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Review article

Structural and evolutionary aspects of algal blue light receptors of the cryptochrome and aureochrome type☆

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ABSTRACT

Blue-light reception plays a pivotal role for algae to adapt to changing environmental conditions. In this review we summarize the current structural and mechanistic knowledge about flavin-dependent algal photoreceptors. We especially focus on the cryptochrome and aureochrome type photoreceptors in the context of their evolutionary divergence. Despite similar photochemical characteristics to orthologous photoreceptors from higher plants and animals the algal blue-light photoreceptors have developed a set of unique structural and mechanistic features that are summarized below.

1. Introduction

The reception of light is an almost ubiquitous feature among organisms of prokaryotic and eukaryotic origin. Especially when their natural habitats *i.e.* aquatic systems, land surfaces or hosts for symbiotic and parasitic life styles are characterized by changing illumination conditions. The reception of blue light (BL) by photosynthetic organisms that thrive in water is of particular importance due to its large penetration depths in open oceans compared to other light qualities (red, green). Altering blue/green or blue/red intensity ratios can furthermore provide positional habitat information, *e.g.* towards coastal waters, where green light is significantly more effective at penetrating the water column.

Terrestrial plants, which originated from green algae about 450 Ma ago (Clarke et al., 2011), have only three different types of BL receptors, cryptochromes, phototropins and members of the Zeitlupe family (Christie et al., 2015). In contrast algae, *i.e.* photosynthetic eukaryotes living in aquatic systems, have originated more than 1500 Ma ago (Yoon et al., 2004). One prominent type of BL photoreceptors is represented here by the flavin-chromophore dependent cryptochrome-photolyase family (CPF). Photolyases, which are ubiquitously found in algae, have an enzymatic function by catalyzing the repair of UV lesions within DNA, namely of cyclobutane pyrimidine dimers (CPD) or (6-4) pyrimidine-pyrimidone photoproducts (Essen, 2006). This makes photolyases essential algal components for maintaining genome integrity due to the unavoidable presence of sun-derived UV radiation. In contrast, the structurally related cryptochromes act just as signaling proteins (Chaves et al., 2011) and are likewise found in all branches of photosynthetic eukaryotes. For comparison phototropins that act as light-activated protein kinase have only been described in green algae, the direct predecessors of land plants (Huang and Beck, 2003; Prochnik et al., 2010; Veetil et al., 2011). Although major parts of phototropin-mediated downstream signaling pathways are still unresolved in plants, the ortholog from the green alga *Chlamydomonas reinhardtii* can functionally replace its plant counterpart (Onodera et al., 2005).

Given their wide occurrence and diversification, additional BL photoreceptors can be found in algae. One example is the blue-light activated adenylyl cyclase PAC from *Euglena gracilis* (Iseki et al., 2002) that is associated with the eyespot of this flagellated species. Its flavin-comprising photoreceptor domain belongs to the BLUF (blue light using FAD) family, whose members otherwise occur in bacterial species (Masuda, 2013). Finally, even non-flavoprotein BL photoreceptors occur in algae. One type of BL photoreceptors actually belongs to the family of canonical phytochromes (Anders and Essen, 2015), which harbor a tetrapyrrole chromophore within their photosensory module. In plants, fungi and bacteria these phytochromes with a complex photosensory module consisting of PAS-, GAF- and PHY-domains are well known for their ability to undergo photochromic transitions between red and far-red light-sensitive states. Instead, orthologs from glaucophytes such as *Cyanophora* and *Gloechaete* show blue/far-red and blue/red transitions, respectively, whereas other algal phytochromes can cover different parts of the visible/near-IR spectrum (Rockwell et al., 2014). Another well-studied type of flavin-independent BL photoreceptors is represented by channelrhodopsins, a class of microbial

