Origin, Evolution and Efficiency of Photosynthesis

Robert E. Blankenship
Washington University in St. Louis
Departments of Biology and Chemistry

CUNY
April 7, 2011

Photosynthesis- The Conversion of Light Energy into Chemical Energy

PS is the source of all our food and most of our energy resources on Earth

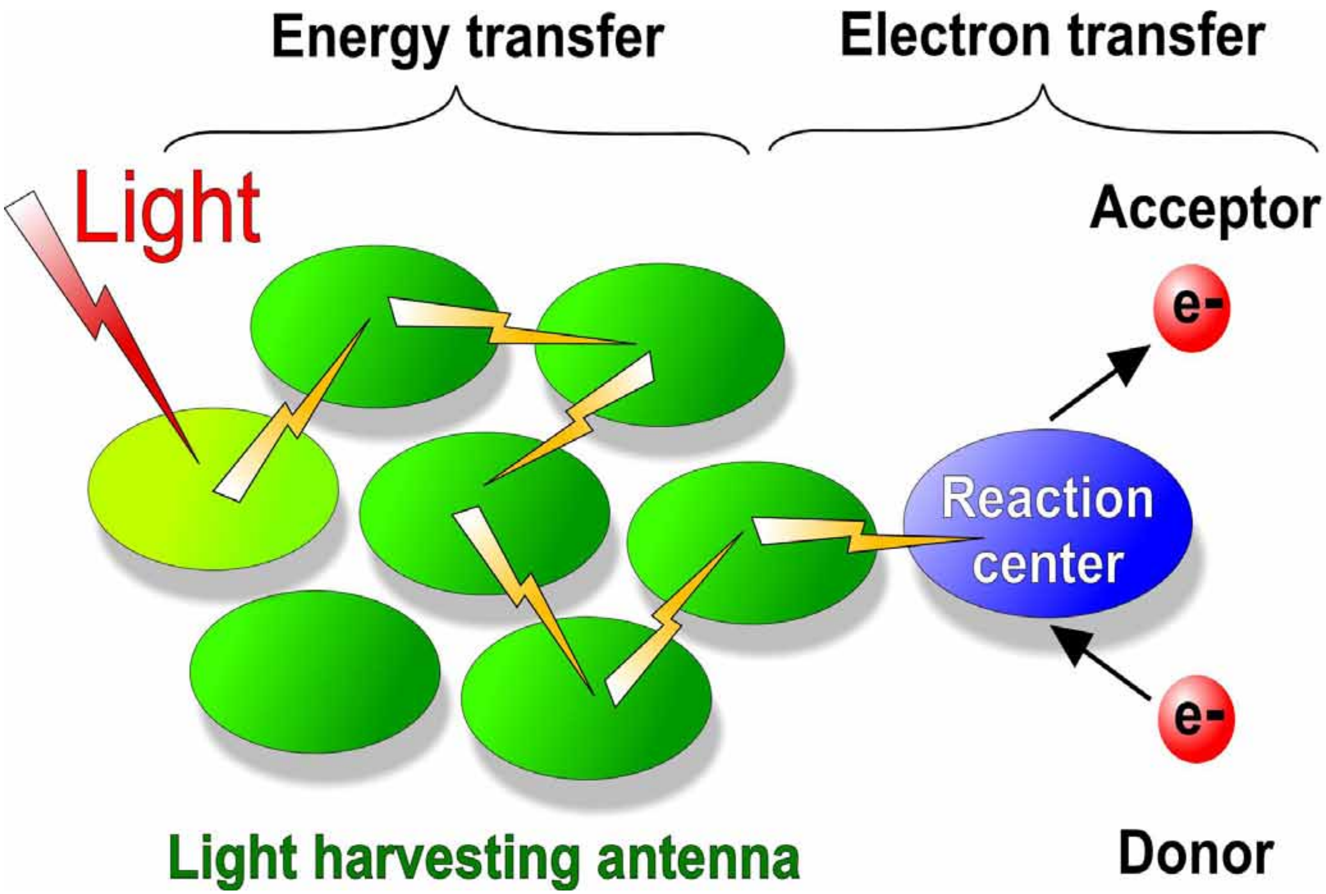
Top 10: Life's greatest inventions

1. Multicellularity
2. The eye
3. The brain
4. Language
5. **Photosynthesis**
6. Sex
7. Death
8. Parasitism
9. Superorganism
10. Symbiosis

04 September 2006

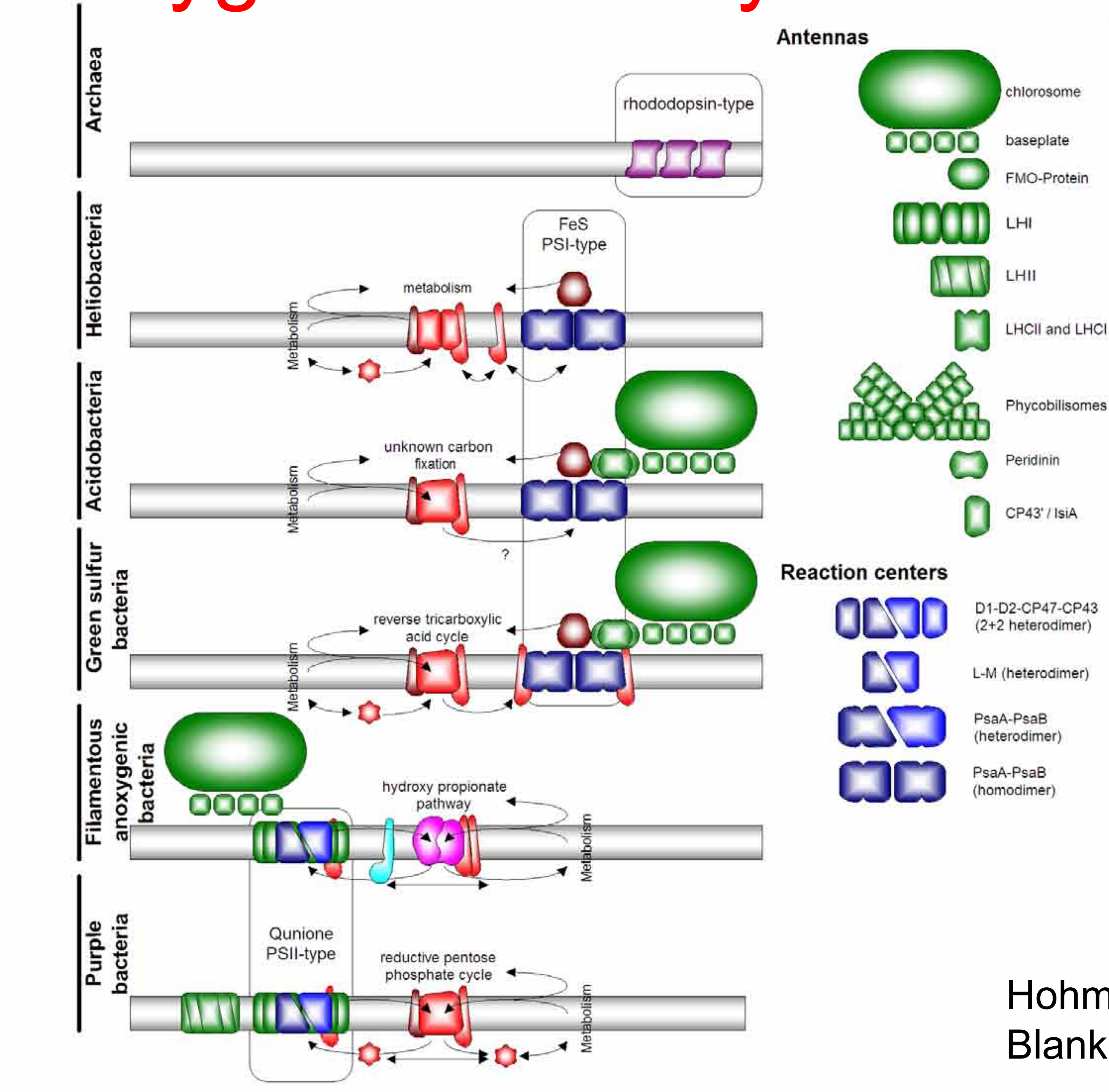
NewScientist.com

Photosynthetic Energy Storage



All PS organisms contain a light-gathering antenna system

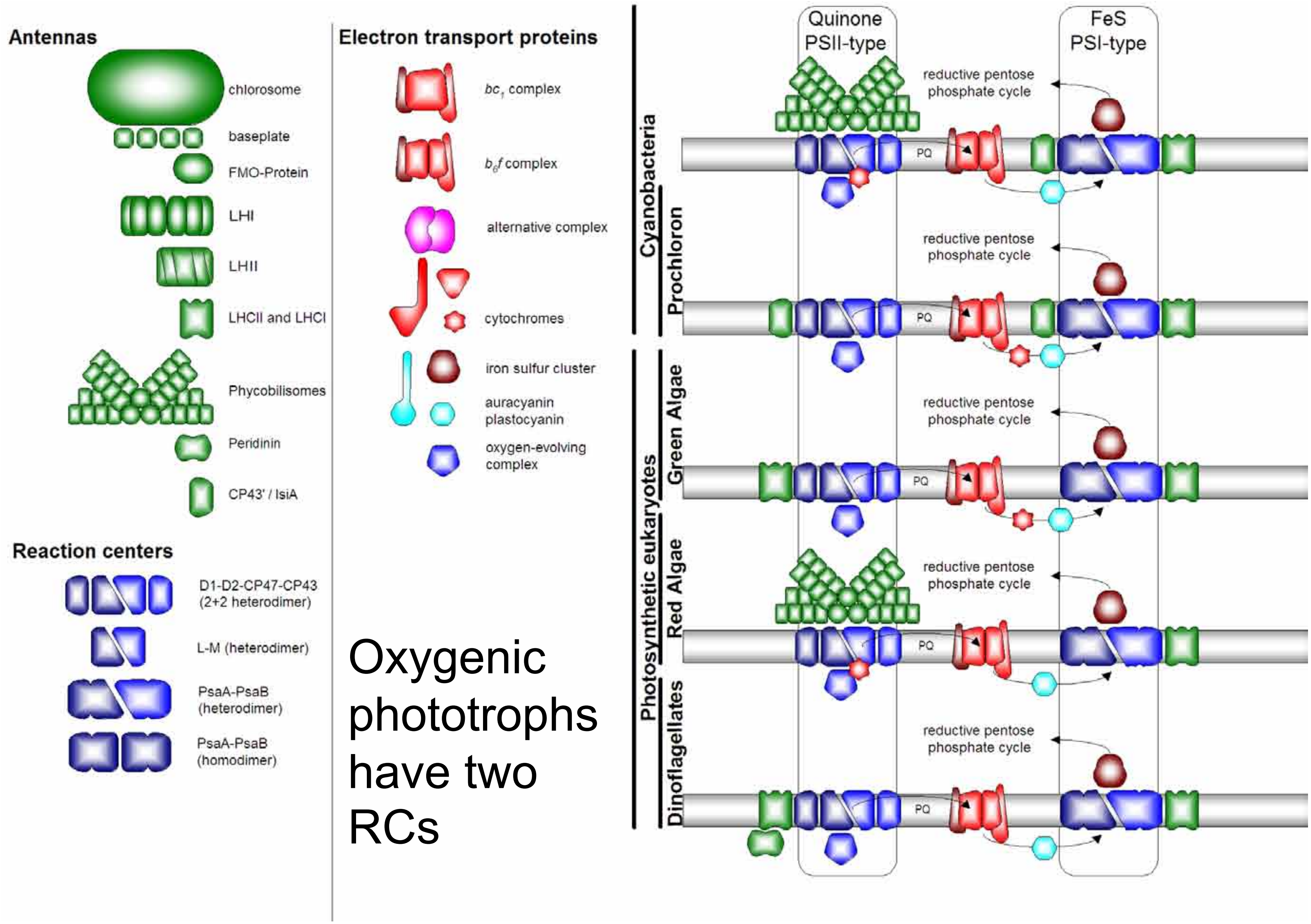
Anoxygenic Photosynthetic Organisms



Anoxygenic phototrophs have one reaction center (RC)

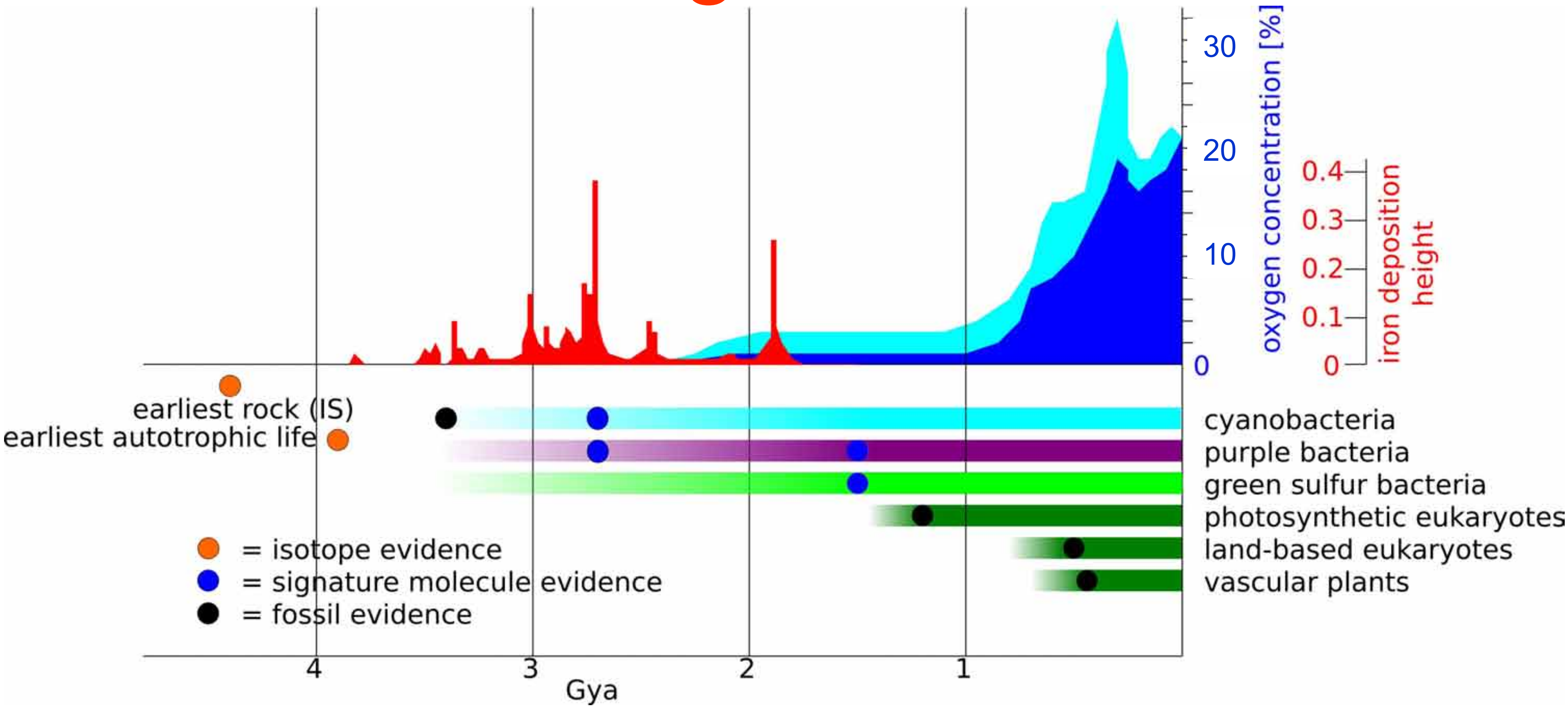
Hohmann-Marriott and Blankenship (2011)

Oxygenic Photosynthetic Organisms



Oxygenic phototrophs have two RCs

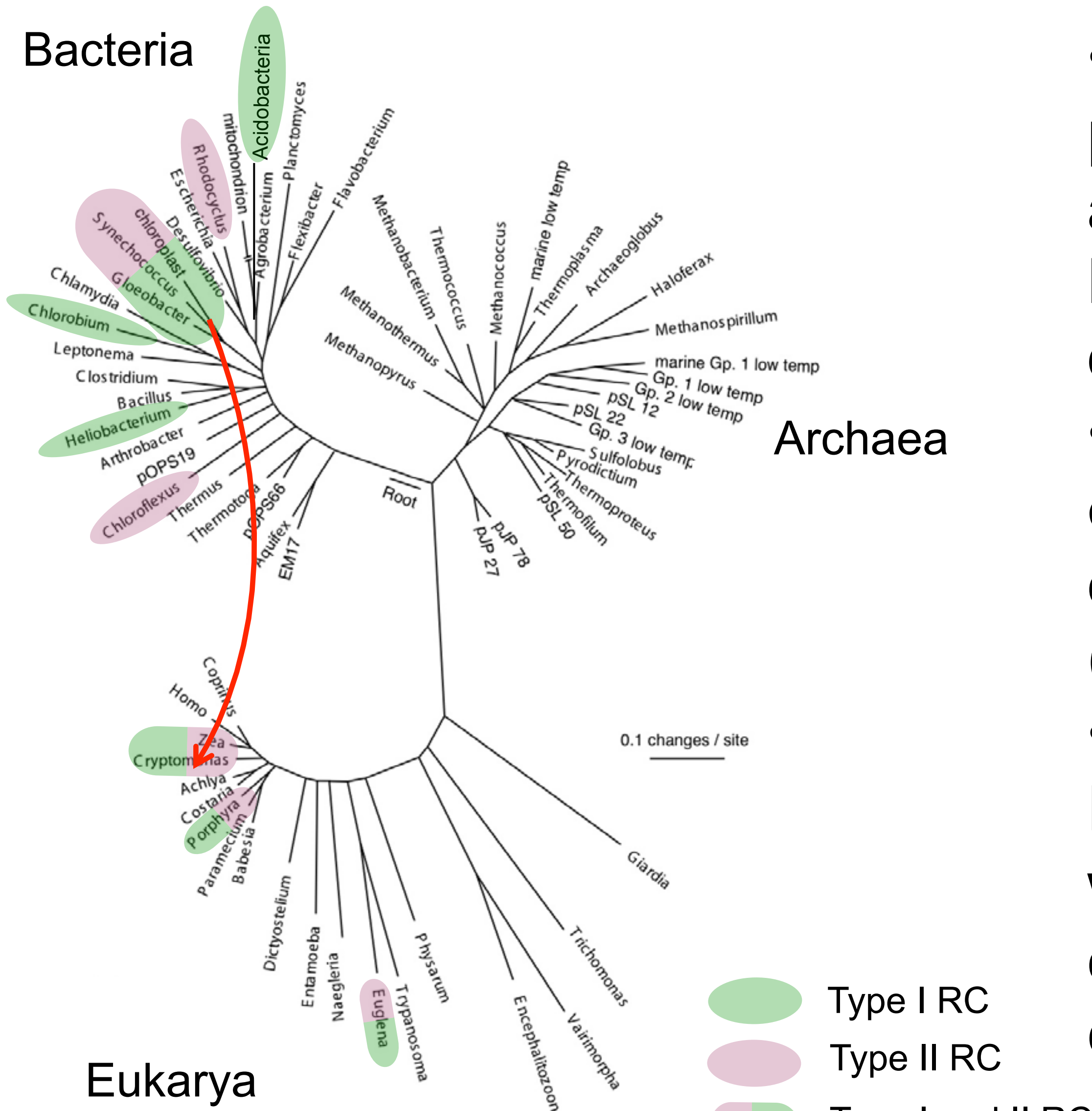
Geologic Record



Photosynthesis originated at least 3 GYA with anoxygenic forms; oxygenic came later.

