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Minireview

The FMO protein*

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Abstract

In this article I review the history of research on the Fenna–Matthews–Olson (FMO) protein with emphasis on my contributions. The FMO protein, which transfers energy from the chlorosome to the reaction center in green sulfur bacteria, was discovered in 1962 and shown to contain bacteriochlorophyll *a*. From the absorption and circular dichroism spectra, it was clear that there was an exciton interaction between the bacteriochlorophyll molecules. Low temperature spectra indicated a seven-fold exciton splitting of the Q_y band. The FMO protein was crystallized in 1964, and the X-ray structure determined in 1979 by B.W. Matthews, R.E. Fenna, M.C. Bolognesi, M.F. Schmidt and J.M. Olson. The structure showed that the protein consisted of three subunits, each containing seven bacteriochlorophyll molecules. The optical spectra were satisfactorily simulated in 1997. In living cells the FMO protein is located between the chlorosome and the reaction centers with the C3 symmetry axis perpendicular to the membrane. The FMO protein may be related to PscA in the reaction center.

Abbreviations: BChl – bacteriochlorophyll; *Cb.* – *Chlorobium*; FMO – Fenna–Matthews–Olson; *Pr.* – *Prosthecochloris*; RC – reaction center

Introduction

Most chlorophyll proteins are water-insoluble proteins containing membrane-spanning α-helices, but the Fenna–Matthews–Olson (FMO) protein is an unusual water-soluble bacteriochlorophyll protein (see Figure 1 for absorption spectrum) found only in green sulfur bacteria. It transfers excitation energy from the chlorosome to the reaction center (RC). The FMO protein is a trimer (Figure 2), and each subunit (Figure 3) contains seven bacteriochlorophyll (BChl) *a* molecules wrapped in a string bag of protein (365/366 amino acids) consisting of 15 strands of β-sheet, six short lengths of α-helix, and a few regions of irregular conformation (Matthews et al. 1979; Li et al. 1997; Camara-Artigas et al. 2003).

I discovered the FMO protein in 1962 at Brookhaven National Laboratory while scanning an alkaline extract of *Chlorobium (Cb.) limicola f. thiosulfatophilum* with a Cary 14R recording spectrophotometer. I was looking for evidence of cytochrome in the extract, and I found it. Being a spectroscopist, I decided to run the spectrophotometer as far as it would go in the near infrared, and I found a small blip at about 805–810 nm. After some thought I remembered that bacteriochlorophyll (BChl) *a* had a peak at 770 nm in organic solvents. (Fortunately

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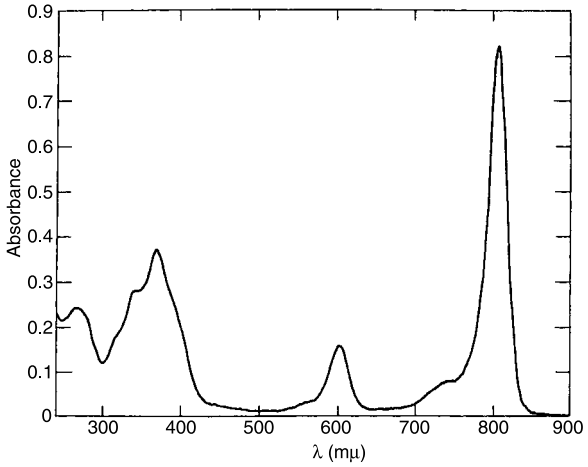

Figure 1. Absorption spectrum of the FMO protein (*Pr. aestuarii*) dissolved in 0.25 M NaCl and 20 mM phosphate buffer, pH 7.8. Reproduced from Sybesma and Olson (1963), by permission of the National Academy of Sciences (USA). (At that time, wavelength of light was written in millimicrons (mμ) instead of namometers (nm) used today.)

