



# Evolution of circadian clocks along the green lineage

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## Abstract

Circadian clocks govern temporal programs in the green lineage (Chloroplastida) as they do in other photosynthetic pro- and eukaryotes, bacteria, fungi, animals, and humans. Their physiological properties, including entrainment, phase responses, and temperature compensation, are well conserved. The involvement of transcriptional/translational feedback loops in the oscillatory machinery and reversible phosphorylation events are also maintained. Circadian clocks control a large variety of output rhythms in green algae and terrestrial plants, adjusting their metabolism and behavior to the day-night cycle. The angiosperm *Arabidopsis* (*Arabidopsis thaliana*) represents a well-studied circadian clock model. Several molecular components of its oscillatory machinery are conserved in other Chloroplastida, but their functions may differ. Conserved clock components include at least one member of the CIRCADIAN CLOCK ASSOCIATED1/REVEILLE and one of the PSEUDO RESPONSE REGULATOR family. The *Arabidopsis* evening complex members EARLY FLOWERING3 (ELF3), ELF4, and LUX ARRHYTHMO are found in the moss *Physcomitrium patens* and in the liverwort *Marchantia polymorpha*. In the flagellate chlorophyte alga *Chlamydomonas reinhardtii*, only homologs of ELF4 and LUX (named RHYTHM OF CHLOROPLAST ROC75) are present. Temporal ROC75 expression in *C. reinhardtii* is opposite to that of the angiosperm LUX, suggesting different clock mechanisms. In the picoalga *Ostreococcus tauri*, both ELF genes are missing, suggesting that it has a progenitor circadian “green” clock. Clock-relevant photoreceptors and thermosensors vary within the green lineage, except for the CRYPTOCHROMES, whose variety and functions may differ. More genetically tractable models of Chloroplastida are needed to draw final conclusions about the gradual evolution of circadian clocks within the green lineage.

## Introduction

The daily environment influences the fitness and growth of photosynthetic organisms. Fluctuating conditions such as day–night or temperature cycles orchestrate their physiological processes. Cyanobacteria, algae, and terrestrial plants evolved an endogenous clock that drives a large variety of output processes, called circadian rhythms. This clock delivers an advantage in their fitness and survival as shown with competition experiments in cyanobacteria. Cyanobacterial fitness enhanced substantially when the circadian period was close to the period of the environmental cycle (Johnson

et al., 1998). Also in land plants, the circadian clock increases plant growth, survival, and competitive advantage (Dodd et al., 2005). As cyanobacteria and photosynthetic eukaryotes produce the oxygen on Earth, are responsible for carbon dioxide fixation and form the base of food-webs, the influence of the circadian clock on their temporal programs is of key importance for life on Earth.

Circadian rhythms have key physiological properties that are maintained in all organisms, including prokaryotes (Kondo et al., 1993; Eelderink-Chen et al., 2021). They

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- Key components of the endogenous oscillator are conserved within the green lineage; their genomes encode at least one member of the PRR and at least one member of the RVE family.
- The angiosperm EC members ELF3 and ELF4 are conserved to a large extent in streptophytes, but at least one of them is missing in select chlorophyte algae. Expression patterns of the EC LUX differ in *A. thaliana* and *C. reinhardtii*.
- ZTL and GI are found in most streptophytes but are absent in the select chlorophyte algae.
- The clock-related effect of CK1 differs in *A. thaliana* and *O. tauri* compared to that in the flagellate *C. reinhardtii*.
- The variety of CRYs in algae is higher than in land plants, and their properties, as well as functions may differ.

continue with a period of about 24 h when the plant is removed from the natural fluctuating conditions and put under free-running conditions of constant light or darkness and temperature (Hsu and Harmer, 2014). One of the first demonstrations of such an endogenous rhythm was done by the French scientist de Mairan (de Mairan, 1729) observing the leaf movement of a mimosa (*Mimosa pudica*) plant. Moreover, circadian rhythms can be entrained to Zeitgebers (Aschoff, 1954). Not only the daily light-dark (LD) cycles and temperature cycles, but also cycles of nutrients like endogenous sugars entrain the circadian clock (Haydon et al., 2013). The phases of circadian rhythms can be shifted either forward or backward depending on the time of the day and the organism. This relationship is summarized in phase-response curves. Finally, circadian rhythms are temperature compensated, meaning that their period is similar when the organism is released to different temperatures under free-running conditions ( $Q_{10}$  is  $\sim 0.8$ – $1.3$ ) (Pittendrigh, 1993).

Circadian rhythms have been broadly studied in photosynthetic organisms, fungi, and animals. Despite the conservation of physiological properties and the discovery of transcriptional/translational feedback loops in the oscillatory system of these organisms, the molecular components of circadian clocks in cyanobacteria, plants, fungi, and animals are different. Exceptions are select kinases and the involvement of CRYPTOCHROMES (CRYs) in eukaryotes (Mittag et al., 2005; Doherty and Kay, 2010; Dunlap and Loros, 2017; Rosbash, 2021). Interestingly, peroxiredoxins are conserved markers of circadian rhythms (Edgar et al., 2012). Thus, metabolic switches of oxidation–reduction cycles of peroxiredoxin proteins have been found across the domains of life, including select animals, fungi, plants, algae, and

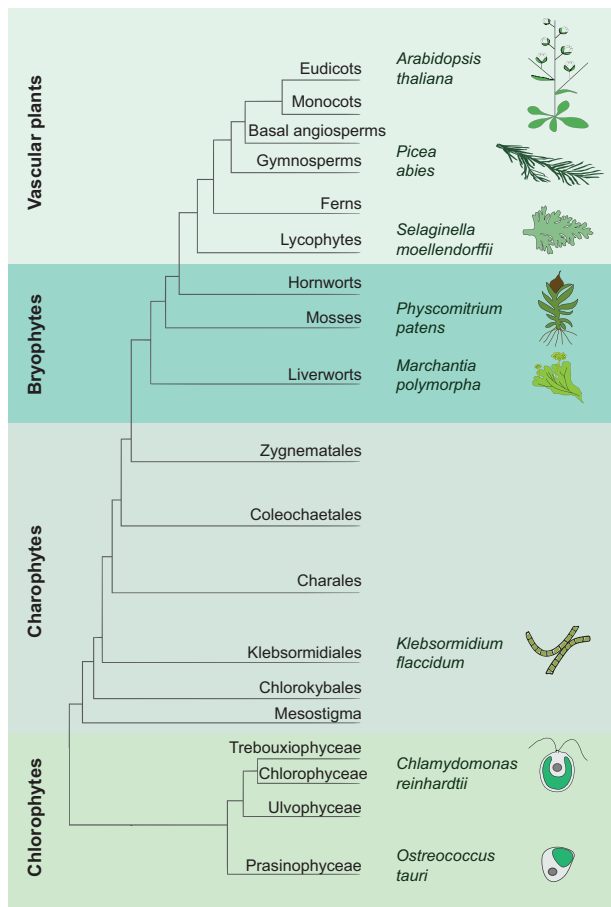
cyanobacteria (Edgar et al., 2012). Currently, it is assumed that circadian rhythms emerged multiple times in evolution, underlining their importance (Rosbash, 2021).

