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Chlorophyll-Protein Complexes of the Cyanophyte, *Nostoc* sp.[1]

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ABSTRACT

Four chlorophyll-protein complexes have been resolved from the cyanophyte, *Nostoc* sp., by sodium dodecyl sulfate (SDS) polyacrylamide gel electrophoresis at 4 C. Complexes solubilized by SDS from *Spinacia oleracea* were run for comparison. As has been well documented, the P700-chlorophyll *a*-protein complex from the higher plant and blue-green algal samples are similar, and the light-harvesting pigment protein complex is present only in the former. Most noteworthy are two closely migrating chlorophyll proteins in *Nostoc* sp. which have approximately the same mobility as a single chlorophyll-protein band resolvable from spinach. The absorption maximum of the complex from spinach is at 667 nanometers, and those of the two complexes from *Nostoc* sp. are at 667 and 669 nanometers; the fluorescence emission maximum at −196 C is at 685 nanometers, and the 735 nanometer fluorescence peak, characteristic of the P700-chlorophyll *a*-protein complex, is absent. The apoproteins of these new complexes from *Nostoc* sp. and spinach are in the kilodalton range. It appears that at least one of these two chlorophyll-protein complexes from *Nostoc* sp. compares with those recently described by others from higher plants and green algae as likely photosystem II complexes, perhaps containing P680, although no photochemical data are yet available.

Nonionic and anionic detergent treatment to disrupt thylakoid membranes, followed by electrophoresis in a variety of polyacrylamide gel systems (8, 10, 16, 17, 21-23) or chromatography on hydroxylapatite (31) or DEAE-cellulose (23), has allowed the identification of three Chl complexes, two of which are proteinaceous in nature and the third of which is a detergent-Chl micelle. The Chl-protein of lowest electrophoretic mobility contains the P700 reaction center and has been named P700-Chl *a*-protein (11), also called CPI (31); it appears to be ubiquitous in all Chl *a*-containing organisms (7). The second pigment protein complex is of greater electrophoretic mobility, contains both Chl *a* and *b*, is found in higher plants and green algae, and is called light-harvesting pigment protein complex or LHPP[2], formerly termed CPII (21). The mol wt of the apoprotein of the P700-Chl *a*-protein complex from higher plants and green algae is approximately 60-70 kD (5, 6, 33), whereas LHPP has two or three polypeptides, ranging from 25 to 35 kD (16, 31). Both Chl-protein complexes have been well characterized and are the subject of a number of reviews (5, 6, 33).

As improved methods of both Chl-protein extraction from membranes and PAGE developed, several less stable Chl-protein complexes have become reproducibly seen. One class of these complexes appears to be dimers and oligomers of LHPP (1, 4, 12, 14, 17, 20, 26). The second class of new Chl-protein complexes, first reported by Hayden and Hopkins (15), contains Chl *a* and no Chl *b*, migrates in SDS-PAGE between CPI and the dimer of LHPP, and is found in relatively low concentrations. This complex has since been found in a number of higher plants (1, 17, 28, 34) and green algae (10). Chl *b* (15) and the −196 C fluorescence emission band at 735 nm characteristic of CPI (18) are lacking in this complex. Moreover, this complex's polypeptides are absent from mutants lacking PSII activity (8, 10) and are enriched in PSII particles (2, 22, 34). These data collectively suggest that this complex is associated with PSII and may contain P680.

Examination of the blue-green algal Chl-proteins has been less extensive. The P700-Chl *a*-protein complex was first isolated from *Phormidium luridium* by hydroxylapatite chromatography of SDS-solubilized membranes (24). The complex was composed of a 110,000-kD component (24), which after reduction with β-mercaptoethanol and electrophoresis in a urea buffer system, yielded two components of 46 and 48 kD (33). Klein and Vernon (23) treated *Anabaena flosaquae* thylakoid membranes with Triton X-100 and obtained three Chl-containing bands by sucrose gradient centrifugation. Two fractions gave similar electrophoretic patterns, except that a 46-kD polypeptide was unique to the 25% layer. Although Klein and Vernon did not demonstrate enriched PSII activity in the band sedimenting in 25% sucrose, Apel *et al.* (2), using an identical gradient with membranes from *Acetabularia mediterranea*, showed PSII activity associated primarily with the 25% sucrose band. Newman and Sherman (27) isolated PSI and PSII-enriched particles from *Synechococcus cedrorum* with polypeptides of 61, 18, 17, 15, and 14 kD for PSI particles and 71, 63, 52, 47, 36, 18, and 14 kD for PSII particles.

