Evolution of Photosynthesis on Earth

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

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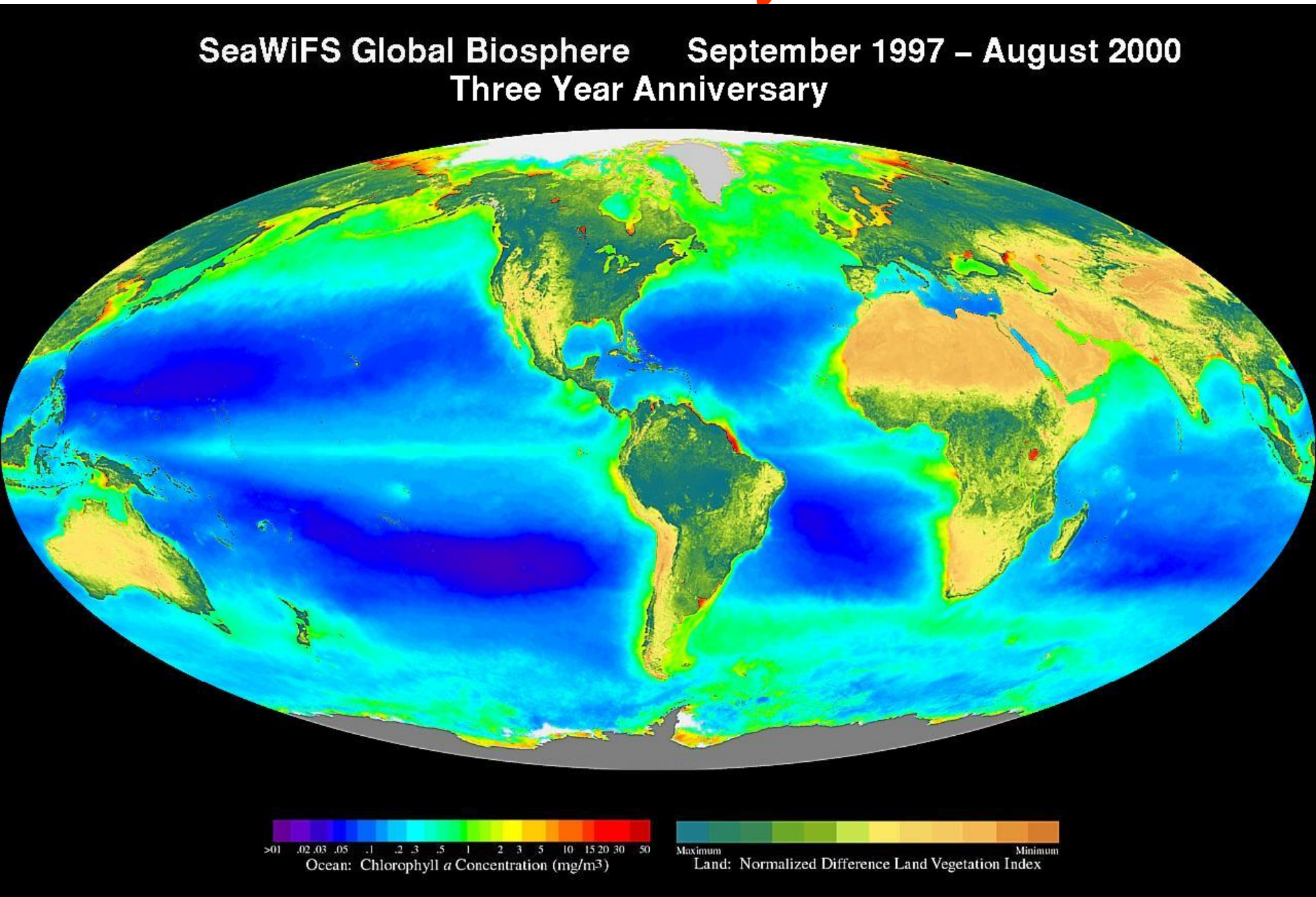
Caltech

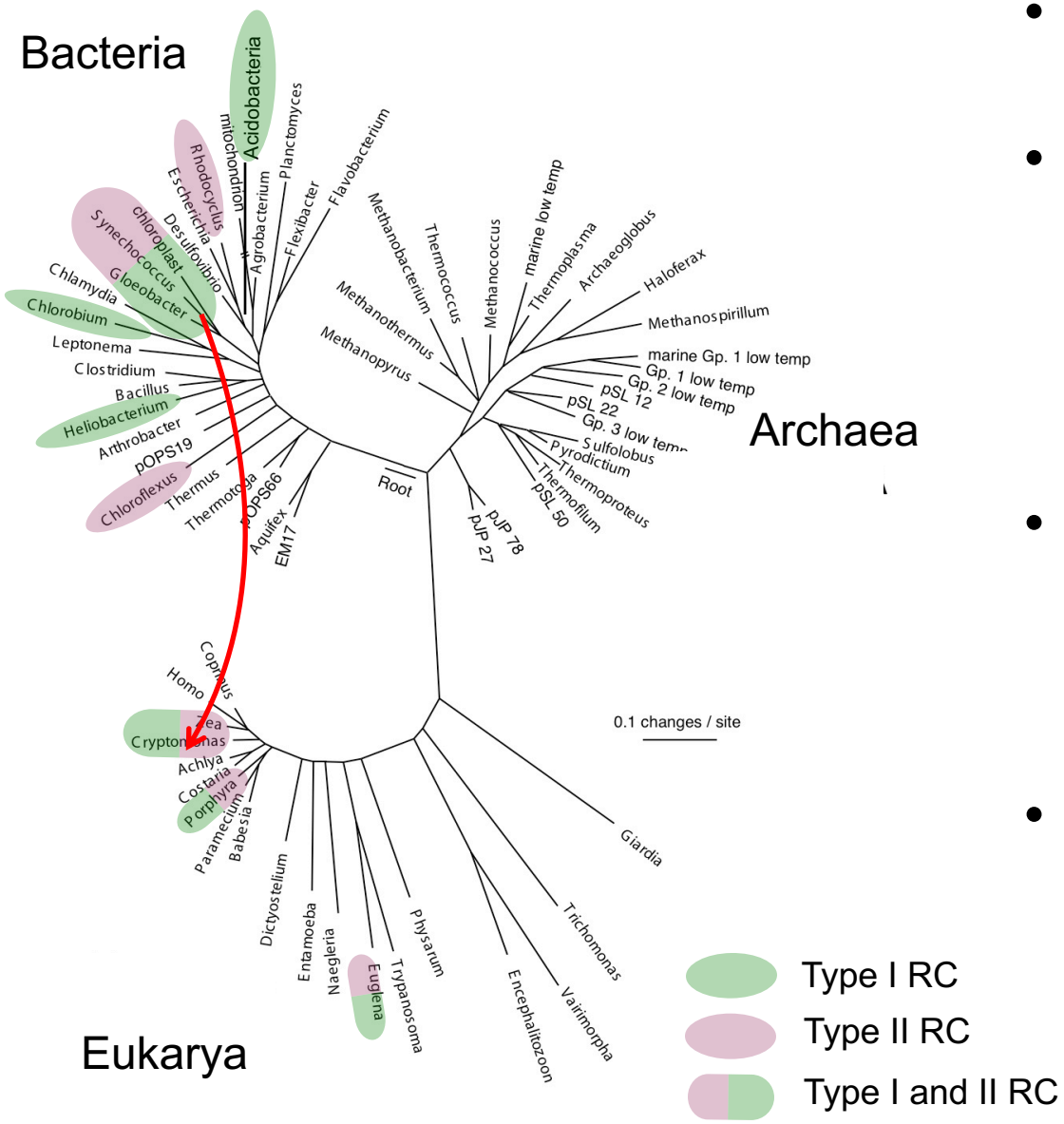
Photosynthesis- The Conversion of Light Energy into Chemical Energy

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

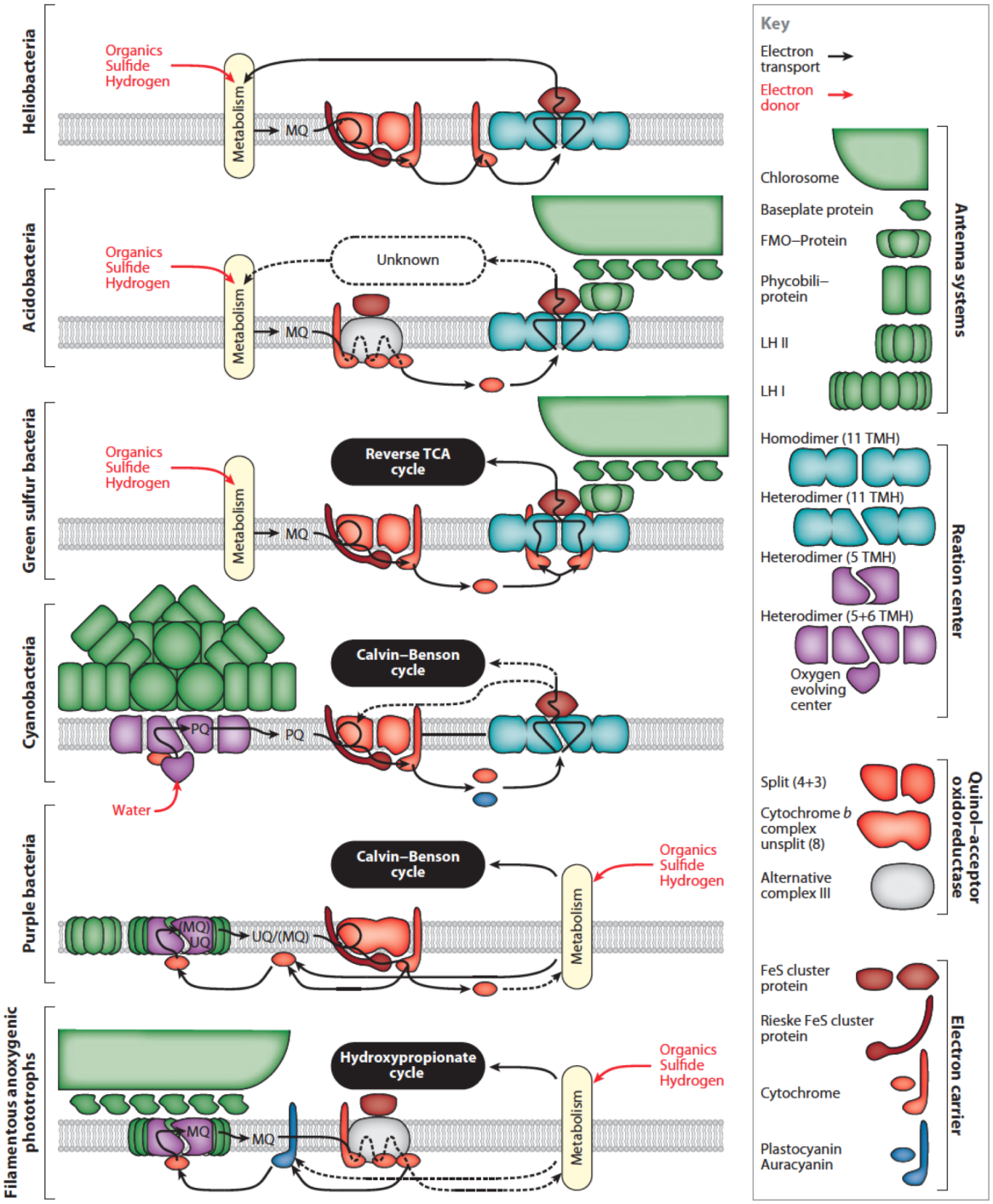
Global Photosynthesis



Types of Phototrophic Organisms



- Photosynthesis is light-driven redox chemistry.
- 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.