In this review, we will focus on circadian clocks of the green lineage (Bowman et al., 2007; Bowman, 2013; Bowman et al., 2017). The green lineage (Figure 1) covers a broad range of photosynthetic eukaryotes with high relevance for life on Earth. It comprises chlorophyte algae ranging from unicells to the advanced Charophyceae streptophyte macroalgae as well as all terrestrial plants. These include bryophytes, ferns, gymnosperms, and angiosperms. All these organisms are summarized as Chlorplastida (Adl et al., 2012). They represent primary endosymbionts whose plastids are derived by the engulfment of a cyanobacterium into a eukaryotic cell. Secondary endosymbionts (Keeling et al., 2005) are not part of this review. Here, we wish to highlight a recent review of the “brown” clock in secondary red photosynthetic organisms (Farré, 2020). Crop plants will also not be part of this review, as they will be covered in a separate article of this special issue. We also wish to highlight a recent review on clock evolution and climate change regarding bacterial rhythms (Jabbur and Johnson, 2022).

Currently, there is a solid number of genome sequences from the green lineage and first functional data from select model organisms to study the clock traits of evolution in this lineage at the molecular basis. These studies will enable us to understand how photosynthetic eukaryotes that govern our planet adapted their lifestyles to temporal programs using clock systems. The focus of this review is thus on select model species of the green lineage (Figure 1) whose genomes are available and that are genetically tractable. Models include two green microalgal species, *Ostreococcus tauri*, a marine picoalga (Keeling, 2007), and *Chlamydomonas reinhardtii*, a freshwater alga, that lives primarily in wet soil (reviewed in Sasso et al., 2018). Under focus are also gametophyte-dominated plants, namely the liverwort *Marchantia polymorpha* and the bryophyte *Physcomitrium patens* (Linde et al., 2017; Rensing et al., 2020), formerly known as *Physcomitrella patens*. The sporophyte-dominated angiosperm *Arabidopsis thaliana* is also part of this review, as it serves as the advanced model of the plant circadian system (Hsu and Harmer, 2014; Webb et al., 2019; Pajjanen et al., 2021).

### The variety of output processes and easily tractable circadian rhythms in the green lineage

In land plants, circadian rhythms of leaf, flower, and stomatal movement or circumnutation of inflorescence stems have been observed (de Mairan, 1729; Engelmann et al., 1992; Webb, 2003; Niinuma et al., 2005; Dornbusch et al., 2014; Yon et al., 2016; Creux et al., 2021). In the liverwort *M. polymorpha*, nyctinastic thallus movement was reported (Lagercrantz et al., 2020). As described above, sessile land plants profit from a clock-controlled program that initiates specific physiological processes within a given time frame. For example, it is advantageous for C3 and C4 plants to



**Figure 1** Schematic phylogenetic relationship in the green lineage. Only species discussed in this review have been highlighted. The phylogenetic tree was modified after Bowman et al. (2007) and Chang et al. (2016). It covers all green algae and terrestrial plants described in the review. Later phylogenetic trees have a focus on Charophytes (Bowman, 2013) or Bryophytes (Bowman et al., 2017).

open their stomata during the day to gain carbon dioxide for the Calvin cycle of photosynthesis. Yet, environmental stresses may overrule the clock-driven processes. On a hot sunny day, the plant will close its stomata to avoid the loss of water. For the crosstalk of plants between circadian regulation and responses to the abiotic environment, we refer to a recent review (Paajanen et al., 2021).

In contrast to land plants, unicellular algae can move within the water column or in wet soil. Microalgal movement can be passive, driven by the current of the ocean, or active driven by cilia. In the biflagellate alga *C. reinhardtii*, tactic movements are controlled by the circadian clock. Green macroalgae of the species *Aegagropila linnaei* perform a circadian rhythm of buoyancy when formed into spherical aggregates (Cano-Ramirez and Dodd, 2018). Recordings of the rhythm of photo orientation in *C. reinhardtii*, also called phototaxis can be automatically collected and were even done on a spacecraft in space (Bruce, 1970; Mergenhagen and Mergenhagen, 1987). While this rhythm peaks during subjective day, the rhythm of chemotaxis to a nitrogen source (ammonium) is highest at subjective night (Byrne

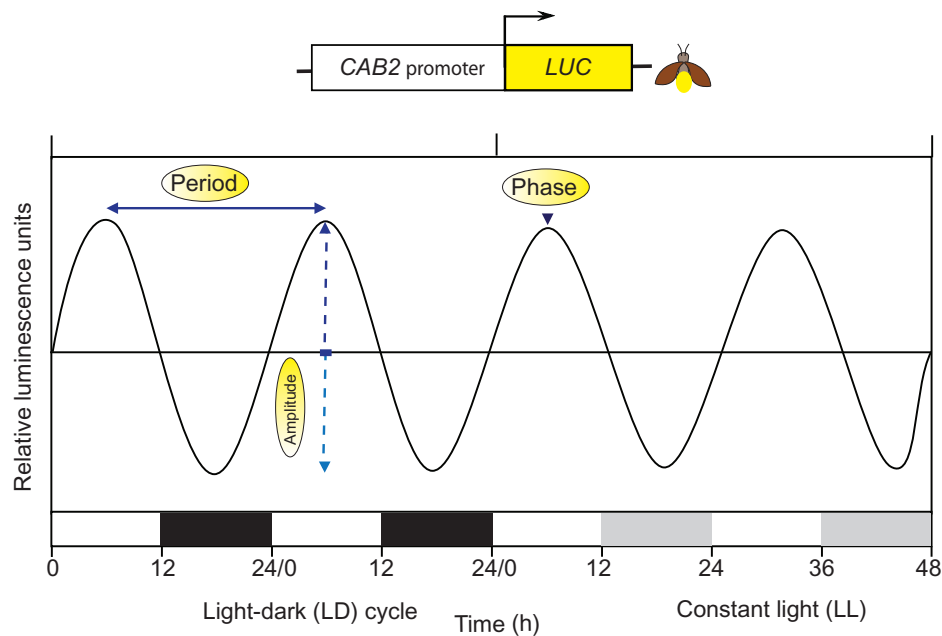
et al., 1992; reviewed in Mittag et al., 2005). Yet, the alga waits until the beginning of day to take up ammonium. Also, nitrite uptake occurs at dawn where the activity of nitrite reductase rises (Pajuelo et al., 1995). Thus, the unicellular algae show simple but coordinated clock-controlled behavioral responses. Moreover, rhythms of cell division, UV light sensitivity, stickiness to glass, and starch accumulation were reported (reviewed in Mittag et al., 2005; Matsuo and Ishiura, 2010).

