Chapter 1

Introductory Chapter: Evolution of Photosynthesis

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Additional information is available at the end of the chapter

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1. Evolution of photosynthetic systems

Photoautotrophy is a complex process that some eukaryotic organisms can carry out. Some bacteria, algae, and plants share this capacity to transform light and carbon dioxide into biomass. Photosynthesis requires chlorophyll and other accessory pigments. There are three evolution lines that are recognized according to the types of pigments present in chloroplasts (specialized organelle where photosynthesis is performed) of these organisms (**Figure 1**).

From the above figure,

A. blue lineage is a primary endosymbiosis in which chlorophyll a (Chl *a*) is the only type of chlorophyll present, and chloroplast has cell walls with peptidoglycans is typical of cyanobacteria;

B. in the green lineage, a primary endosymbiosis also occurred, with the difference that in this lineage, Chl *a* is associated to chlorophyll b (Chl *b*). All chlorophyceae algae belong to this group and account for more than 6000 species. From these types of algae, terrestrial plants emerged with the same trait, that is, Chl *a* associated to Chl *b*; and

C. red primary endosymbiosis lineage has only Chl *a* as the only type of chlorophyll present but with different kinds of accessory red carotenoid pigments. Most marine algae belong to this group [1].

It is believed that a second endosymbiosis event occurred and can explain the presence of additional membranes in chloroplasts. The members of the secondary red endosymbiotic event constitute a very diverse group of organisms, and the most important from the pharmaceutical point of view are diatoms (Heterokonta) and the dinoflagellate (Alveolata) [2].

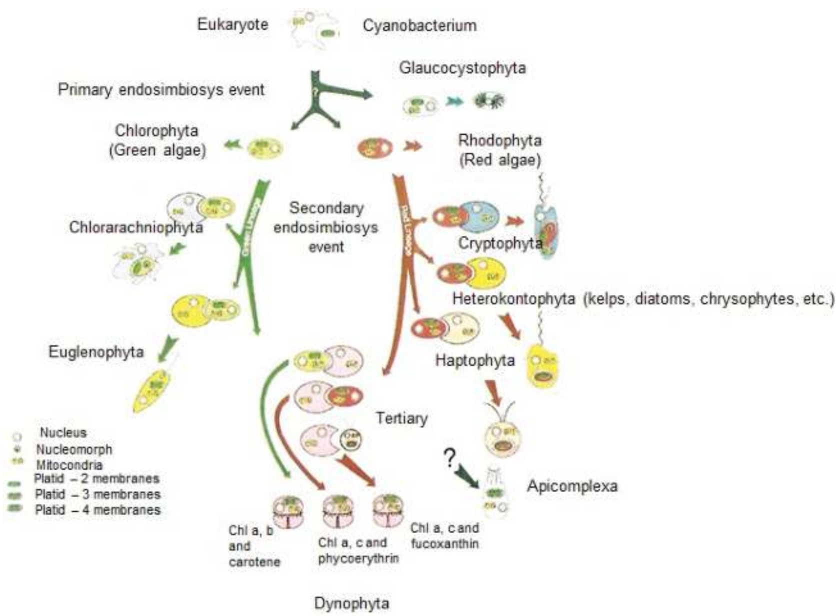

Figure 1. Schematic representation of the primary and secondary endosymbiosis events that gave origin to mayor taxonomic division of organisms that perform oxygenic photosynthesis. All terrestrial plants have their origin from a green primary endosymbiosis event. Most of the aquatic photoautotroph organisms are secondary endosymbionts with red plastids lineage [1].

What are the differences between algae and land plants? Algae are thallophyte, that means they lack of roots, leafs, stomas, and complex reproductive organs [3]. Algae do not form embryos, all reproductive structures are potentially fertile, and protective sterile cells are absent. Development of parenquimatic structures is only present in some groups and finally they exhibit sexual and nonsexual reproduction. By contrast, plants have an elevated level of differentiation like, for example, roots, leafs, vascular network xylem/phloem [4, 5], and other specific characteristics.

2. Protein structure for light harvesting and reaction centers evolved in different pathways

Proteins are encoded in the genetic code of every organism. But new genes must evolve from preexisting genes. This means that through mutations, new biological functions arise that make a protein with one enzymatic or structural function to gain a new function. Some authors have concluded that the proteins of photosynthetic systems may have had originally a photoprotective function. However, given the evolution process, different proteins have been recruited along with different pigment molecules ordered in arrays that enable efficient transfer of excitation energy into the reaction centers where charge separation takes place to fulfill the function of the photosynthetic process [6].

