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Review

Biogenesis of thylakoid membranes☆

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ABSTRACT

Thylakoids mediate photosynthetic electron transfer and represent one of the most elaborate energy-transducing membrane systems. Despite our detailed knowledge of its structure and function, much remains to be learned about how the machinery is put together. The concerted synthesis and assembly of lipids, proteins and low-molecular-weight cofactors like pigments and transition metal ions require a high level of spatiotemporal coordination. While increasing numbers of assembly factors are being functionally characterized, the principles that govern how thylakoid membrane maturation is organized in space are just starting to emerge. In both cyanobacteria and chloroplasts, distinct production lines for the fabrication of photosynthetic complexes, in particular photosystem II, have been identified. This article is part of a Special Issue entitled: Chloroplast Biogenesis.

1. Introduction

The origin of oxygenic photosynthesis dates back more than 2.4 billion years. At that time, primordial cyanobacteria first succeeded in harnessing solar energy to drive the extraction of electrons from water; these are then fed into a transmembrane photosynthetic electron transport chain (PET; [1]). PET takes place across specialized membranes named thylakoids, which represent one of the most elaborate bioenergetic machines known to date [2]. Thylakoids form an intracellular membrane system which harbors most of the constituents involved in the harvesting and utilization of light energy. As a consequence of PET, the chemical energy carriers NADPH and ATP are generated, and utilized for the synthesis of carbohydrates from CO_2. Photosynthesis thus forms the basis of nature's food chains.

The main protein components of thylakoids include the mobile, low-molecular-weight carriers plastoquinone and plastocyanin, which shuttle electrons between huge multisubunit protein/pigment complexes, i.e., photosystem II (PSII) and photosystem I (PSI), via the cytochrome b_6f (Cytb_6f) complex. Finally, an ATPase complex utilizes the energy stored in the proton gradient established across the thylakoid membrane by PET to synthesize ATP. This core molecular machinery mediating PET is highly conserved from cyanobacteria to plants [3], although the light-collecting systems are more diverse, varying from soluble phycobilisomes in cyanobacteria and red algae to membrane-integrated light-harvesting (LHC) systems in plants [4]. The ultrastructure of these various components has been determined at close to atomic resolution in recent years, providing a detailed picture of the structure and function of the PET chain [5,6].

However, despite this in-depth knowledge of their structure, the processes that guide the construction of the various photosynthetic complexes during thylakoid membrane biogenesis are only beginning to emerge. As the available structural data imply, dozens of integral and peripheral protein subunits and hundreds of organic cofactors including chlorophylls, carotenoids, cytochromes and quinones, as well as metals and other ions, have to be brought together and properly assembled. And of course these diverse building materials must be synthesized and supplied in amounts reflecting at least approximately their final stoichiometry. Then the components must be brought together in a lipid environment and assembled in a strictly determined and stepwise sequence. Thus, the entire process must be highly ordered both in space and in time.

The current status of our understanding of the biogenesis of particular complexes is reviewed in detail in Chapters 11–14 [7–10] of this special issue. Therefore, we focus here on how different biosynthetic pathways for thylakoid membrane constituents might be interconnected to enable coordination of biogenesis in the temporal domain. In

Abbreviations: PET, photosynthetic electron transport; NADPH, nicotinamide adenine dinucleotide phosphate; ATP, adenosine triphosphate; CO_2, carbon dioxide; Cytb_6f, cytochrome b_6f complex; PSI, photosystem I; PSII, photosystem II; LHC, light-harvesting complex; MGDG, monogalactosyldiacylglycerol; DGDG, digalactosyldiacylglycerol; SQDG, sulfoquinovosyldiacylglycerol; PG, phosphatidylglycerol; PDC, pyruvate dehydrogenase complex; ACCase, acetyl-CoA carboxylase; PA, phosphatidic acid; DAG, diacylglycerol; MGS, monoglucosyldiacylglycerol synthase; CURT1, CURVATURE THYLAKOID1; THF1, thylakoid formation 1; POR, protochlorophyllide oxidoreductase; ChlG, chlorophyll synthase; CTM, chloroplast translation membrane

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addition, the cytological aspects of the whole process are emphasized by reviewing current findings regarding the spatial organization of thylakoid membrane biogenesis and architecture. Despite differing significantly in structural organization, the functions of thylakoids have been highly conserved throughout evolution. Hence, the biogenesis process will be discussed in the light of recent findings in organisms ranging from cyanobacteria to vascular plants.

2. Forming the matrix of thylakoid membranes — the lipids

2.1. Composition and function of the thylakoid lipidome

Thylakoids represent remarkably conserved energy-transducing membranes with a high protein content that can reach up to 80% in stacked grana regions of eukaryotic chloroplasts accumulating PSII [2]. Like the photosynthetic protein/pigment complexes that account for this high protein/lipid ratio, the lipophilic matrix in which they are embedded is unique, and has been conserved during the course of evolution. This suggests that a specific lipid environment is required to ensure the stability and activity of photosynthetic complexes [11].

With minor deviations, thylakoids from cyanobacteria to plants contain four major lipid types, i.e., the galactoglycerolipids MGDG (monogalactosyldiacylglycerol) and DGDG (digalactosyldiacylglycerol), the sulfolipid SQDG (sulfoquinovosyldiacylglycerol) and the phospholipid PG (phosphatidylglycerol). The glycolipids comprise more than 70% of thylakoid lipids, with MGDG accounting for >50% of the total. The relative proportions of the lipid classes are stable, underlining their defined structural/functional roles which are dependent on their physicochemical properties [12,13]. These properties include the presence of negatively charged headgroups in only SQDG and PG, and the small size of MGDG's headgroup, which allows it to form inverse hexagonal structures (the so-called HII phase), unlike DGDG, SQDG and PG [14,15]. As a functional consequence, DGDG forms and stabilizes membrane bilayers, whereas MGDG is likely to favor curvature of thylakoids. This idea is supported by the finding that highly stacked grana regions with a high content of curved membrane regions exhibit higher MGDG/DGDG ratios than do stroma lamellae [16]. Recent analyses support the critical role of the MGDG/DGDG ratio for membrane phase transitions and highlight the function of DGDG for membrane stacking via the formation of hydrogen bonds between the headgroups of adjacent bilayers [17]. In addition to their matrix role, all glycerolipid classes have been shown to interact closely with photosynthetic protein complexes, in particular with PSII, as deduced from X-ray crystallographic analyses [18–20]. This suggests that individual lipids may also play critical roles for the structure and function of the protein complexes. Indeed, genetic studies of mutants with defects in glycerolipid accumulation in plants and cyanobacteria have confirmed that MGDG is essential for thylakoid formation generally [21], while DGDG and PG are important for the function of PSII in particular [11,22,23].

