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Minireview

How the chlorophyll-proteins got their names

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Abstract

This is the story of how we started studying the green bands seen on SDS-polyacrylamide gels of thylakoid membranes dissociated with the non-ionic detergent β-octyl-D-glucopyranoside. We explain some of the complications we and other workers encountered along the pathway to untangling the chlorophyll-protein complexes of higher plants, and give a concise summary of the complexes, their polypeptides and their genes.

Abbreviations: Chl – chlorophyll; DG – digalactosyldiacylglycerol; LHCII – major light-harvesting complex of Photosystem II; OG – β-D-octyl glucoside; PC – phosphatidylcholine; PS II – Photosystem II; SDS – sodium dodecyl sulfate

Introduction

Progress in science does not always occur in a straight line. We got into the business of chlorophyll-protein complexes because we were trying to find out what proteins could be synthesized by isolated chloroplasts and therefore were likely to be encoded by the chloroplast genome. In 1977, no chloroplast gene had been sequenced, and the sequencing of an entire chloroplast genome was a distant dream (Ohyama et al. 1986; Shinozaki et al. 1986). This was just the beginning of the plant molecular biology era, eloquently reviewed by L. Bogorad and M. Sugiura in an earlier volume (Bogorad 2003; Sugiura 2003).

The giant green alga *Acetabularia* could continue development in the absence of its nucleus (Green 1976a), so it seemed like a good source of chloroplasts for our purpose. We were able to isolate chloroplasts of sufficient quality to be capable of incorporating labeled amino acids *in vitro* using *Acetabularia*, and later spinach. What we found out was that much of the label ended up in a number of discrete bands in the thylakoid membrane fraction (Camm and Green 1978; Green 1980, 1982). However, at the time of the 1978 Photosynthesis Gordon Conference almost none of the thylakoid membrane proteins had been identified. In fact, when one of us (Beverley) asked attendees to help list the identified chloroplast polypeptides, less than a dozen of them were thylakoid-associated (Table 1; see also Nelson and Ben-Shem 2002).

Intrinsic proteins identified by electrophoresis on sodium dodecyl sulfate (SDS) gels

So we decided to identify some of the polypeptides ourselves. One of our strategies was to 'purify' thylakoid membranes by careful washing to remove soluble and peripheral proteins (Strotmann et al. 1973) and then to treat the thylakoids with various detergents at low detergent/Chl ratio. When we applied these extracts directly to gels and electrophoresed them in the

Table 1. Identified chloroplast proteins in 1978 (reproduced from an informal list obtained at the 1978 Gordon Conference on Photosynthesis). Names and molecular weights are exactly as supplied at the time by attendees. Note the contributions of N. Nelson, reviewed in this series (Nelson and Ben-Shem 2002)

Please add any polypeptides you can identify – soluble or membrane (subunit molecular weight on SDS-gels)
>70 kDa
(no entries)
60–70 kDa
68 kDa apoprotein of CPI
63 kDa α subunit of CF1
Ru5P kinase
50–60 kDa
56–58 kDa β subunit of CF1
52–56 RuBPCase (LSU) (now called Rubisco)
40–50 kDa
PGA kinase
G3P dehydrogenase
30–40 kDa
37 FNR (ferredoxin–NADP reductase) – 38 kDa in algae
37 aldolase
34.5 γ subunit of CF1
33–37 cytochrome *f*
33 algal bd cytochrome *c* (*f*)
32 associated w/PS II activity but probably not RX center
20–30 kDa
30, 25, 23 LHC complex
25, 20 PS I reaction centre (N. Nelson)
20 δ subunit of CF_1
10–20 kDa
18, 16 PS I reaction centre (N. Nelson)
17 Fo (binding site for CF_1)
15 ε subunit of CF_1
12–14 RUBPCase (SSU)
11–12 soluble cytochrome *c*
11 plastocyanin
<10 kDa
PS I proteolipid
8 sol. cytochrome *c* from an alga
8 F0 proteolipid
8 ferredoxin
5.6 b559

cold, we saw a number of green bands migrating down the gel. Ordinarily we saw CP1 (the P700 Chl *a* protein of Photosystem I (PS I)) and CPII (the light-harvesting Chl *a/b* complex) as described in the 1975 review by Philip Thornber (Thornber 1975; see also Ogawa 2003), as well as the putative oligomer of CPII that had been reported by several groups (Hiller et al. 1974; Apel 1977; Remy et al. 1977; Anderson et al. 1978; Henriques and Park 1978; Dunkley and Anderson 1979). Because each of these bands possessed a number of polypeptides when completely denatured and re-electrophoresed, the term chlorophyll-protein *complex* was particularly apt! On our gels run in the cold, we could also detect a pair of minor green bands with apparent molecular weights of 47 and 43 kDa. Other workers had found minor complexes on their gels but it was not clear how our bands related to theirs (Hayden and Hopkins 1977; Anderson et al. 1978; Henriques and Park 1978; Krishnan and Gnanam 1979).

