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Algae hold clues to eukaryotic origins of plant phytochromes

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Plants use phytochrome photoreceptors to determine their proximity to other plants, to gauge the intensity of vegetational shade, and to determine whether they are near the surface of bare soil or buried under leaf litter. In each case, phytochromes are measuring the ratio of red (R) to far-red (FR) light in the environment, and plants are using the information to elicit critical developmental responses, such as delaying the germination of seeds under a leaf litter or growing taller and reproducing earlier when neighbors impinge on their access to light (1). In open environments, the R:FR ratio is near 1; under a dense canopy or under leaf litter, it may fall to as low as 0.2, due to absorption of most of the light available for photosynthesis (400–700 nm) by plant pigments. Similarly, in soils, short wavelengths are scattered in the first few millimeters, whereas longer wavelengths penetrate more

deeply. The ability of phytochrome to measure the R:FR ratio arises from its photo-reversibility. It interconverts between two forms, a red absorbing form (Pr) and a far-red absorbing form (Pfr), which occur in a dynamic equilibrium determined by the R:FR ratio in ambient light. Although phytochromes have diversified independently in mosses, ferns, and seed plants (2), the different members of the phytochrome family in these lineages and across plants have very similar absorption maxima, centered on 660 nm for Pr and 730 nm for Pfr. For plants in terrestrial environments, the importance of the R:FR ratio is universal, and the spectral properties of phytochromes appear to have changed little through the ~500 million years of land plant evolution. The origins of phytochrome, however, have remained mysterious. In PNAS, Duanmu et al. (3) provide evidence that contradicts the prevailing

theory, which holds that plant phytochromes were acquired by gene transfer from the cyanobacterial endosymbiont (EGT) that gave rise to chloroplasts.

Until relatively recently, phytochromes were unknown outside of land plants, except in closely related streptophyte algae. This changed with the discovery of phytochrome-like proteins in cyanobacteria (4, 5), and thereafter, with the discovery of a vast diversity of phytochrome-related proteins in bacteria, fungi, diatoms, and brown algae. Among these are phytochromes tuned to yellow, green, blue, and violet wavelengths, as well as to R and FR, and in some, the bilin chromophore confers redox instead of light sensing abilities (6). Early phylogenetic analyses to understand diversity in this larger phytochrome superfamily were inconclusive regarding relationships among plant and bacterial phytochromes, but they suggested that cyanobacterial phytochromes were more closely related to bacterial than to plant phytochromes (7, 8). In one study, the N-terminal photosensory core and the C-terminal regulatory region were analyzed separately, providing strong evidence that C termini of plant and cyanobacterial phytochromes were not closely related (9). Together, the results of these studies contradicted EGT. Herdman et al. (10) also failed to resolve relationships among cyanobacterial, bacterial, and plant phytochromes, but nonetheless argued that similarity among the three types resulted from EGT. Vierstra and Davis (11) argued for EGT based on examination of sequence alignments and the organization of domains, and EGT has remained the favored hypothesis.

A major obstacle to resolving the question of plant phytochrome origins has been the lack of phytochrome data from a greater diversity of eukaryotes, especially from eukaryotes in the Archaeplastida, Viridiplantae (green plants and algae), Rhodophyta (red algae), and Glaucophyta (microalgae with Cyanobacteria-like chloroplasts) (relationships