2.2. Synthesis of lipids

The biosynthesis of thylakoid lipids follows a complex pathway which requires the production and combination of fatty acids and polar head precursors [11,24]. Fatty acid synthesis begins in the chloroplast stroma with the conversion of pyruvate into acetyl-CoA by the pyruvate dehydrogenase complex (PDC). Subsequently, acetyl-CoA is carboxylated to malonyl-CoA by the acetyl-CoA carboxylase (ACCase), which is considered to be the rate-limiting "committed step" in fatty acid synthesis [24]. Interestingly, recent studies of the regulation of chloroplast gene expression have revealed that the E2 dihydrolipoyltransferase subunit of the PDC acts as a regulator of the synthesis of the D1 protein of the PSII reaction center by localizing its mRNA to specialized biogenic membrane regions in *Chlamydomonas reinhardtii* as outlined below (Fig. 2B, Section 3.2 and [25]). Thus, the moonlighting activity of a metabolic enzyme appears to provide for reciprocal regulation of plastid fatty acid synthesis and protein synthesis. This kind of crosstalk in the initial phase of thylakoid membrane biogenesis would guarantee that lipid and protein syntheses are harmonized from the beginning to avoid unbalanced accumulation of the major classes of thylakoid constituents during chloroplast biogenesis [25]. In line with this, transcriptomic studies in *Arabidopsis thaliana* have recently revealed tight coordination between the expression of nuclear genes involved in later steps of both lipid and chlorophyll syntheses and genes coding for photosynthetic proteins [26]. Whether similar regulatory principles also operate in cyanobacteria is currently unknown.

Fatty acid synthesis is completed within the chloroplast, and thylakoid lipids are then synthesized via the resident prokaryotic pathway in the chloroplast or the extra-organellar eukaryotic route, which requires the export of fatty acids into the cytoplasm, their assembly into lipid precursors in the ER and subsequent reimport into plastids [27]. Irrespective of their precise derivation, the lipid precursors phosphatidic acid (PA) and diacylglycerol (DAG) are conveyed to the inner envelope, and further processed by the key enzymes MGD1 and DGD1, which catalyze the formation of the most abundant lipids MGDG and DGDG, respectively. While MGD1 is localized to the inner envelope membrane, DGDG is synthesized at the outer envelope, as revealed by proteomic approaches following membrane fractionation [27–29]. Interestingly, the MGDG/DGDG ratio of membranes has a direct influence on the association of MGD1 with the membrane and its self-organization into reticulated structures; this in turn suggests the existence of specialized membranous microdomains for plastid galactolipid synthesis [30].

Interestingly, recent membrane fractionation experiments have revealed that galactolipid synthesis in cyanobacteria seems to occur at both the plasma membrane and the thylakoids [31]. Formation of MGDG in cyanobacteria differs from that in chloroplasts insofar as the former lack MGD1 activity. Instead, DAG is first converted into monoglucosyldiacylglycerol by the essential enzyme monoglucosyldiacylglycerol synthase (MGS) and then further processed by an epimerase to yield MGDG [32]. In agreement with a broader distribution of lipid synthesis, MGS was found to localize to both plasma membrane and thylakoids [31].

2.3. Trafficking of lipids

One crucial but still unanswered question is how lipids are transferred from the plastid envelope to the internal thylakoid membrane system during its maturation. In principle, three forms of trafficking can be envisaged, based on (i) lateral fusions between inner envelope and thylakoids, (ii) vesicular transport, or (iii) soluble lipid carriers (Fig. 1 and [33]).

In algal chloroplasts and proplastids of vascular plants, thylakoids appear to develop via local invaginations of the inner envelope membrane [34,35]. Less frequently, connections between envelope and thylakoids have been observed in mature chloroplasts also, suggesting that intraplastidic lipid transfer occurs via lateral diffusion (Fig. 1A and [36]). In support of this scenario, in the *A. thaliana mgd1* mutant, which does not form photosynthetically active thylakoids, invaginations of the inner envelope membrane are observed [37].

However, ultrastructural evidence for vesicle-based transfer processes has also been repeatedly obtained (Fig. 1B and [34,38–40]). Furthermore, inhibitors of the cytoplasmic secretory pathway similarly affect vesicle formation in isolated chloroplasts, suggesting that related systems exist in both cellular compartments [40–42]. More recently, comprehensive bioinformatic studies have provided evidence for chloroplast localization for several proteins that share high sequence similarity with known components of the vesicle-based secretory pathway in the cytoplasm [43–45]. Based on these analyses, it seems likely that a complete vesicle transport system which resembles the cytosolic COPII system is active in the chloroplast, whereas COPI and clathrin-

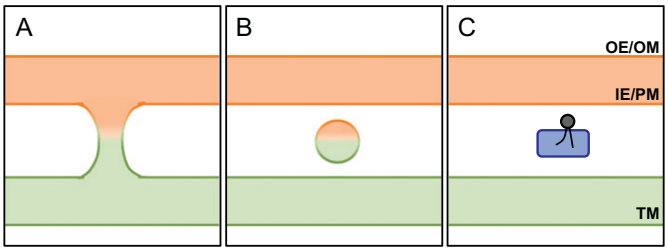

Fig. 1. Modes of lipid trafficking. Three possibilities of lipid trafficking between the inner envelope/plasma membrane (red) and the thylakoid membrane (green) are illustrated: transport via lateral fusions between the membranes (A), vesicles (B) and soluble lipid carriers (C). OE: outer envelope membrane, OM: outer membrane, IE: inner envelope membrane, PM: plasma membrane, TM: thylakoid membrane.

coated vesicles are probably absent from plastids [45,46]. However, in the case of most components of the putative chloroplast vesicle transport system, unequivocal experimental validation of their localization and function is still missing. So far, only two, the small plastid GTPases CPSAR1 and CPRabA5e, have been investigated in molecular detail [47–49].

