Trends in Microbiology

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Review

Structural diversity and modularity of photosynthetic RC–LH1 complexes

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Bacterial photosynthesis is essential for sustaining life on Earth as it aids in carbon assimilation, atmospheric composition, and ecosystem maintenance. Many bacteria utilize anoxygenic photosynthesis to convert sunlight into chemical energy while producing organic matter. The core machinery of anoxygenic photosynthesis performed by purple photosynthetic bacteria and Chloroflexales is the reaction center–light-harvesting 1 (RC–LH1) pigment–protein supercomplex. In this review, we discuss recent structural studies of RC–LH1 core complexes based on the advancement in structural biology techniques. These studies have provided fundamental insights into the assembly mechanisms, structural variations, and modularity of RC–LH1 complexes across different bacterial species, highlighting their functional adaptability. Understanding the natural architectures of RC–LH1 complexes will facilitate the design and engineering of artificial photosynthetic systems, which can enhance photosynthetic efficiency and potentially find applications in sustainable energy production and carbon capture.

Highlights

The photosynthetic reaction center–light-harvesting 1 (RC–LH1) complex is a membrane-protein core supercomplex that plays a crucial role in the primary reactions of anoxygenic photosynthesis.

Recent developments of structural biology techniques have greatly promoted the structural characterization of various RC–LH1 complexes.

The structural analysis provides insight into the assembly principles and functionality of RC–LH1 supercomplexes.

The studies highlight the structural variations and modularity of RC–LH1 complexes among different phototrophic bacteria in an evolutionary and adaptive context.

Advanced understanding of natural photosynthetic RC–LH1 structure and function could aid in the design and engineering of efficient artificial photosynthetic systems.

Introduction

Photosynthesis is considered the most important photobiochemical process on Earth. Through photosynthesis, **phototrophs** (see Glossary), including plants, algae, and some bacteria, can capture and utilize energy from sunlight to produce organic compounds and chemical energy that support almost all life forms [1,2]. The photosynthetic light-reactions occur in the specialized membranes, termed the photosynthetic membranes, which involve a series of highly ordered membrane-embedded and membrane-associated pigment–protein complexes [3–5].

Plants, algae, and cyanobacteria produce chlorophylls and perform **oxygenic photosynthesis** to split water into oxygen, and provide protons and electrons for the generation of ATP and NADPH. By contrast, some bacteria, including **purple non-sulfur bacteria**, **purple sulfur bacteria** and green sulfur bacteria, synthesize different pigments and conduct **anoxygenic photosynthesis** without the release of oxygen [6]. As an ancient process that has been present on Earth for billions of years, anoxygenic photosynthesis played an essential role in shaping the early atmosphere of our planet [7]. Although it represents a simpler photosynthetic form, today, it is still a dominant form of photosynthesis in many ecological niches, including hot springs, deep-sea thermal vents, aquatic and soil ecosystems where oxygen is scarce, and contributes significantly to the global carbon cycle [8–10]. The studies of anoxygenic photosynthesis have provided fundamental insights into the mechanisms of photosynthesis and have led to the discovery of new types of pigments, proteins, and photosynthetic supercomplexes in evolutionarily divergent species.

The photosynthetic light-reactions of purple bacteria take place in the photosynthetic apparatus located in the intracytoplasmic membrane (ICM), which is composed typically of reaction centers (RCs), light-harvesting complex 1 (LH1), light-harvesting complex 2 (LH2), cytochrome bc_1 (Cyt

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bc_1), and ATP synthases (ATPases) (Box 1). Sunlight is initially captured by LH2 and LH1 and then transferred to the RC, in which energy is used to drive the primary reduction/oxidation (redox) reactions of anoxygenic photosynthesis. These reactions involve conversion of quinone molecules to their completely reduced form and electron flow from the RC to the Cyt bc_1 complex as part of a cyclic electron-transport pathway, which finally leads to the generation of a proton gradient across the membrane for ATP synthesis through ATPases [11].

Understanding the structures and interactions of natural photosynthetic complexes is key for elucidating at the molecular level how they function and work together to perform efficient energy and electron transfer in photosynthesis. The RC–LH1 core complex is central to purple bacterial photosynthesis, but resolving the RC–LH1 structures at a high resolution has been challenging due to their structural variability and flexible organizations [12,13]. In recent years, the development of structural biology techniques, especially cryo-electron microscopy (cryo-EM), has remarkably advanced the structural characterization of photosynthetic RC–LH1 complexes from various purple bacterial species at the molecular resolution [14–27] (Box 2). These studies have provided unprecedented insights into the architectural diversity and modularity of the RC–LH1 cores.

Although the RC–LH1 core complexes have conserved functions, protein sequences, and general composition, as well as similar mechanisms of energy transfer and quinone/quinol exchange, recent studies have clearly shown that the RC–LH1 structures are naturally modular and are highly variable among different phototrophic species of bacteria of the phyla Proteobacteria, Chloroflexi, and Gemmatimonadetes (Figure 1). These characteristics manifest in various aspects, including the RC structure, the LH1 organization, pigment forms and content, and additional polypeptides (Table 1). The natural diversity of the RC–LH1 structure highlights the diverse evolutionary strategies utilized by different groups of phototrophic bacteria for optimizing light-harvesting and electron transfer, and it provides the foundation for the functional adaptation of the photosynthetic apparatus, ensuring the fitness of phototrophic bacteria to thrive in competitive ecological environments while also facilitating their roles in the carbon cycle.

The RC and cofactors

The RC is a multicomponent pigment–protein complex that captures light excitation energy, transferred from LH2 and LH1, and conducts the primary **charge separation** across the

Box 1. Intracytoplasmic membranes of purple bacteria: the sites for anoxygenic photosynthesis

In purple bacteria, the ICMs (also known as chromatophores) are specialized photosynthetic membranes to compartmentalize protein complexes and molecules involved in light-dependent photosynthetic reactions and energy transduction. These protein complexes include light-harvesting complexes, RCs, Cyt bc_1 complexes, and ATPases (Figure I) [15]. The RC is the only photosystem in purple bacteria, which is homologous to photosystem II in oxygenic photosynthesis, both belonging to type-II RC characterized as a quinone/non-heme Fe^{2+}/quinone electron acceptor system. Purple bacteria typically have two types of antenna complex: (i) the LH1 intimately encircles the RC to constitute the RC–LH1 'core' complex, which is ubiquitous in all species of purple bacteria; (ii) LH2 locates outside the LH1 ring, serving as a peripheral antenna to enhance absorption cross-section of RC–LH1. The photochemical RC and its associated LHs constitute the photosynthetic unit (PSU). The PSU organization in ICMs of many purple photosynthetic bacteria has been characterized by atomic force microscopy (AFM) [5].

BChl and carotenoid pigments within the LH complexes absorb photons of light as resonance energy. This excitation energy is then transferred through a network of pigments in the LH complexes towards the special pair of BChls within the RC, where energy is used to drive the primary reduction/oxidation (redox) reactions of anoxygenic photosynthesis and lead to the release of excited electrons. These electrons are then passed to RC-bound quinone electron carriers. After two electron transfers, the quinone (Q) is fully reduced to quinol (QH_2) by binding two protons, which is then released from the RC and diffuses to Cyt bc_1 as part of a cyclic electron-transport pathway. The quinol is subsequently oxidized by Cyt bc_1, releasing two protons into the periplasm of the cell, while one electron is passed to the soluble Cyt c_2 and eventually back to the special pair of BChl in the RC and the other returns to the Q pool via a quinone carrier. The cyclic electron flow results in the generation of an electrochemical proton gradient across the ICM, which is utilized by ATPases for the synthesis of ATP [11].

Glossary

Anoxygenic photosynthesis: a process used by certain bacteria to absorb light energy and drive biochemical reactions that produce ATP and organic matter, without releasing oxygen.
Charge separation: a photochemical process that occurs in the RC. When the SP of BChls is excited and promoted to a higher energy state, it donates an electron to a neighboring BChl molecule, then to a BPhe molecule, and finally to quinone molecules. During this process, the electron donors become positively charged, while the electron acceptors become negatively charged. This separation of charges initiates an oxidation–reduction process that leads to a continuous flow of electrons across the photosynthetic membrane, ultimately generating a proton gradient that is utilized for ATP production.
Cofactors: in photosynthetic complexes, cofactors typically involve non-protein molecules or chemical groups that are required for light absorption, electron transfer, and energy transfer. For example, bacterial photosynthetic complexes include pigments, quinones, lipid molecules, and metal ions as cofactors.
Oxygenic photosynthesis: a process by which photosynthetic organisms, such as plants, algae, and cyanobacteria, utilize energy from sunlight to produce organic matter and split water to release oxygen.
Photodamage: the harmful effects caused by excess light energy on phototrophs. Excessive exposure to light can lead to the production of reactive oxygen species and heat, which can damage photosynthetic proteins, lipids, and DNA, ultimately resulting in a decrease in photosynthetic efficiency and bacterial growth.
Phototrophs: a group of organisms that obtain energy from sunlight, either directly or indirectly, to drive metabolism. This includes photoautotrophic organisms that use light energy and CO_2 as a carbon source to produce organic matter, and photoheterotrophic organisms that use light energy and organic compounds as a carbon source instead of CO_2.
Purple non-sulfur bacteria: a type of phototrophic bacteria that can carry out anoxygenic photosynthesis in the absence of sulfur compounds and harness organic acids as carbon resources and electron donors.