Hohmann-Marriott and Blankenship (2011) *Ann. Rev. Plant Biol.*

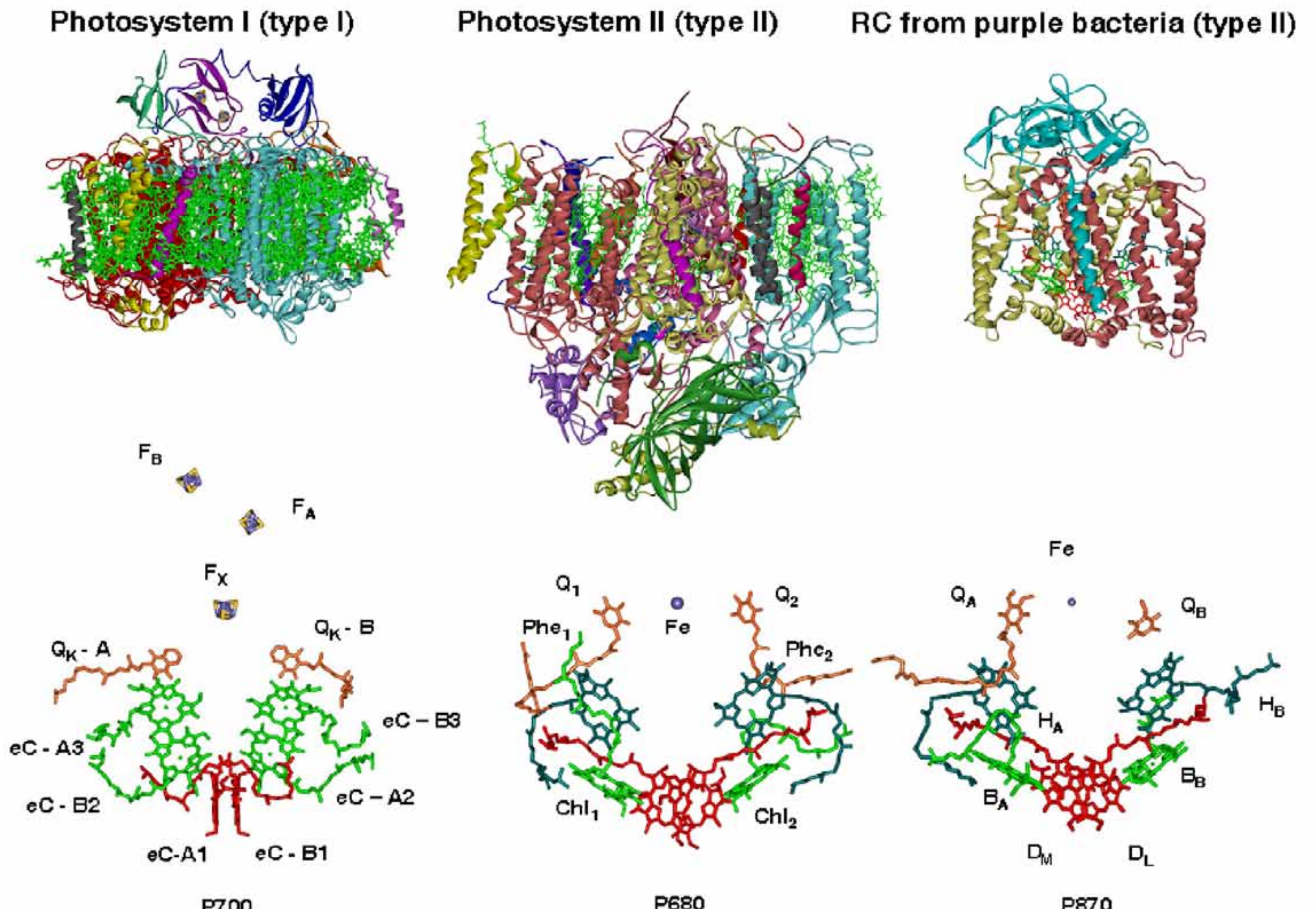
Types of Phototrophic Organisms



- Chlorophyll-based phototrophic organisms are found only in the Bacterial and Eukaryal domains.
- Phototrophs are either **oxygenic** (oxygen evolving) or **anoxygenic** (non-oxygen evolving)
- All phototrophic Eukaryotic chloroplasts were derived via endosymbiosis of cyanobacteria.

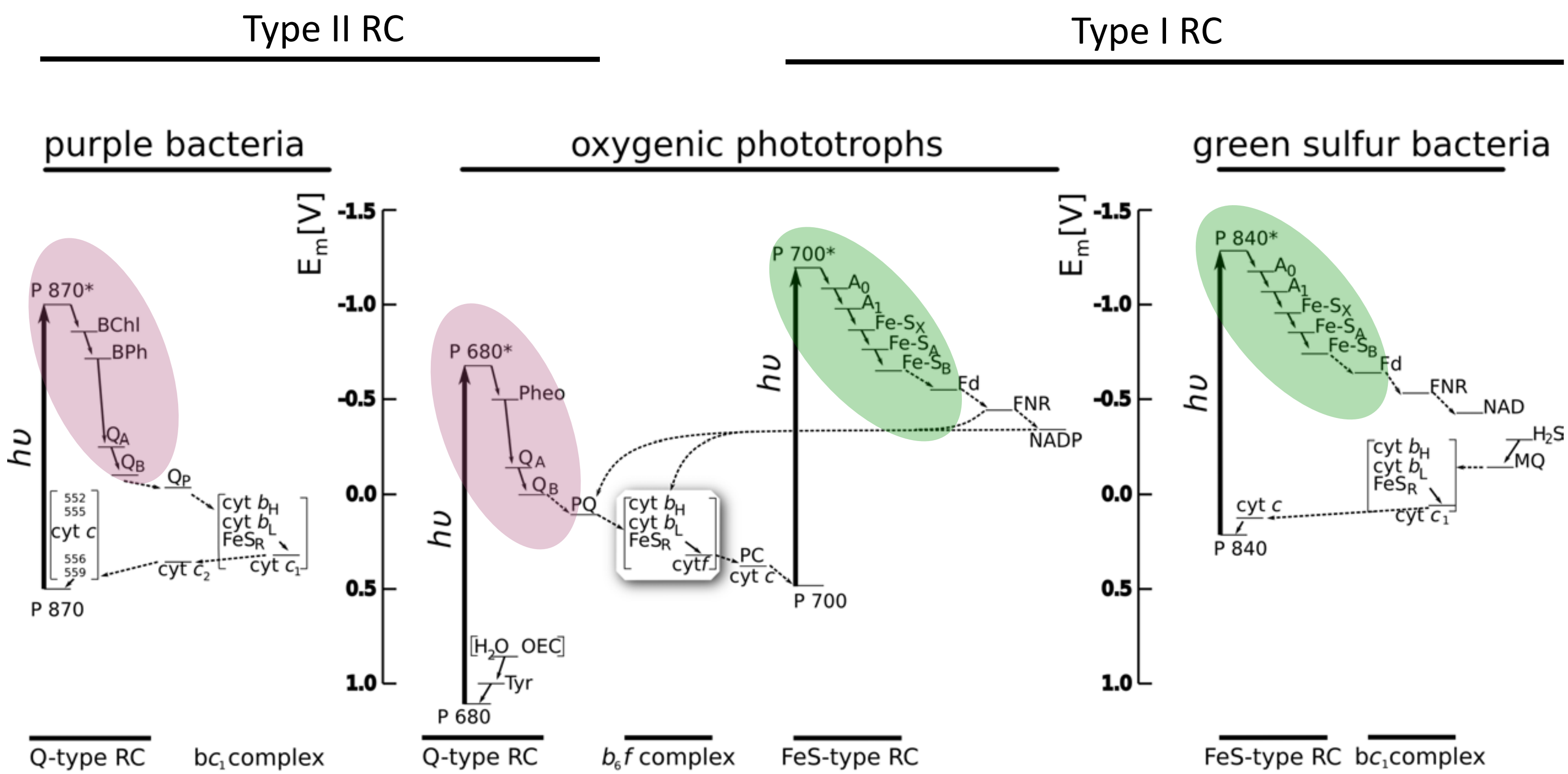
Figure adapted from N. Pace

Photosynthetic Reaction Centers



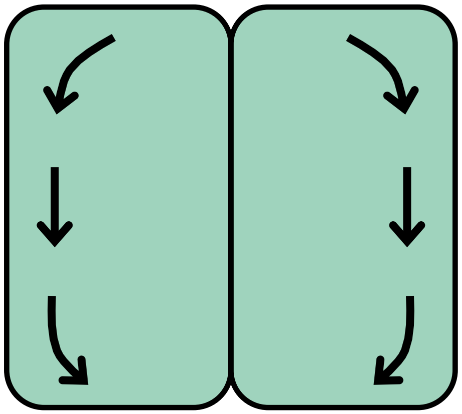
Structural conservation of RCs suggests a single evolutionary origin.

RC Energy-Kinetic Diagrams

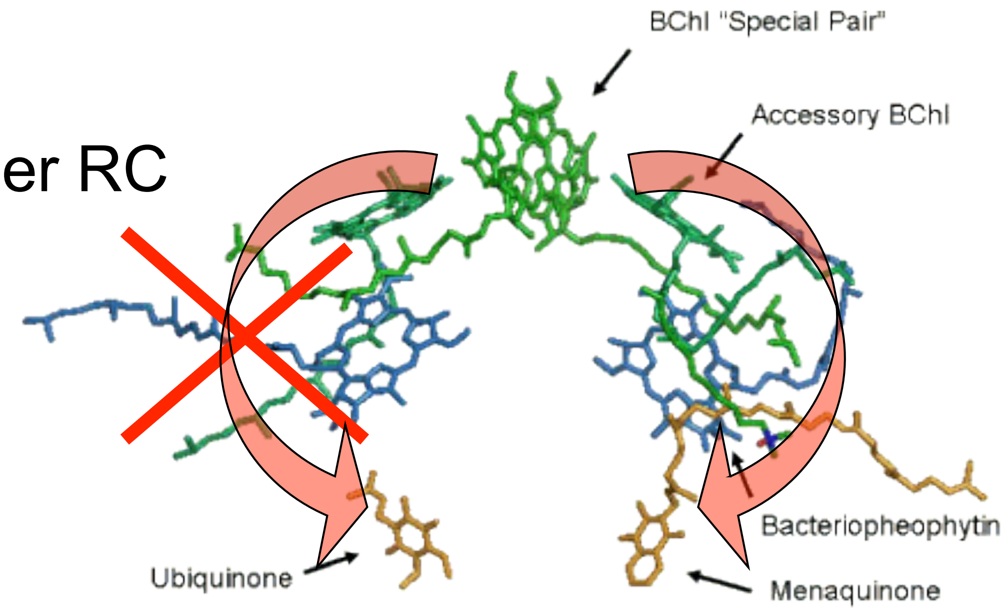


These diagrams incorporate both kinetic and thermodynamic information, and also suggest evolutionary relationships among photosynthetic reaction centers.

Gene Duplication in RC Evolution

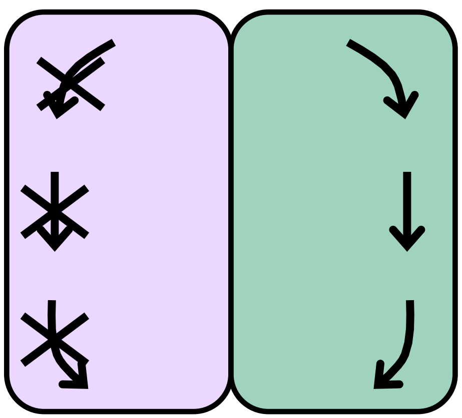


Homodimer RC



↓ Gene duplication

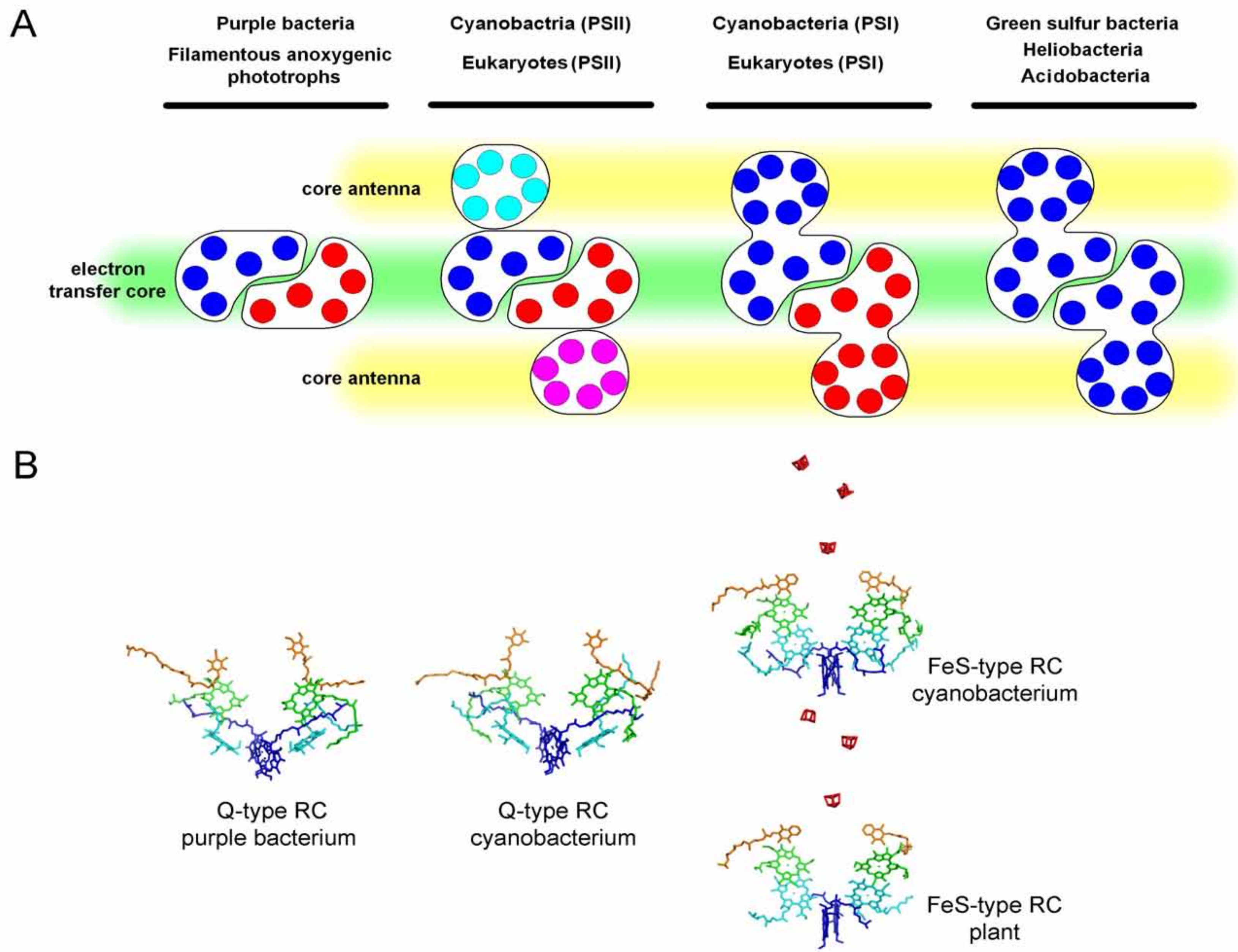
↓ Gene divergence



Heterodimer RC

Gene duplication and divergence is source of directionality of electron transfer

Evolution of Reaction Centers

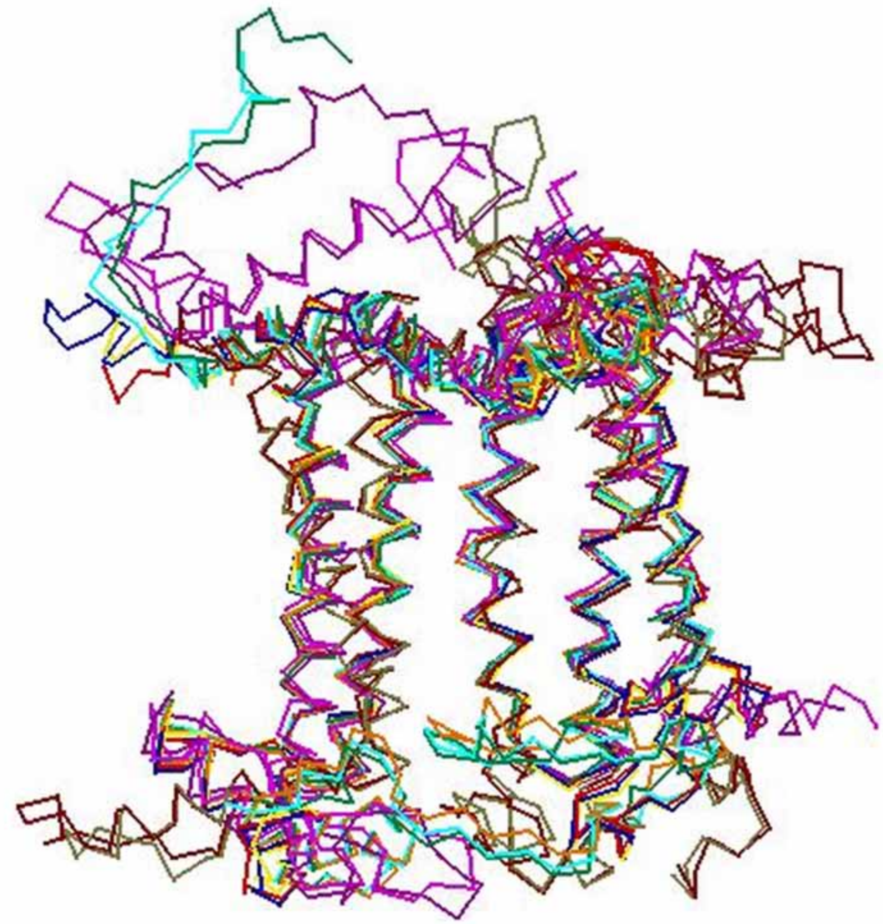


Structural Comparisons of RCs

- X-ray structures of purple bacterial RC, PS I and PSII compared using Combinatorial Extension-Monte Carlo (CE-MC method*.

