necessary to fit the spectra from strain 2K. These six components are ascribed to an exciton interaction between the seven bacteriochlorophyll *a* molecules in each subunit. The clear difference between the exciton splitting in the two bacteriochlorophyll *a* proteins shows that the arrangement of the chlorophyll molecules in each subunit must be slightly different.

The spectra for the bacteriochlorophyll *a* reaction center complexes have a component at 834 nm (absorption) and 832 nm (CD) which does not appear in the spectra of the bacteriochlorophyll *a* proteins. The new component is ascribed to a reaction center complex which is combined with bacteriochlorophyll *a* proteins to form the bacteriochlorophyll *a* reaction center complex. The complete absorption (or CD) spectrum for a given bacteriochlorophyll *a* reaction center complex can be described to a first approximation in terms of the absorption (or CD) spectrum for the corresponding bacteriochlorophyll *a* protein plus the new component ascribed to the reaction center complex.

INTRODUCTION

The bacteriochlorophyll *a* protein from the green bacterium *Chlorobium*

* Contribution No. 546 from Charles F. Kettering Laboratory.

Supplementary data to this article, giving details of computer resolved components of absorption and CD spectra can be obtained on request f om: Elsevier Scientific Publishing Company, BBA Data Deposition, P.O. Box 1527, Amsterdam, The Netherlands. Reference should be made to No. BBA/00/037/47091/XXX(1976)XXX.

limicola 2K† has three subunits, each consisting of a core of seven bacteriochlorophyll *a* molecules wrapped in a polypeptide blanket of at least 327 residues [1]. The average center-to-center distance between neighboring bacteriochlorophyll *a* molecules is 12 Å within one subunit, and is 24 Å between nearest chlorophyll molecules in different subunits of the same trimer. From the close packing within subunits, an exciton interaction between the seven chlorophyll molecules is expected to give rise to splittings in the energy levels of the Q_x- and Q_y-bands. Such an exciton splitting may give rise to multiple components (maximum of seven) in both the absorption spectrum (dipole strength) and the CD spectrum (rotational strength). The total dipole strength (given by the area under the absorption curve) is not greatly affected by the exciton interaction, but the rotational strenghts (given by the positive and negative areas of the components in the CD spectrum) are largely induced by the exciton interaction. (Monomeric bacteriochlorophyll *a* shows very weak optical activity [2].)

An exciton splitting has already been observed in the absorption and CD spectra of the bacteriochlorophyll *a* protein at 77 °K [2, 3]. In the absorption spectrum the Q_x-band was split into three sharp components and the Q_y-band was split into three sharp components plus one broad component [3]. The CD spectrum further showed that the Q_y-band was split into at least five components [2]. By means of computer program GAMET* the absorption and CD spectra were resolved concurrently in terms of five asymmetric Gaussian components [2] which are listed in Table I. These components indicated the existence of a strong exciton interaction

TABLE I

FIVE COMPUTER-RESOLVED COMPONENTS OF ABSORPTION AND CD SPECTRA OF BACTERIOCHLOROPHYLL *a* PROTEIN FROM STRAIN 2K

FWHM, full width at half maximum for left half of asymmetric Gaussian curve.

Component pair	λ (nm)		Relative dipole strength	Relative rotational strength	FWHM (nm)	Skew
	A	CD				
1	(a) 792	787	13	− 8	13.2	0.65
	(b) 791	791	12	− 5	18.7	0.41
2	(a) 804	800	37	18	9.8	0.65
	(b) 805	798	41	11	13.7	0.56
3	(a) 813	812	35	35	6.6	0.75
	(b) 810	811	2	3	5.5	0.52
4	(a) 817	814	3	−22	6.6	0.65
	(b) 814	814	33	− 5	7.1	0.89
5	(a) 824	823	13	−17	8.3	0.82
	(b) 825	822	12	− 7	8.4	0.75

(a) Philipson and Sauer [2] and (b) this work.

† *Chlorobium limicola* 2K is the green component of the mixed culture known as "*Chloropseudomonas ethylica* 2K" [4, 5].

* Computer program GAMET was written in 1973 by C. Lederer at the Lawrence Berkeley Laboratory, University of California.

rather than the existence of five difference protein environments for bacteriochlorophyll *a*, because the relative dipole strengths varied from 3 to 37 instead of all values being the same or multiples of the lowest value. Therefore Philipson and Sauer [2] proposed an exciton interaction between at least five chlorophyll molecules spaced 12–15 Å apart in each subunit of the bacteriochlorophyll *a* protein. Since it is now known from the X-ray diffraction study of Fenna and Matthews [1] that each subunit contains seven chlorophyll molecules, we were interested to determine whether there is any empirical spectral evidence for more than five components in the exciton splitting of the Q_y-band of chlorophyll in the bacteriochlorophyll *a* protein from *C. limicola* 2K.