The automated recording of circadian rhythms facilitates studies on their circadian clocks. In land plants, the measurement of the rhythm of leaf movement was automated. Leaf movements such as in *A. thaliana* were analyzed bioinformatically using video cameras or time lapse photography and subsequent bioinformatics analyses of leaf movements (Engelmann et al., 1992; Wagner et al., 2017). Simultaneously the invention of easily tractable reporters supported research in *A. thaliana* on chronobiology as well as the development of new model organisms in this field. Circadian controlled promoters were often fused to the reporter and this chimera served as a basis for genetic screens in the search for clock components. The most used reporter system involves bioluminescence and the enzyme LUCIFERASE (LUC). Based on the automated measurement of the natural rhythm of bioluminescence in a dinoflagellate alga (Broda et al., 1986), artificial-based bioluminescence imaging was deployed rapidly by the chronobiological community as a tool to track for example gene expression. LUC reporters from marine bacteria, from a soft coral or the firefly (Figure 2) were used to study circadian systems in *O. tauri*, *C. reinhardtii*, *P. patens*, *M. polymorpha*, and *A. thaliana* (Millar et al., 1995; Matsuo et al., 2006; Voytsekh et al., 2008; Thommen et al., 2012; Aoki et al., 2014; Linde et al., 2017).

## Components of the core oscillators in the green lineage

### The core oscillatory system in the angiosperm model *A. thaliana*

The angiosperm clock model of *A. thaliana* (Figure 3) is the best studied in the green lineage. Its endogenous oscillator is composed of interlocking transcription–translation feedback loops (Hsu and Harmer, 2014). There are more than 20 clock and clock-related components known in *A. thaliana*. They are grouped into morning-, day-, afternoon-, and evening-phased components. The MYB-like transcription factors CIRCADIAN CLOCK-ASSOCIATED 1 (CCA1) and LATE ELONGATED HYPOCOTYL (LHY) are expressed at dawn (Schaffer et al., 1998; Wang and Tobin, 1998). They interact with each other and act as transcriptional repressors on genes containing the so-called evening element (EE) promoter motif (Harmer et al., 2000; Harmer and Kay, 2005). Knockout plants of *cca1* or *lhy* show a shortened period in the expression of target genes and the double mutant shows an even shorter period (Green and Tobin, 1999; Mizoguchi et al., 2002). Initially, the PSEUDO RESPONSE REGULATOR 1 (PRR1), also known as TIMING OF CAB EXPRESSION 1



**Figure 2** Measurement of circadian-controlled bioluminescence under a light–dark cycle and free-running conditions. A chimeric construct consisting of the clock-controlled *cab2* promoter and the firefly LUC reporter is shown (Millar et al., 1995). The rhythm of bioluminescence is measured in relative luminescence units. Period, amplitude, and phase, peaking during the day, are indicated with arrows. Plants were grown in a LD cycle and then released under constant light (LL) and temperature. LD0 indicates the start of the day and LD12 the beginning of the night. Under constant light (LL), subjective days (white bars) and nights (gray bars) are highlighted. Hours indicate how long the plant has been kept under LL.

(*TOC1*), with peak expression in the early evening, was found to be a target of this repression and to directly regulate *CCA1* and *LHY* expression. Based on these findings, the first single transcriptional–translational feedback loop was proposed (Alabadi et al., 2001). At first, it was suggested that *TOC1* functions as an activator of morning-expressed oscillator genes (Pruneda-Paz et al., 2009). Later it was found that *TOC1* acts as a repressor by its rhythmic association to promoters of oscillator genes, thus connecting the morning and evening feedback loops through the repressing activity of *TOC1* (Huang et al., 2012; Nohales and Kay, 2016). Other members of the PRR family, *PRR3*, *PRR5*, *PRR7*, and *PRR9*, are also part of the plant oscillator whose transcripts increase over the course of the day. The *PRR9* transcript peaks after dawn directly following *CCA1/LHY* expression, with *PRR7*, *PRR5*, and *PRR3* following over the course of the day and *TOC1* peaking in the evening (Matsushika et al., 2000; Farré and Liu, 2013). *PRR9*, *PRR7*, and *PRR3* are partially redundant in repressing the morning genes *CCA1* and *LHY*, forming a second loop (Nakamichi et al., 2010).

During the evening, the genes *EARLY FLOWERING 3* (*ELF3*), *ELF4*, and *LUX ARRHYTHMO* (*LUX*) are expressed and interact to form the evening complex (EC; Nusinow et al., 2011; Herrero et al., 2012). The EC represses the expression of *PRR9*, *PRR7*, and *TOC1*, releasing the lock they form on *CCA1* and *LHY* expression, giving way to a transcript increase of the two morning genes (Nohales and Kay, 2016). *BROTHER OF LUX ARRHYTHMO* (*BOA/NOX*) is another evening phased component that forms a complex with *ELF3* and *ELF4* and indirectly promotes expression of *CCA1* (Dai et al., 2011; Nusinow

et al., 2011). *LUX* also forms an autoinhibitory loop by repressing its own and the transcription of *PRR9* (Helfer et al., 2011). In addition, *CCA1* and *LHY* repress the expression of the EC genes *LUX*, *ELF3* and *ELF4* by binding to their EE motif, closing the loop (Adams et al., 2015; Nagel et al., 2015; Kamioka et al., 2016; Adams et al., 2018).

Furthermore, the activating MYB-like transcription factor *REVEILLE 8* (*RVE8*) forms a complex with *LNK1* (*NIGHT LIGHT-INDUCIBLE AND CLOCK-REGULATED 1*) and *LNK2* to induce *TOC1* and *PRR5* expression (Xie et al., 2014; Pérez-García et al., 2015). It was also shown that *RVE4*, *RVE6*, and *RVE8* promote expression of *PRRs* and the EC (Farinas and Mas, 2011; Rawat et al., 2011; Hsu et al., 2013; Xie et al., 2014). Repression of these positive regulators is facilitated by the *PRRs* on *RVE8* (Nakamichi, 2020) and on the *LNKs* (Nakamichi et al., 2012; Rugnone et al., 2013; Liu et al., 2016).