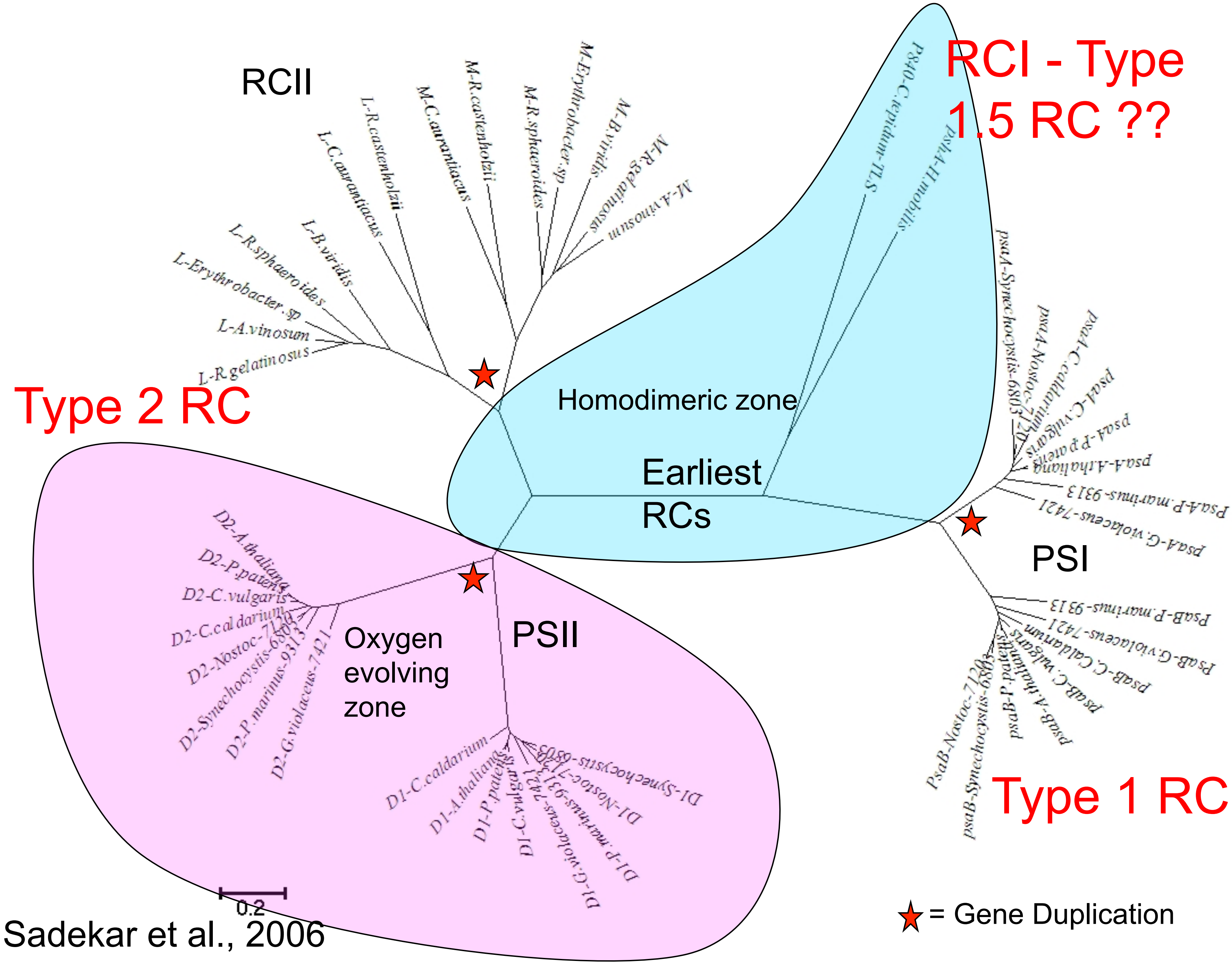
- Algorithm finds best structural alignment of all proteins compared (α C only). X-ray structure is not changed.

- Overall topology of structure-based trees is the same as sequence-based trees.



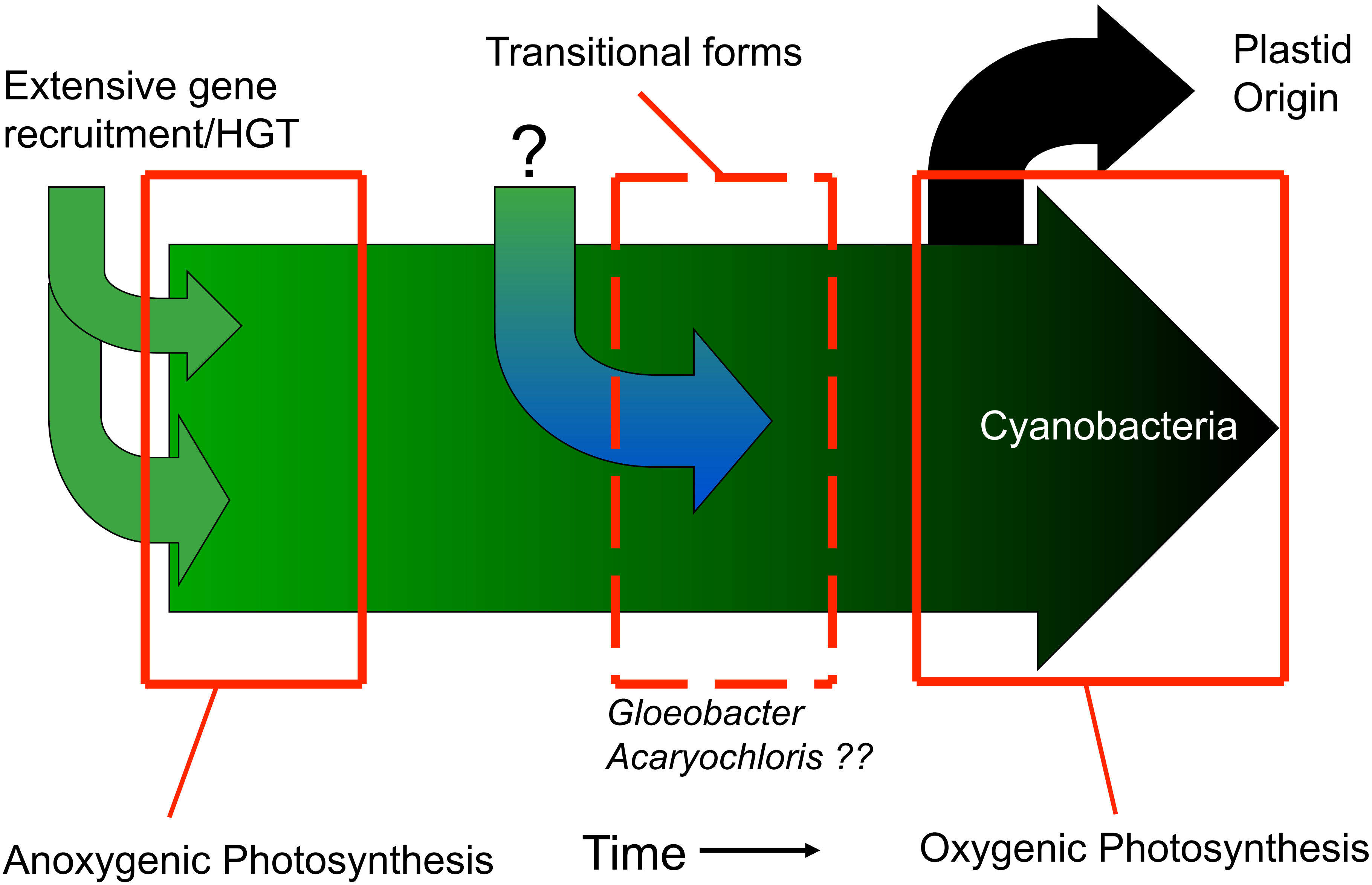
*Guda et al. *Nucl. Acids Res.* 2004

Sadekar et al. *Mol. Biol.Evol.* 2006



Sadekar et al., 2006

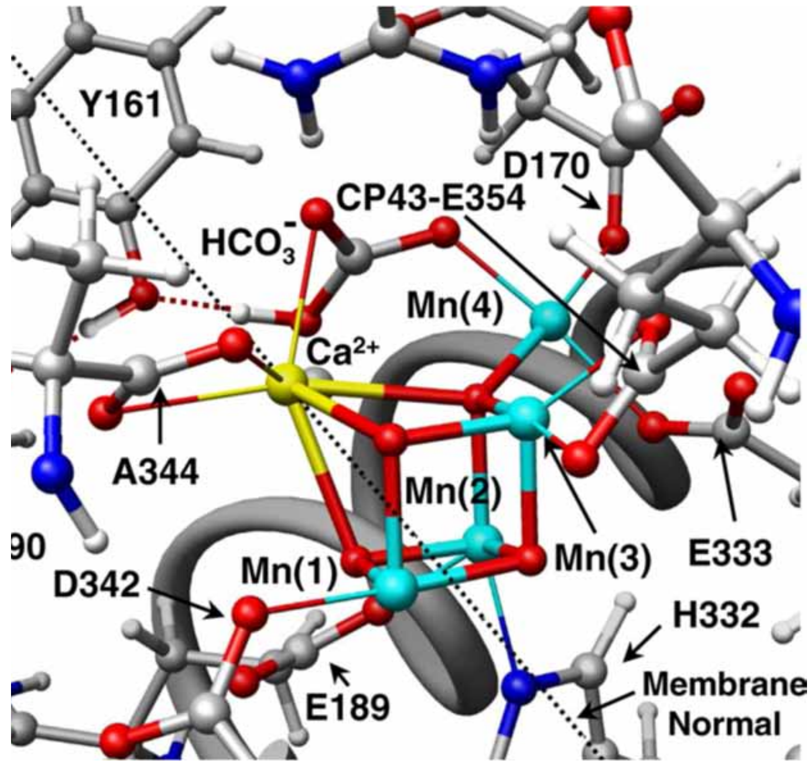
Transition to Oxygenic Photosynthesis



Origin of Oxygen Evolution

Changes between the anoxygenic RC and PS2 are:

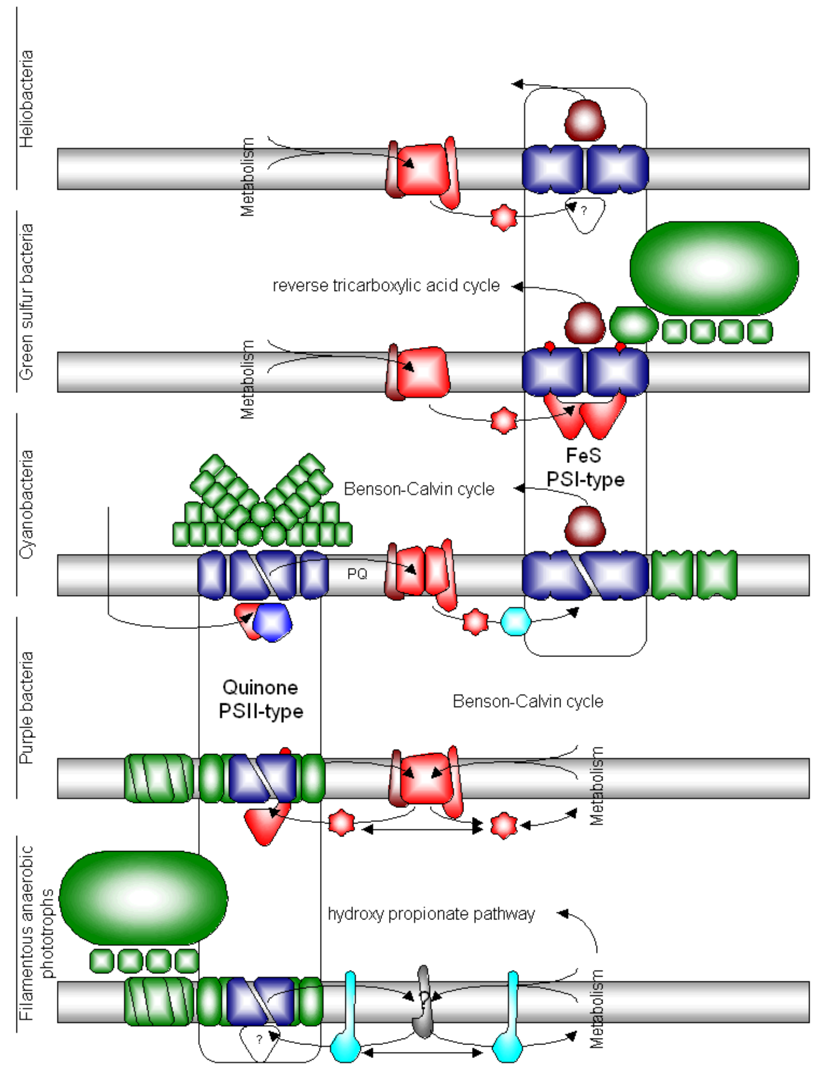
- A redox potential > 1 V, which requires change from BChl (870 nm) to Chl (680 nm)
- A charge accumulating system to interface 1 e- photochemistry to 4 e- oxygen chemistry - Mn cluster--Singular event!
- A much more complex protein complement
- Linked photosystems ??



Sproviero et al., CCR 2008

Evolution of PS-What we (think) we know

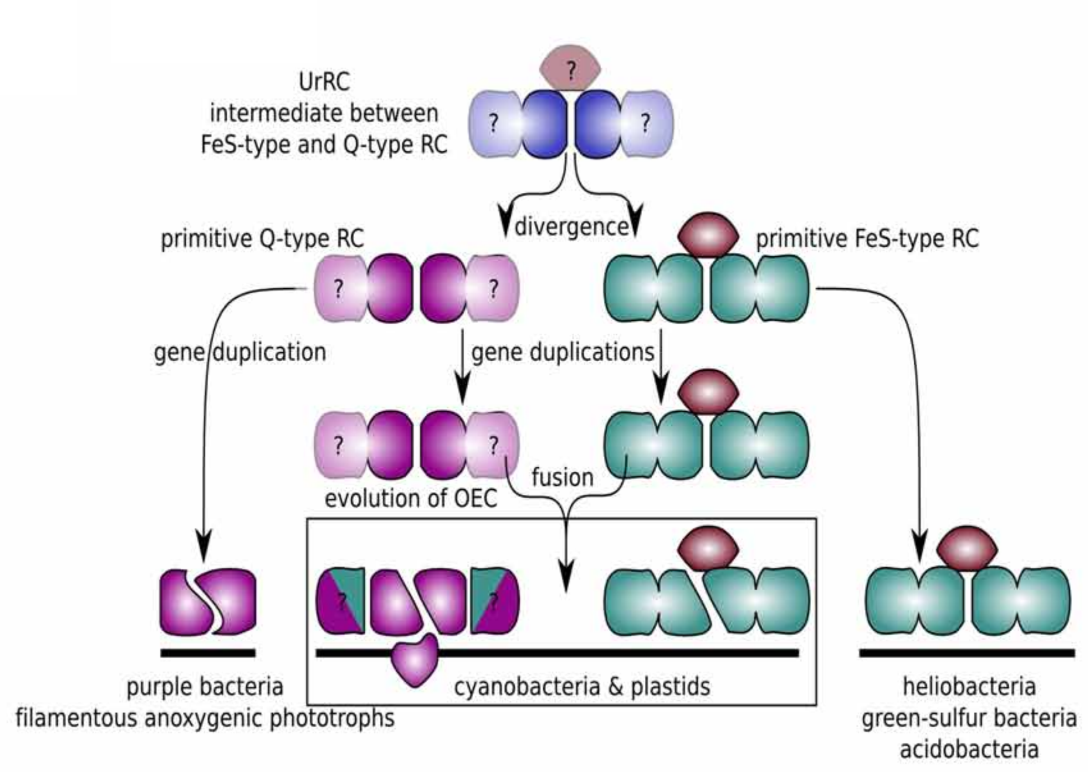
- Photosynthetic reaction centers all have a common ancestor and are related by divergent evolution
- Earliest RCs were homodimeric and not oxygen-evolving
- Multiple gene duplications have taken place to produce heterodimeric RCs
- Tree topology suggests that oxygen evolution arose after the major RC lines diverged
- Ancestral RC may have been intermediate between Type I and Type II
- Antennas have arisen multiple times during evolution



Origin and Evolution of Photosynthesis-Remaining Challenges

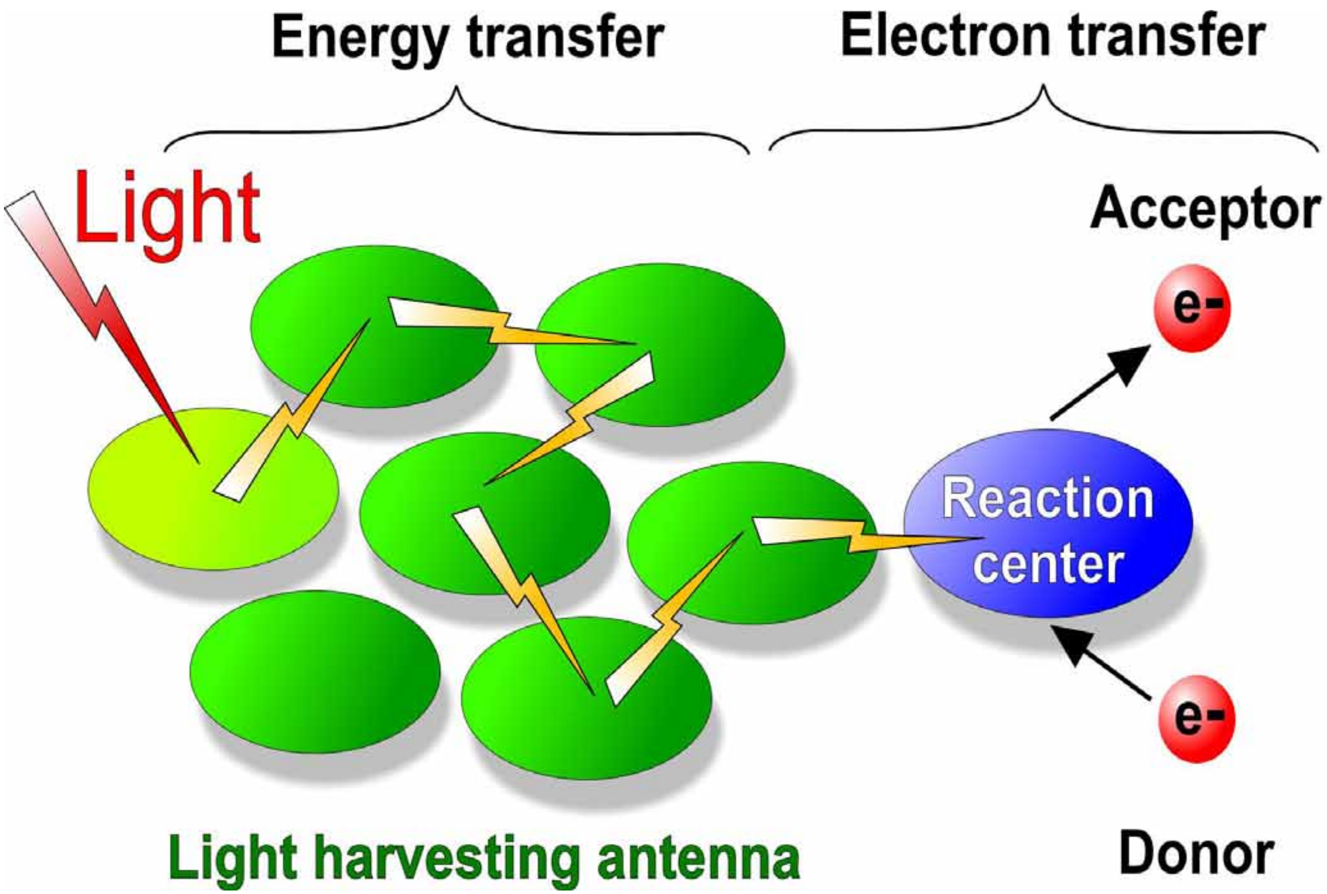
- Nature of the earliest PS systems not known
- Significance of gene duplications in RC evolution not understood
- Evolutionary origin of the oxygen evolving complex not known
- No good understanding of how two photosystems were linked in series

Fusion Hypothesis



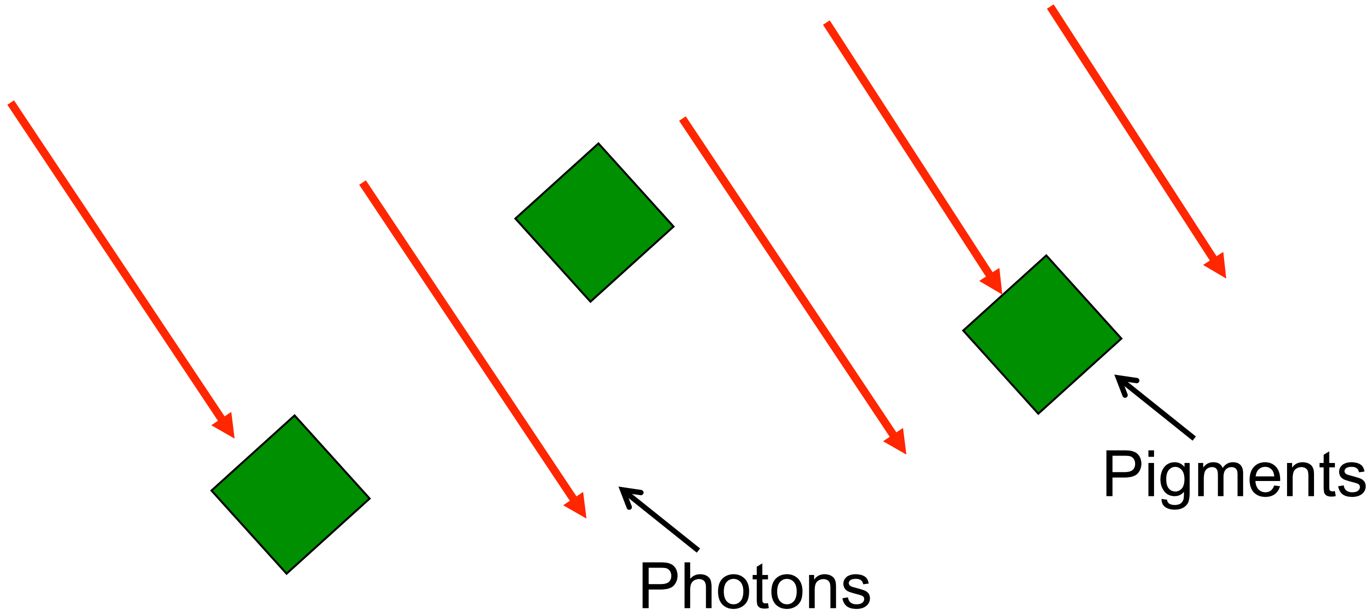
Hohmann-Marriott and Blankenship (2011)
Ann. Rev. Plant Biol.

