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Minireview

Evolution of photosystem I – from symmetry through pseudosymmetry to asymmetry

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Abstract The evolution of photosystem (PS) I was probably initiated by the formation of a homodimeric reaction center similar to the one currently present in green bacteria. Gene duplication has generated a heterodimeric reaction center that subsequently evolved to the PSI present in cyanobacteria, algae and plant chloroplasts. During the evolution of PSI several attempts to maximize the efficiency of light harvesting took place in the various organisms. In the Chlorobiaceae, chlorosomes and FMO were added to the homodimeric reaction center. In cyanobacteria phycobilisomes and CP43′ evolved to cope with the light limitations and stress conditions. The plant PSI utilizes a modular arrangement of membrane light-harvesting proteins (LHCI). We obtained structural information from the two ends of the evolutionary spectrum. Novel features in the structure of *Chlorobium tepidum* FMO are reported in this communication. Our structure of plant PSI reveals that the addition of subunit G provided the template for LHCI binding, and the addition of subunit H prevented the possibility of trimer formation and provided a binding site for LHCII and the onset of energy spillover from PSII to PSI.

Key words: Photosystem I; Evolution; Green bacteria; Membrane proteins; Photosynthesis; Light-harvesting

1. Introduction

Oxygenic photosynthesis is the main energy provider for the synthesis of organic matter on earth. The first step in this process, light-induced charge separation, is driven by photosystems (PS) I and II, two large chlorophyll-containing protein complexes acting in series and located in the thylakoid membranes of cyanobacteria and chloroplasts [1,2]. Molecular biology evidence and recent phylogenetic studies suggest that PSI, which probably emerged 3.5 billion years ago, preceded the appearance of cyanobacteria and it may have evolved from organisms resembling today's green and gliding bacteria [3–5].

Gene duplication followed by evolution of homodimeric to heterodimeric structures is one of the most crucial steps in the advancement of organisms from primitive to advanced life forms [6]. Beginning with the structure of hemoglobin by Perutz et al. [7], a growing number of proteins were identified whose functional unit consisted of two or more subunits. Several more complex organizational forms are often based on dimeric substructures [2,6]. Gene duplication and the subsequent formation of pseudoheterodimeric structures were essential for the evolution of most multisubunit oligomeric protein complexes [6,8]. PSI and PSII are prime examples of such an evolutionary trend [4,9,10].

Even though PSI reaction centers (RCs) from bacteria and plants are homologous and evolved from a single ancestor the light-harvesting complexes (LHCs) that accompany these RCs are highly diverged and have no genetic relations. In green sulfur bacteria, the soluble bacteriochlorophyll *a* protein FMO (after Fenna, Matthews and Olson) transfers light energy from the large ellipsoidal complex, the chlorosome, to the photosynthetic RC [3]. Cyanobacteria utilize a phycobilin–protein complex called phycobilisome and chloroplasts contain specialized chlorophyll–protein complexes that are organized as LHCI complex [11,12]. We obtained structural information from the two ends of the evolutionary spectrum. Intact FMO was crystallized and solved to about 2.4 Å resolution and the entire plant PSI was crystallized and solved to 4.4 Å resolution [13,14]. The two structures reveal several features that are pertinent for understanding the evolution of PSI and light harvesting by this intricate complex.

2. Novel features in FMO from *Chlorobium tepidum*

While attempting to crystallize the RC complex from the green sulfur bacterium *C. tepidum*, we discovered conditions that permitted FMO crystallization from a solution that contained only the purified RC complex (and no free FMO). The RC was isolated after dodecyl maltoside extraction from cell membranes by a modified procedure that was published previously [13,15]. When added to the purified RC, a crystallization buffer containing hexanediol and magnesium chloride had a triple effect: aggregation of the RC, detachment of FMO from the RC and later, crystallization of this trimeric light-harvesting protein. The structure was solved by molecular replacement using the original FMO structure (that was published at 1.9 Å resolution). Surprisingly our structure, solved at 2.4 Å resolution, revealed novel features that were not detected in the previous structures [16–18]. We ascribe these to the fact that the FMO described here was kept in its native form, as part of the intact RC complex, just until