CPSAR1 resembles the cytosolic COPII coat-forming protein Sar1, exhibits GTPase activity in vitro and is distributed between the chloroplast envelope and the stroma, all of which are consistent with a Sar1-like function during vesicle induction [48]. In agreement with this, thylakoid formation is severely affected during the early embryo phase in a CPSAR1-deficient *A. thaliana* mutant. Interestingly, CPSAR1 – also named ObgC – has been implicated in the biogenesis of a second macromolecular structure, i.e., the plastid ribosome [50].

The Rab GTPase CPRabA5e is a close homolog of the vesicle transport protein Ypt31/32 from yeast and has recently been shown to complement the *ypt31/32* mutant [49]. CPRabA5e localizes to the chloroplast stroma and thylakoids, and an *A. thaliana* knock-out mutant displayed enhanced chloroplast vesicle formation at low temperatures and under oxidative stress [49]. Interestingly, this small GTPase interacts with the recently discovered thylakoid membrane-shaping factor CURT1A (Section 5) in yeast two-hybrid screens. Whether this is of functional relevance for the control of thylakoid morphology remains to be seen [47].

Other plastid-specific factors besides these homologs of cytosolic secretory proteins have been implicated in vesicle transport from the inner envelope to thylakoids. These include the VIPP1 protein, which is homologous to the bacterial phage shock protein PspA. VIPP1 has been implicated in thylakoid biogenesis and/or thylakoid maintenance in both cyanobacteria and chloroplasts [51–53]. The molecular details of VIPP1 functions are addressed in Chapter 21 [54] of this issue.

In addition, the protein THF1 (thylakoid formation 1), named Psb29 in cyanobacteria, is considered as a potential constituent of a chloroplast vesicle-based transport system based on its loss-of-function phenotype. The mutant is sensitive to high-level light, has a less efficient PSII and forms variegated leaves, with chloroplasts accumulating vesicles instead of organized thylakoids [27,55,56]. THF1 interacts with light-harvesting LHCB proteins and plays a role in the dynamics of PSII supercomplexes – even during leaf senescence – which suggests that it serves a much broader function throughout the lifetime of thylakoid membranes [57,58].

Vesicular thylakoid membrane biogenesis is also severely affected in knock-out mutants for a thylakoid disulfide isomerase named SCO2 or CYO1 [59,60]: *sco2/cyo1* mutants display a cotyledon-specific albino phenotype with unusually large chloroplast vesicles which appear to emerge from the inner envelope. Remarkably, SCO2 interacts directly with LHCB1 proteins and was therefore proposed to be involved in vesicle-mediated transport of membrane proteins in the early stages of plant development [61].

The overall picture that emerges is that in early stages of chloroplast development, i.e., in proplastids of meristematic tissues, thylakoid membrane biogenesis proceeds via local invaginations of the inner chloroplast envelope, whereas a vesicle-based transport system takes over in mature chloroplasts. However, a characteristic biogenesis process takes place during the transformation of proplastids into etioplasts in the dark. Etioplasts harbor semi-crystalline structures named prolamellar bodies, which represent accumulations of several photosynthetic proteins in "pre-complexes" with associated components such as the light-dependent protochlorophyllide oxidoreductase (POR), protochlorophyllide and MGDG [62,63]. Upon illumination and the ensuing synthesis of chlorophyll, the prolamellar body transforms into thylakoid lamellae within a matter of hours. How lipids and protein subunits of photosynthetic complexes are conveyed to this intraorganellar structure is still an open question, but it appears likely that systems involved in the transport of material during the proplastid-to-chloroplast transition are also involved in this case [64,65].

As in chloroplasts, the precise mechanism of lipid transport to thylakoids in cyanobacteria, which contain an internal thylakoid membrane system, remains mysterious. The aforementioned presence of MGS activity in cyanobacterial thylakoids might suggest that extensive transport is not required because lipids are synthesized in situ. Indeed, cyanobacterial vesicles emerging from the plasma membrane have yet to be unambiguously identified [66]. Nevertheless, bioinformatic studies recently suggested that proteins involved in cytoplasmic vesicular transport, e.g., the Tvp38 vesicle-associated protein from yeast, also share homologies with gene products from cyanobacteria [67]. However, the function of these cyanobacterial components remains to be determined.

As an alternative to vesicles, lateral fusions of the cyanobacterial plasma membrane with thylakoid membranes have been considered to mediate transport of membrane material including lipids, proteins and pigments to growing thylakoids. This hypothesis is directly related to the longstanding question whether the cyanobacterial plasma and thylakoid membranes are physically connected, in which case the periplasmic space and the thylakoid lumen could form a continuum [68–71]. For several decades the fact that ultrastructural analyses of cyanobacterial membranes have been unable to unambiguously demonstrate such continuity has resulted in controversial discussions [72,73]. More recently, the analysis of *Synechocystis* sp. PCC 6803 cells grown under low light intensities revealed that such a connection between the two membrane types indeed exists at sites where thylakoid membranes converge on the plasma membrane (Fig. 2 and [74]). These convergence sites, named "thylakoid centers", have recently attracted much attention as potential regions at which PSII biogenesis is initiated (Section 3.2).

3. Forming the functional heart of thylakoids — the protein/pigment complexes

Whereas lipids form the matrix of thylakoids and provide the necessary hydrophobic milieu, the complexes that comprise the photosynthetic apparatus represent the main functional units of PET. Since they constitute the vast majority of thylakoid proteins and pigments,