Photosynthetic Energy Storage



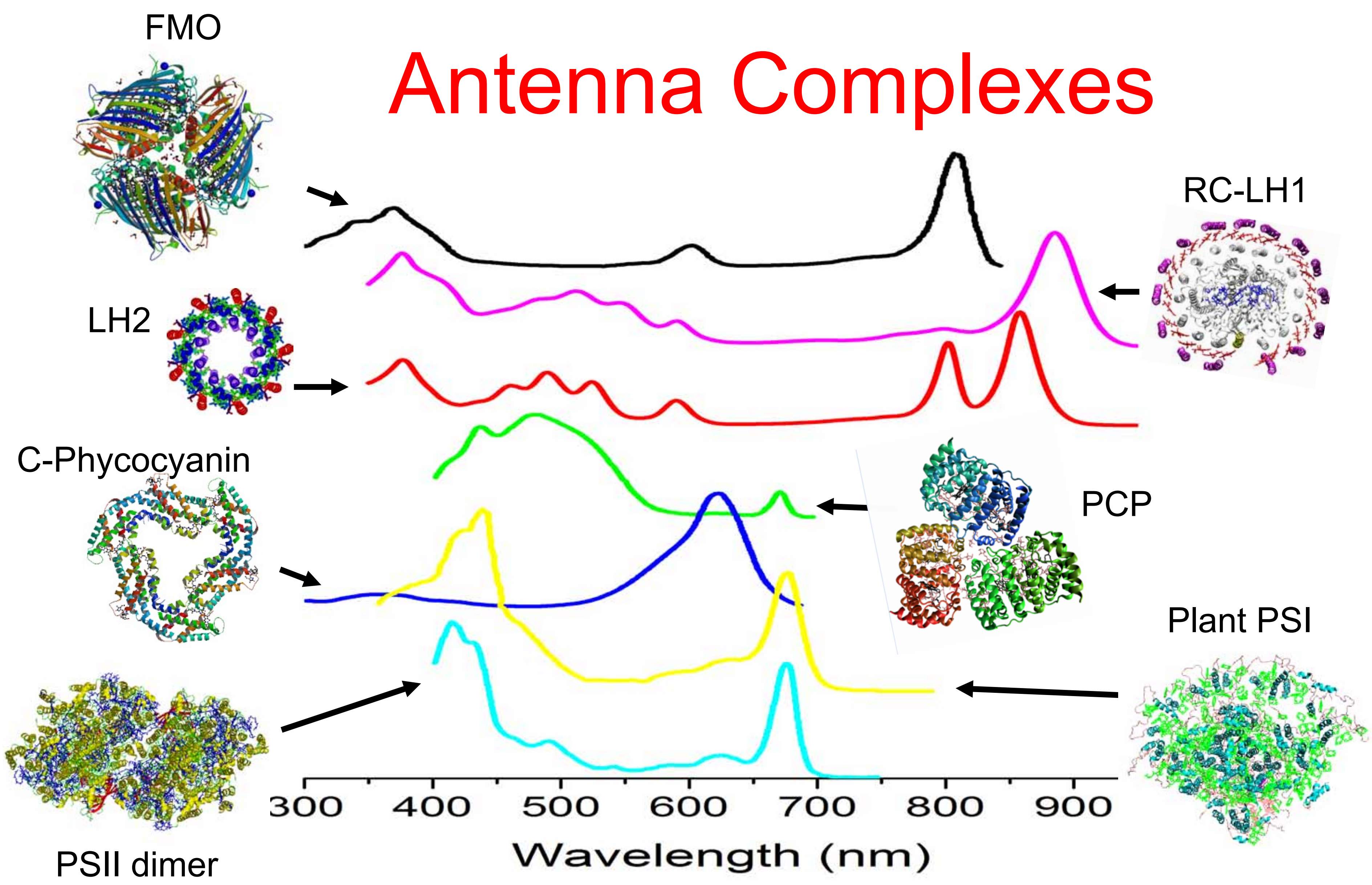
All PS organisms contain a light-gathering antenna system

Why Antennas?



- Each chlorophyll molecule absorbs about 10 photons per second in full sun
- Antenna size is an economic balance in efficient use of cellular resources
- Too large and system saturates at low intensity and suffers photodamage
- Too small and not enough energy for cellular needs

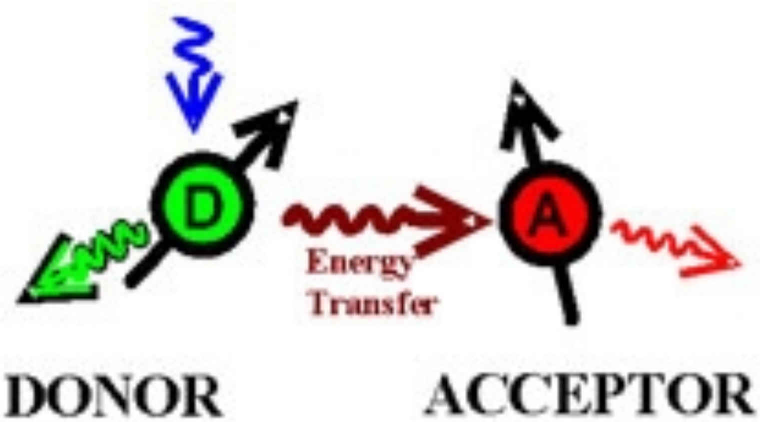
Antenna Complexes

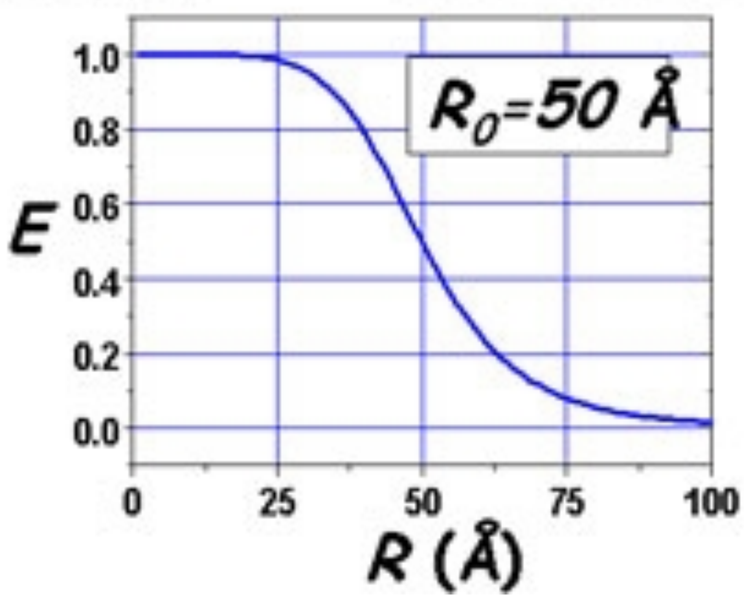


Extreme diversity of antenna systems strongly suggests multiple independent evolutionary origins

Aaron Collins 2010

Förster Resonance Energy Transfer (FRET)

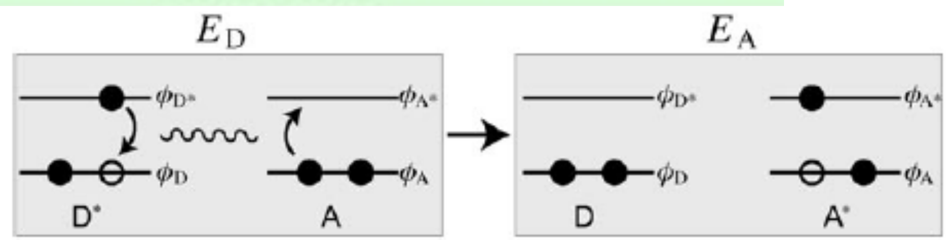




Energy Transfer Efficiency

$$E = \frac{1}{1+(R/R_0)^6}$$

R_0=50% transfer efficiency distance
3nm~7nm



- Rate of energy transfer from donor to acceptor depends on distance, orientation and spectral overlap.
- Förster description breaks down when pigments are close.

Chlorosome Antenna Complexes

Cells of green bacteria contain ~100 chlorosomes appressed to the cytoplasmic membrane

Connected via a complex internal structural network

Each chlorosome contains ~250,000 molecules of BChl *c*

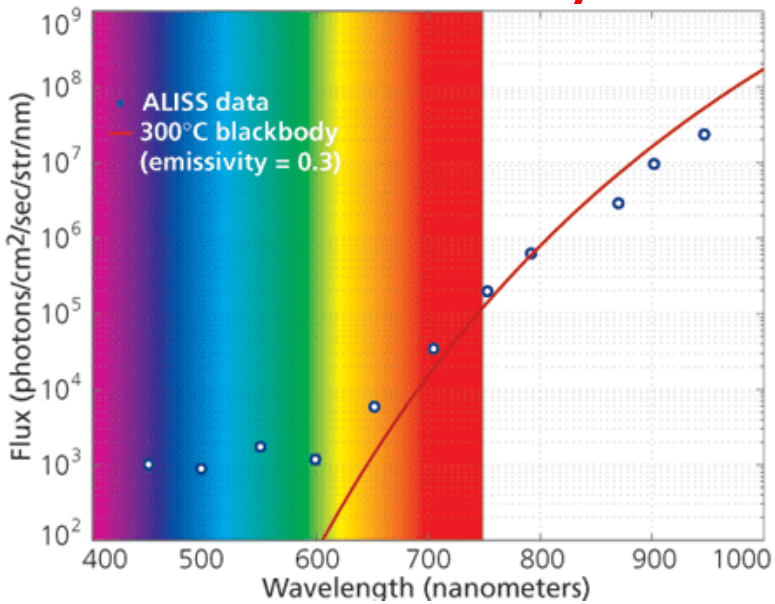
Martin Hohmann-Marriott

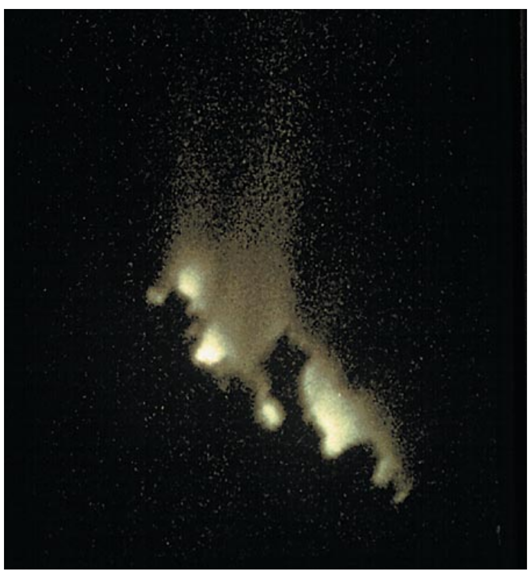
Phototrophic Bacteria at Deep Sea Hydrothermal Vents

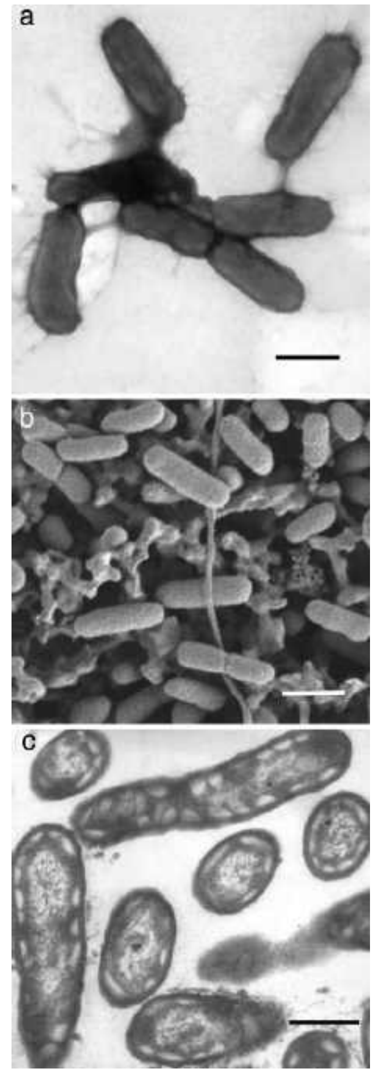
•July-August 2000 Juan de Fuca Ridge
•December 2001 9 North

2200 meters deep
Temp gradient --
350ºC to 2ºC

Light Emission and Photosynthesis at Hydrothermal Vents



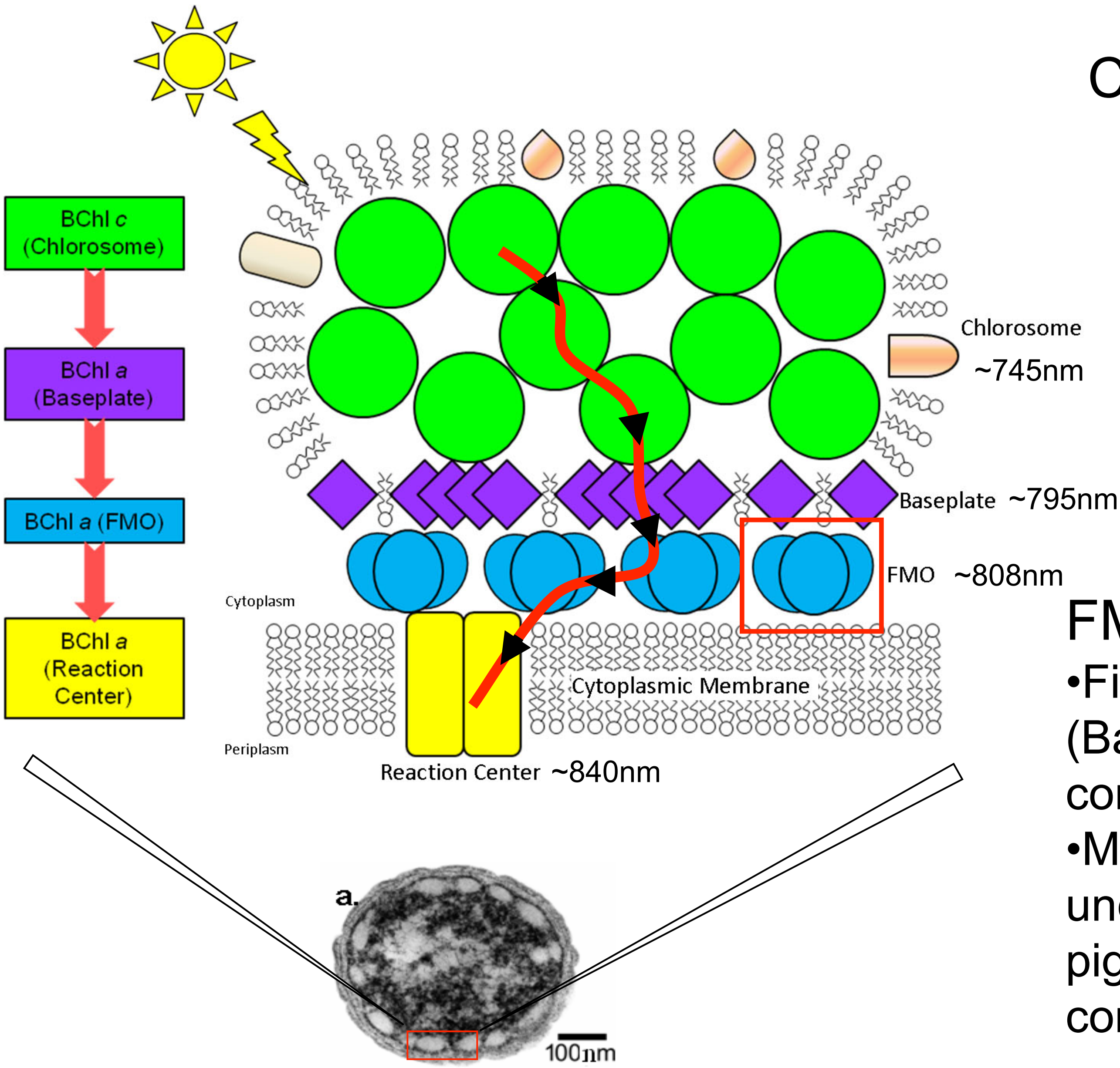




White et al. (2000)
Geophys Res Lett

Beatty et al. PNAS (2005)

Photosystem from Green Sulfur Bacteria



Chlorosome:

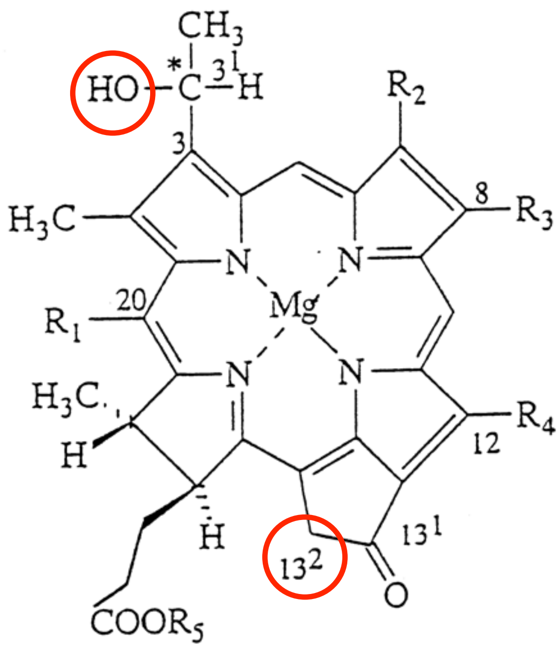
Length: 110–180 nm
Width: 40–60 nm
Height: 20-30 nm
Mass: >100 MDa
BChl *c/d/e*: ~ 250,000
BChl *a* ~2000

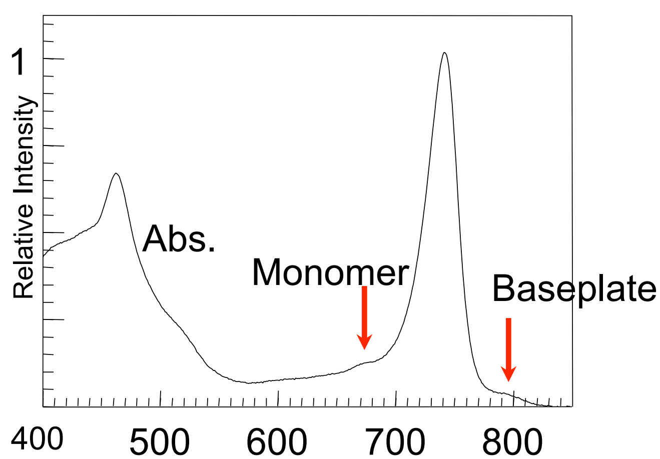
FMO protein:

- First crystal structure of (Bacterio)chlorophyll containing protein.
- Much of the current understanding of how pigments bind to proteins comes from this protein.