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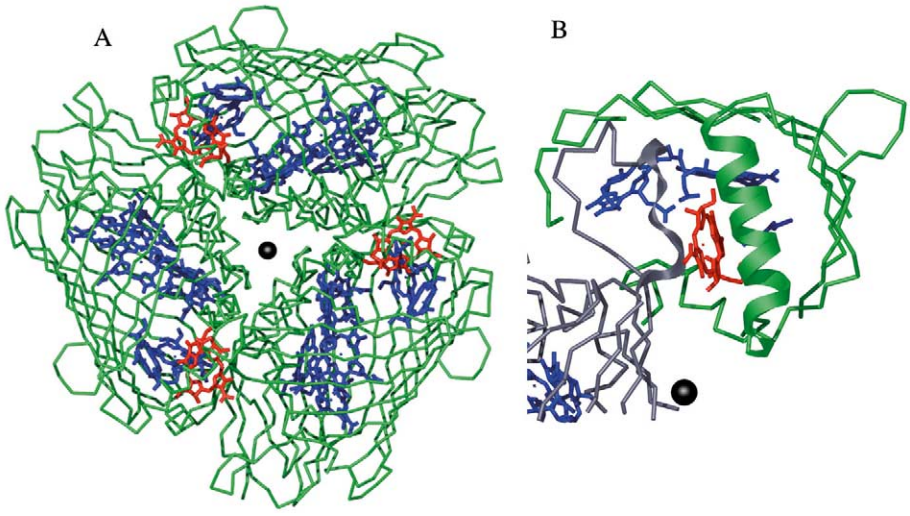

Fig. 1. Structural model of *C. tepidum* FMO at 2.4 Å resolution. A: The C-α chain (green) of the trimeric FMO is shown from the wider opening of the funnel that runs along the three-fold symmetry axis. The seven chlorophyll residues that were previously detected are in blue. The new suspected chlorophyll residue is in red and the two metal ions along the three-fold axis are depicted as black balls. B: Position of the new putative chlorophyll (red) at the interface of two FMO monomers (green and gray).

crystallization occurred. A model of our structure of trimeric FMO is depicted in Fig. 1. Two metal ions are positioned at the narrowest points of the funnel that passes along the three-fold symmetry axis. No such metal ions were previously reported in crystals formed by FMO though the protein's activity and trimeric assembly were verified [17,18]. The most prominent new detail in the electron density map that was not reported in previous works appears in the interface between the monomers, positioned in a pocket formed by an α-helix of one monomer (residues 157–175) and a protruding loop from the second (residues 122–130) (Fig. 1B). This additional electron density shows no similarity to any ingredient of the purification or crystallization buffers. We propose that this electron density is the result of the presence of an eighth chlorophyll molecule in each FMO monomer within the RC. The fact that this addition was not previously detected in any preparation of FMO but only when the FMO was crystallized directly from the purified RC strongly suggests that it is positioned at the interface between FMO and the RC. This prompts us to propose a model for FMO binding to the RC. Recent studies by electron microscopy pointed to the possibility that all the FMO in the cell is attached to the RC probably as two trimers per RC [3]. Fig. 2 depicts a model of the interaction of the two FMO trimers with a theoretical model of the PscA dimer that forms the core of the *Chlorobium* RC. The homodimer of PscA was constructed from the coordinates of the cyanobacterial PsaB [19], leaving the transmembrane helices unchanged and modifying the loops connecting between them according to the lengths obtained from the hydropathy plot (TMHMM Server v. 2.0). A similar model of the homodimer of PscA was previously proposed [20]. Two alternatives for FMO binding to the RC are given in Fig. 2. In the first one (Fig. 2A) the FMO is attached to the RC at the wider side of the 'funnel' that runs along its three-

