

The structure of photosystem I and evolution of photosynthesis

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Summary

Oxygenic photosynthesis is the principal producer of both oxygen and organic matter on earth. The primary step in this process—the conversion of sunlight into chemical energy—is driven by four multi-subunit membrane protein complexes named photosystem I, photosystem II, cytochrome *b₆f* complex and F-ATPase. Photosystem I generates the most negative redox potential in nature and thus largely determines the global amount of enthalpy in living systems. The recent structural determination of PSI complexes from cyanobacteria and plants sheds light on the evolutionary forces that shaped oxygenic photosynthesis. The fortuitous formation of our solar system in a space plentiful of elements, our distance from the sun and the long time of uninterrupted evolution enabled the perfection of photosynthesis and the evolution of advanced organisms. The available structural information complements the knowledge gained from genomic and proteomic data to illustrate a more precise scenario for the evolution of life systems on earth. *BioEssays* 27:914–922, 2005.

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Introduction

The opportunistic feature of life existence is epitomized by our location in the Milky Way galaxy.⁽¹⁾ A search through the Milky Way identified a galactic habitable zone with a narrow span of between 25,000 and 32,000 light years from the galaxy center. This zone complies with the four conditions that may allow evolution of life systems; the presence of a host star, enough heavy elements to form terrestrial planets, sufficient time for

biological evolution, and an environment free of life-extinguishing supernovae. The distance of the life-supporting planet from the star is also critical for maintaining water-based life. Our terrestrial planet is situated at an ideal distance from the sun that maintains on most of its surface a life-supporting temperature at night and day as well as in winter and summer. Earth is also plentiful with atoms covering most of the periodic table. Remarkably they had to be generated by a multitude of supernovae yet, as far as we can judge, we are no longer under danger of being extinguished by a supernovae in the foreseeable future. In any case the energy for sustaining complex life forms should be provided by light and photosynthesis is vital for life formation.

During the early events in their evolution, photosynthesis pigments functioned mainly in the protection of the primordial nucleic acids and proteins from photochemical damage. Later they assembled together with specific proteins to form primordial reaction centers that were adopted by the DNA/protein-based organisms and eventually evolved into the different current photosynthetic apparatuses. There are numerous photosynthetic processes that can harness the light energy for supporting life processes, but as far as we know only oxygenic photosynthesis is capable to energize life by utilizing water as an electron donor, thus maintaining the oxygen and the ozone layer in our atmosphere.^(2–5)

Can the genomic and proteomic data obtained from investigating current organisms paint a precise picture of the early evolution on earth? How has modern photosynthesis evolved? When and how were the different photosynthetic systems formed and what is the connection between them? What can we learn from the recently determined structures of photosynthetic systems on their function and evolution? These are the main questions that we attempt to address here.

The biochemistry of oxygenic photosynthesis

Oxygenic photosynthesis—the use of light energy to synthesize ATP and NADPH with the production of oxygen from water—underpins the survival of virtually all higher-life forms on earth. Producing oxygen and assimilating carbon dioxide into organic matter determine to a large extent the composition of our atmosphere and provide all life forms with essential food and fuel. Oxygenic photosynthesis that operates in cyanobacteria, algae and plants is catalyzed by four biochemically defined membrane complexes.⁽⁴⁾ According to the partial