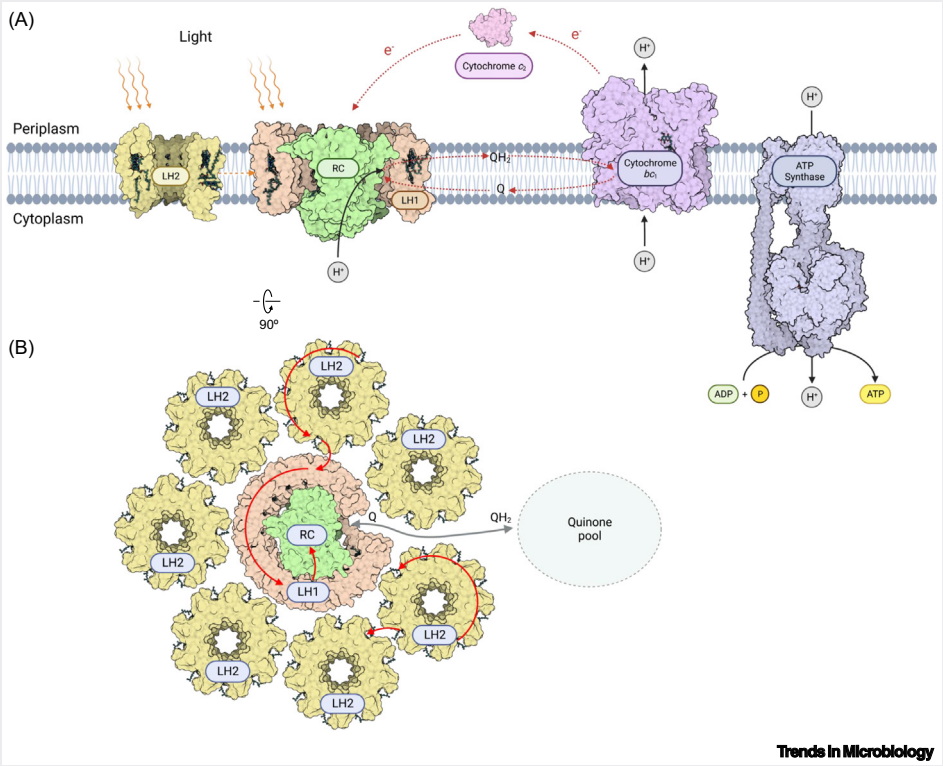

Figure I. Schematic models of the photosynthetic apparatus in the intracytoplasmic membrane (ICM) of purple bacteria. (A) Side view of the photosynthetic apparatus including membrane-spanning light-harvesting 2 (LH2), LH1 that binds with the reaction center (RC) to form an RC–LH1 core complex, cytochrome bc_1 (Cyt bc_1), and ATPase. Light energy is captured by LH2 and LH1, and excitation energy is then transferred to the RC to initiate charge separation. The electrons are then passed to Cyt bc_1 and are shuttled back to the RC by the soluble Cyt c_2 or via the Q-cycle in the ICM membrane. This cyclic electron transfer creates an electrochemical gradient across the ICM membrane, which is used by ATPase to drive ATP production. Protein Data Bank (PDB) ID: 7PBW for LH2, 7DDQ for RC–LH1, 1ZRT for Cyt bc_1, and 6OQU for ATPase. (B) Top view of the photosynthetic unit (PSU). The RC–LH1 is surrounded by multiple LH2, forming a tightly organized PSU to enable efficient energy transfer between the antenna complexes and RCs. Schematic pathways of energy transfer in the PSU and pathways of Q/QH_2 diffusion between RC–LH1 and Q pool within the ICM are indicated. Note that the exact locations of Cyt bc_1 and ATPase remain to be verified.

Purple sulfur bacteria: unlike purple non-sulfur bacteria, purple sulfur bacteria are obligate anaerobes capable of photosynthesis, and cannot grow in the presence of oxygen; they use hydrogen sulfide (H_2S) as an electron donor for photosynthesis and produce sulfur as a byproduct. Purple non-sulfur bacteria belong to α-Proteobacteria and the β-Proteobacteria, and purple sulfur bacteria belong to the γ-Proteobacteria, categorized based on 16S rDNA sequence similarities.

Quinone transport: movement of quinone electron carriers across photosynthetic membranes for electron transport. Quinones accept electrons from the reaction center and pass them to the cytochrome complexes to generate a proton gradient for the production of ATP.

Special pair: in the reaction center, two bacteriochlorophylls form a strongly interacting dimer known as the special pair (SP). When excitation energy is transferred from LH1 to the RC, an electron within the special pair is promoted to an excited state to initiate charge separation and electron transfer that leads to the generation of energy.

photosynthetic membrane, thereby resulting in the generation of a voltage gradient that drives ATP synthesis. The RC of *Blastochloris* (*Blc.*) *viridis* was the first membrane protein complex structurally resolved [28]; this was recognized by the award of the 1988 Nobel Prize in Chemistry. Over the past two decades, several RC–LH1 structures from different purple bacterial species have been characterized at high resolution, advancing our understanding of the RC structural and functional variations (Table 1).

The RC is typically composed of three transmembrane polypeptides: L, H, and M subunits along with their associated **cofactors**. The RC-M and RC-L subunits are highly conserved among all species of purple bacteria and are present in all the RC structures determined, implicating their crucial functions in accommodating the cofactors and electron transport. The cofactors associated with the subunits M and L of the RC typically include four bacteriochlorophylls (BChls), two bacteriopheophytins (BPhes), two quinones (Qs), a carotenoid, and a Fe^{2+}; they are organized into two symmetrically related branches (Figure 2A). Close to the periplasmic surface, a

Box 2. Milestones in RC–LH1 structural determination

Over the past 20 years there has been a tremendous endeavor to unravel the molecular details and explore the structural variations of photosynthetic RC–LH1 complexes, owing in particular to the rapid advancement of cryo-EM technology. Resolved RC–LH1 structures and milestones in RC–LH1 structural determination are highlighted in Figure II.

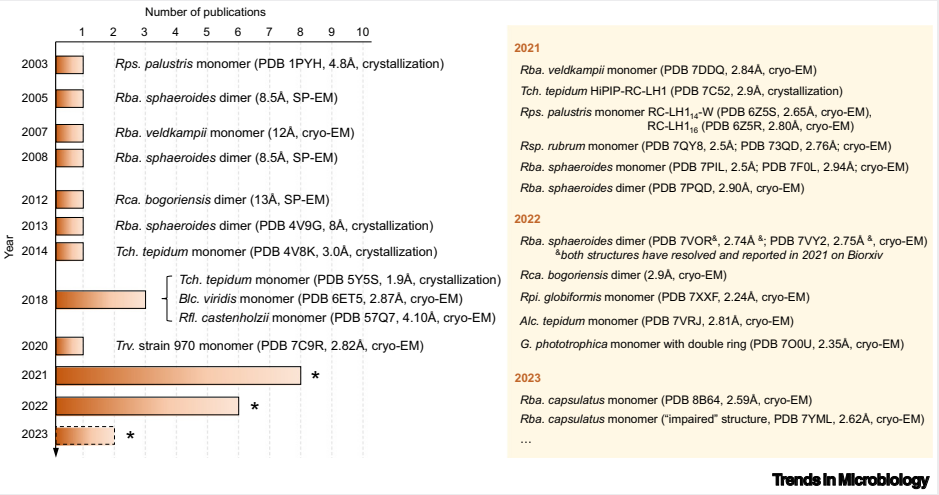

Figure II. Publications related to the studies of photosynthetic reaction center–light harvesting 1 (RC–LH1) core complex structures over time. The numbers were calculated based on publications that focused on RC–LH1 structural determination and Protein Data Bank (PDB) deposits. The resolution, PDB ID (if available), and the method of obtaining the structures of individual RC–LH1 core complexes are also indicated. Details of the published structural information for 2021–2023 (indicated by *) are listed on the right side. The number of publications in 2023 was calculated only to the end of May 2023 when the manuscript was prepared, thereby being indicated by a dashed line. The publications for these reported RC–LH1 structures involve [12–27,30,37,38,47,52,57,58,64–67]. Abbreviations: *Alc.*, *Allochromatium*; *Blc.*, *Blastochloris*; *G.*, *Gemmatimonas*; *Rba.*, *Rhodobacter*; *Rca.*, *Rhodobaca*; *Rpi.*, *Rhodopila*; *Rps.*, *Rhodopseudomonas*; *Rsp.*, *Rhodospirillum*; *Tch.*, *Thermochromatium*; *Trv.*, *Thiorhodovibrio*.

