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RESEARCH

Phylogenetic and spectroscopic insights on the evolution of core antenna proteins in cyanobacteria

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Abstract

Light harvesting by antenna systems is the initial step in a series of electron-transfer reactions in all photosynthetic organisms, leading to energy trapping by reaction center proteins. Cyanobacteria are an ecologically diverse group and are the simplest organisms capable of oxygenic photosynthesis. The primary light-harvesting antenna in cyanobacteria is the large membrane extrinsic pigment-protein complex called the phycobilisome. In addition, cyanobacteria have also evolved specialized membrane-intrinsic chlorophyll-binding antenna proteins that transfer excitation energy to the reaction centers of photosystems I and II (PSI and PSII) and dissipate excess energy through nonphotochemical quenching. Primary among these are the CP43 and CP47 proteins of PSII, but in addition, some cyanobacteria also use IsiA and the prochlorophyte chlorophyll *a*/*b* binding (Pcb) family of proteins. Together, these proteins comprise the CP43 family of proteins owing to their sequence similarity with CP43. In this article, we have revisited the evolution of these chlorophyll-binding antenna proteins by examining their protein sequences in parallel with their spectral properties. Our phylogenetic and spectroscopic analyses support the idea of a common ancestor for CP43, IsiA, and Pcb proteins, and suggest that PcbC might be a distant ancestor of IsiA. The similar spectral properties of CP47 and IsiA suggest a closer evolutionary relationship between these proteins compared to CP43.

Keywords Cyanobacteria · Antenna proteins · Evolution · Spectroscopy · Phylogeny · Chlorophyll

Introduction

Bacteria capable of oxygenic photosynthesis constitute the phylum cyanobacteria. Initially placed together with algae as *Schizophytae* by Ferdinand Cohn in 1872 (Stanier et al. 1971), cyanobacteria were not included in the Bacterial taxonomical scheme until 1978 (Stanier et al. 1978). Cyanobacteria are a diverse group of prokaryotes, with the phycobilin and chlorophyll pigments imparting the cells a blue-green color. It is generally agreed that cyanobacteria are the most ancient among the oxygenic photoautotrophs and that a cyanobacterial precursor was the progenitor of the chloroplasts of plants and algae (Bonen and Doolittle 1975, 1976; Bonen et al. 1979; Giovannoni et al. 1988). As such, the basic mechanisms of light-harvesting and photosynthetic electron transport has remained unchanged across all oxygenic photoautotrophs.

Like all oxygenic photoautotrophs, cyanobacteria have two photosystems, PSI and PSII, connected through the Z-scheme (Blankenship 1992). Photosynthetic electron transport functions to chemically fix the light energy absorbed by the chlorophyll pigments bound to the photosystems. However, the photosynthetic apparatus in general, and photosystem II in particular, is prone to damage under strong irradiance that can result in a phenomenon called photoinhibition (Nishiyama et al. 2006). Light absorption and energy transfer to the PSII reaction center are, thus, tightly regulated in both cyanobacteria and eukaryotic photoautotrophs through chlorophyll-binding antenna (CBA) proteins. Among the oxygenic photoautotrophs, cyanobacteria have evolved unique CBA proteins like iron-stress-induced A (IsiA) and prochlorophyte chlorophyll-*b* binding (Pcb) that,

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together with the closely related CP43 and CP47 proteins of PSII, form the larger CBA protein family in cyanobacteria.

Chlorophyll-binding antenna proteins in cyanobacteria

Based on the terminal electron acceptors, PSI and PSII have been suggested to have evolved from two different types of reaction centers classified as Type I and Type II, respectively (Blankenship 2001). However, the CBA proteins CP43 and CP47 of PSII were initially suggested to have evolved from the truncation of a gene-encoding a Type I reaction center (Mix et al. 2005). This view was later challenged, and a new hypothesis was proposed suggesting that remodeling of a Type I reaction center gave rise to the CP43 and CP47 proteins (Cardona 2016). The *psbC* gene-encoding CP43 in cyanobacteria has been hypothesized to be the progenitor of the *isiA* and *pcb* gene families (Chen et al. 2005b). Despite similar to CP43, in both IsiA and Pcb proteins, the large thylakoid lumen-exposed loop E connecting helices V and VI is truncated (Murray et al. 2006).

All oxygenic photoautotrophs contain CP43 and CP47, but the presence of IsiA and Pcb proteins depends on specific ecological niches or genera (Chen et al. 2018; Chen et al. 2008a, b; Chen et al. 2005b). The *isiA* gene was first identified as a gene upstream to flavodoxin expressed under iron-limiting conditions (Laudenbacht and Straus 1988). It was later confirmed that the chlorophyll-protein (CP) complex (CPVI-4) seen accumulating under iron stress (Pakrasi et al. 1985) contained the *isiA* gene product (Burnap et al. 1993). Under iron-limiting conditions, IsiA is known to form individual or concentric rings that may associate with trimeric PSI (Bibby et al. 2001; Boekema et al. 2001; Kouřil et al. 2005). The recent structures of IsiA-PSI protein complexes (Toporik et al. 2019; Akita et al. 2020; Cao et al. 2020; Nagao et al. 2023) show IsiA subunits surrounding the PSI monomer or trimer and detail the energy transfer from IsiA to PSI (Harris et al. 2023). The IsiA protein was initially proposed to act as a chlorophyll-storage protein (Burnap et al. 1993); later, roles like photoprotection (Ihalainen et al. 2005), light harvesting (Yeremenko et al. 2004) and excitation energy dissipation (Sandström et al. 2001; Chen et al. 2017) were also proposed. More recently, spectroscopic observations confirmed that IsiA indeed acts as a quencher that involves a conserved cysteine residue (Chen et al. 2021).