In this sense, reaction centers of photosystems I and II (PSI and PSII) of photosynthetic prokaryotes have similar elements and homologous structures, and therefore it is believed that photosynthetic reaction centers have evolved only once. On the contrary, light harvesting complexes are very different between taxa, share no sequence, and have very little structural similarity (**Figure 2**). This indicates that light harvesting complexes of higher plants, cyanobacteria, purple bacteria, and green sulfur bacteria evolved independently from each other [6, 7]. This means that genes of the antenna may have duplicated and

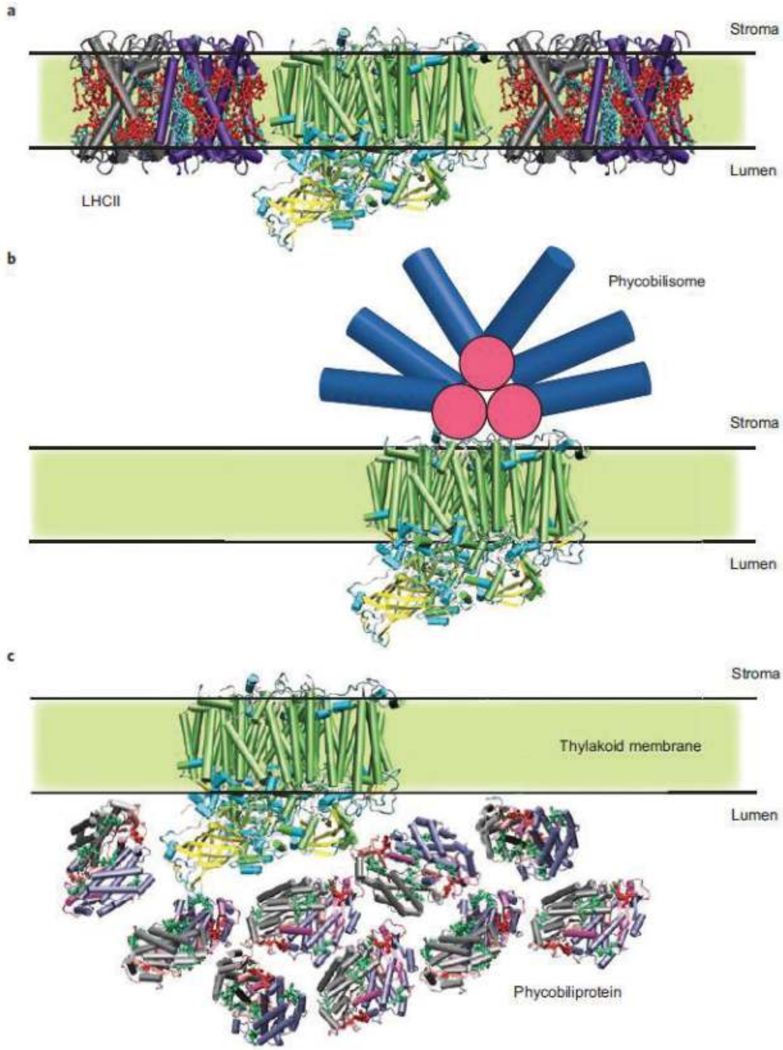

Figure 2. Representation of the reaction center and antenna structures of different taxa of photosynthetic organisms. Reaction centers have similar structures. While the organization of light harvesting antenna complexes relative to the photosynthetic membrane have very different structure. Examples shown are representative of: a, Higher plants and green algae. b, Cyanobacteria and red algae. c, Cryptophytes (Image from Scholes et al., 2011).

diverged, resulting in the multitude of antenna proteins that is present in photosynthetic organisms today. Although the evolution has been from photoprotection to light harvesting, in some branches of the evolutionary tree, there may have been a back conversion into a protective function.

Evolution of light harvesting complex proteins is considered an example of how new protein functions are created by recruitment, and if there is a selective advantage conferred with the new function, it will be fixed in the gene pool. The events creating the recent antenna structure may have took place around 300 million years ago, after which the genes have been fixed in the different organisms with slight variations with adaptive significance that we may find today [6].

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