Light-dependent regulation by protein degradation is facilitated by the protein *GIGANTEA* (*GI*) together with the photoreceptor *ZEITLUPE* (*ZTL*). *GI* binds to the LOV domain of *ZTL* in a light-dependent manner, stabilizing both proteins (Kim et al., 2007). In darkness, this complex dissociates. *GI* and *ZTL* induce degradation of *TOC1* and *PRR5* via the proteasome pathway (Más et al., 2003; Kim et al., 2007). In turn, *GI* promotes transcription of the morning genes *CCA1* and *TOC1* (Martin-Tryon et al., 2007). *GI* is regulated by *CCA1* binding to its *CCA1* binding site, reducing its expression (Lu et al., 2012).

Recently, the circadian clock of the wild tobacco *Nicotiana attenuata* has been studied not only under laboratory conditions, but also in its native habitat (Yon et al., 2016; Cortés

Llorca et al., 2020). Also, transcriptome dynamics of *Arabidopsis halleri* were investigated in natural environments under seasonal conditions (Nagano et al., 2019).

### Clock components in the moss *P. patens*

A set of conserved circadian core components that share similarity in gene expression with vascular plants was found in the bryophyte *P. patens*. These genes include the Myb-like transcription factors *PpCCA1a* and *PpCCA1b*, homologs of *CCA1/LHY1* and the PRRs *PpPRR1* to *PpPRR4*. One *LUX* putative ortholog (*Phypa-47310*) and two *ELF3*-like genes (*Phypa-66647* and *Phypa-165364*) are described as putative circadian clock-related genes (Holm et al., 2010; Satbhai et al., 2011; Figure 3). However, homologous genes coding for proteins like *TOC1*, *GI*, or *ZTL* in *A. thaliana* are missing in *P. patens* (Linde et al., 2017). *PpCCA1a* and *PpCCA1b* both showed expression peaks like *CCA1/LHY* of *A. thaliana* at dawn in LD cycles and under continuous darkness, but not under continuous light. Like in *A. thaliana*, a knockout of the two genes resulted in a reduced amplitude and shorter period; a negative feedback regulation was suggested (Okada et al., 2009). The PRRs and *ELF3*-like genes have expression profiles similar to their *A. thaliana* counterparts (Holm et al., 2010). The function of the putative *ELF4* ortholog in *P. patens* is poorly understood. However, constitutive expression of *PpELF4* in the *A. thaliana elf4* mutant completely rescued its early flowering phenotype. The same study suggests that *PpELF4* can regulate the expression of *CCA1*, *LHY*, and PRRs, which implies an overlapping function with the circadian clock of *A. thaliana* (Zhao et al., 2019). Thus, the molecular components of the central moss clock seem to be closely related to the select angiosperm clock.

### Time keeping in the liverwort *M. polymorpha*

There have been recent functional studies of clock gene homologs of the liverwort *M. polymorpha*. These include the PRR, RVE, and *TOC1* genes (Figure 3) and suggest their involvement in the *M. polymorpha* circadian clock as well as experimental studies of *ELF3*, *LUX*, and *GI* (Linde et al., 2017). It was suggested that the core clock genes PRR, RVE, and *TOC1* form a core transcriptional feedback loop (Lagercrantz et al., 2020). In addition, a DE-ETIOLATED1 homolog was studied in *M. polymorpha* as *AtDET1* is associated with *AtCCA1/LHY*, which are missing in liverworts (Linde et al., 2017; Lagercrantz et al., 2021). The circadian rhythm of *MpDET1* expression was disrupted in mutants of key clock and putative EC genes (Lagercrantz et al., 2021). *MpDet1* knockdown disturbed the circadian rhythm of nyctinastic thallus movement and rhythmic gene expression patterns (Lagercrantz et al., 2021).

## Comparative clock gene analysis in green chlorophyte algae compared to Streptophytes

Streptophytes comprise the freshwater Charophyceae algal clade (Figure 1) as the most advanced green algae with

similarities to land plants as well as all embryophyte plants including the mosses, ferns, gymnosperms, and angiosperms (Bowman, 2013). A recent study compared the angiosperm clock genes of *A. thaliana* with genes of other organisms of the green lineage. These include the gymnosperm *Picea abies*, the moss *P. patens*, the liverwort *M. polymorpha*, the fern *Selaginella moellendorffii*, a representative from Charophyceae *Klebsormidium flaccidum*, and the chlorophyte model algae *C. reinhardtii* and *O. tauri* (Linde et al., 2017).

The search for clock gene homologs revealed that the large REVEILLE (RVE) family consisting of the members *CCA1* and *LHY* and other RVE genes is represented with at least one member in all investigated photosynthetic organisms of the green lineage (Linde et al., 2017; de los Reyes et al., 2017). This is also the case for the PRR family; at least one member is present in all investigated species of the green lineage. However, the sequence similarity may be relatively low. Thus, two *TOC1* homologs were found in *C. reinhardtii*, named *CrPRR1* and *CrPRR2*, but are rather distinct from the angiosperm *TOC1* (Satbhai et al., 2011). In the case of *M. polymorpha*, the *CCA1/LHY* homolog is missing, as mentioned above, but a RVE member is present. Functional analysis is needed in all cases and has been executed in some members as described in other subchapters.