Octyl glucoside permitted separation of relatively stable chlorophyll-protein complexes

By 1978 we had become more and more interested in the structure of the complexes in the green bands. It was clear that detergents like SDS were a double-edged sword. On the one hand, they were necessary for membrane fractionation and electrophoresis, but at the same time, they tended to denature complexes. Thus, Baron and Thompson's paper (1975) reporting preservation of enzyme activity in the presence of non-ionic alkyl glucosides was very interesting. We soon got a sample of β-D-octyl glucoside (OG) and established that it had several advantages in solubilizing complexes for electrophoresis. First, when membranes were prewashed with very low ionic strength buffer (2 mM Tris–maleate, pH 7), CP1 was almost insoluble and could thus be separated from other CP complexes. Second, almost all the chlorophyll remained attached to proteins so that there was a relatively small amount of free chlorophyll on the gels. This plus the fact that CPII appeared primarily in the putative oligomeric form suggested that complexes were maintained in a native form. Finally, several minor complexes were routinely visible in our gels (Figure 1).

In the region of the gel normally dominated by the CPII monomer, we identified a new Chl *a/b* complex that we called CP29, and showed by peptide mapping that its major polypeptide constituent was distinct from the two major polypeptides of CPII and its oligomer (then called CP64, later CPII*) (Camm and Green 1980). The Chl *a* complexes of about 43 and 47 kDa occasionally seen in SDS gels were routinely and clearly present in gels of OG extracts (Camm and

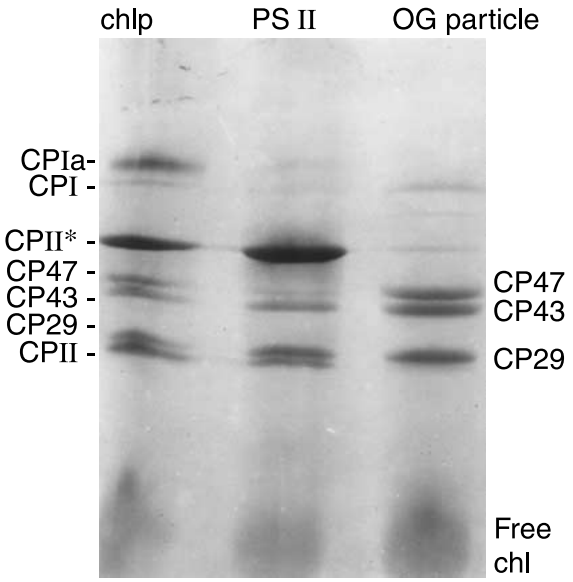

Figure 1. An early 'green' (i.e., unstained) gel showing Chl–protein complexes extracted from spinach chloroplasts by the non-ionic detergent OG. Chlp, OG extract of intact thylakoids; PS II, OG extract of thylakoids prewashed with low ionic strength buffer (note that the amounts of PS I components have been decreased); OG particle, OG extract of thylakoids pre-treated with divalent cations.

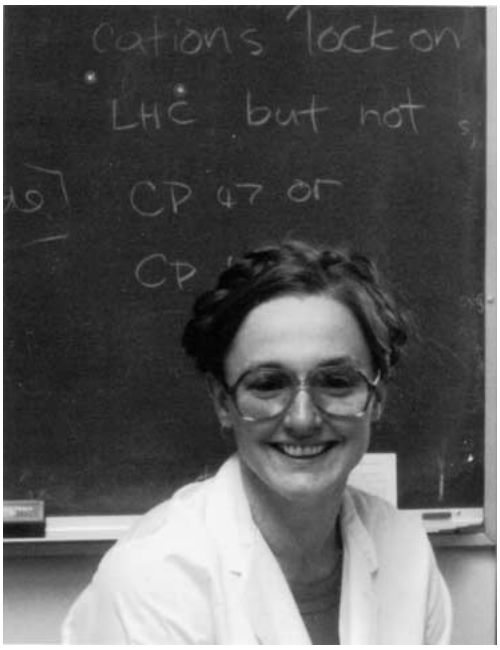

Figure 2. Edith Camm in 1980, in front of blackboard notes on effect of cations on extractability of Chl-proteins (Camm and Green 1982).