In addition we wished to record for comparison the exciton splitting in the bacteriochlorophyll *a* protein from a second green bacterium, *C. limicola* f. *thiosulfatophilum* 6230 (Tassajara). Strain Tassajara comes from Lake Tassajara in California, whereas strain 2K comes from Kuyal'nik estuary of the Black Sea [5]. The biochemical properties of the two chlorophyll proteins are sufficiently different (Olson, Shaw and Engelberger, unpublished) to warrant an investigation of possible differences in chlorophyll-chlorophyll interactions.

Finally, we wanted to compare the spectral properties of pure bacteriochlorophyll *a* proteins with the properties of bacteriochlorophyll *a* reaction center complexes. These complexes (mol. wt. $> 1.5 \cdot 10^6$) are derived from *Chlorobium* vesicles, are free of *Chlorobium* chlorophyll, and are photochemically active [7]. Their absorption spectra at 77–100 °K show striking similarities to the spectra of the corresponding bacteriochlorophyll *a* proteins [8, 9]. We wished to determine the CD spectra of the complexes at 77 °C in order to show more precisely the relationship between the exciton interaction in a given bacteriochlorophyll *a* protein and the interaction in the corresponding bacteriochlorophyll *a* reaction center complex.

MATERIALS AND METHODS

Bacteriochlorophyll *a* proteins and bacteriochlorophyll *a* reaction center complexes were prepared at Brookhaven National Laboratory from *C. limicola* 2K and *C. limicola* f. *thiosulfatophilum* 6230 (Tassajara) as described previously [8].

Absorption and CD spectra of samples at 77 °K were recorded at the Kettering Laboratory with a Cary 14 recording spectrophotometer and a custom built CD recording spectrophotometer [10].

The experimental spectra were analyzed in terms of asymmetric Gaussian curves by means of computer program GAMET used in conjunction with a Control Data Corporation 6600 computer in the Central Scientific Computing Facility at Brookhaven National Laboratory. Each pair of spectra (absorption and CD) was analyzed as a single composite spectrum with the requirement that each pair of components (absorption and CD) share a common bandwidth and skew. The analysis shown in Table II and Fig. 1 (bacteriochlorophyll *a* protein from strain 2K) is described in detail to illustrate the general procedure.

Each Gaussian component is specified by four parameters: wavelength, area, bandwidth and skew. Six pairs of components are chosen by the scientist to fit the absorption and CD spectra. Since each pair shares the same bandwidth and skew, only six parameters are necessary to specify each pair of components, and only

TABLE II

SIX COMPUTER-RESOLVED COMPONENTS OF ABSORPTION AND CD SPECTRA OF BACTERIOCHLOROPHYLL *a* PROTEIN FROM STRAIN 2K

FWHM, full width at half maximum for left half of asymmetric Gaussian curve.

λ (nm)		Relative dipole strength	Relative rotational strength	FWHM (nm)	Skew
A	CD				
(1) 789.2	791.0	9.2	−5.5	18.6	0.43
(2) 799.5	798.4	15.0	10.5	14.3	0.49
(3) 805.4	805.4F*	28.1	0.1	8.9	0.78
(4) 810.1	810.8	1.6	3.3	5.7	0.48
(5) 813.9	813.6	34.1	−5.3	7.3	0.86
(6) 825.1	821.6	12.0	−6.7	8.4	0.75

* The symbol F denotes a fixed parameter.