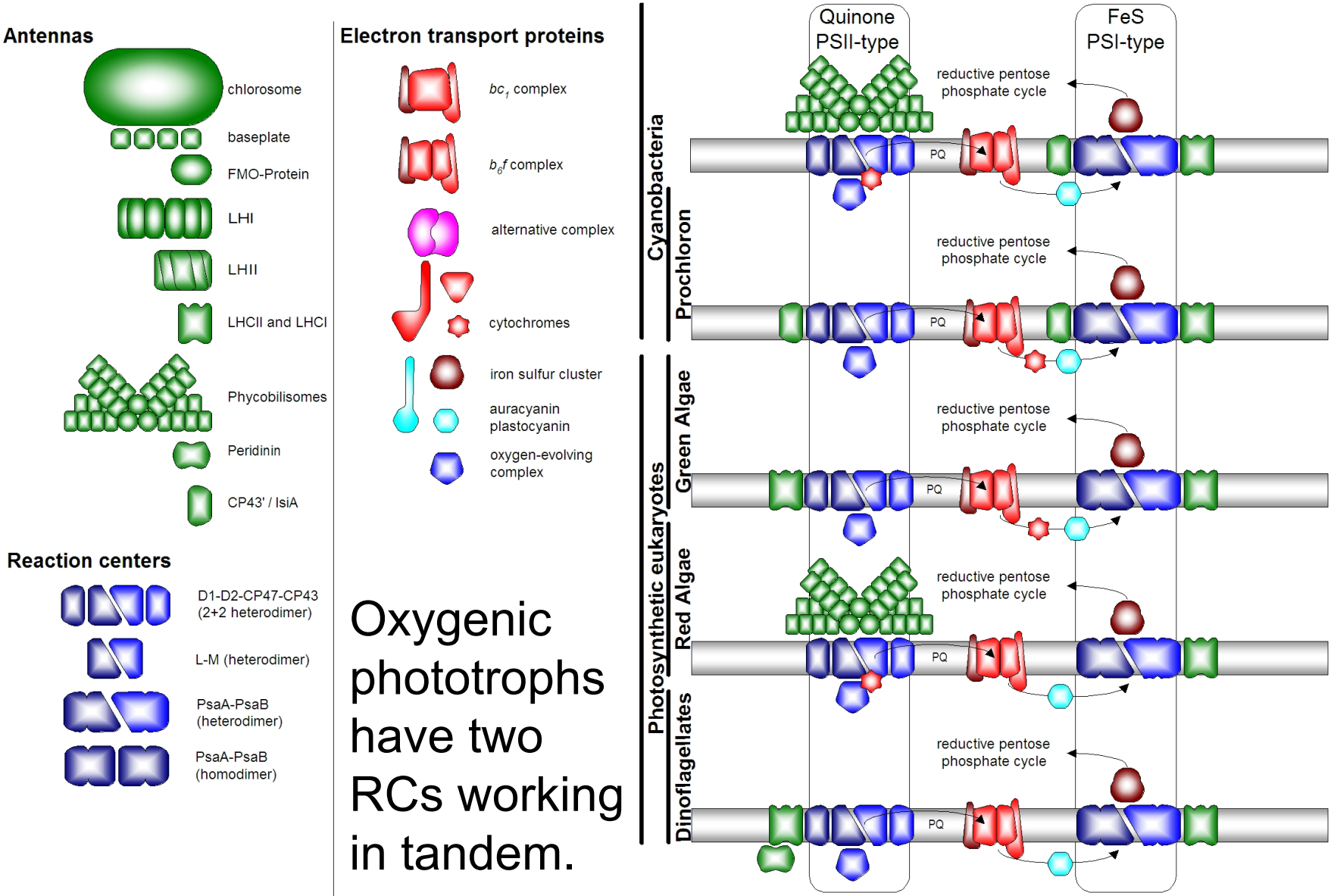


Photosynthetic Prokaryotes

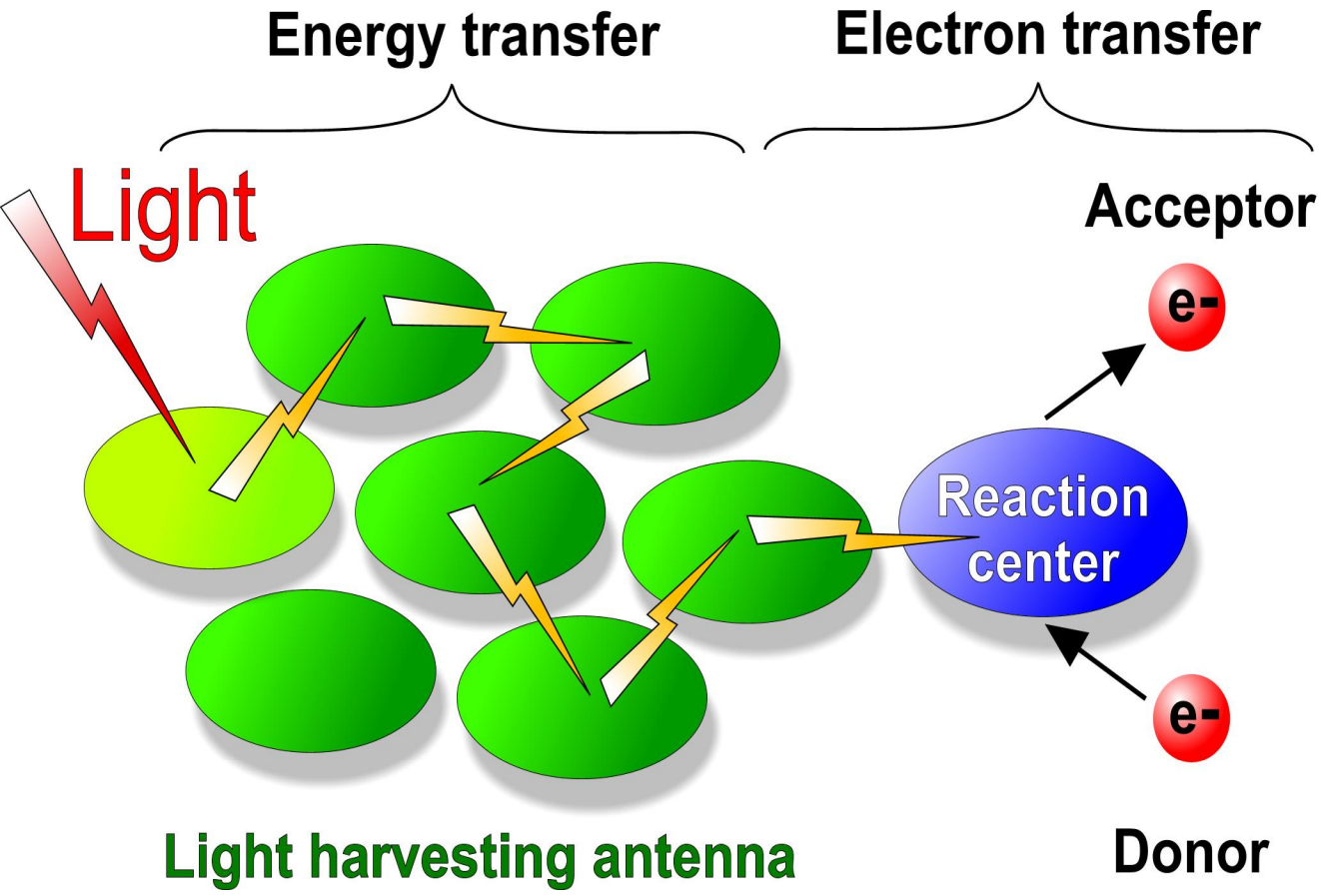
- There are ~~six~~ seven known bacterial phyla with chlorophyll-based photosynthetic members.
- They have varied modules of antennas, reaction centers, cofactor biosynthesis, and carbon fixation pathways.
- Each module has a unique evolutionary history.

Homann-Marriott and Blankenship, *ARPB* (2011)

Oxygenic Photosynthetic Organisms

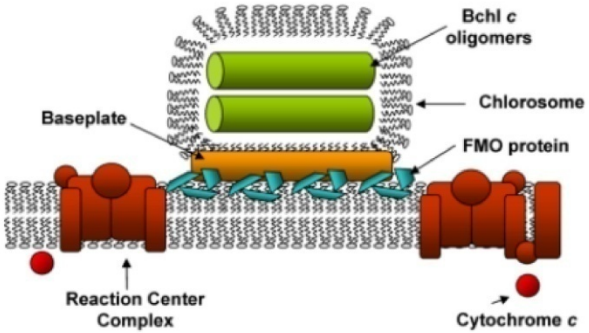


Photosynthetic Energy Storage

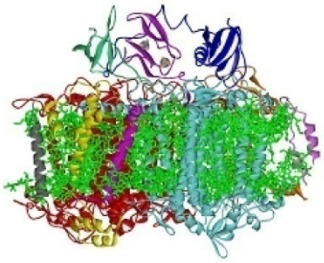


All PS organisms contain a light-gathering antenna system and an electron-transferring reaction center.