Within the cyanobacterial phylum, prochlorophytes lack the phycobilisome light-harvesting complex and are sometimes referred to as green cyanobacteria (Pinevich et al. 2012; Barrera-Rojas et al. 2018). Another unique feature of prochlorophytes is the presence of Pcb proteins that act as membrane-intrinsic light-harvesting antenna for either PSI or PSII. The *pcb* gene family to date is restricted to the three known genera of prochlorophytes (*Prochlothrix*, *Prochlorococcus,* and *Prochloron*) and chlorophyll *d*-containing cyanobacteria belonging to the genus *Acaryochloris* (Geiß et al. 2001; Chen et al. 2002; Bibby et al. 2003a; Saer and Blankenship 2017). Pcb proteins, unlike IsiA that binds only chlorophyll *a,* can bind both mono- and divinyl forms of chlorophyll *a* and *b* (Ito and Tanaka 2011; Barrera-Rojas et al. 2018) along with chlorophyll *d* in *Acaryochloris* species (Chen et al. 2005a). Besides using chlorophyll *d* as the major light-harvesting pigment, *Acaryochloris* is unique in having both IsiA and Pcb as well as phycobiliproteins (Chen et al. 2008a, b). The *pcb* gene family, depending on the species, can include multiple *pcb* genes (*pcbA*-*pcbH*) linked to low light adaptation in *Prochlorococcus* (Bibby et al. 2003a). Unlike IsiA, which preferentially forms supercomplexes with PSI, Pcb proteins are known to associate with both PSI and PSII (Bibby et al. 2003b; Bumba et al. 2005; Boichenko et al. 2007; Chen and Bibby 2005).

Structural and amino acid sequence similarities between the CBA proteins of cyanobacteria suggest that these proteins have evolved from a common ancestor. However, most studies of the evolution of CBA proteins were performed before high-resolution structures of these proteins were available. With the current advancements in spectroscopic assessment of excitation energy transfer and cryo-EM structures, revisiting the evolution of CBA proteins in cyanobacteria is worthwhile. In this report, we look at the evolution and function of CBA proteins from phylogenetic and spectroscopic perspectives to improve our understanding of these proteins.

Materials and methods

Sequence selection

Amino acid sequences of proteins presented in Fig. 1 were downloaded from the UniProt database (www.uniprot.org) on May 5, 2023. The genes were selected to include Pcb protein sequences from the representative genera belonging to *Prochlorococcus marinus*, *Prochloron didemni*, *Prochlorothrix hollandica*, *Acaryochloris marina*, and *Fischerella muscicola*. The IsiA protein sequence from *Acaryochloris marina*, *Fischerella muscicola*, and *Prochlorococcus marinus* were identified by BLAST sequence analysis (www.uniprot.org) of respective genomes against the IsiA sequence from *Synechocystis* sp. PCC 6803. The species of selected sequences (Fig. 1) are abbreviated as PROHO (*Prochlorothrix hollandica*, taxon ID 1223), PRODI (*Prochloron didemni*, taxon ID 1216), ACAMR (*Acaryochloris marina*, taxon ID 155978), ACAM1 (*Acaryochloris marina* strain MBIC 11017, taxon ID 329726), FISMU (*Fischerella muscicola*, taxon ID 92938), SYNY3 (*Synechocystis* sp. PCC

6803, taxon ID 1111708), SYNE7 (*Synechococcus elongatus* PCC7942, taxon ID1140), PROMA (*Prochlorococcus marinus* strain SS120, taxon ID167539), PROM4 (*Prochlorcoccus marinus* strain MIT 9211, taxon ID 93059), and GLOVI (*Gloeobacter violaceus* PCC 7421, taxon ID 251221).

Amino acid sequence alignment and phylogenetic analysis

All alignment and phylogenetic analysis were performed using MEGA 11 (64-bit) software (www.megasoftware.net) for Windows. The protein sequences were aligned using the MUSCLE algorithm inbuilt in the software using default settings. Before phylogenetic analysis, the best data-fitting amino acid substitution model was identified (Settings used—Gap/Missing Data Treatment: use all sites; Branch Swap Filter: Very strong and Number of Threads: 4). The identified model (LG + G + I) was then used to construct a Maximum Likelihood tree (bootstrapped 50 times).

Structure analysis of CP43, CP47, and IsiA

All structure analysis was performed using ChimeraX (https://www.rbvi.ucsf.edu/chimerax). The individual chains corresponding to the CP43 and CP47 proteins were extracted from PDB entry-7N8O (Gisriel et al. 2022) (https://doi.org/10.2210/pdb7n8o/pdb), and IsiA was extracted from PDB entry-6NWA (Toporik et al. 2019) (https://doi.org/10.2210/pdb6nwa/pdb). Inbuilt functions with default settings were used to align the proteins and cofactors.

