Biochimica et Biophysica Acta, 681 (1982) 248–255
Elsevier Biomedical Press

BBA 41115

THE CHLOROPHYLL-PROTEIN COMPLEXES OF *ACETABULARIA*

A NOVEL CHLOROPHYLL *a / b* COMPLEX WHICH FORMS OLIGOMERS

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(Received August 28th, 1981)
(Revised manuscript received February 1st, 1982)

Key words: Chlorophyll-protein complex; Thylakoid membrane Light-harvesting chlorophyll a / b complex; Octylglucoside; (Acetabularia)

(1) Five minor chlorophyll-protein complexes were isolated from thylakoid membranes of the green alga *Acetabularia* by SDS-polyacrylamide gel electrophoresis, after SDS or octylglucoside solubilization. None of them were related to CP I (Photosystem I reaction center core) or CP II (chlorophyll *a / b* light-harvesting complex). (2) Two complexes (CPa-1 and CPa-2) contained only chlorophyll (Chl) *a*, with absorption maxima of 673 and 671 nm, and fluorescence emission maxima of 683 nm compared to 676 nm for CP II. The complexes had apparent molecular masses of 43–47 and 38–40 kDa, and contained a single polypeptide of 41 and 37 kDa, respectively. They each account for about 3% of the total chlorophyll. (3) Three complexes had identical spectra, with Chl *a / b* ratios of 3–4 compared to 2 for thylakoid membranes, and a pronounced shoulder around 485 nm indicating enrichment in carotenoids. One of them was the complex 'CP 29' (Camm, E.L. and Green, B.R. (1980) Plant Physiol. 66, 428–432) and the other two were slightly different oligomeric forms of CP 29. They could be formed from CP 29 during reelectrophoresis; but about half the complex was isolated originally in an oligomeric form. Together they account for at least 7% of the total chlorophyll. Their function is unknown.

Introduction

When chloroplast thylakoid membranes are solubilized with low concentrations of SDS and electrophoresed on SDS-polyacrylamide gels, a large proportion of the chlorophyll is found as chlorophyll-protein complexes [1]. The major complexes are CP I (P-700-Chl *a* protein) which contains the reaction center of PS I, and CP II (light-harvesting Chl *a/b* complex, or LHC) which is associated with PS II but does not contain the reaction center. In addition, various dimers and oligomers of the LHC have been reported [2–8]. In the case of the green alga, *Acetabularia*, a prominent oligomer with an apparent molecular mass of 64 kDa has been characterized [9,10]: it will be referred to here as CP II*.

We have recently reported an improved procedure for fractionating thylakoid membranes using the nonionic detergent octylglucoside [11,12]. This detergent allows the preservation of three minor chlorophyll-protein complexes, which can be resolved on polyacrylamide gels containing 0.1% SDS. Two of the complexes contain only Chl *a* and appear to be similar to CP III and CP IV of

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Abbreviations: Chl, chlorophyll; CP I, P-700-Chl *a* protein; LHC, light-harvesting Chl *a / b* protein complex; CP II, 'monomer' form of LHC; CP II*, oligomer form LHC; PS; photosystem.

Chlamydomonas [13] and Chla-P2 and -P3 of barley [14]. On the basis of genetic evidence, one or both of these complexes may be derived from PS II reaction center [13,14]. The third complex isolated from octylglucoside extracts contains both Chl *a* and *b* but is quite distinct from the LHC. It has a higher Chl *a/b* ratio than the LHC and contains a single 29 kDa polypeptide which gives a different proteolytic digestion pattern from those of the two LHC polypeptides [11]. It resembles the Chl *a/b* complex isolated from *Vicia* by Machold and Meister [15]. This complex, termed CP 29, has been isolated from a number of higher plants as well as a green alga [12]. We have proposed that it is associated with PS II, perhaps as an internal antenna [16].