pair of BChl molecules, known as the '**special pair**' BChls, are positioned closely together, playing a crucial role in initiating the photosynthesis process. The active Branch A consists of an accessory $BChl_A$, $BPhe_A$, and a quinone Q_A. The inactive Branch B is usually equivalent to the A branch, consisting of a $BChl_B$, a $BPhe_B$, a Q_B and an additional carotenoid pigment, but the energy levels between $BPhe_B$ and Q_B are greater than those of $BPhe_A$ and Q_A, thereby facilitating the transfer of two subsequent electrons to Q_B [29]. Unlike the conserved Branch A pigments, the Branch B pigments vary (Table 1). For example, in RC–LH1 of *Rhodobacter* (*Rba.*) *veldkampii* [15] and *Rhodobaca* (*Rca.*) *bogoriensis* [30], an additional BPhe was identified in Branch B. In the RC–LH1 of *Roseiflexus* (*Rfl.*) *castenholzii*, a green non-sulfur bacterium of the phylum Chloroflexi [21], the accessory BChl is swapped for a BPhe. The nature of primary quinones Q_A and Q_B also differs among species. Q_A has been found to either be a ubiquinone (UQ) [14–20], a menaquinone (MQ) [21–24] or, in the case of *Rhodospirillum* (*Rsp.*) *rubrum* [26,27], a rhodoquinone made from a pre-existing ubiquinone [31,32]. The RC of *Rfl. castenholzii*, which belongs to a phylum that diverged from other anoxygenic photosynthetic bacteria at an early stage in their evolution [33,34], contains MQ in both Q_A and Q_B sites [21], instead of a UQ in the Q_B site found in purple bacteria. Additionally, the carotenoid pigment in Branch B differs depending on species and growth conditions [35,36].

The RC-H subunit is anchored into the photosynthetic membrane with a single transmembrane helix, and a globular domain is attached to the cytoplasmic side of RC-M and RC-L

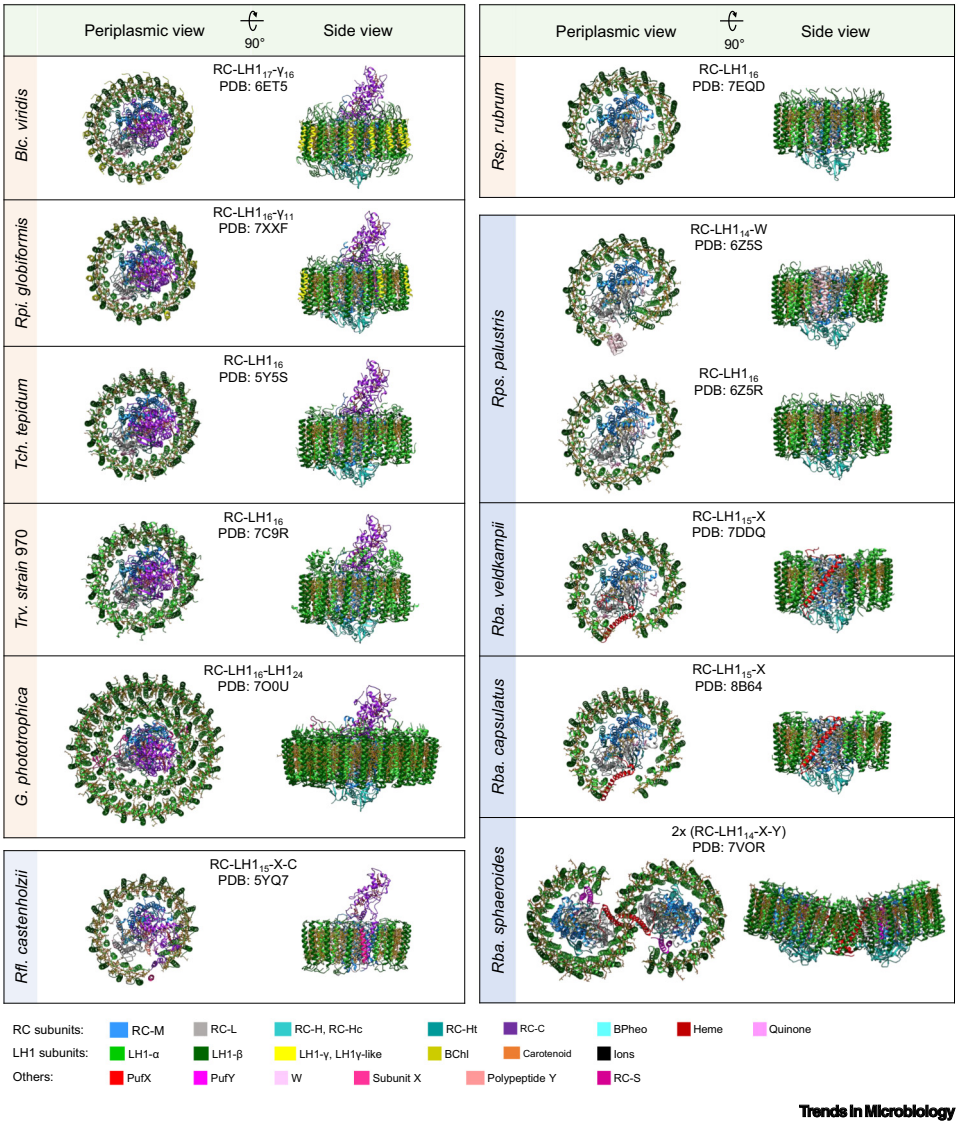

Figure 1. Overview of the structures of photosynthetic reaction center–light harvesting 1 (RC–LH1) core complexes in various phototrophic bacterial species. Studies on the RC–LH1 complexes shed light on their structural diversity and modularity. The RC–LH1 core complexes can be classified into two groups based on whether the LH1 ring is closed (orange) or has an opening mediated by additional polypeptides (blue). They can be also categorized into monomers that contain one RC with its LH1 ring and dimer with two RCs joined by a ribbon of LH1. It appears that monomeric RC–LH1 core complexes are more common in nature than dimeric RC–LH1. See also Table 1. The color scheme is presented at the bottom. Abbreviation: PDB, Protein Data Bank.

[14–20,22–24,26,27,37,38] (Figure 2B). While the RC could be still functional without the RC-H subunit [39,40], RC-H shields the quinone sites from the ions in the cytoplasm, suggesting its role in providing specific proton channels for Q_B protonation [41,42]. In contrast to the RCs of purple photosynthetic bacteria, the RC of *Rfl. castenholzii* lacks the RC-H subunit [21] (Figure 2B), and the *puhA* gene encoding RC-H subunit was missing in *Gemmatimonas phototrophica* [38], a phototrophic representative of the bacterial phylum Gemmatimonadetes. Instead, the RC of *G. phototrophica* contains two H subunits: a smaller transmembrane polypeptide Ht and a

Table 1. Structural and compositional comparison of the reported RC–LH1 core complexes from anoxygenic phototrophs[a,b]