The blue-green algae contain no Chl *b* and therefore no LHPP as do higher plants. Analysis of the blue-green algal system facilitates the identification of a band with possible PSII association as the absence of LHPP also would eliminate the bands of intermediate mobilities, dimers and oligomers of LHPP, found between CPL and LHPP.

We have compared the Chl-protein complexes of a higher plant (spinach) with those of a blue-green alga (*Nostoc* sp.), using the PAGE system of Henriques and Park (18). After SDS gel electrophoresis at 4 C, characterization of Chl-containing bands included low temperature fluorescence spectra, room temperature absorption spectra, and reelectrophoresis on Laemmli (25) gels, where the sample is heated to 100 C for 5 min prior to electrophoresis. We have resolved four major Chl-protein complexes from the cyanophyte *Nostoc* sp. by SDS-PAGE at 4 C. Two of these show mobilities of their apoproteins in the 45-kD range. It appears that at least one of the two Chl-protein complexes from *Nostoc* sp.

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[2] Abbreviations: LHPP: light-harvesting pigment protein complex; kD: kilodalton; PAGE: polyacrylamide gel electrophoresis.

compares with those tentatively identified by Henriques and Park (18) and Delepelaire and Chua (10) as PSII complexes, perhaps containing P_{680}, although no photochemical data are yet available.

MATERIALS AND METHODS

The blue-green alga *Nostoc* sp. (strain Mac) was grown in a 14-liter New Brunswick Scientific fermentor supplied with 1% CO_2 in air in medium "CG 10" (13) and illuminated with Gro-light bulbs (General Electric FIST8). Spinach was greenhouse-grown.

The thylakoid membranes from *Nostoc* sp. were prepared as follows. Two liters of cells were harvested and washed with 0.5 M K-phosphate (pH 7.0). The cells were resuspended in 0.5 M K-phosphate (1 g wet weight/10 ml buffer), homogenized with a glass tissue homogenizer, and broken in a French pressure cell at 12,000–16,000 p.s.i. The pressate was centrifuged at 20,000*g* for 20 min. The supernatant was centrifuged at 200,000*g* for 45 min in an International Equipment Co. ultracentrifuge (A-237 rotor) at 20 C. The pellet was used immediately for further analysis. *Nostoc* sp. thylakoid membranes for electrophoresis were suspended in 1 mM Na-phosphate (pH 6.9) to a concentration of 1–2 mg Chl/ml, and homogenized with a tissue homogenizer. Prior to electrophoresis, the membrane samples were diluted 1:1 with sample buffer kept at 20 C (10% glycerol, 5% mercaptoethanol, 25 mM Tris [pH 6.8], and SDS for a final SDS to Chl ratio of 10:1).

Spinacia oleracea L. thylakoid membranes and samples for electrophoresis were prepared according to the method of Henriques and Park (18), with precautions made to keep all steps at 4 C and in the dark.

