If, as suggested above, GSK-3/*zw3*[sgg] provides a tonic negative signal, keeping its targets inactive until a positive stimulant causes their dephosphorylation, deletion of the kinase would have the same effect as chronic stimulation, consistent with the dramatic *Drosophila* phenotypes demonstrating that you really can have too much of a good thing.

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Chlorophyll *a/b*-binding proteins: an extended family

Beverley R. Green, Eran Pichersky and Klaus Kloppstech

A large proportion of the chlorophyll in a plant is engaged in harvesting light energy and transferring it to the photochemical reaction centres. These 'antenna' chlorophylls are non-covalently bound to specific proteins to form chlorophyll–protein complexes. The chlorophyll *a/b*-binding (CAB) polypeptides are encoded by an extended family of nuclear genes. It has recently been discovered that other proteins not known to bind chlorophyll, the early light-inducible proteins (ELIPs), are also related and could be considered part of this family. We suggest that the latter proteins may be involved in pigment biosynthesis or in assembly of the thylakoid membrane.

THE MOLECULAR ORGANIZATION of the elaborate apparatus responsible for the efficient conversion of light to chemical energy in photosynthesis is one of the most interesting and challenging areas of modern biochemistry. All photosynthetic organisms that evolve oxygen have two photosystems, PSII and PSI, which operate in series to remove electrons from water and deliver them energetically uphill to NADP$^+$ (Fig. 1). The energy to drive this electron flow comes from the light energy absorbed by the 100–300 chlorophyll (Chl) molecules associated with each photosystem. The only Chl molecules to lose and gain electrons, i.e. contribute to electron flow, are one special pair of Chl *a* molecules in the 'reaction centre' (RC) of each photosystem (labelled P680 in RCII and P700 in RCI). Most of the Chl is not involved in moving electrons around, but is organized in light-harvesting antennae, which surround the reaction centres and transfer absorbed light energy to them.

The chlorophyll–protein complexes

Green plants have two kinds of chlorophyll, Chl *a* and Chl *b*, which are non-covalently bound to intrinsic membrane proteins. These chlorophyll–protein complexes can have only Chl *a* or both Chl *a* and *b*. Both types of chlorophyll–protein complex also contain several carotenoid molecules which are thought to protect them from the damaging effects of light. The functional cores of both PSI and PSII consist of a number of hydrophobic proteins that are chloroplast-encoded and synthesized[1]. Several of these bind Chl *a* and act as internal antennae to the nearby RCs. The subject of this article is the second class of chlorophyll–protein complexes, those containing both Chl *a* and *b* (hatched or dotted in Fig. 1). In contrast to the polypeptides of the Chl *a* antenna complexes, the Chl *a/b* or 'CAB' polypeptides are encoded by nuclear genes, synthesized on cytoplasmic ribosomes, imported across the two membranes of the chloroplast envelope, and finally inserted into the thylakoid membrane[2].

One of the first Chl–protein complexes discovered was what we now call LHCII (light-harvesting complex II, originally CPII), the major Chl *a/b* antenna of PSII[3,4]. It accounts for about 50% of the total Chl in the plant, which is an indication of its importance. It is particularly interesting because of its involvement in both short-term and long-term adaptation to different light and temperature conditions[5]. It was discovered

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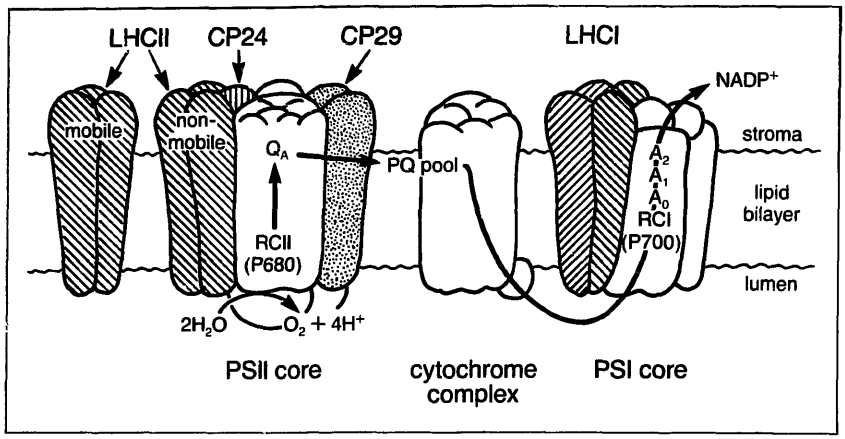