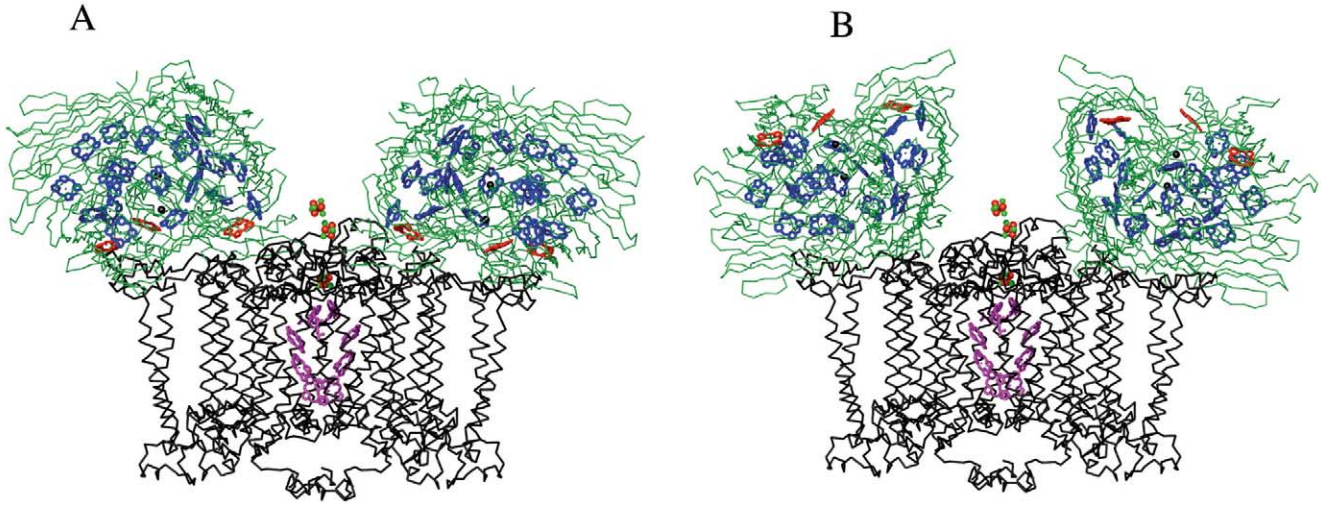

Fig. 2. Two possible theoretical models for the interaction of FMO trimers with the main subunits of the RC. The homodimeric RC was modeled as described in the text. A: The FMO was placed on the RC with the new 'chlorophylls' close to the membrane surface onto the cytoplasmic side of the RC. B: The FMO was fitted with chlorophyll 3 closest to the membrane (180° rotation relative to A).

fold symmetry axis. The novel putative chlorophylls are positioned close to the membrane suggesting that they play a crucial role in excitation energy transfer to the RC. In the second possibility (Fig. 2B), where FMO is rotated by 180°, chlorophyll 3 (nomenclature as in [16]) of each monomer is closest to the membrane. Calculations aiming at simulating spectroscopic data of FMO suggest that excitation energy is eventually localized on this chlorophyll 3 [21]. However, these calculations were performed on isolated, oxidized FMO that lacks the possible additional chlorophyll. For reasons described above and because of better fitting to the electron microscope models [3,22,23], we favor the first possibility.

Regardless of the orientation of the FMO moieties, the structure of the *Chlorobium* RC must keep a two-fold symmetry because it is based on a homodimeric core that is a single gene product [9,24]. Accordingly in the ancestral PSI, symmetry is kept both within the RC and in its immediate light-harvesting antenna, the homotrimeric FMO.