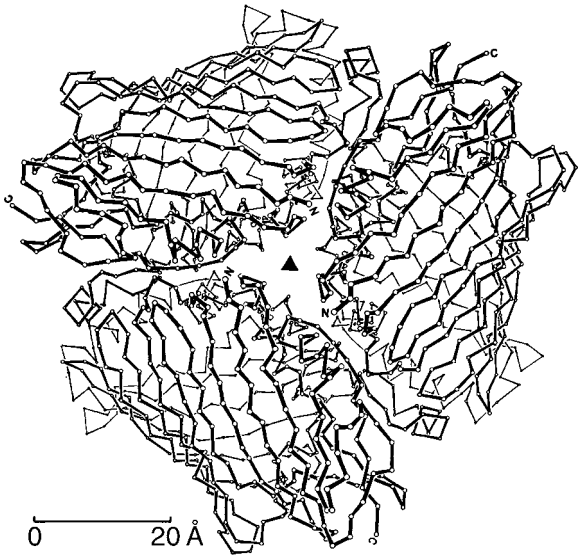

Figure 2. The FMO protein (*Pr. aestuarii*) viewed down the three-fold symmetry axis. Only the backbone of the protein portion is shown, with each α-carbon atom shown as a circle. The BChl *a* molecules have been omitted. Reproduced from Matthews et al. (1979) by permission of Academic Press (London).

the extract was largely free of aggregated BChl *c*, which has a large peak at about 740 nm.) My assistant, Carol Romano, concentrated the extract and dialized it against buffer, and Geoff Zubay showed us how to make a DEAE-cellulose column. That way we were able to get rid of all the remaining BChl *c*. The eluate contained only the beautiful blue-green stuff. At this

Figure 3. One subunit of the FMO protein (*Pr. aestuarii*) showing the seven BChl *a* molecules enclosed within an envelope of protein. For clarity the phytyl tail and other ring substituents of each BChl have been omitted. The three-fold symmetry axis of the trimer extends from left to right across the front of the subunit. Reproduced from Matthews et al. (1979) by permission of Academic Press (London).

point we were quite sure we had a chlorophyll protein, and we were quite sure the chlorophyll was very similar to BChl *a* (Olson and Romano 1962). We first called our chlorophyll protein 'protein-chlorophyll-770 complex.' (Olson et al. 1963), then 'BChl protein' (Olson 1966), later 'BChl *a* protein' (Olson et al. 1976), and finally 'FMO protein' (Olson 1994).

Molecular weight and composition

Being eager to find out the size of the 'protein-chlorophyll-770 complex' from *Prosthecochloris (Pr.) aestuarii* 2K (part of a mixed culture called '*Chloropseudomonas ethylicum* 2K') I enlisted the aid of Dave Filmer to show me how to use the Spinco Model E Ultracentrifuge, and we found a molecular weight of $(167 \pm 17) \times 10^3$ (Olson et al. 1963; Olson 1966). We also found that there were 21–23 BChl *a* molecules associated with the complex, and I speculated that the complex might consist of seven subunits, each containing three BChl *a* molecules (Olson 1966).

In 1968, Philip Thornber determined the chemical composition of the BChl *a*-protein from *Pr. aestuarii*, and we found that the data could be explained by a model with either three or four subunits, each con-

taining seven or five BChl *a* molecules, respectively. Unfortunately, we published 'four subunits with five BChl *a* molecules each' (Thornber and Olson 1968; J.M. Olson et al. 1969).

Energy transfer

Chris Sybesma had been investigating energy transfer in green sulfur bacteria, and he discovered that light energy absorbed by BChl *c* in *Pr. aestuarii* is transferred to chlorophyll-770 (BChl *a*) (Sybesma and Olson 1963). The clear implication of the absorption and fluorescence data was that the protein-chlorophyll-770 complex existed *in vivo*, and accepted excitation energy from BChl *c*.

Spectral characteristics

In 1966 I found that the 809-nm absorbance band split into three peaks at 805, 814 and 824 nm at 77 K, while the 603-nm band split into two peaks at 601 and 607 nm (Olson 1966). Ken Sauer suggested that there might be excitonic interaction between some of the BChl *a* molecules in the protein, so I sent regular shipments to Berkley for circular dichroism (CD) studies. Eventually Philipson and Sauer (1972) concluded that four absorption and five CD components in the Q_y band at 77 K meant that at least five BChl *a* were involved in an excitonic interaction.