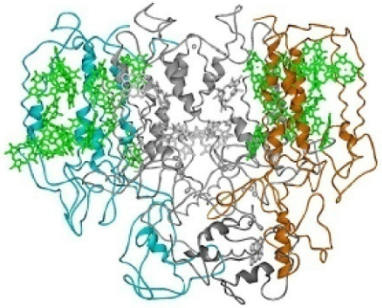
Photosynthetic Antenna Complexes



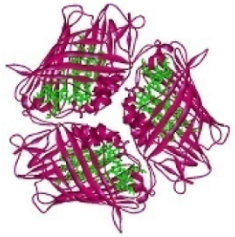
Chlorosomes



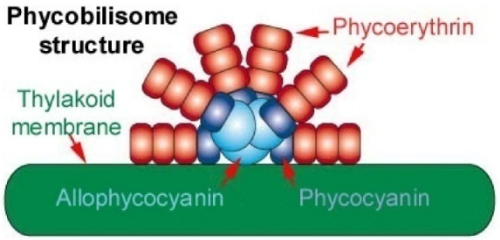
Photosystem I Core

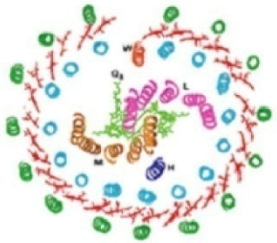


CP43 and CP47 from PSII

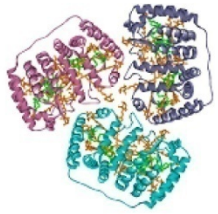


Fenna-Matthew-Olson Protein

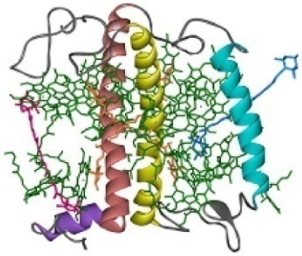




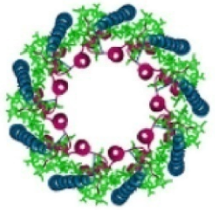
LH1 Core



Peridinin-Chl Complex



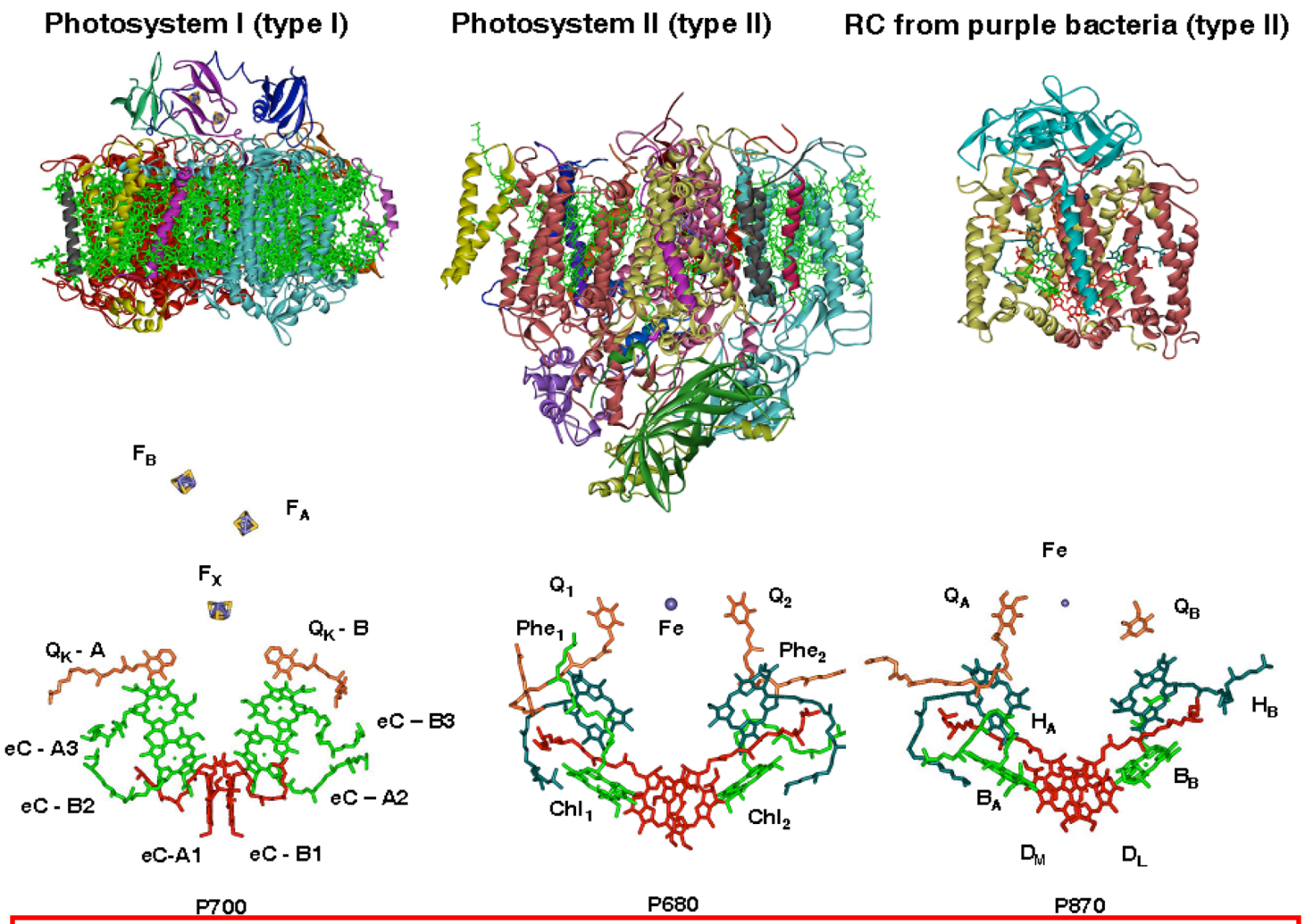
LHCII and LHCI



LH2

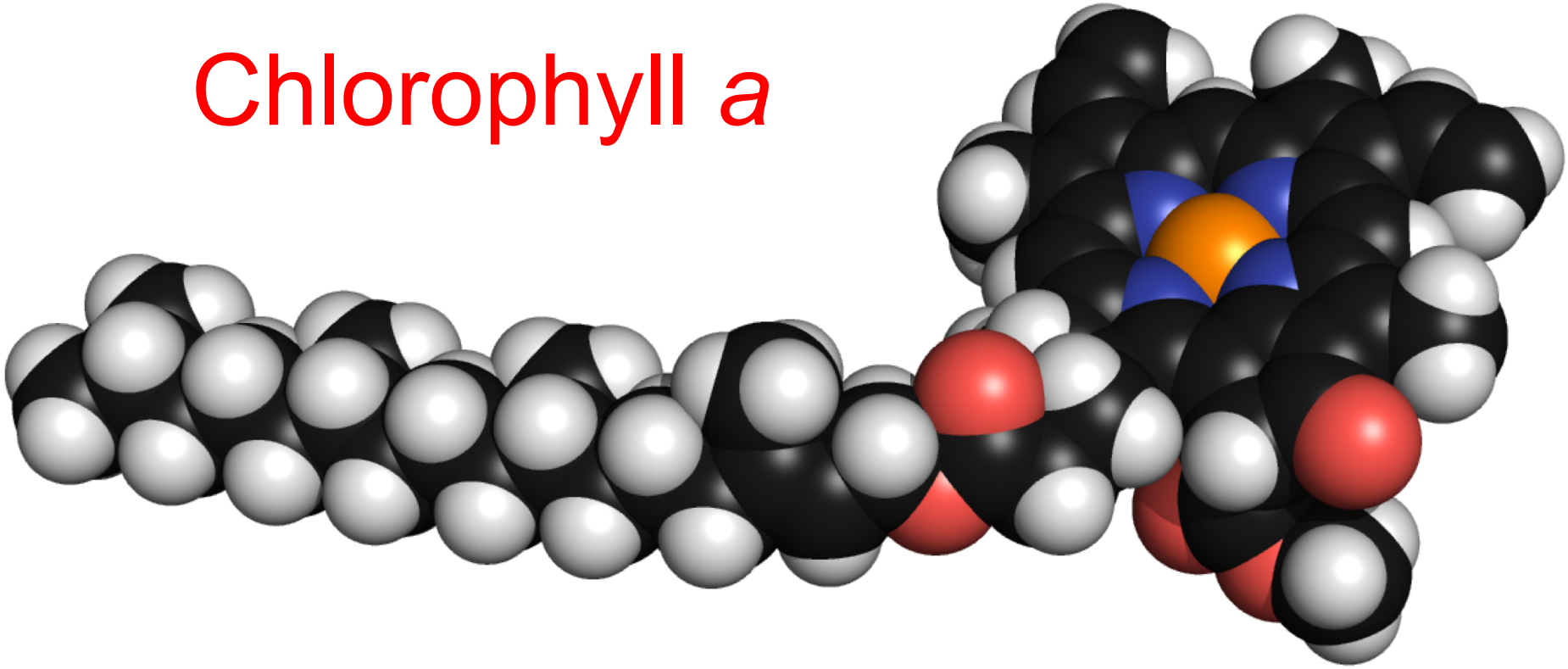
Extreme diversity of antenna systems strongly suggests multiple independent evolutionary origins - Adaptation to different photic environments.

Photosynthetic Reaction Centers



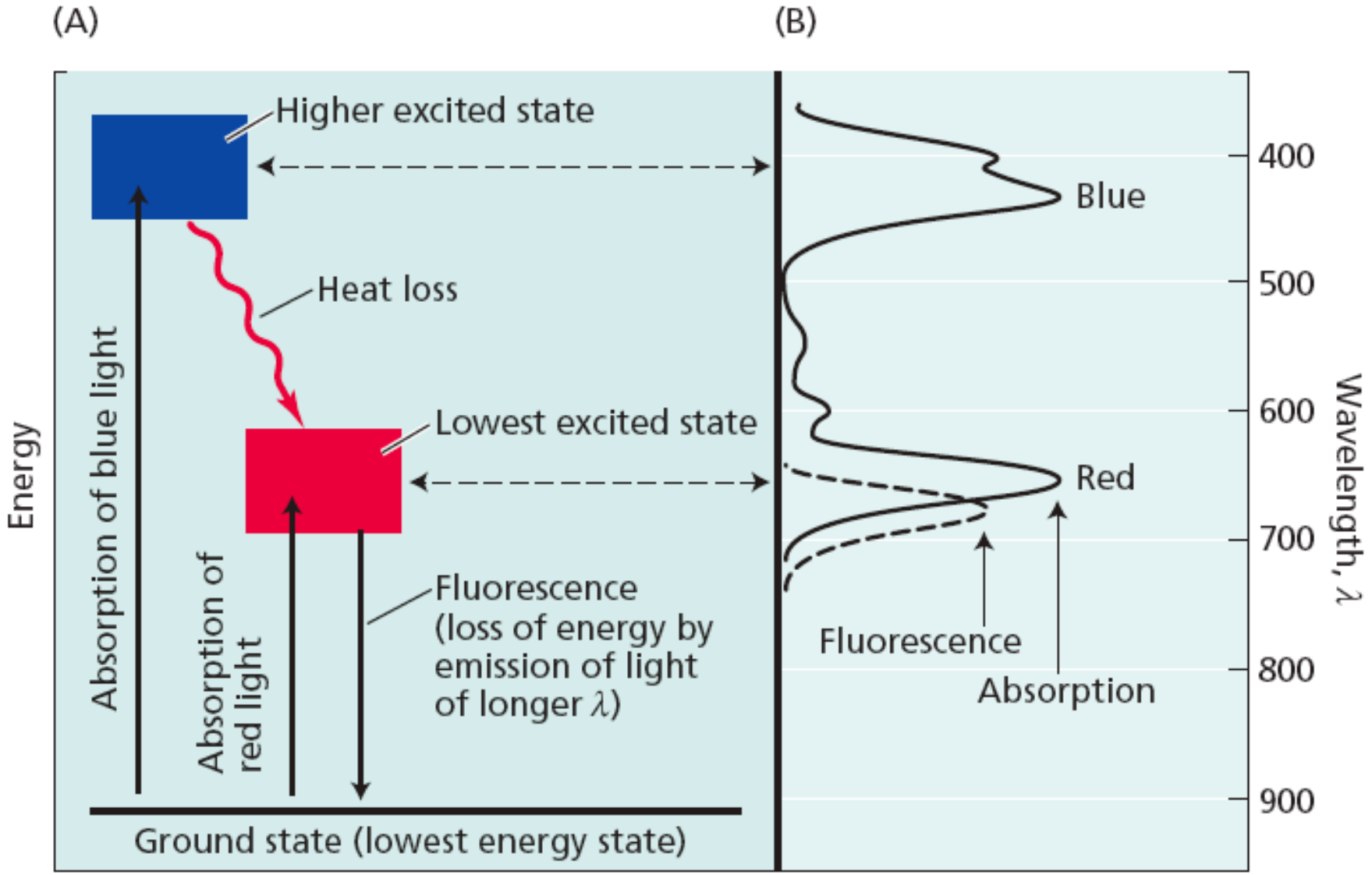
Structural conservation of RCs suggests a single evolutionary origin.

Chlorophyll *a*



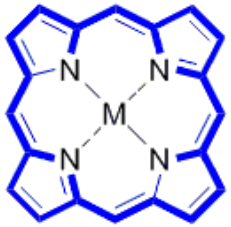
- Chlorophyll is a highly colored molecule that is central to photosynthesis.
- Light must first be absorbed by chlorophyll or other pigments before it can be stored as chemical energy.
- Chlorophyll is usually associated with specific proteins.

Chlorophyll Photon Absorption

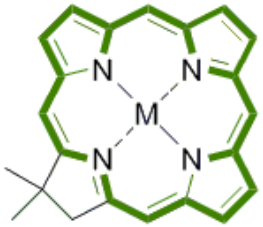


Electron transfer takes place from the lowest excited state.

Pigment Conjugation and Electronic Properties

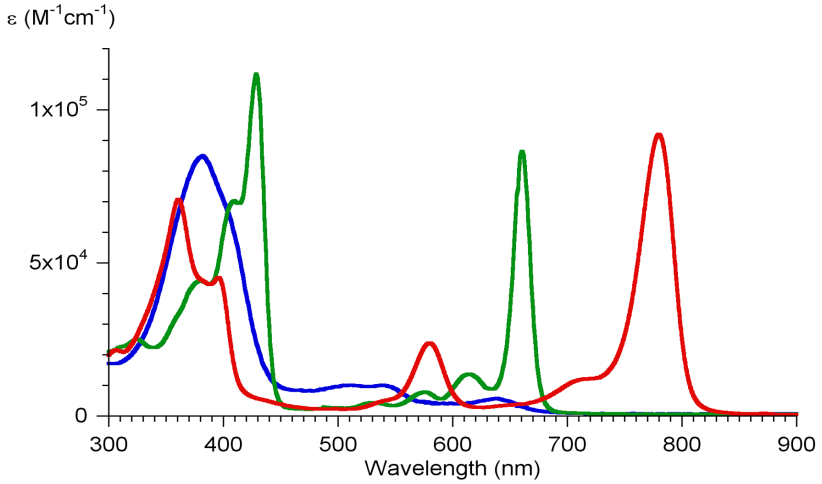


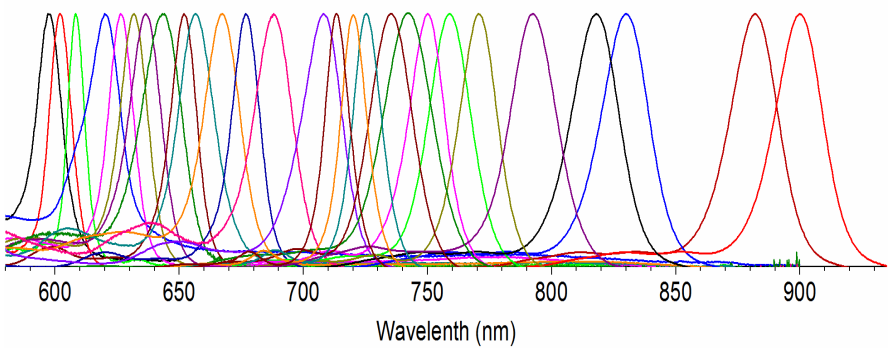
Porphyrin



Chlorin

Bacteriochlorin

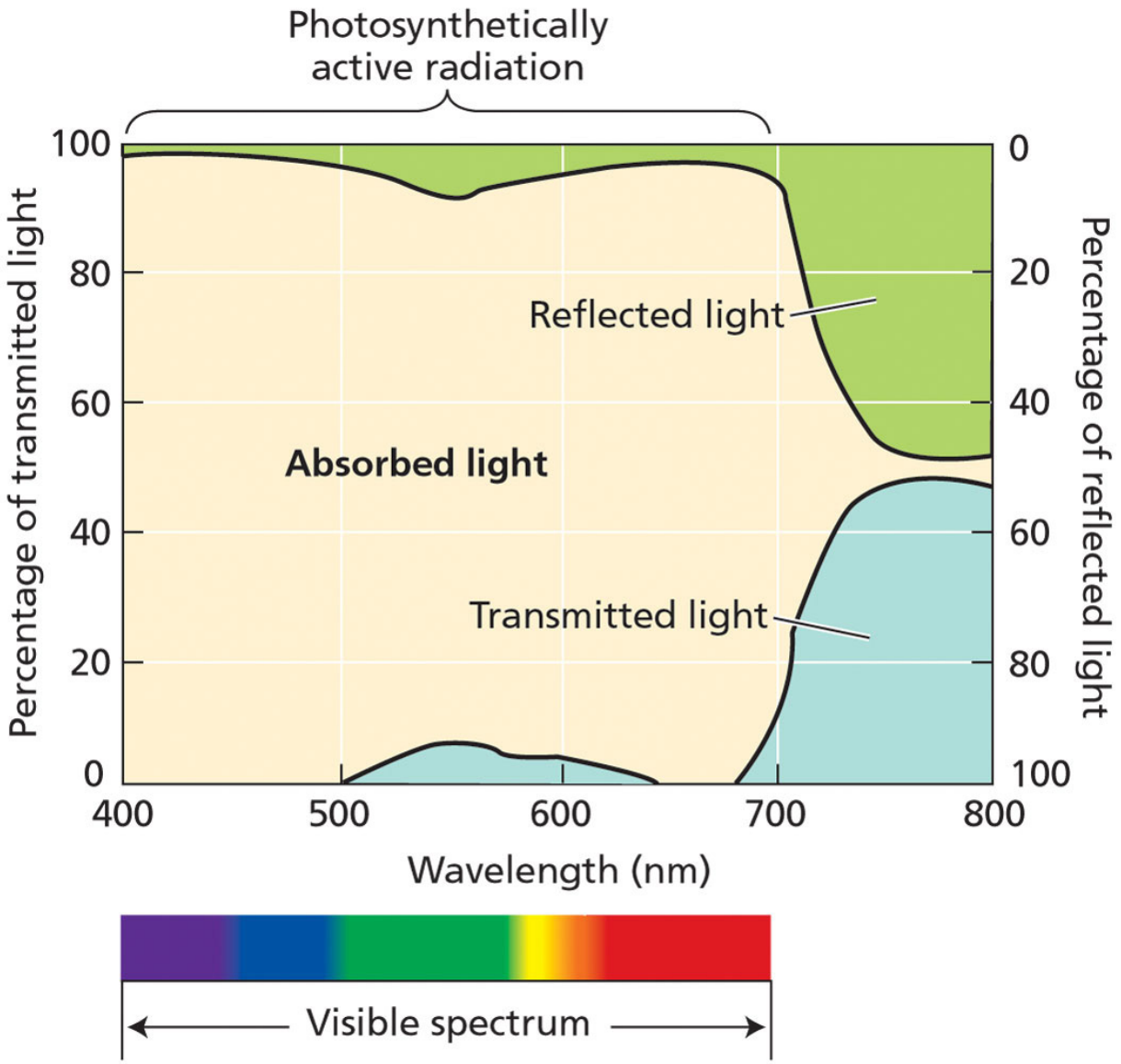




- Pyrrole-ring reduction: Decreased size of π-e^- system (porphyrin $\rightarrow$ chlorin $\rightarrow$ Bchlorin) gives bathochromic Q_y shift.
- Substituent type and position: 3-formyl etc. add conjugation length and give bathochromic Q_y shift; 7-formyl (chlorin) and 7-oxo (bacteriochorin) do the opposite.