3. Advancement in evolution and deviation from symmetry in protein complexes

From the time that two partially homologous adjacent chloroplast genes, encoding polypeptides of the P700 chlorophyll *a*–protein complex of PSI (PsaA and PsaB), were discovered, it was apparent that the core of PSI evolved by gene duplication of an ancestral gene [25–28]. Thus the fundamental core of PSI RC (subunits PsaA and PsaB) is composed of a heterodimeric structure that likely evolved from a homodimeric ancestor. Indeed cloning of the gene encoding the main subunit of *Chlorobium* RC together with polypeptide sequences of the large subunit revealed that only one gene encodes the dimer of subunit I [9,24,29]. Thus, the core of *Chlorobium* RC represents an ancestral homodimeric RC from which PSI of cyanobacteria and plants evolved. It was proposed that the homodimeric RC is more suitable for the specific metabolic requirements of *Chlorobium* [1,3]. This trend is general for the evolution of many protein complexes. Fig. 3 depicts a schematic presentation of a protein complex that evolved from a single gene that encodes a polypeptide that initially operated as a homodimer. It is apparent that additional gene products that are involved in increasing affinity to ligands or substrates, regulation or proper assembly could be added only in a symmetric fashion. This limits the possibilities to achieve a delicate tuning of the system. Gene duplication and subsequent separate evolution of the two genes could solve this problem. The instance that a single mutation occurs in one of the genes, depicted in Fig. 3 as the emerging of α′, the structure of the complex changes from a symmetric to a pseudosymmetric organization. At this stage addition of a β subunit can take place in a symmetric or asymmetric fashion depending on whether the mutation changes the structure of the respective binding sites on the α and α′ subunits. Further deviation in the amino acid sequences of α and α′ subunits will enforce deviation from symmetry with every addition of subunits to the protein complex (Fig. 3). The protein complex may now maintain the pseudosymmetry of α and α′ subunits or let these two subunits evolve into two entirely different proteins with no sequence homology. In PSI of cyanobacteria, algae and higher plants the pseudo-two-fold symmetry was maintained by virtue of sequence homology between PsaA and PsaB. However, the structure of the entire complex deviated from symmetry with the advancement of evolution. The deviation from symmetry is attributed to the more peripheral subunits PsaC, PsaD, PsaE, PsaF, PsaJ and PsaL. Since the position of these subunits is almost identical in cyanobacteria and plants, the deviation from symmetry was probably initiated at the onset of oxygenic photosynthesis following the initial gene duplication and the emerging of PsaA and PsaB (Fig. 3).

4. Going from trimeric PSI in cyanobacteria to monomeric PSI in higher plants

While plant PSI is purified as a monomer its cyanobacterial counterpart assembles in vivo into trimers [12,30–33]. The three-fold symmetry of cyanobacterial PSI dictates that any addition of subunits to the complex is necessarily symmetric and placed equally in each of the three monomers. Recently it was discovered that under certain stress conditions, the trimeric cyanobacterial PSI is surrounded by a membrane antenna protein called CP43′. Eighteen identical copies of CP43′ form a circle around the periphery of the PSI trimer that keeps an almost constant distance from the core [34–36]. This arrangement of LHCs perfectly maintains the symmetric structure of the trimeric RC. We propose that this evolution-

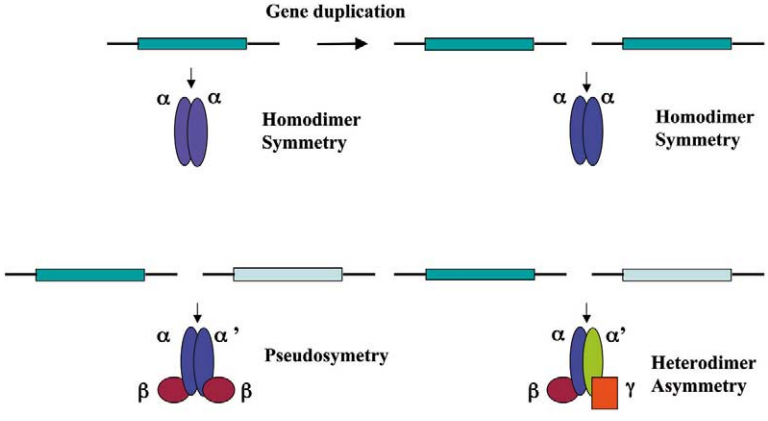

Fig. 3. Gene duplication and deviation from symmetry increase the possibility for the addition of different subunits in evolving protein complex.

ary attempt to add LHC into the RC did not prevail in higher plants because its symmetric arrangement could not support a modular LHC of varying composition. Following this line of thinking, the evolutionary force that drove the trimeric RC into a monomeric one in eukaryotic organisms was the generation of modular light-harvesting machinery that would be able to cope with the ever-changing light intensities and quality on the surface of the ocean and even more so on land.