Species	RC–LH1 structure	PDB ID (Refs)	Resolution (Å)	RC		LH1			Additional subunits	Quinone (Q_A, Q_B)
				Subunits	Pigments	Ring shape	Subunits	Pigments per LH-αβ		
Blc. viridis	Monomer	6ET5 [23]	2.87	H,M,L,C	4 BChl *b*, 2 BPhe *b*, 1 1,2-dihydroneurosporene	Closed	$\alpha\beta_{17}$	2 BChl *b*, 1 all-*trans*-1,2-dihydroneurosporene or dihydrolycopene	16 γ	MQ-9, UQ-9
Tch. tepidum	Monomer	5Y5S [22]	1.90	H,M,L,C	4 BChl *a*, 2 BPhe *a*, 1 spirilloxanthin	Closed	$\alpha\beta_{16}$	2 BChl *a*, 1 spirilloxanthin	–	MQ-8, UQ-8
Alc. tepidum	Monomer	7VRJ [53]	2.81	H,M,L,C	4 BChl *a*, 2 BPhe *a*, 1 15-*cis*-spirilloxanthin	Closed	$\alpha\beta_{16}$	2 BChl *a*, 1 all-*trans* spirilloxanthin	–	MQ-8, UQ-8
Trv. strain 970	Monomer	7C9R [37]	2.82	H,M,L,C	4 BChl *a*, 2 BPhe *a*, 1 3,4,3',4'-tetrahydrospirilloxanthin	Closed	$\alpha\beta_{16}$	2 BChl *a*, 1 3,4,3',4'-tetrahydrospirilloxanthin	–	MQ-8, UQ-8
Rsp. rubrum	Monomer	7EQD [26]	2.76	H,M,L	4 *trans*-geranyl BChl *a*, 2 (*trans*-geranyl) BPhe *a*, 1 15-*cis*-spirilloxanthin	Closed	$\alpha\beta_{16}$	2 *trans*-geranyl BChl *a*, 1 all-*trans*-spirilloxanthin	–	RQ-10, UQ-10
		7OY8 [27]	2.5							UQ-10, UQ-10
Rpi. globiformis	Monomer	7XXF [24]	2.24	H,M,L,C	4 BChl *a*, 2 BPhe *a*, 1 *cis*-keto-carotenoid	Closed	$\alpha\beta_{16}$	2 BChl *a*, 1 *trans*-keto-carotenoid	11 γ-like	MQ-9, UQ-10
Rps. palustris	Monomer	6Z5R [14]	2.80	H,M,L	4 BChl *a*, 2 BPhe *a*, 1 *cis*-rhodopin	Closed	$\alpha\beta_{16}$	2 BChl *a*, 1 spirilloxanthin	–	UQ-10, UQ-10
	Monomer	6Z5S [14]	2.65			Open	$\alpha\beta_{14}$		W	
Rba. veldkampii	Monomer	7DDQ [15]	2.84	H,M,L	4 BChl *a*, 3 BPhe *a*, 1 *cis*-spheroidene	Open	$\alpha\beta_{15}$	2 BChl *a*, 1 spheroidene	PufX	UQ-10, UQ-10
Rba. capsulatus	Monomer	8B64 [25]	2.59	H,M,L	4 BChl *a*, 2 BPhe *a*, 1 *cis*-spheroidene	Open	$\alpha\beta_{15}$	2 BChl *a*, 2 spheroidene	PufX	UQ-10, UQ-10
Rba. sphaeroides 2.4.1	Monomer	7VNY [20]	2.79	H,M,L	4 BChl *a*, 2 BPhe *a*, 1 *cis*-spheroidene	Open	$\alpha\beta_{14}$	2 BChl *a*, 2 spheroidene	PufX, PufY	UQ-10, UQ-10
	Dimer	7VOR [20] 7VOT [20]	2.74 2.90	H,M,L	4 BChl *a*, 2 BPhe *a*, 1 *cis*-spheroidene	Open	2x $\alpha\beta_{14}$	2 BChl *a*, 2 spheroidene	2 PufX, 2 PufY	UQ-10, UQ-10
Rba. sphaeroides 2.4.1 *pufX*	Monomer	7VOY [20]	4.20	Uncertain		Closed	$\alpha\beta_{17}$		uncertain	
Rba. sphaeroides 2.4.1 *pufY*	Monomer	7VNM [20]	2.86	H,M,L	4 BChl *a*, 2 BPhe *a*, 1 *cis*-spheroidene	Open	$\alpha\beta_{13\text{-}14}$	2 BChl *a*, 2 spheroidene	PufX	UQ-10, UQ-10
	Dimer	7VA9 [20] 7VB9 [20]	3.08 3.45	H,M,L	4 BChl *a*, 2 BPhe *a*, 1 *cis*-spheroidene	Open	2x $\alpha\beta_{14}$ $\alpha\beta_{14}$ + $\alpha\beta_{7\text{-}9}$	2 BChl *a*, 2 spheroidene	2 PufX	UQ-10, UQ-10
Rba.	Monomer	7F0L	2.94	H,M,L	4 BChl *a*, 2 BPhe *a*, 1	Open	$\alpha\beta_{14}$	2 BChl *a*, 2 spheroidene	PufX,	UQ-10,

sphaeroides IL106		[16]			*cis*-spheroidene				PufY	UQ-10
	Dimer	7VY2 [17]	2.75	H,M,L	4 BChl *a*, 2 BPhe *a*, 1 *cis*-spheroidene	Open	2x $\alpha\beta_{14}$	2 BChl *a*, 2 spheroidene	2 PufX, 2 PufY	UQ-10, UQ-10
Rba. sphaeroides IL106 *pufY*	Monomer	7VY3 [17]	2.63	H,M,L	4 BChl *a*, 2 BPhe *a*, 1 *cis*-spheroidene	Open	$\alpha\beta_{10\text{-}11}$	2 BChl *a*, 2 spheroidene	PufX	UQ-10, UQ-10
Rba. sphaeroides R53L	Monomer	7PIL [19]	2.50	H,M,L	4 BChl *a*, 2 BPhe *a*, 1 *cis*-spheroidene	Open	$\alpha\beta_{14}$	2 BChl *a*, 2 spheroidene	PufX, PufY	UQ-10, UQ-10
Rba. sphaeroides DBCΩG	Dimer	7PQD [18]	2.90	H,M,L	4 BChl *a*, 2 BPhe *a*, 1 3,4-dihydrospheroidene	Open	2x $\alpha\beta_{14}$	2 BChl *a*, 2 3,4-dihydrospheroidene	2 PufX, 2 PufY, 4 Protein-Z	UQ-10, UQ-10
Rca. bogoriensis	Dimer	– [30]	2.9	H,M,L	4 BChl *a*, 3 BPhe *a*, 1 spheroidenone	Open	2x $\alpha\beta_{15}$,	2 BChl *a*, 2 spheroidenone	2 PufX, 2 protein Y	UQ-10, UQ-10
Rfl. castenholzii	Monomer	5YQ7 [21]	4.10	M,L,C	3 BChl *a*, 3 BPhe *a*	Open	$\alpha\beta_{15}$	2 BChl *a* (B880), 1 BChl *a* (B800), 1 keto-γ-carotene	Subunit X, Y	MQ-11, MQ-11
G. phototrophica	Monomer	7O0U [38] 7O0V [38] 7O0W [38] 7O0X [38]	2.35 2.50 2.47 2.44	H (c,t),M,L,C	4 BChl *a*, 2 BPhe *a*, 1 15-*cis*-spirilloxanthin	Closed, double ring	$\alpha\beta_{16}$ (inner) $\alpha\beta_{24}$ (outer)	Inner: 2 BChl *a*, 1 gemmatoxanthin Outer: 3 BChl *a*, 1 gemmatoxanthin	RC-S, RC-U	–, MQ-8

[a]Some cofactors were tentatively assigned based on the current resolutions. *Rfl. castenholzii* is Gram-negative and is classified as a green non-sulfur bacterium of the bacterial phylum Chloroflexi; *G. phototrophica* is, so far, the only phototrophic species of the bacterial phylum Gemmatimonadetes. PufY was also named protein Y or protein U.
[b]Abbreviations: MQ, menaquinone; RQ, rhodoquinone; UQ, ubiquinone.