The electrophoresis system used for both *Nostoc* and spinach was modeled after the procedure of Henriques and Park (18) except that instead of a 9% acrylamide running gel, either a 10 or 12.5% running gel was used. The 12.5% acrylamide running gel was found to give better resolution of the lower mol wt Chl-protein complexes. Gel dilutions were made from a 30% acrylamide-0.8% bisacrylamide stock. Both tube gels and slab gels were run. Tube gels had a 5-mm i.d. with a 2-cm stacking gel and a 13-cm running gel. A 3% acrylamide stacking gel was used with the 12.5% running gel, and a 5% stacking gel was used with the 10% gel. The proteins on tube gels were electrophoresed at 1 mamp per tube through the stacking gel and at 2.5 mamp per tube in the running gel. The slab gels were run in a Bio-Rad model 221, 30 slab apparatus (30 × 0.15 cm) with a 5% stacking gel and a 10% running gel. A 20-mamp current was applied through the stacking gel and 40 mamp through the running gel. All gels were run in the dark at 4 C. Reservoir buffers were precooled to 4 C. Samples were run in the range of 10–120 μg Chl per slot or tube. Chl concentration was estimated according to the method of Arnon (3).

After electrophoresis, gels were scanned at 672 and 650 nm in a Gilford spectrophotometer equipped with a linear transport device. Some gels were stained with Coomassie brilliant blue R, destained in a 25% isopropyl alcohol, and 10% acetic acid mixture, followed by 10% acetic acid, and scanned at 563 nm.

Following electrophoresis and prior to staining, room temperature absorption spectra and −196 C fluorescence spectra were taken. Absorption spectra were measured on slab gel slices in a Cary 17D spectrophotometer. Fluorescence spectra were taken in an Aminco-Bowman spectrofluorometer equipped with a R446S Hamumatsu TV photomultiplier tube. The gel slices were positioned for front surface illumination in a Dewar flask after being frozen with liquid N_2. The band pass on the excitation side was 11 nm and 2.7 nm on the emission side. The spectra were uncorrected for lamp output and emission grating phototube efficiency.

Reelectrophoresis of gel bands was done with proteins from unstained tube gels. After electrophoresis at 4 C, the Chl-containing bands were sliced from the gel and stored at −20 C until use. For reelectrophoresis, a Laemmli (25) buffer system was used with a 12.5% running gel and a 3% stacking gel. Gel slices were removed from the freezer, homogenized, mixed with 50–100 μl Laemmli sample buffer plus 2 μl bromophenol blue tracking dye, and were then either applied directly to the top of the gel or were first heated for 10 min in a boiling H_2O bath and then applied to the gel. Gels were run at 0.5 mamp through the stacking gel and 2.5 mamp through the running gel. Mol wt of polypeptides were calculated using BSA, ovalbumin, carbonic anhydrase, *myo*-globin, and β-lactoglobulin as standards.

RESULTS AND DISCUSSION

Figure 1 shows the separation obtained of the Chl-protein complexes from *Nostoc* sp. and spinach thylakoid membranes in a SDS discontinuous gel system with a 3% acrylamide stacking gel and 12.5% acrylamide running gel, run at 4 C. The spinach sample shows the presence of CPI and LHPP as the major complexes. The free pigment zone is also present, directly behind the tracking dye. This gel system also allows for the resolution of the intermediate bands between CPI and LHPP (Fig. 1). The major band of intermediate mobility is labeled in Figure 1 as CPIII, after the nomenclature of Delepelaire and Chua (10). It is of interest as it co-migrates with two bands from *Nostoc* sp. Two very minor Chl-protein bands can also be seen in these gels (seen more clearly in Fig. 2) which migrate in a SDS gel between CPI and CPIII. These were not analyzed because of their very small concentrations, but they are likely to be oligomers of LHPP as described by Henriques and Park (18).

Figure 1 also shows the Chl-protein complexes from *Nostoc* sp. The major Chl-protein band present in *Nostoc* sp. is a band which compares in mobility to CPI of spinach. Three additional Chl-containing bands are also seen, one very similar in mobility to the major CPI band, and two closely migrating bands with mobilities comparable to CPIII from spinach. The free pigment zone composed of Chl-detergent micelles is immediately preceded by the major bands of the phycobiliproteins.