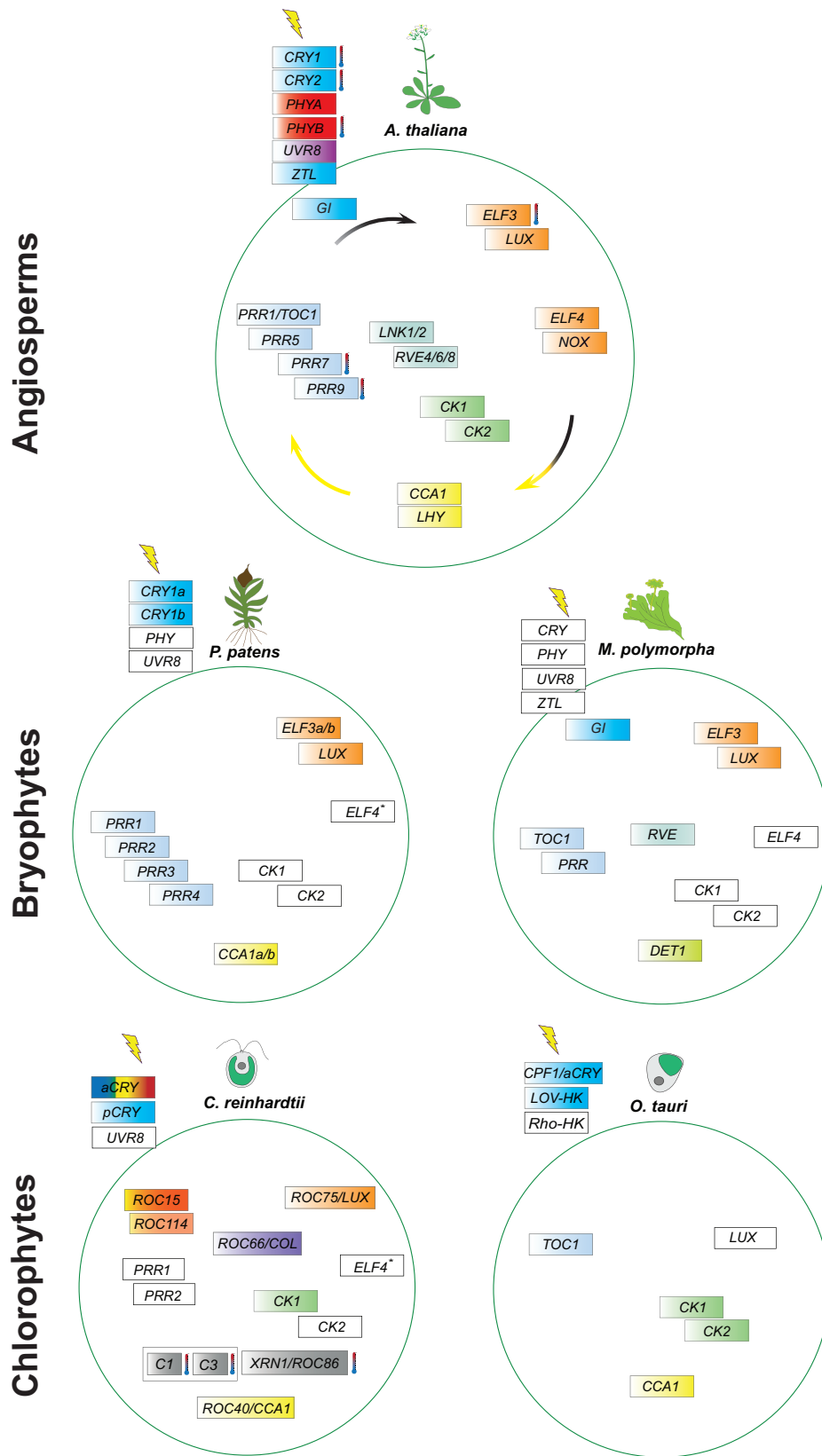
Genes of the angiosperm EC, *ELF3*, *ELF4*, and *LUX* are found in all members of the green lineage within the streptophytes with one exception. *ELF3* seems to be absent in *P. abies* (Linde et al., 2017). This is also the case for the chlorophyte alga *C. reinhardtii*; EC members are found except for *ELF3* (Mittag et al., 2005; Linde et al., 2017). In contrast, all above mentioned EC members seem to be missing in the picoalga *O. tauri* (Linde et al., 2017). However, a *LUX*(-like) was reported elsewhere (Serrano-Bueno et al., 2017; Matsuo et al., 2020) and awaits further functional characterization. These data indicate that *O. tauri* has the least conserved circadian key clock members.

The *ZTL* and *GI* duo that is closely associated with light input is present in all streptophytes, except for the moss *P. patens* and for the Charophyceae *K. flaccidum* regarding *GI*. Both *ZTL* and *GI* are missing in the select chlorophyte algae (Linde et al., 2017).

Altogether, this analysis suggests that some key clock genes of the Chloroplastida seem conserved from chlorophyte unicellular algae to advanced Charophyceae algae and land plants. However, the functional data on the involvement of these genes in the clock machinery of the respective organism are still under investigation. Complementation assays were done with *ELF4* from *C. reinhardtii* and *P. patens* as mentioned above. Notably, both *CrELF4* and *PpELF4* rescued the *A. thaliana elf4* mutant (Zhao et al., 2019) and are thus labeled with a star in Figure 3. The rescues involved the early flowering phenotype and affect the expression of circadian clock-controlled genes in *A. thaliana*.

### The picoalga *O. tauri*

*O. tauri*, belonging to the Prasinophyceae (Figure 1) is a chlorophyte algal model with minimal cellular organization



**Figure 3** Comparison of molecular components of the circadian clock of select angiosperms, mosses, and chlorophyte algae. The molecular components of the circadian clock of select angiosperm, moss, and chlorophyte algae are shown. A simplified scheme of the angiosperm *A. thaliana* clock (Webb et al., 2019) is taken as a base model. The temporal series of the main oscillatory components that are shown in between the arrows is indicated by the flow of the arrows. It starts with CCA1/LHY expression at dawn (yellow color) and ends with the EC (black color). Functional details are explained in the main text. For clarity, arrows for other models than *A. thaliana* have been omitted as differences in expression can

(continued)

(Corellou et al., 2009). It contains two homologs of the *A. thaliana* core clock proteins. These are OtTOC1 and OtCCA1 with high conservation within the PRR, CCT, and MYB domains (Corellou et al., 2009; Figure 3). Members of the angiosperm EC, *ELF3*, and *ELF4* have not been found in *O. tauri* (Linde et al., 2017). The *O. tauri* genome encodes genes containing GARP and B-box transcription factors, but it remains unknown if they are involved in its clock machinery (Corellou et al., 2009). A LUX-like protein was also reported (Serrano-Bueno et al., 2017; Matsuo et al., 2020). Expression profiles of *OtTOC1* peak like the *A. thaliana* homolog at subjective dusk, whereas *OtCCA1* expression has a broader and earlier peak compared to *A. thaliana* (Corellou et al., 2009; reviewed in Noordally and Millar, 2015). Notably, relevant clock-related kinases involved in the angiosperm clock, CASEIN KINASE1 (CK1) and CK2, are conserved in *O. tauri* (Box 1).

Another important feature in *O. tauri* is that 90% of its daily transcriptome is rhythmic (de los Reyes et al., 2017). Thus, this picoalga is heavily influenced by light switches. In contrast, there is a reduction in the size of diurnal transcriptomes in the flagellate alga *C. reinhardtii* (down to 70%) and in the land plant *A. thaliana* (only 40%, Covington et al., 2008; Zones et al., 2015; de los Reyes et al., 2017). Altogether, it seems that the clock of *O. tauri* is reduced in core clock components of the EC and may only have one transcription–translation feedback loop. However, this seems to be compensated by the high number of genes regulated by the daily change of light and darkness.