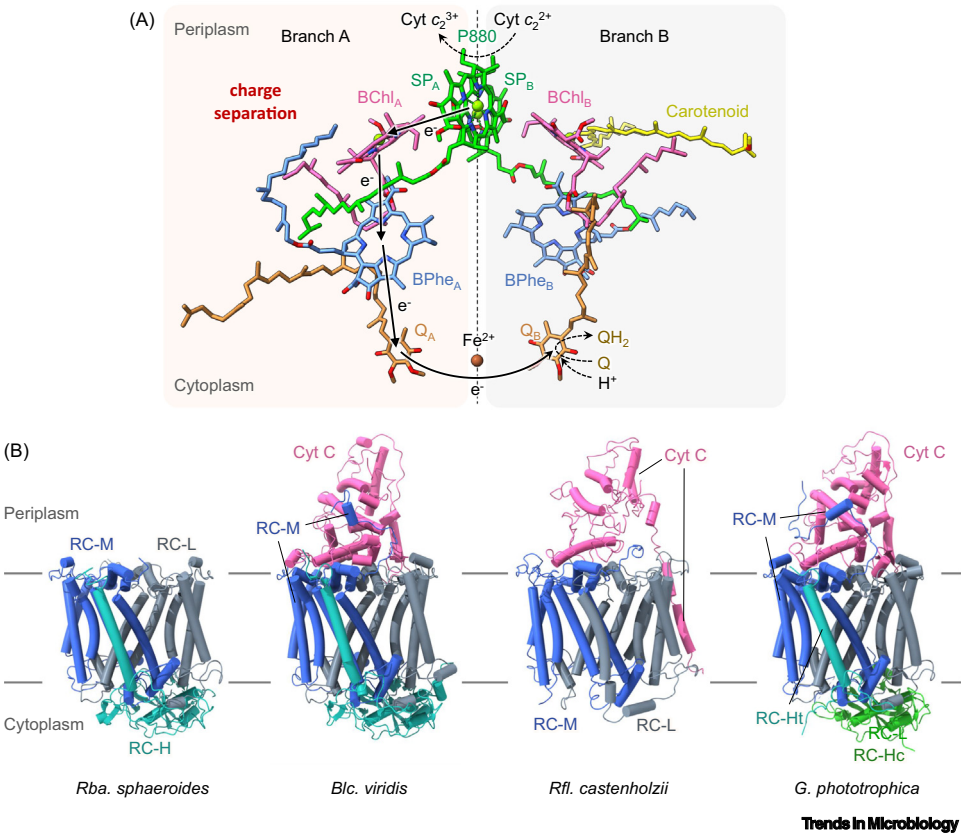

Figure 2. Reaction center (RC) structure and function. (A) Charge separation and electron transfer through the RC. The RC-L and -M subunits of purple bacteria act as a scaffold to arrange four bacteriochlorophylls (BChls) (SP_A, SP_B, $BChl_A$, $BChl_B$), two bacteriopheophytins (BPhes) ($BPhe_A$, $BPhe_B$), two ubiquinones (Q_A, Q_B), one carotenoid, and one non-heme iron. The cofactors form two separate membrane-spanning branches, A and B, with a pseudo twofold symmetry (broken line). Charge separation and electron transfer occur through Branch A (or active). In addition to the cofactors in Branch A, Branch B (also 'inactive') contains an extra photoprotective carotenoid. The transfer of excitation energy to the RC induces the separation and stabilization of charge across the photosynthetic membrane. The special pair (SP) of BChls acts as the primary electron donor and is excited to P880*; this excited state then transfers an electron to $BChl_A$ and $BPhe_A$, and subsequently to Q_A. Q_B accepts the electron from Q_A. At this point, an electron has been transferred across the membrane and the primary reactants are ready for the next electron transfer. Once quinone receives two electrons, it binds two protons from the cytoplasm and escapes from the RC to neighboring Cyt bc_1. A Cyt c_2 or a Cyt C subunit reduces oxidized SP by transferring electrons back to the SP from Cyt bc_1. The cofactors are shown as sticks, with Mg^{2+} and Fe^{2+} ions shown as spheres. Arrows indicate the routes of light-driven electron transfer, and dashed arrows show quinone/quinol association/disassociation and delivery of electrons to $P880^+$ by Cyt c_2^{2+}. The figure was constructed using Protein Data Bank (PDB) 7VOR. (B) Variability of the RC protein composition and structure. In many phototrophic bacteria, for example *Rhodobacter sphaeroides* (PDB 7VOR), the RC is formed by only three core subunits: RC-L (Light, PufL), RC-M (Medium, PufM), and RC-H (Heavy, PuhA) (left). In these species, the soluble electron carrier Cyt c_2 docks directly to the RC periplasmic surface through electrostatic interactions for electron transfer to the SP of BChls within the RC. By contrast, the RC in some species, such as *Blastochloris viridis* (PDB 6ET5), contains a nonmembranous heme-containing cytochrome subunit (Cyt C or PufC) that noncovalently links to the RC-L and RC-M subunits (middle). The association of Cyt C facilitates the transfer of electrons from Cyt c_2 electron carriers to the RC. The RC-M and RC-L subunits are highly conserved among all species of purple bacteria and are present in all the RC structures determined. The RC-H subunit binds to the cytoplasmic face of RC-L and RC-M subunits. The RC of the green non-sulfur bacterium *Roseiflexus castenholzii* (PDB 5YQ7) is composed of Cyt C, RC-L, and RC-M, without RC-H (right). The RC-H subunit of *Gemmatimonas phototrophica* (PDB 7Q0U) is fragmented into two domains: Ht as a smaller transmembrane polypeptide and Hc as a larger polypeptide located on the cytoplasmic side of RC–LH.

cytoplasmic subunit Hc on top of the quinone sites. In addition, a unique short α-helix of RC-H above the Q_A site was identified in *Rhodobacter Rba. capsulatus* [25], which differs from the less-defined secondary structures in the same region resolved in other purple bacteria species.

The structural rigidity of this additional α-helix of RC-H might play a role in further insulating the Q_A site from the cytoplasm.

The released electron is replenished within the RC by a soluble protein electron carrier, which is commonly Cyt c_2 [43]. There are also other types of small Cyt molecules identified in certain species, such as Cyt c_8 [44], Cyt c_y [45], Cyt c_{2m} [46], or a high-potential iron–sulfur protein (HiPIP) [47]. Many RCs – such as those in *Rba. sphaeroides* [16–20], *Rba. veldkampii* [15], *Rba. capsulatus* [25], *Rhodopseudomonas* (*Rps.*) *palustris* [14], and *Rsp. rubrum* [26,27] – bind the protein electron carrier directly onto the periplasmic surface of RC-M and RC-L subunits [48]. By contrast, some other RCs have an additional nonmembranous heme-containing protein, namely Cyt C, which is noncovalently attached to the RC-M and RC-L subunits on their periplasmic sides (Figure 2B). By 'pulling out' the Cyt C subunit from the photosynthetic membrane, atomic force microscopy (AFM)-based single-molecule force spectroscopy revealed the stepwise unfolding process of Cyt C from the *Blc. viridis* RC–LH1 complex [49]. The Cyt C subunit typically coordinates four heme groups [21–24,37,38] and transfers electrons from Cyt c_2 to the special pair of BChls, improving electron transport and complex thermostability [50,51]. It was revealed that the electron carrier HiPIP binds to the Cyt C of the thermophilic purple sulfur bacterium *Thermochromatium* (*Tch.*) *tepidum* (γ-Proteobacteria) near its 1st heme group via hydrophobic interactions [52]. In some species, the N-terminal transmembrane domain of the Cyt C subunit is post-translationally truncated at a cysteine residue [22,23,37,53], and the anchoring of Cyt C to the membrane is mediated by a lipid, which occupies less space between the RC and LH1 ring compared to a transmembrane helix. By contrast, the Cyt C subunits of *Rfl. castenholzii* [21] and the acidophilic *Rhodopila* (*Rpi.*) *globiformis* [24] lack the cysteine residue and their N-terminal transmembrane helices are inserted into the membrane. This form has been proposed to be more ancient than the lipid-anchored form.

LH1 structure and cofactors

The LH1 complex is composed of a ring of LH1 heterodimers formed by transmembrane α- and β-polypeptides with their associated pigments: BChls and carotenoids. The α- and β-polypeptides are generally 40–70 amino acids long, comprising a hydrophobic transmembrane domain and the polar C- and N-terminal domains extending out on either side of the photosynthetic membrane. BChls are coordinated through their central Mg^{2+} atoms by conserved histidine residues in the transmembrane region of LH1. The distance between neighboring LH1 subunits appears consistent among species, enabling efficient excitation energy transfer along the LH1 ring [15,23]. The high absorption cross-section and long excited-state lifetime of LH1 make it an efficient antenna complex for light harvesting and transferring the excitation energy to the RC. LH1 could also protect the RC complex from **photodamage** by quenching the excess energy and preventing the formation of harmful reactive oxygen species (ROS) [35,36,54].

A striking feature of the natural RC–LH1 structures is the diversity in the shape of LH1 and the number of LH1 subunits. Many RC–LH1 complexes occur as slightly elliptical monomers, with a closed LH1 ring comprising 16 or 17 αβ-heterodimers surrounding the RC [14,22,26,27,37,55], or an open LH1 ring consisting of 14 or 15 αβ-polypeptides along with additional transmembrane polypeptides [14,15,20,21,56]. Dimeric RC–LH1 structures are found in a few purple bacterial species, with an S-shaped LH1 array composed of 28 LH1 αβ-heterodimers surrounding two RCs [17,18,20,30,57]. The RC–LH complex of *G. phototrophica* uniquely consists of two concentric LH rings encircling the central RC, including an inner ring of 16 LH1 subunits and an outer ring of 24 LH (named LHh) subunits [38]. This complex is the largest photosynthetic RC–LH1 core complex characterized to date.