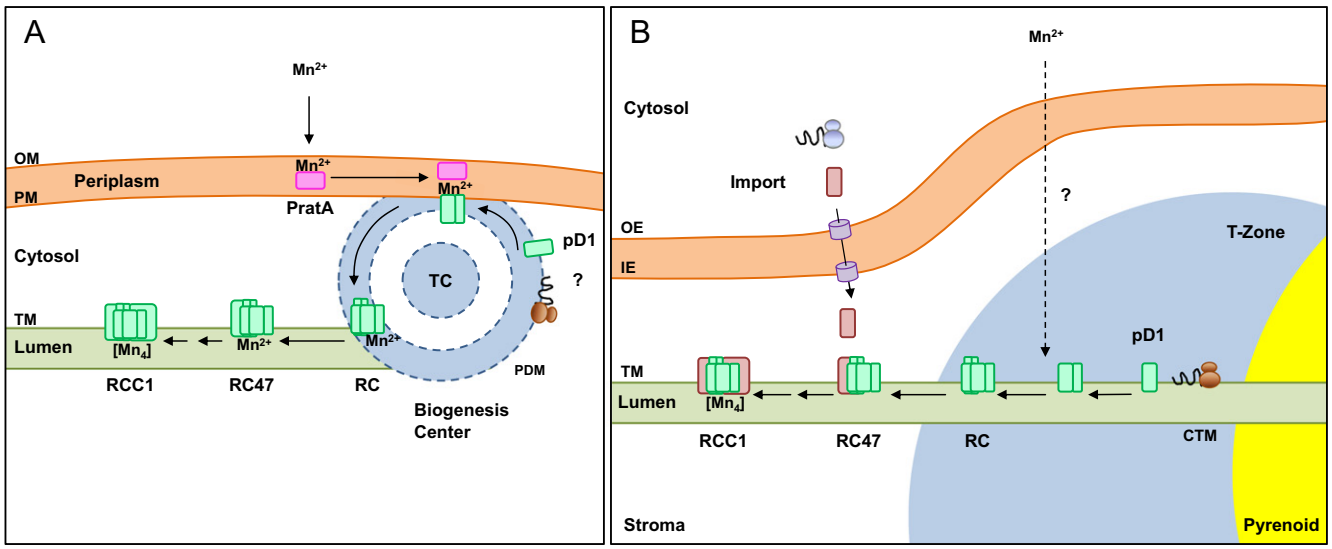

Fig. 2. Organization of specific regions dedicated to PSII assembly. Comparison of a biogenesis center in *Synechocystis* sp. PCC 6803 (A) and a T-zone in *C. reinhardtii* (B). For further explanation see Sections 3 and 4 of the text. OM: outer membrane, PM: plasma membrane, TM: thylakoid membrane, TC: thylakoid center, PDM: PratA-defined membrane, OE: outer envelope membrane, IE: inner envelope membrane, CTM: chloroplast translation membranes. (B) is adapted from Schottkowski et al. 2012.

their mode of integration into and assembly within the membrane is a central question in chloroplast research.

As the complexity of thylakoid architecture has increased during evolution, so too has the need for coordination of the assembly process (for further details see section 4 and Fig. 3). Gene expression and synthesis of the necessary proteins are already highly regulated (Chapters 1–9 [75–83]), and the same holds for the subsequent phase of complex assembly and cofactor integration (Chapters 11–14 [7–10]). Moreover, with the advent of chloroplasts after the endosymbiotic engulfment of a cyanobacterial cell, the whole process became much more complicated, due to the constraints imposed by the transfer of photosynthetic genes from the chloroplast to the nucleus. As a consequence, the biogenesis process now required the import of many protein subunits of photosynthetic complexes into the organelle, offering a new opportunity for regulatory control (Chapters 15–18 [84–87]). Accumulating evidence indicates that most if not all of these processes are coordinated by regulatory factors which catalyze distinct assembly steps in a stepwise manner, but do not form constituents of the final photosynthetic machinery [88–91]. As such, they can serve as markers which enable one to assign specific biogenesis steps to organellar subfractions or substructures. At least in theory, it should therefore be possible to dissect the cytological landscape of thylakoid membrane biogenesis. Two main experimental approaches have recently been exploited to discern the design of the production line for photosynthetic membranes — the application of membrane fractionation and imaging techniques.

3.1. Lessons from membrane fractionation experiments — thylakoid heterogeneity

Cyanobacteria usually possess three different membrane systems. The outer membrane and the plasma membrane, together with the intervening peptidoglycan layer, form the cell envelope, which encloses the thylakoid membranes. Early cell fractionation studies using sucrose-gradient centrifugation had revealed that distinct subunits of both PSI and PSII are present not only in thylakoids but also in plasma membranes from the cyanobacterium *Synechococcus elongatus* [92,93]. Other subunits of PSII, including CP43 and CP47, were found exclusively in thylakoids. In line with these findings, no PSII activity (as measured by oxygen evolution) was detectable in plasma membranes, which led to the hypothesis that biogenic intermediates of photosynthetic complexes might accumulate in the plasma membrane [93]. This idea was later revisited by applying a two-phase partitioning technique to separate different membrane fractions [94]. Again, in addition to being found in thylakoids, core subunits of PSII and PSI including D1, D2, Cytb559, PsaA, PsaB, PsaC and PsaD were immunologically detected – in minor amounts – in plasma membrane fractions. Moreover, substantial amounts of the assembly factors CtpA, Ycf3 and Ycf4 were also found in the plasma membrane, suggesting that the initial steps in the assembly of both PSII and PSI take place in plasma membranes [94]. These early assembly intermediates already contain chlorophyll and are capable of light-induced charge separation [55].

More recent membrane fractionations involving two consecutive sucrose-gradient centrifugation steps have led to the identification and characterization of a membrane subfraction that is distinct from both plasma and thylakoid membranes. Because the PSII assembly factor PratA was found to accumulate in this fraction, it was named the PratA-defined membrane (PDM; [95]). A detailed characterization of the PDM revealed that it contains – besides PratA – substantial amounts of the pD1 precursor protein. Importantly, in a *pratA* mutant, pD1 accumulation in PDMs was further enhanced [95]. In addition, the D2 reaction-center protein and early PSII assembly factors like YCF48 and YidC, but not the thylakoid marker proteins CP47 and CP43, were detected, in agreement with earlier membrane fractionation studies described above. Interestingly, the protochlorophyllide oxidoreductase (POR) required for chlorophyll synthesis, and its interaction partner Pitt, as well as the chlorophyll precursor chlorophyllide *a*, were also found in PDMs, suggesting that the two biosynthesis pathways might intersect at PDMs [96]. A tight connection between apoprotein synthesis/assembly and chlorophyll synthesis was recently confirmed by the close physical linkage between the chlorophyll synthase (ChlG) and the PSII assembly factors YCF39 and YidC revealed by co-elution of these proteins together with chlorophylls during tag-based affinity purification of ChlG [97,98]. However, in contrast to plasma membrane fractions described above, neither PSI subunits nor assembly factors were detected in PDMs [99]. Taken together, these data suggest that PDMs might represent a specialized membrane region where assembly of PSII is initiated, and that a tight connection between assembly and chlorophyll synthesis/insertion exists, at least in cyanobacteria (Fig. 2A).