Figure 1

Diagram of thylakoid membrane organization, emphasizing the Chl *a/b*-protein complexes. LHCII (diagonal hatching), CP24 (vertical hatching) and CP29 (stipple) are antennae of photosystem II (PSII); LHCI (hatching) is the antenna of photosystem I (PSI). RCI and RCII are the reaction centre chlorophyll pairs of PSI and PSII. In the chloroplast, PSI units would be segregated in unappressed regions of the thylakoid membrane (stroma lamellae) whereas a large fraction of PSII units would be in regions where two or more thylakoids were appressed (grana lamellae). The 'mobile' fraction of LHCII is able to move between grana and stroma regions to alter the distribution of excitation energy between the two photosystems.

about ten years ago (for review see Ref. 1) that 75–80% of the PSII units were concentrated in regions where two or more thylakoid membrane sacs were appressed (the so-called grana lamellae) whereas almost all the PSI units were in non-appressed regions (stroma lamellae). It was subsequently found that a subpopulation of LHCII (mobile LHCII) was able to respond to excess light by separating itself from the core of PSII and migrating into the non-appressed regions of the thylakoid where it is closer to PSI (Ref. 5). This changes the distribution of light energy between the two photosystems.

In the past few years, a number of other Chl *a/b* complexes have been isolated, and shown to have different locations and roles in the two photosystems[3,6]. CP29 has two polypeptides and a Chl *a/b* ratio of 4–5, which is significantly higher than the 1.2 ratio of LHCII (Table I). It is associated more tightly with the central core of PSII than is LHCII (Ref. 7), and its attachment is not affected by physiological conditions[8]. It never migrates into the non-appressed regions of the thylakoid membrane. Detergent treatments that remove CP29 from PSII core preparations also damage their ability to transfer electrons to quinone acceptors; however, there is no evidence that CP29 itself is involved in quinone binding[9]. PSII also has a small amount of a complex called CP24[10], which appears to have only one CAB polypeptide on SDS-PAGE and has a Chl *a/b* ratio of less than 1. It is removed from PSII core (and CP29) along with LHCII, so it is probably on the periphery of PSII. The specific role of CP24 is unknown.

PSI was at first believed to lack Chl *b*, but a few years ago it was found that it has its own light-harvesting antenna (LHCI) with four polypeptides and an *a/b* ratio of 3–4 (Ref. 11).

LHCI can be subdivided into at least two different Chl–protein complexes, one of which appears to be responsible for the 730 nm fluorescence of PSI at low temperature (LHCI–730)[12]. The other complex (LHCI–680) fluoresces at lower wavelength (higher energy) suggesting a different type of Chl organization. The path of energy flow among LHCI–680, LHCI–730 and the Chl *a* antennae of PSI is under investigation in several laboratories.

Table I. The tomato chlorophyll *a/b* proteins and their genes

Complex	Role/location	Chl *a/b* ratio	Polypeptides	Gene types	No. gene copies	No. introns
LHCII	Major antenna PSII	1.2	2 major	Type I	8	0
				Type II	2	1
			1 minor	Type III	ND	–
CP29	Core antenna PSII	4–5	2	Type I	1	5
				Type II	ND	–
CP24	Minor PSII antenna	<1	1–2	–	2	1
LHCI	PSI antenna	3–5	4	Type I	2	3
				Type II	1	4
				Type III	1	2
				Type IV	2	2

ND = not determined.

