



Review

Evolution and function of light harvesting proteins[☆]

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ABSTRACT

Photosynthetic eukaryotes exhibit very different light-harvesting proteins, but all contain membrane-intrinsic light-harvesting complexes (Lhcs), either as additional or sole antennae. Lhcs non-covalently bind chlorophyll *a* and in most cases another Chl, as well as very different carotenoids, depending on the taxon. The proteins fall into two major groups: The well-defined Lhca/b group of proteins binds typically Chl *b* and lutein, and the group is present in the 'green lineage'. The other group consists of Lhcr/Lhcf, Lhcz and Lhcx/LhcSR proteins. The former are found in the so-called Chromalveolatae, where they mostly bind Chl *c* and carotenoids very efficient in excitation energy transfer, and in their red algae ancestors. Lhcx/LhcSR are present in most Chromalveolatae and in some members of the green lineage as well. Lhcs function in light harvesting, but also in photoprotection, and they influence the organisation of the thylakoid membrane. The different functions of the Lhc subfamilies are discussed in the light of their evolution.

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Introduction

All photosynthetic organisms rely on different kind of light-harvesting systems to enhance the absorption cross section of their photosystems (PSs) and, more specifically, enlarge the spectral range used for photosynthesis. During evolution many different ways have evolved, *i.e.*, nowadays a number of different light harvesting complexes (Lhcs) exist, sometimes even in the same

species. This review focuses on the family of membrane intrinsic light harvesting proteins (Lhc) found in most eukaryotic photosynthetic organisms (Wolfe *et al.*, 1994). The most prominent and best studied member of this group is the major Lhc of photosystem (PS) II, LHCII, of higher plants. By analogy all light harvesting proteins of the family are predicted to have three membrane spanning α -helices, connected by loops of different sizes (Fig. 1). The protein family also comprises smaller (one or two helices) as well as larger (four helix) proteins (for a recent review see Engelken *et al.*, 2010). Except for the 4-helix protein PsbS none of them will be in the focus of this review.

All primary plastids derived from a common endosymbiosis event, where an ancient cyanobacterium became the later

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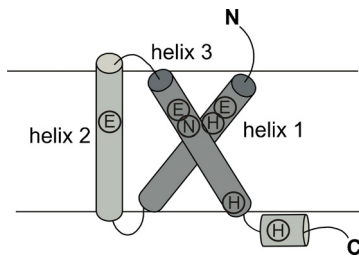


Fig. 1. Schematic representation of the structure of Lhc proteins with three membrane spanning α -helices in the thylakoid membrane. Conserved Chl binding sites are shown as well.

chloroplast. This led to the nowadays Glaucophytes, red and green algae and all groups which evolved from the latter like e.g. higher plants. In addition, endosymbiosis involving a cyanobacterium independently lead to the chromatophores of *Paulinella chromatophora* (Nowack et al., 2008), but this issue is not covered here. However, secondary endosymbioses led to further groups of organisms related either to the green or the red lineage. The former became endosymbionts for Chlorarachniophytes and Euglenophytes. From the latter all so-called Chromalveolates evolved, i.e., cryptomonads, haptophytes, heterokontophytes (including brown algae, diatoms and Xanthophyceae amongst others) and dinoflagellates (Archibald and Keeling, 2002) (Fig. 2). Although members of the Lhc family exist in all eukaryotic photosynthetic organisms, this review will focus on those taxa where sufficient functional and biochemical data are available, i.e. on (a) green alga, mosses and higher plants of the green lineage and (b) mainly on diatoms of the chromalveolate lineage.

Lhcs are proteins integral to the thylakoid membrane that consist of three membrane spanning α -helices and are binding chlorophylls (Chls) and carotenoids (Cars), whereby amount and kind of these pigments depend on the taxa. All Lhc are nuclear encoded. Structurally they are assumed to be very similar to each other (Fig. 1). Helix 1 and 3 are homologous and likely originated from internal sequence duplication (Green and Pichersky, 1994).