Green 1980, 1981). Under some conditions, they were the only complexes extracted (Camm and Green 1982; Figure 2 is a photograph of one of us (Edith)). Because 'CP47' and 'CP43' were relatively stable after OG solubilization, it was possible to excise the green bands from the gel and purify the Chl-proteins by re-electrophoresis on a polyacrylamide gel of a different concentration, taking advantage of the fact that the relative mobility of hydrophobic Chl-proteins changes as a function of the acrylamide concentration to separate them from polypeptides without Chl (Chua et al. 1975). After denaturing the purified Chl-proteins, we were able to show that they contained one polypeptide each (Camm and Green 1980; Green et al. 1982) and were therefore probably the same as Chl *a*-protein complexes III and IV described by Delepelaire and Chua (1979) in *Chlamydomonas*, and Chl_a-P2 and Chl_a-P3 purified by Otto Machold and his collaborators from higher plants (Machold et al. 1977; Machold and Meister 1979). The genes for these polypeptides were later cloned and sequenced in Reinhold Herrmann's lab (Alt et al. 1984; Morris and Herrmann 1984), and are now called *psb*B and *psb*C.

We originally dubbed the minor complexes 'CP47', 'CP43' and 'CP29' according to the apparent molecular weights of the spinach complexes on our gel system, since we were uncertain how they related to the complexes that had been observed and given various names or symbols by other workers. All these minor complexes were present in gels of OG extracts from several kinds of plants (Camm and Green 1981), so it was clear that they represented some kind of common elements in thylakoids. Since the apparent molecular weight of a green band is strictly 'apparent' and varies markedly depending on the electrophoresis system, we later tried to introduce the more rational terms CPa-1 and CPa-2 for the minor Chl *a* proteins (Green et al. 1982; Camm and Green 1983a, b), since several workers had used 'CPa' for a single band that migrated at roughly the same position on shorter gels (Hayden and Hopkins 1977; Anderson et al. 1998; Anderson 2002). However, these names were not as distinctive as 'CP47' and 'CP43' and did not catch on in the same way. 'CP29' had a more chequered career (see below).

Chlorophyll *a/b* complexes

At first it seemed that it would be a simple job to identify the polypeptide components of all the complexes and figure out how the complexes related to each other. However, the story turned out to be more complicated than at first thought, accounting for the

subtitle of a 1988 review paper: 'Just what green band is that?' (Green 1988). Different results were obtained in each lab depending on the gel systems and detergent combinations in use. Photographs of 'green gels' obtained by the groups of Phil Thornber, Otto Machold and David Simpson, Jan Anderson, Nam-Hai Chua, Andrew Staehelin and ourselves are compared in two Thornber reviews (Thornber 1986; Thornber et al. 1991), and one of Jan Anderson's gels is shown in Figure 6 of her contribution to this series (Anderson 2002). Of course, each group had its own system of naming the Chl-proteins and their polypeptides which caused even more confusion!

Most of the complexity resides in the Chl *a*/*b*-protein complexes of PS II. The polypeptide composition of light-harvesting complex (LHC) II, the major Chl *a*/*b* complex of PS II was a particularly difficult problem that was tackled in one way or another by all the workers in the field, with a variety of results, not to mention nomenclatures (reviewed in Anderson 1986; Thornber 1986, 1995; Green 1988; Thornber et al. 1991). There are a variety of reasons for this problem: LHC II is somewhat unstable on gels so that a green band may comigrate with de-pigmented polypeptides from other Chl-proteins (Green and Camm 1982), some of the polypeptides are phosphorylated some of the time (Allen 1992), and there are several populations of LHC II in the thylakoid (Anderson 1986; Allen 1992). In contrast, the four Chl *a*/*b*-proteins associated with PS I, collectively described as LHC I, were more easily sorted out (Haworth et al. 1983; Lam et al. 1984), probably because of the prior existence of good methods for isolating purified active PS I preparations with defined polypeptide compositions (nicely reviewed by Nelson and Ben-Shem 2002).