Two new eukaryotic subunits PsaG and PsaH were crucial for the initiation of this evolutionary step and eventually the emerging of land plants. In addition modification of PsaL played a role in the advancement towards monomeric PSI. As depicted in Fig. 4, the protruding C′-terminus of the cyanobacterial PsaL is essential for PSI trimer formation [19,37]. A forced model of trimeric plant PSI (Fig. 4) shows not only that this part of PsaL is missing in plants but also that the added subunit H prevents any possibility of forming a trimeric structure. Thus, the three-fold symmetry that governs the structure of the cyanobacterial PSI was broken about 1 billion years ago (beginning of chloroplast evolution).

The evolution of PsaG is of particular interest with respect to the deviation from symmetry. Sequence alignment demonstrates that PsaG arose through gene duplication of PsaK [38], which therefore originally added a symmetric feature to the RC. But evolution, through random mutations, had designed distinct roles for these subunits that are now becoming clear. There seems to be an inherent difference in the rigidity of these subunits and in the stability of their binding to PsaA/PsaB. Even in the 2.5 Å resolution structure of cyanobacterial PSI [19], large parts of PsaK are not resolved (stromal loop, half of second helix), attesting to their flexibility and accessibility to proteases. On the other hand, PsaG is almost fully traceable, including its water-exposed loops, even at our 4.4 Å electron density maps [14,39]. This difference is well reflected in the roles of these subunits. PsaG serves as the anchor site for LHCI binding. It forms a helix bundle with helix C of Lhca1 thus contributing the only intramembrane interaction between the core and the antenna belt (Fig. 5). We propose that this strong and stable anchor site facilitates the modular nature of LHCI. The rest of the antenna may change its composition and use Lhca1 (and perhaps Lhca4) attached to PsaG as a stronghold for assembly and binding to the core. This notion is given credence by a recent work that recorded LHCI stoichiometry in plants growing under different light intensities [40]. Lhca2 and Lhca3 levels fluctuated strongly as a function of light intensity, the concentration of Lhca4 was reduced dramatically at high intensities, and only Lhca1 levels remained constant under all conditions. Plants also used the instability of PsaK to their advantage. We find that Lhca3 binds to the core through relatively weak interactions with water-exposed loops: on the luminal side with PsaA and on the opposite side with an electron density that we attribute to the stromal loop of PsaK as suggested by cross-linking experiments [14,41]. We propose that this weak binding and the instability of PsaK facilitates, in eukaryotes, fast alterations in the composition of LHCI. This underlies