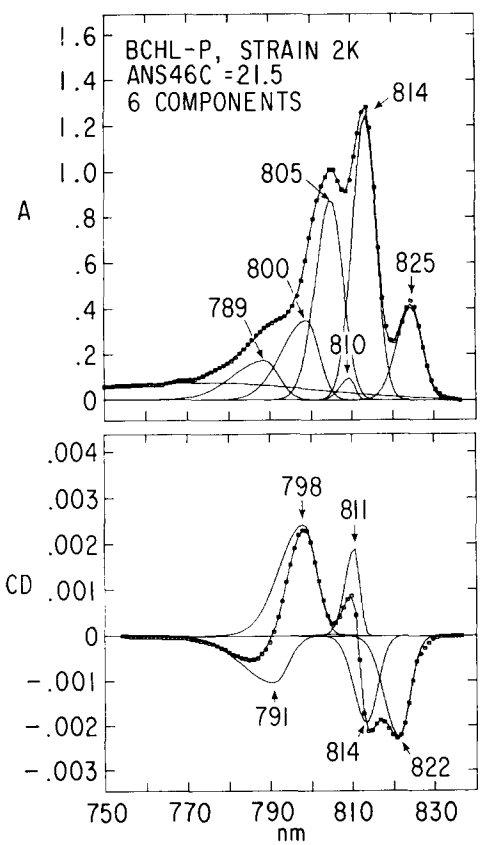

Fig. 1. Six computer-resolved component pairs for absorption and CD spectra of bacteriochlorophyll *a* protein from strain 2K (ANS46c). Out of 39 parameters, 38 were free to vary. $\chi^2 = 21.5$.

36 parameters are required to specify six pairs of components. In addition to the six pairs of components, the absorption spectrum requires a broad "baseline" component centered at the blue end of the spectrum to compensate for the fact that the absorption spectrum never returns to zero on the blue side of the spectrum. Since only half of the "baseline" component is used in the analysis, the skew is fixed at 1.0, and only three parameters are allowed to vary in the process of refining the analysis. The total number of parameters for this analysis is thus 36+3 = 39. An initial guess is prepared in which initial values are assigned to each of the 39 parameters. Then the computer improves the initial guess with certain parameters held fixed and other parameters allowed to vary. If enough parameters are held fixed, the computer finds a solution which converges (i.e. "Chi Sq.", the sum of squares of difference between computed solution and experimental data, reaches a local minimum). The solution then becomes the initial guess for further improvement with fewer parameters held fixed. The final solution (with minimum Chi square) is obtained when the computer finds a solution which converges with all (or almost all) parameters allowed to vary. Each final solution was graphed on the CalComp plotter by the computer.

RESULTS AND DISCUSSION

Bacteriochlorophyll *a* reaction center complexes from both strains were prepared with the reaction centers either fully reduced (by ascorbate) or fully oxidized (by ferricyanide). As shown in Fig. 2 the absorption spectra for both reduced and oxidized complexes show a pattern of three peaks at 805, 814 and approx. 825 nm (strain 2K) or 805, 815 and approx. 823 nm (strain Tassajara) quite similar to the pattern for the corresponding bacteriochlorophyll *a* protein. Likewise the CD spectra for the complex and the protein from strain 2K show a pattern with peaks and troughs at approx. 784 (−), approx. 796 (+), approx. 804 (−), 810 (+), 814 (−), and 821 nm (−). For strain Tassajara the CD spectra show a different pattern with peaks and troughs at approx. 797 (+), approx. 806 (−), approx. 813 (+), and 821 nm (−). Two new spectral features are unique to bacteriochlorophyll *a* reaction center complexes: an absorption peak at 834 nm and a positive CD peak at 831 nm. These new features are tentatively ascribed to chlorophyll other than *P*-840 in the reaction center, while the other components are ascribed to bacteriochlorophyll *a* proteins in each complex. The previous comparison at room temperature of bacteriochlorophyll *a* protein and complex from strain Tassajara indicated a new CD band at 837 nm for the complex, but failed to show the correspondence between the other CD peaks and troughs for protein and complex [8].

Analysis of spectra for bacteriochlorophyll a proteins

Initially we analyzed our data (Fig. 2) for the bacteriochlorophyll *a* protein from strain 2K in terms of five asymmetric Gaussian components as did Philipson and Sauer [2] with their earlier data. (This analysis required 129 refinements.) As shown in Table I this analysis contained one major flaw, a 7-nm difference between the components of absorption (805.1 nm) and CD (798.1 nm) in the second pair. This flaw was rectified by adding a sixth component at 799.5 nm to the absorption spectrum and a sixth component at 805.4 nm to the CD spectrum. After 13 refinements these additions greatly improved the resolution of the absorption spectrum with little effect

on the CD spectrum (see Table II and Fig. 1). The addition of a seventh component at 825 nm improved the fit to the CD spectrum in that region, but we attributed the anomalous shape of the spectrum to the effect of powerful xenon emission lines at 828.0 and 823.2 nm [11], in the light source of the CD spectrophotometer. Therefore on spectral evidence alone only six components can be justified for the resolution of our data.