The CAB polypeptide family: modular proteins

A new light was cast on the diversity of Chl *a/b* antenna protein complexes when it was discovered that both monoclonal and polyclonal antibodies raised against protein(s) from one purified complex recognized the polypeptides of the other complexes[13–15], suggesting that all these proteins might share some common amino acid sequences. Gene sequencing has now verified this and has shown that these CAB proteins comprise an extended family. We have recently discovered that some apparently unrelated proteins, the 'early light-inducible proteins' (ELIPs) are even more distant relatives[16].

The protein sequences deduced from DNA sequences reveal a family pattern (Fig. 2). The proteins themselves can be considered to be made up of modules, some of which are almost identical in sequence in all the CAB proteins, and others that appear to have diverged (evolved) much more rapidly. They all have three hydrophobic regions, each of a sufficient length to span the thylakoid membrane. There has been some discussion about the number of transmembrane helices but the most widely accepted folding model for the LHCII proteins[18], supported by protease digestion and chemical labelling experiments[19,20], has three transmembrane helices with the amino terminus exposed on the stroma side and the carboxyl terminus tucked away in the thylakoid lumen (inset in Fig. 2). By analogy, the other Chl *a/b* proteins could have the same topology. In all the CAB proteins, the two regions preceding the first and

third transmembrane helices have a very distinctive pattern of conserved residues (zigzags, Fig. 2). These modules, on the stroma side according to our model, are highly enriched in turn-promoting amino acids (Gly, Pro, Asp). The CAB proteins show substantially more diversity in the region of the second predicted transmembrane helix. Family ties break down in the amino-terminal regions, which are quite dissimilar.

Transmembrane helices 1 and 3 and the segments preceding them are the most highly conserved sequences (shaded in Fig. 2). In fact, homology matrix analysis shows that these two regions are homologous to each other, suggesting that they could have resulted from an internal gene duplication in the evolutionary history of the family[21]. Note that the ELIPs have detectable sequence homology to CABs only in the helical part of the conserved regions, although they are predicted to have β-turns in the same positions as those in the CABs.

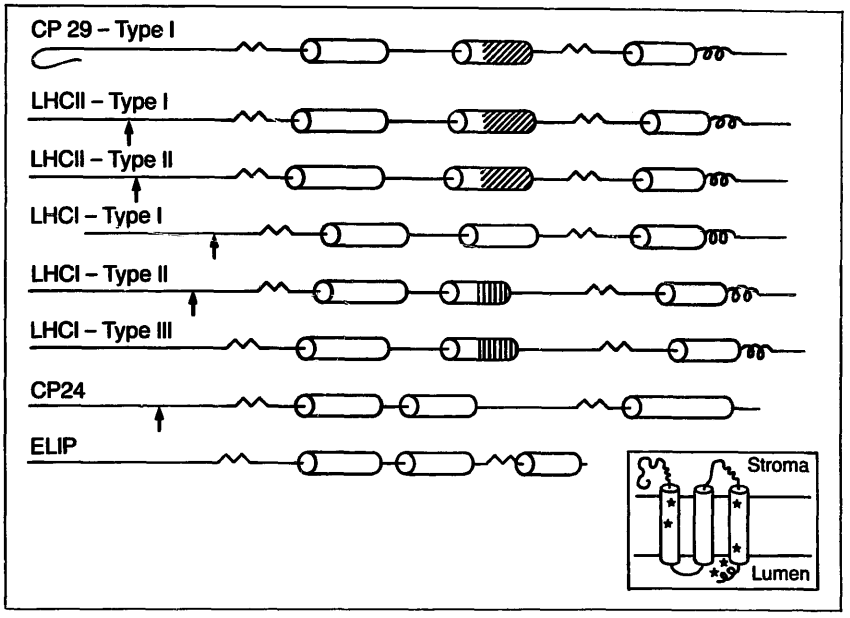

Figure 2

Schematic diagram of the structure of the chlorophyll *a/b* (CAB) proteins and the early light-induced proteins (ELIPs). Shaded areas indicate the two conserved regions, shared by all CABs. Diagonal hatching indicates additional regions of homology between CP29 Type I and LHCII sequences; vertical hatching, homology between Type II and Type III LHCI sequences. Type IV LHCI (not shown) is similar to Type II. Structure prediction was done by a combination of methods[17]. Predicted transmembrane helices are represented by cylinders; amphipathic helices by a coil; β-turns by zig-zags; transit peptide cleavage sites by arrows. Insert: model of protein folding as originally proposed by Karlin-Neumann *et al.*[18] Stars represent the conserved residues (His, Gln, Asn) that could be ligated to Mg^{2+} ion of chlorophylls.