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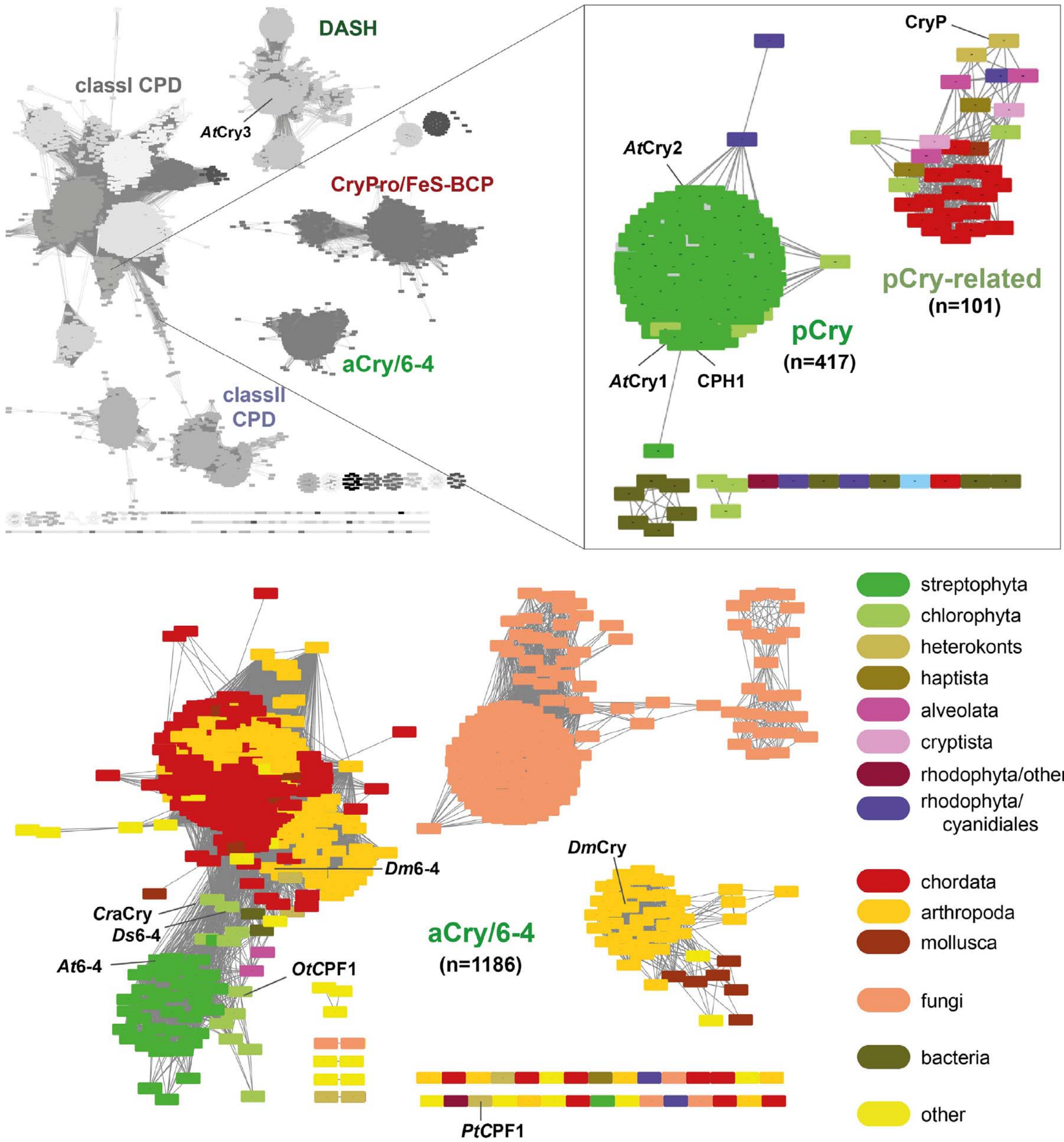

Fig. 1. Sequence-similarity network analysis (Gerlt et al., 2015) of the CPF with 13779 orthologs (Jan. 2017) using PFAM families PF00875 and PF04244. Left, each of the 7503 independent nodes represents sequences with more than 90% sequence identity, the edges correspond to BLAST E-value scores of below 10^{-90}. Obviously, the CPF dissolves in a set of highly distinct subfamilies. Right, view of the pCry and pCry-like cryptochromes after reclustering. Bottom, view on the family of animal-like cryptochromes/6-4 photolyases after decreasing the E-value cutoff to 10^{-150}. Used accession codes including further information are found in the Supplementary Information for the aCry/(6-4) photolyases as well as pCry and pCry-like orthologs.

rhodopsins with a photoisomerizable retinal chromophore that occur in flagellated green algae and mediate mostly proton/cation flow for triggering plasma membrane depolarization (Schneider et al., 2015). Finally, a distinct class of microbial rhodopsins in green algae is fused with a C-terminal histidine kinase domain and a response regulator and apparently function *via* a form of two-component signaling (Luck et al., 2012; Luck and Hegemann, 2017).

In this review, we will focus only on flavin-comprising cryptochromes and aureochromes that have been extensively studied during the last few years by others and us with biophysical and structural approaches. Other aspects of algal photoreceptors, which are not covered in this review, are covered elsewhere in depth (Duanmu et al., 2017; Fortunato et al., 2015; Hegemann, 2008; Arash Kianianmomeni and Hallmann, 2014; Suetsugu and Wada, 2013).

2. Dual function cryptochromes – a new class of photoreceptors found in algae

Cryptochromes have been evolutionary derived multiple times, either from class I CPD photolyases, like the plant and DASH-type cryptochromes, or from (6-4) photolyases as the animal-like cryptochromes (Fig. 1). The common feature between photolyases and cryptochromes is their ability to subject their inbuilt FAD chromophore to BL-induced photoreduction from an oxidized state (FAD) to a semi-reduced form ($FAD^{\bullet -}$, $FADH^{\bullet}$) and, in the case of photolyases, to the fully reduced $FADH^{-}$ state (Chaves et al., 2011). The mode of light-dependent downstream signaling by many cryptochromes has not yet been entirely understood in structural terms, although a multitude of light-dependent interactors have been identified for plant- and animal-like cryptochromes (pCry and aCry). For example, the animal type I cryptochrome