Photoreceptive Proteins and Their Evolution

13

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13.1 Introduction

Many of the photoreceptor molecules have two main parts: one light-sensing part and another part transmitting the signal, often by transfer of a phosphate group. These two parts may have different evolutionary histories and have been united at a later stage in evolution. Thus the signaling parts of two different photoreceptors, such as two protein domains acting as kinases, may be related, while the light-sensing parts may be unrelated. This makes it impossible to compose completely correct evolutionary relationships in the form of "trees."

In his book *In the Blink of an Eye*, Parker (2004) vividly describes how the "invention" of vision triggered the so-called Cambrian explosion, the rapid evolution by which all the animal phyla of the present-day fauna emerged within only a few million years (see also Parker 2011; Alvarez 2008). But long before the Cambrian explosion organisms were able to use light for gathering information about the world around them, and light has had an impact on evolution since the origin of life.

In a distant past, when our earliest ancestors inhabited the planet, there were no continents. An ocean covered all of the young Earth's surface except for volcanoes here and there. The ocean volume was probably about twice the present, and plate tectonics had not yet sculpted the Earth with high mountains and great ocean depths (Flament et al. 2008; Arndt and Nisbet 2012). Water transmits best light of short wavelength, from UV-A to blue. It is therefore not surprising that the earliest light-recording pigments had their absorption bands in this spectral region. Specializing at light of very high wavelength, as plant phytochromes or the vision of some fishes, is of more recent date. Even in the phytochrome superfamily of proteins, which we often regard as typical long-wavelength sensors, there are bacterial members that tune the bilin absorption to the blue-violet region of the spectrum (Narikawa et al. 2008), so this may be the original wavelength region for this photoreceptor family as well.

13.2 Problems with the Classification of Photoreceptors

Photoreceptors can be classified in various ways, according to:

1. Function, e.g., photoperiodism, stomata regulation, vision, phototaxis
2. Spectral coverage, e.g., ultraviolet-B, blue light, red light
3. Type of chromophore, e.g., flavine, retinal, bilin
4. Occurence in the cell, e.g., cell membrane, other membrane, cytosol, nucleus
5. Domain (e.g., PAS (Möglich et al. (2009), GAF, BLUF, LOV, EAL) structure (domain architecture) of the protein part
6. Overall tertiary and quaternary structure of the protein
7. Signal output, e.g., phosphorylation, reduction, or oxidation

To a certain degree some of these classifications are correlated, but the correlation is not strict. There are, for instance, photoreceptors with the same chromophore, but with completely different proteins. Cryptochromes and BLUF domain blue light sensors (Gomelsky and Klug 2002) both contain FAD as chromophore. Members of two families of rhodopsins without any sequence similarity have retinal as chromophore. The same protein may have two different functions, e.g., serve both as cryptochrome (light-sensing protein) and photolyase (repair enzyme) (Bayram et al. 2008). The amino acid sequence may be unrelated, but the overall protein structure related, as in the two families of rhodopsins. Proteins containing flavin (FMN or FAD) as chromophore are mostly active in the UV-A to blue spectral band, but in some cases in the green (Bouly et al. 2007; Wang et al.

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2013) or even red (Beel et al. 2012) parts of the spectrum. Finally, there are sensor proteins which have more than one chromophore. Thus Jiang et al. (1999) described a xanthopsin-phytochrome combination, and phototropin-phytochrome combinations (neochromes) have arisen at least twice during evolution (Suetsugo et al. 2005).

For these reasons and others it is difficult to find a completely logical and still useful classification of chromophores. We have chosen to divide the sensor proteins into eight major groups mainly based on type of chromophore and try to follow a phylogenetic classification within each of these main groups. We will use the following classification:
Cryptochromes
Rhodopsins
Xanthopsins (PYPs)
Phytochromes and phytochrome-like photosensors
Light, oxygen, voltage (LOV) domain-containing proteins
Sensor of blue light using FAD (BLUF) domain-containing proteins
Ciliate photoreceptors (stentorin-related)
Ultraviolet-resistance locus eight family (UVR8)