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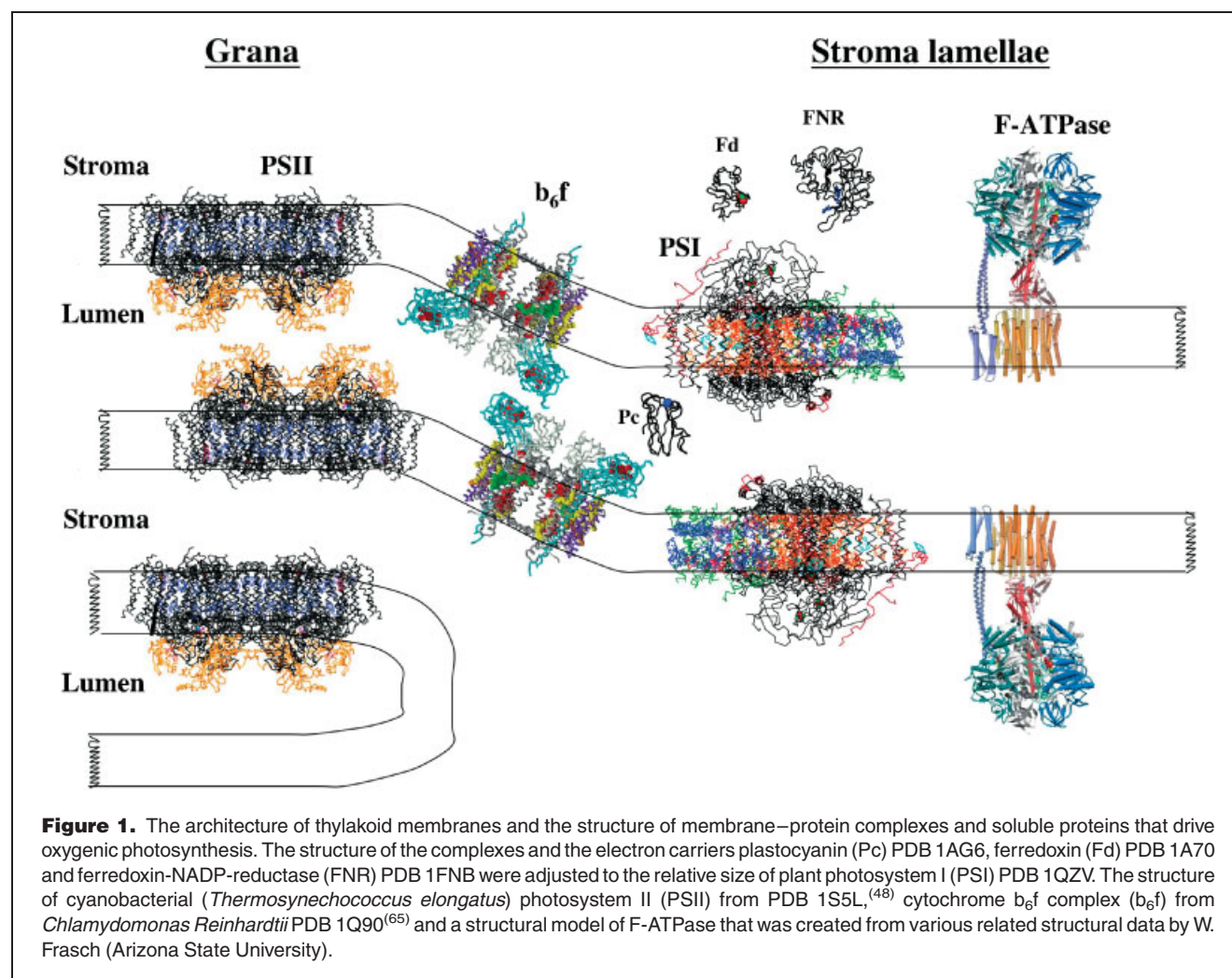
Abbreviations: RC, reaction center; RC1, type I reaction center; RC2, type II reaction center; PSI, photosystem I; PSII, photosystem II; Fr, ferredoxin; Pc, plastocyanin; F-ATPase, ATP synthase; UV, ultra violet light; TM, transmembrane; Q, quinone; pmf, protonmotive force.

reactions that they catalyze, photosystem II (PSII) is defined as a water–plastoquinone oxidoreductase, cytochrome b_6f complex as a plastoquinone–plastocyanin oxidoreductase, photosystem I (PSI) as a plastocyanin–ferredoxin oxidoreductase and the F-ATPase as a Protonmotive force (pmf)-driven ATP synthase (Fig. 1). PSI and PSII contain chlorophylls and other pigments that harvest the light and funnel its energy to a reaction centre (RC). Energy captured by the reaction centre induces the excitation of a special chlorophyll pair, which initiates the translocation of an electron across the membrane through a chain of cofactors.⁽⁴⁾ Water, the electron donor for this process, is oxidized to O_2 and $4 H^+$ by PSII. The electrons extracted from water are shuttled through a quinone pool and the cytochrome b_6f complex to plastocyanin, a small soluble copper protein. Solar energy absorbed by PSI induces the translocation of an electron from plastocyanin at the inner face of the membrane (lumen) to ferredoxin on the opposite side (stroma).⁽⁶⁾ The reduced ferredoxin is subsequently used in numerous synthetic reactions and regulatory cycles,

including nitrate assimilation, fatty-acid desaturation and NADPH production. The charge separation in PSI and PSII, together with the electron transfer through the cytochrome b_6f complex, leads to the formation of an electrochemical potential, which powers ATP synthesis by the fourth protein complex, F-ATPase.⁽⁷⁾ In the dark, CO_2 reduction to carbohydrates is fuelled by ATP and NADPH.⁽⁸⁾

Early events in the evolution of photosynthesis

Since the onset of life on earth about four billion years ago, the atmosphere and earth surface underwent drastic changes.^(9,10) While life began under highly reducing conditions with very little oxygen in the atmosphere, today it operates with 21% oxygen in the atmosphere and in most ecological niches, under highly oxidative conditions. Consequently, life began in an environment plentiful of available metal ions and today it operates with a general shortage, which prompts organisms to compete on the available metal ions. This competition dictated drastic changes in metabolic pathways and led to the



development of highly sophisticated metal-ion homeostasis in higher organisms.⁽¹¹⁾

The first life forms were most likely non-photosynthetic, existing on the redox contrast between the atmosphere–ocean and the mantle.^(12–16) Studies with carbon isotopes imply that the enzyme ribulose-1,5-bisphosphate carboxylase has controlled the global distribution of carbon in the atmosphere–ocean system for at least 3.5 billion years, selectively mobilizing carbon into the biosphere from an abundant atmospheric reservoir.^(9,17) Modern biochemical reactions of carbon and nitrogen fixation already operated very productively by then.^(17–19) The early events in the evolution of photosynthesis are not clear. Although many of the key enzymes including metal proteins containing Mn, Cu and iron-sulfur clusters already existed, their recruitment into photosynthetic systems required several adaptations. Pigment-containing proteins and chlorophyll-proteins also preceded the onset of photosynthetic systems.