### The biflagellated unicellular alga *C. reinhardtii*

The chlorophyte alga *C. reinhardtii* belongs to the Chlorophyceae (Figure 1). In contrast to *O. tauri* and all other presented plant models, *C. reinhardtii* is a motile organism that can use its flagella for clock-controlled tactic movements (Mittag et al., 2005).

Molecular characterization of a clock component was made by identification of the CHLAMY1 RNA-binding complex that binds to UG-repeat sequences in the 3'-UTR of mRNAs (reviewed in Mittag et al., 2005). CHLAMY1 consists

of the subunits C1 and C3 (Zhao et al., 2004). An increase or decrease of the protein level of the C3 subunit, present in overexpression and knockdown lines, respectively, results in a shift in the acrophase, while changes in the level of C1 cause arrhythmicity (Iliev et al., 2006). However, it should be emphasized that the alterations on the C1 level automatically cause changes in the level of C3 due to a co-regulatory mechanism (Iliev et al., 2006). C3 has high sequence similarity to mammalian CUG-binding proteins that are involved in myotonic dystrophy (Zhao et al., 2004; Koshelev et al., 2010). Myotonic dystrophy is associated with variable circadian rhythms (Okumura et al., 2002).

Deeper insights into the clock of *C. reinhardtii* were obtained through forward genetic approaches screening a library of insertional mutants using a LUC reporter gene that is controlled by the *psbD* clock-controlled chloroplast promoter (Matsuo et al., 2006, 2008). The screen identified 105 genes that showed alterations in the amplitude, phase and/or period, termed “RHYTHM OF CHLOROPLAST” (ROC) mutants (Matsuo et al., 2008). Some of the proteins contain conserved domains that are also found in the core clock components of *A. thaliana* (reviewed in Matsuo and Ishiura, 2010; Ryo et al., 2016). *ROC15* and *ROC75* encode domains with sequence similarity to the GARP DNA-binding domain that can also be found in *LUX*. *ROC15* is associated with the light signaling pathway (see section below). *ROC40* encodes a Myb domain like *CCA1/LHY*. It has a UG-repeat in its 3'-UTR and thus may be connected to *CHLAMY1* (Ryo et al., 2016). *ROC15* and *ROC40*, mRNAs accumulate from subjective midnight until dawn.

*ROC66* encodes a B-box and the CCT similar to CO proteins. Another CO family protein, which is different from *ROC66*, *CrCO*, affects circadian output regarding growth, diurnal starch content rhythms, and cell cycle-related gene expression (Serrano et al., 2009). It is notable that *CrCO* can complement the *co* mutation in *A. thaliana* regarding the timing of flowering phenotype. *ROC114* encodes an F-box and is a potential ubiquitin ligase. As mentioned above, *TOC1* homologs (*CrPRR1* and *CrPRR2*) have been found in *C. reinhardtii* but are not functionally studied yet.

### Figure 3 (Continued)

occur or expression times are not always known. Genes that are conserved in the central oscillator in mosses and chlorophyte algae, but not functionally characterized, are indicated by white boxes. Further clock components in a select liverwort (*M. polymorpha*) and a select flagellate alga (*C. reinhardtii*) are shown. The asterisk in *ELF4* refers to complementation assays. Photoreceptors that have been characterized and found to participate in the circadian clock machinery are shown outside the green circles for each organism. Colors represent their absorption range. Representative photoreceptors that may relate to the clock are indicated by white boxes. Please note that *PRR1* has no sequence similarity to *TOC1* in some of the mentioned organisms. Not all potential clock-relevant photoreceptors have been added for clarity. For example, the genome of *C. reinhardtii* encodes 18 photoreceptors (Greiner et al., 2017). Several may be involved in the circadian clock, but only few have been studied so far. Clock components that can integrate temperature information and thus may be involved in temperature entrainment are labeled with a thermometer. aCRY, animal-like CRYPTOCHROME; C1, subunit 1 of the RNA-binding protein CHLAMY1; C3, subunit 3 of the RNA-binding protein CHLAMY1; CCA1, CIRCADIAN CLOCK-ASSOCIATED1; CK, CASEIN KINASE; COL, CONSTANS-like; CPF, CRYPTOCHROME PHOTOLYASE FAMILY; CRY1, Arabidopsis CRYPTOCHROME 1; CRY2, Arabidopsis CRYPTOCHROME 2; DET1, DEETIOLATED1, ELF, EARLY FLOWERING; GI, GIGANTEA; LHY, LATE ELONGATED HYPOCOTYL; LNK, NIGHT LIGHT-INDUCIBLE AND CLOCK-REGULATED; LOV-HK, LOV-HISTIDINE KINASE, LUX, LUX ARRHYTHMO; NOX, BROTHER OF LUX ARRHYTHMO; pCRY, plant CRYPTOCHROME; PHYA, PHYTOCHROME A; PHYB, PHYTOCHROME B; PRR, PSEUDO RESPONSE REGULATOR; Rho-HK, RHODOPSIN-HISTIDINE KINASE; ROC, RHYTHM OF CHLOROPLAST; RVE, REVEILLE; TOC1, TIMING OF CAB 1 EXPRESSION; UVR-8, UV RESISTANCE LOCUS 8; XRN1, 5'-3' EXORIBONUCLEASE 1; ZTL, ZEITLUPE.

### Box 1 POSTTRANSLATIONAL CONTROL AND CKS

In all model species studied thus far including angiosperm plants, posttranslational control has been found to be of high importance (Yan et al., 2021). Among the diverse modifications of clock-related proteins ubiquitination, O-glycosylation, SUMOylation, methylation, and phosphorylation play important roles. We will not detail all these processes in this review because they have not been studied for all members in the green lineage. But we would like to highlight that reversible phosphorylation plays a major role in diverse organisms including not only algae and land plants (Kusakina and Dodd, 2012; Noordally and Millar, 2015; Krahmer et al., 2021), but also fungi (Liu et al., 2000), flies, and mammals (Narasimamurthy and Virshup, 2021). CKs (CK1 and CK2) are well conserved across species and are also found to be of importance in unicellular algae (Mittag et al., 2005; Schmidt et al., 2006; van Ooijen et al., 2013). The role of CKs has been demonstrated in the circadian systems of the chlorophyte algae *O. tauri* and *C. reinhardtii*, but also in the *A. thaliana* angiosperm clock. A CK1 knockdown shortens the period in *C. reinhardtii* (Schmidt et al., 2006) while inhibition of CK1 in *O. tauri* and *A. thaliana* lengthens the period (van Ooijen et al., 2013; Uehara et al., 2019). These effects underline that the clocks of *O. tauri* and *A. thaliana* may be closer in their mechanisms than the *C. reinhardtii* clock (Matsuo et al., 2020). It is also notable that CK1 is located in the flagella and the eyespot of *C. reinhardtii* (Schmidt et al., 2006). CK2 was also shown to be clock-relevant in *O. tauri* (Le Bihan et al., 2015). Data are still missing on CK2 and clock function in *C. reinhardtii*. In *A. thaliana* CK2 is involved in CCA1 and LHY phosphorylation (Sugano et al., 1998, 1999).