Results

Phylogenetic assessment of CBA proteins

Multiple studies examining the evolution of CBA proteins have reached two conclusions: (1) Pcb proteins are not related to the light-harvesting complex (LHC) of algae and higher plants (Palenik and Haselkorn 1992; La Roche et al. 1996; Chen et al. 2008a, b), and (2) CP43, CP47, IsiA, and Pcb proteins have common ancestry (Mix et al. 2005; Zhang et al. 2007). However, in recent years, advancements in biochemistry, spectroscopy, and protein-pigment structure elucidation allow studying the evolution of CBA proteins with better resolution. Our phylogenetic assessment (Fig. 1) using the entire sequence of proteins agrees with previous studies showing that the CP43 protein (PsbC) is more closely related to IsiA and Pcb proteins compared to CP47 (PsbB) (Chen and Bibby 2005). Examination of the tree reveals an early bifurcation of the CP43 family from CP47. The CP43/IsiA/Pcb family progenitor split into two groups, one including the CP43 proteins and a few Pcb (primarily PcbC) proteins, and the other group comprised of IsiA and most Pcb proteins. This suggests that post-divergence, IsiA and Pcb (specifically PcbA and PcbB) might have followed an independent evolutionary path. Another interesting feature quite evident in the tree is the grouping of Pcb sequences between prochlorophytes. It seems that the CBA proteins of the genus *Prochlorococcus* diverged early and have evolved within the genus. The closer grouping in the tree of Pcb proteins from different prochlorophyte genera suggests that lateral gene transfer between genera further specialized these proteins to suit light-harvesting needs and that the ability of Pcb proteins to bind mono- and divinyl forms of chlorophyll *a* and *b* followed. This hypothesis seems quite probable as chlorophyll *a* is suggested to be the most ancient among the chlorophylls (Björn et al. 2009).

One of the primary questions concerning IsiA is the evolution of the iron stress response and the association of IsiA with PSI. However, for the Pcb proteins, no clear-cut pattern can be seen in which proteins associate with PSI and/or are involved in iron stress versus which proteins associate with PSII. The PcbC protein shows similarity to IsiA in terms of forming complexes with PSI, and at least two PcbC proteins (Accession numbers: Q7VC57 and Q9F487) are known to be upregulated under iron stress (Geiß et al. 2001; Bibby et al. 2003a). Like IsiA, the PcbC protein of *Prochlorothrix hollandica* (Accession number: P95505) forms an 18-mer protein complex with PSI (Bumba et al. 2005). These similarities between PcbC and IsiA, along with the grouping of PcbC with CP43 suggests that the IsiA protein could have evolved from a precursor form of PcbC. Based on phylogeny derived from 16S rRNA sequences, *Prochlorothrix hollandica* is placed among the early cyanobacterial lineage (Tomitani et al. 2006; Moore et al. 2019). It is possible that an ancestor of the PcbC protein of *Prochlorothrix hollandica* was a progenitor of the IsiA protein that was retained in *Acaryochloris* and *Fischerella* and was later acquired and became specialized into the current form of IsiA.

Developing the above hypothesis further, we looked at the multiple protein sequence alignment to compare the conservation of amino acid residues between PcbC (Q7VC57, P95505, Q6Q974, and Q9F487), IsiA (Q55274), and PsbC (P09193). The data in Table 1 do not show any pattern consistent with PcbC of *Prochlorothrix hollandica* as a progenitor of IsiA. An important feature that was exclusively observed in the IsiA protein in *Synechocystis* sp. PCC 6803 (IsiA SYNY3, Fig. 1) and other cyanobacteria, but not in CP43, was the presence of a conserved Cys residue (Chen et al. 2017). Exploring the alignment (Fig. 2) shows that the IsiA SYNY3 Cys 260 (Q55274) residue aligns with Cys 263 of PcbC (Q7VC57) from *Prochlorococcus marinus*. Moreover, PcbC from *Prochlorothrix hollandica* (P95505) and *Acaryochloris*

