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The family of phytochrome-like photoreceptors: diverse, complex and multi-colored, but very useful

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Bilin-dependent GAF domain photoreceptors cover the whole spectrum of light with their absorbance properties. They can be divided into three groups according to the domain architecture of their photosensory module. Group I and Group II harbor phytochromes with PAS-GAF-PHY and GAF-PHY domain architecture, respectively. Group III consists of stand-alone GAF domain photoreceptors, the cyanobacteriochromes. Crystal structures of all three groups are now available to shed light on possible downstream signaling pathways. Structures of Group I and III photoreceptors in both states display changes in the secondary structures during photoconversion. The knowledge about the photoconversion in phytochromes and CBCRs make them promising targets for applications in life science and synthetic biology.

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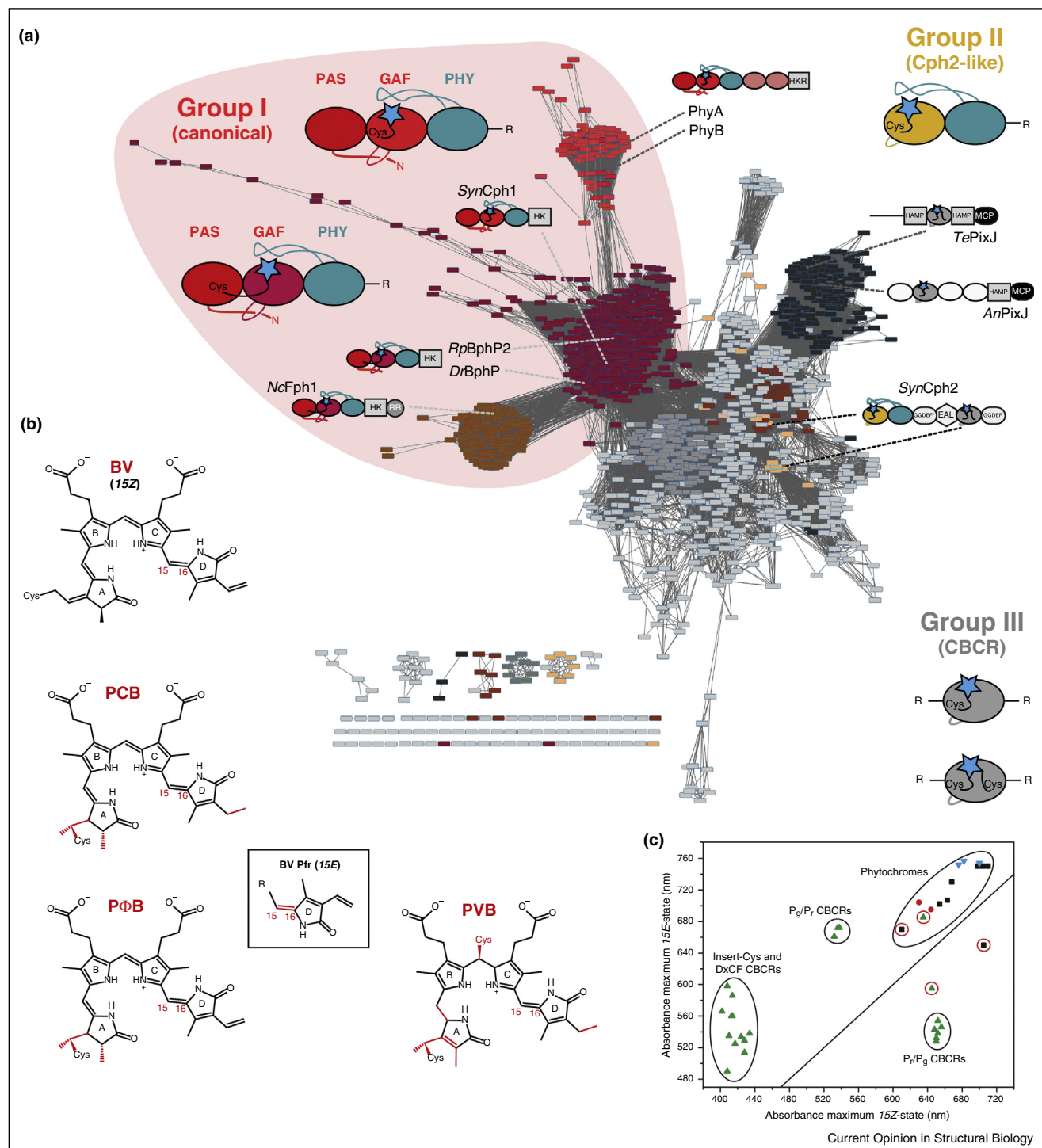
Introduction