SDS solubilization of *Acetabularia* thylakoid membranes followed by SDS-polyacrylamide gel electrophoresis produced a total of five minor chlorophyll-protein complexes, three of which contained both Chl *a* and *b* [16,17]. The same complexes could also be detected using octylglucoside solubilization. This paper reports the isolation and characterization of these complexes, none of which are related either to CP I or to the various forms of LHC. The Chl *a/b* complexes are particularly interesting in this organism because they consist of a monomer (CP 29) and two slightly different oligomers, both of which can be formed by reassociation of the monomer during electrophoresis.

Methods

Acetabularia cliftonii was cultured and chloroplasts were isolated as previously described [18,19]. Soluble proteins were removed by three to four washes with $Na_4P_2O_7$-HCl (pH 7.6) and coupling factor and several other polypeptides by overnight dialysis against 0.1 M Tris-HCl, 10 mM EDTA, 10 mM mercaptoethanol (pH 7.6) [20], or by several washes with 2 M NaBr [21]. If the membranes were not used immediately, they were suspended in a small volume of sample buffer (65 mM Tris-HCl, 5 mM dithiothreitol, 10% glycerol, pH 6.8) and stored at −70°C. All other operations, including electrophoresis, were carried out at 4°C unless otherwise noted.

For the isolation of chlorophyll-protein complexes using SDS solubilization, the washed membranes were suspended in sample buffer at 1 mg Chl/ml. SDS (British Drug House) was added from a 20% (w/v) solution to give an SDS/Chl ratio of 10 (w/w), and the samples were left on ice for 45–60 min before electrophoresis. We have not experienced any difficulty with this SDS precipitating in the cold. In some experiments, membranes were preincubated for 30 min in sample buffer containing 5 mM $MgCl_2$, pelleted at 35000 $\times g$, and suspended in the same buffer before addition of SDS.

In some experiments, washing solutions included the protease inhibitors *p*-aminobenzamidine (6 mM), phenylmethylsulfonyl fluoride (1 mM) and ϵ-aminocaproic acid (40 mM). Sample buffer contained the same inhibitors at concentrations of 6, 1 and 4 mM, respectively.

For octylglucoside solubilization, membranes were washed once in 2 mM Tris-maleate (pH 7.0) and pelleted at 20000 $\times g$. The pellet was suspended in 30 mM octylglucoside in 2 mM Tris-maleate (pH 7.0) to give a detergent/Chl ratio of about 20, left on ice for 30 min, then centrifuged at 105000 $\times g$ for 30 min. The extract was used for the isolation of complexes.

Complexes were separated on nondissociating gels in the cold as previously described [11,20]. The gel was protected from light with a loose aluminum foil cover. For purification of complexes, the first step was a 3 mm thick, 7.5% polyacrylamide gel with 60–80 μg Chl per 10 mm wide slot. Electrophoresis was continued for 6–7 h, or until the free chlorophyll front had migrated 8–9 cm in the running gel. Complexes were cut out, pooled and rerun on a 1.5 mm thick 10% gel with 25 mm long sample slots. The complexes eluted efficiently and formed a narrow band in the stacking gel if the gel slices were chopped into pieces of about 1–2 mm^3 and the current was kept at 10–15 mA for the first hour. Slices containing purified complexes were cut and stored at −70°C.

For analysis of polypeptides, gel slices were broken up into small particles, then extracted with 2% SDS in sample buffer and heated to 50 or 100°C depending on the experiment.

The proportions of chlorophyll in each complex were determined by scanning gels of whole membranes with a Helena R and D scanning densitom-

eter equipped with a 680 nm filter.

Absorption spectra were determined on gel slices at room temperature with a Unicam SP1750 spectrophotometer, using a gel slice from an empty lane as a blank. Reproducible results were obtained with samples having an A_{max} of less than 0.01. Chl *a*/*b* ratios were determined by the method of Ogawa and Shibata [22]. Gel slices were homogenized with a small volume of methanol in the cold, and the polyacrylamide removed by centrifugation at 12000 × *g* for 10 min. The change in absorbance at 665 nm after the addition of hydroxylamine was monitored until the reaction went to completion (4–5 min).