The advent of proteomic approaches then allowed the question of cyanobacterial membrane heterogeneity to be addressed more systematically [70]. The proteomes of the thylakoid and plasma

membranes have now been investigated in cells grown under various conditions [100–103]. These analyses revealed that cyanobacterial thylakoids display heterogeneity with respect to the distribution of photosynthetic complexes [101], This also holds for plasma membranes, which have also been shown to exhibit non-uniform protein distributions [100]. Recently, comparative proteomic studies have been performed on membrane fractions which had been purified via the two-phase partitioning technique. Many of the subunits of thylakoid membrane complexes, including in particular PSI and the ATP synthase were identified in the plasma membrane fraction, leading to a model which predicts transient "hemifusions" between plasma and thylakoid membranes [104]. At these sites, it was proposed, that proteins are inserted into the membrane and subsequently directed to either the plasma membrane or thylakoids [104].

Perhaps the most striking example of structural and functional membrane heterogeneity is provided by the primordial cyanobacterium *Gloeobacter violaceus*. *G. violaceus* does not contain an internal thylakoid membrane system; instead its photosynthetic complexes are inserted into the plasma membrane [105,106]. As a consequence, photosynthetically active patches with a mean diameter of 140 nm can be detected by spectroscopic means within the plasma membrane of *G. violaceus* (section 4, Fig. 3 and [107]). When these membranes are fractionated via sucrose-gradient centrifugation, a lighter, carotenoid-rich "orange" and a heavier "green" fraction are obtained, which have related lipid compositions. However, comparison of their protein and pigment compositions revealed that the orange membranes resemble the plasma membrane, while the green moiety is more reminiscent of photosynthetically active thylakoids [107]. The accumulation of PSII assembly factors in orange membranes further suggests that spatially separated biogenic and photosynthetically active membrane microdomains exist even in the plasma membrane of *G. violaceus*. These green microdomains are likely to represent the evolutionary starting point for the development of an internal thylakoid membrane system (section 4, Fig. 3 and [107]).

Chloroplast outer and inner envelopes, as well as thylakoids, can be efficiently separated by centrifugation techniques, and their respective proteomes have been extensively characterized [28,108–110]. These data revealed that lipid and carotenoid synthesis is localized to the envelope membranes. The spatial organization of chlorophyll synthesis is, however, more complex, since it is initiated in the stroma, proceeds at the envelope and is completed at thylakoids (Chapter 24 [111,112]).

In *C. reinhardtii*, the integration of freshly synthesized D1 protein of PSII has been shown to take place at stromal thylakoids and the protein subsequently moves towards grana regions [113]. Moreover, membrane fractionation experiments using sucrose gradients have revealed the existence of membranes distinct from thylakoids in which putative RNA-binding regulators of chloroplast gene expression accumulate [114]. More recently, the concept of specialized chloroplast translation membranes (CTMs) in *C. reinhardtii* has been further elaborated by following the distribution of translation factors, ribosomes and assembly factors of photosynthetic complexes in sucrose gradients after floatation of membranous material (Fig. 2B and [115]). CTMs were found to be denser than thylakoids due to their association with ribosomes, and contained translation and assembly factors for PSII including the *psbD*-specific translation activator RBP40, the aforementioned *psbA* translation factor DLA2 and the assembly protein HCF136 [25,115,116]. Interestingly, no PSI subunits nor PSI assembly factors were immunologically detectable in CTMs, indicating that this fraction represents a PSII-specific biogenic compartment [115].

Moreover, proteomic analysis of the eyespot has identified the PSI assembly factor YCF4, leading to speculation that this alga-specific, carotenoid-rich structure might serve as the site of PSI biogenesis in *C. reinhardtii* [117,118].

In vascular plants, there is currently less evidence for the existence of related biogenic membrane regions. Ribosomes are excluded from grana regions for steric reasons, but bind to non-stacked stromal thylakoids [119]. Here, co-translational insertion of membrane proteins is assumed to take place and subsequent assembly steps are likely to occur here too. This idea is supported by the finding that stromal thylakoid fractions are enriched for PSII assembly intermediates [120]. By employing a detergent-free, two-phase partitioning approach, the distribution of PSII subunits and PSII assembly factors in spinach thylakoid subfractions, i.e., grana core, grana margin and stromal thylakoids, has recently been assessed in detail [121]. Their content of several assembly factors was clearly enhanced relative to grana regions, which is compatible with a biogenic function for stromal thylakoids [121].

3.2. Cytological organization of thylakoid biogenesis

With the identification of factors involved in the synthesis and assembly of photosynthetic complexes, their subcellular/suborganellar localization could be determined using in situ FISH/IF techniques or GFP-based live-cell imaging. Pioneering work by Zerges and coworkers showed that, upon illumination at moderate light levels, both mRNAs and ribosomes in the chloroplasts of *C. reinhardtii* colocalize to two or three punctate regions at the periphery of its single pyrenoid, which were named T (for translation) zones (Fig. 2B and [122]). Strikingly, as in the case of CTMs (Section 3.1), only chloroplast mRNAs coding for subunits of PSII were found to be localized to T-zones. Therefore, it was suggested that CTMs represent T-zone-related membrane material [115]. This idea is further supported by the accumulation of PSII assembly intermediates around the pyrenoid in a PSII assembly mutant [122]. Moreover, the DLA2 subunit of pyruvate dehydrogenase (Section 2.2) has been identified as a critical determinant for light-dependent localized translation of the *psbA* mRNA at T-zones [25]. DLA2 binds to an A-rich element in the 5′ untranslated region of the *psbA* mRNA, cofractionates with CTMs and colocalizes with *psbA* mRNA at T-zones in a light- and acetate-dependent manner [25,123]. Most importantly, localization of *psbA* mRNA to T-zones is lost in DLA2 RNAi lines, and D1 synthesis is affected [25]. All these findings strongly suggest that DLA2 is involved in targeted translation of the *psbA* mRNA at T-zones and thereby determines the starting point of the path for PSII biogenesis [25,124]. Furthermore, application of translational elongation inhibitors revealed that accumulation of mRNAs in T-zones does not require active chloroplast protein synthesis, which rules out the alternative possibility that targeting is mediated via signals in the nascent polypeptide [125].