Family relations

The two major LHCII polypeptides are the most closely related members of the CAB family. The numerous genes encoding them fall into two types (I and II), which code for the higher and lower molecular weight polypeptides, respectively. All the amino acid sequences within a type in the same species are nearly identical. Between Type I and Type II the sequences are about 85% identical, although the transit peptides are only 50% identical[4]. Most plants are endowed with 5–15 of these genes and this is reflected in the high relative abundance of the major LHCII proteins compared to other thylakoid membrane proteins.

In contrast to these 'siblings', a group of CAB 'cousins', including the four LHCI polypeptides and one CP29 polypeptide, share quite a few family characteristics with the LHCII polypeptides but are all distinctly different (Fig. 3). CP29 Type I and the LHCIIs share some homology in the second transmembrane helix (hatched in Fig. 2) as well as a small conserved motif in the amino terminal region. LHCI Types II, III and IV have detectable homology with each other in the second transmembrane helix (vertical hatching), and have less homology with Type I LHCI, which is about as related to them as it is to CP29 Type I. With these exceptions, there is very little in common among these proteins outside of the conserved regions. The CAB polypeptides whose genes have not yet been cloned (the second CP29 polypeptide and one or more minor LHCII polypeptides) are immunologically related to the other CABs, so we expect they will share the same general structural pattern.

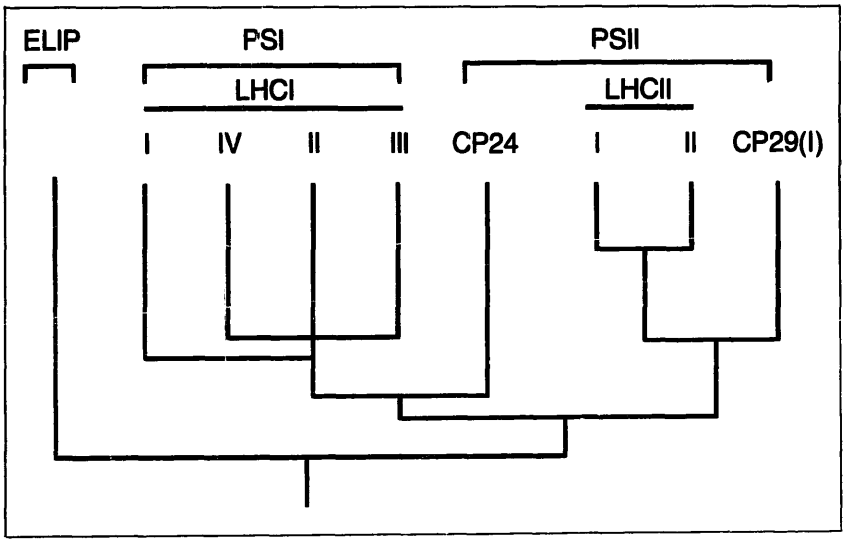

Figure 3

Family tree showing relationship of CAB and ELIPs polypeptides. The lengths of branches do not indicate a rigorous calculation of evolutionary distances. Most CAB proteins, with the exception of LHCII Types I and II, are 60–70% divergent (see text). The branching points were based both on overall sequence similarity and on comparison of shared deletions/insertions.