Fluorescence emission spectra were obtained using 442 nm light from a Spectrophysics He-Cd laser, filtered through a Corning CS5-58 or 5-61 filter to remove He and Cd lines above 500 nm. Gel slices were held between two small pieces of microscope slide glass in a brass holder immersed in liquid N_2 in a small Dewar flask with unsilvered windows, and oriented at approx. 45° to the source so that the front surface was illuminated. The light emitted at 90° to the source was filtered through a Corning CS3-70 filter and detected with a Bausch and Lomb monochromator equipped with an RCA 8645 photomultiplier. The filter-monochromator-photomultiplier combination was calibrated for wavelength using a neon instrument lamp, and for variations in instrumental response as a function of wavelength using a National Bureau of Standards L-101 lamp.

Results and Discussion

Dissociation of thylakoid membranes with SDS and octylglucoside

The complexes separated electrophoretically from SDS or octylglucoside extracts are shown in Fig. 1. In the samples solubilized with SDS, the major bands are CP I and CP II, as expected. The sample dissociated in the absence of Mg^{2+} also has a fairly prominent CP II* band. This band is markedly reduced when samples are preincubated and solubilized in the presence of 5 mM $MgCl_2$. Addition of $MgCl_2$ after the addition of SDS does not have this effect. Three minor complexes, labelled D, CPa-1 and CPa-2, are found in the 38–50 kDa region of the gel, between CP II and

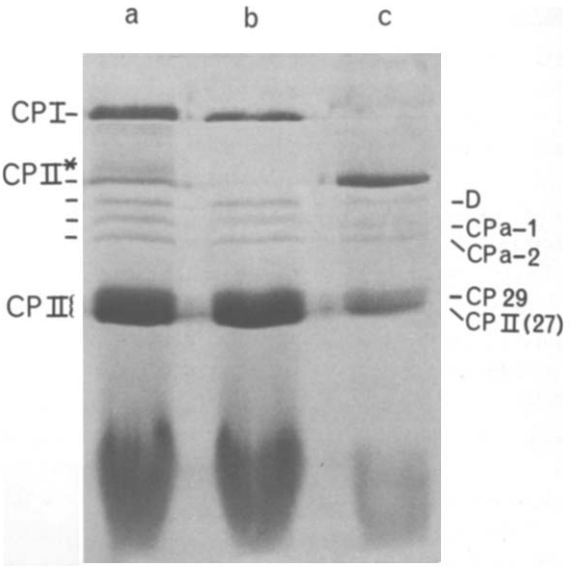

Fig. 1. Chlorophyll-protein complexes of *Acetabularia cliftonii*. First electrophoresis on SDS-polyacrylamide gel. (a) Solubilized with SDS in the absence of Mg^{2+}, (b) solubilized with SDS in the presence of 5 mM Mg^{2+}, (c) solubilized with octylglucoside, 105000 × *g* supernatant. Gel is unstained. Symbols are defined in the text.

CP II*. The percentage of total chlorophyll in each minor complex is about 3%, regardless of whether or not Mg^{2+} is present. The decrease in chlorophyll background in the region near the minor complexes makes it easier to purify these complexes after Mg^{2+} treatment of the membranes. Our observations on the effect of Mg^{2+} on the LHC are in agreement with those of Aro and Valanne [5] and are discussed elsewhere [23].

There are several differences in samples solubilized with octylglucoside. As we have previously reported for higher plants [11,12], most of the LHC is preserved as the CP II* oligomer and the CP II band is drastically decreased (Fig. 1c). There is no band at the CP I position, although there is a small amount of Chl *a*-containing material higher up on the gel, which is thought to be a CP I oligomer [11]. Most of the CP I remains in the 105000 × *g* pellet, which can be solubilized with 2% SDS (data not shown).