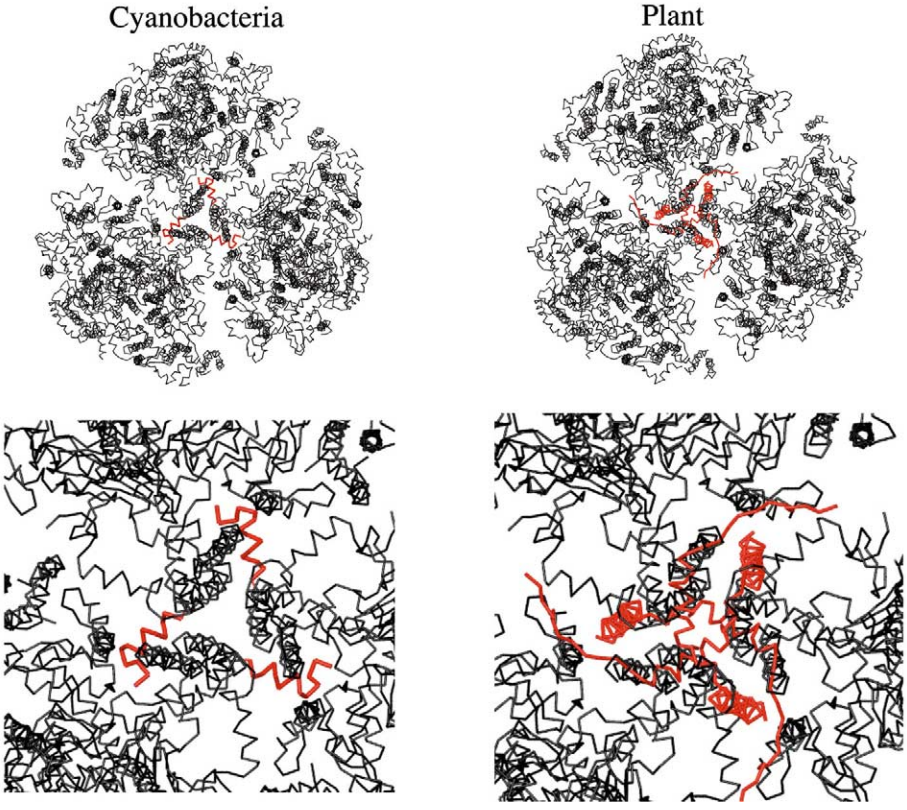

Fig. 4. Subunit H prevents the possibility of trimer formation in plant PSI. Left panels: A model of PSI trimer from *Synechococcus elongatus* [19]. The enlarged middle section illustrates the contribution of the C′-terminus of subunit L (red) for trimer formation. Right panels: A computer-generated forced-trimer of plant PSI-RC. The enlarged middle section shows that subunit H (red) prevents any possibility of trimer formation.

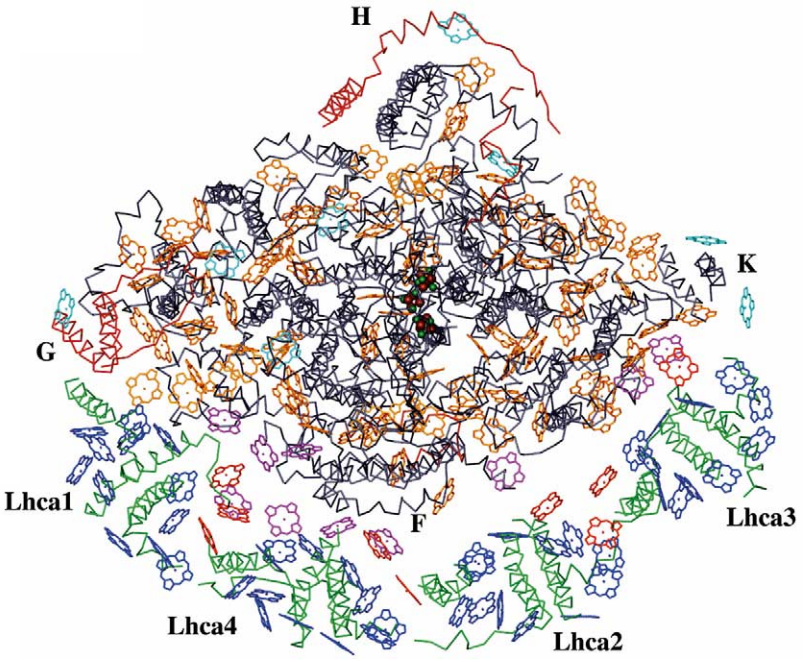

Fig. 5. The entire plant PSI crystal structure revealed at 4.4 Å resolution. A look from the stromal side of the membrane on the C-α backbone and the cofactors of plant PSI. The solution of the crystal structure was as previously described [14,39]. Chains with structural similarity to the cyanobacterial RC are in black; new additions to the RC core are in red and the LHCI proteins are in green. The assignment of Lhca1–4 and the positions of F, G, H and K subunits are indicated. The chlorophylls are depicted in different colors according to their assigned location and/or putative function: LHCI chlorophylls (blue), energy transfer between LHCI monomers (red), special function in energy migration between LHCI and the RC (magenta), conserved chlorophylls in the RC (yellow), added chlorophylls to the RC (cyan).

the recent finding concerning PSI from *Chlamydomonas* under iron deprivation [42]. Under these conditions, PsaK is degraded, the Lhca2–Lhca3 heterodimer detaches from the complex and alternative Lhca proteins are expressed. Thus an important aspect of eukaryotic PSI deviation from symmetry lies in the fact that LHCI is strongly bound to the core only at one pole (PsaG). The modularity of LHCI, which, contrary to FMO and CP43′, is composed of four different proteins with varying stoichiometry, is further facilitated by a unique binding mode between LHCI dimers and monomers which does not involve interactions between transmembrane helices.