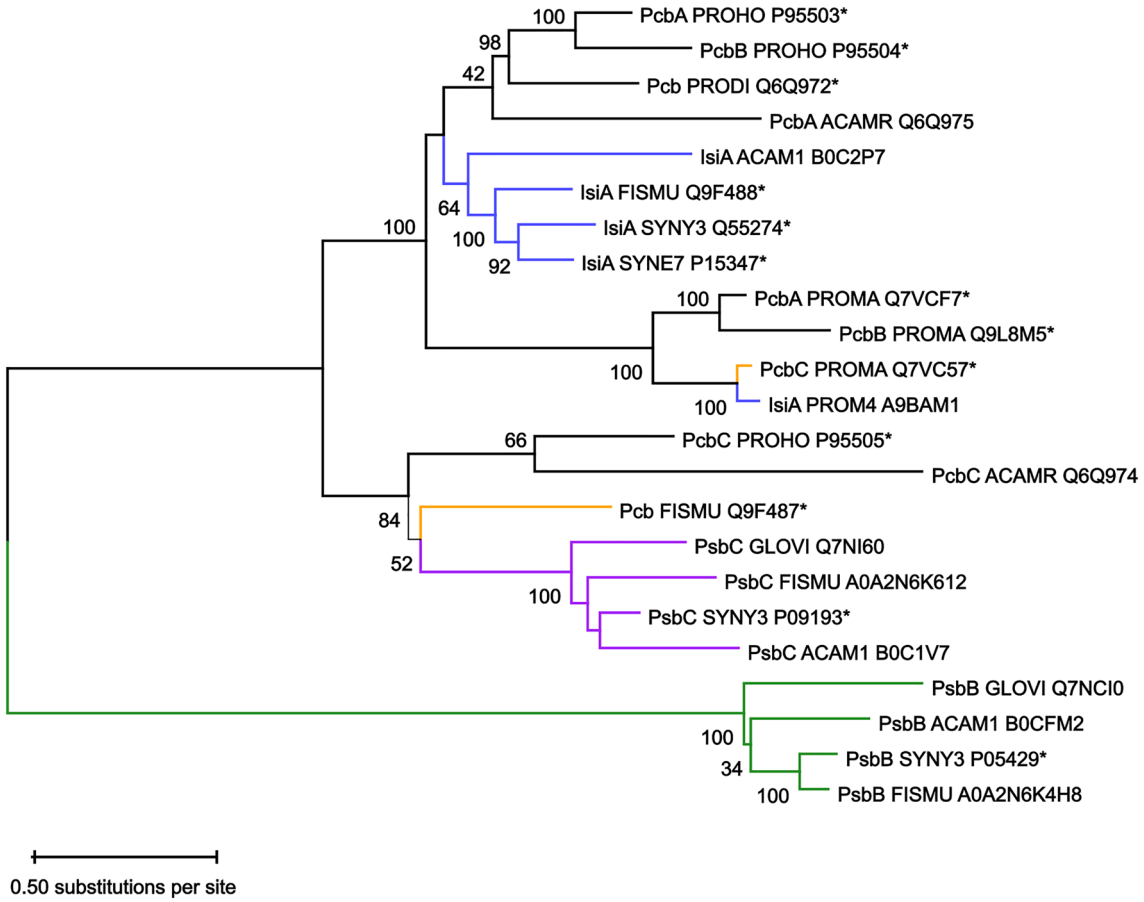


Fig. 1 Bootstrap consensus phylogenetic assessment using the entire protein sequence of the proteins CP43, CP47, IsiA, and Pcb. The branches are labeled as the name of the protein followed by abbreviated name of the organism and Accession number as it appears in the UniProt database. Labels with an asterisk are proteins that are reviewed entries in the database. Branches with the CP43 (PsbC) protein sequences are shown in purple, CP47 (PsbB) in green, and IsiA in blue to highlight their location in the tree. The branches with the PcbC proteins upregulated under iron stress are colored orange. Refer to the methods section for details. Bootstrap frequencies greater than 30 are shown at the nodes

Table 1 Comparison of IsiA and PsbC protein sequences from *Synechocystis* sp. PCC 6803 with PcbC protein sequences

Protein name	Length	Percent identity	Aromatic amino acid percentage (except His)	Charged amino acid percentage	Number of cysteine residues	Number of glycine residues	Number of histidine residues	Number of proline residues
IsiA SYNY3 Q55274	342	Reference	14.9	10.5	1	39	15	15
PcbC PROMA Q7VC57	351	50.1	15.1	13.7	4	41	15	9
PcbC PROHO P95505	375	39.5	12.3	13.3	4	55	14	27
PcbC ACAMR Q6Q974	352	32.4	11.6	12.8	5	37	12	16
Pcb FISMU Q9F487	324	47.8	12.7	10.8	0	36	13	13
PsbC SYNY3 P09193	460	36.1	13.5	13.9	2	60	13	24

Fig. 2 Multiple protein sequence alignment of IsiA and PsbC from *Synechocystis* sp. PCC 6803 with the PcbC proteins. The conserved histidines are highlighted with red boxes. Blue box highlights the position of Cys 260 from IsiA and shows the presence of Cys residues of PcbC that either aligns or is close to Cys 260 of IsiA SYNY3 Q55274. The asterisk after the name shows reviewed entries in the Uniprot database. The spectroscopic properties of IsiA SYNY3 Q55274, PcbC PROHO P95505, and PsbC SYNY3 P09193 have been studied and summarized later in the text