In 1975, I visited Bacon Ke in Yellow Springs, Ohio, in order to examine in detail the absorbance and CD properties of BChl *a* proteins and BChl *a*-RC complexes from *Pr. aestuarii* and *Cb. limicola f thiosulfatophilum* at 77 K. The exciton interaction was different in the two proteins. For the *Pr. aestuarii* protein the highest peak in the absorbance spectrum was at 814 nm (type A), while for the *Cb. limicola* protein it was at 806 nm (type B). The resolution of the absorbance and CD spectra of the *Prosthecochloris* protein required six asymmetric Gaussian component, but only five were required for a satisfactory resolution of the spectra of the *Chlorobium* protein. The absorbance (or CD) spectrum for either BChl *a*-RC complex was to a first approximation the sum of the spectrum of the corresponding BChl *a* protein plus a new absorbance (or CD) band at 834 nm (or 832 nm). This suggested that the BChl *a*-RC complex may be composed of BChl *a* proteins combined with a RC complex with absorbance and CD bands at 834 and 832 nm, respectively. [An 833-nm band had previously been observed in the absorbance spectrum of the *Chlorobium* BChl *a*-RC complex at 100 K (Olson et al. 1976).]

In my quest for really low-temperature spectra, I contacted Robert (Bob) Pearlstein at Oak Ridge National Laboratory, and together with William (Bill) Whitten he looked at the BChl *a* protein and the BChl *a*-RC complex from *Cb. limicola f. thiosulfatophilum* at 5 K. The absorption spectrum (type B) of the BChl *a* protein closely resembled the 77 K spectrum, and the spectrum of the BChl *a*-RC complex was similar to the 77 K spectrum with the addition of a slight shoulder at 838 nm. We confirmed that about half of the BChl *a* in the complex was in the form of BChl *a* protein trimers and the other half in a related conformation (Olson 1978; Whitten et al. 1979). [It now appears that two BChl *a* proteins may be associated with each RC *in vivo*, but only one is firmly bound in some photoactive BChl *a*-RC complexes (Remigy et al. 1999, 2002).] In our final paper (Whitten et al. 1980) we compared the BChl *a* proteins from both *Chlorobium* and *Prosthecochloris* and found evidence for seven absorbance and CD components in the 810-nm band. We ascribed them to a seven-fold exciton splitting.

Pr. aestuarii and *Cb. vibrioforma* contain BChl *a* proteins with type A spectra, while *Cb. limicola f. sulfatophilum*, *Cb. tepidum* and *Cb. phaeovibrioides* contain proteins with type B spectra (Olson et al. 1976; Miller et al. 1994; Francke and Amesz 1997).

After I moved to Odense University in Denmark in 1982, I turned to the low temperature spectrum of the BChl *a* protein (now called the FMO protein) from a new species of bacteria (*Cb. tepidum*) in collaboration with new colleagues (Mette Miller and Raymond Cox). From the absorbance spectrum (type B) of the FMO protein and the spectrum of a photoactive FMO-RC complex at 77 K, we calculated the putative spectrum of the RC core complex by subtracting the FMO protein spectrum from the FMO-RC complex spectrum. The RC core complex showed peaks at 795, 817, 833 and 836 nm but lacked the peak at 825 nm found in the FMO protein (Vasmel et al. 1983; Miller et al. 1994). The splitting of the 835-nm band into two peaks at 833 and 836 nm had been observed earlier (Swarthoff and Amesz 1979; Whitten et al. 1979; Otte et al. 1991). These experiments were repeated at 6 K in Jan Amesz' lab in Leiden, and the RC core complex showed peaks at 797, 808, 818, 834 and 836 nm (the 808 nm peak had not been detected at 77 K). The efficiency of energy transfer from carotenoid to BChl