5. The role of subunit H in excitation energy distribution between PSII and PSI

The emergence of subunit H and modification of PsaL as novel features of eukaryotic PSI not only prevented the possibility of trimer formation but also provided a template for

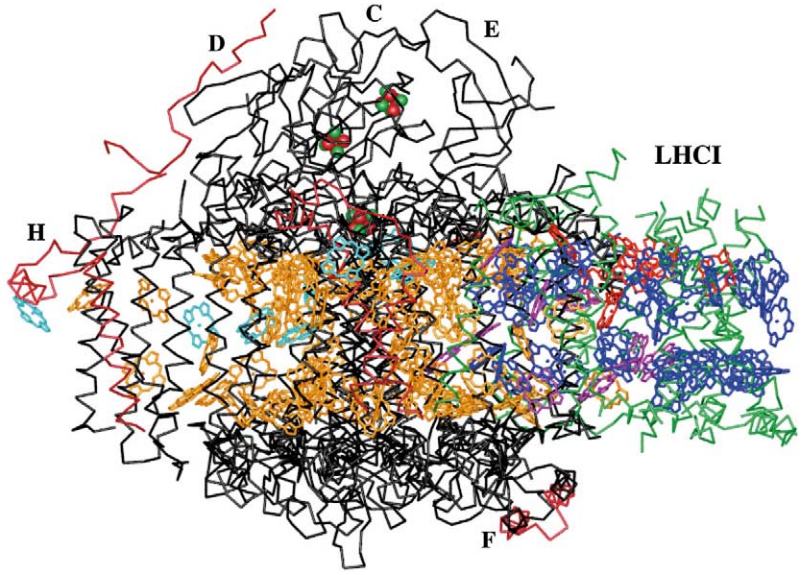

Fig. 6. A side view of the plant PSI. A look from the side of subunit G. The positions of subunits C, D, E, F and H as well as LHCI are indicated. The three iron–sulfur clusters are visible with Fe as red balls and S as green balls. The color code of the proteins and the chlorophylls is as in Fig. 5.

LHCII binding [14,43]. It is remarkable that in contrast to PSI, which operates at a quantum efficiency of close to one, PSII loses up to a fifth of the quanta that it absorbs [44]. Consequently PSII produces destructive reactive oxygen species that constantly damage its subunits and in particular D1 [45,46]. This destruction increases with increasing light intensities and thus an ingenious mechanistic solution had to evolve in order for algae to colonize the surface of water bodies and even more so for the evolution of land plants. Part of this mechanism is the 'spillover' of light energy from PSII to PSI [47]. Under strong light intensities or light preferentially absorbed by PSII, a sub-population of LHCII trimers is phosphorylated, dissociates from PSII and binds to PSI. This effect decreases the light harvesting by PSII and decreases the rate of its destruction and at the same time increases light harvesting by the resilient PSI that could be utilized for energy-requiring processes such as cyclic photophosphorylation [47,48]. This regulated process is reversible and at low light intensities, the phosphate is removed from LHCII, it dissociates from PSI and either moves back to PSII or is degraded.

Attempts to purify the complex of PSI with LHCII demonstrated the lability of the association between these moieties [49]. This lability serves well the need to quickly respond to changes in light conditions and stands as another example of the tools that enhance the modularity of the light-harvesting apparatus in plants. To fulfill the need for a weak, yet specific docking site for LHCII (and not LHCI) that will mediate energy transfer from LHCII to the core, a specifically designed site had to be incorporated into PSI structure. Such a delicate and specific design probably could not be simply achieved by changes in LHCI or perhaps required modification that would have compromised LHCI's modularity or function. Thus, a novel subunit PsaH, dedicated to the task of LHCII binding, was added. Cross-linking studies have recently shown that PsaH together with PsaL and PsaI form the LHCII binding site in PSI [49]. The modularity of LHCI is facilitated by relatively weak binding, between its monomers and between them and the core, that does not involve transmembrane helix interactions. It is tempting to deduce that nature applied a similar binding mode to the association of LHCII and PSI and that solvent-exposed regions play the major part in this association.

As shown in Fig. 6, subunit H is bound to the core in an asymmetric manner. This arrangement further pushes PSI out of its original pseudo-two-fold and later three-fold symmetries leaving numerous possibilities for specific interactions for fine-tuning of a remarkably efficient energy-converting machine.

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