The function of these primordial chlorophyll–protein complexes and the way that the reaction centers evolved from them is arguable. It was suggested that the ancestral chlorophyll–protein complexes were evolved for the protection of the primordial organisms against UV damage.⁽²⁰⁾ In addition to the protection of the proteins and DNA from UV damages, the chlorophyll–protein complexes had to develop protective mechanisms against their own excited states.^(21,22) Thus it was suggested that to prevent damage by the excited chlorophylls, some of them were established as chlorophyll-dimers (which are called “red traps” since their absorption peak is shifted to lower energy). As long as the two chlorophylls in the dimers were kept in an environment that did not allow oxidation–reduction reactions, the excitation in these traps preferentially decayed as singlets.^(21,22) This prevented the formation of long-lived damaging triplets.^(23,24) By letting the chlorophylls in one of these dimers get close enough, and by evolving the environment of this chlorophyll-dimer to promote electron transfer from it, a primordial reaction center was formed from the ancient chlorophyll–protein complex. For an unknown mechanistic reason, the chlorophyll dimer capable of oxidation–reduction activity evolved from a homodimeric protein, with each monomer donating one chlorophyll molecule.^(21,25–27) Now being a productive entity of converting light to chemical energy, it had to be protected from its own photochemical activity.

Tracing of sequential events during the onset of life on earth

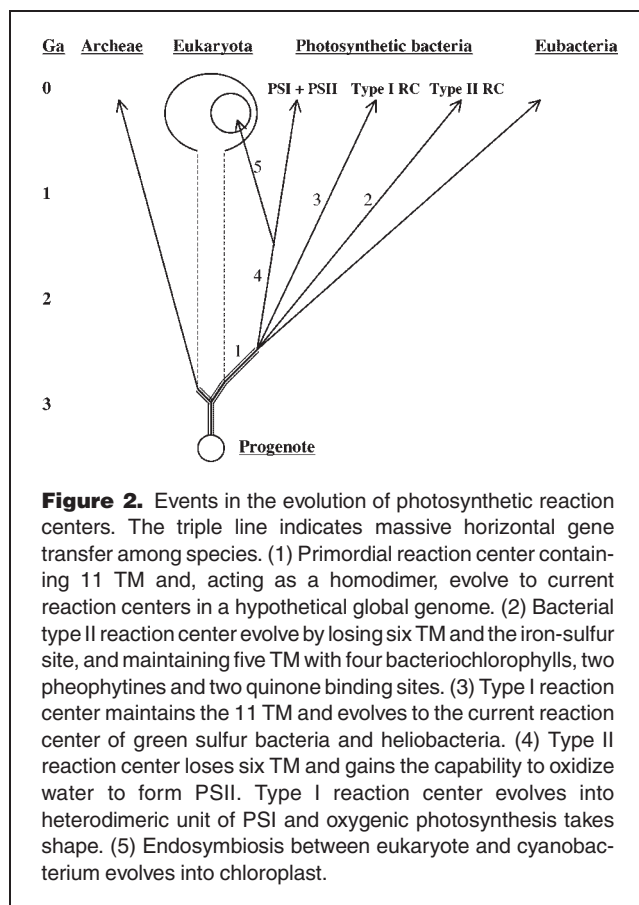
Evolutionary timing using a phylogenomic dating approach advanced our understanding of the deep-branching relationships in *Eubacteria*, *Archaea* and *Eukaryota*. Utilization of a large number of genes from whole genome sequences reduced the long-branch artifacts. Recent phylogenetic trees revealed the evolutionary relationships between diverse

bacterial groups that left traces in geological records.⁽¹⁰⁾ For example, it was shown that large-scale bacterial sulphate reduction began in marine environments around 2.45 billion years ago (Ga), followed by rapid oxygenation of the atmosphere about 2.3 or 2.2 Ga. Oxygenation was then followed by the disappearance of banded iron formations by 1.8 Ga.^(10,28) However, oxygenic photosynthesis may operate as long as 3.0 to 3.2 Ga and it took more than 1 billion years to reach the atmospheric environment that current organisms experience. Thus, phylogenomic dating that is based on the organisms that currently live on earth may be prone to erroneous conclusions.

Before the eukaryotes started to evolve about 1.5 Ga, prokaryotes governed the life on earth. In prokaryotes, photosynthetic capability is present within five major groups of bacteria: (i) the low G + C Gram-positive bacteria such as heliobacteria, (ii) green nonsulfur or filamentous bacteria such as *Chloroflexus*, (iii) green sulfur bacteria such as *Chlorobium*; (iv) proteobacteria, and (v) cyanobacteria. Of these, only cyanobacteria, which contain two different reaction centers (PSI and PSII), are capable of carrying out oxygenic photosynthesis. After Carl Woese presented the first comprehensive bacterial evolutionary tree in his landmark 1987 paper,⁽²⁸⁾ some investigators deduced that the major bacterial groups arose simultaneously in a fashion that could be described as a large adaptive radiation form.^(29–31) However, dating with ribosomal RNA produced conflicting topologies where the resulting phylogenies are not very well resolved. Conflicting topologies may be interpreted as evidence for lateral gene transfer.^(32,33) Indeed one has to assume a rampant lateral gene transfer to conciliate the unresolved questions raised by phylogenomic dating during the primordial evolution of life on earth.⁽¹⁹⁾ We propose to go even one step further, and to look upon the gene pool that existed over 2.5 Ga as a single genome and, instead of attempting to analyze the evolution of species, to study the functional evolution of the various metabolic systems and membrane complexes (Fig. 2).^(34,35) Accordingly, regardless of the evolutionary dating of heliobacteria that is supposed to be more ancient than green sulfur bacteria,^(5,16) the reaction center that currently operates in green sulfur bacteria could be more ancient than its relative in heliobacteria.