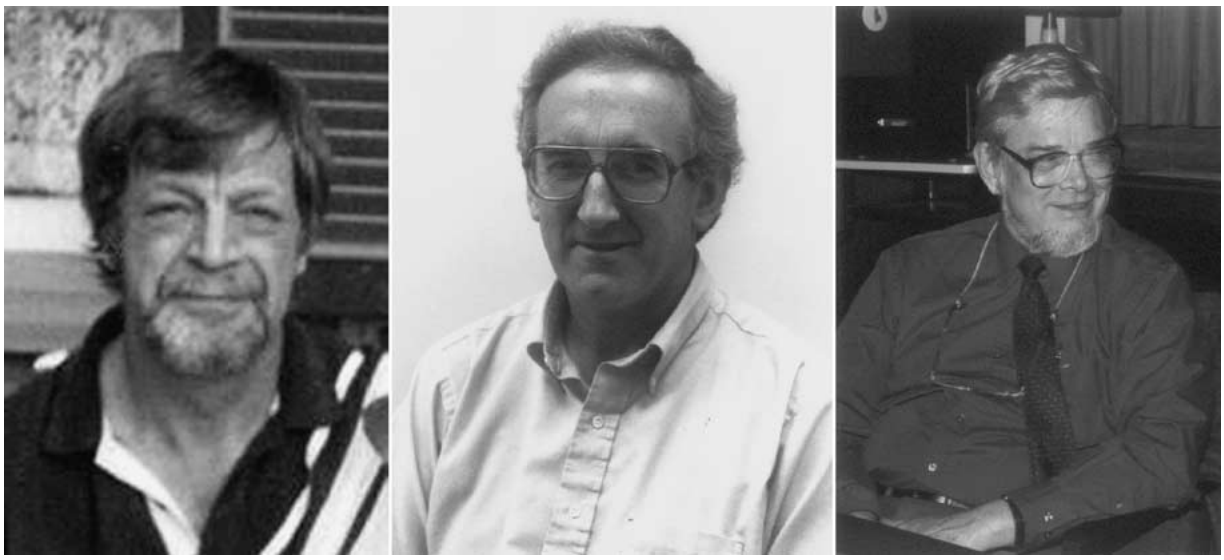

Figure 4. Left: Roger Fenna (taken in 2002). *Middle:* Brian W. Matthews (taken in 1998). *Right:* John M. Olson (taken in 1994).

a in the core complex was 23% and from the FMO protein to the core 35% (Francke et al. 1996). This low efficiency seemed strange in view of the presumed function of the FMO protein to transfer energy from the chlorosome to the RC *in vivo*. A possible explanation is that excited state quenching occurs in the FMO protein at neutral or oxidizing redox potentials (Zhou et al. 1994).

Structure

In 1964 my assistant, Frances Roskosky, had accidentally crystallized the BChl *a* protein by concentrating a solution almost to dryness and leaving it in the refrigerator. Patricia Cole (summer student) spent the summer of 1966 growing crystals up to 1 mm long and 0.3 mm wide in anticipation of future X-ray crystallography. The absorbance spectrum (420–850 nm) of crystalline BChl *a* protein is essentially the same as that for BChl *a* protein dissolved in buffer containing 250 mM NaCl (Sybesma and Olson 1963; R.A. Olson et al. 1969).

After our failure to obtain good X-ray data at Brookhaven National Lab, I asked Benno Schoenborn, Brookhaven's neutron diffraction expert, to recommend an X-ray crystallographer, and he suggested Brian Matthews at the University of Oregon (Figure 4). We sent Matthews three crystals in December 1971, and in 1972 the crystallization process was transferred to Oregon. In 1973 Roger Fenna (see Figure 4) joined the team as a postdoc in Matthew's lab, and the results began to come out. The first paper (Fenna et al. 1974) showed that the BChl *a* protein was a trimer instead of a tetramer and that each subunit contained seven BChl *a* molecules. Also the molecular weight was revised downward from 170 to 150×10^3. From 1973 until 1975 my laboratory was devoted to producing all the BChl *a* protein needed by Fenna and Matthews. (At one point the chairman of the Biology Department, at Brookhaven, suggested that I needed to spend more time writing papers.) A preliminary structure appeared in 1975 (Fenna and Matthews 1975), and the complete structure (2.8-Å resolution) was published in 1979 (Matthews et al. 1979). I was very proud of my contribution to the project, but as a result of this structure determination the BChl *a* protein became known as the 'Fenna–Matthews protein' until Robert (Bob) Blankenship introduced the name 'Fenna–Matthews–Olson' or 'FMO protein' (Dracheva et al. 1992). The structure was later refined to 1.9 Å (Tronrud et al. 1986) and eventually combined with the amino acid sequence (Daurat-Larroque et al. 1986; Tronrud and Matthews 1993). Dracheva et al. (1992) sequenced the FMO protein from *Cb. tepidum*, and Li et al. (1997) then determined the three-dimensional structure by X-ray diffraction to 2.2 Å. [The structure determination

was repeated by Camara-Artigas et al. (2003) using slightly different crystals than used by Li et al. (1997).]