Slide courtesy of Dewey Holten and Jon Lindsey

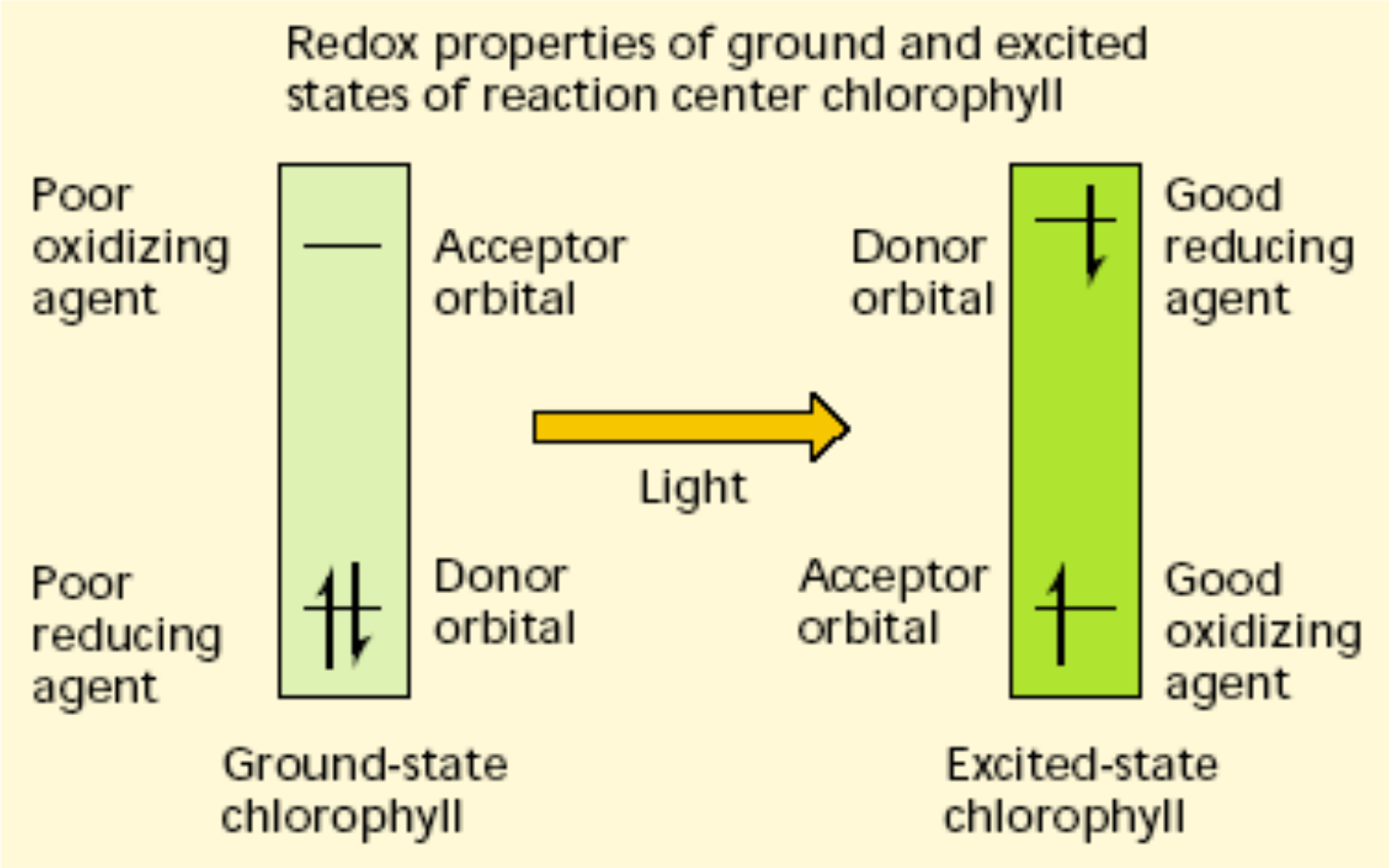
Plants are not green, they are **Black**!



PLANT PHYSIOLOGY, Third Edition, Figure 9.3 © 2002 Sinauer Associates, Inc.

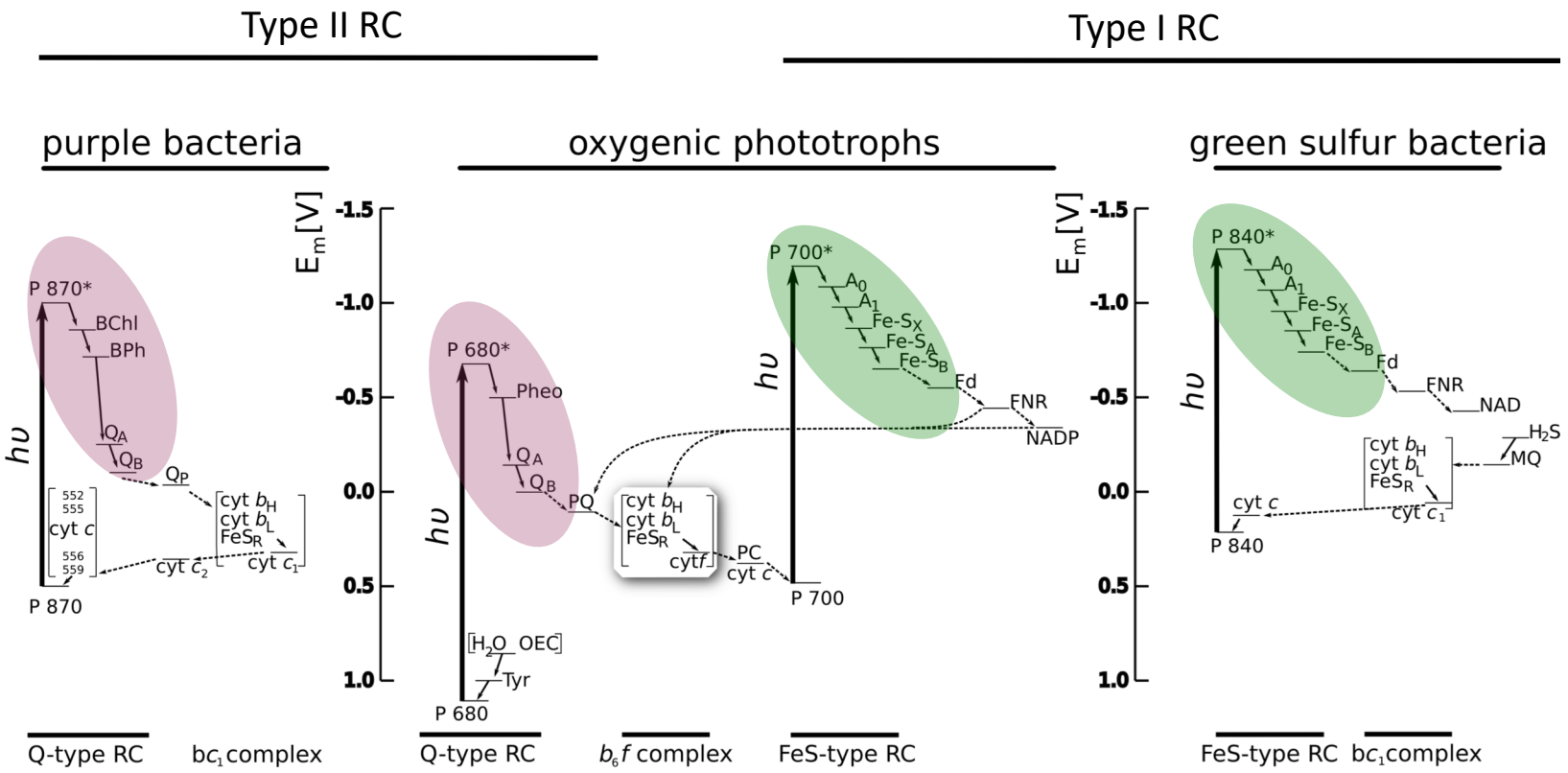
- Plants absorb almost all of the visible light.
- They transmit and reflect light at longer wavelengths—Red Edge.
- The red edge will shift if the organism contains a different type of pigment.

Excited state redox processes



- Excited states can be both strong oxidizing and strong reducing agents--very chemically reactive.
- The primary energy storing step in chlorophyll-based photosynthesis is the excited state acting as a reductant.

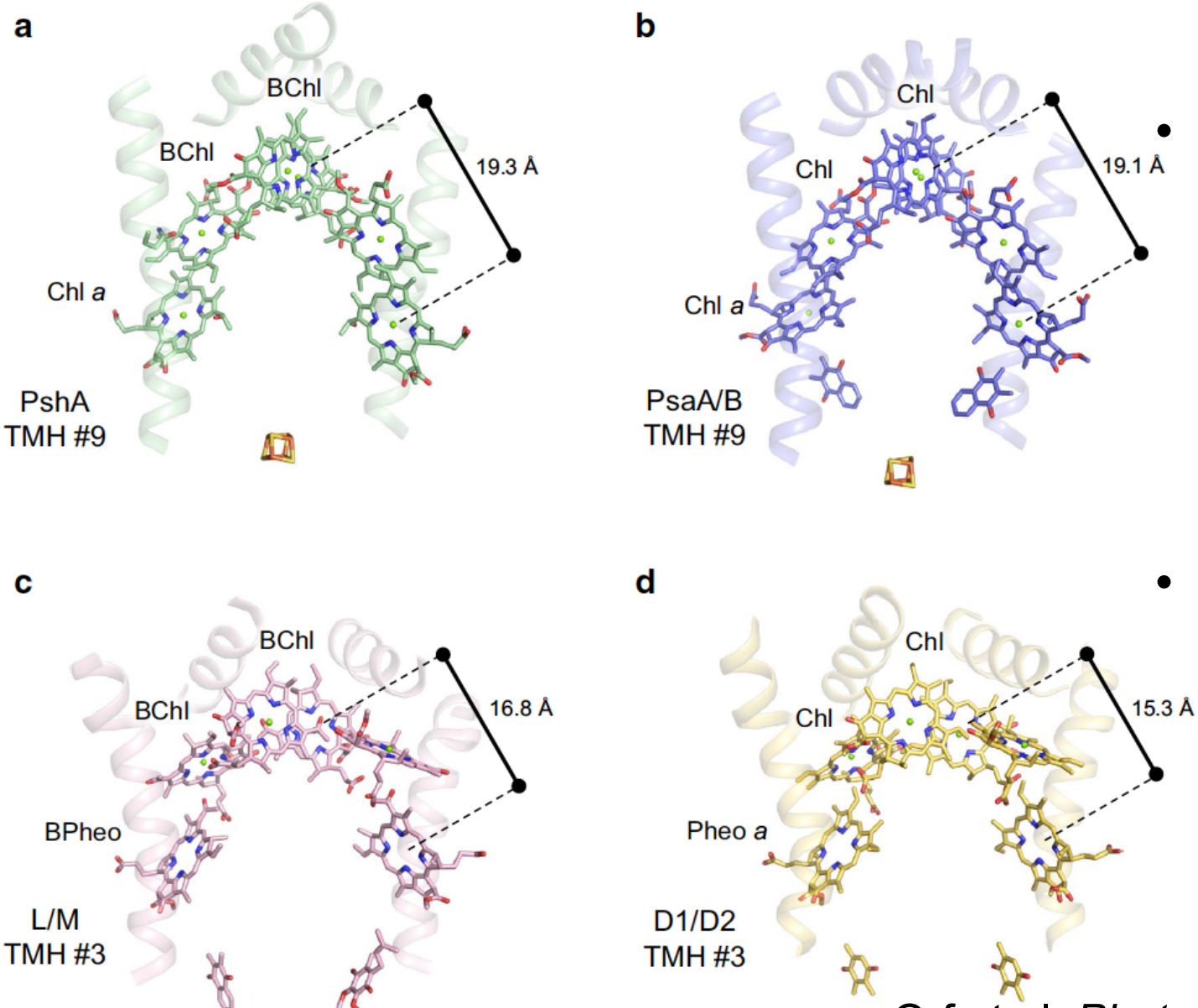
RC energy-kinetic diagrams



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

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

Cofactor arrangement in RCs

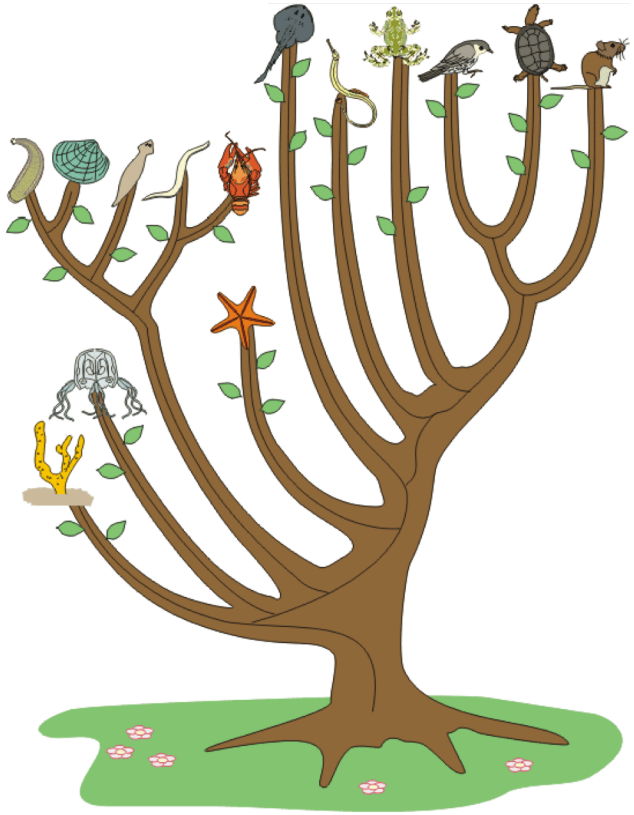


- Cofactors in all types of RCs have the same basic structural arrangement.
- This strongly suggests that they have a common evolutionary history.