13.3 Photolyases/Cryptochromes

The function of the earliest representatives of this group seems to have been to act as photolyases, i.e., to repair damaged DNA by a light-dependent process. Only later did some members of the group acquire a role as photoreceptor pigments, and this switch of function has taken place more than once during evolution. Some of the proteins can function both as photolyase and as photoreceptor, such as one in the fungus *Aspergillus niger* (Bayram et al. 2008) [and one in *Trichoderma harzianum* (Berrocal-Tito et al. 2000)] so the distinction between photolyase and cryptochrome is diffuse. All members of this class contain an FAD chromophore that is involved in photochemistry, and most of them also contain a secondary chromophore that acts as an "antenna" that can collect light energy and transfer it to the FAD (Müller and Carell (2009). The antenna chromophore is in some cases 5,10-methenyl tetrahydrofolate (MTHF) (Öztürk et al. 2008). but can also be FMN, FAD, 8-hydroxy-5-deazaflavin, or 6,7-dimethyl-8-ribityl-lumazine (Geisselbrecht et al. 2012). The cryptochrome found in *Rhodobacter sphaeroides*, which carries the 6,7-dimethyl-8-ribityl-lumazine antenna chromophore, is special also because it has, in addition to FAD, an iron-sulfur cluster at the catalytic site Oberpichler et al. (2011).

The photolyase/cryptochrome superfamily has representatives in all three domains of life (Archaea, Eubacteria, and Eukaryota) and thus seems to have been present in the last common ancestor of present-day organisms, "LUCA." An alternative could be horizontal (lateral) gene transfer. Photolyase genes occur in virus (*Entomopoxvirinae*) that have been involved in horizontal transfer of photolyase genes among insects (Afonso et al. 1999; Nalcacioglu 2010; Biernat et al. 2011). Photolyase genes occur also in baculovirus (van Oers et al. (2004), in *Chordopoxvirinae* that infect vertebrates (Afonso et al. 2000), and in marine *Cafeteria roenbergensis* giant virus (Fischer et al. 2010) that infects zooplankton; researchers do not seem to think that lateral gene transfer has been important in the macroevolution and spread of these proteins.

There is no complete consensus regarding the phylogenetic relationships between the major classes of photolyases/cryptochromes, and different phylogenetic trees have been published (e.g., Lucas-Lledó and Lynch 2009; Rivera et al. 2012; Oberpichler et al. 2011; Kiontke et al. 2011; Asimgil and Kavakli 2012). Different authors also use different names for the various groups, which makes the literature somewhat confusing. We follow here, with simplification, the scheme from Rivera et al. (2012) (CPD and (6–4) refer to different kinds of DNA damage that are described in Chap. 22.):

1. Class 1 CPD photolyases
2.
   - 2.1. Class 2 CPD photolyases
   - 2.2. Plant cryptochromes (probably evolved from early form of 2.1)
3.
   - 3.1. Single DNA strand photolyases/DASH cryptochromes
   - 3.2.
     - 3.2.1. (6–4) photolyases
     - 3.2.2. Animal cryptochromes
       - 3.2.2.1. Insect type 1 + sponge + Cnidaria cryptochrome
       - 3.2.2.2. Insect type 2 + vertebrate cryptochrome

The above scheme indicates that cryptochromes have evolved from photolyases at least three times, i.e., plant cryptochromes from CPD photolyases, DASH cryptochromes from single strand DNA photolyases, and animal cryptochromes from (6–4) photolyases. The strange name DASH comes from the four genera in which representatives for the group were first found: *Drosophila*, *Arabidopsis*, *Synechocystis*, *Homo* (Brudler et al. (2003). As the name indicates, these proteins are widely distributed among eukaryotes, but there are also representatives from Eubacteria. Most of the proteins in category 3.1 above are probably only photolyases. One member with cryptochrome activity is *Fusarium fujikuroi* CryD DASH cryptochrome (Castrillo et al. 2013).

Essen (2006) points to the similarities between function in DNA repair and in photoreception. In both functions light-induced electron transfer is involved. So it is not surprising that some enzymes can carry out both functions, and a plant

photolyase may acquire cryptochrome function by substitution of a single amino acid (Burney et al. 2012). The separation between single-strand DNA photolyases and DASH cytochromes is not clear. Some authors regard these as two names for the same proteins rather than two groups of proteins.