Evolution of the photosynthetic reaction centers

Photosynthetic reaction centers are generally divided, according to the identity of the last electron acceptor, into two groups: Type I (RC1) with Fe-S cluster as a last acceptor as in PSI and the RC of green sulfur bacteria and heliobacteria and type II (RC2) with a mobile quinone as a last acceptor, as in PSII and the RC of purple and green filamentous bacteria.⁽³⁶⁾ Phylogenetic analyses of the core reaction center proteins of PSI and PSII from cyanobacteria and higher plants reveal several striking structural similarities that are also in common with the



type I RC of green sulfur bacteria and type II RC of purple bacteria.^(37–39) These similarities support the long-standing hypothesis of a common evolutionary origin for all reaction center complexes.^(2,20,38,40) Type II reaction center is considered to be the precursor of cyanobacterial PSII,⁽⁴¹⁾ and it was recently suggested that it was also the progenitor of PSI.^(38,42,43) However, this RC2 probably also had some type I characteristics. A basic difference between existing RC1 and existing RC2 is that in the RC1 the core protein contains both electron transfer components and intrinsic antenna chlorophylls within its 11 transmembrane (TM) helices. These functions are split between different proteins, with a smaller number of TM helices in the existing RC2 (PSII). It was recently shown that the PSII intrinsic antenna proteins, CP43 and CP47, bear primary sequence resemblance to the antenna domain in the core protein of the heliobacteria RC1, but not to any purple bacteria protein. This supports the hypothesis that the primordial type II RC was similar to existing type I reaction centers in the sense that it was constructed of large 11 TM helix proteins that contained both the electron transfer components and the intrinsic antenna, as opposed to the current PSII and purple bacteria reaction centers. However, as a type II RC, it operated with quinones as electron acceptors

and contained no iron-sulfur clusters. The purple bacteria are now placed as the most ancient of all emerging photosynthetic lineages.⁽⁴⁴⁾ However, heliobacteria that contain RC1 use BChl-g as a pigment, which is the closest evolutionary pigment precursor to Chl-a used by cyanobacteria and higher plants.⁽⁴⁵⁾ It was thus considered that, although heliobacteria appear to have the closest pigment precursor to Chl-a, they have the “wrong” reaction center type for water oxidation (RC1).

We favor the hypothesis that the RC1 (Fig. 3), such as the one present in the current green sulfur bacteria (*Chlorobiaceae*), was the common ancestor of all photosynthetic reaction centers.^(25,26) Sequence analysis of type I and type II reaction centers suggested that they evolved by gene duplication that led to the heterodimeric reaction centers currently operating in most photosynthetic organisms.^(9,36) A relict of the ancient homodimeric reaction center was identified in green sulfur and heliobacteria, i.e. in “old” bacteria.^(25–27) The green sulfur bacterial RC harbors both an iron-sulfur cluster and loosely bound quinones. Its resemblance to PSI and the involvement of loosely bound quinones suggest that the origin of both PSI and perhaps PSII reaction centers was a similar homodimeric PSI-like reaction center. At a relatively short time, PSI was evolved to contain the basic structure of the PsaA–PsaB heterodimer—several new subunits added in an asymmetric manner⁽²¹⁾—and this kind of reaction center contained about 90 chlorophyll molecules. Since the homodimeric reaction center was considered to predate the heterodimeric reaction center and no RC2 homodimeric reaction center was found, it is conceivable that the homodimeric RC1 was indeed the precursor for all reaction centers.

According to this scenario, the evolution of photosynthetic reaction centers started with a gene encoding large protein that operated as a homodimer much like PscA of the *Chlorobiaceae* (Fig. 3). Each monomer was capable of binding 20–40 chlorophyll molecules that were of the bacterial-type, where two of them were held in close proximity and appropriate environment to form the excitation trap capable of oxidation–reduction reactions.⁽³⁶⁾ In the opposite side of the membrane, there were two identical quinone-binding sites (one for each monomer). A strategically located cysteine residue per each monomer provided the template for the formation of the electron acceptor non-heme iron center. This kind of reaction center was capable of functioning as the type II of the current purple bacteria in cyclic electron transport for ATP production, as well as the type I reaction center such as the current PSI. This kind of reaction center was ideal for operating under anaerobic conditions that governed the atmosphere during the onset of life on earth. At that time, reducing substances were abundant and, due to the lack of free oxygen, ATP could not be formed by respiration. Cyclic photophosphorylation was the main source of ATP for the photosynthetic organisms. One obstacle that hampered the smooth operation of cyclic