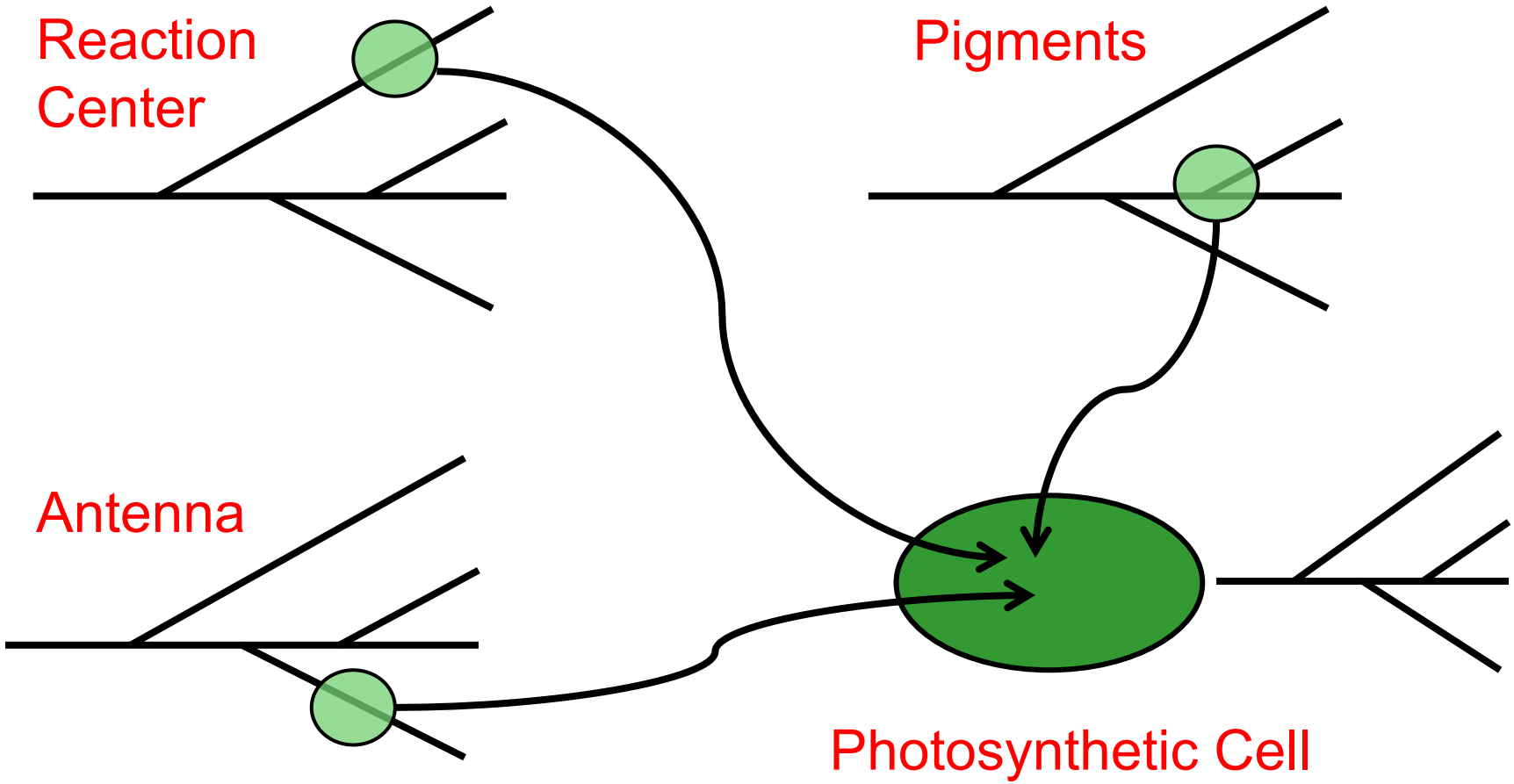
Orf et al. *Photosynth. Res.* (2018)

Origin and Early Evolution of PS

- To understand the origin and early evolution of photosynthesis, must consider mechanisms and evolution of many subsystems and processes:
  - **Reaction centers (including**
  - **O_2 Evol Center)**
  - Pigments (Chls, carotenoids, bilins)
  - Antenna complexes
  - Electron transfer pathways
  - Carbon fixation pathways
  - Photoprotection mechanisms
- Horizontal gene transfer has been widespread.

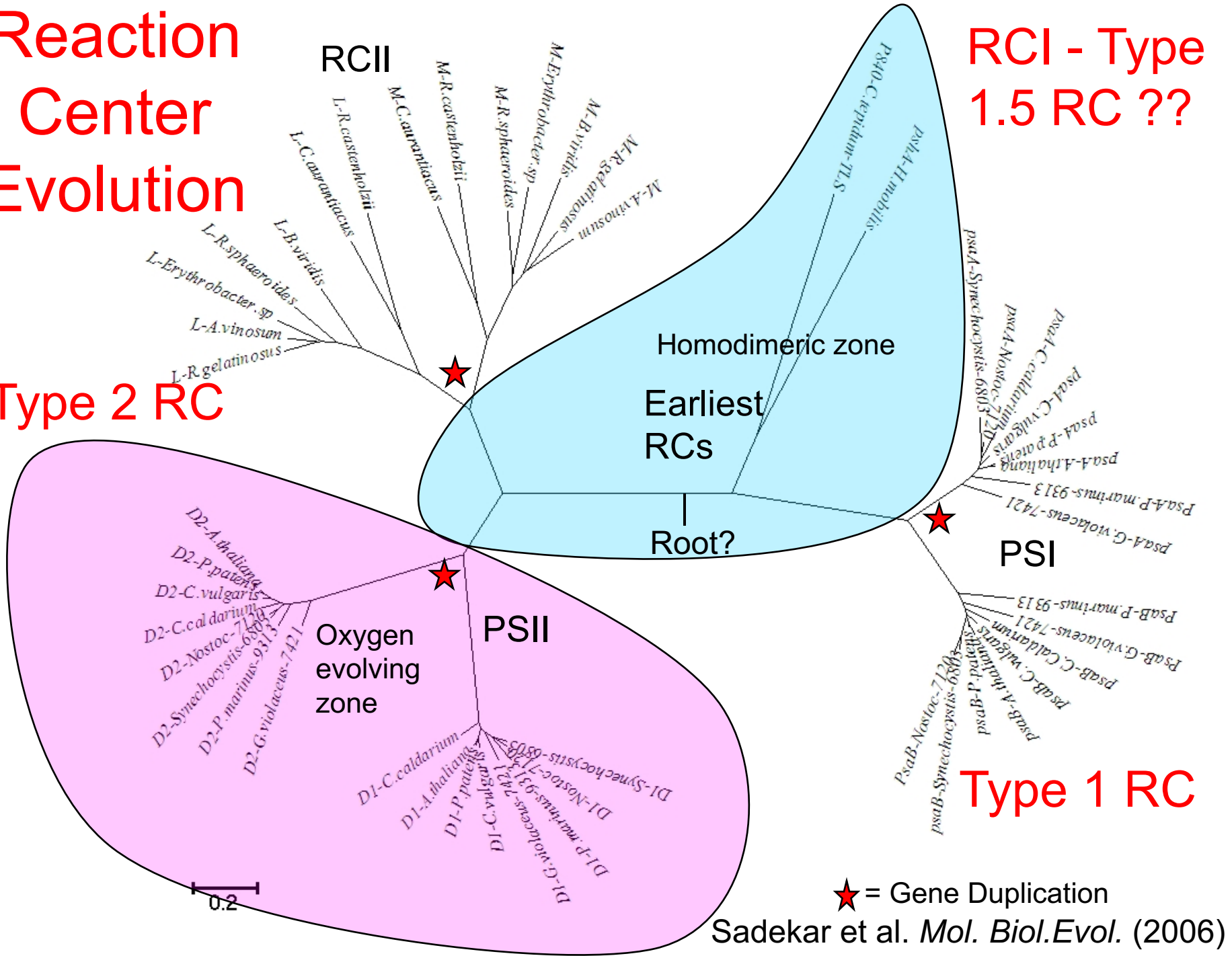


Mosaic Evolution of Photosynthesis



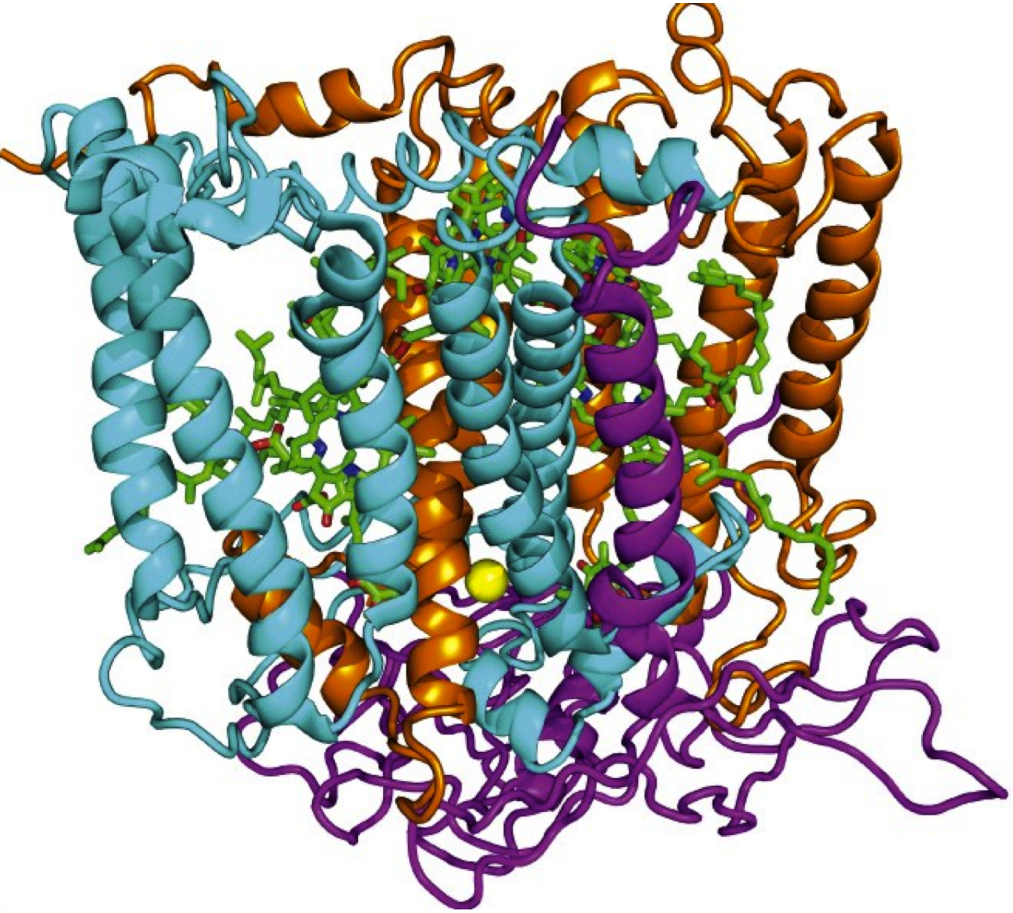
- All photosynthetic organisms are chimeric.
- Different parts of the photosynthetic machinery have distinct evolutionary histories.
- There is no simple path for “evolution of photosysnthesis”.