Figure 2 shows a densitometric scan at 672 nm of spinach and *Nostoc* sp. Chl-protein complexes in a 12.5% acrylamide gel. The CPI of spinach is indicated, and it appears to have the same mobility as the major band from *Nostoc* sp. We have also designated this band from *Nostoc* as CPI. The CPI from *Nostoc* contains at least 50% of the Chl-protein isolated by gel electro-

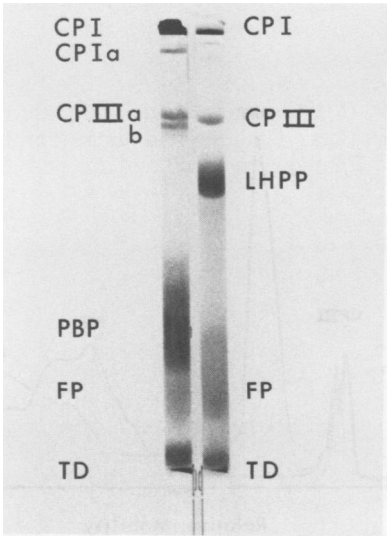

FIG. 1. Electrophoretogram of spinach (right) and *Nostoc* sp. (left) SDS-solubilized thylakoid membranes before staining. PBP: phycobiliproteins; FP: free pigment; TD: tracking dye.

phoresis. In addition to CPI, three additional bands from *Nostoc* are resolved (Fig. 2). Band CPIa, as seen in Figures 1 and 2, has a slightly greater mobility than CPI. The quantity of CPIa resolved is often variable. It is not certain if it represents a breakdown product of CPI during electrophoresis or if it is the same protein with a varying amount of complexed detergent. It is present as 5–10% of the total Chl-protein isolated. CPIIIa and CPIIIb from *Nostoc*, in Figures 1 and 2, are the two bands of greatest interest for these appear to have the same mobility as CPIII from spinach. CPIIIa and CPIIIb are always present in equal quantities and collectively represent 20–30% of the total Chl-protein present.

Figure 3 shows the absorption spectra of the major Chl-protein bands from *Nostoc* sp. and spinach. The absorption spectra were taken from a 10% acrylamide slab gel slice at room temperature. The P700-Chl *a*-protein complex of spinach in our system exhibits an absorption maximum of 673 nm. A similar absorption maximum is seen for the complex from *Nostoc* sp. which demonstrates the same electrophoretic mobility as spinach CPI. CPIII from spinach has an absorption maximum of 667.5 nm. CPIIIa and CPIIIb from *Nostoc* have maxima at 669 and 667 nm, respectively. The LHPP spectrum is also shown; in addition to its peak at 667 nm, it has a prominent shoulder at 650 nm, indicative of Chl *b*, which is noticeably absent in all other spectra. Band CPIa of *Nostoc* (spectrum not shown) has an absorption maximum of 671 nm. We do consider the 673 nm complex to be the P700-Chl *a*-protein complex even though its wavelength maximum is lower than that of 677 nm of CPI isolated by Thornber from blue-greens (31). Shiozawa (30) showed that incubation in SDS of the P700-Chl *a*-protein complex of higher plants (which is considered to be homologous to the blue-green algal system because of its similar amino acid and pigment composition [32] shifted the red wavelength maximum from 677 to 673 nm after 30 min of incubation, and to 671 nm after 155 min incubation, followed by the onset of pheophytinization. It is possible that the longer electrophoresis time of 3 h compared to that of Thornber of 20 min may influence the spectral properties of CPI and may be the cause of the variable appearance and quantity of band CPIa from *Nostoc*.