From the above one could get the impression that the only roles for proteins in this superfamily are DNA repair and photoreception. However, many cryptochromes, including the human ones, serve other functions, especially as parts of circadian oscillators (Chap. 18) and as photo-magnets in animal orientation (Chap. 20).

Both the photolyase repair function and the cryptochrome light-sensing function depend on the light-induced electron transfer. For cryptochrome also blue-light-induced proton transfer, phosphorylation (Zuo et al. 2012) and conformational change (Kondoh et al. 2011) of the protein have been observed. The signaling state contains the FAD chromophore in the semiquinone state (Banerjee et al. 2007), but the signaling mechanism is not established (Chaves et al. 2011) and may differ between different kinds of cryptochrome. The downstream signaling of plant cryptochrome 2 involves at least two pathways (Liu et al. 2011).

13.4 Rhodopsins

Based on their structure, rhodopsins can be divided into two main groups, i.e., microbial (type 1) and animal (type 2) rhodopsins. Type 1 rhodopsins occur mainly in archaeans and fungi but also in some bacteria (Hoff et al. 1995; Jung et al. 2003) and some algae (see Ruiz-González and Marín 2004). Rhodopsins can also be classified according to function as ion-transporting, sensory, and others. The two classifications divide the rhodopsins in quite different ways. Rhodopsins that are structurally closely related can be found in organisms that are only very distantly related, indicating the occurrence of lateral (horizontal) gene transfer. Therefore it is not surprising that rhodopsin genes can also be found in viruses (Yutin and Koonin 2013). Furthermore, very different types of rhodopsin can be found in closely related organisms (or even within the same organism). This has contributed to making the elucidation of rhodopsin evolutionary history a difficult task.

Type 1 and type 2 rhodopsins share almost no amino acid sequences (Taylor and Agarwal 1993; Soppa 1994). However, all type 1 rhodopsins are clearly related as are all type 2 rhodopsins. From this one could draw the conclusion that they have independent origins, but by applying a method based on the probabilities of nucleotide replacement in DNA (Fitch 1970), Shen et al. (2013) could trace a distant relationship, and the theory of a common origin has been strengthened by the finding of Devine et al. (2013) that the structural

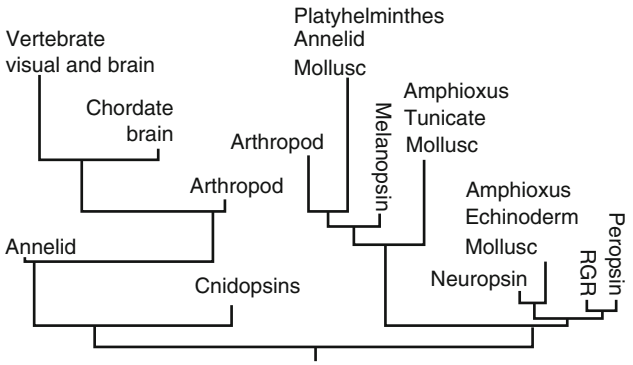

Fig. 13.1 Evolutionary tree of type 2 rhodopsins (Redrawn and simplified after Porter et al. 2012)

similarity cannot be explained by functional constraint. The retinal chromophore is attached to a lysine residue in both clades, but in different conformations. Shen et al. (2013) speculate that at some point during evolution the function as light sensors and the attachment of a chromophore have been abandoned, releasing the conservation of the chromophore-binding structure of the protein. The split between type 1 and type 2 rhodopsins must have taken place at least 1.5 billion years ago (Taylor and Agarwal 1993).

Of the rhodopsins in fungi some are of type 1 and others of type 2 (Novikov et al. 2012). Those of type 1 are rather different from those present in Archaea (Brown 2004; Washuk et al. 2005; Fan et al. 2011; Ito et al. 2012), while those of type 2 fall among the metazoan ones. Rhodopsins usually have one (as the human ones) or two photoactive states (and either the 11-cis or the all trans form or both can be photoactive), but one kind of type 1 rhodopsin has been shown to possess a complicated photocycle with three photoactive states (Sudo et al. 2011; Inoue et al. 2012). The evolution of type 1 rhodopsins is further discussed by Ruiz-González and Marín (2004) and Zhang et al. (2011).