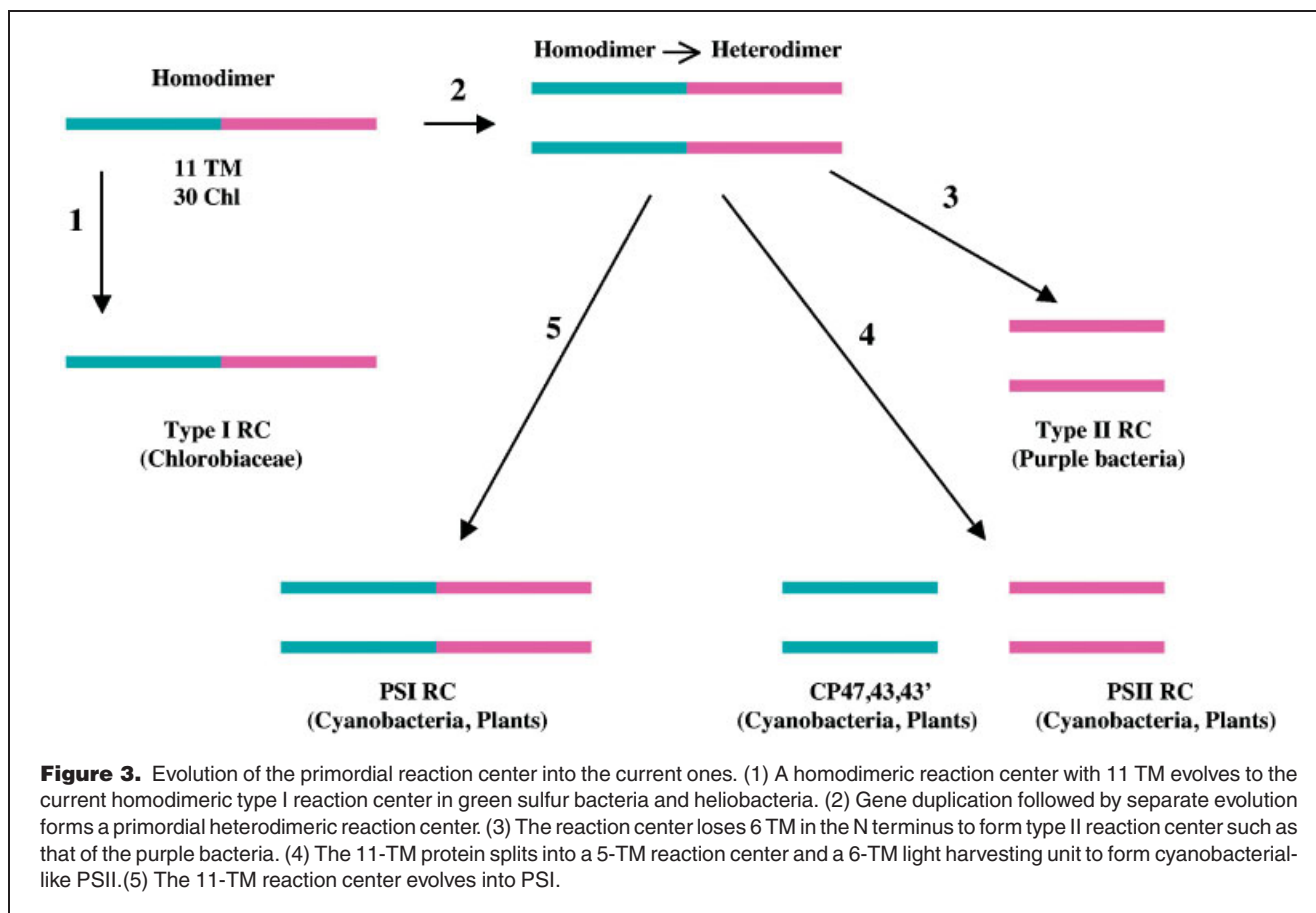


Figure 3. Evolution of the primordial reaction center into the current ones. (1) A homodimeric reaction center with 11 TM evolves to the current homodimeric type I reaction center in green sulfur bacteria and heliobacteria. (2) Gene duplication followed by separate evolution forms a primordial heterodimeric reaction center. (3) The reaction center loses 6 TM in the N terminus to form type II reaction center such as that of the purple bacteria. (4) The 11-TM protein splits into a 5-TM reaction center and a 6-TM light harvesting unit to form cyanobacterial-like PSII. (5) The 11-TM reaction center evolves into PSI.

electron transport was the frequent over-reduction of all the electron carriers that might inhibit the electron transport due to lack of oxidized electron acceptors. Reduction of CO_2 and especially the evolution of the enzyme hydrogenase, which reduces protons to hydrogen molecules, solved this problem.^(14,43) The current RC from green sulfur bacteria that live under anaerobic conditions might be similar to that primordial RC.

The formation of the type II reaction center from the above primordial RC is relatively straight forward (Figs. 2 and 3). For the formation of heterodimeric RC, an initial gene duplication that was followed by some sequence diversification took place. Next, the cysteine residues were mutated out to eliminate the assembly of non-heme iron electron acceptor. An iron-binding site was generated between the two quinone-binding sites and the latter were further evolved to exhibit a differential binding affinity to form Q_A and Q_B , respectively. The genes encoding the reaction center were shortened to eliminate five transmembrane helices at the N terminus and consequently most of the antennae chlorophyll molecules were lost. This established the current type II bacterial reaction center that consists of a heterodimeric structure containing four bacterial chlorophylls, two bacterial pheophytine, Q_A , Q_B and an iron

atom in-between them. Comparison of several genes from the green nonsulfur bacterium *Chloroflexus aurantiacus*, containing RC2, and the green sulfur bacterium *Chlorobium tepidum*, containing RC1, demonstrated that these organisms are closely related and thus may represent the earliest known branching point of the two reaction center types.⁽⁴⁴⁾ However, as mentioned above we favor evolution of systems over that of species.