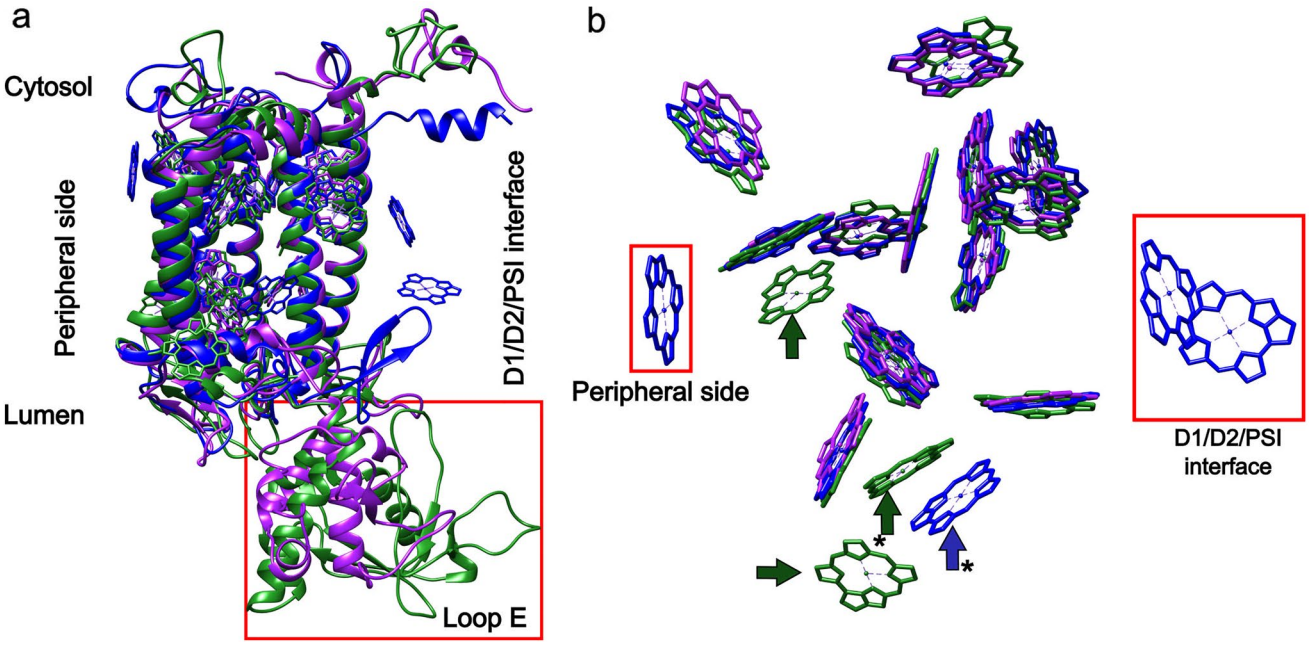
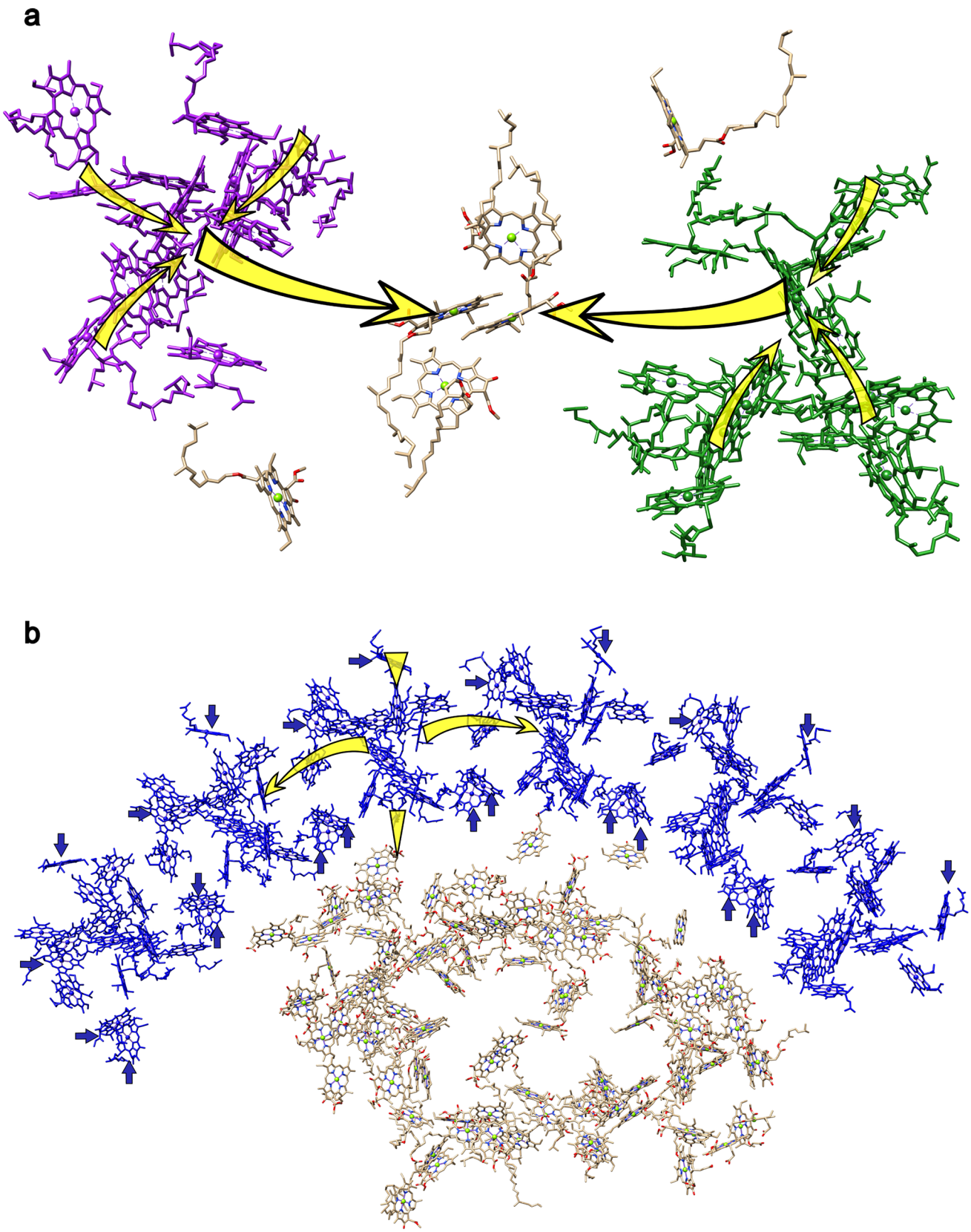


