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Introduction

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This volume of *Journal of Bioenergetics and Biomembranes* contains a set of papers that review recent developments in structure–function of proteins involved in photosynthetic energy transduction. The first paper in the set (U. Ermler, H. Michel, and M. Schiffer) reviews studies on a membrane protein complex, the bacterial photosynthetic reaction centre, that is the paradigm for X-ray structural analysis of integral membrane proteins. Diffraction analysis of a new crystal form of the reaction center from *Rhodobacter sphaeroides* that has a resolution of 2.65 Å is described. This manuscript is particularly interesting, not only because of the higher-resolution studies of the *sphaeroides* complex, but because it involves a joint perspective (i) from two of the major laboratories working on the structure, and (ii) consideration of information from both crystal structure analysis and site-directed mutagenesis.

The manuscript contains a review of the crystallization protocols that have been used in the different laboratories, and a discussion of the *trans*-membrane helices, pigment locations, chromophore–protein interactions, quinone binding site, and electron transfer asymmetry in light of the higher resolution data for *Rb. sphaeroides*.

The other five papers in this set discuss the complexes and proteins involved in the electron transport from H_2O to $NADP^+$ in oxygenic photosynthesis:

$$H_2O \rightarrow PSII \rightarrow PQ \rightarrow Cyt\, b_6f \rightarrow plastocyanin$$
$$\rightarrow PSI \rightarrow ferredoxin \rightarrow FNR \rightarrow NADP^+$$

In article 2, Boekema *et al.* discuss electron microscopic analysis of photosystems II and I (PSII, PSI) and the cytochrome b_6f complex. The article contains a summary of the experimental principles of EM structure determination. The results from image analysis are shown of (i) monomeric and dimeric PSII complexes, and (ii) monomeric and trimeric PSI complexes with and without the stromal or *n*-side extrinsic *psa*C,D,E subunits, isolated from cyanobacteria and higher plant chloroplasts. The large size of these complexes, 64 Å × 75 Å × 123 Å for the PSII monomer, MW > 10^6 for the PSI trimer from cyanobacteria, is an indicator of the difficulty of the structure analysis. (In the case of PSI, structure information is also available from X-ray diffraction analysis at 6 Å resolution carried out in the laboratories of W. Saenger and H.T. Witt.) EM analysis by Boekema *et al.* shows a cyanobacterial cytochrome b_6f complex that is monomeric. It is of interest to compare the existence of the monomeric form of this complex in the cyanobacterial cytochrome b_6f complex with the dimeric complex that is abundant in the plant chloroplast thylakoid membrane and is discussed in article 3 by Cramer *et al.* The latter article discusses sequence and structure aspects of the b_6f complex, and the recently completed 2.3 Å structure of the lumen-side domain (252 residues) of cytochrome *f*.

In article 4, M. R. Redinbo, T. O. Yeates, and S. Merchant analyze structure–function of the small (97–104 amino acids) soluble copper protein, plastocyanin, that is the electron acceptor of cytochrome *f* and, as shown above, the electron donor to the photosystem I complex. Plastocyanin has been crystallized from three algal and three plant chloroplast sources. Despite sequence divergence, the three-dimensional structure of the protein involving an eight-stranded antiparallel β-barrel has been well conserved. The pathways of intramolecular electron transport are discussed. The role is discussed of negative and neutral patches on the surface of the plasto-

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cyanin molecule in the binding interactions with cytochrome *f* and photosystem I that are required for intermolecular electron transfer. This article together with article 3 on the structure of cytochrome *f* allow one to consider molecular details of the successful encounter interactions between them.

Light absorbed by PSI drives electrons from the positive redox potential associated with the reaction center, P700, and its electron donors, plastocyanin and cytochrome *f* on the *p*- or lumen side of the membrane, to the bound iron-sulfur electron acceptors at a negative reducing potential on the *n*- or stromal side, from which ferredoxin is reduced.

H. Holden *et al.* discuss "Structure–Function Studies of [2Fe-2S] Ferredoxins." A complete review is presented of sequence, and structure data where available, of ferredoxins representative of the plant, vertebrate, and bacterial type, the metal cluster binding pocket, and the solvent channel in plant ferredoxin. A particularly strong aspect of the structure discussion is the use of both X-ray and NMR data, and the presentation of the latter in comparative studies of (i) vegetative and heterocyst ferredoxin, and (ii) ferredoxin-mediated reduction of the ferredoxin : $NADP^+$ reductase (FNR).

P. A. Karplus and C. M. Bruns discuss "Structure–Function Relations for Ferredoxin Reductase" that catalyzes the reduction of $NADP^+$, the ultimate electron acceptor of noncyclic electron transport, to NADPH that is the reducing agent for carbon fixation. The three-dimensional structure of FNR from spinach chloroplasts was solved at 2.2 Å resolution by Karplus and co-workers in 1991, and is now known to 1.7 Å.

The structure of FNR is a prototype for a two-domain motif for enzymes including human NO synthase, human cytochrome P450 reductase, tobacco nitrate reductase, and bacterial methane monoxygenase and phthalate dioxygenase, that transfer electrons from a nicotinamide dinucleotide to a one-electron acceptor. From the X-ray structure, it is possible to identify particular residues that are important for structural integrity, and binding of FAD, $NADP^+$, and ferredoxin.

The above six articles provide an up-to-date overview of a significant fraction of the structural studies on proteins involved in photosynthetic energy transduction, yielding structural information at the molecular level. One other membrane protein system that is not covered here, but should be mentioned, is the light-harvesting chlorophyll protein of chloroplast thylakoid membranes. It is being analyzed with two-dimensional crystals and tilted stage electron microscopy, and its structure solution is proceeding rapidly in the laboratory of W. Kühlbrandt.