In contrast, all three of the minor complexes found in SDS extracts are also present in octylglucoside extracts. Complex CPa-1 migrates in a

TABLE I

CHARACTERISTICS OF CHLOROPHYLL-PROTEIN COMPLEXES

	Apparent molecular mass (kDa)	Absorption maximum (nm) at 25°C	Chl *a*/*b*	Fluorescence emission maximum (nm) at 77 K [a]	% total Chl	Polypeptides (kDa)
Major complexes						
CP I	82–98	676	35	677, 710	20–30	66
CP II*	55–60	673,654	1.0	675	>50	
CP II	19–21	673,654	0.8 [b]	676, 736		26,27
Minor complexes						
D1/D2	49–51	676, 651	3–4	677	5–7	30
D3 (CP 29)	27–29	675, 652		677		
CP a-1	43–47	673	8	683	3	41
CP a-2	38–40	671	10	683	3	37

[a] Maxima corrected for energy sensitivity of monochromator-photomultiplier combination.

[b] Crude CP II has a Chl *a*/*b* ratio of about 1.1 depending on whether CP 29 is included, but the complex loses Chl *a* on reelectrophoresis [4].

slightly different position, but when cut out and rerun on a second gel it has the same relative mobility as the CPa-1 band from the SDS extract. As a result of the decreased amount of chlorophyll in the CP II band, a fourth minor complex can be seen running just behind the CP II band, in the same position as the higher plant complex CP 29. In some gels, it is quite clearly separated from CP II (Fig. 3a).

The percentages of total membrane chlorophyll associated with each complex were estimated from densitometer scans of both SDS and octylglucoside extracts and are given in Table I.

The 'D' family of complexes: oligomers of CP 29

When the chlorophyll-protein complexes separated by electrophoresis from extracts of either detergent were rerun on a second gel, most of them migrated in the same relative positions (Fig. 2). Some of the CP II* broke down to CP II, providing a convenient marker. The one exception was complex D, which split into three bands: two closely spaced bands (D-1 and D-2) at the original D position, and a third band (D-3) migrating just behind the CP II band with an apparent molecular mass of 27–29 kDa. All samples of D gave the three bands on reelectrophoresis. Reelectrophoresis of the trailing edge of the CP II band from an SDS extract revealed a band at the same position as D-3 (Fig. 2, lane f). Since this is the position where CP 29 would be expected to run if it were present but obscured by CP II, it suggested that CP 29 and D-3 might be the same.

When this hypothesis was tested by reelectrophoresing the CP 29 band from an octylglucoside extract, CP 29 not only gave a band at the same position as D-3, but it also gave two faint bands at the D-1/D-2 position (Fig. 3). The spectrum of a gel slice containing the two new bands was identical to the spectra of D-1, D-2, D-3 and the twice-electrophoresed CP 29 (Fig. 4). This rather surpris-

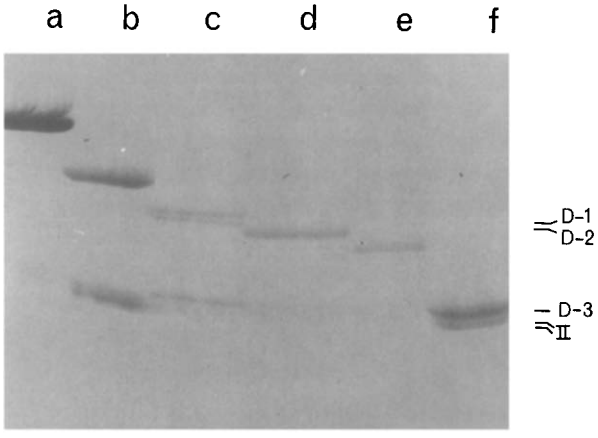

Fig. 2. Second electrophoresis of chlorophyll-protein complexes. (a) CP I, (b) CP II*, (c) complex D, (d) CPa-1, (e) CPa-2, (f) trailing edge of CP II band. Gel is unstained.