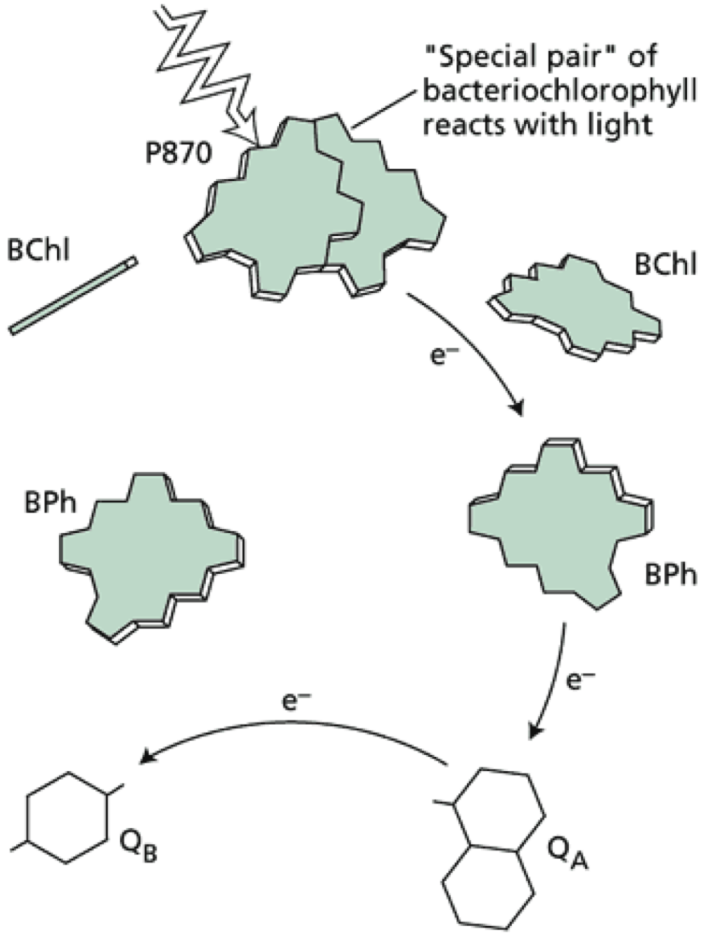
Reaction Center Evolution



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

Purple Bacterial Heterodimeric Type II Reaction Center

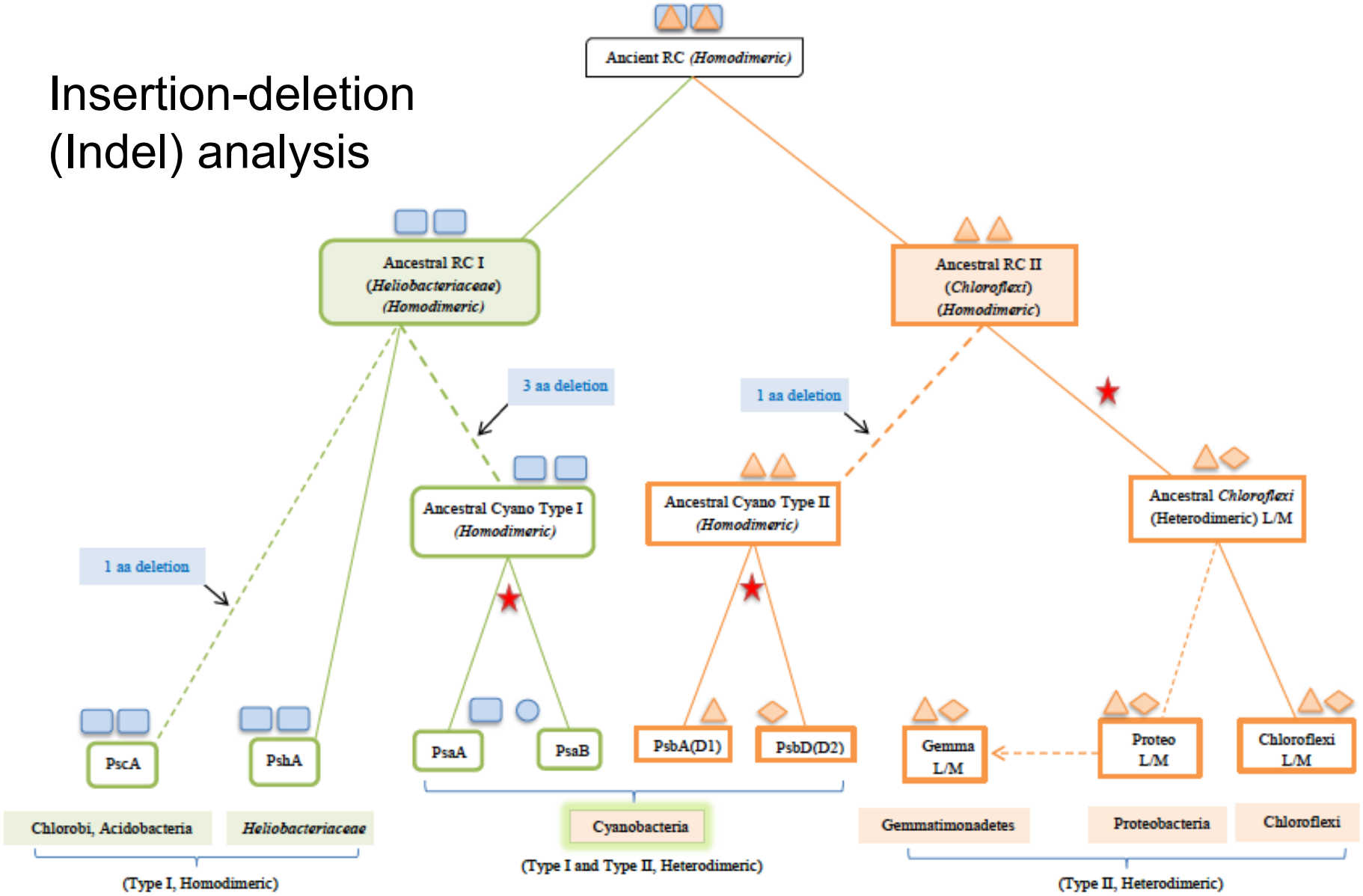




The slight structural asymmetry of the reaction center L and M subunits gives rise to a strong functional asymmetry of electron transfer pathway and the 2 e^- Q_A/Q_B gate.

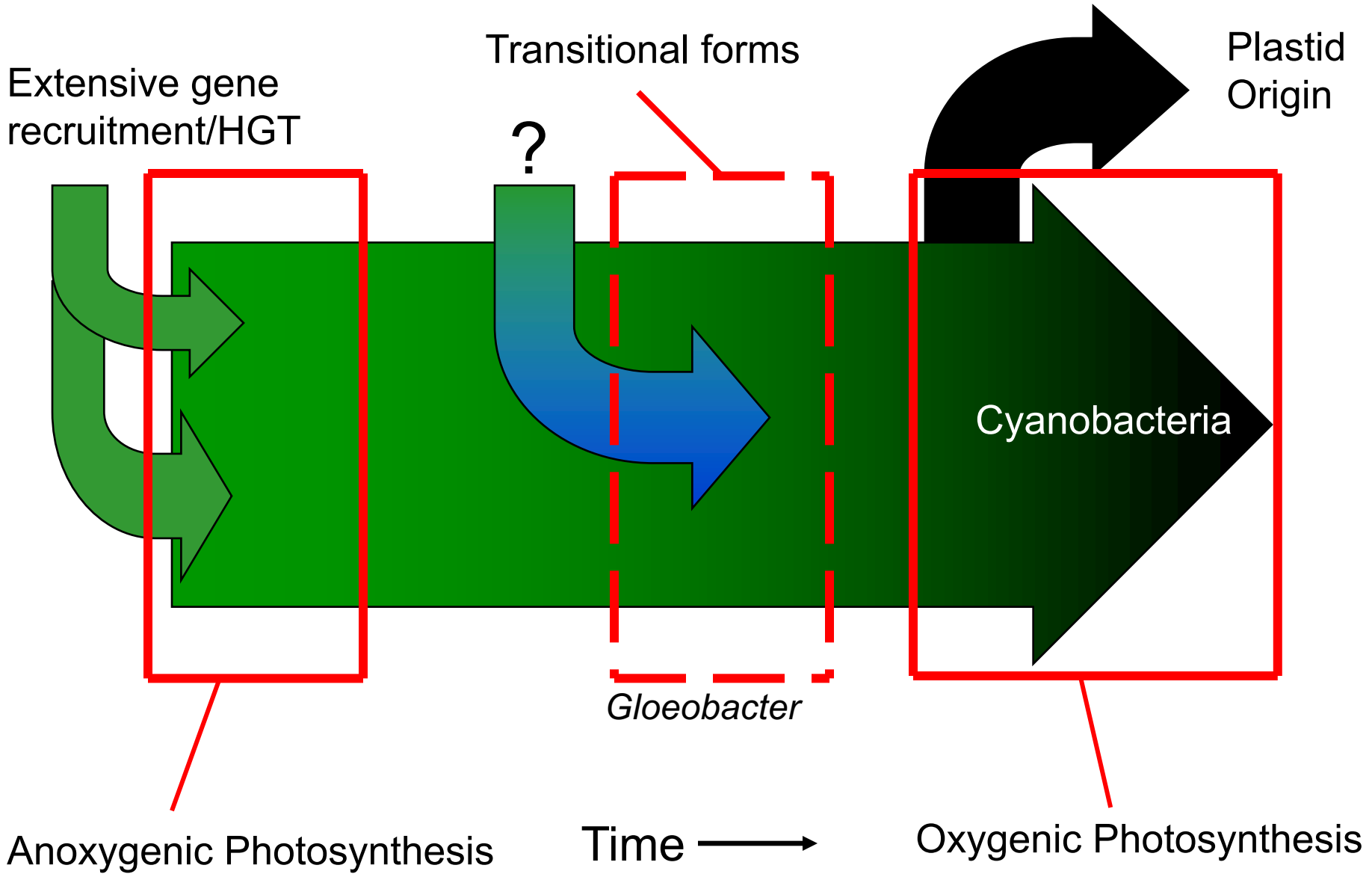
Reaction Center Evolution

Insertion-deletion (Indel) analysis



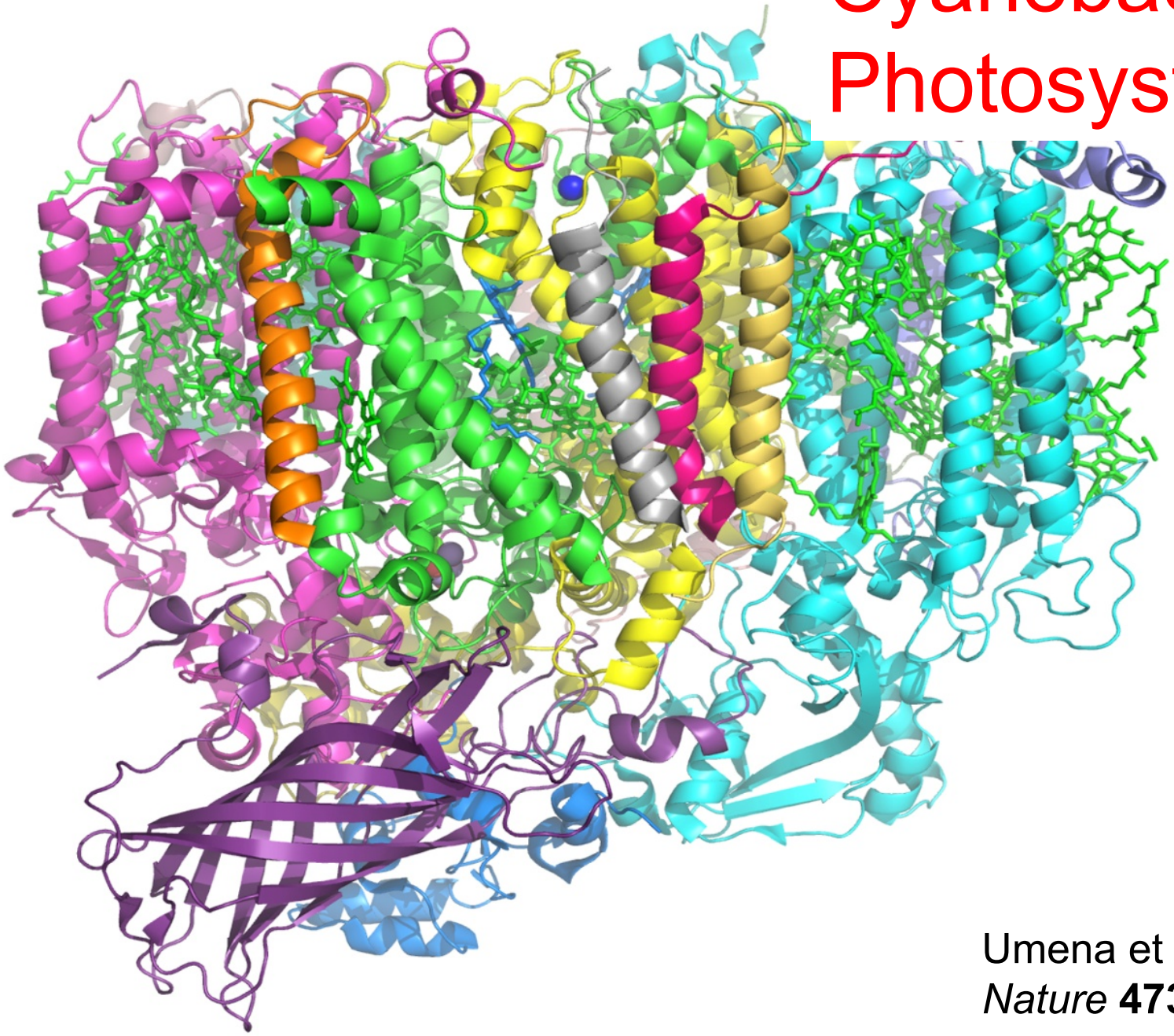
Khadka et al. *Photosynth. Res.*, (2018)