Fig. 3 Structure comparison of the CP43 (purple), the CP47 (green), and the IsiA (blue) proteins from *Synechocystis* sp. PCC 6803. **a** The three closely related chlorophyll-binding proteins show six transmembrane helices. All six helices align with each other; the IsiA protein shows the absence of the lumenal loop E (red box) that is present in CP43 and CP47. **b** Chlorophyll *a* arrangement in the CP43, CP47 and IsiA proteins as seen from the cytosolic side of the thylakoid membrane. All 13 chlorophyll *a* pigments of CP43 align with the chlorophylls present in CP47 and IsiA proteins. Three extra chlorophylls of CP47 (green arrows) are toward the lumenal side of the PSII. When eighteen IsiA monomers form a ring surrounding PS I, the four extra chlorophylls of an IsiA monomer have two chlorophylls that face the PSI side, while one chlorophyll is on the periphery of the ring (highlighted by red boxes). The fourth chlorophyll (shown by blue arrow) is closely placed to one of the additional chlorophylls from CP47. PDB: 7N8O and 6NWA. Asterisks designate closely associated chlorophylls, see text for details. Only tetrapyrrole rings are shown for chlorophyll *a* for image clarity


a
b

◂**Fig. 4** Excitation energy transfer pathways (yellow arrows) in (**a**) PSII and (**b**) IsiA-PSI. **a** In PSII, the chlorophylls associate with CP43 (purple), CP47 (green), and the D1 and D2 subunits (colored by elements). The chlorophylls of CP43 and CP47 direct energy toward the special pair of chlorophylls of the P680 reaction center to drive the reduction of the primary electron acceptor Q_A. **b** The chlorophyll arrangement of six IsiA (blue)-PSI monomer (colored by elements) complex is hypothesized to act as a photoprotective association that dissipates excitation energy by distributing the energy across the IsiA ring or by directing the energy toward PSI. Blue arrows represent the additional chlorophylls of IsiA, two facing PSI and one at the periphery of the IsiA ring. The additional chlorophyll aligning with one chlorophyll from CP47 is also shown

marina (Q6Q974) have Cys 285 and 306 that aligns with the Cys 260 of IsiA. This further supports the possibility that PcbC is an IsiA progenitor, despite the limited spectroscopic and structural data available.

Structure comparison of CP43, CP47, and IsiA

Structural data for the Pcb proteins are unfortunately lacking, so we examined and compared the available structures of CP43, CP47, and IsiA. Structure superimposition of CP43, CP47, and IsiA (PDB source: 7N8O and 6NWA) from *Synechocystis* sp. PCC 6803 shows matches of the six transmembrane helices (Fig. 3a). The thirteen chlorophylls from CP43 align with the thirteen chlorophylls of CP47 and IsiA (Fig. 3b). Out of the additional chlorophylls associating with the CP47 and IsiA proteins (marked with red boxes and arrows in Fig. 3b), one chlorophyll from each of the two proteins is closely aligned (Fig. 3b, arrows with asterisks) and might be influencing the spectroscopic similarities of the two CBA proteins (examined below).

Tracing the possible excitation-energy path (Fig. 4) that the CP43 and CP47 proteins have evolved to direct energy to the P680 reaction center shows the contrast with IsiA-PSI complexes in which IsiA probably transfers the excitation energy captured by the chlorophyll on the peripheral side toward PSI through two chlorophylls on the PSI side (shown by boxes and blue arrows in Fig. 3b) and to neighboring IsiA.

General spectroscopic properties of CP43-like protein family

CP47, CP43, and IsiA have been extensively studied spectroscopically for the last few decades. Therefore, the basic spectroscopic properties of the complexes, including the main absorption and fluorescence bands and the chlorophyll *a* fluorescence decay lifetime or carotenoid-to-chlorophyll excitation-energy transfer, determined at various temperatures, could be gathered. Such spectroscopic characteristics for CP47, CP43, IsiA, and Pcb are listed in Table 2. The table clearly demonstrates that the least spectroscopically studied sub-family is Pcb with only one PcbC subclass representative investigated at room temperature (Durchan et al. 2010). However, for others, the availability of results from numerous studies allowed us to determine if any spectroscopic trends for each complex class existed. For that purpose, it is more convenient to convert some results from the table to the graphical representation shown in Fig. 5. Because there is limited data available for Pcb, the figure focuses only on CP43/47 (including pC43/47) and IsiA. The graph shows the positions of the main chlorophyll *a* absorption (Q_y) and fluorescence bands as a function of temperature and shows interesting trends that could be not easily deduced from the table.

Spectroscopic complexities of IsiA

It is apparent that for IsiA, there is a significant variation of the chlorophyll *a* Q_y band position (Fig. 5, blue oval) in the room-temperature absorption spectra reported by various researchers. The band varies between 669 and 675 nm and reflects that in some studies, the samples were very likely copurified with PSI, which naturally coexists with IsiA and if present will spectrally shift the overall absorption spectrum to longer wavelengths. The presence of PSI would also explain the existence of the very fast phase of chlorophyll fluorescence decay (< 100 ps time constants) that likely is associated with excitation-energy transfer to PSI that is not present in later studies using IsiA samples of higher purity. However, as seen in the table, even high-purity IsiA samples still demonstrate multiphasic decay of chlorophyll fluorescence. Fluorescence quenching that initially was thought to be associated with excitation-energy transfer to the carotenoid S_1 state was recently proposed to be related with electron-transfer processes mediated by a cysteine amino acid residue uniquely positioned within the chlorophyll array to serve as a quencher under specific environmental conditions (Chen et al. 2021). This mechanism is comparable to that observed in the Fenna–Matthews–Olson (FMO) pigment-protein complex from green sulfur bacteria (Orf et al. 2016) and is very likely behind the observed chlorophyll fluorescence quenching because mutating the cystine residue essentially eliminates the effect (Chen et al. 2021). Interestingly, the fast chlorophyll fluorescence decay component was also observed in another member of the family, the PcbC complex. It is possible that the cysteine residue of PcbC aligning with Cys 260 plays a similar role; however, participation of the carotenoid zeaxanthin bound to the complex cannot be ruled out (Durchan et al. 2010).