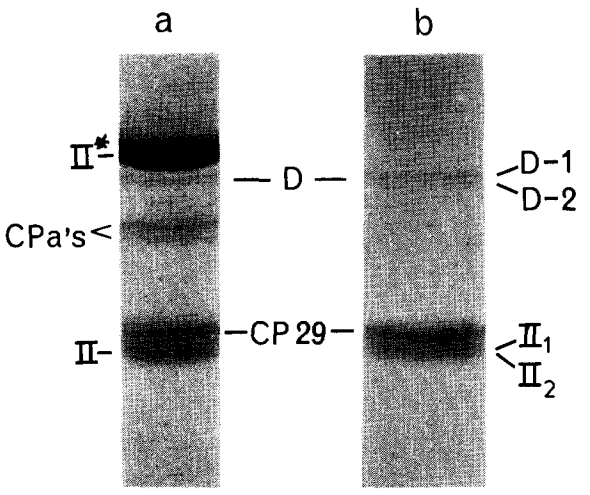

Fig. 3. Reassociation of CP 29 during reelectrophoresis (a) Octylglucoside extract, showing separation of CP 29 and CP II (CP 27) bands; (b) CP 29 excised from first gel and reelectrophoresed. Note that CP II has split into two closely spaced bands [24]. Gels unstained.

ing observation suggested that D-1 and D-2 might be oligomers of CP 29. In support of this, a D-1/D-2 band from the reelectrophoresis of D (as in Fig. 2) gave rise to some D-3 when it was subjected to yet a third electrophoresis. Since the bands had electrophoresed twice at a position corresponding to a molecular mass of 50 kDa, it was highly unlikely that there would be any residual impurity of apparent molecular mass 29 kDa.

These conclusions were confirmed by analysis of the polypeptides. When completely solubilized with 2% SDS, the complexes D-1, D-2 and D-3 gave a single polypeptide of 30 kDa (Fig. 5b–d). The putative D-1/D-2 band formed by reassociation also gave a single 30 kDa band (Fig. 5f). The 30 kDa bands were clearly separated from the 26 and 27 kDa polypeptides of the light-harvesting complex. CP II* was used in this experiment to avoid contamination with several colorless polypeptides which comigrate with CP II [20,24].

The D-1 and D-2 bands can also be formed during reelectrophoresis of the trailing edge of the CP II band from SDS solubilization, or from a similar CP II fraction originating from an octylglucoside pellet solubilized with 2% SDS. The latter shows that not all the CP 29 is solubilized by octylglucoside and that this complex may account

