

## 1.3 Complexes of oxygenic photosynthesis

In the last decade significant progress in the elucidation of three-dimensional structures of complexes of oxygenic photosynthesis (see Fig. 7) has been made. Complete structures of the three main complexes PSI [37, 38], *cyt b<sub>6</sub>f* [39, 40] and PSII [41, 42] were resolved from different organisms with good resolution around 3.0 Å and better.

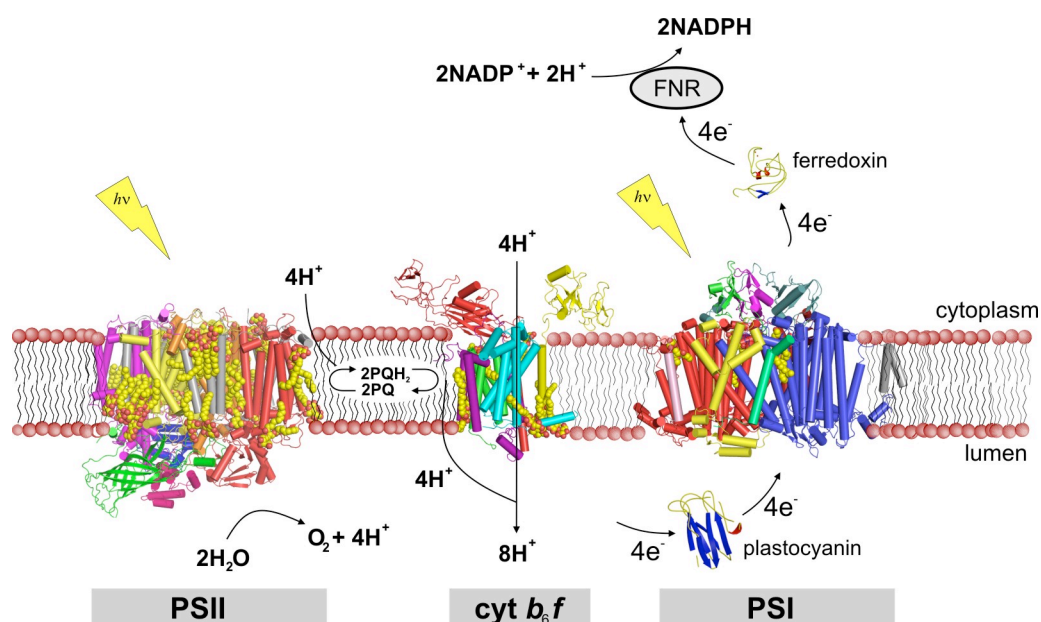


Figure 7. Complexes of oxygenic photosynthesis: schematic view of the thylakoid membrane with PSI, PSII, and *cyt b<sub>6</sub>f* embedded. For simplicity only a monomer of each complex is shown, TMHs are shown as cylinders, all cofactors except lipids are omitted. The lipids intrinsic to the structures are shown in space filling representation with yellow spheres for carbon and red spheres for oxygen. Arrows indicate proton as well as electron fluxes.

### 1.3.1 Photosystem II

PSII is a large multisubunit protein-pigment-lipid complex, consisting of at least 20 protein subunits and 92 bound cofactors (35 chlorophyll molecules, two pheophytine and two haem molecules, twelve  $\beta$ -carotenoids, 25 lipids, seven detergent molecules, three plastoquinones, unique  $\text{Mn}_4\text{Ca}$  cluster, bicarbonate, two  $\text{Ca}^{2+}$ , one  $\text{Fe}^{2+}$  and one  $\text{Cl}^-$  ion) per monomer (see Figs. 8, 9). PSII acts as light-driven water-quinone oxidoreductase. PSII occurs as homodimer, where the monomers are related by a non-crystallographic pseudo-twofold axis. Two membrane intrinsic protein subunits D1 (PsbA) and D2 (PsbB) form the RC core and harbour all cofactors of the ETC. D1 additionally provides the binding site for the  $\text{Mn}_4\text{Ca}$  cluster, therefore this subunit is prone to radiation damage, arising from side reactions during charge separation. Therefore special mechanism called D1-turnover [43-45] is employed to

replace the damaged subunit (see section 3.2.1.3 for discussion of possible role of lipids in D1-turnover). In both D1 and D2 subunits five TMHs are arranged in two semicircles interlocked in a handshake motif and related by the local twofold axis.