The origin of type 2 rhodopsins (Fig. 13.1), also called GPCR, can be traced back to the ancestor of opisthokonts (1100 MYA) (Krishnan et al. 2012).

Type 2 rhodopsins can be phylogenetically divided into seven subfamilies, and only one of them is involved in imaging vision. According to Feuda et al. (2012) the first group to branch off from the path that leads to human rhodopsins is the one that contains melanopsin and placopsin. Placopsin is a pigment present in placozoans, a kind of primitive eyeless animal, possibly on the first evolutionary track branching off from the path leading to other Metazoa (Osigus et al. 2013). Melanopsin is involved in the setting of the biological clock by light (Chap. 18) in many different kinds of animal. This phylogeny differs from that of other authors, such as Terakita (2005) who regard the so-called rhabdomeric rhodopsins as splitting off together with the melanopsins.

13.5 Photoactive Yellow Proteins (PYPs, Xanthopsins)

The first photoactive yellow protein (PYP) was discovered in 1985 (Meyer 1985) in the purple photosynthetic bacterium *Ectothiorhodospira halophila* (later renamed *Halorhodospira halophila*). Soon thereafter it was found to exhibit light-induced changes reminiscent of rhodopsin (Meyer et al. 1987). Now 140 related gene sequences are known from a variety of bacteria, but the corresponding proteins have not been characterized in all cases. No PYP genes are known from Archaea or Eukaryota.

PYP genes can be classified into eight main groups based on base sequences. This classification is completely different from the classification of the bacteria in which the proteins occur (Kumauchi et al. 2008; Meyer et al. 2012), indicating widespread horizontal transmission of the PYP genes. Thus the distribution of the eight PYP groups of Meyer et al. (2012) among bacterial taxa is as follows:

I. α-, γ-, and δ-Proteobacteria
II. α- and γ-Proteobacteria
III. Bacteroides and Spirochaetes
IV. α-Proteobacteria
V. Bacteroides, β-, γ-, and δ-Proteobacteria
VI. δ-Proteobacteria
VII. γ-Proteobacteria
VIII. α–Proteobacteria

The PYPs are involved in a great number of functions, and within a single one of the groups above there may be representatives having different functions. The chromophore is p-hydroxy-cinnamic acid, which is bleached by a trans-cis isomerization upon exposure to light and quickly reverses in the dark (Meyer et al. 2012). It is thought that signal transmission occurs by association of some protein with the PYP in the bleached state.

Most PYPs occur in proteobacteria, but there are also two *Bacterioides* species and one spirochaete known to contain PYP. They appear sometimes to be involved in phototaxis, but in *Rhodospirillum centenum* it regulates a polyketide synthase gene.

Some proteins contain both a PYP part and a bacteriophytochrome domain (Kyndt et al. 2007, 2010).

13.6 Phytochrome-Like Photoreceptor Proteins

Phytochromes were first discovered in land plants and then also in green algae. These first discovered members of the superfamily are receptors specialized for red and far-red light. Now we know that this type of protein occurs in all domains of life and that, in general, they are tuned (spectrally adapted) to shorter wavelengths.

Phytochromes are photochromic, i.e., change absorption spectrum when they are exposed to light, and do this in a reversible way, such that they can change in one way under one kind of light, and in the opposite way under another kind of light. More about this in Chap. 11. They are proteins having an open-chain tetrapyrrole as chromophore. This chromophore is slightly different in different kinds of phytochromes. Bacteria utilize biliverdin, while cyanobacteria and plants use phycocyanobilin or phytochromobilin. The wavelength of the main absorption peak of the ground ("dark") state varies from 400 nm to 754 nm depending on species (Auldridge and Forest 2011), so the tuning range is comparable to that of rhodopsins. In most cases the active form absorbs at longer wavelength than the inactive form, but the reverse is found in some cases.

One hypothesis concerning the origin of this superfamily of photoreceptors is that the proteins originated as bilin sensors (and, indirectly, as sensors of molecular oxygen). The bilin requires oxygen for its formation, so this type of sensor is likely to have originated later than oxygenic photosynthesis.