It is worth noting that historically IsiA was called CP43', which is logical considering that the absorption spectra of CP43 and IsiA are comparable. In addition, in the absence of a molecular structure of IsiA, pigment analysis suggested

Table 2 Spectroscopic properties of CP43-like CBA proteins. Including main absorption and fluorescence bands, fluorescence decay lifetime, lifetime of the S_1 excited state of bound carotenoids, and carotenoid-to-chlorophyll (Chl *a*) excitation-energy transfer recorded in various temperatures

	Chl *a*			Chl *b*			Chl *a* Fluo (nm)	Chl *a* t_F	Car (No.)	Car S_2 (0–0)	Car → Chl *a* EET (%) (method)	Car S_1 t (ps)	Temp. (K)	Refs.
	No	Abs (nm)		No	Abs (nm)									
		Soret	Q_y		Soret	Q_y								
CP47 inner antenna (monomeric)														
CP47	16			n.p					β-Car (3)					Shen et al. (2019)
								1.9–2.4 ns 4.8–5.6 ns					277–10	Huyer et al. (2004)
		436	673				693			503	~40 (FE)		4	van Dorssen et al. (1987)
			674.5										77	de Weerd et al. (2002a)
			675					5.8					77	de Weerd et al. (2002b)
		438	675				695						48	Alfonso et al. (1994)
			675				683	2.3 ns					293	Casazza et al. (2010)
								3.22 ns			66.5		293	He et al. (2001)
			676.5				695						4.5	Neupane et al. (2010)
											35 (FE)		293	de Weerd et al. (2003)
								3.22 ns 5.41 ns					293	de Paula et al. (1994)
														Boehm et al. (2011)
pCP47		436	674										293	Boehm et al. (2011)
			676							502			5	Boehm et al. (2011)
														Boehm et al. (2011)
CP43 inner antenna (monomeric)														
Subclass														
CP43	13			n.p					β-Car (4)					Shen et al. (2019)
			669										77	de Weerd et al. (2002b)
		438	671				683			495			48	Alfonso et al. (1994)
			671				684	2.2 ns					293	Casazza et al. (2010)
								3.54 ns			47.5		293	He et al. (2001)
		437	669				682.8			487			5	Groot et al. (1999)
		436	671				683				34 (FE)		293	Qu et al. (2020)
			669				683						4.2	Jankowiak et al. (2000), Dang et al. (2008)
											35 (FE)		293	de Weerd et al. (2003)
							684						77	Boehm et al. (2011)
pCP43	n.d	437	670.5				683	3.5 ns	β-Car (n.d.)	492	39 (FE)	10.5	293	Biswas et al. (2023)
		437	669.5				685	5.1 ns		498		13.2	77	Biswas et al. (2023)
		436	671										293	Boehm et al. (2011)

Table 2 (continued)

	Chl *a*			Chl *b*			Chl *a* Fluo (nm)	Chl *a* t_F	Car (No.)	Car S_2 (0–0)	Car → Chl *a* EET (%) (method)	Car S_1 t (ps)	Temp. (K)	Refs.
	No	Abs (nm)		No	Abs (nm)									
		Soret	Q_y		Soret	Q_y								
			668.5							499			5	Boehm et al. (2011)
IsiA (also known as CP43') outer antenna, Chl *a* storage (oligomeric, ring)														
Subclass														
Native IsiA	17			n.p					β-Car (4)					Akita et al. (2020), Toporik et al. (2019)[a]
			669				683.5						5	Reinot et al. (2022)
			669							~495			293	Andrizhiyevskaya et al. (2004, 2002)
			675							~500			293	Berera et al. (2009)
			672				679	66 ps 210 ps		496			293	Ihalainen et al. (2005)
							687						4.2	Ihalainen et al. (2005)
							684						77	Wahadoszamen et al. (2015)
		435	675					71 ps 402 ps		~500	26–37 (TA)	7.6	293	Berera et al. (2010)
			671.5										293	Feng et al. (2011)
			669				687						5	Feng et al. (2011)
			671										293	Melkozernov et al. (2003)
		437	670				678	280–400 ps 1.6–2 ns (oxidative)		~487	~0 (FE)	10.5	293	Chen et al. (2017)
								1 ns 4.1 ns (reducing)					293	Chen et al. (2017)
		436	669				686	1.9 ns 6.8 ns (oxidative)		503		6.6	77	Chen et al. (2017)
C260V IsiA		437	671					2.05 ns 5.3 ns (oxidative)					293	Chen et al. (2021)
Pcb outer antenna (oligomeric, ring)														
Subclass														
PcbC	17			4					Zea (1) β-Car (2) α-Car (1)					Herbstová et al. (2010)[b]
PcbC		437	671		465	645	685[c]	200 ps long (n.d.)	Zea β-Car	495	~25 (TA)	9	293	Durchan et al. (2010)

n.d. not determined, *n.p.* not present, *TA* transient absorption, *FE* fluorescence excitation, *pCP43/47* preassembly CP complexes