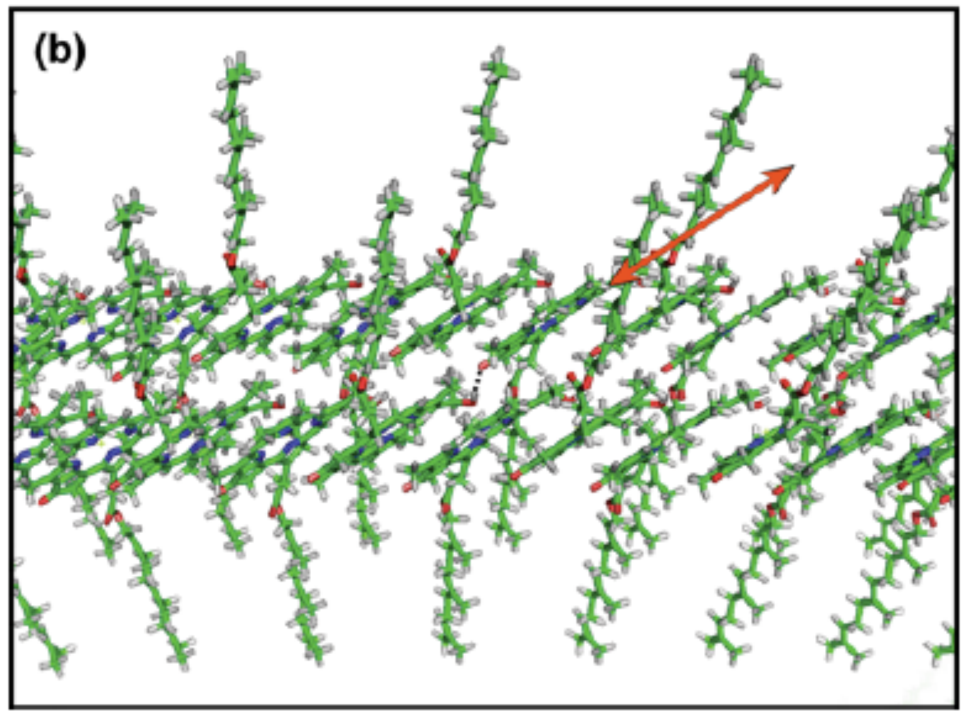
Chlorosome Bacteriochlorophyll Organization

Bchl *c,d or e*



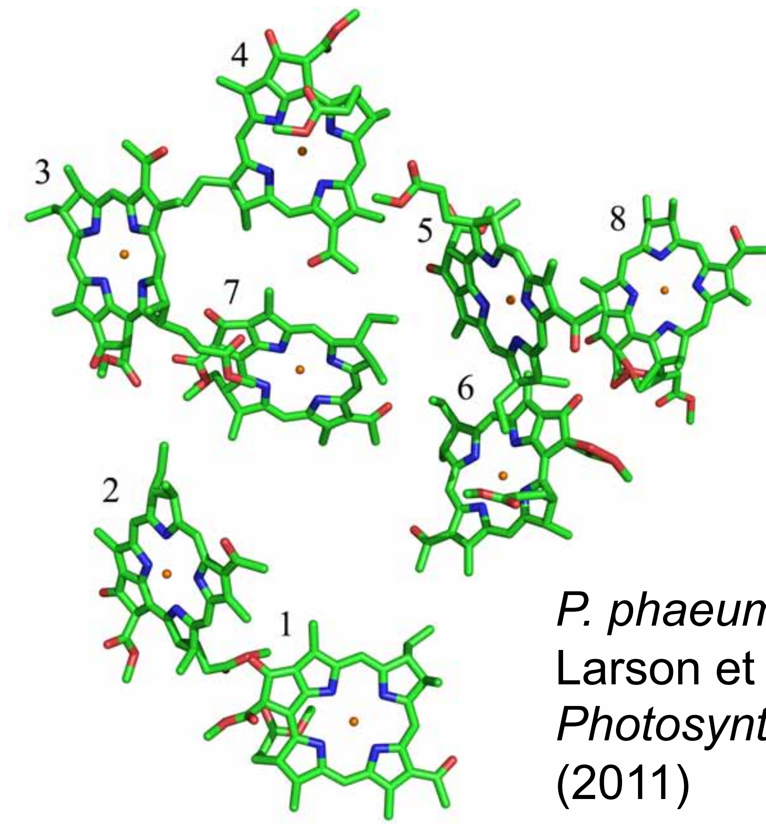


- No protein!
- Pigment oligomers
- Reversible self-assembly
- Similar to J aggregates



Oostergetel et al. *Photosynth. Res.* (2010)

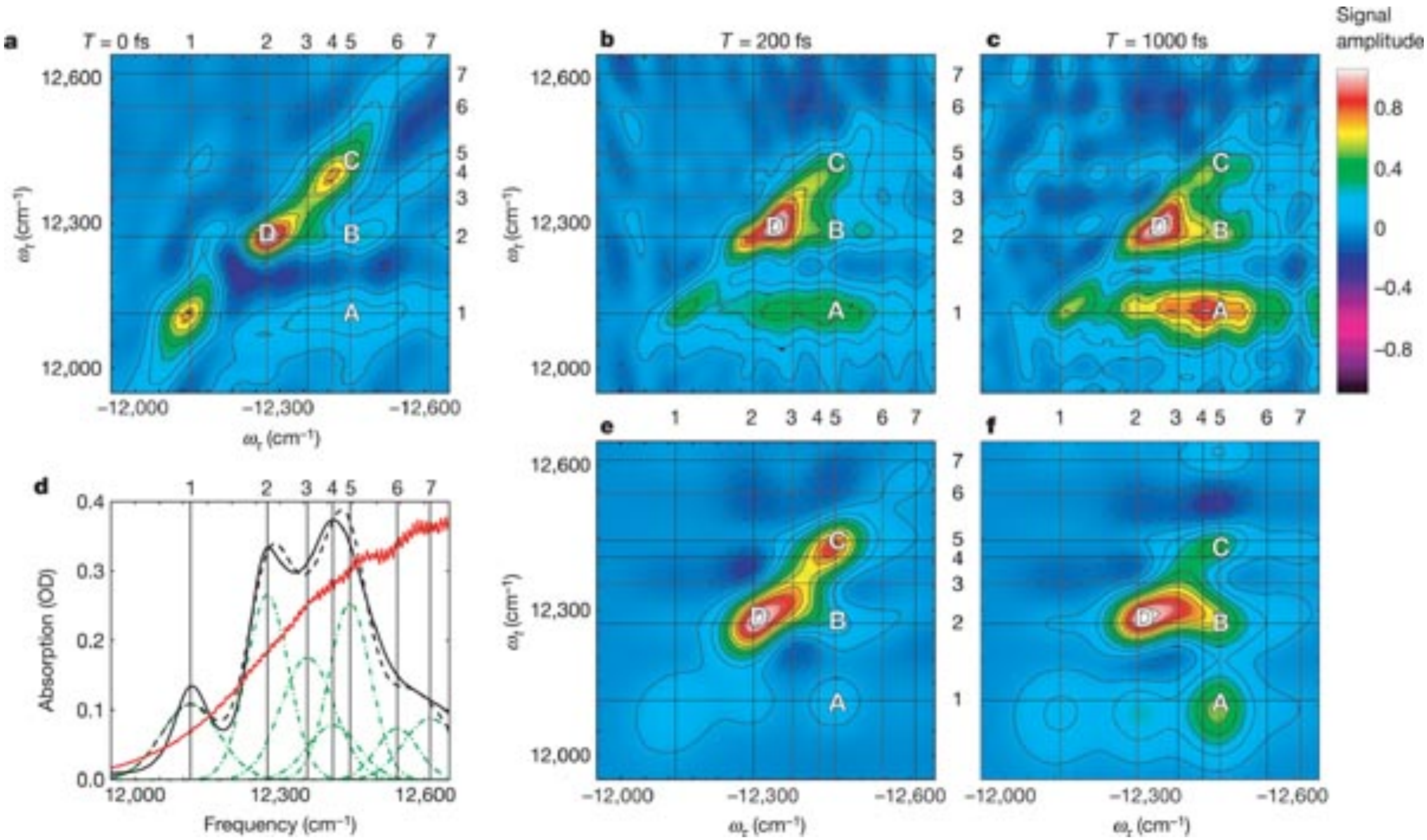
Fenna-Matthews-Olson (FMO) Protein



P. phaeum FMO
Larson et al.
Photosynth. Res.
(2011)

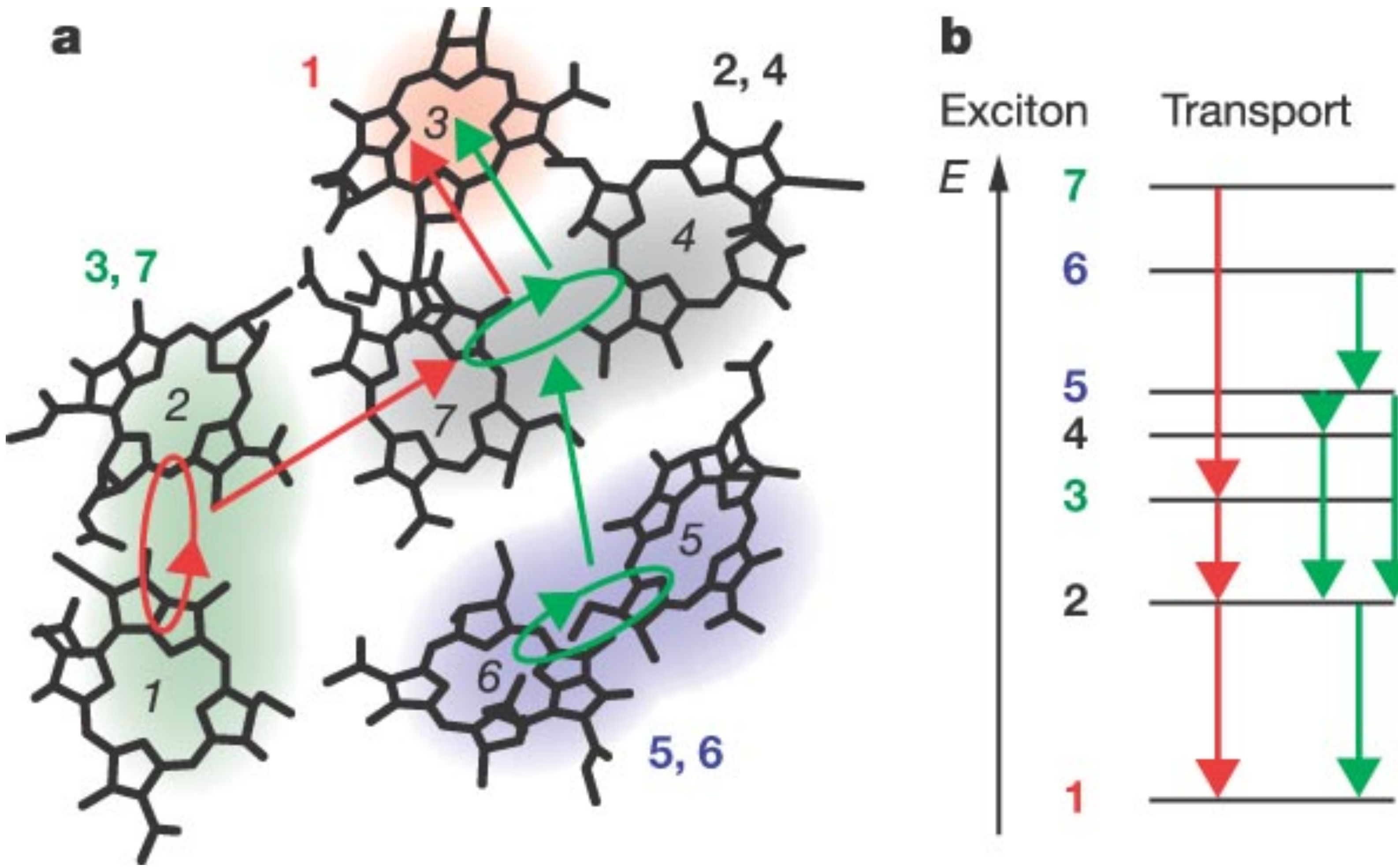
- Made of three identical subunits, each 46.5 kDa
- Predominantly β-sheet
- Each subunit contains 7 or 8 BChl *a* molecules
- Each subunit forms a “taco shell” around the BChl *a* molecules.

2D Ultrafast Spectroscopy



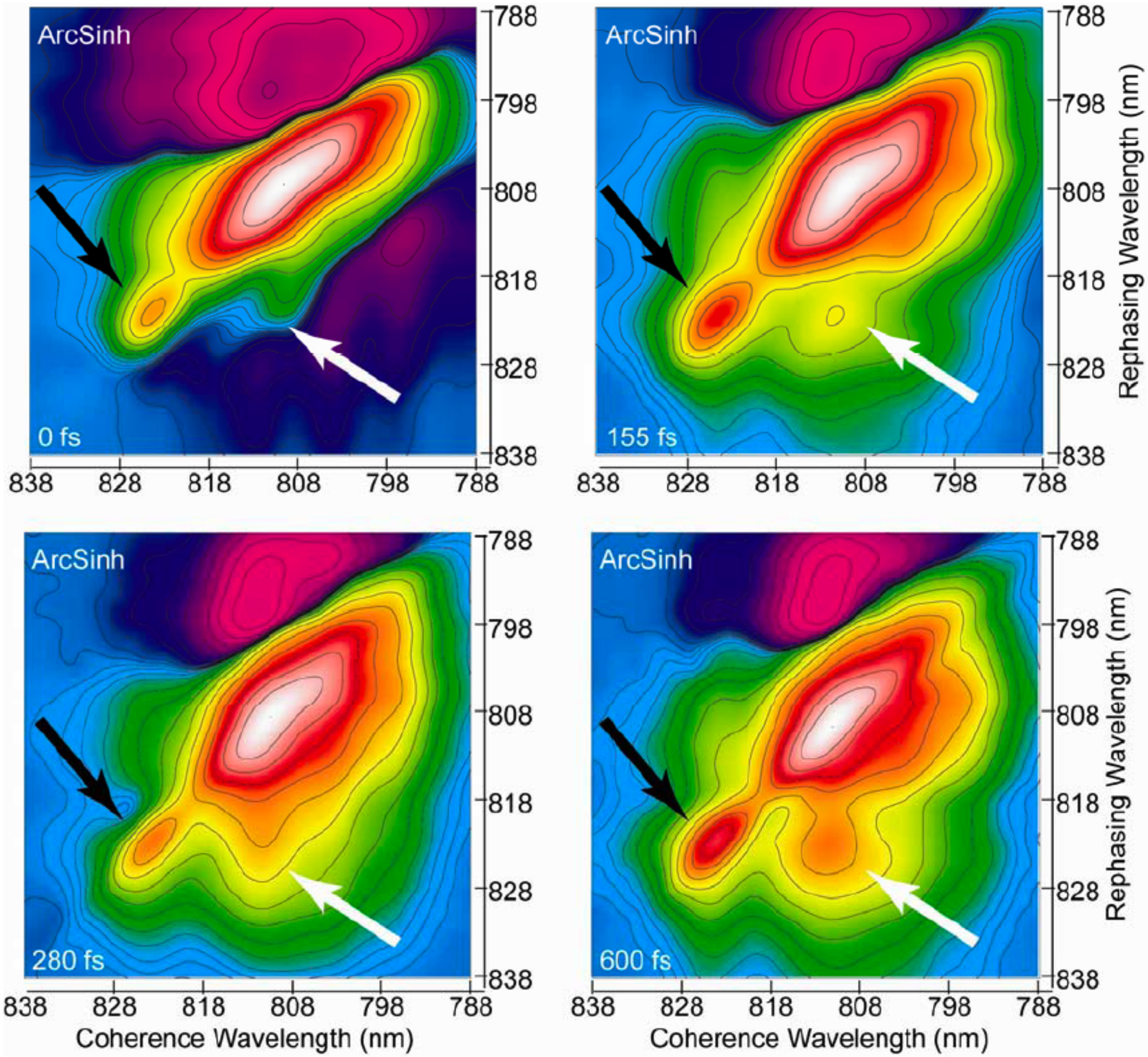
Brixner et al. *Nature* (2005)

Pathways of Energy Transfer



Brixner et al. *Nature* (2005)

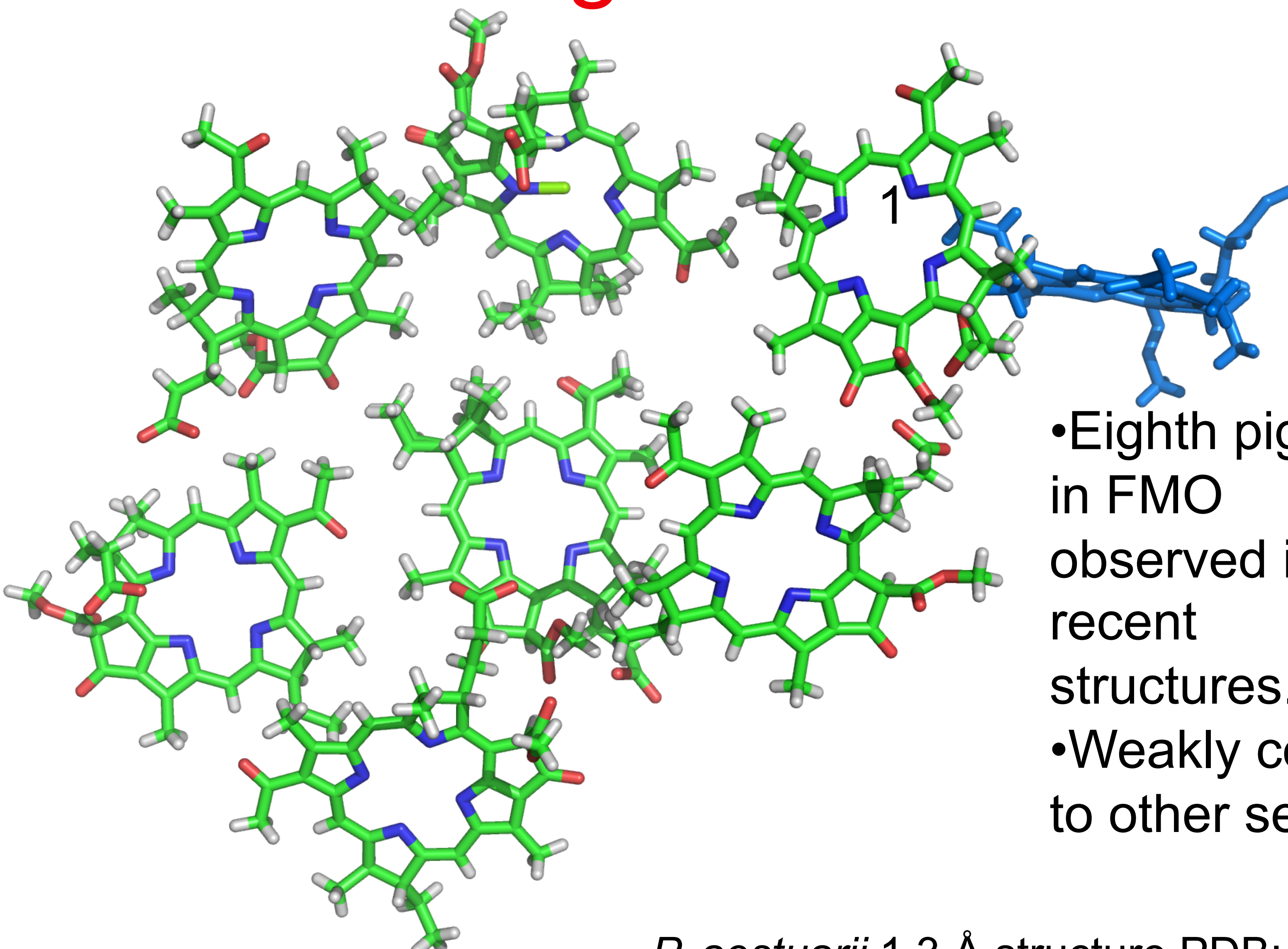
Quantum Coherence in FMO



- FMO exhibits quantum coherence effects.
- May increase efficiency of energy transfer.
- Has also been observed in some other PS antenna complexes.