Recently, the T-zone model for the initial steps of PSII synthesis and assembly has been expanded by incorporating the later steps of PSII maturation [115]. IF-based localization experiments have defined an extended biogenesis region which includes the region in the vicinity of T-zones forming the junctions with thylakoid lobes [115]. At these junctions TOC and TIC components of the envelope's protein import machinery were shown to accumulate upon moderate illumination. This led to the hypothesis that the integration of nucleus-encoded PSII subunits – in particular the oxygen-evolving complex (OEC) subunits and LHC proteins – into an assembling PSII core complex is spatially connected to the T-zone area (Fig. 2B and [115]). As depicted in Fig. 2B, this would provide a continuous assembly pathway for PSII, without release or transfer of intermediates, even when subunits originating in the cytoplasm must be incorporated. Whether similar coordination points are utilized in plastids of other organisms remains to be clarified.

In cyanobacteria, the situation is less complex due to the lack of organelle-based intracellular compartmentalization. Nevertheless, as already suggested by the identification of biogenic PDM fractions (Section 3.1) a distinct cellular substructure in which the initial steps of PSII biogenesis take place has recently been defined in the model organism *Synechocystis* 6803. Transmission electron microscopy in combination with immunogold labeling of the PSII assembly factor PratA revealed that this PDM marker protein accumulates at so-called "thylakoid centers", i.e., sites where the thylakoid membranes converge towards the plasma membrane (Fig. 2A and [126]). Thylakoid centers

were initially described as cylindrical, rod-like structures at the cell periphery [73,127].

These rods are ~50 nm in diameter and 1 μm in length, and in EM tomography studies on *Synechocystis* 6803 their ends are occasionally seen to be connected to the plasma membrane [73]. Cross-sections through the rods revealed a 14-fold symmetry resembling that of assemblies of recombinant VIPP1 protein [128]. Therefore, it has recently been suggested that VIPP1 is the major constituent of thylakoid centers [129]. Recent GFP-based live-cell imaging using confocal microscopy has revealed that, under low light conditions, VIPP1 is localized in a punctate manner preferentially at the cell periphery [53]. However, under high light levels, the number of punctate accumulations associated with internal thylakoid membranes increases substantially, suggesting a highly dynamic subcellular redistribution of VIPP1 under stress conditions (Chapter 21 [53,54]).

The central electron-dense rod structures appear to be surrounded by a semicircular membranous halo, from which thylakoid lamellae appear to originate [126]. In PratA-deficient cells, this halo does not form, leading to distortion of thylakoid convergence sites [126]. This suggests that, besides functioning in Mn^{2+} transport, PratA also fulfills a structural role at PSII biogenesis centers [126]. The current model for the organization of de novo PSII biogenesis predicts that its initial steps take place at PDMs of thylakoid centers (Fig. 2A and [89]). At this site, freshly synthesized pD1 precursor protein is loaded with Mn^{2+} directly from the periplasm via PratA, and the first PSII assembly intermediate – the RC complex – is formed, probably cotranslationally, Chl is incorporated into this precomplex at PDMs, which then move into thylakoid lobes. Here, PSII assembly proceeds along its conserved path until functional PSII is generated (Chapter 11 [7]). As in the case of CTMs/T-zones in *C. reinhardtii*, no evidence for the assembly of other photosynthetic complexes, e.g., PSI, at PDMs has been obtained to date.

4. Biogenic centers — a common model for thylakoid assembly?

The work described in the previous sections, mainly on the fabrication of PSII, outlines the design of a thylakoid membrane assembly line in both cyanobacteria and chloroplasts. The results reveal that the biogenic process is initiated at distinct, subcellular membranous structures. From there on, it proceeds in a strictly determined sequence of maturation steps to form a complete functional photosynthetic apparatus. Essential cofactors like metal ions and chlorophyll molecules are incorporated into assembly intermediates during the initial phase. This underlines the fact that spatial organization of the process helps to ensure that provision and assembly of proteins and synthesis and incorporation of cofactors are properly synchronized. Moreover, crosstalk with other metabolic pathways – particularly lipid synthesis – at these sites could facilitate the coordination of thylakoid biogenesis.

As discussed earlier, besides providing a nucleation point for physical interaction between different biosynthetic machines and the ordered insertion of components via substrate channeling, such a focused biogenesis pathway should have two major advantages [89,124]. First, the local increase in concentrations of cofactors and assembly intermediates, such as Mn^{2+} ions, in biogenic microcompartments would favorably shift the chemical equilibrium towards assembly. Second, defined biogenic microcompartments, well separated from photosynthetically active membranes, could minimize the release of toxic intermediates of the assembly process such as photoreactive chlorophyll molecules [89,124].

This raises the question of where such biogenic substructures might best be sited in the cell/organelle. As described above, to date, two biogenic centers have been analyzed in greater detail, i.e., biogenesis centers/PDMs in cyanobacteria and T-zones/CTMs in the chloroplast of the green alga *C. reinhardtii* (Fig. 2). Interestingly, both are clearly dedicated to the assembly of PSII but not of PSI. Why PSII biogenesis should be highly organized in space is not immediately obvious. Based on the function of the marker protein PratA, one may speculate that the PSII-specific requirement for Mn^{2+} favors the use, and determines the site, of an organized assembly line.

Another feature specific to PSII assembly is that two quite different pathways have to be considered. One mediates its de novo construction and requires the synthesis and assembly of the entire set of PSII components, as described above. The second is devoted to the maintenance of PSII after photo-damage to its D1 subunit, and involves partial disassembly, and repair synthesis and integration of the D1 protein alone (Chapter 12 [10]). Judging from the suborganellar distribution of *psbA* mRNA after exposure of cells to high light levels that damage D1, D1 repair synthesis and integration into PSII apparently occur at sites that are spatially separated from biogenic centers. Under these conditions, no localization to T-zones is observed. Instead, *psbA* mRNA is more or less evenly distributed all over stromal thylakoid lobes, suggesting an on-site mode of D1 repair [122]. In both *C. reinhardtii* and vascular plants, repair synthesis and reassembly are excluded from thylakoid grana regions due to steric constraints, and therefore take place at stromal thylakoids and/or grana margin regions [113,130,131]. Moreover, D1 repair synthesis appears to be regulated at the level of translational elongation, whereas D1 synthesis for de novo PSII assembly is controlled at the initiation step via the 5′ untranslated region of the *psbA* mRNA [132]. This evidence suggests that the two processes are strictly separated both spatially and functionally. In cyanobacteria too, biogenic and repair regions are distinctly separated. Recent studies of the PSII repair-related FtsH protease revealed that it accumulates in thylakoids, and not in biogenesis centers [133]. Taken together, these findings suggest that localized *de novo* assembly of PSII might be needed in order to isolate it from PSII on-site repair, thereby avoiding the risk of interference between synthesis/assembly machineries that obviously operate in different modes [89]. In addition, centers are likely to facilitate the incorporation of Mn^{2+} into growing PSII, whereas metal ions might be recycled during D1 repair.