[a]From Cryo-EM

[b]Based on pigment stoichiometry

[c]At 77 K

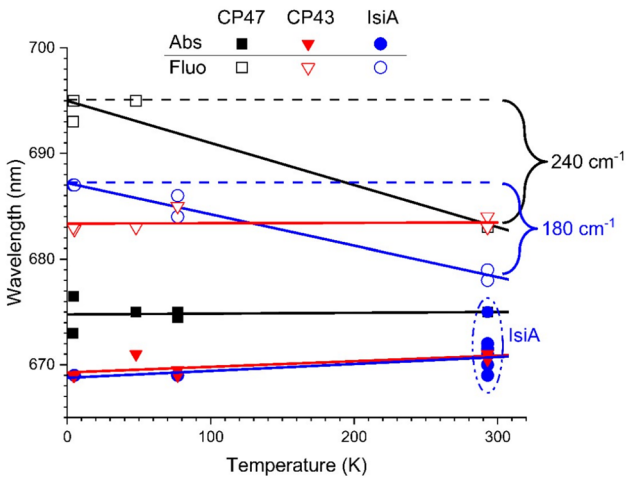


Fig. 5 Graphical representation of the selected data (main absorption and fluorescence bands of chlorophyll *a*) gathered in Table 2. The temperature-induced trends in positions were fitted with linear functions. For IsiA absorption, the point corresponding to the Chl *a* Q_y band at 675 nm was omitted in the fit. Temperature is in Kelvin, and energy gaps are in wavenumbers

that there was only a small difference between the number of chlorophyll molecules bound in the complexes. However, the newest molecular projections of the PSI-IsiA supercomplex (Toporik et al. 2019; Akita et al. 2020) demonstrated that IsiA has 17 chlorophyll molecules in its structure, which makes it more comparable to CP47 with 16 chlorophylls. In addition, CP47 and IsiA show a similar trend in the temperature-induced shift of the fluorescence emission spectra that is not observed for CP43.

Temperature effect on absorption and fluorescence emission

As seen in Fig. 5, temperature has a small effect on the position of the main absorption band for all complexes, which only varies within 1 nm through the entire 4-293 K temperature range. However, there is an apparent difference between complexes in how temperature affects position of fluorescence emission. For CP47 and IsiA, there is an apparent shift in the fluorescence band toward longer wavelengths when temperature decreases. The overall energetic shift toward lower energies is slightly different for both complexes (240 cm^{-1} for CP47 vs 180 cm^{-1} for IsiA), but generally it is very close to a loss of thermal energy upon going from 293 to 4 K, which is 200 cm^{-1}. Therefore, the strong correlation of the spectral shift with available thermal energy could be interpreted that, in those complexes, excitation energy is not specifically trapped anywhere within the complex but always tries to equilibrate to the lowest energy site and then emits. Therefore, the emission band shifts linearly with temperature simply because thermal energy is a linear function of temperature ($E = kT$, k—Boltzmann constant). However, no such trend is seen for CP43, for which the shift of the fluorescence band is marginal, a pattern observed in multiple independent studies. This could be interpreted that the emitters in CP43 are acting as excitation traps with narrower excited state energies that more efficiently facilitate excitation-energy transfer to the reaction center. In this case, loss of chlorophyll in the structure, in respect to other protein family members, is evidently beneficial and could originate from evolutionary pressure to optimize protein assembly more efficiently.

Efficiency of carotenoid-to-Chl *a* excitation-energy transfer

We examined the available data for any trend in carotenoid-to-chlorophyll excitation-energy transfer and if so, how it correlates with changes in protein structure and pigments. Unfortunately, the data are too scattered and inconclusive, though most likely the efficiency of the process is below 50% in all CP43-like family members. To find out more about this property more specifically direct experimental studies are needed.

Discussion and conclusions

The transmembrane light-harvesting antenna proteins and their evolution has been an area of interest since their identification in oxygenic photoautotrophs. Such studies hold importance for classifying proteins and predicting functions based on the phylogenetic assessment of their amino acid sequences. Two major classes of CBA proteins canonical to oxygenic photoautotrophs are the CP43 and the CP47 proteins. In cyanobacteria, however, other CBA proteins like IsiA and the Pcb family of proteins are also found. Phylogenetic assessment of these proteins in cyanobacteria has prompted researchers to propose the hypothesis that CP43 gave rise to the IsiA and Pcb proteins (Chen et al. 2005b), while other researchers have proposed that a precursor protein was the ancestor of the CP43, IsiA, and Pcb proteins (Murray et al. 2006). Based on the observations presented in this study, we side with the observations of Murray et al. (2006). It is likely that the CP43 protein evolved into the PcbC protein of *Prochlorothrix hollandica* and *Acaryochloris marina* or Pcb-like protein of *Fischerella muscicola* (Fig. 1). A possible reason for CP43 and not CP47 evolving into other CBA proteins could be because of the complex life cycle of PSII involving frequent damage and repair. During repair, PSII is disassembled to release CP43, and such processing might have made CP43 more susceptible to evolutionary pressure. The similarity of the spectroscopic properties (Table 2), association with PSI (Bumba et al. 2005),

transcription under iron stress (Bibby et al. 2003a), and conservation of the cysteine residue (Fig. 2) would suggest a close relation between the IsiA and PcbC proteins. The grouping of PcbA, PcbB, and IsiA and their placement in a separate branch from CP43 in the phylogenetic tree further supports the notion presented by Murray et al. (2006). Determining if PcbC is a progenitor of IsiA depends on further studies of the PcbC protein. In general, structural information on Pcb proteins would provide critical information to better understand this group of proteins and provide more evidence to support our hypothesis. Lateral gene transfer between organisms and further evolution of the IsiA and Pcb family of proteins with specific adaptations to suit the light-harvesting needs is also a likely scenario to be explored.

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Data availability All data related to this study are contained in the manuscript.

Declarations

Conflict of interest The authors declare no competing interests.

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