Engel et al. *Nature* (2007)

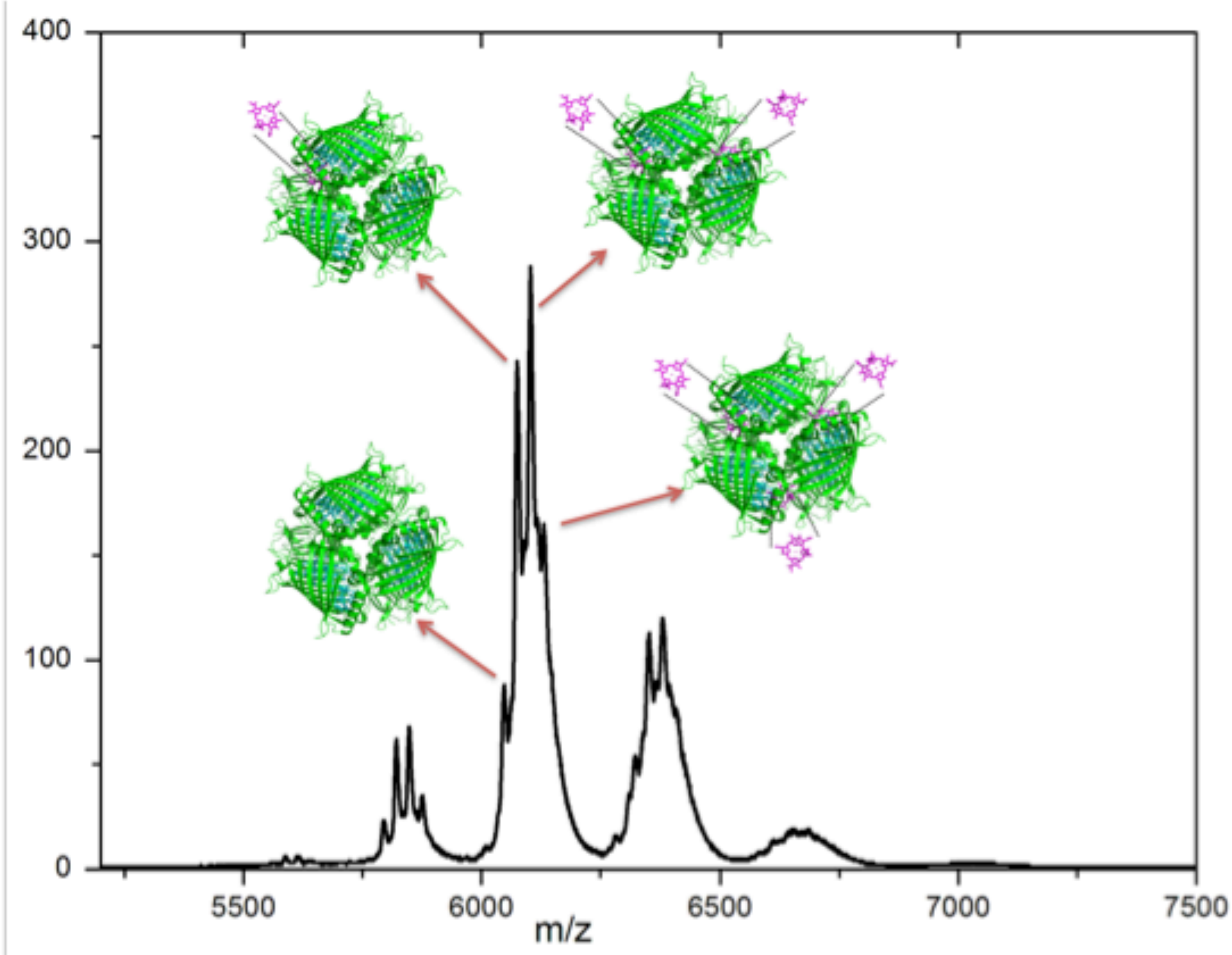
Another Pigment in FMO!!



- Eighth pigment in FMO observed in recent structures.
- Weakly coupled to other seven.

P. aestuarii 1.3 Å structure PDB: 3EOJ
Tronrud et al. *Photosynth. Res.* (2009)

Native Spray MS of FMO

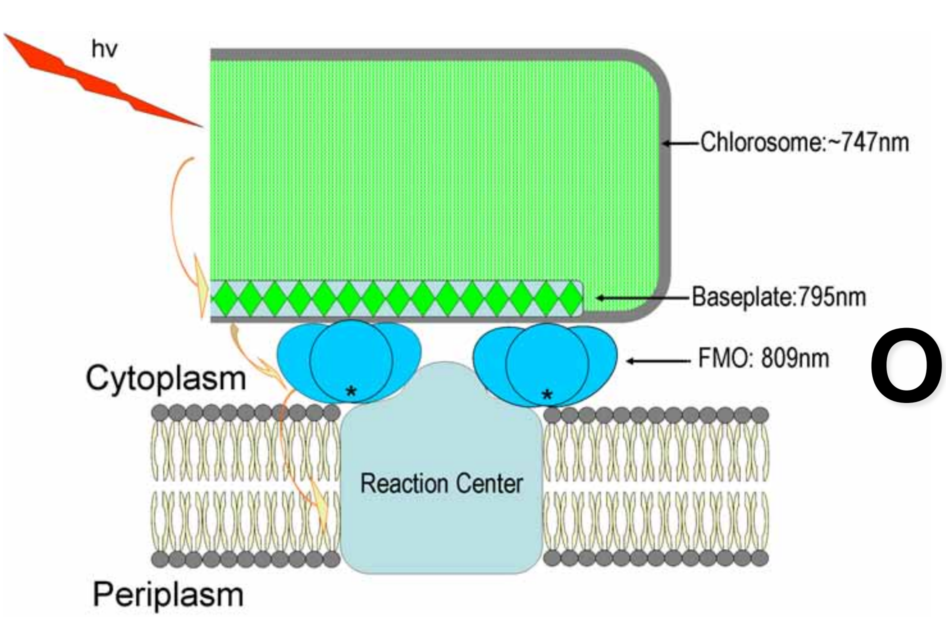


- Native spray MS of FMO protein indicates that the intact complex contains up to 24 BChl *a* molecules.
- Some of the 8th BChl molecules are lost during purification.

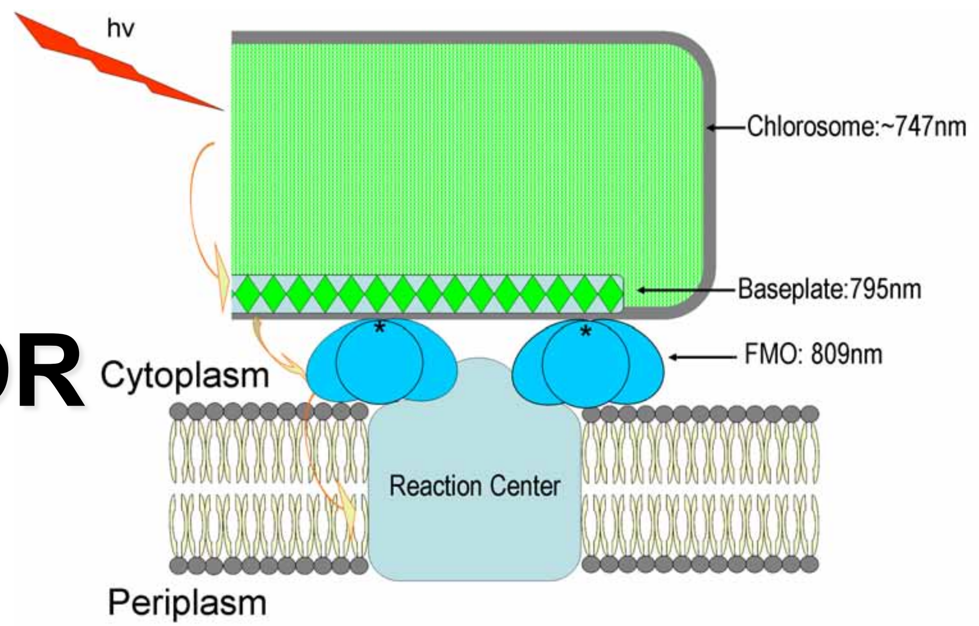
Wen et al. *Biochemistry* (2011)

Orientation of FMO on the membrane

How does the FMO protein interact with the membrane?



OR

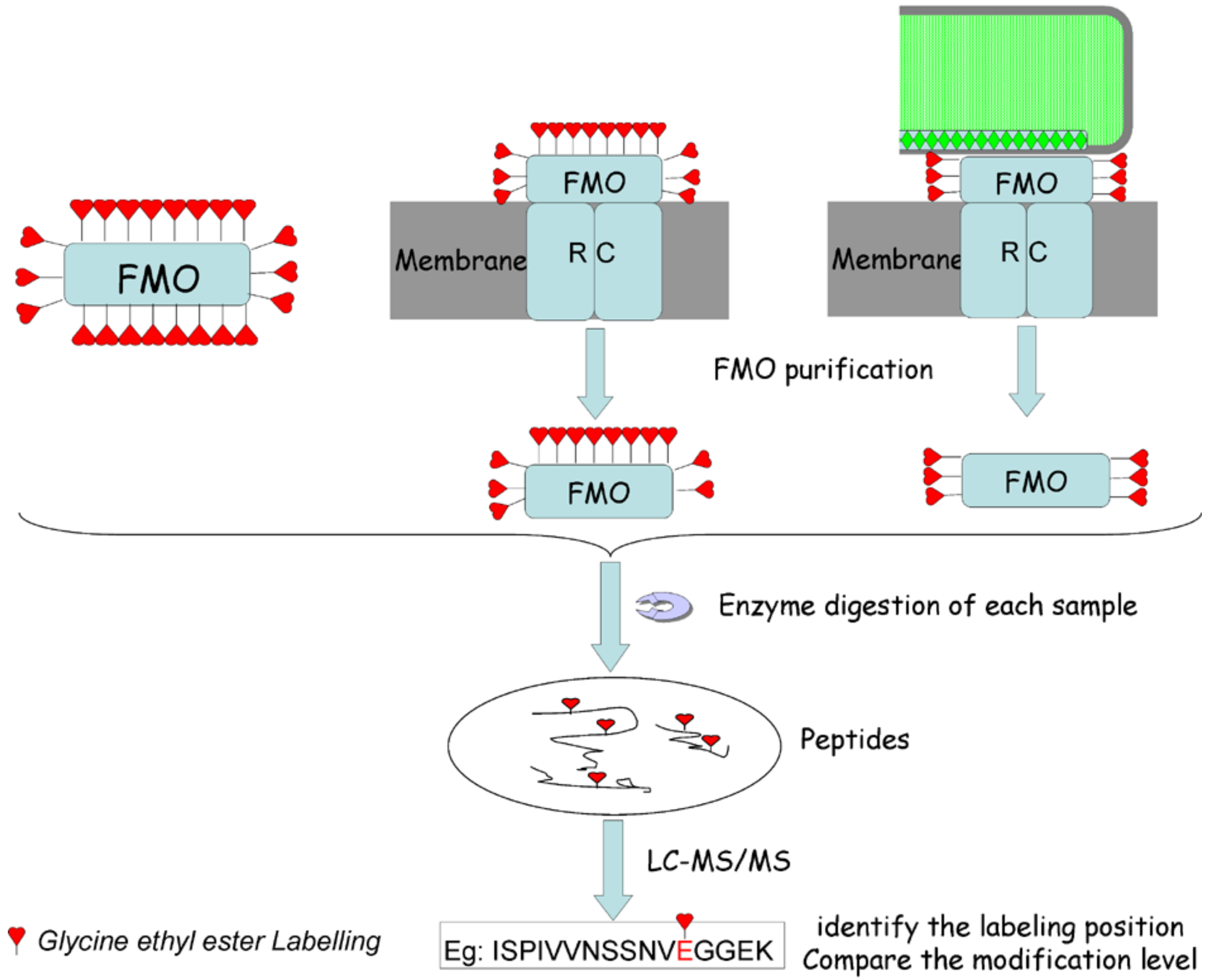


* Bchl *a* #3

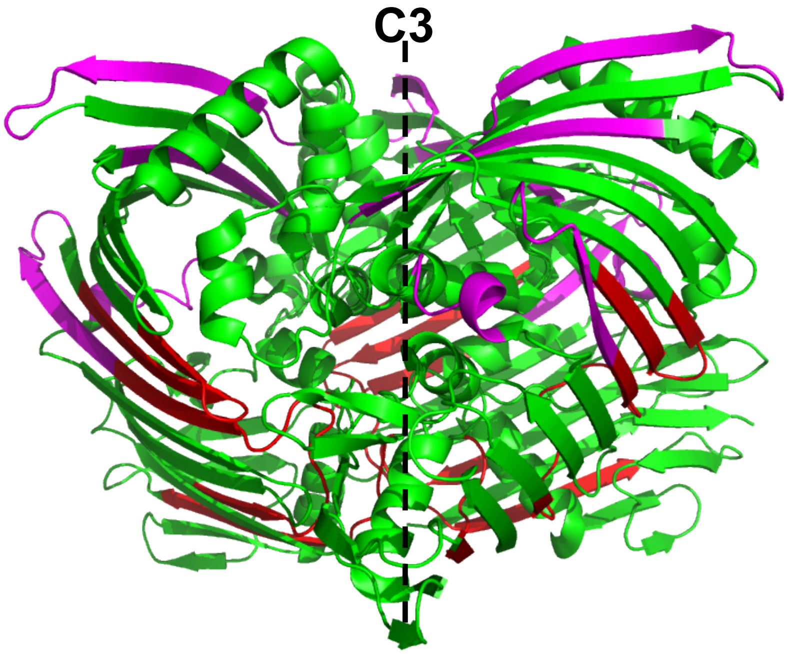
- The two sides of the FMO protein are distinguishable.
- Previous work has not established which side faces the membrane.

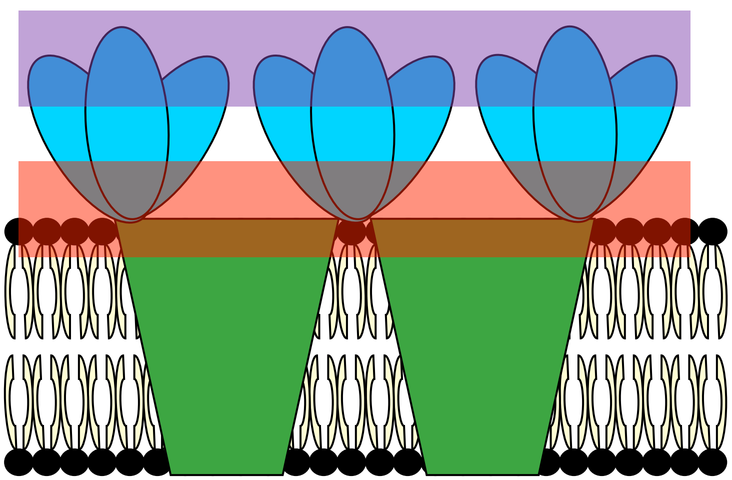
Wen et al. *PNAS* (2009)