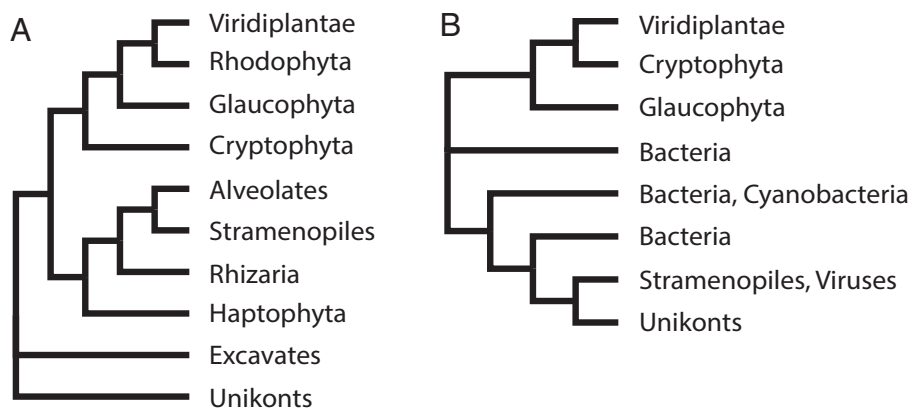


Fig. 1. (A) Simplified unrooted tree of eukaryotes [after Burki et al. (16)] showing the major lineages: Viridiplantae (green algae and land plants), rhodophytes (red algae), glaucophytes (microalgae with Cyanobacteria-like plastids), Cryptophytes and Haptophytes (unicellular algae, some that retain plastids obtained via secondary endosymbiosis), Alveolates (dinoflagellates, ciliates, and ampicomplexan parasites), Stramenopiles (water molds, diatoms, brown and golden algae), Rhizaria (including amoebafagellates and radiolarians), Excavates (free-living parasitic and unicellular forms, including parasitias such as *Euglena*, *Trypanosoma*, and *Giardia*), and Unikonts (including animals and fungi). (B) Simplified unrooted tree of phytochromes in prokaryotes and eukaryotes (3). In stramenopiles, phytochromes are found in diatoms and brown algae. In unikonts, phytochromes are found in fungi. The diverse bacterial lineage that is sister to unikonts and stramenopiles includes photosynthetic, nitrogen-fixing, and plant pathogenic bacteria, including the common vector for genetic transformation of *Arabidopsis thaliana*, *Agrobacterium tumefaciens*. Cyanobacteria are sister to another, similarly diverse clade of photosynthetic and heterotrophic bacteria that includes the extremophile *Dienococcus radiodurans* and methylotrophic species of *Methylobacterium*. The remaining, unplaced bacterial lineage is exclusively photosynthetic.

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among eukaryotes are summarized in Fig. 1A). Duanmu et al. address this by sequencing and assembling transcriptomes from a glaucophyte and several prasinophyte algae and by including phytochrome sequences from these assemblies in a matrix with a good representation of published eukaryotic and prokaryotic phytochromes. Two important phylogenetic results emerge from their analyses of the three domains of the N-terminal photosensory core module (PCM). First, there is clear evidence for two independent origins of eukaryotic PCM; sequences from diatoms and brown algae (stramenopiles) and fungi form one lineage nested within bacteriophytochromes, whereas sequences from Archaeplastida and the cryptophyte, *Guillardia theta*, form another monophyletic lineage (Fig. 1B). The distinctness of the two eukaryotic phytochrome lineages is also reflected in the domain structures of their C-terminal regions. Second, cyanobacterial PCM are nested within prokaryotic PCM and are more closely related to bacterial, fungal, and stramenopile PCM than they are to archaeplastid PCM. This suggests that the heterotrophic ancestor of Archaeplastida may have possessed a phytochrome before the primary endosymbiotic event, or that EGT from the cyanobacterial endosymbiont occurred very early, before the divergence of Viridiplantae, Rhodophyta, and Glaucophyta from one another. The photosensory core of plant phytochromes thus has been evolving independently from that of cyanobacterial phytochromes for up to 1,200 million years, based on fossil records for green algae (12).

Notably, phytochromes have not been detected in red algal genomes, and in this context, the position of the cryptophyte *Guillardia theta* in the PCM trees (Fig. 1B) is interesting. Cryptophytes are among the several organisms that obtained plastids from red algae via a secondary endosymbiosis event (13). Rhodophytes are sister to Viridiplantae in the organismal tree, and this is the position of *G. theta* in the PCM tree of Duanmu et al., suggesting that phytochromes were present in red algae before the secondary endosymbiosis event. The structure of one of the *G. theta* phytochromes is consistent with this

scenario. It is the only phytochrome thus far detected that shares with Viridiplantae phytochromes a double internal PAS (PerARNT-Sim) repeat that separates the PCM from the C-terminal histidine-kinase-related module (HKM). Glaucophytes have a single internal PAS (14), whereas prokaryotic phytochromes lack an internal PAS (6). The phylogenetic analysis of the HKM by

Duanmu et al. demonstrate that the strategic choice of a relatively small number of study organisms can greatly advance our understanding of phylogeny and function.

Duanmu et al. was less conclusive. The results do not provide statistically strong support for a close relationship between green plant and cyanobacterial HKM, but they do suggest that the history of glaucophyte HKM differs from that of cryptophytes and Viridiplantae. Puzzles clearly remain to be addressed in this regard.

Within Viridiplantae, however, the findings of Duanmu et al. fill important gaps in our knowledge of phytochrome evolution and function. Their focus on

prasinophyte algae allowed them to establish that diverse members of the chlorophyte algae do possess phytochromes, despite their absence in sequenced genomes of species from *Chlamydomonas*, *Chlorella*, *Volvox*, *Bathycoccus*, and *Ostreococcus*. Moreover, they establish that phytochromes of prasinophytes share light-mediated signaling mechanisms with those of land plants, including strong diurnal regulation of gene expression preceded by redistribution of phytochrome from the cytoplasm to the nucleus. Unlike plant phytochromes, however, prasinophyte phytochromes are tuned to wavelengths that travel farther through seawater than do R and FR, and their HKM retain histidine kinase catalytic activity.

As significant players in carbon cycling, prasinophytes are ecologically important in their own right. Phylogenetically, they also occupy a key position. They split earlier from the chlorophyte branch of Viridiplantae than do the model organisms such as *Chlamydomonas reinhardtii*, *Chlorella vulgaris*, and *Volvox carteri* (12), and they retain certain features of land plants not retained by the model species (15). Altogether, the results of Duanmu et al. demonstrate that the strategic choice of a relatively small number of study organisms can greatly advance our understanding of phylogeny and function.

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