Simulation of optical spectra

Pearlstein and Hemenger (1978) were the first to attempt a simulation of the low-temperature absorbance and CD spectra of the 800-nm band of FMO protein from *Pr. aestuarii*. In order to obtain a reasonable fit to the experimental spectra, they had to assume that the lowest energy singlet transition was x-polarized in each of the seven BChl *a* molecules considered. This seemed to be an unrealistic assumption, and Pearlstein (1992) recalculated the simulation assuming y-polarization and using all 21 BChl *a* molecules in the trimer. He also assumed $51.6\,D^2$ for the Q_y transition dipole moment. The resulting simulation of both absorbance and CD spectra were about as good as in the earlier paper (Pearlstein and Hemenger 1978), and Pearlstein concluded that BChl 7 is the largest contributor to the lowest energy exciton state in each subunit. Lu and Pearlstein (1993) further improved the simulation by introducing a computer search of unspecified parameters such as the site wavelengths of individual BChl *a* molecules.

Gülen (1996) tried a different approach and based the simulation on absorbance, linear dichroism, and triplet-minus-singlet spectra. However, the parameters, which gave acceptable simulations of these spectra failed to give a satisfactory simulation of the CD spectrum. Louw et al. (1997a, b) finally were able to simulate absorbance, linear dichroism, circular dichroism, triplet-minus-singlet, and linear dichroism-minus-(triplet-minus-singlet) spectra for just seven BChl *a* molecules in one subunit with a single set of parameters. The new approach in this simulation was to assume much lower interaction energies between the BChl *a* molecules. This meant a much lower effective dipole strength ($28.7\,D^2$) for each BChl *a* molecule in the FMO subunit. The best simulation of the spectra was obtained when BChl 3 was assumed to have the lowest site energy. This approach was extended to the FMO protein from *Cb. tepidum* by Vulto et al. (1998), and an even better simulation was achieved than for the FMO protein from *Pr. aestuarii*.

With the advent of three-dimensional structures, the FMO proteins proved to be a godsend for physicists and physical chemists interested in spectral properties, excited states, and energy transfer. For a comprehensive list of relevant publications, I refer the reader to an excellent review by Blankenship and Matsuura (2003).

How is the FMO protein oriented *in vivo*?

In living bacteria FMO proteins are thought to be located between chlorosomes and the reaction center complexes embedded in the cytoplasmic membrane. Twenty-three years ago I proposed that these FMO proteins self assembled into two-dimensional crystals (trigonal space group $P3_1$) in which the 3_1 screw axis (the C3 symmetry axis of the trimer) made an angle of 25° with the plane of the cytoplasmic membrane (Olson 1980). Several years later this idea was shown to be wrong by Melkozernov et al. (1998), who showed that the C3 symmetry axis of the trimer is perpendicular to the membrane plane in *Cb. tepidum*. (I was pleased to be on the team that made this correction.)

Where did the FMO protein come from?

In the fall of 2000 I had the idea that the FMO protein might have evolved from a primitive reaction center protein. If this were the case, there might be some homology between the FMO proteins and PscA, the reaction center protein of green sulfur bacteria. Most of my colleagues thought that this was a crazy idea, but Bob Blankenship was willing to help me test my hypothesis by lending me his graduate student, Jason Raymond. For about a year Jason and I looked for homology between FMO proteins from *Pr. aestuarii*, *Cb. limicola*, and *Cb. tepidum* and PscA proteins from *Cb. limicola* and *Cb. tepidum*. We found a 220-residue C-terminal segment with an identity score of 13% and a signature sequence (LxHHxxxGxFxxF) common to both proteins. Probability-of-random-shuffle analysis showed that the 220-residue alignment is better than 96% of randomized alignments. We believe that this evidence supports the hypothesis that the FMO protein is related to PscA (Olson and Raymond 2003).

Acknowledgments

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