Our data for the bacteriochlorophyll *a* protein from strain Tassajara were also

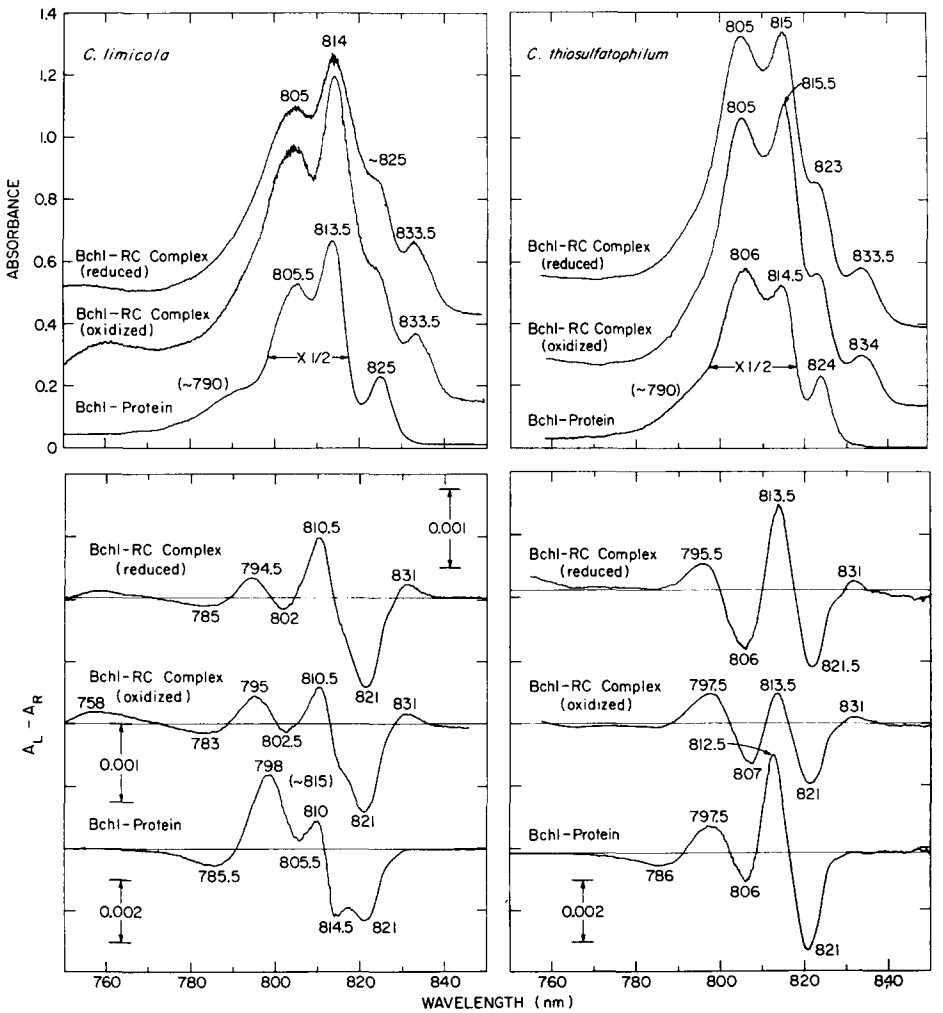

Fig. 2. Absorption and CD spectra of bacteriochlorophyll *a* proteins and bacteriochlorophyll *a* reaction center complexes in 50 % glycerol at 77 °K. Light path, 1.0 mm. Spectra for strain 2K are on the left; for strain Tassajara on the right. Bacteriochlorophyll *a* proteins were dissolved in 10 mM Tris (pH 8) and approx. 0.1 M NaCl before mixing with 60 % glycerol (1:4, v/v). Bacteriochlorophyll *a* reaction center complexes were dissolved in 10 mM phosphate (pH 7.4) and approx. 35 % sucrose. Either $K_3Fe(CN)_6$ (35 mM) or sodium ascorbate (solid) was added to oxidize or reduce the reaction centers before mixing with 60 % glycerol (1:4, v/v).

TABLE III

FIVE COMPUTER-RESOLVED COMPONENTS OF ABSORPTION AND CD SPECTRA OF BACTERIOCHLOROPHYLL *a* PROTEIN FROM STRAIN TASSAJARA

FWHM, full width at half maximum for left half of asymmetric Gaussian curve.