How did oxygenic photosynthesis evolve from this primordial homodimeric RC1? Naturally, The evolution of type I (PSI) is more apparent. Gene duplication for the formation of a heterodimeric reaction center was followed by substitution of Bchl-a to Bchl-g to chlorophyll a. The quinones became firmly bound, the environment of the electron transfer components was adjusted and the size of the intrinsic antenna increased. The more difficult task was to form an oxygen-evolving type II (PSII) from the proposed primordial reaction center. Most of the above steps that were described for the bacterial type II reaction center can be adopted for the evolution of PSII. The Bchl-a had to be substituted by chlorophyll a and the most difficult task was to form the water-oxidizing complex. We should consider how the PSII photochemical apparatus evolved to generate a sufficiently strong one-electron

photooxidant that is found in contemporary PSII. All the suggestions in the literature for the evolution of type II reaction centers to PSII should be considered.^(2,20,37,38)

Evolutionary attempts at light harvesting

While there is a consensus that the increase in free oxygen was the result of oxygenic photosynthesis, very little is known about the evolutionary steps that had to take place for this event to happen. A variety of lines of evidence, including comparative biochemistry, structural biology and genomics, shed some light on how oxygenic photosynthesis shaped life on earth as we know it today. The buildup of oxygen in the earth's atmosphere, which began about 2.2 billion years ago,^(10,28) was one of the most important events in the history of the planet. However, there are several evidences that oxygenic photosynthesis already operated 3.2 billions years ago.^(5,15) Apparently, the oxygen produced during those 1 billion years was reduced by the reducing components on the earth crest and could be accumulated into the atmosphere only after this gigantic titration was completed.^(10,28) Oxygenic photosynthesis operates under vastly different conditions, which are dictated by the ecological niches that are occupied by different organisms. Whereas green algae and plants are mainly present on the surface of oceans and on land, cyanobacteria usually proliferate deep into oceans and other water bodies. Consequently, they are protected from high light intensities and compete for the dim light of their environment.⁽²²⁾ A life at dim light intensities probably drove the formation of the trimeric PSI that is present in cyanobacteria.⁽²¹⁾ In addition, several light harvesting assemblies have evolved to cope with the limited light conditions. The recent discovery that, under certain stress conditions (depletion of iron), the trimeric cyanobacterial PSI is encircled with a ring of 18 copies of CP43' is a fine example for such attempt.^(46,47) The CP43' is a membranal light-harvesting protein, similar to CP43 of PSII that probably coordinates 14–16 chlorophyll-a molecules.⁽⁴⁸⁾ It was demonstrated that the CP43' ring can efficiently transfer energy to the PSI-RC.⁽⁴⁹⁾ Thus, it is possible that when chloroplasts formed, 1.2 billions years ago, the RC of cyanobacteria was already adapted to utilization of light absorbed either directly, by its own intrinsic antenna chlorophylls, or by a peripheral membrane antenna bound to the subunit F side of the RC. Furthermore, it was shown that, in a deep-living strain of *prochlorococcus* (a member of cyanobacteria taxon) that lives under dim light, PSI-RC is augmented with a ring of 18 copies of Pcb, a protein similar to CP43 but capable of binding chlorophyll-b as well as chlorophyll-a.⁽⁵⁰⁾ Thus, we may suggest that the ability of the RC to receive energy from a membrane antenna is much older even than 1.2 billion years.