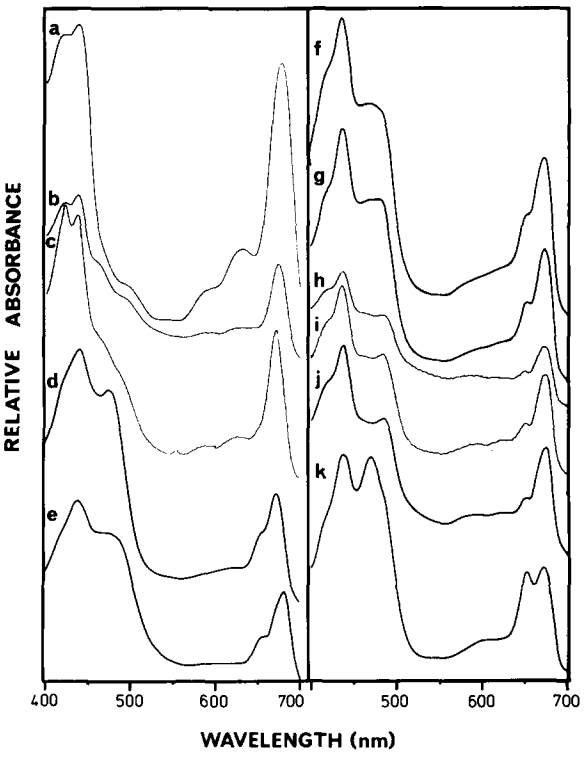

Fig. 4. Absorption spectra of membranes and purified chlorophyll-protein complexes on gel slices at room temperature. All complexes had been subjected to two rounds of electrophoresis with the exception of f. (a) CP I, (b) CP a-1, (c) CP a-2. (d) Membranes solubilized with 2% SDS, in sample buffer; λ_{max} = 652, 673 nm. (e) Membranes suspended in sample buffer, without SDS; λ_{max} = 653, 681 nm. (f) Crude D, (g) CP 29, (h) D-1, (i) D-2, (j) D-1/D-2 formed by reassociation during electrophoresis, (k) CP II*. Absorption maxima of the complexes are given in Table I.

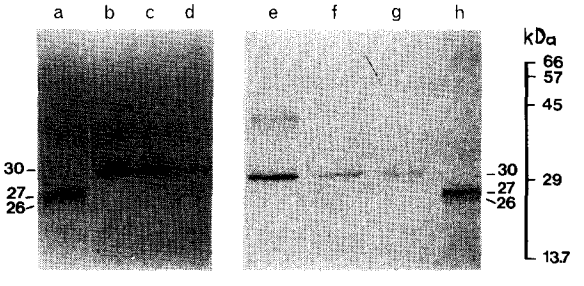

Fig. 5. Polypeptides from purified complexes dissociated with 2% SDS (see Methods). (a) CP II*, (b) D-1, (c) D-2, (d) D-3, (e) D-1/D-2 from reelectrophoresis of D, (f) D-1/D-2 from reassociation of CP 29, (g) D-3, (h) CP II*.

for more than 7% of the total chlorophyll (Table I). Not all samples of CP 29 or the trailing edge of CP II do reassociate, for reasons which we have been unable to discover. Our impression is that the reassociation of CP 29 may simply be a function of its concentration in the stacking gel band. This is the first reported case of reassociation of a chlorophyll-protein complex during reelectrophoresis. Various oligomers of CP I and CP II have been shown to dissociate into the 'monomer' form [1,2,4,6], but none of the monomers has been observed to reassociate.

We have also been unable to find anything which affects the dissociation of D into the three bands, or to determine the difference between D-1 and D-2. The addition of 5 mM Mg^{2+}, 10 mM EDTA, 60 mM dithiothreitol, or the negatively charged thiol reagent 3-thiopropanoic acid (10 mM) [25] to the sample buffer had no effect, nor did several cycles of freeze thawing. The only result of isolating membranes in the presence of proteolysis inhibitors (1 mM phenylmethylsulfonyl fluoride, 6 mM *p*-aminobenzamidine, 40 mM ϵ-aminocaproic acid) was to increase the amount of CP II* relative to CP II. When membranes were tested for the presence of a latent protease by preincubating them in 0.1% SDS at room temperature for 1 h [26], there was no detectable difference in the polypeptide pattern. We suspect that the difference between D-1 and D-2 may be due to some minor conformational change. It must be remembered that the chlorophyll-protein complexes are being deliberately electrophoresed under conditions where the protein is not completely denatured although it may be coated with detergent.

The D complexes contain Chl b

The D complexes have identical absorption spectra, with two very distinctive features (Fig. 4). They have a marked peak at 480–490 nm, which suggests the presence of relatively large amounts of carotenoid, and they all contain Chl *b* (Table I). Estimation of the Chl *a*/*b* ratio by the hydroxylamine method [22] gave a figure of 3–4, compared to 1.9 for whole membranes and 1.0 for CP II*. Due to the small amount of material available, identification of the carotenoid(s) was not attempted.