λ (nm)		Relative dipole strength	Relative rotational strength	FWHM (nm)	Skew
A	CD				
(1) 789.4	789.5	0.5	−4.2	18.2	0.40
(2) 800.8	799.2	26.8	5.9	21.8	0.37
(3) 807.0	807.4	50.1	−6.0	9.5	1.54
(4) 815.7	812.5	13.1	8.9	5.8	0.86
(5) 824.0	821.0	9.4	−7.3	5.5	1.07

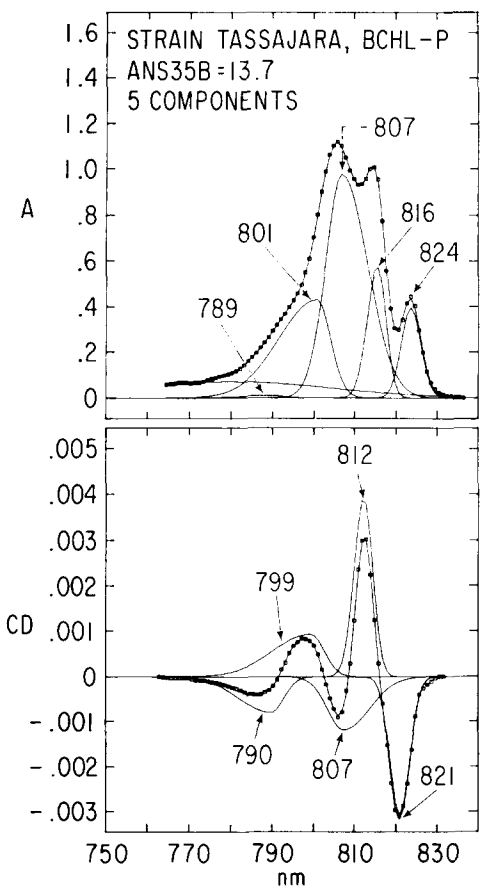

Fig. 3. Five computer-resolved component pairs for absorption and CD spectra of bacteriochlorophyll *a* protein from strain Tassajara (ANS35b). All 33 parameters were free to vary. $\chi^2 = 13.7$.

analyzed in terms of five components as shown in Table III and Fig. 3. This resolution is unsatisfactory because the third component, 807.0 (807.4), has a large skew (1.54) toward the red. This large skew suggests that at least six components would be required to resolve these data in terms of components either symmetrical or skewed toward the blue. (Our attempt to obtain a satisfactory resolution in terms of six components was not successful.)

Analysis of spectra for bacteriochlorophyll a reaction center complexes

In order to fit the spectral data for the oxidized bacteriochlorophyll *a* reaction center complex from strain 2K, a seventh component pair at approx. 833 (831) nm was added to the six-component analysis for the bacteriochlorophyll *a* protein (Table II and Fig. 1.) The analysis was refined until convergence was obtained with 53 parameters out of 58 allowed to vary. As shown in Table IV and Fig. 4 this analysis is

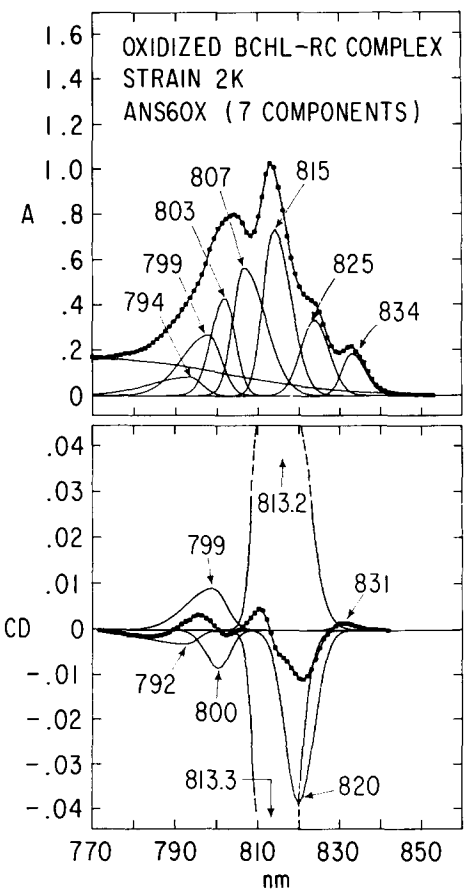

Fig. 4. Seven computer-resolved component pairs for absorption and CD spectra of oxidized bacteriochlorophyll *a* reaction center complex from strain 2K (ANS6OX). Out of 45, 41 parameters were free to vary. $\chi^2 = 22.4$.