Transition to Oxygenic Photosynthesis



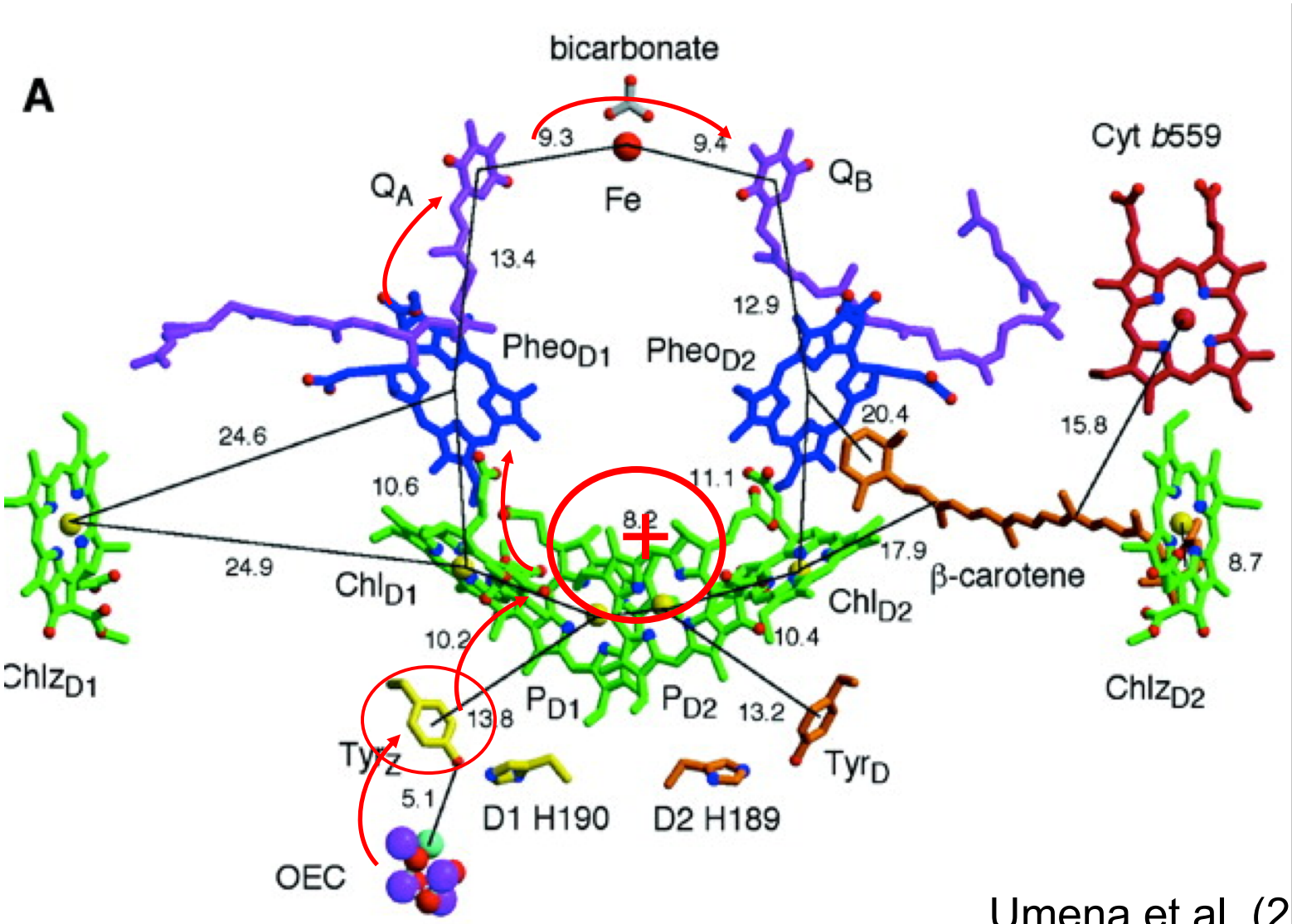
Raymond and Blankenship *BBA* (2004)

Cyanobacterial Photosystem II



Umena et al. (2011)
Nature **473**: 55-61

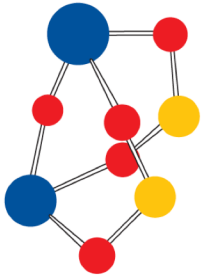
Photosystem II from cyanobacteria



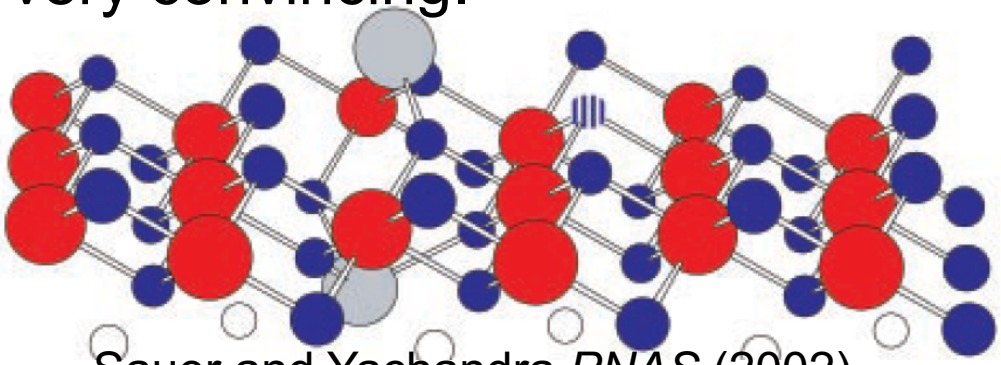
Umena et al. (2011)
Nature **473**: 55-61

Evolutionary origin of the oxygen evolution center of Photosystem II

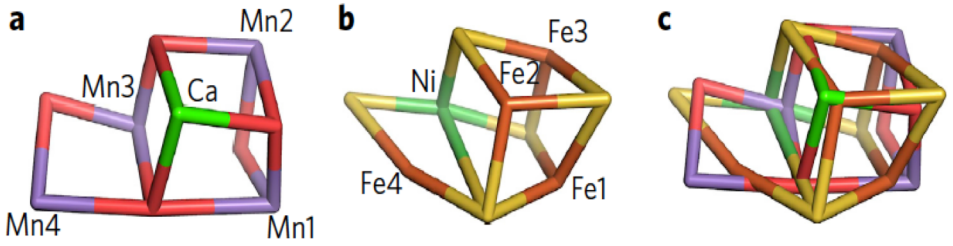
- Many suggestions have been made for the evolutionary origin of the OEC.
- These include Mn catalase, Mn minerals, carbon monoxide dehydrogenase.
- None of them are very convincing.



Blankenship and Hartman, *TIBS* (1998)



Sauer and Yachandra *PNAS* (2002)



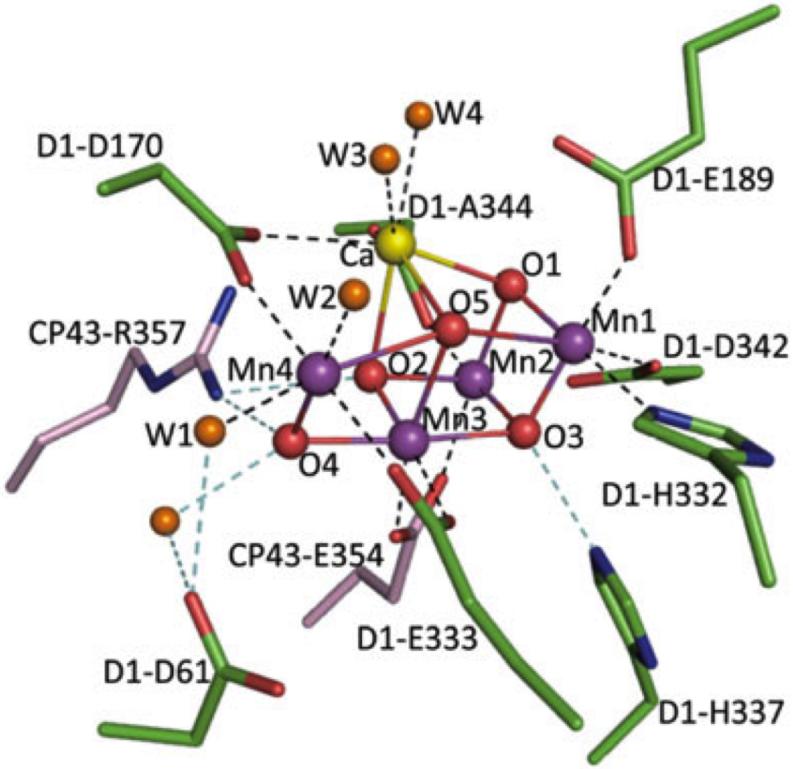
Barber *Nature Plants* (2017)

Origin of Oxygen Evolution

Reaction: $2H_2O \rightarrow O_2 + 4H^+ + 4e^-$

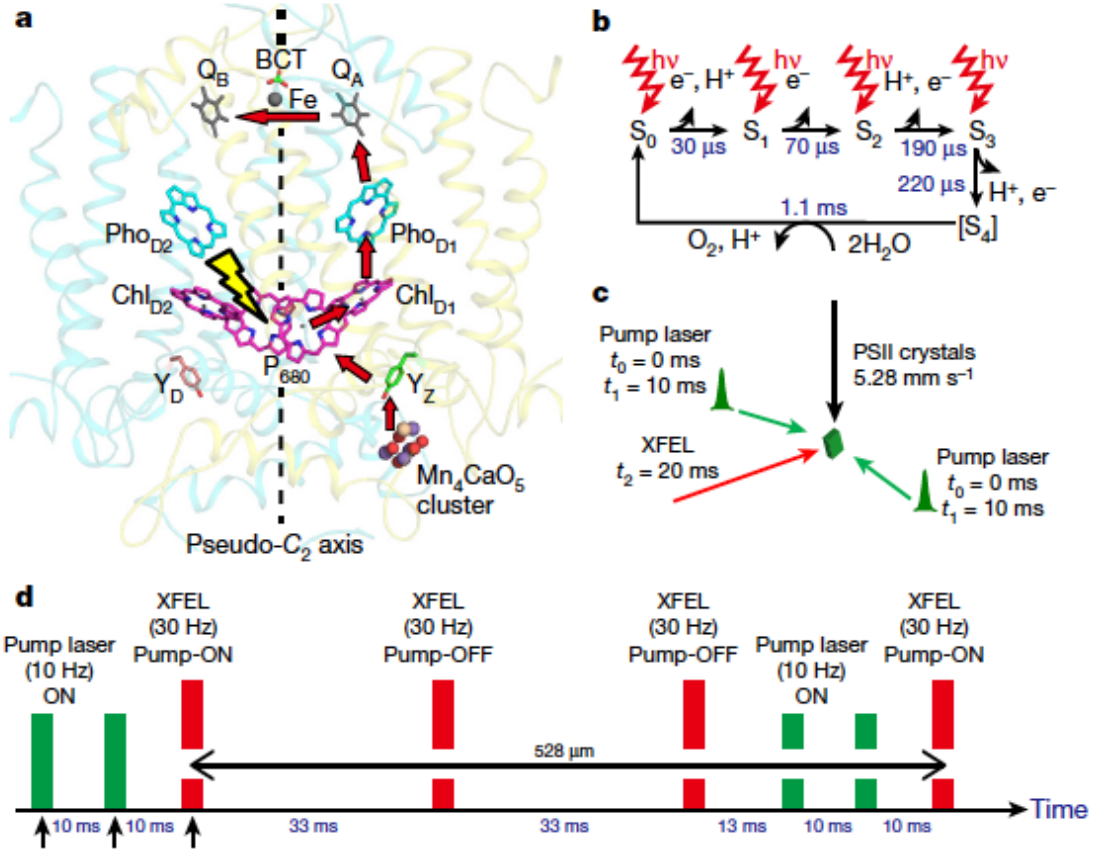
Changes between the anoxygenic RC and PS2 are:

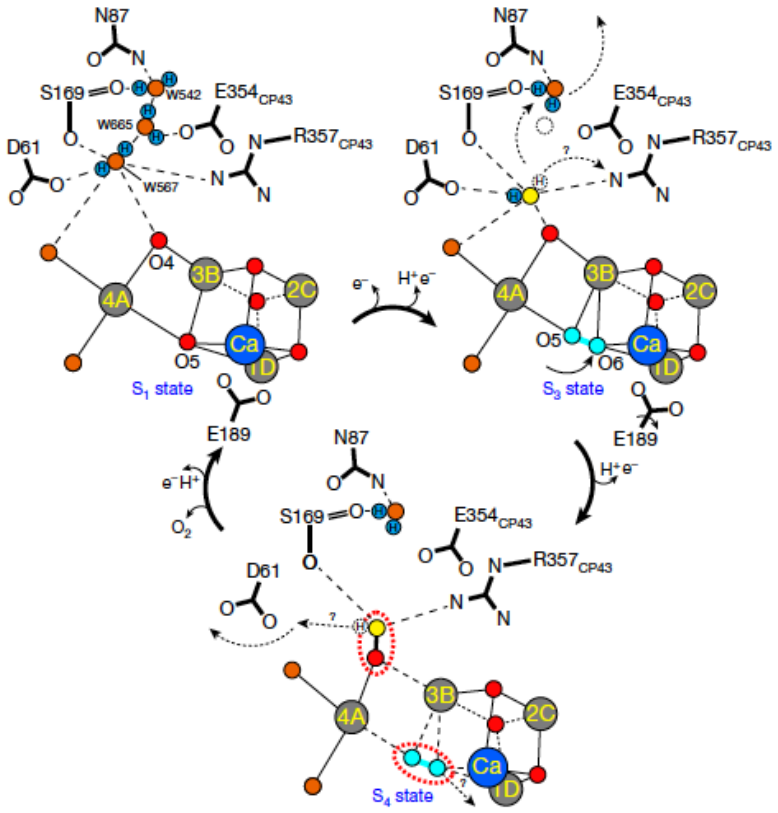
- A redox potential > 1 V, which requires change from BChl (870 nm) to Chl (680 nm)
- A charge-accumulating system to interface 1 e^- photochemistry to 4 e^- oxygen chemistry - Mn cluster - Singular event!
- A much more complex protein complement
- Linked photosystems ??



Umena et al.
Nature (2011)

Mechanism of O_2 production

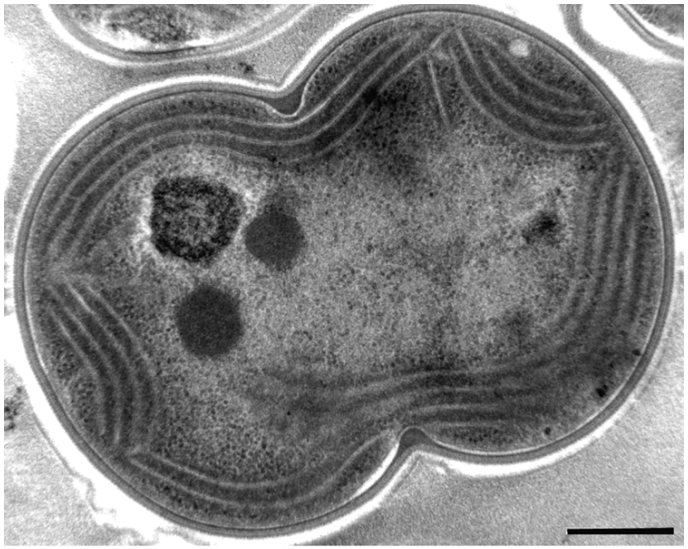




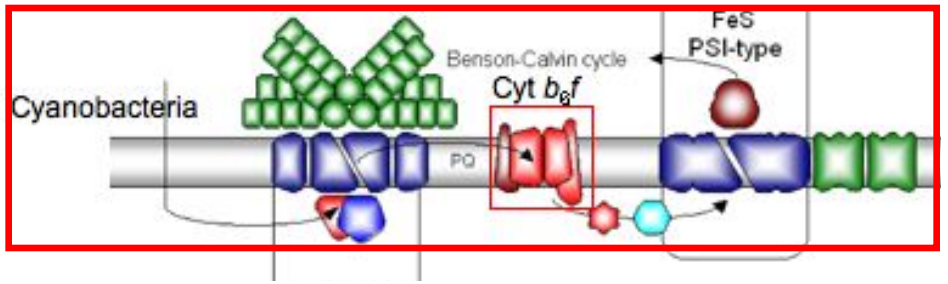
- Laser flashes coupled with X-ray pulses shows structural changes associated with S state advances.
- Details of mechanism are not yet certain.