The LUX homolog ROC75 is a day-phase expressed nuclear-localized protein (Matsuo et al., 2020). ROC75 represses the key clock-related genes *ROC15*, *ROC40*, and *ROC66*, during subjective day. The acute downregulation of *ROC15* and *ROC40* mRNAs by light is, however, independent of ROC75.

Contrary to the evening expression of angiosperm *LUX* and the *LUX*-like transcript in *O. tauri*, the *ROC75* transcript accumulates during daytime (Monnier et al., 2010; Matsuo et al., 2020). Thus, it was postulated that the *C. reinhardtii* clock may have a contrasting mechanism compared to *A. thaliana* and *O. tauri* (Matsuo et al., 2020). This hypothesis is consistent with a different effect on period caused by a knockdown mutant or inhibition of CK1 from *O. tauri* and *A. thaliana* compared to *C. reinhardtii* (Box 1; Schmidt et al., 2006; van Ooijen et al., 2013; Uehara et al., 2019). In general, CK1 and CK2 are involved in posttranslational regulation of the clock in several organisms and are recently even discussed with regard to temperature compensation (Kusakina and Dodd, 2012; Hu et al., 2021; Narasimamurthy and Virshup, 2021).

It may be that the circadian clock of flagellate algae has partially different properties compared to the clock of sessile plants and nonflagellate algae. The *C. reinhardtii* genome encodes conserved genes from the plant and animal kingdom, especially with regard to the flagella (Merchant et al., 2007). It should also be noted that six genes involved in flagellar function were included in the mutant clock screen suggesting the requirement of normal flagellar function to maintain the robustness of chloroplast rhythmicity (Matsuo et al., 2008). Also, CK1 is found in the flagellum and has many targets there (Schmidt et al., 2006; Boesger et al., 2012).

## Sensors of light and temperature in the green lineage

### Photoreceptors in land plants

In *A. thaliana*, four families of photoreceptors (Figure 3) have been described to be involved in the clock machinery:

(1) PHYTOCHROMES (PHY); (2) CRYs; (3) the ZTL family, and UV RESISTANCE LOCUS 8 (UVR8; reviewed in Sanchez et al., 2020). These photoreceptors absorb light at specific wavelengths, ranging from the UV-B area to UV-A, blue and red/far red light.

It should be noted that the PHYs and CRYs seem to contribute only partially to clock entrainment in *A. thaliana* (reviewed in Sanchez et al., 2020). An Arabidopsis mutant lacking main photoreceptors such as *phyA-201 phyB-5 cry1-201 cry2/fha-1* still shows clock entrainment (Balcerowicz et al., 2021). A recent study with RNA-sequencing time-series data identified light- and temperature-sensitive bursts of transcription factor activity. It suggests that PHY and CRY signaling is important for fine-tuning, but separate pathways can activate much of the program (Balcerowicz et al., 2021). Low-intensity UV-B radiation acts as an entraining signal for the clock. UVR8 and CONSTITUTIVELY PHOTOMORPHOGENIC 1 (COP1) are required for this process and their interactions were shown (Fehér et al., 2011; Podolec et al., 2021). We hypothesize that the coordination of several light sensors is needed for the final entrainment programs. Also, it should be kept in mind that the biological function of some light sensors such as for CRY3, a *Drosophila*, Arabidopsis, *Synechococcus*, and Human-CRY in *A. thaliana*, are not yet known.

Light can also induce the expression of clock genes (Nohales and Kay, 2016). PHYB regulates the phase of several clock genes (Palágyi et al., 2010). It was also shown that a constitutively active allele of PHYB maintains circadian robustness in the absence of light (Jones et al., 2015). All these data implicate a complex interplay. The CRYs are involved in different physiological processes. Both CRY1 and CRY2 play an important role for the functioning of the endogenous oscillator (reviewed in Sanchez et al., 2020). A *cry* double mutant exhibits a longer period compared to wild-type (Devlin and Kay, 2000). Recently, it was shown that CRYs



mediate blue light regulation of N<sup>6</sup>-methyladenosins modifications of mRNAs, especially those regulated by the circadian clock (Wang et al., 2021). This aspect of blue light signaling by CRYs allows an influence on posttranscriptional regulation.

The function of ZTL and GI has been detailed above. ZTL is found in select bryophytes, ferns, monocots, and dicots (Linde et al., 2017; Gil and Park, 2019), but is missing in *O. tauri*, *C. reinhardtii*, and *P. patens*. In *P. patens* two CRYs seem to be involved in blue light signaling in connection with the circadian clock (Ichikawa et al., 2004). It is too early to predict if the function of the CRYs fulfills the ZTL functions in plants where ZTL is missing. UVR8 is present in bryophytes (Soriano et al., 2018), but a clock function has not been described so far.

### Photoperception in unicellular alga

Photoreceptors and their role for circadian clocks have been investigated in the model algae *C. reinhardtii* and *O. tauri*. Like *A. thaliana*, both algae have CRYs. However, the complexity of the CRY system in these algae is broader than in land plants (Petersen et al., 2021). The plant CRY in *C. reinhardtii* (called pCRY) has been shown to be involved in phase resetting of the circadian clock. A knock-down mutant results in period lengthening and after a few days under constant conditions in arrhythmicity (Müller et al., 2017). A functional connection to the clock-component ROC 75 was recently described (Kamrani et al., 2018). It is worth noting that the unicellular algae also has an animal-type CRY (aCRY) that is grouped closely to the CRYPTOCHROME PHOTOLYASE FAMILY (CPF1; Beel et al., 2012; Petersen et al., 2021). It absorbs not only in the blue range of the visible spectrum, but also in the yellow and red (Beel et al., 2012). Despite the dogma that CRYs have lost photolyase activity the algal animal-like CRYs that group to the CPF have maintained it (Coesel et al., 2009; Heijde et al., 2010; Franz et al., 2018). Moreover, the CPF1 from *O. tauri* exhibits clock function in a heterologous system (Heijde et al., 2010). aCRY from *C. reinhardtii* alters light-induction/reduction of some clock genes, like for the C3 subunit of the circadian RNA-binding protein CHLAMY 1 (Beel et al., 2012).