The superfamily consists of two main groups of photoreceptors (also some non-photoreceptor proteins are closely related):

1. Cyanobacteriochromes
2. Phytochromes
   2.1. Bacteriophytochromes
   2.2. Cyanobacterial phytochromes
   2.3. Fungal phytochromes
   2.4. Plant phytochromes
   2.5. Phytochrome-like proteins

As many other photoreceptor proteins, phytochromes can be clearly divided into a light-sensing ("signal input") part on the N-terminal side and one "signal output" part on the C-terminal side. The latter, in the active form, has kinase activity. All phytochrome-like proteins contain two typical domains, a PHY domain and a GAF domain. GAF stands for cyclic guanosine monophosphate phosphodiesterase/adenylate cyclase/formate hydrogen lyase. The GAF domain is of very ancient origin and occurs in many other proteins, too (Aravind and Ponting 1997; Anantharaman et al. 2001). As the name implies it binds cyclic guanosine monophosphate (cGMP). Although there is no sequence homology, some GAF domains have an unexpected structural similarity to some PAS domains (Ho et al. 2000). Although the light-sensing part of plant phytochromes is derived from the corresponding in cyanobacteria, the output part (the kinase)

probably is not. Plant phytochromes thus are, in a sense, chimeric.

The cyanobacteriochromes (at least those in the DXCF-cyanobacteriochrome subfamily) differ from the phytochromes by forming a photolabile thioether linkage between the chromophore (in this case phycoviolobilin) and a cysteine in the apoprotein in addition to the stable cysteine-chromophore linkage common for all proteins in the superfamily (Burgie et al. 2013).

The sensor proteins in this category signal by transphosphorylation. The prokaryotic versions are histidine kinases, while the plant phytochromes phosphorylate serine and threonine. More about this in Sect. 12.2.5.

13.7 BLUF Photoreceptors

BLUF stands for **B**lue **L**ight photoreceptor **U**sing **F**AD, but the concept does not include the likewise FAD-containing cryptochromes. They are defined by a typical amino acid sequence in the FAD-binding BLUF domain. This type of photoreceptor is one of those which (as also the plant UV-B receptor UVR8) long evaded discovery. BLUF receptors were first reported almost simultaneously in a prokaryote, the proteobacterium *Rhodobacter sphaeroides* (Braatsch et al. 2002; Masuda and Bauer 2002), and in a eukaryote, *Euglena gracilis* (Iseki et al. 2002). After this BLUF domains have been identified in ca 10 % of all fully sequenced bacteria. A BLUF photoreceptor is involved in the regulation of photosynthesis in *Rhodobacter sphaeroides*, in phototaxis in the cyanobacterium *Synechocystis sp*. PCC6803 and in *Euglena gracilis*, and in the latter it also mediates light-induction of adenylyl cyclase activity. Otherwise the functions are so far unknown. Mandalari et al. (2013) have constructed a BLUF phylogeny showing a few major clades containing several members, while many other BLUF domains remain as isolated single-member clades.

13.8 LOV Domain Photoreceptors

The workings of this type of photoreceptor have been observed as long as people have noticed the ability of plants to grow toward light, an ability described in more detail by Darwin and Darwin (1881). But the nature of the photoreceptor for this ability was long debated. Both flavin compounds and carotenes have absorption spectra that approximately match the action spectrum for phototropism. Finally the mystery was solved by a research team lead by Winslow Briggs at the Carnegie Institution of Washington (Huala et al. 1997; Christie et al. 1998) who identified the receptor as a novel type of flavoprotein, later named phototropin 1 and found to be a member of a widespread family called LOV domain proteins, distributed over all three domains of life (Krauss et al. 2009). The chromophore is flavin mononucleotide (FMN), in contrast to the redox-active chromophore (FAD) in cryptochromes.

In plants and algae there are three types of LOV domain photoreceptors, namely, phototropin, Zeitlupe, and aureochrome (Wada and Suetsugu 2013), and other types occur in bacteria (Losi 2004). Unlike phytochrome and cryptochrome, phototropins characteristically localize to the plasma membrane (Christie 2007). Kinetically LOV proteins are divided into two groups, i.e., slow-cycling and fast-cycling.