Light perception allows life to adapt to changing illumination, for example, for controlling morphogenesis, photosynthesis or avoidance of harmful radiation. Phytochromes utilize bilins as chromophore and occur in most kingdoms of life, for example, algae, plants and cyanobacteria, as well as in non-photosynthetic organisms such as bacteria and fungi, but interestingly not in animals and archaea [1]. Their chromophore senses two different light qualities by adopting two stable, photoconvertible isomers: In plant, fungal and many bacterial phytochromes the P_r state absorbs red light to convert to the P_{fr} state, whereas the latter converts back by far-red light absorption. Furthermore, conversion can proceed independently of light as dark reversion [1]. Rockwell *et al.* [2] classified GAF domain photoreceptors with bilin

chromophores into three subfamilies dependent on their common domain architecture (Figure 1a). Group I includes canonical phytochromes whose sensory region adopts a PAS-GAF-PHY domain architecture. Firstly discovered in plants this domain organization is characteristic of bacterial, algal and fungal phytochromes as well (Figure 1a). One consequence of their complex topology is a figure-of-eight knot structure, where the variable N-terminus is threaded through an elongated loop of the GAF domain [3,4] (Figure 2a). Cyanobacteria harbor diverse phytochrome-like photoreceptors of Groups II and III (Figure 1a). Cyanobacterial phytochromes of Group II (Cph2) lack only the N-terminal PAS domain, whereas Group III, the cyanobacteriochromes (CBCRs), form a diverse subfamily of bilin-binding stand-alone GAF domains. Together with their effector domains most of these phytochromes apparently exist as dimers. Accordingly, the crystal structures of their photosensory modules are often found as parallel or antiparallel dimers. Interestingly, the two photostates of Group III members can cover any region of light from ultraviolet (UV) to near infrared radiation (NIR).

As linear tetrapyrroles, bilins form long-lived excited states by their highly conjugated ring system [5] without being toxic to the cell while allowing enhancement and fine-tuning of their absorption by the protein environment. Bacteriophytochromes (BphP) and fungal phytochromes (Fph) link biliverdin IX α (BV), a degradation product of heme, autocatalytically to an N-terminal cysteine residue as chromophore. Bilin reductases catalyze BV reduction to the other phytybilins (Figure 1b), phytychromobilin (P Φ B) and phycocyanobilin (PCB) from plant and cyanobacterial phytochromes that are attached to a conserved cysteine in the GAF domain [3,4,6 \bullet]. The photocycle of these bilin chromophores depends on the $Z \rightarrow E$ and $E \rightarrow Z$ photoisomerization of their C15 = C16 double bond (Figure 1b). BV-binding phytochromes absorb NIR by their $15E$ -state and are thus the most red-shifted GAF-containing photoreceptors. So far, all bathyphytochromes (bathy-BphPs) that form P_{fr} as ground state belong to this group of BV-binding phytochromes. Compared to bathy-BphPs P Φ B-binding plant phytochromes are blue-shifted for their $15Z$ -states and $15E$ -states (Figure 1c). This is further pronounced in PCB-binding phytochromes of Groups I and II with the latter displaying the most blue-shifted absorbance maxima, especially in the P_r state [7]. In contrast, CBCRs undergo very diverse photocycles [8–15] with currently four major types: Two types have opposite photocycles

Figure 1



Domain architecture, chromophores and spectral diversity of members of the phytochrome family. **(a)** Sequence-similarity network of phytochrome-like GAF domains (INTERPRO entry 16032; edges correspond to pair-wise BLAST E -values of $<10^{-75}$; each node to sequences of $>70\%$ sequence identity) as calculated by the EFI-enzyme similarity web tool (efi.igb.illinois.edu/efi-est). Group I phytochromes are clustered in plant (light-red), bacterial (dark-red) and fungal (brown) subfamilies. PAS and PHY domains are depicted in red and green, respectively. Blue stars indicate the bilin chromophore and the location of the cysteine as chromophore attachment site that is either part of the GAF domain (light red) or the N-terminus (GAF domain: dark red). Red lines depict the knot regions, dark-green loops the tongue-region of the PHY domain. Effector domains are abbreviated by R; CBCRs (gray) may also have N-terminal domains. Domain organizations of Group I, II (orange) and III (gray, black) members including the effector domains are shown as ellipses and rectangles (PAS: red; effector domains: white, gray or black; HKR domain: histidine kinase related domain; *Syn*: *Synechocystis* sp. PCC 6803; *Nc*: *Neurospora crassa*; *An*: *Anabaena* sp. PCC 7120; *Te*: *Thermosynechococcus elongates*; *Rp*: *Rhodospseudomonas palustris*).

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