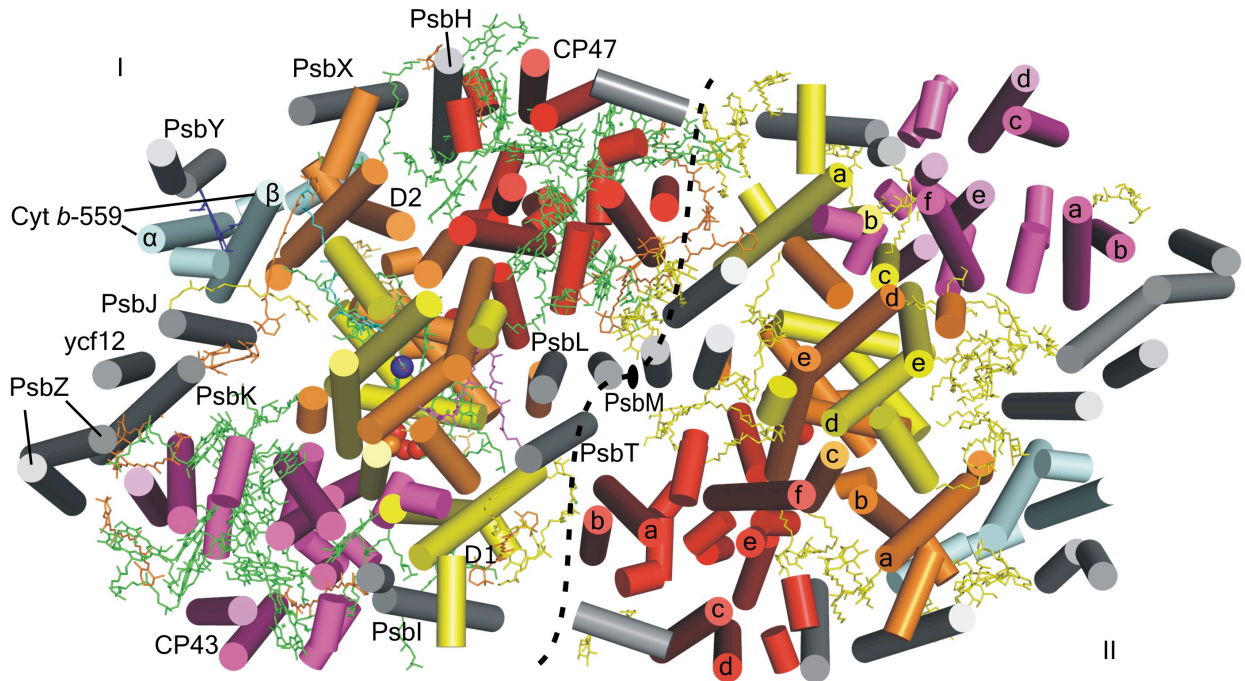


Figure 8. Dimeric PSII from *Thermosynechococcus elongatus* (*T. elongatus*) (pdb codes: 3bz1 and 3bz2), view is onto the membrane plane from the cytoplasmic side, membrane extrinsic parts are omitted. The monomer-monomer interface is indicated by a black dotted line, the  $C_2$  axis relating the two monomers by a black ellipse. In monomer I (left) protein subunits are indicated and Chl (green), Car (orange), Haem (blue) and PQ (olive) cofactors shown. In monomer II (right) TMHs of D1, D2, CP43 and CP47 are named a-e/f and lipid and detergent molecules (yellow) are shown.

D1 and D2 subunits are flanked with chlorophyll-binding antenna proteins CP43 (PsbC) and CP47 (PsbB) respectively, each composed of six TMHs and with 13 and 16 bound Chl *a* molecules correspondingly.

Next to the *a* and *b* TMHs of D2, cytochrome *b-559* (cyt *b-559*) is located. It consists of two subunits  $\alpha$  and  $\beta$ , between which the haem group of cytochrome ligated by histidines is found. This cytochrome possesses unusual redox properties [46] and occurs in several forms with high, intermediate and low midpoint potentials [47]. Several functions have been proposed for cyt *b-559*, but the most important is the participation in cyclic electron transfer as an emergency electron donor or acceptor [46, 48, 49] to protect PSII from photoinhibition.