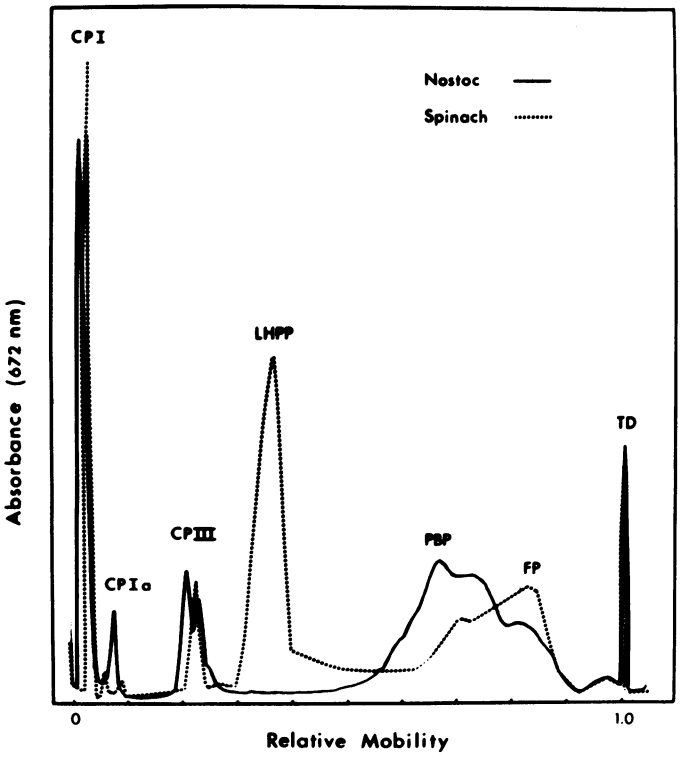

FIG. 2. Densitometric scan at 672 nm of Chl-containing bands of spinach and *Nostoc* sp. in 12.5% SDS-polyacrylamide disc gel. Abbreviations as in Figure 1.

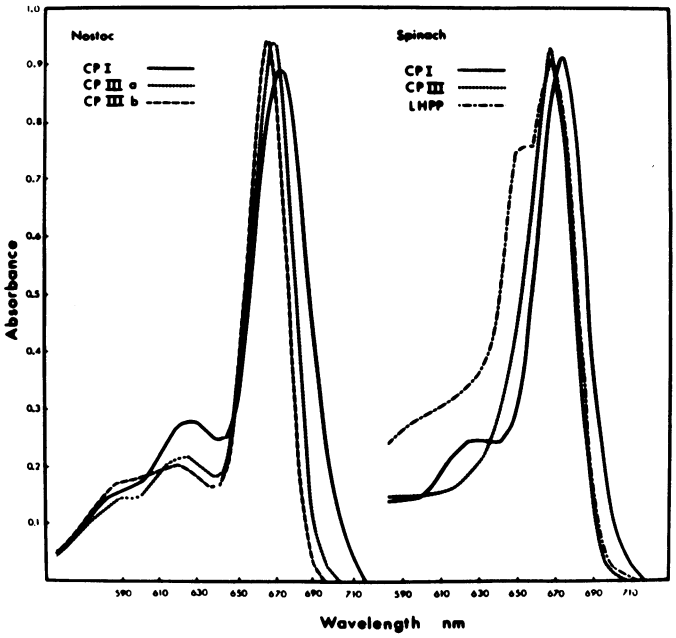

FIG. 3. Room temperature absorption spectra of the major Chl-protein complexes of *Nostoc* sp. and spinach taken from slab gel slices.

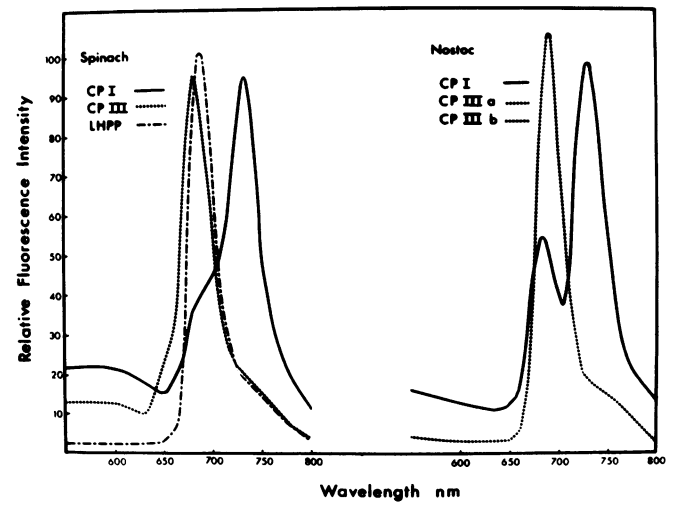

FIG. 4. Fluorescence emission spectra at −196 C of Chl-protein complexes of spinach and *Nostoc* sp. from slab gel slices. Excitation was at 435 nm.