UV-B perception via UVR8 is conserved in *C. reinhardtii* (Tilbrook et al., 2016; Serrano-Bueno et al., 2017; Han et al., 2019). Like *A. thaliana*, UVR8 interacts with COP1. However, a UVR8 receptor seems to be missing in *O. tauri* (Han et al., 2019) as well as PHYs that are also absent in *C. reinhardtii* (Mittag et al., 2005; Han et al., 2019).

Furthermore, ROC15 of *C. reinhardtii* is involved in triggering the reset of the algal circadian clock along with the F-box protein ROC114 (Niwa et al., 2013). In a mutant called LRR that affects a RAS signaling-related leucine-rich-repeat protein, ROC15 degradation and resetting of the clock by red and violet light was impaired (Kinoshita et al., 2017).

In *O. tauri*, a LOV-HISTIDINE KINASE (LOV-HK) and a RHODOPSIN-HISTIDINE KINASE (Rho-HK) have been reported (Djouani-Tahri et al., 2011) and discussed

(Thommen et al., 2015; Luck et al., 2019), to be involved in the circadian clock machinery.

These data highlight that conserved but also different types of known photoreceptors are involved in green algae and land plants (Figure 3). The genome of *C. reinhardtii* encodes for 18 different photoreceptors (Greiner et al., 2017) whose influence on the circadian clock is little understood.

### Temperature sensing

Information on temperature sensing and signaling in the physiological range is still rare. In *C. reinhardtii* the two subunits of CHLAMY1 integrate changes in temperature in the physiological range with regard to protein expression (C3 subunit) or to reversible phosphorylation (C1 subunit) (Voytsekh et al., 2008). Two interaction partners of C3, the 5′–3′ EXORIBONUCLEASE XRN1 (also known as ROC86; Dathe et al., 2012) and splicing variant 12 of a further RNA recognition motif-containing RNA-binding protein, MUSASHI, react to changes in ambient temperature with regard to their protein abundance (Li et al., 2018). It is assumed that these proteins are part of a thermal signaling network in the green alga.

In *A. thaliana*, the EC is temperature responsive. It was recently shown that ELF3 of *A. thaliana* Col-0 contains a polyglutamine (polyQ) repeat whose length corresponds with thermal responses. The ELF3 polyQ repeat is missing in stiff brome (*Brachypodium distachyon*), whereas potato (*Solanum tuberosum*) contains an intermediate in comparison to *A. thaliana*, suggesting that it is not universal for land plants (Jung et al., 2020). The temperature sensitivity of ELF3 is altered by the levels of ELF4. Plants lacking functional PRR7 and PRR9 are unable to entrain the clock to cold pulses after entrainment to thermocycles, which indicates a role in the clock temperature signaling (Salomé and McClung 2005).

Another thermosensor in *A. thaliana* is the red-light photoreceptor PHYB (reviewed in Gil and Park, 2019). It senses temperature through the temperature-dependent reversion of the active Pfr to inactive Pr state (Legris et al., 2016). It was shown that PHYB associates in a temperature-dependent manner with promoters of target genes like the PHYTOCHROME-INTERACTING FACTORS (Jung et al., 2016; Legris et al., 2016). Also, for the photoreceptors CRY1 and CRY2 it was recently shown that their protein levels are substantially altered by temperature and that the photocycle is affected (Pooam et al., 2021).

A detailed overview of abiotic factors besides light and temperature influencing the period of the circadian clock is shown in (Webb et al., 2019) and will not be detailed here.

### Conclusions

Genome-based data on circadian clock members of the green lineage and first functional studies suggest that several of its clock members are conserved and evolved from chlorophyte Prasinophyceae picoalgae (Linde et al., 2017; Serrano-Bueno et al., 2017). The green lineage includes a

large number of clock gene homologs that can be found in all/most of its members (Figure 3) and that are missing in fungi and animals except for CKs (Box 1) and CRYs (Figure 3). In several cases, functional data are still missing to draw final conclusions about a conserved mechanism of clocks in the green lineage. It seems that the clock complexity increases from the picoalga *O. tauri* to the flagellate *C. reinhardtii* and from the mosses to the angiosperm *A. thaliana*. The higher complexity may be since land plants are sessile and thus need more clock components to react to all possible environmental conditions. There is also some evidence that the clock-controlled tactic movements of the ciliated *C. reinhardtii* may result in an at least partially different clock mechanism. To confirm or disregard this hypothesis, studies on another flagellate green alga would be needed (see “Outstanding Questions Box”). More genetically tractable model organisms of the Chloroplastida, especially within the Charophytes (Figure 1), the transition zone of advanced streptophyte algae to terrestrial plants, would help to get a more comprehensive picture of circadian clocks in the green lineage.

Regarding the influence of light on the angiosperm clock, it is important to mention that the photoreceptor ZTL and GI have been found in all investigated streptophyte species (Linde et al., 2017) except for *P. patens* and *K. flaccidum* where ZTL is present, but GI is missing. Both are absent in the select chlorophyte algae. These findings suggest that the negatively light regulated protein degradation mediated by ZTL is a component that arose during the transition to terrestrial habitats. Photoreceptor classes that can be found in most and all the presented species of this review, respectively, are the UVR8s that are only missing in *O. tauri* (Han et al., 2019) and the CRYs. CRY functions within the clock were already shown for *C. reinhardtii*, *O. tauri*, *P. patens*, and *A. thaliana* (Ichikawa et al., 2004; Beel et al., 2012; Müller

et al., 2017; Sanchez et al., 2020). For this reason, it seems that CRYs are mainly conserved as mediators of the light input and clock control within the green lineage. The broad variety in their properties and functions has been discussed above and is especially visible in different algal species (Petersen et al., 2021). Apart from this, CRYs are involved in the clock-light input pathway in fungi and insects, whereas in mammals they have a role as key clock components within the endogenous oscillator (Foley and Emery, 2020).

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## OUTSTANDING QUESTIONS

- How conserved are circadian clock components and their mechanisms within the different phyla of Chloroplastida?
- Which conserved clock genes along the green lineage have similar functions?
- Have ZTL and GI been lost in the moss *P. patens* or have they evolved independently in liverworts and mosses?
- Do flagellate algae have an individual additional set of clock components?
- Are there main differences in the circadian clock between sessile plants and motile flagellate algae?
- How conserved is photo perception in the green lineage?
- How conserved is temperature sensing in the green lineage?

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