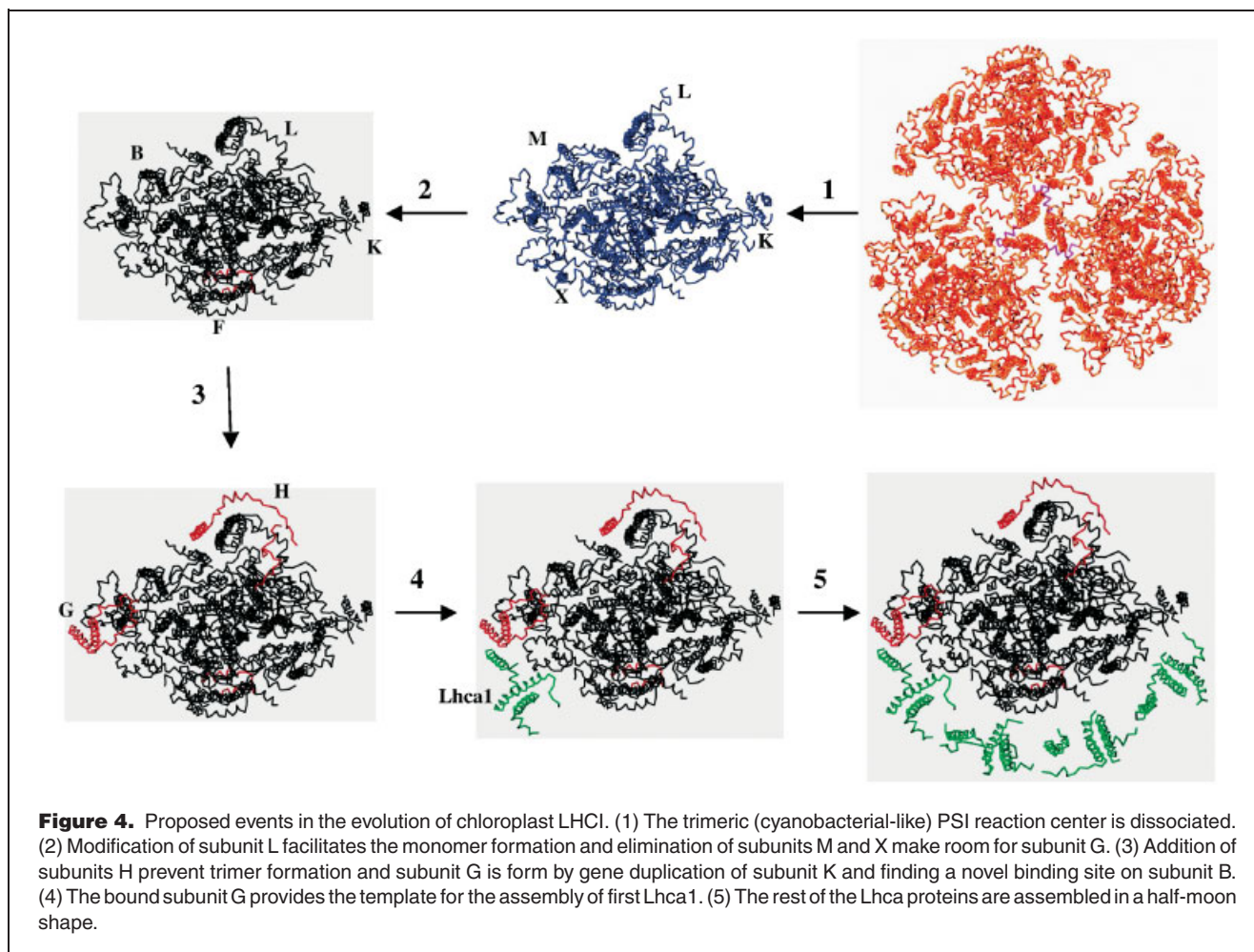
Attesting to the antiquity of the chlorophyll arrangement in PSI-RC, the crystal model of plant PSI reveals that the majority of the RC chlorophylls retained the same position and tilting

angle as in the PSI from the cyanobacteria *S. elongatus*.^(51,52) Furthermore, sequence alignment of PsaA from plant and from that of the most ancient cyanobacterium *Gloeobacter violaceus*,⁽⁵³⁾ supports the notion that the designing principles of the chlorophyll arrangement in PSI have remained unchanged for more than 1.2 billion years. This sequence alignment reveals that 90% of the histidines in plant PsaA also appear in *Gloeobacter* (compared to 72% identity in the entire sequence). Since the majority of chlorophylls in PSI-RC are coordinated by histidines, and since according to 16S rRNA analysis *Gloeobacter* is the species closest to the ancestral cyanobacteria, this attests to the antiquity of the chlorophyll arrangement in PSI.

Capturing the ocean surface and land

The organisms that populated the ancient oceans were protected from the possible damages of high light intensities by the depth of water under which they lived. Living under dim light forced them to compete for this vital energy source and several mechanisms were "tested" according to the different ecological niches. Thus phycobilisomes evolved to capture light that is not absorbed by chlorophyll, and various other attempts to develop light-harvesting systems appeared. One of these attempts probably resulted in the formation of a trimeric reaction center that may facilitate capturing of the dim light.⁽⁵⁴⁾ Habitation of the surface of the oceans and, even more so, capturing the land required the generation of modular light-harvesting machinery that would be able to cope with the ever-changing light intensities and quality on their surface. The evolution of eukaryotic photosynthesis by endosymbiosis between heterotrophic organisms with autotrophic cyanobacteria was in concert with capture of the niches that are occasionally bombarded by very high light intensities. Therefore one of the most important parameters that enabled the capture of these niches was the evolution of protective mechanisms against nonproductive excited states that can decay through damaging triplets, because singlet oxygen generated via such chlorophyll triplets can destroy basic components of the photosynthetic apparatus.^(24,55) The trimeric PSI present in cyanobacteria prevented the formation of the modular light-harvesting system because most of the surface of each monomer was occupied by the trimer formation.⁽²¹⁾ Therefore, one of the crucial evolutionary events towards establishing oxygenic photosynthesis in chloroplast and populating the ocean surface and land was the conversion of trimeric RC to a monomeric RC (Fig. 4).