Two types of BChls, BChl *a* and BChl *b*, are present in purple photosynthetic bacteria and the reported RC–LH1 structures (Table 1). BChl *a* is the most prevalent one and absorbs light at wavelengths between 800 and 970 nm (Q_y band; Q_y refers to 'quantum yield'). Some species, like *Blc. viridis*, use BChl *b* to absorb light with even longer wavelengths ranging between 960 and 1050 nm. The incorporation of BChls *a* and *b* in purple photosynthetic bacteria and certain anoxygenic phototrophs enables them to harness near-infrared light that is not accessible to plants or cyanobacteria. In purple bacteria, each LH1 αβ-subunit typically contains two BChl pigments (Figure 3A). However, the LH1 subunit of the green nonsulfur bacterium *Rfl. castenholzii* and the LH subunit in the outer LHh ring from *G. phototrophica* were found to coordinate three BChl pigments [21,38], in contrast to the typical two in other species. Carotenoids also play a crucial role in coordinating with the BChls in RC–LH1, facilitating light energy

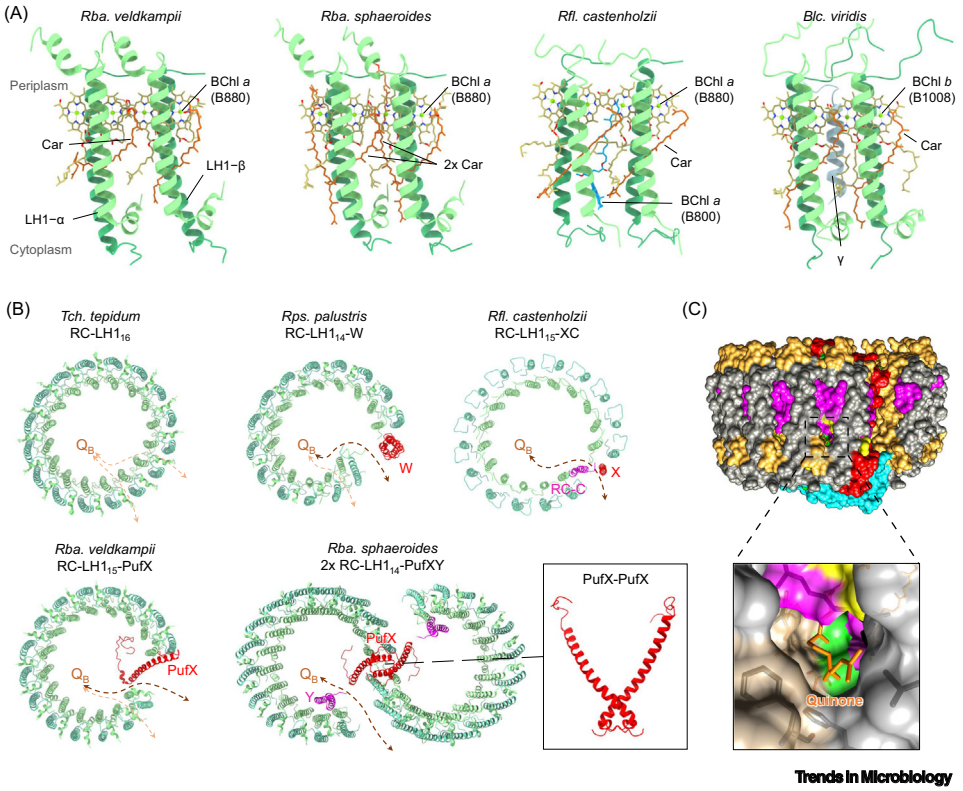

Figure 3. Variability of the light harvesting 1 (LH1) organization and quinone transport pathways. (A) Diversity of the LH1 αβ-heterodimer pigment arrangement in different representative species. Each LH1 αβ-heterodimer accommodates two bacteriochlorophyll (BChl) *a* (B880) and one Car in *Rhodobacter veldkampii*, two BChl *a* (B880) and two Car in *Rhodobacter sphaeroides*, two BChl *a* (B880), one BChl *a* (B800) and one Car in *Roseiflexus castenholzii*, two BChl *b* (B1008) and one Car in *Blastochloris viridis*. See also Table 1. (B) The organizational variation of LH1 rings, providing specific channels for quinone/quinol transport in and out of the RC–LH1 core complexes. Quinone can travel through the space between LH1 subunits in the closed LH1 ring (orange arrows). For open LH1 rings, quinone can pass the LH1 barrier through the gap mediated by additional polypeptides (brown arrows), in addition to the potential holes between LH1 subunits (orange arrows). The additional polypeptides were identified as protein-W in *Rhodopseudomonas palustris*, subunit-X and RC Cyt C transmembrane polypeptides in *Roseiflexus castenholzii*, PufX in *Rhodobacter veldkampii* and *Rhodobacter capsulatus*, as well as PufX and PufY in *Rhodobacter sphaeroides*. In certain species, for example *R. sphaeroides*, two RC–LH1 monomers form a dimer having an S-shaped LH1 ring with two large gaps for quinone/quinol traffic. The dimerization of reaction center (RC)–LH1 is mediated by the specific orientation and coupling of two PufX polypeptides (box). (C) A hole identified between two adjacent LH1 αβ-heterodimer of *Rhodobacter veldkampii*, where a quinone tail was particularly observed. This hole represents the potential channel in both closed and open LH1 rings to enable passage of quinone/quinol molecules.

capture and transfer and providing photoprotection. The number of carotenoids per LH1 heterodimer varies across different species and even within the same genus. For instance, each LH1 αβ-subunit of *Rba. sphaeroides* [20], *Rba. capsulatus* [25], and *Rca. bogoriensis* [30] noncovalently binds two carotenoid pigments instead of one, which is typical in other species (Figure 3A and Table 1). The diversity in the content of BChls and carotenoids in the LH1 ring may have implications for quinone/quinol transport, a topic further discussed in the subsequent text.

In addition to variations in pigment composition and content, some RC–LH1 complexes exhibit unique biochemical features. For example, the RC–LH1 complexes of the thermophilic purple sulfur bacterium *Tch. tepidum*, *Allochromatium (Alc.) tepidum,* and the mesophilic purple sulfur bacterium *Thiorhodovibrio* (*Trv*.) strain 970 (γ-Proteobacteria) incorporate Ca^{2+} ions in the C-terminal-loop region of LH1 [22,37,52,53,58]; this Ca^{2+} ion is bound by a pair of αβ-polypeptides and two water molecules, resulting in an unusual red-shifted Q_y absorption at 915 nm and enhanced thermostability of LH1. This biochemical feature may contribute to the fitness of these bacteria in their specific ecological niches [59,60].

Quinone/quinol transport in RC–LH1

While the LH1 ring facilitates excitation energy migration to the central RC, the high pigment density within the LH1 creates a physical barrier that may impede the rapid traffic of quinones between the RC and Cyt bc_1. Therefore, a channel or a gap in the LH1 ring is crucial for the functionality of the core complex. Recent structural studies have identified small hydrophobic channels between neighboring LH1 αβ-polypeptides in RC–LH1 structures, both with closed and open LH1 rings [14,15,22,26,27,58]. These channels are thought to act as the portals for quinone/quinol transport into and out of the core complex (Figure 3B,C). In addition, in RC–LH1 complexes with an opening in the LH1 ring, one or more LH1 subunits and their pigments are often sacrificed in the vicinity of the RC; instead, additional polypeptides are incorporated at the same position to maintain the LH1 ring shape and structural integrity necessary for the opening (Figure 3B). These openings are consistently located in the same place, adjacent to the Q_B site, in distinct RC–LH1 complexes, indicating their crucial roles in facilitating quinone traffic across the LH1 ring as an intriguing illustration of convergent evolution.

In most *Rhodobacter* species, the RC–LH1 core complexes contain an additional transmembrane polypeptide PufX, which mediates the opening of LH1 and dimerization of RC–LH1 (Figure 3B). The first high-resolution structure of PufX was obtained through cryo-EM analysis of *Rba. veldkampii* RC–LH1 at 2.8 Å resolution [15]. Recent studies have further elucidated the structural characteristics of PufX in the RC–LH1 complexes from other *Rhodobacter* species, including *Rba. capsulatus* [56] and *Rba. sphaeroides* [16–20]. The PufX peptide, which is approximately 80 amino acids long, consists of a short N-terminal tail, a C-terminal loop, and a central transmembrane helix that is positioned diagonally to the membrane plane. The C-terminal loop of PufX is exposed on the periplasmic side of RC–LH1 and connects to the RC-L subunit; the N-terminal tail of PufX is exposed on the cytoplasmic side of RC–LH1 and is close to the first LH1 subunit next to the opening. It was proposed that the association of PufX with the RC precedes the encirclement of the RC by LH1 [20]. Although the number of LH1 subunits in RC–LH1 varies depending on the species (e.g., 15 LH1 subunits per RC–LH1 in *Rba. veldkampii* and *Rba. capsulatus*, 14 or 28 LH1 subunits in *Rba. sphaeroides* RC–LH1 monomer or dimer, respectively), the specific organization of PufX with the RC–LH1 complex impedes the formation of a fully encircled LH1 ring and leads to the generation of a large gap in the LH1 ring. This gap serves as a unique portal for efficient quinone/quinol transport in and out of the core complex, which is confirmed by computational simulations [15,20].

Unlike the *Rba. veldkampii* counterpart with two BChls and one carotenoid, each LH1 subunit of *Rba. sphaeroides* and *Rba. capsulatus* contains two BChls plus two carotenoids, resulting in a more intense pigment array that could impede quinone/quinol passage through the small channels between adjacent LH1 subunits, necessitating the existence of this PufX-mediated gap for rapid quinone/quinol traffic. Consistently, when PufX is deleted from *Rba. sphaeroides*, the complex assembles with a fully closed ring of 17 LH1 around an inconsistently positioned RC, resulting in a loss of efficient photosynthesis [20].