The fluorescence emission spectra at −196 C are shown in Figure 4 for both *Nostoc* and spinach. The emission maximum for the CPI complexes from both *Nostoc* and spinach is at 735 nm with a shoulder at 685 nm. Although the ratios of fluorescence intensity at 685 and 735 nm varied from preparation to preparation, the 735 nm emission maximum was consistently predominant. Differences in ratios may be due to reabsorption of fluorescence with more concentrated samples or by the technical problems attendant upon freezing gel slices. Band CPIa from *Nostoc* sp. also exhibits a 735 nm fluorescence emission peak with a shoulder at 685 nm. The fluorescence emission maxima of CPIII from spinach and CPIIIa and CPIIIb from *Nostoc* are all similar with a peak at 685 nm, and no 735 nm fluorescence. Table I presents a summary of these spectral data.

Reelectrophoresis of the Chl-protein complexes from *Nostoc*

and spinach was done on Laemmli (25) gels to determine the polypeptide composition of their apoproteins. Figure 5 shows the representative patterns obtained. *Nostoc* CPI reelectrophoresed with the appearance of three bands at 84, 75, and 58 kD. Spinach CPI reelectrophoresed with a single polypeptide in the 64 kD range. Reelectrophoresis of CPIa tended to give inconsistent results, ranging from one band of 54 kD to four bands with mol wt of 87, 77, 71, and 50 kD. CPIIIa reelectrophoresed with major bands at 48 and 44 kD. CPIIIb reelectrophoresed with a major band at 48 kD and a minor band at 43 kD. CPIII from spinach reelectrophoresed with polypeptides of 49 and 44 kD. Apoprotein sizes of spinach and *Nostoc* sp. Chl-proteins are summarized in Table II.

Band CPIa appears to be related spectrally to CPI. Its different mobility on the 4 C SDS gels may be due to greater denaturation of CPI by SDS, Detergent binding is also likely to differ with greater denaturation. The electrophoretic mobility of a protein in a SDS environment is affected by two states, the size of the electrostatic charge per unit mass (the charge of the anionic head group of the detergent), and the size of the rod-like particle formed in the SDS environment (29). Band CPIa could therefore represent a modified CPI with a greater anionic charge or different rod-like

Table I. *Spectral Characteristics of Chl-Protein Complexes*

	Spinach			*Nostoc* sp.	
	Abs. λ Max.	Fl. λ Max.		Abs. λ Max.	Fl. λ Max.
	nm			*nm*	
CPI	673	685, 735 (major)	CPI	673	685, 735 (major)
LHPP	668	686	LHPP	—	—
CPIII	667.5	680	CPIIIa	669	685
			CPIIIb	667	685