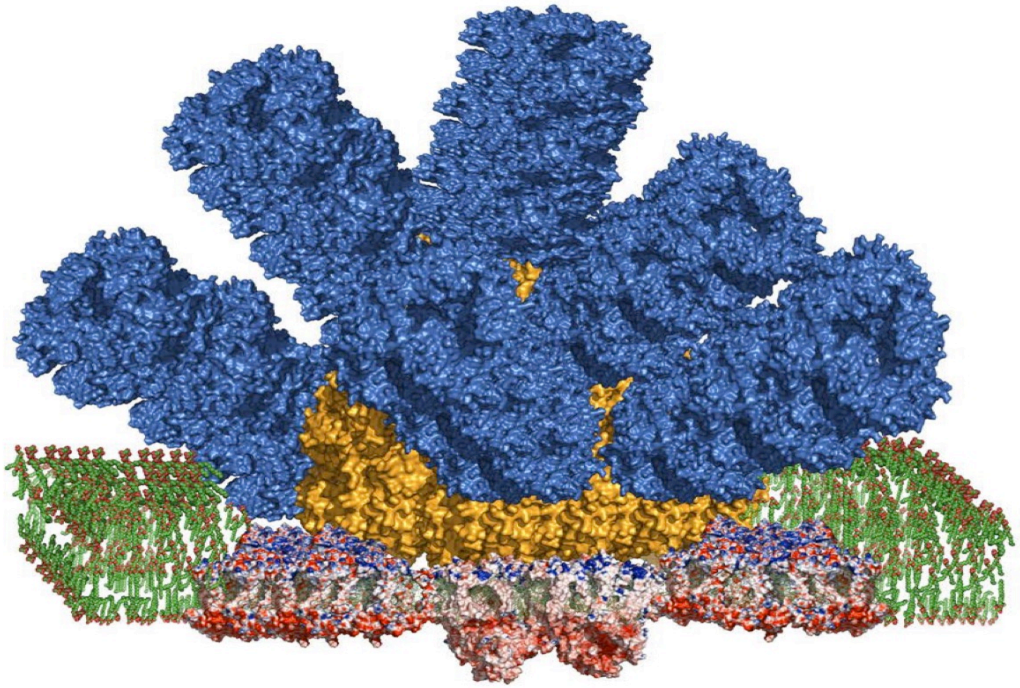
Suga et al. *Nature* **533**: 131-135 (2017)

Cyanobacteria



Synechocystis PCC6803





Liu et al. *Science* (2013)

- The cyanobacteria are the only group of oxygenic PS prokaryotes.
- They contain both Type I and Type II RCs.
- They are the source of chloroplasts via endosymbiosis.

Cyanobacterial Origins

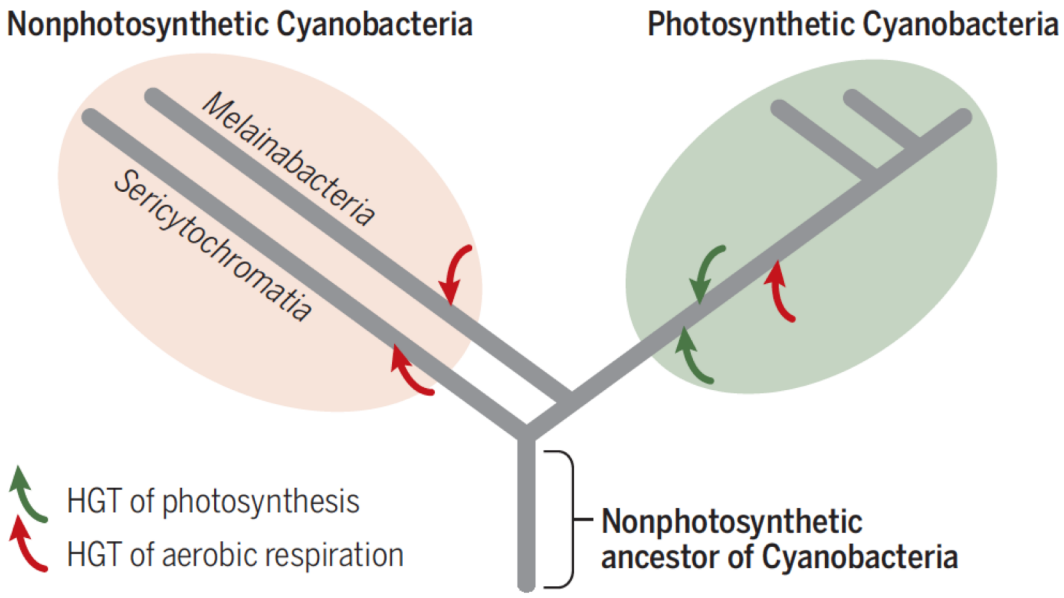
On the origins of oxygenic photosynthesis and aerobic respiration in Cyanobacteria

Rochelle M. Soo,[1]* James Hemp,[2]* Donovan H. Parks,[1]
Woodward W. Fischer,[2]† Philip Hugenholtz[1]†

Science (2017)

Early branching cyanobacteria show no trace of having ever had the abiilty to do photosynthesis.

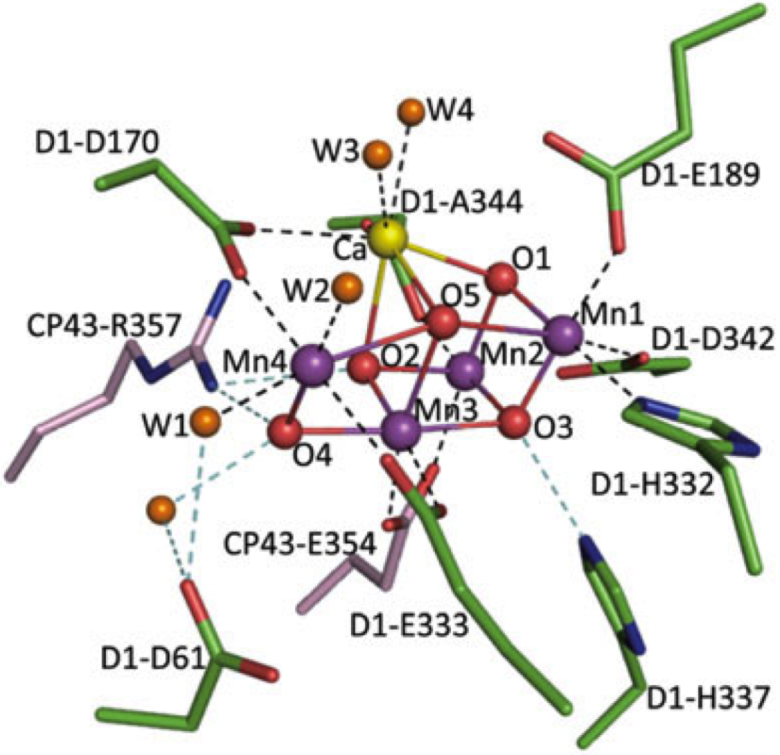
Photosynthetic cyanobacteria probably arose by horizontal gene transfer of PS genes from existing phototrophs to bring Type I and Type II reaction centers together.



Blankenship *Science* (2017)

Is oxygenic photosynthesis an inevitable evolutionary development?

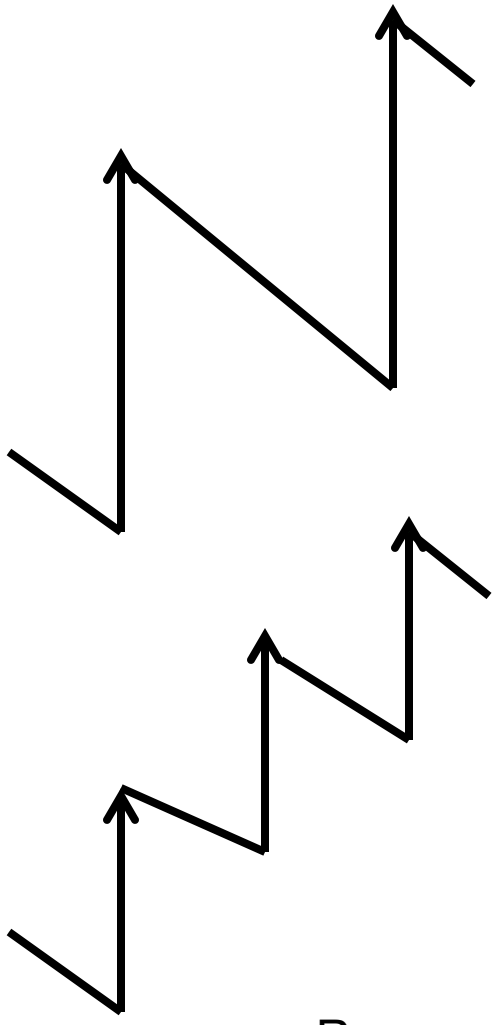
- Oxygenic photosynthesis is mechanistically much more complex than anoxygenic PS.
- It is very unlikely to be an early form of PS on any world.
- Oxygenic PS uses a ubiquitous electron donor molecule, H_2O, and produces a high energy form of stored products.
- It is so efficient that it is likely to be the dominant form of PS, providing that the very high barrier to its evolution can be surmounted.



Umena et al.
Nature (2011)

What is the long wavelength limit for oxygenic photosynthesis?

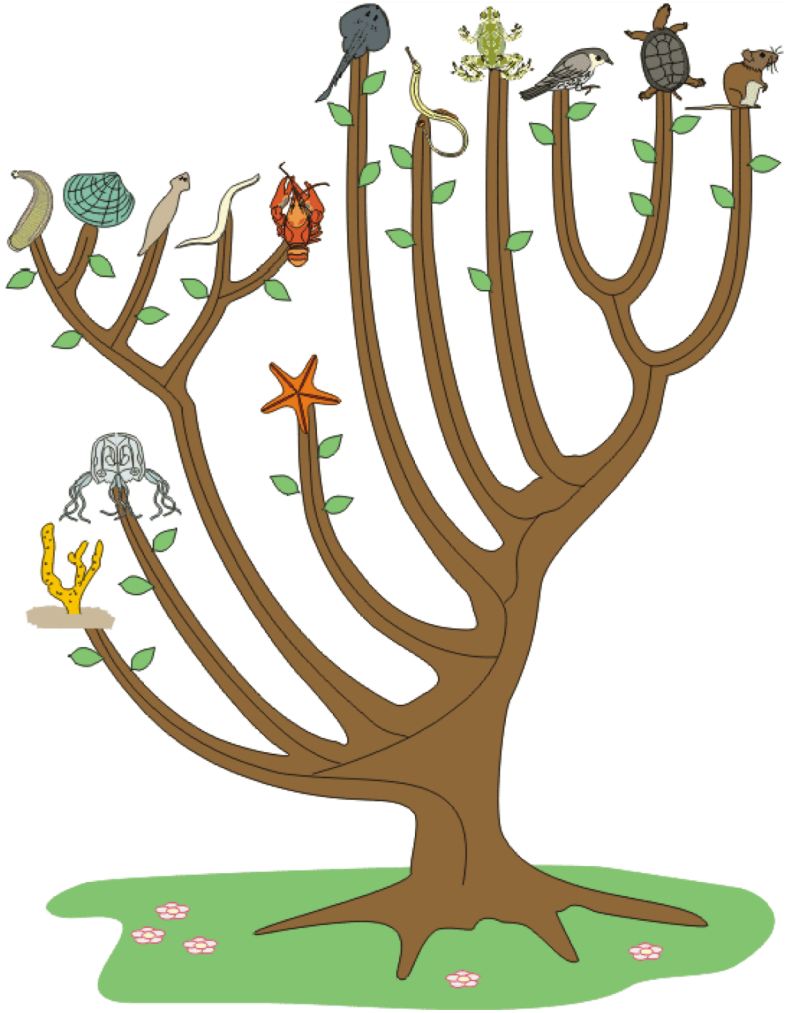
- The red limit for oxygenic PS using the familiar two photosystem architecture is not certain but is probably about 750 nm.
- Using a three or more photosystem architecture, it could be at significantly longer wavelengths.
- Anoxygenic PS works out to 1000 nm.
- Depending on the type of photopigments used, the red edge might be in the visible or near IR or there may be multiple red edges or a gradual one.
- It is difficult to see how photosynthesis could be driven using infrared light that only excites vibrational transitions.



Raven

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.
- Not certain how two photosystems were linked in series.



Acknowledgements

Former Group Members

Jason Raymond

Wes Swingley

Martin Hohmann-Marriott

Sumedha Sadekar

Collaborators

Peter Gogarten-U Conn.
Hyman Hartman-MIT
Radhey Gupta-McMaster U

Nancy Kiang-NASA Goddard
Niki Paranteau-NASA Ames

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