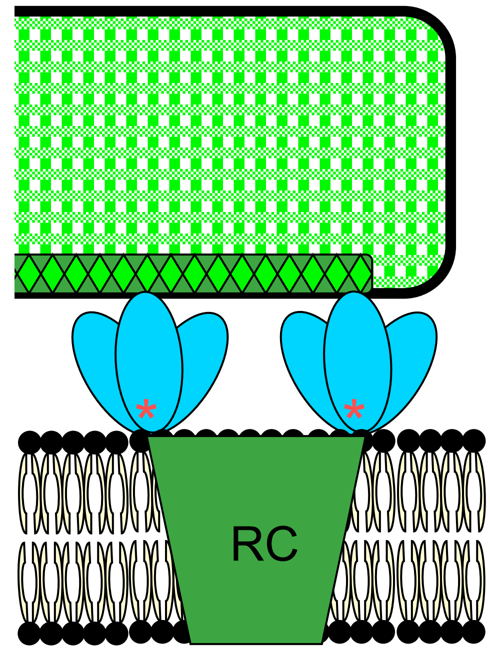
Experimental design



Membrane Architecture

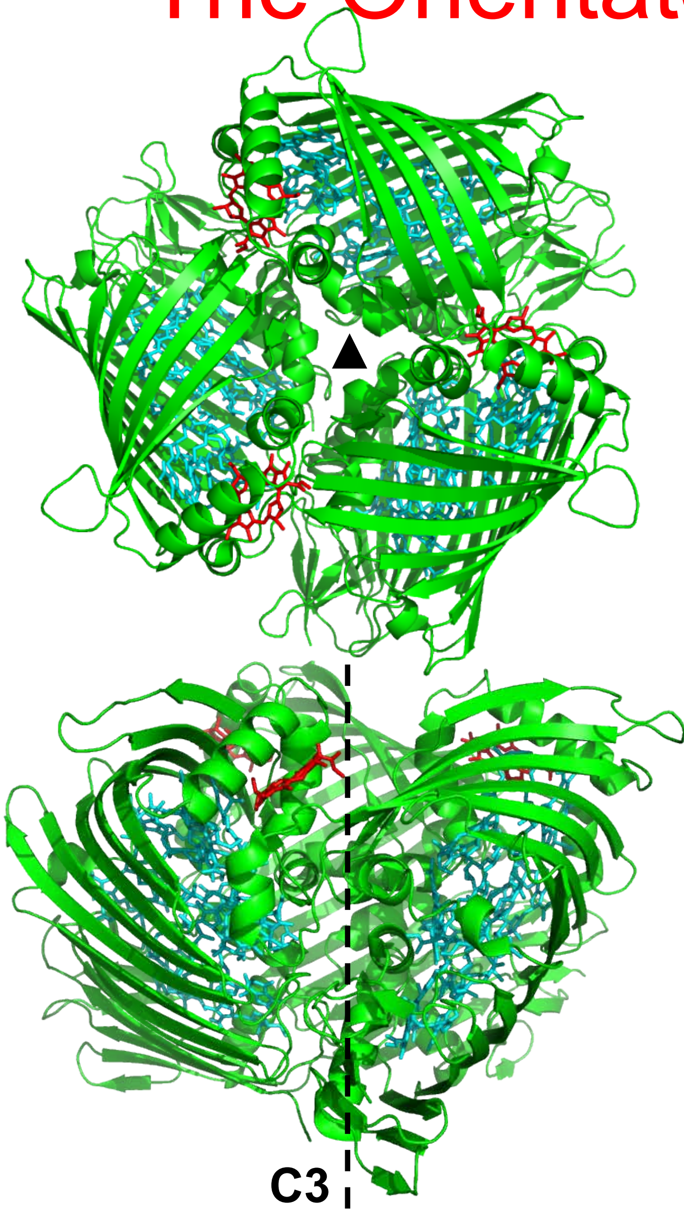


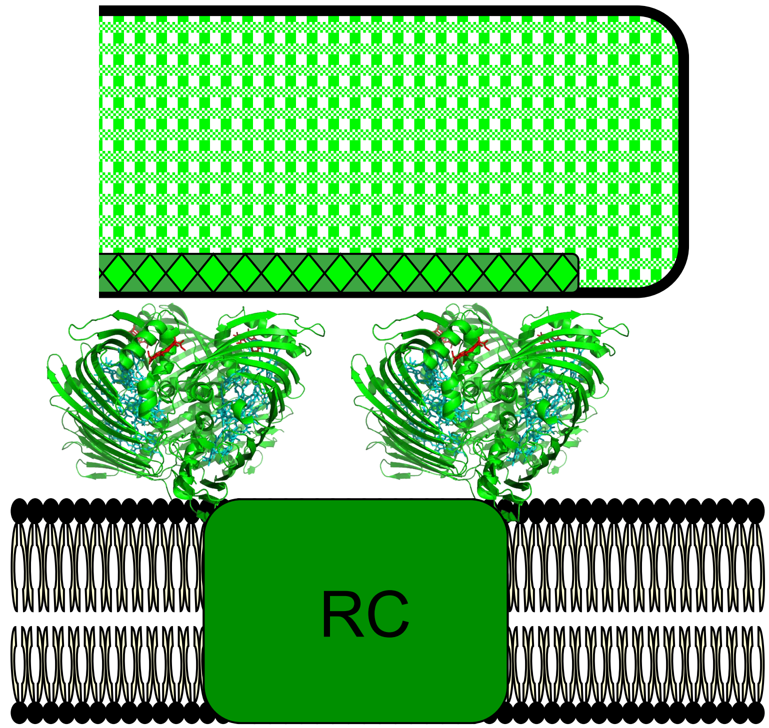




Bchl *a*3 side of the protein interacts with the membrane

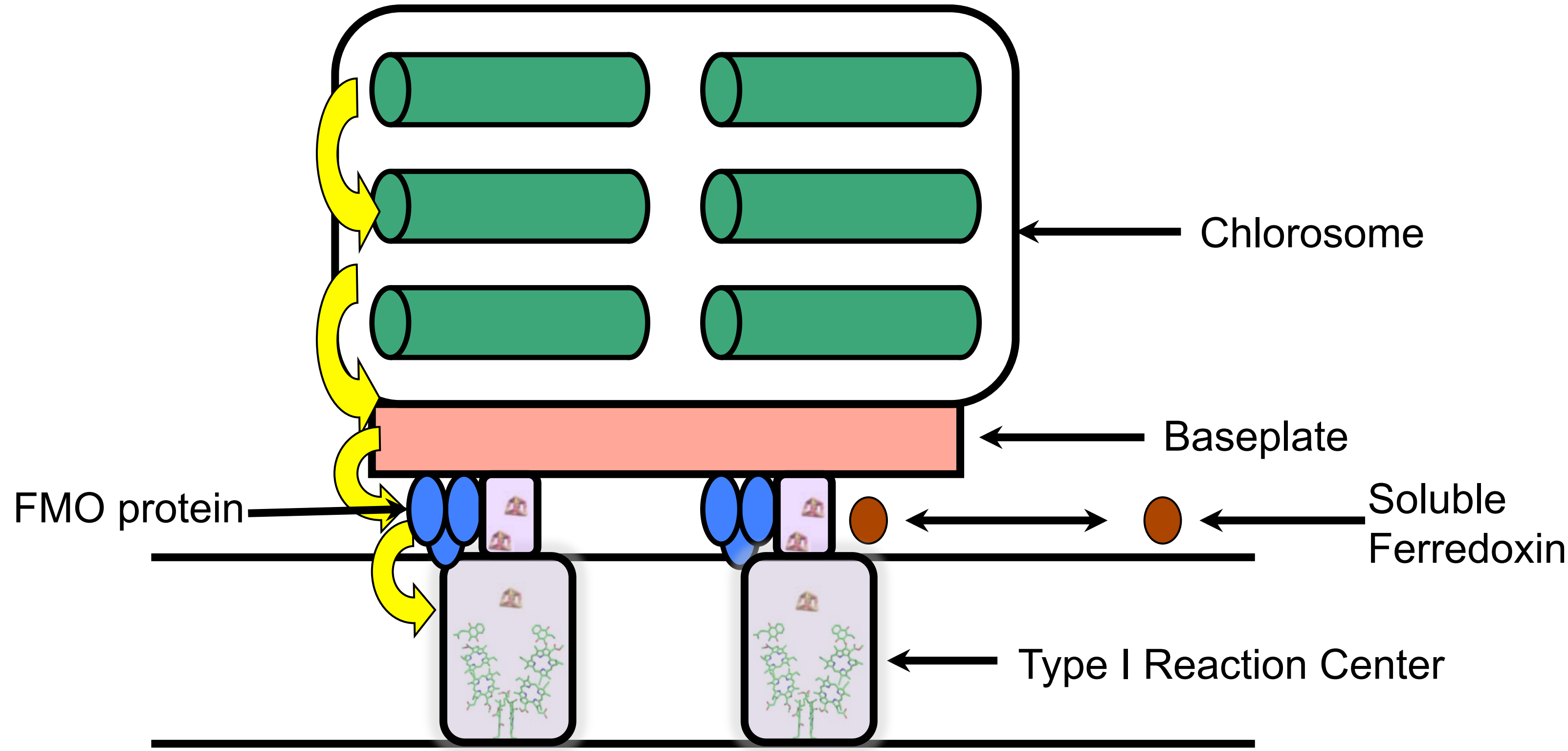
The Orientaton of the 8th BChl *a*





- The 8th BChl *a* is positioned to facilitate energy transfer from the chlorosome baseplate to the core pigments in FMO.
- Theoretical work predicts that it is blue shifted.

Antenna Organization in Green Sulfur Bacteria

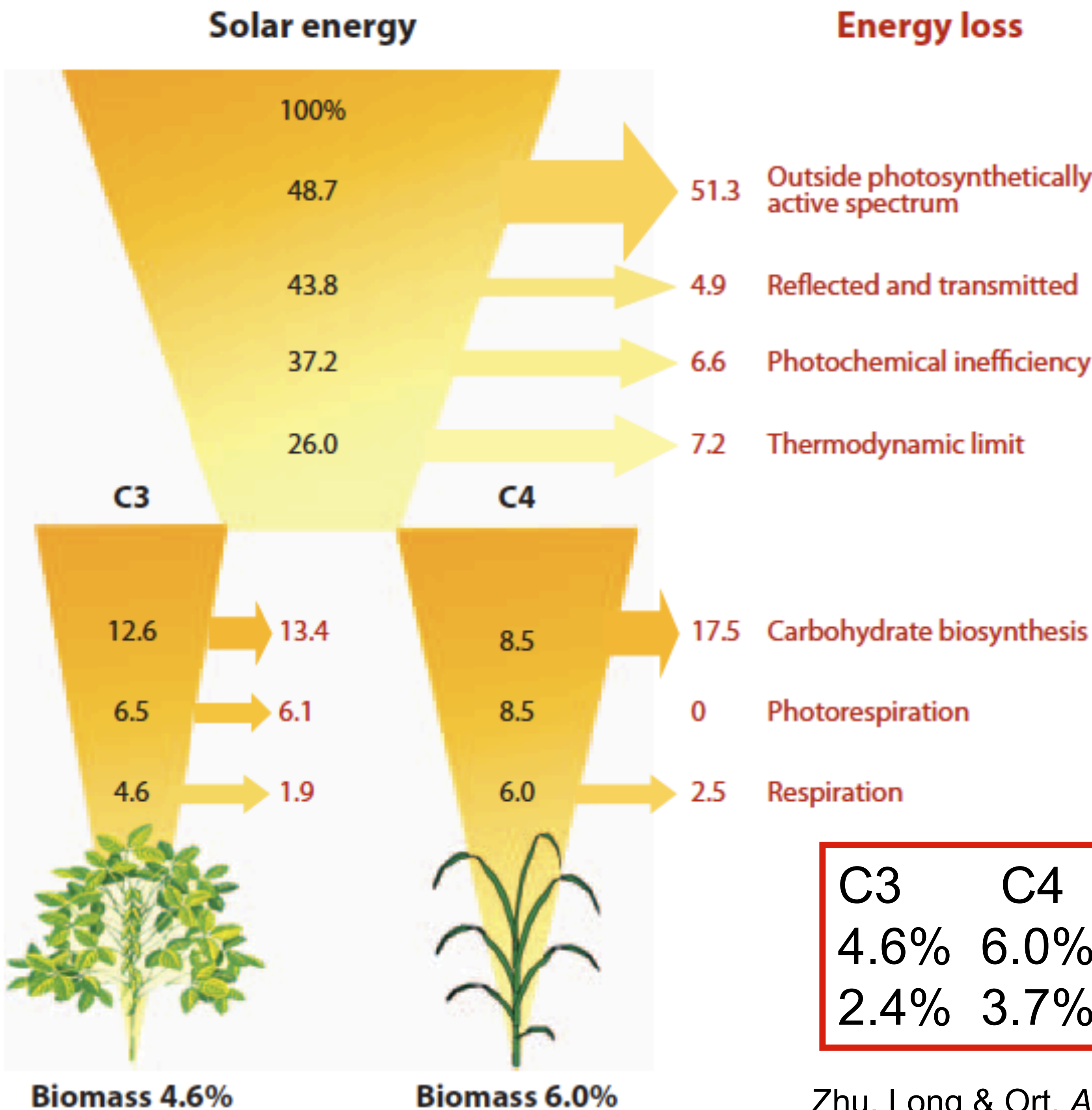


The FMO protein acts as a "conductive wire" or spacer that simultaneously gives soluble ferredoxin access to the FeS centers of the RC and maintains efficient energy transfer from the chlorosome.

Photovoltaics vs Photosynthesis

- Which is more efficient at solar energy conversion?
- What other factors are involved?

Solar conversion efficiency of plants

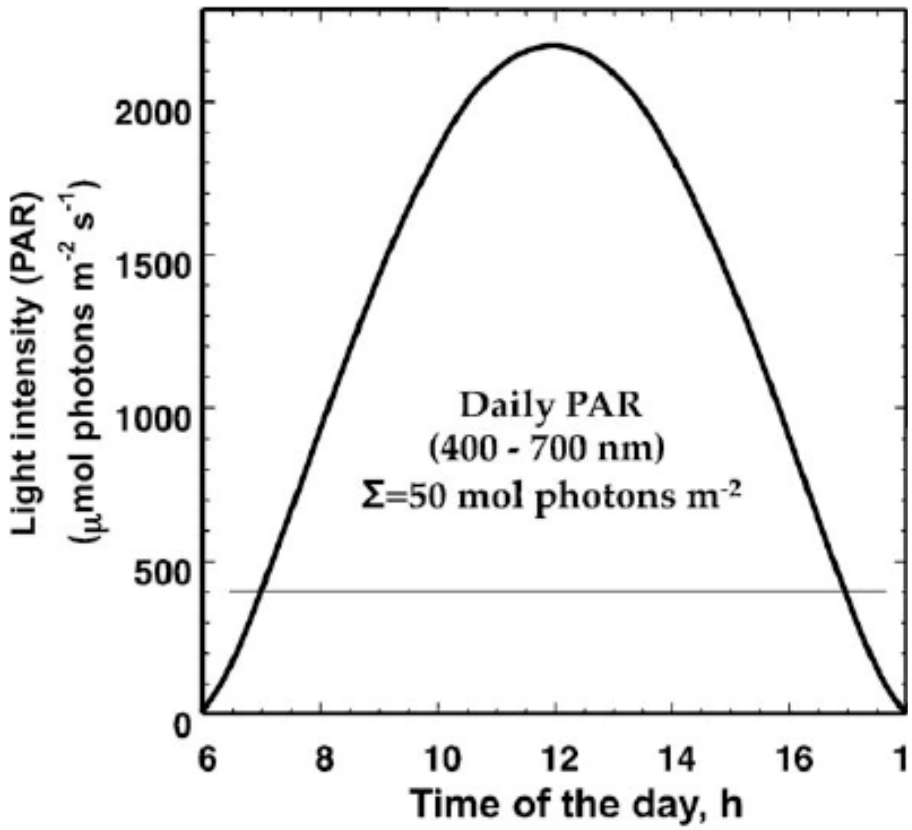


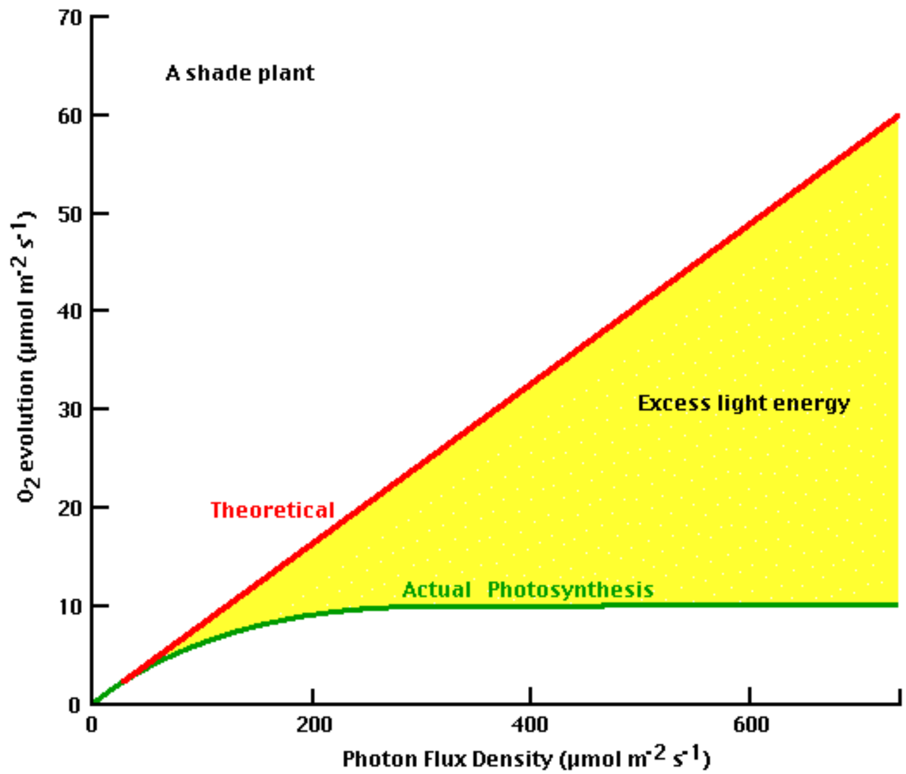
Plants are significantly less efficient at solar energy conversion than are photovoltaics.

C3	C4	
4.6%	6.0%	expected
2.4%	3.7%	max field PS

Zhu, Long & Ort, *Ann Rev Plant Biol* (2010)

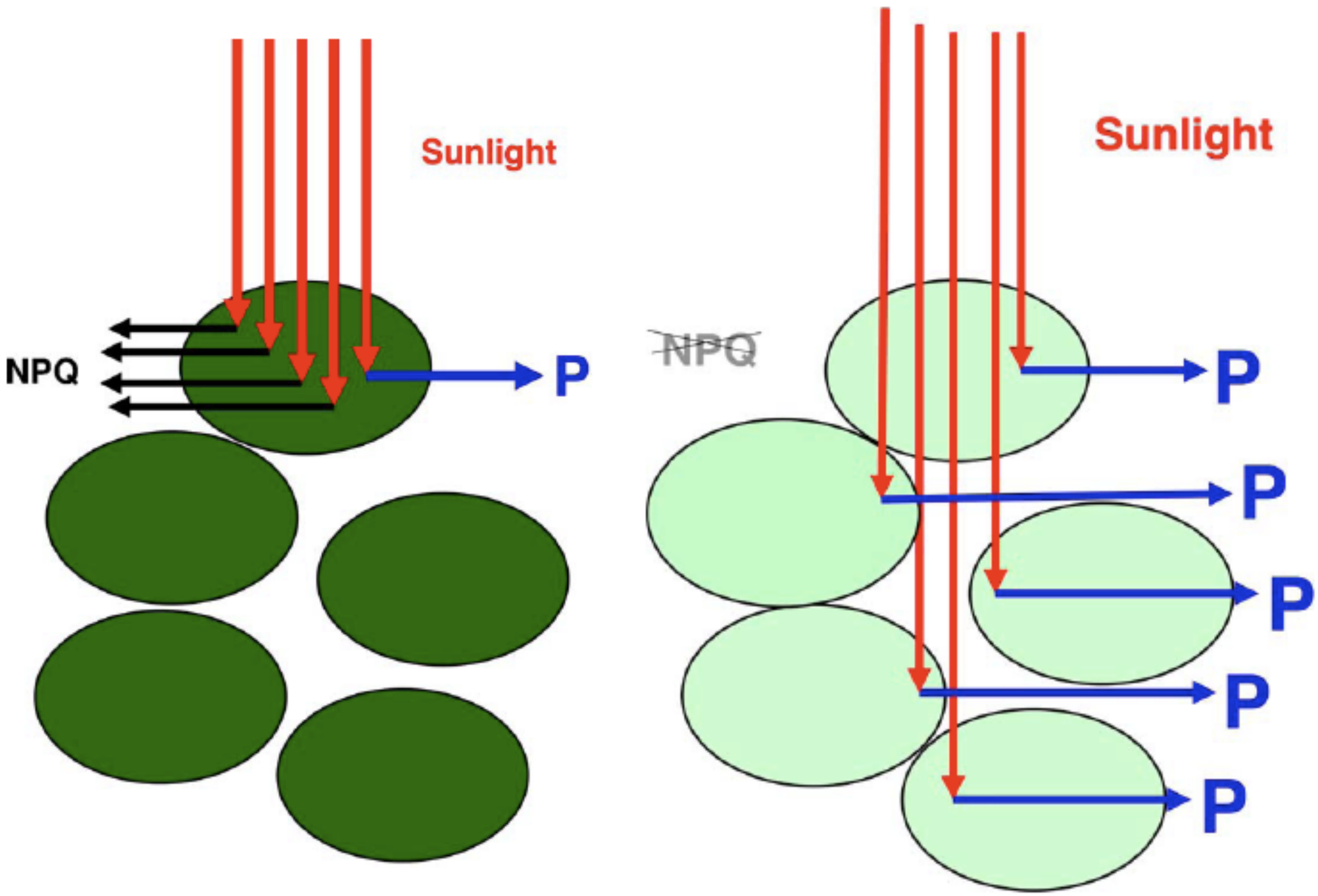
Light saturation curve of PS





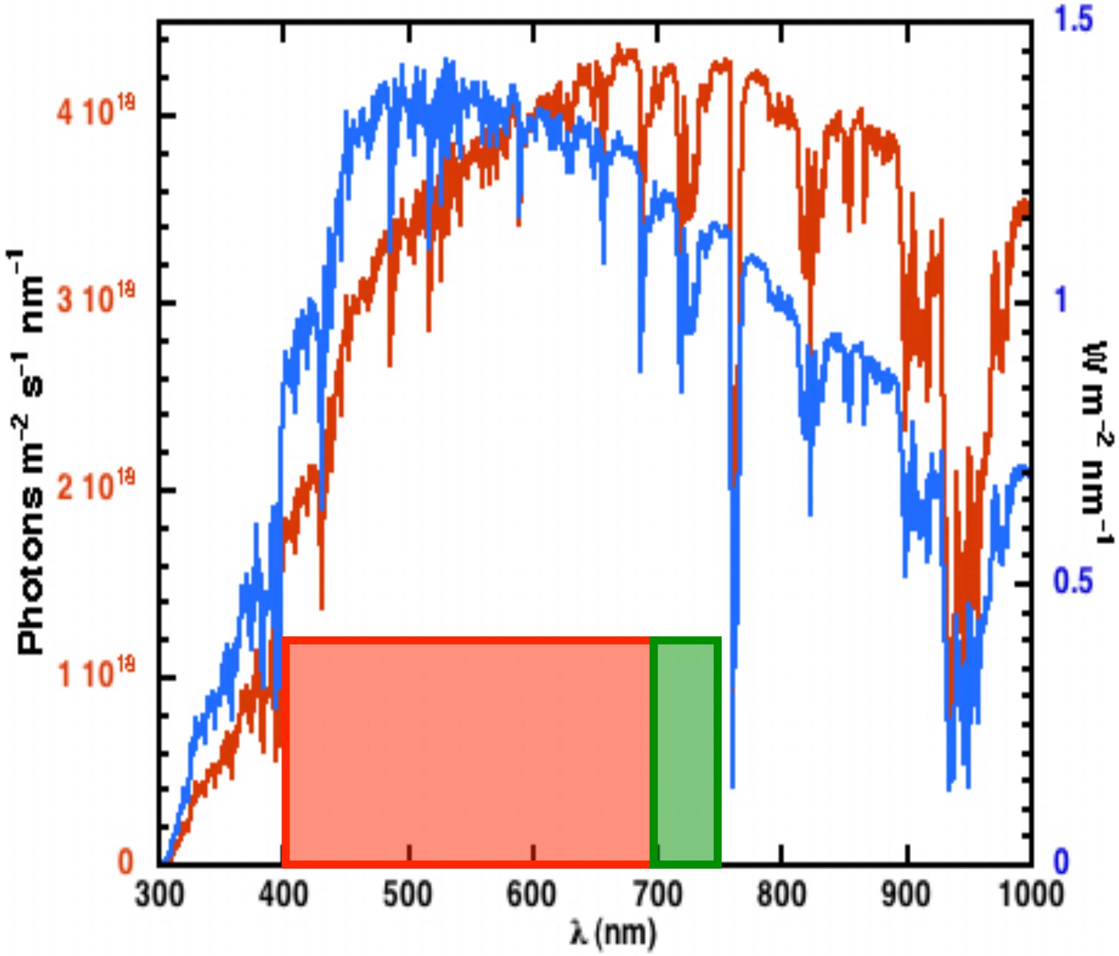
Photosynthesis saturates at light intensities well below maximum solar intensity--antenna too big!