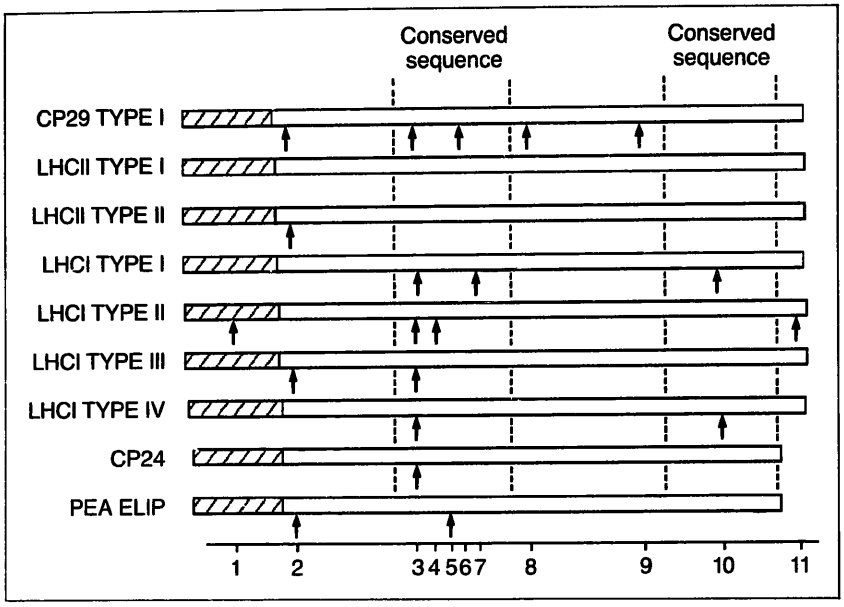

Figure 4

Positions of introns (arrows) in tomato CAB genes and a pea ELIP gene. Only in three positions (2,3,10) do introns occur in the same position in more than one type of CAB gene. Hatched region represents the transit sequence that is cleaved once the protein is transported into the chloroplast stroma.

CP24 was only recently distinguished from LHCII by improved detergent solubilization methods[10], and its genes were cloned[22,23]. It first appeared to have only two transmembrane helices[22], which posed an interesting topological problem; however, comparison of the spinach and tomato genes and reexamination of the secondary structure prediction showed that there were indeed three transmembrane helices, although the first two are closer together than in other CAB proteins, and there is a very long hydrophilic region (stroma-exposed) following the second transmembrane helix (Fig. 2). CP24 also lacks most of the carboxy-terminal tail, predicted to include an amphipathic α-helix close to the lumenal surface[21]. This putative helix (coil, Fig. 2) is highly conserved in all the other CAB proteins, with invariant His and Asn residues as potential Chl ligands (stars, Fig. 2 insert). Perhaps this explains why CP24 is somewhat unstable and loses its Chl easily, or why it has such a low Chl *a/b* ratio.

Distant relatives

The ELIPS or early light-inducible proteins[24] are more distant relatives of the CAB family. As their name suggests, their genes are turned on very early during greening of etiolated plants, and both mRNAs and proteins are degraded long before chloroplast development is completed. In young green plantlets the level of ELIP mRNAs is governed by a circadian oscillator, and varies by a factor of 20 between the maximum in the morning and the minimum during the middle of the night[24]. Similar oscillations have been observed in mRNA levels of CAB proteins and other light-inducible proteins of PSI and PSII (Ref. 25). Preliminary evidence suggests that the levels of the ELIP proteins themselves may oscillate during the day (K. Kloppstech, unpublished). In both peas and barley there are two groups of closely related ELIP genes, analogous to the multiple Type I and Type II LHCII genes.

Amino acid sequences deduced from ELIP genes of peas and barley show that, like the CAB proteins, ELIPs also have three potential membrane-spanning helices, although the connections between the helices are much shorter[16,26]. Furthermore, the first and third helices have weak but recognizable homology with the corresponding helices of the CAB polypeptides[16]. The conserved His, Asn and Gln are present, although the second Gln is replaced by a Glu. In contrast, the two highly conserved stromal domains of the CABs are not found in the ELIPs, nor is the carboxy-terminal tail with its putative Chl-binding residues. However, trypsinization of thylakoid membranes, as well as the number of predicted helices, indicate that the topology of ELIPs is very similar to that of the CABs (insert, Fig. 2). Furthermore, the stromal domains of the ELIPs are predicted to have several closely spaced β-turns in approximately the same positions as the CAB polypeptides, even though there is no detectable sequence similarity. Thus, as with other protein families such as the globins, the folding pattern of the protein is conserved even when sequence similarity is no longer recognizable[27].