This conversion was governed by the emergence of subunit H and modification of PsaL that facilitates trimer formation in cyanobacteria.^(51,52,56) This novel feature of eukaryotic PSI not only prevented the possibility of trimer formation but also provided a template for the evolution of LHCI (Fig. 4). The evolution of PsaG represents a second crucial evolutionary step that took place about 1.2 billion years ago that enabled the



formation of LHCI.^(21,51) Sequence alignment demonstrated that PsaG arose through gene duplication of PsaK.^(57,58) Random mutations had led to distinct roles for these subunits that are now becoming clear. There seems to be an inherent difference in the rigidity of these subunits and in the stability of their binding to PsaA/PsaB. Even in the 2.5 Å resolution structure of cyanobacterial PSI,⁽⁵²⁾ large parts of PsaK are not resolved, attesting to their flexibility and/or accessibility to proteases. On the other hand, PsaG is more rigid and our 4.4 Å electron density map even revealed potential water-exposed domains.⁽⁵¹⁾ Even though the orientation of PsaG is debatable,⁽⁵⁹⁾ it certainly serves as the anchor site for LHCI binding. It forms a helix bundle with helix C of Lhca1, thus contributing the only intramembrane interaction between the core and the antenna belt (Figs. 4,5). We proposed that this strong and stable anchor site provided the evolutionary template for the formation of the modular LHCI that was one of the prerequisites for the emergence of oxygenic photosynthesis on the ocean surface and land. It was demonstrated that the presence of different LHCI monomers was modulated in

plants growing under different light intensities.⁽⁶⁰⁾ Lhca2 and Lhca3 levels fluctuated strongly as a function of light intensity; the concentration of Lhca4 was reduced dramatically at high intensities, and only Lhca1 levels remained constant under all conditions. We proposed that weak binding between LHCI monomers and the instability of PsaK facilitated alterations in the composition of LHCI. Obviously, the weak interactions among the various LHCI monomers enable exchange of different individual monomers under various stress conditions or in different subdomains of the thylakoid. Indeed proteomic analysis in tomato indicates that several populations of photosystem I that differ in their LHCI composition may exist.⁽⁶¹⁾ The sequential evolutionary scenario depicted in Fig. 4 describes the necessary evolutionary steps that led to the formation of the supercomplex between the RC and LHCI. Fig. 5 shows a top view of plant PSI at 4.4 Å resolution.⁽⁵¹⁾ The assembly of proteins and pigments is optimized for obtaining an unprecedented quantum yield of nearly 1.0.⁽⁴⁾

After that supercomplex was formed, PSI was ready for further interactions with light-harvesting antenna proteins, and

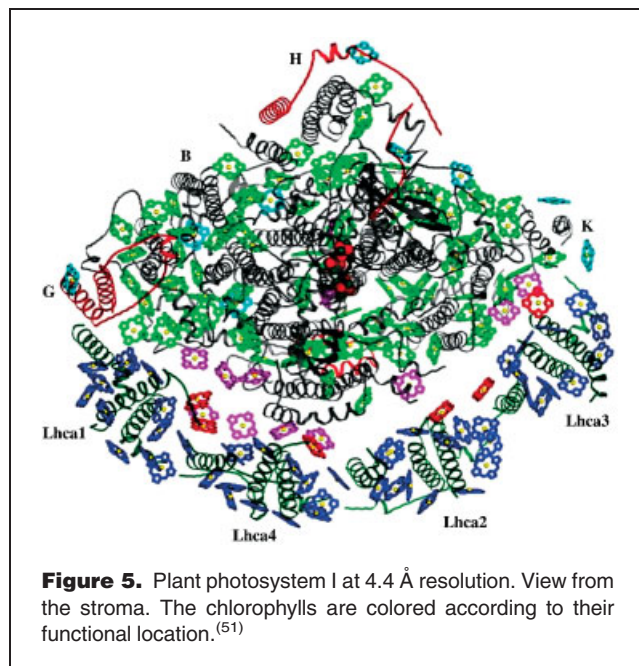


Figure 5. Plant photosystem I at 4.4 Å resolution. View from the stroma. The chlorophylls are colored according to their functional location.⁽⁵¹⁾

especially with LHCII under state-transition conditions. For that, the emergence of subunit H was crucial not only for preventing the possibility of trimer formation but also for provision of a template for LHCII binding.⁽⁶²⁾ Under strong light intensities or light preferentially absorbed by PSII, a sub-population of LHCII trimers is phosphorylated, dissociates from PSII and binds to PSI. This effect decreases the light harvesting by PSII and reduced the rate of its destruction and at the same time increases light harvesting by the resilient PSI that could be utilized for energy-requiring processes such as cyclic photophosphorylation.^(63,64) This regulated process is reversible and, at low light intensities, the phosphate is removed from LHCII, which dissociates from PSI and either moves back to PSII or is degraded. The role of phosphorylation in state-transition is still ill-defined.

Currently, a wide variety of photosynthetic systems operate in a vast number of organisms. One of the most striking observation revealed by the structure of plant PSI was the strict conservation of the chlorophyll positions in comparison to the cyanobacterial reaction center.⁽⁵¹⁾ During 1.2 billion years of separate evolution, an enormous number of random mutations took place, yet both cyanobacteria and higher plants maintained virtually the same chlorophyll arrangement. On the other hand, outside the “heart” of the major protein complexes that carry oxygenic photosynthesis, numerous adjustments to the hostile environment at the water surface and on land took place. The scenario painted in this review neglected all those important evolutionary events with the aim of pointing out possible major steps during the 3.5 billion years that shaped oxygenic photosynthesis.

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