CP29 deserves a special note. Originally, we described CP29 from spinach as having a single 29 kDa polypeptide (Camm and Green 1980). However, in the green alga *Acetabularia*, what appeared to be an oligomeric form of CP29 produced two minor green bands on re-electrophoresis, each enriched in a different polypeptide (Green et al. 1982). When we started using spinach PS II preparations made by the method of Ghanotakis et al. (1987), the CP29 purified from those preparations also had two polypeptides (Camm and Green 1989). Meanwhile, Roberto Bassi and his colleagues had resolved two minor green bands from maize and called them CP29 and CP26, although it was not clear from the polypeptide composition how they related to the original CP29 (Bassi et al. 1987; Dainese and Bassi 1991). Tryptic peptide sequencing of the 26 and 28 kDa polypeptides of tomato CP29 (in collaboration with Ruedi Aebersold) showed that they were different from each other and from the polypeptides of LHCII; this led to the cloning and sequencing of the gene for the 26 kDa polypeptide, which was named CP29 type I (Pichersky et al. 1991). The 28 kDa polypeptide had a very similar sequence to that of the Chl-protein isolated by Henrysson et al. (1989) and was named CP29 type II. In the meantime, Falbel and Staehelin (1992) did a thorough study of the different results obtained with different plants, using different antibodies and different electrophoretic systems, and suggested that to avoid confusion the Chl-protein with the lower molecular weight polypeptide should be called CP26, and higher molecular weight one should be CP29. So that is how CP26 got its name.

It was not until amino acid sequences could be obtained and the corresponding genes cloned that all the Chl *a*/*b*-protein complexes were sorted out. In collaboration with Eran Pichersky and Ruedi Aebersold, 11 of the 12 Chl *a*/*b*-proteins of tomato were identified with their genes (Pichersky et al. 1991; Schwarz et al. 1991; Green et al. 1992; Green and Pichersky 1994). The CP29 polypeptide is now recognized as the product of the *Lhcb4* gene (Morishige and Thornber 1992) and the CP26 polypeptide as the product of the *Lhcb5* gene (Pichersky et al. 1991). The smallest of the minor complexes (encoded by the *Lhcb6* gene) was called CP24 after its apparent molecular weight (Dunahay and Staehelin 1986). The sequences showed that all the Chl *a*/*b* polypeptides were members of the same protein family (Green and Pichersky 1994), which is now referred to as the LHC Superfamily (Green and Durnford 1996).

Although there was still no general agreement on nomenclatures for the Chl-protein complexes, in 1992 Steffan Jansson persuaded everyone to sign onto a common agreed nomenclature for the genes, with some arm-twisting help from Carl Price (Jansson et al. 1992). (It has been suggested that Stefan and Carl deserved the first 'Nobel Peace Prize in Photosynthesis' for this contribution!) The current information on the complexes, their polypeptides and their genes is discussed in several review articles (Jansson 1994, 1999; Green and Durnford 1996; van Amerongen and Dekker 2003) and is summarized in Table 2.

Table 2. A current list of plant chlorophyll-protein complexes

Chlorophyll-protein complex	Pigments	Proteins (genes)	Role
Photosystem I			
CPI (also CP1)	Chl *a*, β-carotene	PsaA (*psaA*), PsaB (*psaB*)	PS I reaction centre
LHCIa (LHCI-680)	Chl *a*, Chl *b*, xanthophylls	Lhca2 (*Lhca2*), Lhca3 (*Lhca3*)	PS I distal antenna
LHCIb (LHCI-730)	Chl *a,* Chl *b*, xanthophylls	Lhca1 (*Lhca1*), Lhca4 (*Lhca4*)	PS I distal antenna
CPIa (CPI + LHCI, seen on 'green' gels)	Chl *a*, Chl *b*, xanthophylls	–	–
Photosystem II			
CP47	Chl *a*, β-carotene	PsbB (*psbB*)	Core antenna
CP43	Chl *a*, β-carotene	PsbC (*psbC*)	Core antenna
CP29	Chl *a*, Chl *b*, lutein, xanthophylls	Lhcb4 (*Lhcb4*)	Inner distal antenna
CP26	Chl *a*, Chl *b*, lutein, xanthophylls	Lhcb5 (*Lhcb5*)	Inner distal antenna
CP24	Chl *a*, Chl *b*, lutein, xanthophylls	Lhcb6 (*Lhcb6*)	Inner distal antenna
CPII (LHCII monomer, also called LHCIIb)	Chl *a*, Chl *b*, lutein, xanthophylls	Lhcb1 (*Lhcb1*), Lhcb2 (*Lhcb2*), sometimes Lhcb3 (*Lhcb3*)	Outer distal antenna
CPII* (LHCII oligomer, seen on 'green' gels)	Chl *a*, Chl *b*, lutein, xanthophylls	Lhcb1 (*Lhcb1*), Lhcb2 (*Lhcb2*), Lhcb3 (*Lhcb3*)	Outer distal antenna

Attempts to model the organization of Photosystem II (PS II) complexes in the native membrane