All of this poses two further questions: (i) Where are other photosynthetic complexes, in particular the Chl-rich PSI complex, assembled? (ii) Are PSII biogenesis centers a recurring feature in thylakoid evolution? What little information is available regarding the site of PSI biogenesis suggests that some assembly occurs at the eyespot in *C. reinhardtii* or in cyanobacterial plasma membranes. In *Synechocystis* 6803, thylakoid lobes protruding into the interior of the cell have been hypothesized to represent a thylakoid membrane subfraction that is distinct from biogenesis centers and may serve as sites of biogenesis and/or repair. These membranes are frequently associated with ribosomes, suggesting that they are highly active sites of protein synthesis [68,73]. However, whether a specific subset of polypeptides is synthesized at these locations is currently unclear. Similarly, almost nothing is known about the site or mode of assembly of the cytb_6f and ATPase complexes.

The same can be said with respect to the evolution of thylakoid biogenesis machineries. Fig. 3 schematically depicts the structures of various thylakoid membrane systems to illustrate their differing complexities. Based on available structural data, some but not all cyanobacteria, e.g., *Synechocystis* 6803, contain thylakoid convergence sites that might form biogenic centers for thylakoids [127]. *G. violaceus*, however, lacks an internal thylakoid membrane system and utilizes distinct green patches within the plasma membrane instead, while *Synechoccoccus* sp. PCC 7942 has an internal membrane system without thylakoid convergence sites (Section 3.1 and [107,134]). It should be noted here that thylakoid centers have alternatively been hypothesized to represent remnants of cyanobacterial cell division, simply marking the sites on the plasma membrane at which division has occurred [72].

In the case of chloroplasts, particularly of unicellular algal species, the pyrenoid appears to represent an important landmark which might serve to define the starting point of thylakoid maturation by providing a structural nucleation point. In *C. reinhardtii* the pyrenoid is penetrated by a network of thylakoid tubules [135]. By analogy to the

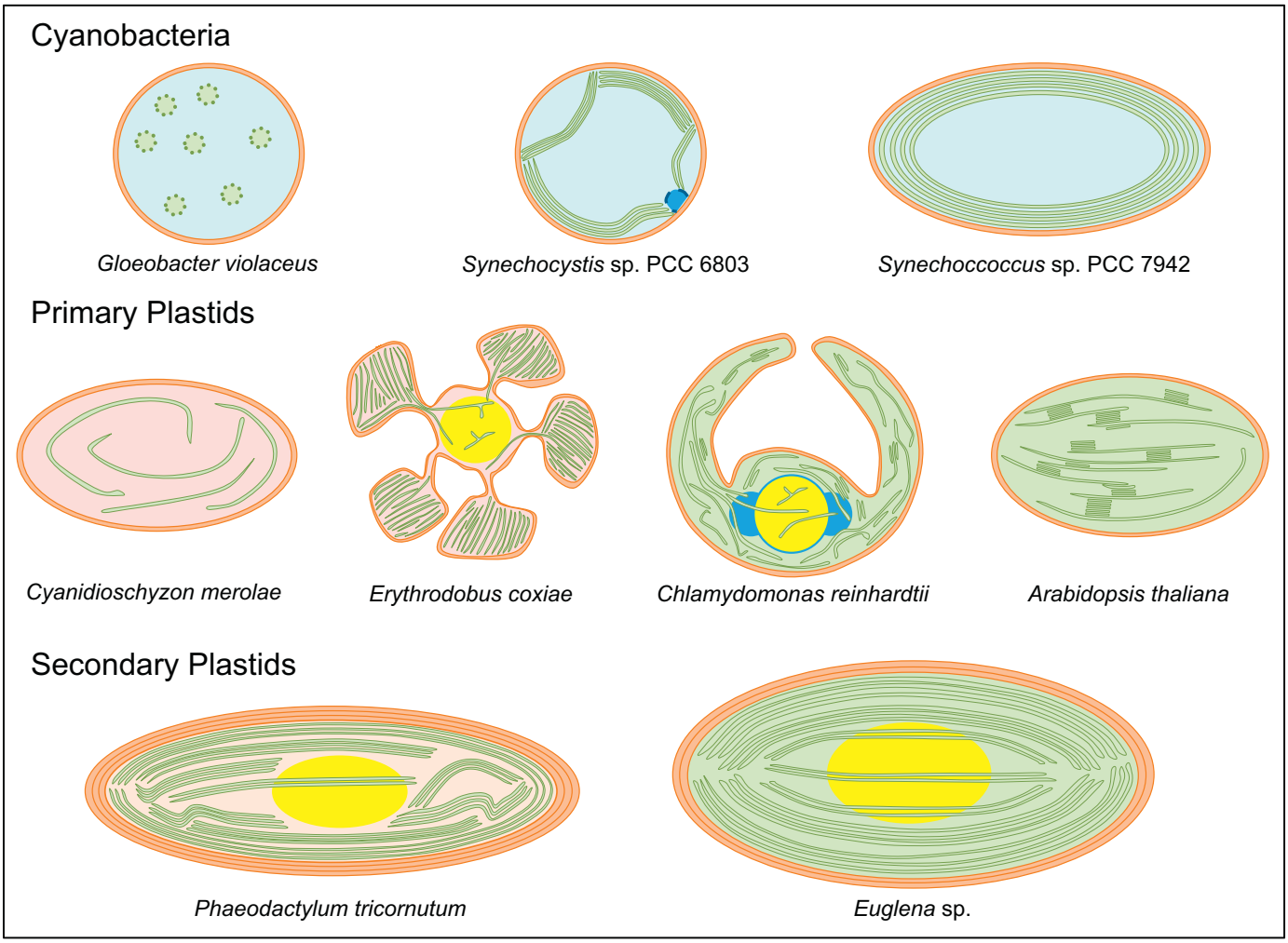

Fig. 3. Architectures of thylakoid membranes. Models of the diverse structures of thylakoid membranes (green) in cyanobacteria and in primary and secondary plastids. Biogenesis center and T-zones are depicted in blue, pyrenoids are shown in yellow, envelope and plasma membranes are indicated in red.

situation in *C. reinhardtii*, other algae might contain CTMs that either surround or traverse the pyrenoid (Fig. 3).