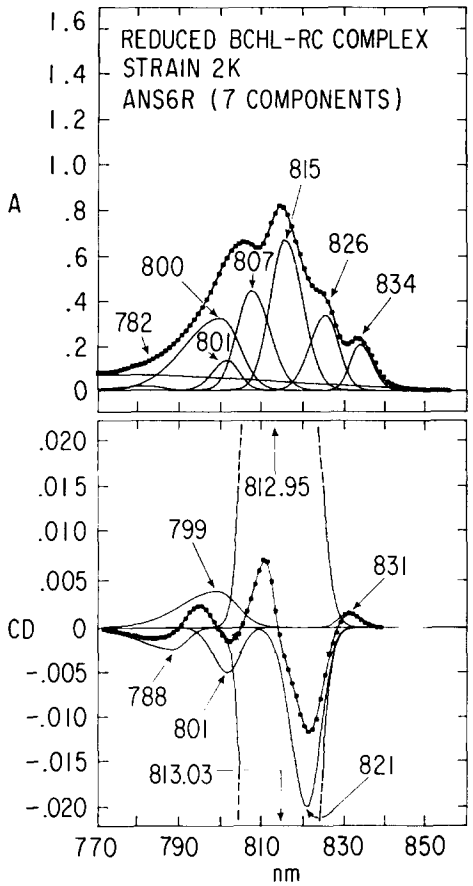

Fig. 5. Seven computer-resolved component pairs for absorption and CD spectra of reduced bacteriochlorophyll *a* reaction center complex from strain 2K (ANS6R). Out of 45 parameters, 42 were free to vary. $\chi^2 = 41.2$.

unsatisfactory in the following respects. Two CD components (813.2 and 813.3 nm) are only 0.1 nm apart, and the fourth, fifth and seventh component pairs have skews far in excess of 1.0.

The analysis (Table IV and Fig. 4) for the oxidized complex was then further refined to fit the data for the reduced complex. Convergence was finally obtained with 54 parameters out of 58 allowed to vary. As shown in Table IV and Fig. 5 this analysis is less than satisfactory for the same reasons that the analysis for the oxidized complex is unsatisfactory.

For the spectral data from the reduced bacteriochlorophyll *a* reaction center complex from strain Tassajara the analysis was carried out for five component pairs only. Final convergence occurred with 32 out of 33 parameters free to vary. Results are shown in Table V and Fig. 6. These results were then combined with the spectral data from the oxidized complex to give the results shown in Table V and Fig. 7. Final convergence was again obtained with 32 out of 33 parameters free to vary.

TABLE IV

COMPARISON OF SPECTRAL COMPONENTS FOR BACTERIOCHLOROPHYLL *a* PROTEIN AND BACTERIOCHLOROPHYLL *a* REACTION-CENTER COMPLEXES FROM STRAIN 2K

RDS, relative dipole strength. RRS, relative rotational strength. FWHM, full width at half maximum for left half at asymmetric Gaussian curve.

Component	Parameter	Bacteriochlorophyll *a* protein	Bacteriochlorophyll *a* reaction center complex	
			Oxidized	Reduced
I	λ_A	789.2	794.0	782.0
	λ_{CD}	791.0	792.2	788.0
	RDS	9.2	5.5	1.2
	RRS	−5.5	−2.1	−1.6
	FHWM	18.6	23.4	19.0
	Skew	0.43	0.29	0.41
II	λ_A	799.5	798.7	799.6
	λ_{CD}	798.4	799.0	798.9
	RDS	15.0	13.8	24.4
	RRS	10.5	4.6	3.0
	FWHM	14.3	15.8	20.9
	Skew	0.49	0.46	0.53
III	λ_A	805.4	802.6	801.2
	λ_{CD}	805.4F	800.2	801.2
	RDS	28.1	13.4	4.8
	RRS	0.1	−2.6	−1.8
	FWHM	8.9	7.8	8.3
	Skew	0.78	0.78	0.86
IV	λ_A	810.1	807.3	807.0
	λ_{CD}	810.8	813.2	812.95
	RDS	1.6	23.6	20.1
	RRS	3.3	62.0	193.9
	FWHM	5.7	6.3	8.2
	Skew	0.48	1.98	1.33
V	λ_A	813.9	814.7	815.2
	λ_{CD}	813.6	813.3	813.03
	RDS	34.1	25.9	29.8
	RRS	−5.3	−51.0	−188.5
	FWHM	7.3	6.2	8.2
	Skew	0.86	1.56	1.27
VI	λ_A	825.1	824.8	825.5
	λ_{CD}	821.6	820.0	820.6
	RDS	12.0	12.2	13.4
	RRS	−6.7	−14.1	−7.9
	FWHM	8.4	8.1	9.0
	Skew	0.75	1.04	0.87
VII	λ_A		834.0	834.0
	λ_{CD}		831.2	830.8
	RDS		5.5	6.3
	RRS		0.4	0.5
	FWHM		5.7	5.5
	Skew		1.36	1.35