In addition to PufX, another additional polypeptide, namely PufY (also called protein-Y or protein-U), has been recently identified in the RC–LH1 monomer and dimer of *Rba. sphaeroides* [16–20]. The name 'PufY' was given in order to be consistent with the nomenclature used for other RC–LH1 components, such as PufX, PufL/M, for RC-L/M, and PufA/B for LH1 α/β, which are encoded by genes in the *puf* operon, although the gene encoding PufY (RSP_7571) is far from the *puf* operon [20]. Deletion of PufY destabilized the neighboring LH1 subunits located next to the opening [17,20], which may affect the rates of **quinone transport**.

The native photosynthetic membranes of *Rps. palustris* contain RC–LH1 monomers with either a closed 16-subunit LH1 ring (RC–$LH1_{16}$, 90% of total RC–LH1) or an open LH1 ring with an additional polypeptide Protein-W (RC–$LH1_{14}$–W, 10% of total RC–LH1) [13,14,55]. Protein-W features three transmembrane helices and replaces an LH1 subunit, creating a gap in the LH1 ring. Biochemical assays have shown that RC–$LH1_{14}$-W has a greater Cyt c_2 oxidation rate than RC–$LH1_{16}$, suggesting the role of Protein-W-mediated LH1 opening in facilitating quinone/quinol diffusion.

The LH1 ring of *Blc. viridis* RC–LH1 is composed of 17 LH1 αβ-heterodimers, each of which binds two BChls and one carotenoid, as well as 16 γ-polypeptides that occupy the space between neighboring β-chains on the outer side of the LH1 ring [23]. The presence of γ-polypeptides may enhance the rigidity of the LH1 ring and generate a unique microenvironment for the redshift of BChl *b*, whereas the absence of a γ-polypeptide between two LH1 heterodimers creates space for the passage of quinone/quinol molecules.

In contrast, the RC–LH1 complex of the acidophile *Rpi. globiformis* features a closed LH1 ring composed of 16 αβ-heterodimers and 11 additional γ-like polypeptides located between β-polypeptides outside the LH1 ring [24]. It is noteworthy that the gene encoding the γ-like polypeptide and the gene encoding the γ-polypeptide in *Blc. viridis* exhibit low sequence similarity and are located in distinct genomic positions. The asymmetric numbers of αβ- and γ-like polypeptides in *Rpi. globiformis* provide several pores in the LH1 ring, which might be highly flexible and facilitate quinone transport.

The LH1 ring of *Rfl. castenholzii* is comprised of 15 αβ-heterodimers and a gap formed by the transmembrane helix of Cyt C and another transmembrane helix, subunit X [21]. As each LH1 subunit of *Rfl. castenholzii* coordinates three BChls and one carotenoid, which forms a compact pigment barrier surrounding the RC, this opening appears to be essential for effective quinone/quinol transport.

Dimerization of RC–LH1

Although monomeric RC–LH1 core complexes are common in many phototrophic bacteria, some *Rhodobacter* species and an alkaliphilic purple bacterium, *Rca. bogoriensis*, have been found to contain dimeric RC–LH1 complexes [17,18,20,30,57,61]. The RC–LH1 dimer consists of a continuous S-shaped array of LH1 αβ-subunits surrounding two RCs, and two copies of

PufX are located in the center, mediating the dimerization of two C-shaped monomers. However, in the *Rhodobacter* species, like *Rba. veldkampii* and *Rba. capsulatus*, the PufX-containing RC–LH1 complexes appear purely as monomers [15,25], raising the question of how PufX has diversified among extant lineages to result in distinct RC–LHC configurations.

In native RC–LH1 monomers of *Rba. sphaeroides*, *Rba. veldkampii*, and *Rba. capsulatus*, the PufX transmembrane polypeptide enhances the association between the RC and LH1, and prevents complete encirclement of LH1, resulting in an open LH1 ring. Deletion of PufX in *Rba. sphaeroides* resulted in exclusive formation of monomeric RC–LH1 with a closed LH1 ring, causing the loss of capability to perform photoheterotrophic growth [20]. This signifies the role of PufX in mediating a gap in the LH1 ring and the dimerization of RC–LH1 in *Rba. sphaeroides*. The two PufX polypeptides at the dimerization interface have a crossing angle of approximately 73° (Figure 3B), but intriguingly, no strong interaction was identified at the PufX–PufX interface. It was proposed that the interactions could be mediated by unobservable water molecules [20] or the two PufX polypeptides are close enough to form a hydrophobic surface [17]. Instead, it is evident that PufX interacts with its neighboring RC–LH1 monomer, stabilizing the dimeric structure. The N-terminal region of PufX forms hydrogen bonds with the RC-H subunit and interacts with LH1 subunits of the neighboring monomer [20], explaining why deletion of PufX N terminus impeded the dimerization [62,63]. The C-terminal region of PufX binds with the RC within the monomer, which is thought to be important for the PufX incorporation and Cyt c_2 navigation [15,20,30], and also interacts with LH1 of the neighboring monomer [20].

Concluding remarks

The advancement of structural biology techniques has revolutionized the studies of photosynthetic supercomplex structures by providing molecular-level details that aid in uncovering the molecular mechanisms of photosynthesis. Recent studies on the three-dimensional architecture of RC–LH1 core complexes from various microbial phototrophs have provided valuable insights into their structural diversity, modularity, and pigment organization. Advanced knowledge is critical for understanding the assembly principles and functionality of RC–LH1 supercomplexes, as well as their evolutionary relationships and adaptive roles in prokaryotic photosynthesis and fitness to thrive in a challenging environment. An in-depth comprehension of the molecular mechanisms underlying the assembly and functional regulation of photosynthetic pigment–protein complexes can be leveraged to design and engineer efficient, robust artificial photosynthetic systems. These systems can mimic or surpass natural structures in performance, meeting the demands of sustainable development. Future research should focus on elucidating how distinct RC–LH1 components self-assemble to form a specific architecture and eventually a functional photosynthetic complex, how pigments and cofactors are organized spatially and functionally coordinate with others, how rapid quinone/quinol exchange occurs in and out of the RC–LH1, and how RC–LH1 complexes are arranged physiologically together with other complexes in the photosynthetic membrane to ensure efficient electron transfer (see Outstanding questions). To address these questions, researchers can integrate a combination of techniques, including cryo-EM, time-resolved X-ray crystallography, AFM, spectroscopy, genetic engineering, computational simulations, and quantum calculations to conduct systematic studies on the structure, function, and regulation of RC–LH1 core complexes.

Outstanding questions

What mechanisms determine the structural variation and modularity of RC–LH1 complexes across species of different genera or phyla and varying environments?

What are the assembly processes of distinct RC–LH1 structures, and what regulatory factors are involved?

How to achieve higher resolution to determine the types and content of cofactors for a better understanding of their functionalities in the RC–LH1 core complex?

What are the energy transport and quinone/quinol transport mechanisms in RC–LH1 and the photosynthetic unit in its native membrane context?

How do RC–LH1 complexes interact with other photosynthetic complexes in the electron transport chain (e.g., LH2, Cyt bc_1, ATPase) to ensure efficient energy transfer and electron flow in the photosynthetic machinery?

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Declaration of interests

No interests are declared.