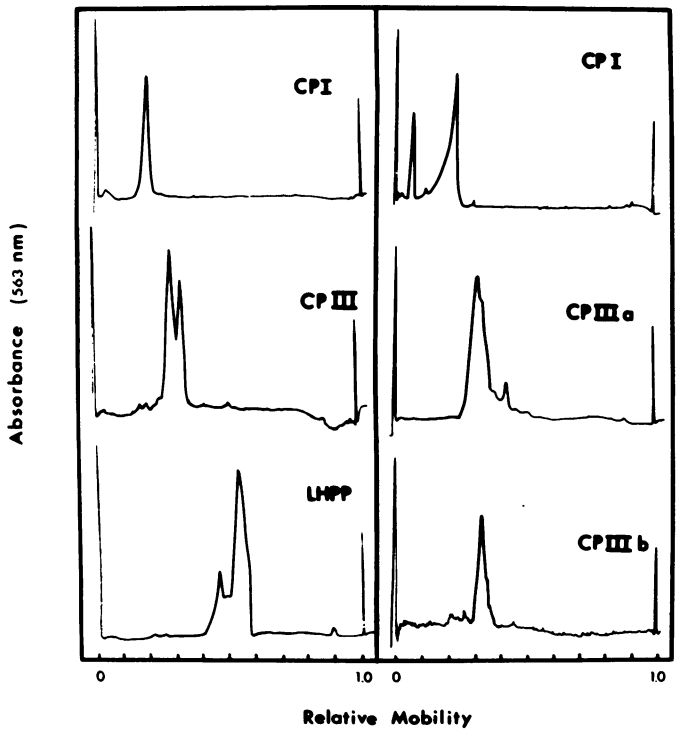

FIG. 5. Densitometric scan at 563 nm of Coomassie blue-stained apoproteins of the Chl-protein complexes from *Nostoc* sp. and spinach. Reelectrophoresis for apoproteins as described under "Materials and Methods."

Table II. *Apoprotein Molecular wt of Chl-Protein Complexes by SDS-PAGE*

Spinach		*Nostoc* sp.	
CPI	64,000	CPI	84,000
			75,000
			58,000 (major)
LHPP	34,000		
	27,500 (major)		
	26,300		
CPIII	49,000 (major)	CPIIIa	48,000
	44,500		44,000
		CPIIIb	48,000
			43,000

dimensions. The variations in gel patterns of CPIa upon reelectrophoresis do not allow for further comparisons with CPI.

CPIIIa and CPIIIb are not likely to be similar modifications or denaturation products of CPI; most significantly they completely lack the 735 nm emission band. CPIIIa and CPIIIb are essentially identical. Their absorption maxima differ by 2 nm, and their fluorescence maxima are the same. CPIIIa and CPIIIb each reelectrophorese as two apoprotein bands, of nearly identical sizes. It is not certain if these two Chl-protein complexes reflect minor changes in the tertiary structure of the SDS Chl-protein complex occurring during detergent treatment, or if they are, in fact, two distinct Chl-protein complexes. They repeatedly appear as two bands in approximately equal quantities on SDS gels run at 4 C.

CPIIIa and CPIIIb show clear similarities with CPIII of Delepelaire and Chua (10), band A of Henriques and Park (18), and our CPIII from spinach. They share similar spectral characteristics, mobilities in SDS-PAGE at 4 C, and apoprotein electrophoretic mobilities in SDS-PAGE of complexes heated to 100 C. The slight differences observed are probably due to species variation. In the blue-green algal system, one can avoid the complications of the higher plants and green algae where, in addition to the above described Chl-protein complex, one often finds several other complexes thought to be dimers or oligomers of LHPP (1, 26, 28) which have electrophoretic mobilities intermediate between those of CPI and LHPP and contain approximately equimolar amounts of Chl *a* and *b*. With a blue-green alga, *Nostoc* sp., we have obtained a pair of Chl-containing protein bands whose apoproteins are in the mol wt range of 43–48 kD. These two bands neither represent complexes of LHPP nor likely dissociation products from the major Chl-protein, CPI. These Chl-proteins are devoid of PSI Chl, as seen in the low temperature fluorescence data where there is only an emission band at 685 nm. The work of Delepelaire and Chua (10) in which mutants of *Chlamydomonas* deficient in PSII activity also lack the 46 to 47 kD CPIII apoproteins together with their spectral data (10) and those of Henriques and Park (18) suggest by analogy that CPIIIa and/or CPIIIb from the cyanophyte, *Nostoc* sp., may be associated with PSII and perhaps even contain P680. No photochemical data are yet available. This Chl-protein complex has been reported only in plants containing Chl *b* (*i.e.* higher plants and green algae). Its presence in a blue-green, procaryotic alga may indicate that like the P700-Chl *a*-protein complex, it is ubiquitous among all Chl-containing organisms and may contain P680.

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