The existence of a Chl *a*/*b* complex other than the LHC has only recently been reported [11,15]. Machold and Meister [15] were able to isolate a complex, which they called Complex III, from *Vicia* thylakoids, using a 12–18% gradient gel. Judging by its spectrum, and its single 29 kDa polypeptide, it is probably the same as our complex CP 29, which can also be isolated from *Vicia* using octylglucoside solubilization [12].

The complex CP 29 has been found in all higher plants examined to date, as well as in *Acetabularia* [11,12]. The novelty of the *Acetabularia* CP 29 is that it is able to form oligomers, and that a certain proportion of it is isolated in the oligomer form after initial solubilization with either detergent (Fig. 1). This suggests that the complex may occur as the oligomer form in vivo. No bands comparable to D-1, D-2 or the original D band have ever been seen in higher plant material. It appears that the oligomers of CP 29 are unique to *Acetabularia*.

The Chl a complexes

The major complex CP I is identical to the P-700-Chl *a* complex of higher plants and blue-green algae [20]. The minor complexes, CPa-1 and CPa-2, have absorption maxima of 673 and 671 nm respectively, compared to 676 nm for CP I (Table I). Like CP I, they contain little or no Chl *b* and are not as highly enriched in carotenoids as the D complexes (Fig. 4). Using the hydroxylamine method [22], CP I had an average Chl *a*/*b* ratio of 35 with a range of 16–75, while CPa-1 and a-2 had ratios of about 8.

As reported by others [14], we experienced considerable difficulty in ridding the complexes of extraneous polypeptides. However, when the membranes were washed with 6 M guanidine hydrochloride [27] before detergent solubilization, CPa-1 and CPa-2 each contained a single polypeptide of 41 and 37 kDa respectively.

CPa-1 and a-2 are very similar to the Chl *a* complexes isolated from *Chlamydomonas* [13], barley [14] and a number of other higher plants [11,12], and referred to as CP 47 and CP 43 in our previous papers [11,12,16]. A number of workers have reported that there is only one Chl *a* complex in this region of the gel, accounting for a higher percentage of the total chlorophyll [1,28]. However, the fact that the two complexes have

apoproteins of different molecular mass and different antigenic specificities [13] shows that there are indeed two minor Chl *a* complexes.

Fluorescence emission spectra

The Chl *a* complexes have been suggested to be part of the PS II reaction center for a number of reasons. Their polypeptides are absent or diminished in a *Chlamydomonas* mutant defective in PS II [13]. They contain only Chl *a*, as would be expected for a reaction center, and are present in mutants defective in Chl *b* synthesis [14,29]. A reaction center preparation from *Chlamydomonas* is enriched in the 47 and 50 kDa polypeptides of the two Chl *a* complexes well as in a third polypeptide of about 35 kDa [30].