They form a kind of cross, induced by a conserved motive of Arg and Glu at each helix, forming two ion pairs and stabilising these two helices in the middle of the membrane in a left-handed supercoil (Kühlbrandt et al., 1994). Conserved Chl binding sites are located at helix 1 and 3, leading to a symmetric arrangement of Chls around this pair. Helix 2 is different from the others and runs almost perpendicular to the membrane. The space between helix 2 and the pair of helix 1 and 3 is crowded by pigments, which were also shown to be indispensable for maintaining the three-dimensional structure of the complexes. Despite these overall similarities, pigmentation as well as sequences differs. Only two high resolution molecular structures are available so far, from LHCII (Liu et al., 2004; Standfuss et al., 2005) and from CP29 (Pan et al., 2011), one of the minor antenna proteins of PSII. Both are structurally very similar supporting the hypothesis of the overall structural similarity of members of the Lhc-family.

What do we learn from sequence comparison?

During the last years many fully sequenced genomes of algae from different phyla became available, fuelling tremendous work on the evolution, but also on the function of Lhc proteins. Thus, many excellent reviews have dealt with the phylogenetic relationships of Lhcs lately (Dittami et al., 2010; Neilson and Durnford, 2010; Hoffman et al., 2011; Ballottari et al., 2012), which will only be shortly summarised here.

The Lhc gene family

The genes for the Lhc proteins fall into two well-defined groups: coding for the Chl *a/b* binding proteins of the green lineage, i.e., of green algae, mosses and higher plants, and the other Lhc sequences (see e.g. Neilson and Durnford, 2010) (Fig. 3a). The genes for Chl *a/b* binding proteins can be subdivided again into two major groups: the *Lhca* genes coding for proteins serving as PSI antenna, and *Lhcb* genes, coding for Lhcs associated with PSII. The remaining group in turn can be subdivided in *Lhcf*, *Lhcr*, *Lhcx* (former *L1818*

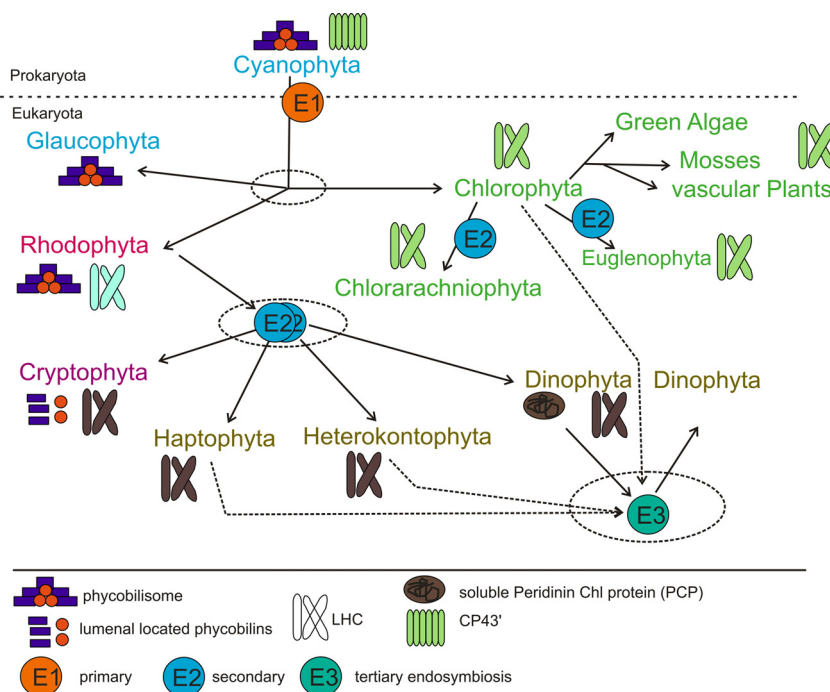


Fig. 2. Phylogenetic relationships between the different algal groups and their light harvesting systems. Phylogenetic relationships still under debate are marked by a circle, dotted lines point out alternative routes for tertiary endosymbioses, see text for detail.

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