As we were trying to untangle the proteins in the Chl-protein complexes, we were also trying to understand how they fit together in PS II in the membrane. We continued with our technique of gently and systematically peeling off layers from PS II. In 1983, we successfully separated the Chl *a*/*b* complexes from the rest of the PS II complex on sucrose density gradients, and found that PS II biochemical activity coincided with the presence of CP47 (CPa-1) (Camm and Green 1983a, b). From this evidence we postulated that CP47 could be the reaction center polypeptide, although CP43 (CPa-2) could also have a role. However, the work of Nanba and Satoh (1987) showed conclusively that D1/D2 represented the reaction center, and that CP47 and CP43 were, in fact, internal antenna complexes. That story has been very nicely told by Kimiyuki Satoh in his historical review (Satoh 2003). At that point, the intimate association of CP47 with the PS II reaction center core became just another intriguing and hard-to-interpret observation. However, the current model of the PS II reaction center based on crystallographic work (Zouni et al. 2001; Kamiya and Shen 2003) and earlier nearest-neighbor analysis (Harrer et al. 1998) show that CP47 is located between D1 and D2 while CP43 is more peripheral. This association may explain why our photosynthetically active, detergent treated particles were more likely to contain CP47 than CP43.

We were also successful in using various detergents to prepare particles containing the PS II reaction center plus CP29 and CP26, but lacking the LHC II Chl *a*/*b* complex (Camm and Green 1989). This suggested to us that CP29 and CP26 were located in closer proximity to the PS II reaction center core, inside a shell of LHC II. In collaboration with Radovan Popovic and colleagues at the Université du Québec à Trois Rivières, Edith carried out photoacoustic spectroscopy on these particles. Among other things, this analysis revealed high energy storage, and the relationship between the action and absorption spectra suggested that these minor Chl *a*/*b* complexes were functional as an internal antenna (Camm et al. 1988). This interpretation is consistent with current models of the supramolecular PS II complex (Boekema et al.

1995; van Amerongen and Dekker 2003). (See James Barber, this issue.)

Our PS II preparations were useful in another way. We teamed up with Sallie Sprague and Andrew Staehelin to see how the LHC II complexes and the PS II core particles behaved in liposomes made of phosphatidylcholine (PC), a minor component of the thylakoid membrane, or digalactosyldiglyceride (DG), the major lipid component. We found that PS II cores were incorporated into DG liposomes where they could be visualized as 7.5 nm intra-membranous particles by freeze-fracture, whereas they were not incorporated into PC liposomes and caused them to become convoluted. We attributed this to charge interaction between the PC head group and the PS II cores (Sprague et al. 1985). Our observations emphasized the contribution of lipids to the overall structure of chloroplast membranes (Webb and Green 1991), an aspect which has received relatively little attention in recent years. Andrew Staehelin has reviewed the history of electron microscopical studies on thylakoid membranes and described how these studies contributed to our current view of the three-dimensional structure of a photosynthetic membrane (Staehelin 2003).

The next chapter

In the early 1990s both the authors moved from a consideration of chlorophyll-protein complexes into other aspects of photosynthesis, and eventually into other aspects of academic life. Beverley's interest in the evolution of the LHC superfamily led her into the field of molecular evolution via the algae that contain Chl *c* (Durnford et al. 1999). These algae are fascinating subjects because their chloroplasts were obtained by secondary or even tertiary endosymbiosis (Ishida et al. 2000; Ishida and Green 2002). Furthermore, the surprising discovery of single gene minicircles in dinoflagellate chloroplasts (Zhang et al. 1999) brought the story 'full circle' (Green 1976b). Edith investigated the effects of environmental factors on the photosynthetic apparatus in evergreen and deciduous conifers (e.g., Eastman and Camm 1995; Rosenthal and Camm 1997), and more recently has applied her problem-solving skills to educational administration. But these are stories for another time.

Figure 3. Beverley Green, having just stumbled into the photosynthesis field at her first of many Gordon Conferences on Photosynthesis (1978).

Figure 4. Elisabeth (Beth) Gantt and Philip (Phil) Thornber enjoying lobster at the 1978 Gordon Conference on Photosynthesis. Beth was preoccupied with understanding phycobilisomes at the time, but later discovered that red algae have a PS I-associated Chl *a*-antenna whose proteins are related to the Chl *a/b* and Chl *a/c* proteins (Wolfe et al. 1994).

In closing, Beverley (Figure 3) would like to thank David Krogmann for finding room for her at the 1978 Gordon Research Conference on Photosynthesis, which got her 'hooked' on photosynthesis! Figure 4 shows two of the pioneers in the field, Beth Gantt and the late Phil Thornber, who were among the attendees at that conference.

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