ELIPs have been found associated with both PSI and PSII. A first hint towards understanding their role may be that they have been found in the stroma thylakoids (unappressed membranes) which are thought to be the site of insertion of PSII (and presumably PSI) proteins. This suggests they may play a role in the assembly of the photosystems, or perhaps in the synthesis and integration of pigments into the mature pigment–protein complexes. An exciting recent discovery is that a protein with high sequence similarity to ELIPs is induced in parallel with accelerated carotenoid synthesis in the green alga *Dunaliella* (A. Lers, H. Levy and A. Zamir, unpublished). Furthermore, the promoter of its gene has two regions with sequence identity to regulatory elements of mammalian genes involved in synthesis and uptake of sterols. Since both sterols and carotenoids are products of the isoprenoid pathway, this suggests that the *Dunaliella* ELIP-like protein might be involved in the synthesis of carotenoids or in their accumulation and transfer to the developing Chl–protein complexes.

The evolution of the CAB family

Since all the chlorophyll–protein complexes are found in all higher plants and green algae examined[6], we expect most of the different types of CAB genes to occur in all plants. An almost complete set of CAB genes has been isolated and characterized in only one species, the tomato *Lycopersicon esculentum* (Refs 21,22, B. Green and E. Pichersky, unpublished), although many reports of one type of CAB gene (mostly LHCII Type I) from various species have appeared. We have recently determined by Southern blotting that *Arabidopsis thaliana* contains all eight different types of CAB genes presently known in tomato (J. M. McGrath and E. Pichersky, submitted).

The eight types of CAB polypeptide are, with one exception, substantially

divergent (60–70%) (Fig. 3) suggesting that the gene duplications that gave rise to them occurred very early in the evolution of CAB-containing organisms. In contrast, the LHCII Types I and II genes are only 15% divergent from each other, indicating a much later gene duplication event, perhaps at the time of divergence between the fern and seed plants[28]. Comparisons of LHCII Type I proteins from diverse species indicate strong conservation of primary sequence (>90%); a similar rate of sequence conservation is observed for LHCII Type II proteins[4]. Lack of substantial sequence data precludes within-type comparisons for the other CAB proteins.

The LHCII Type I is encoded by multiple gene copies in most species[4] (Table I). Within a species, these genes are very similar, encoding identical or almost identical proteins. It is not known whether this is the result of gene conversion events or very recent gene duplications. In contrast, the genes encoding LHCII Type II, LHCI, CP29 and CP24 are present as single or duplicate copies in tomato (Table I) and preliminary data suggests this is the case in other plant species[4].

With the exception of the LHCII Type I CAB genes, all other members of the family contain introns. However, the number and position of introns vary among the different types of CAB genes (Fig. 4). Of the 11 positions in which introns occur, only three positions are common to more than one type of CAB gene. There is also no evidence that introns occur at boundaries between structural domains. In fact, more introns occur in the middle of conserved regions than in the non-conserved regions. The general 'scatter' seen in Fig. 4 would support the idea that some introns were added after the divergence of the different types of CABs, but the paucity of sequence data available makes tracing the evolution of introns within the family uncertain.

Besides the 'green' eukaryotes that have Chl *a/b* antennae (vascular plants, mosses and certain groups of algae), the other large group of oxygenic photosynthesizers is the chromophytic algae, which have Chl *c* instead of Chl *b* in their antennae. Antibodies to Chl *a/b* polypeptides cross-react with the Chl *a/c* polypeptides of several algal groups[29,30]. The sequences of three Chl *a/c* polypeptides from the diatom *Phaeodactylum tricornutum* show clearly detectable homology with the CABs in both the first and third transmembrane helices and their preceding hydrophilic modules, although the Chl *a/c* polypeptides are less related to the CABs than the CABs are to each other[31]. The presence of CAB or CAB-like proteins in all eukaryotic photosynthetic organisms except for the red algae means that this gene family must date from the very early stages of evolution of eukaryotic photosynthetic organisms.