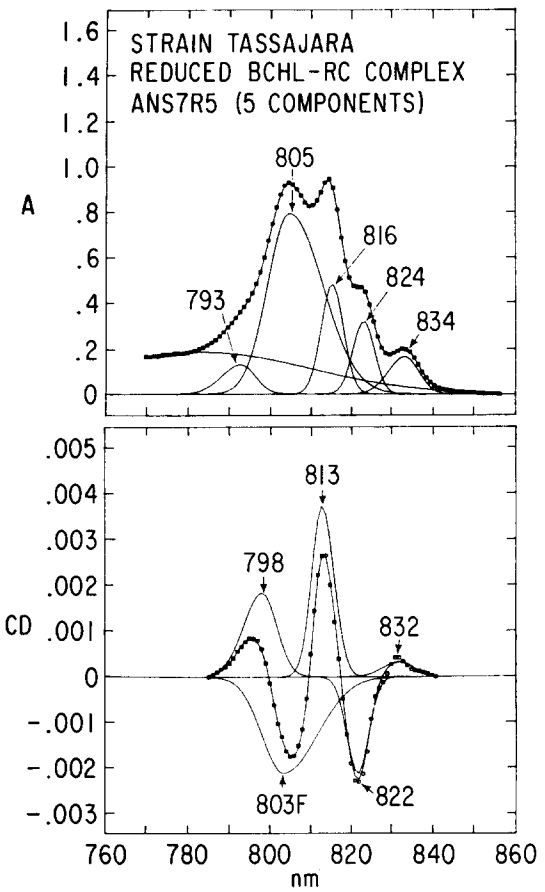

Fig. 6. Five computer-resolved component pairs for absorption and CD spectra of reduced bacteriochlorophyll *a* reaction center complex from strain Tassajara (ANS7R5). Out of 33 parameters, 32 were free to vary. $\chi^2 = 9.0$.

either strain are examined together, it can be seen that the components for strain 2K fall into seven groups (Table IV) and for strain Tassajara into six groups (Table V).

For strain 2K component I in the complex is weaker in both dipole strength and rotation strength than it is in the free protein. Component II is weaker in rotational strength in the complex than in the free protein. Component III in the complex is weaker in dipole strength, but stronger in rotational strength. Component IV in the complex is much stronger in both dipole strength and rotational strength. Component V in the complex is much stronger in rotational strength only. Component VI is about the same in both complex and free protein, while component VII is present only in the complex.

For strain Tassajara, component I in the complex is undetectable. Component II in the complex is weaker in rotational strength. Component III is stronger in rotational strength in the complex. Components IV and V are about the same in both complex and free protein. Component VI is present only in the complex.

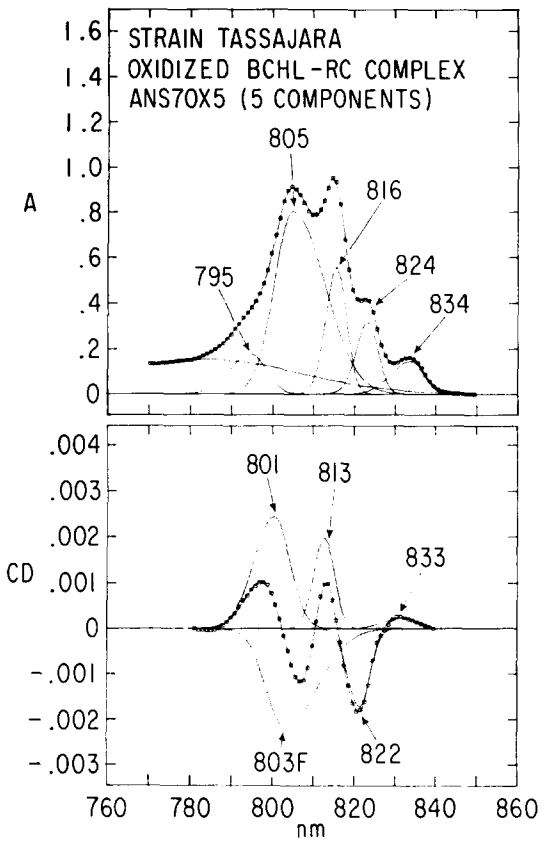

Fig. 7. Five computer-resolved component pairs for absorption and CD spectra of oxidized bacteriochlorophyll *a* reaction center complex from strain Tassajara (ANS7OX5). Out of 33 parameters, 32 were free to vary. $\chi^2 = 8.4$.