Effect of reduced antenna size



Melis *Plant Sci.* (2009)

Solar output spectrum

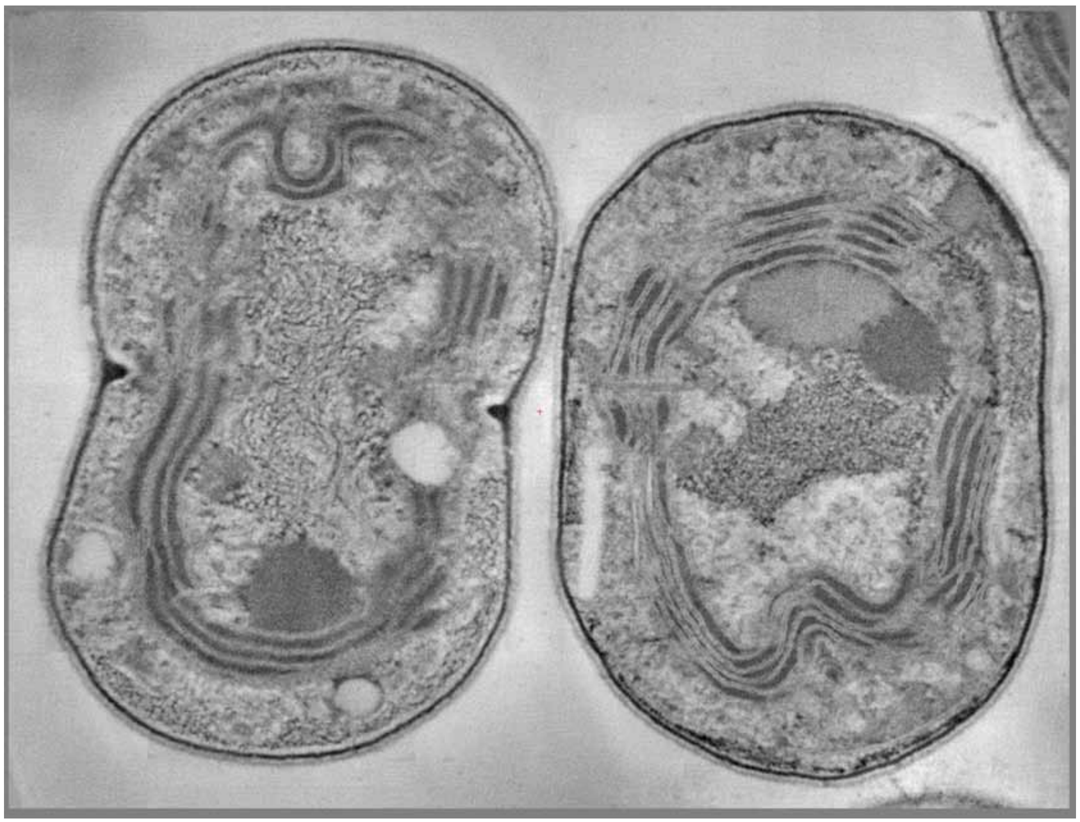


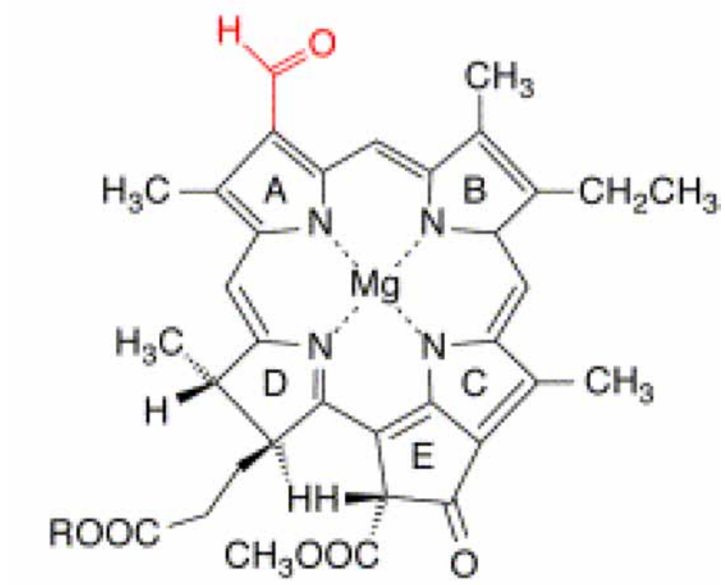
- Oxygen-evolving photosynthetic organisms utilize only the visible region of the solar spectrum.
- Photosynthetically active radiation (PAR) 400-700 nm.
- If PAR extended to 750 nm increases photon flux by **19%**

Photon flux spectrum — Energy spectrum

Acaryochloris marina

Discovered in **1996**, isolated from *didemnid ascidian*, in the Western Pacific Ocean

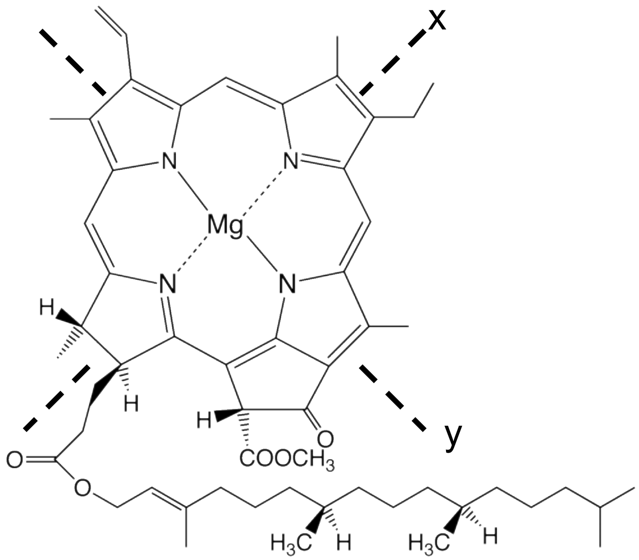




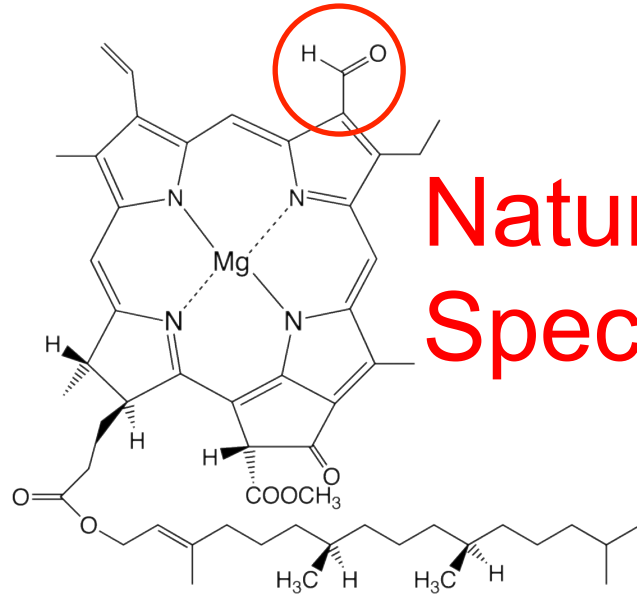
Contains chl *d* as principal pigment

Miyashita et al. *Nature*, 2006

Natural Pigment Spectral Shifts

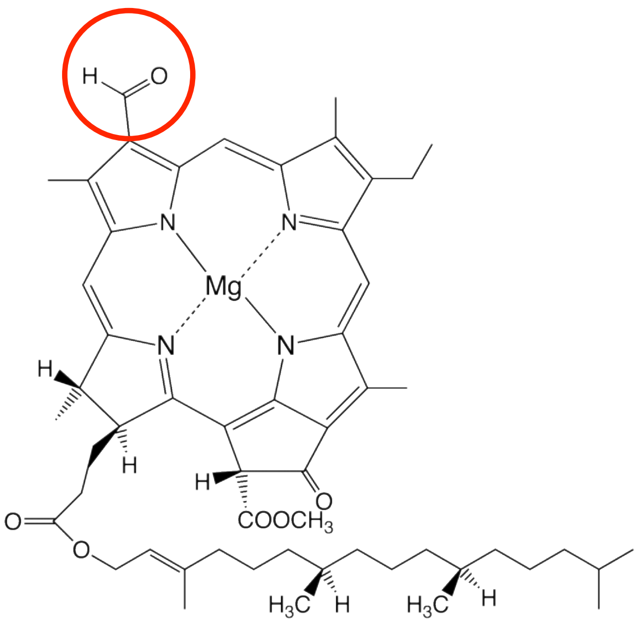


Chlorophyll *a*

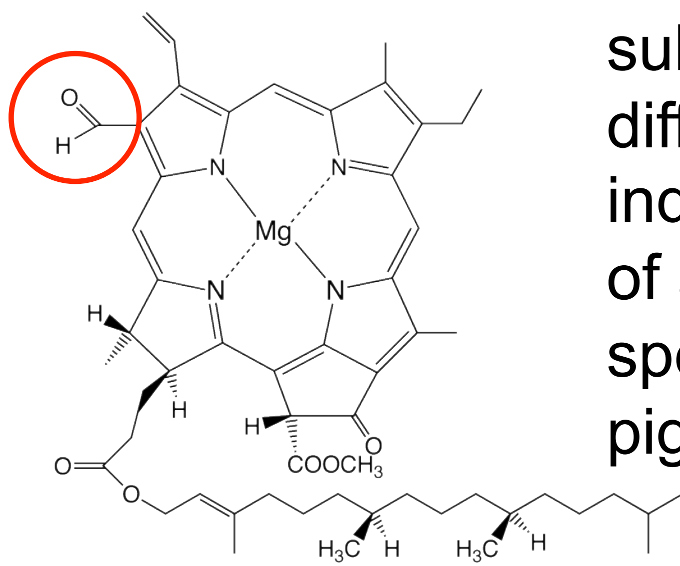


Chlorophyll *b*

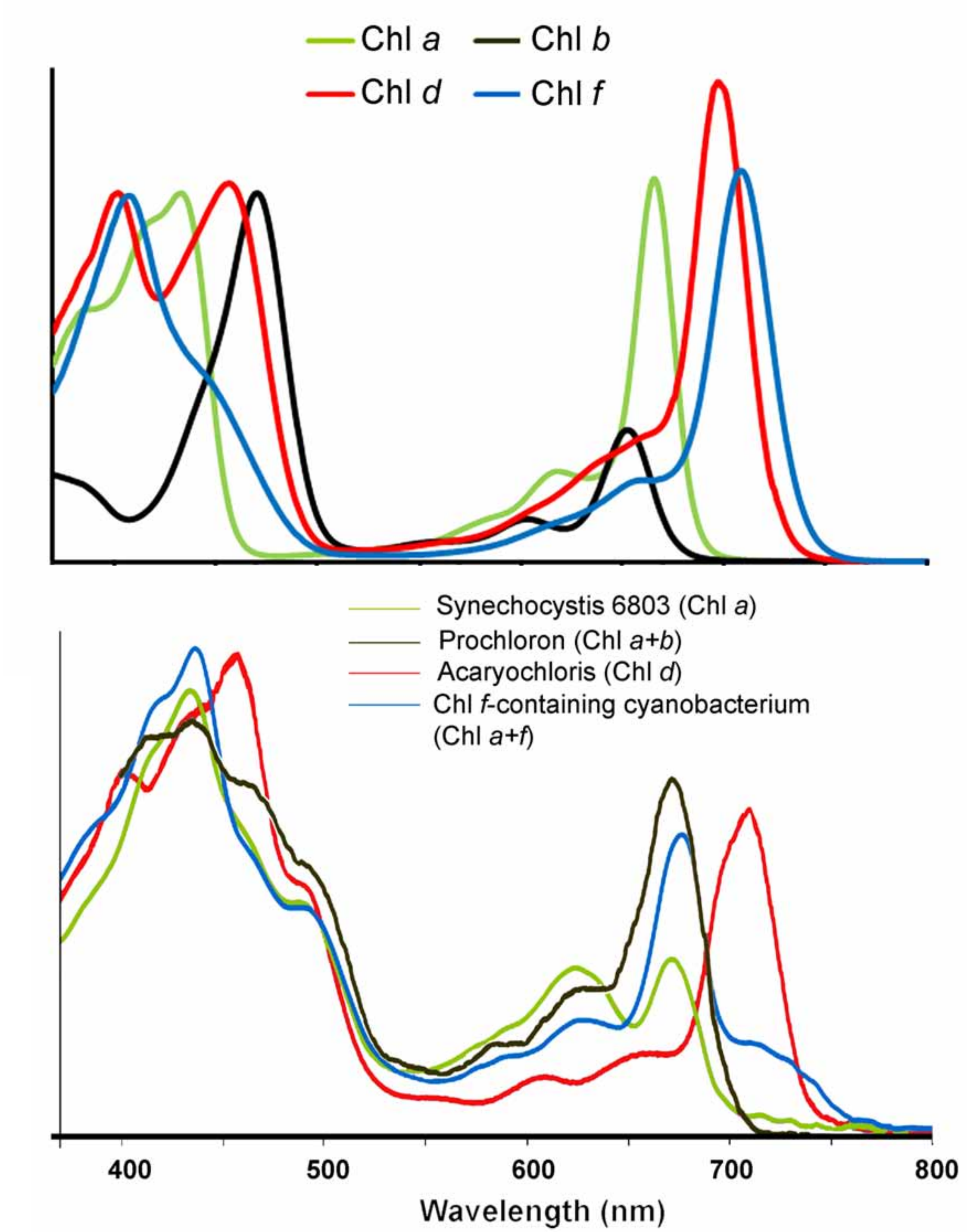
Addition of formyl substituent at different positions induces large shifts of absorption spectra in natural pigments.



Chlorophyll *d*



Chlorophyll *f*



Spectral Extension

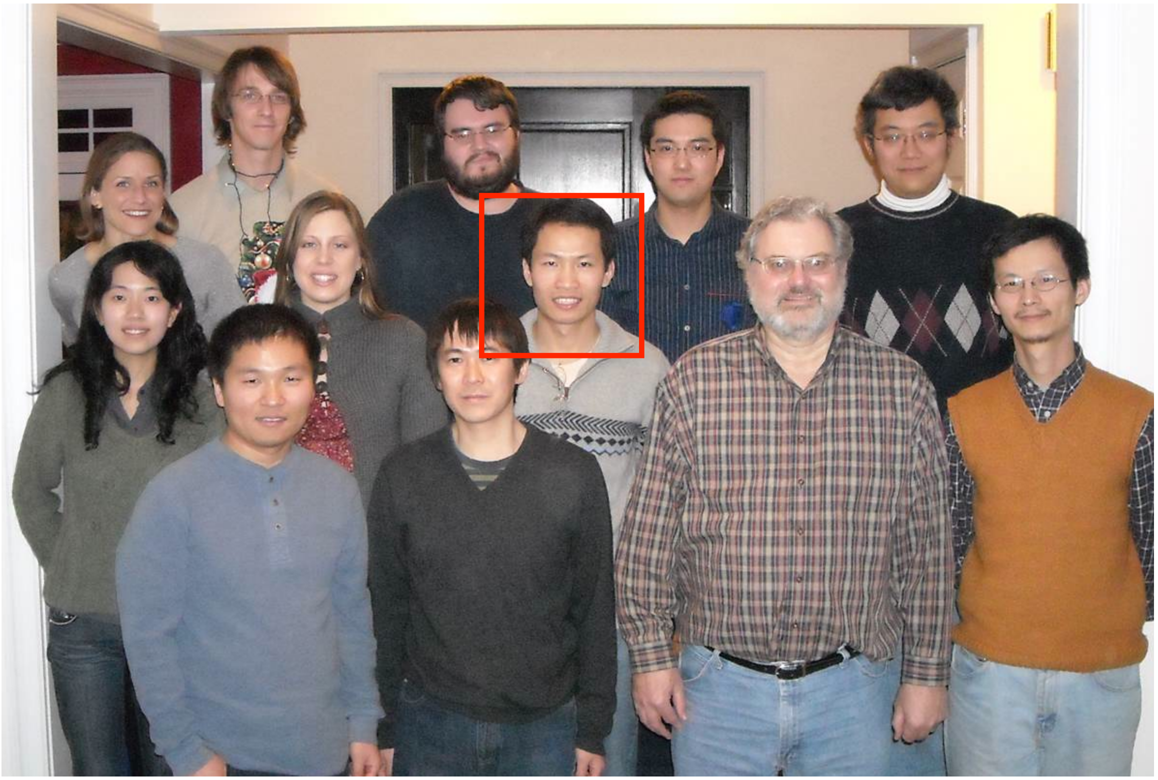
Chlorophylls *d* and *f* absorb well to the red of other pigments that are active in oxygenic photosynthesis, yet still are functional.

Chen and Blankenship, *Trends in Plant Science* (2011)

Other factors to consider

- Costs of
  - Land and capital
  - Water use
  - Operations and maintenance
  - Waste disposal
  - Transmission
  - Transportation and storage
- Risks from manufacturing
- Interactions with the food supply (NYT April 7,2011)
- Climate change issues

Wash. U. Research Group-2011



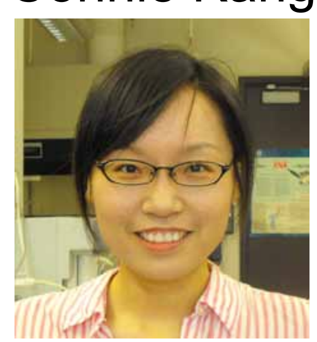
Front Row Xianglu Li, Jiro Harada, Bob Blankenship, Yueyong Xin,
Second Row Xinliu Gao, Jeanne Sheffield, Jianzhong Wen
Third Row Barb Honchak, Aaron Collins, Patrick Bell, Hai Yue, Joseph Tang
UG - Yamini Krishnamurthy, EJ Cho,

Darek Niedzwiedzki

David Bina

Mindy Prado

Connie Kang



Jeremy King

Jing Jiang

Acknowledgements and Support

Dr. Jianzhong Wen

Collaborators

Michael Gross, Weidong Cui
Hao Zhang, Richard Huang
Washington Univ. in St. Louis

Dale Tronrud, Leslie Gay
Univ. of Oregon

Jim Allen, Chadwick Larson
Arizona State Univ.

Don Bryant, Yusuke Tsukatani
Penn. State Univ.