Provenance of the ancestral CAB gene

The evolutionary origin of the Chl *a/b*-binding polypeptides is not known. The bacteriochlorophyll-binding antenna proteins of purple photosynthetic prokaryotes, which are short and cross the membrane once[32], do not have discernible sequence similarity to CABs. Neither do the Chl *a* polypeptides of the PSI and II cores, including those of the Chl *a*-containing prokaryotes, the cyanophytes. The phycobiliproteins, which fill the role of light-harvesting antennae for cyanophytes, are not membrane proteins and share no homology with any of the chlorophyll- or bacteriochlorophyll-binding proteins.

Since the sequences of the two conserved transmembrane helices of all members of the CAB family, including the ELIPs, are highly similar to each other and may indeed have similar functions, e.g. in pigment binding, this suggests that extant CAB genes are descended from an ancestral gene that was created by a tandem gene duplication followed by gene fusion. The middle hydrophobic region might then have evolved simply to maintain the

first and third hydrophobic regions in the same membrane orientation (stroma to thylakoid). If the internal duplication hypothesis is correct, then some related gene(s) may exist that encodes a chlorophyll *a/b* binding polypeptide with a single transmembrane helix. Alternatively, it may no longer bind chlorophyll but instead play some other role in modern plants.

A recently discovered group of prokaryotes, the Prochlorophytes, do not have phycobilisomes and do have a Chl *a/b* antenna[33,34], but their Chl *a/b*-binding polypeptides are not immunologically related to the CAB polypeptides[35]. It is therefore not yet possible to determine whether the prototype CAB gene originated prior to the separation of the prokaryotic and eukaryotic lineages. However, the prokaryotic photosynthesizers of the marine environment are largely unknown; it was only in 1986 that the first free-living prochlorophyte was discovered[34]. It is quite likely that a number of novel antenna complexes are waiting to be discovered!

This leaves the question of where a new chlorophyll-binding protein could have come from. An attractive hypothesis is that the CAB proteins are structurally related to enzymes participating in the last steps of synthesis of chlorophyll or other pigments, since both must have binding site(s) for the pigment molecules. For example, the CAB proteins could have arisen through the duplication of a gene encoding a chlorophyll biosynthesis enzyme and the recruitment of one duplicate copy to encode a structural protein of a new antenna system. The only such enzyme sequenced to date is protochlorophyllide reductase, which does not have any detectable homology with any other protein known[36]. However, the possibility that ELIPs might be involved in carotenoid biosynthesis lends support to this idea, and provides impetus for further research on the enzymes of both chlorophyll and carotenoid biosynthetic pathways.

Acknowledgement

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Note added in proof

Kühlbrandt and Wang have recently published a model of pea LHCII based on electron crystallography to 6Å resolution (*Nature* 350, 130–134, 14 March 1991), which confirms the three-helix model. The two conserved helices are longer than the middle helix (31 and 33 vs. 20 residues), and probably extend out of the bilayer. The two conserved stroma-exposed regions appear as kinked hooks lying along the surface of the protein. A pseudo-twofold symmetry axis relates the two conserved regions. The most exciting new finding is that the 15 Chl are organized in a novel fashion: hanging around the helices like washing on a two-level drying rack, with the rings roughly perpendicular to the membrane plane, and at least partly exposed to the lipid bilayer.

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Solution to Lipsky Acrostic (December)

'That so many experts turn out so much research ... is often brought forward as proving the progress of science. Rate of working, nevertheless, is the product of force by velocity and is not necessarily increased if velocity approaches infinity while force approaches zero.'

C. Truesdell, *[An Idiot's Fugitive] Essays on Science*, Springer-Verlag, New York, 1984, p. 1.

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