Eukaryotic LOV domains are divided into six clades: PHOT LOV1, PHOT LOV2, AUREO LOV, PASLOV PAS, PASLOV LOV, and Hap LOV (Ishikawa et al. 2009). AUREO LOV is subdivided into clades 1, 2, and 3 based on bZIP domain sequences.

13.9 Ciliate Photoreceptors

Some ciliates within the order Heterotrichida exhibit photoresponses which are mediated by any of the main classes of photoreceptors described above. They contain proteins having chromophores related to the well-known plant compound hypericin (Fig. 13.2). The latter is produced by *Hypericum* species and has been used for medical purposes. The ciliates most thoroughly investigated with respect to their photoreactions and photoreceptors are those belonging to genera *Stentor, Maristentor*, and *Blepharisma*. Only for these genera it has been established that the photoreactions are associated with the ciliate-specific photoreceptors described below, while the situation in other cases is at present uncertain, since the organisms contain also rhodopsins and flavin compounds (reviewed by Cadetti et al. 2000). For *Stentor*, action spectroscopy shows stentorin to be the active chromophore for photophobic response (Wood 1976), and for *Blepharisma*, blepharismin (Matsuoka et al. 1992). Another evidence supports the latter conclusion (Matsuoka et al. 1995). The proteins to which the chromophores are attached have so far not been well characterized. The stentorin chromophore is linked to a 50 kDa apoprotein. Several substances have been proposed as parts of a signal transduction chain, but the information so far is very scanty. Because the phylogenetic distribution of this type of photoreceptor is so limited, it is probably of rather late origin compared to other photoreceptors.

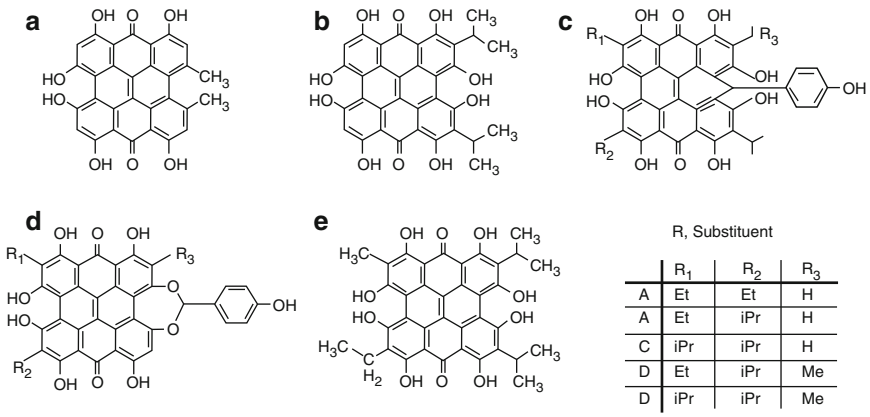

Fig. 13.2 Structures of (**a**) hypericin, (**b**) stentorin, (**c**) blepharismin, (**d**) oxyblepharismin, and (**e**) plausible formula for maristentorin (From Mukherjee et al. 2006)

13.10 The Plant UV-B Receptor, UVR8

It has long been realized that plants possess a UV-B-specific photoreceptor, but only recently has it been characterized on the molecular level. This photoreceptor differs from all others enumerated above by having no non-amino acid chromatophore (Christie et al. 2012; Wu et al. 2012). The UV-B absorption is achieved by a large number of aromatic amino acids in the protein, of which several tryptophan residues are so closely positioned that the π-orbitals overlap. Absorption of UV-B radiation around 290 nm causes the protein to be monomerized from the dimeric state and translocated from the cytoplasm to the nucleus, where it interacts with other proteins and affects gene transcription (see Chap. 11). The photoreceptor is widespread among plants. The green alga *Chlamydomonas* has a similar protein (Christie et al. 2012) that probably has the same function. Related proteins with other functions occur in other organisms, including animals. One of these is RCC1, a regulator of DNA replication (Dasso et al. 1992; Dasso 1993) and mitosis. It thus appears that the UVR8 photoreceptor is specific for green plants, but has an ancient ancestry.

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