Components I, II, III, IV and VII for strain 2K appear comparable to components I, II, III, V and VI for strain Tassajara. For both strains the change in component I is about the same in going from the free protein to the complex. Likewise the change in component II is about the same, and the change in component III is similar. Components VI (2K) and V (Tassajara) hardly change at all.

CONCLUSIONS

(1) The exciton interaction in the bacteriochlorophyll *a* protein from strain Tassajara is distinctly different from that in the bacteriochlorophyll *a* protein from strain 2K. This means that at least some of the positional and rotational coordinates of the chlorophyll molecules in the one subunit must be different from those in the other subunit.

(2) Resolution of the absorption and CD spectra of bacteriochlorophyll *a* protein from 2K requires six asymmetric Gaussian components skewed towards the blue. For bacteriochlorophyll *a* protein from strain Tassajara more than five such

TABLE V

COMPARISON OF SPECTRAL COMPONENTS FOR BACTERIOCHLOROPHYLL *a* PROTEIN AND BACTERIOCHLOROPHYLL *a* REACTION CENTER COMPLEXES FROM STRAIN TASSAJARA

RDS, relative dipole strength. RRS, relative rotational strength. FWHM, full width at half maximum for left half of asymmetric Gaussian curve.

Component	Parameter	Bacteriochlorophyll *a* protein	Bacteriochlorophyll *a* reaction center complex	
			Oxidized	Reduced
I	λ_A	789.4		
	λ_{CD}	789.5		
	RDS	0.5		
	RRS	−4.2		
	FWHM	18.2		
	Skew	0.40		
II	λ_A	800.8	794.7	793.3
	λ_{CD}	799.2	800.7	798.2
	RDS	26.8	9.2	6.1
	RRS	5.9	12.7	8.7
	FWHM	21.8	11.9	11.0
	Skew	0.37	0.76	0.76
III	λ_A	807.0	805.1	805.1
	λ_{CD}	807.4	803.3	803.3
	RDS	50.1	57.6	61.9
	RRS	−6.0	−15.8	−16.5
	FWHM	9.5	10.7	12.4
	Skew	1.54	1.71	1.56
IV	λ_A	815.7	815.9	815.7
	λ_{CD}	812.5	813.1	813.1
	RDS	13.1	16.5	15.2
	RRS	8.9	5.9	11.8
	FWHM	5.8	6.3	6.3
	Skew	0.86	0.91	1.05
V	λ_A	824.0	823.6	823.6
	λ_{CD}	821.0	821.8	821.8
	RDS	9.4	9.9	9.8
	RRS	−7.3	−5.4	−6.5
	FWHM	5.5	6.7	6.3
	Skew	1.07	0.88	0.98
VI	λ_A		834.4	833.7
	λ_{CD}		833.3	832.1
	RDS		6.8	7.0
	RRS		1.1	1.4
	FWHM		11.5	9.6
	Skew		0.64	0.84

Comparison of bacteriochlorophyll a proteins to bacteriochlorophyll a reaction center complexes

When the spectral components for the bacteriochlorophyll *a* protein and the bacteriochlorophyll *a* reaction center complex (oxidized and reduced forms) from

components appear to be required. No satisfactory resolution has yet been obtained.

(3) The absorption (or CD) spectrum for either bacteriochlorophyll *a* reaction center complex is to a first approximation the sum of the spectrum for the corresponding bacteriochlorophyll *a* protein plus a new absorption (or CD) band at 834 nm (or 832 nm). This suggests that the bacteriochlorophyll *a* reaction center complex may be composed of bacteriochlorophyll *a* proteins combined with a reaction center complex with absorption and CD bands at 834 and 832 nm, respectively.

(4) The components of the absorption (or CD) spectrum for either complex are different in relative intensity from the corresponding components in the spectrum for the corresponding bacteriochlorophyll *a* protein. This indicates that the conformation of the bacteriochlorophyll *a* proteins in the complex is slightly different from the conformation in the free state.

(5) The components of the absorption (or CD) spectrum for either complex in the reduced state are slightly different in relative intensity from the components in the spectrum for the oxidized state. This means that the conformation of the bacteriochlorophyll *a* proteins in the complex is sensitive to the oxidization state of the reaction center.

(6) The absorption band at 834 nm and the CD band at approx. 832 nm are relatively insensitive to the oxidation state of the reaction center.

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