Pyrenoids are not found in the chloroplasts of higher plants. In etioplasts, however, prothylakoids emerge from the prolamellar body, which appears as a tubular network of membranes in electron micrographs [65,136]. Hence, one may speculate that, during thylakoid biogenesis in developing etioplasts, prolamellar bodies play a structural role similar to that of pyrenoids in algal chloroplasts.

In red algae a wide variety of different morphotypes of plastids and thylakoids exists. For instance, some unicellular species, like the model organism *Cyanidiioschyzon merolae*, lack a pyrenoid [137], while others, like *Erythrolobus coxiae* and thallus-forming species like *Porphyra* sp., harbor such a structure [138,139]. Indeed, *E. coxiae* has a plastid containing a central pyrenoid surrounded by at least four plastid lobes (Fig. 3 and [139]). The pyrenoids of these red algae are penetrated by several branched thylakoids, giving rise to a network comparable to the thylakoid tubule system in *C. reinhardtii*. Interestingly, the vast majority of secondary plastids also contain pyrenoids but, unlike those in their evolutionary ancestors, these are not penetrated by loosely organized tubular networks but by paired thylakoid stacks. In the case of the diatom *Phaeodactylum tricornutum*, a single thylakoid stack composed of two thylakoid layers extends through the pyrenoid (Fig. 3 and supp. Fig. 2 of [140]). In several *Euglena* species the pyrenoid is, however, traversed by more than one paired thylakoid stack (Fig. 3 and [141]). It is noteworthy that, in both diatoms and euglenoids, stromal thylakoid stacks are normally composed of three parallel thylakoid layers (Fig. 3 and [141,142]).

In addition to its putative role in thylakoid membrane biogenesis, the pyrenoid of *C. reinhardtii* has been shown to be involved in the chloroplast's stress response [143]. Under oxidative stress, RNA granules are formed within the internal perimeter of the pyrenoid, probably to protect mRNA molecules from damage by reactive oxygen species [143]. After release of stress, mRNAs are rapidly reincorporated into polysomes in a highly dynamic manner. These findings underline the significance of the pyrenoid as an alga-specific compartment that acts as an organizer for targeted chloroplast protein synthesis [143].

In contrast, there is so far little evidence for the presence of distinct suborganellar structures dedicated to thylakoid biogenesis in higher plants. One way of addressing this question at the molecular level would be to analyze homologs of factors that are known to mark these biogenic sites in algae and cyanobacteria, in particular, the PratA protein from *Synechocystis* 6803. However, no proteins that show any obvious similarities with PratA have been detected by bioinformatic means. Intriguingly, two factors, namely Rep27 from *C. reinhardtii* and Lpa1 from *A. thaliana*, belong to the tetratricopeptide repeat protein (TPR) family – like PratA – and both have been shown to interact with the D1 protein based on interaction studies and phenotypic assessment of the corresponding mutants [144–146]. These studies revealed a role

for both proteins in facilitating the integration of nascent D1 into PSII pre-complexes. Moreover, recombinant Lpa1 possesses Mn^{2+} binding activity, making this factor a good candidate for a marker which might enable one to determine the localization of PSII biogenesis sites in the chloroplasts of land plants [89,126].

5. The shaping of thylakoid architecture

As summarized in Fig. 3, thylakoid membrane systems can undergo substantial architectural diversification. Whereas red algae and their descendants in the "red lineage" of algae with secondary plastids have retained phycobilisome-like structures during evolution to some extent, green algae and, even more prominently, vascular plants developed membrane-located light-harvesting complexes [142,147]. This transition opened new opportunities for the shaping of thylakoids by removing the steric constraints associated with the assembly of the relatively bulky phycobilisome structure at the surface of thylakoids. This has allowed vascular plants to form an even more highly curved structural element of the thylakoid membrane, i.e., the granum [4]. Although the precise ultrastructure of grana regions remains a matter of debate [65,148–150], in principle, they consist of multiple stacks of flat membrane discs ca. 300–600 nm in diameter, which are linked by single stroma lamellae. Moreover, the photosynthetic complexes are unevenly distributed between the two subsystems, with PSII and LHCII being concentrated in grana regions whereas PSI and the ATPase are mainly found in stroma lamellae — a condition referred to as lateral heterogeneity. The physicochemical forces that drive grana formation have been attributed to stromal moieties of LHCII proteins, which are proposed to determine membrane stacking of adjacent thylakoid discs [151,152]. However, a novel class of thylakoid-shaping proteins, with four members named CURVATURE THYLAKOID1A-D (CURT1A-D), has recently been identified in *A. thaliana* [65,153]. Genetic and biochemical evidence strongly suggests that CURT1 proteins localize to grana margin regions. Here, they induce extreme membrane bending that results in the formation of thylakoid discs, thereby determining the architecture of a granum [153]. Their margin-specific localization makes CURT proteins ideal markers for this thylakoid sub-fraction in land plants, and allows precise tracking of these membranes during fractionation experiments [130]. Moreover, recent work has revealed that the dynamic organization of grana margin regions is a key factor in the control of the PSII repair process after photodamage [130]. Whether CURT1 is also related to biogenic processes at stromal thylakoids is not yet known, but the phenotype of CURT1 mutants lacking grana structures revealed that these are not required for the generation of thylakoids. Surprisingly, CURT1 homologs are present not only in grana-containing land plants and green algae, but also in cyanobacteria. Future work will doubtless uncover the functional role of this class of small thylakoid membrane proteins in the shaping of thylakoids.

Competing interest statement

The authors declare no competing interests.

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