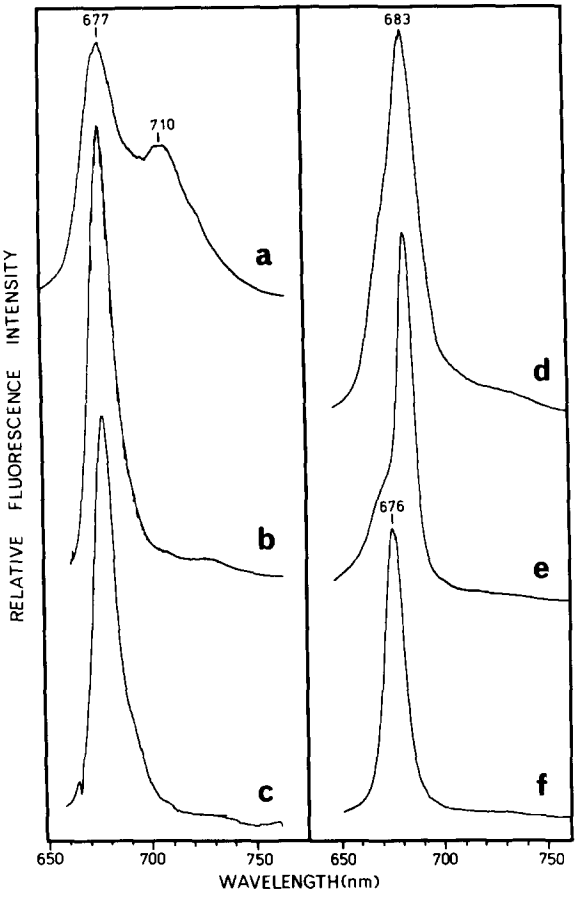

Fig. 6. Fluorescence emission spectra of purified chlorophyll-protein compelxes on gel slices at −196°C. Excitation wavelength 442 nm. (a) CP I, (b) CP II, (c) CP II*, (d) CPa-1, (e) CPa-2, (f) D-2. The shapes of the curves have not been corrected for the wavelength-dependent sensitivity of the apparatus: this is insignificant for all but CP I. The maxima given are corrected.

One characteristic feature of PS II reaction center preparations from higher plants is that they have a fluorescence emission maximum at 77 K of 685–686 nm compared to 681–682 nm for CP II [31–34]. To see if these observations could be related to the *Acetabularia* complexes, the fluorescence emission spectrum of each complex was measured, using gel slices immersed in liquid N_2 (Fig. 6).

Both CPa-1 and CPa-2 had emission maxima at 683 nm. The spectrum of CPa-1 closely resembled that of the single CPa from barley studied by Waldron and Anderson [35]. All the other complexes had emission maxima at 675–677 nm. The spectrum of CP II was similar to that of purified CP II from higher plants [31,36]. A gel slice from the free pigment zone, containing chlorophyll and carotenoids, had a maximum at about 670 nm. When the CP I spectrum was corrected for the wavelength-dependent sensitivity of the apparatus, the 710–712 nm emission was more intense than the 677 nm emission, but there was no distinct peak at 735 nm [6,37]. None of the complexes had the 695 nm peak which is thought by some authors to represent emission from the PS II antenna chlorophylls [36].

Although CPa-1 and CPa-2 have the same emission maxima as a highly purified PS II fraction prepared with the detergent Triton X-100 [34], this is only indirect evidence linking the complexes with the PS II reaction center. We are currently attempting to isolate fractions with PS II activity from octylglucoside extracts to see if they contain these two complexes.

Nomenclature

Since this paper introduces two new chlorophyll-protein complexes to the literature (the dimers of CP 29), a few comments on nomenclature are in order. We have changed our names for the minor Chl *a* complexes from CP 47 and CP 43 [11,12,23] to CP a-1 and CP a-2, since the single complex found by many workers is most often referred to as CP a [28]. Machold and co-workers [14] have proposed a logical system which, however, could be confusing because most of the letters

are common to all of the names. Since we wish to communicate with a general audience, we prefer to use symbols that are more visually distinctive, and for that reason, to continue using symbols such as CP I (CP 1) and CP II which are widely recognized outside the small circle of chlorophyll-protein afficionados. It should be noted, of course, that the usual CP II band on SDS gels includes CP 29 as well as several nonchlorophyll-bound comigrating proteins [24,38], so it should not be used for studies on the molecular organization of the light-harvesting complex. Since we have no data on the function of CP 29, we suggest it should keep this suitably noncommittal name. The oligomers are apparently unique to *Acetabularia*, but since our original name A [16,17] has been used to refer to CP *a* [7] the oligomers have renamed D-1 and D-2.

Acknowledgements

Bernice L. Muir, David Vogt, Rajinder Verdi and Janet Snell provided excellent technical assistance with the *Acetabularia* cultures. We are very grateful to Dr. Gerry Porter, U.B.C. Chemistry Department, for the use of his facilities to do the fluorescence spectra. Ken Jeffries made the sample holder. This research was supported by grants from the Natural Science and Engineering Research Council of Canada.

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