References

1. Croce, R. and van Amerongen, H. (2020) Light harvesting in oxygenic photosynthesis: structural biology meets spectroscopy. *Science* 369, eaay2058
2. Soo, R.M. *et al.* (2017) On the origins of oxygenic photosynthesis and aerobic respiration in Cyanobacteria. *Science* 355, 1436–1440
3. Mullineaux, C.W. and Liu, L.N. (2020) Membrane dynamics in phototrophic bacteria. *Annu. Rev. Microbiol.* 74, 633–654
4. Liu, L.N. (2016) Distribution and dynamics of electron transport complexes in cyanobacterial thylakoid membranes. *Biochim. Biophys. Acta* 1857, 256–265
5. Liu, L.N. and Scheuring, S. (2013) Investigation of photosynthetic membrane structure using atomic force microscopy. *Trends Plant Sci.* 18, 277–286
6. Miller, L.C. *et al.* (2020) Composition, organisation and function of purple photosynthetic machinery. In *Microbial Photosynthesis* (Wang, Q., ed.), pp. 73–114, Springer
7. Hohmann-Marriott, M.F. and Blankenship, R.E. (2011) Evolution of photosynthesis. *Annu. Rev. Plant Biol.* 62, 515–548
8. Liu, L.N. (2022) Advances in the bacterial organelles for CO_2 fixation. *Trends Microbiol.* 30, 567–580
9. Sakarika, M. *et al.* (2020) Purple non-sulphur bacteria and plant production: benefits for fertilization, stress resistance and the environment. *Microb. Biotechnol.* 13, 1336–1365
10. Madigan, M.T. (2003) Anoxygenic phototrophic bacteria from extreme environments. *Photosynth. Res.* 76, 157–171
11. Singharoy, A. *et al.* (2019) Atoms to Phenotypes: Molecular design principles of cellular energy metabolism. *Cell* 179, 1098–1111 e23
12. Qian, P. *et al.* (2013) Three-dimensional structure of the *Rhodobacter sphaeroides* RC-LH1-PufX complex: dimerization and quinone channels promoted by PufX. *Biochemistry* 52, 7575–7585
13. Roszak, A.W. *et al.* (2003) Crystal structure of the RC-LH1 core complex from *Rhodopseudomonas palustris*. *Science* 302, 1969–1972
14. Swainsbury, D.J.K. *et al.* (2021) Structures of *Rhodopseudomonas palustris* RC-LH1 complexes with open or closed quinone channels. *Sci. Adv.* 7, eabe2631
15. Bracun, L. *et al.* (2021) Cryo-EM structure of the photosynthetic RC-LH1-PufX supercomplex at 2.8-Å resolution. *Sci. Adv.* 7, eabf8864
16. Tani, K. *et al.* (2021) A previously unrecognized membrane protein in the *Rhodobacter sphaeroides* LH1-RC photocomplex. *Nat. Commun.* 12, 6300
17. Tani, K. *et al.* (2022) Asymmetric structure of the native *Rhodobacter sphaeroides* dimeric LH1-RC complex. *Nat. Commun.* 13, 1904
18. Qian, P. *et al.* (2021) Cryo-EM structure of the dimeric *Rhodobacter sphaeroides* RC-LH1 core complex at 2.9 Å: the structural basis for dimerisation. *Biochem. J.* 478, 3923–3937
19. Qian, P. *et al.* (2021) Cryo-EM structure of the monomeric *Rhodobacter sphaeroides* RC-LH1 core complex at 2.5 Å. *Biochem. J.* 478, 3775–3790
20. Cao, P. *et al.* (2022) Structural basis for the assembly and quinone transport mechanisms of the dimeric photosynthetic RC-LH1 supercomplex. *Nat. Commun.* 13, 1977
21. Xin, Y. *et al.* (2018) Cryo-EM structure of the RC-LH core complex from an early branching photosynthetic prokaryote. *Nat. Commun.* 9, 1568
22. Yu, L.J. *et al.* (2018) Structure of photosynthetic LH1-RC supercomplex at 1.9 A resolution. *Nature* 556, 209–213
23. Qian, P. *et al.* (2018) Cryo-EM structure of the *Blastochloris viridis* LH1-RC complex at 2.9 Å. *Nature* 556, 203–208
24. Tani, K. *et al.* (2022) An LH1-RC photocomplex from an extremophilic phototroph provides insight into origins of two photosynthesis proteins. *Commun. Biol.* 5, 1197
25. Bracun, L. *et al.* (2023) Cryo-EM structure of a monomeric RC-LH1-PufX supercomplex with high-carotenoid content from *Rhodobacter capsulatus*. *Structure* 31, 318–328
26. Tani, K. *et al.* (2021) Cryo-EM Structure of the Photosynthetic LH1-RC complex from *Rhodospirillum rubrum*. *Biochemistry* 60, 2483–2491
27. Qian, P. *et al.* (2021) Cryo-EM structure of the *Rhodospirillum rubrum* RC-LH1 complex at 2.5 Å. *Biochem. J.* 478, 3253–3263
28. Deisenhofer, J. *et al.* (1984) X-ray structure analysis of a membrane protein complex. *J. Mol. Biol.* 180, 385–398
29. Rutherford, A.W. *et al.* (2012) Back-reactions, short-circuits, leaks and other energy wasteful reactions in biological electron transfer: redox tuning to survive life in O(2). *FEBS Lett.* 586, 603–616
30. Semchonok, D.A. *et al.* (2022) Cryo-EM structure of the *Rhodobaca bogoriensis* RC-LH1-PufX dimeric complex at 2.9 Å. *bioRxiv* Published online 1 March 2022. https://doi.org/10.1101/2022.02.25.481955
31. Brajcich, B.C. *et al.* (2010) Evidence that ubiquinone is a required intermediate for rhodoquinone biosynthesis in *Rhodospirillum rubrum*. *J. Bacteriol.* 192, 436–445
32. Lonjers, Z.T. *et al.* (2012) Identification of a new gene required for the biosynthesis of rhodoquinone in *Rhodospirillum rubrum*. *J. Bacteriol.* 194, 965–971
33. Pierson, B.K. and Castenholz, R.W. (1974) A phototrophic gliding filamentous bacterium of hot springs, Chloroflexus aurantiacus, gen. and sp. nov. *Arch. Microbiol.* 100, 5–24
34. Imhoff, J.F. *et al.* (2017) Photosynthesis is widely distributed among Proteobacteria as demonstrated by the phylogeny of PufLM reaction center proteins. *Front. Microbiol.* 8, 2679
35. Chi, S.C. *et al.* (2015) Assembly of functional photosystem complexes in *Rhodobacter sphaeroides* incorporating carotenoids from the spirilloxanthin pathway. *Biochim. Biophys. Acta* 1847, 189–201
36. D'Haene, S.E. *et al.* (2014) Organization in photosynthetic membranes of purple bacteria *in vivo*: the role of carotenoids. *Biochim. Biophys. Acta* 1837, 1665–1673
37. Tani, K. *et al.* (2020) Cryo-EM structure of a Ca(2+)-bound photosynthetic LH1-RC complex containing multiple alphabeta-polypeptides. *Nat. Commun.* 11, 4955
38. Qian, P. *et al.* (2022) 2.4-Å structure of the double-ring *Gemmatimonas phototrophica* photosystem. *Sci. Adv.* 8, eabk3139
39. Takahashi, E. and Wraight, C.A. (1996) Potentiation of proton transfer function by electrostatic interactions in photosynthetic reaction centers from *Rhodobacter sphaeroides*: first results from site-directed mutation of the H subunit. *Proc. Natl. Acad. Sci. U. S. A.* 93, 2640–2645
40. Lupo, D. and Ghosh, R. (2004) The reaction center H subunit is not required for high levels of light-harvesting complex 1 in *Rhodospirillum rubrum* mutants. *J. Bacteriol.* 186, 5585–5595
41. Ishikita, H. and Knapp, E.W. (2005) Energetics of proton transfer pathways in reaction centers from *Rhodobacter sphaeroides*. The Glu-H173 activated mutants. *J. Biol. Chem.* 280, 12446–12450
42. Wei, R.J. *et al.* (2022) Comparison of proton transfer paths to the Q_A and Q_B sites of the *Rb. sphaeroides* photosynthetic reaction centers. *Photosynth. Res.* 152, 153–165
43. Zannoni, D. and Daldal, F. (1993) The role of c-type cytochromes in catalyzing oxidative and photosynthetic electron transport in the dual functional plasmamembrane of facultative phototrophs. *Arch. Microbiol.* 160, 413–423
44. Vermeglio, A. *et al.* (2002) The role of high-potential iron protein and cytochrome c(8) as alternative electron donors to the reaction center of *Chromatium vinosum*. *Biochemistry* 41, 8868–8875
45. Jenney Jr., F.E. and Daldal, F. (1993) A novel membrane-associated c-type cytochrome, cyt cy, can mediate the photosynthetic growth of *Rhodobacter capsulatus* and *Rhodobacter sphaeroides*. *EMBO J.* 12, 1283–1292
46. Kimura, Y. *et al.* (2007) A new membrane-bound cytochrome c works as an electron donor to the photosynthetic reaction center

complex in the purple bacterium, *Rhodovulum sulfidophilum*. *J. Biol. Chem.* 282, 6463–6472
47. Nagashima, K.V. *et al.* (2002) High-potential iron-sulfur protein (HiPIP) is the major electron donor to the reaction center complex in photosynthetically growing cells of the purple bacterium *Rubrivivax gelatinosus*. *Biochemistry* 41, 14028–14032
48. Vasilev, C. *et al.* (2019) Dissecting the cytochrome c_2-reaction centre interaction in bacterial photosynthesis using single molecule force spectroscopy. *Biochem. J.* 476, 2173–2190
49. Miller, L.C. *et al.* (2020) Unfolding pathway and intermolecular interactions of the cytochrome subunit in the bacterial photosynthetic reaction center. *Biochim. Biophys. Acta Bioenerg.* 1861, 148204
50. Masuda, S. *et al.* (1999) A new cytochrome subunit bound to the photosynthetic reaction center in the purple bacterium, *Rhodovulum sulfidophilum*. *J. Biol. Chem.* 274, 10795–10801
51. Kobayashi, M. *et al.* (2005) Reconstitution of photosynthetic reaction centers and core antenna-reaction center complexes in liposomes and their thermal stability. *Biosci. Biotechnol. Biochem.* 69, 1130–1136
52. Kawakami, T. *et al.* (2021) Crystal structure of a photosynthetic LH1-RC in complex with its electron donor HiPIP. *Nat. Commun.* 12, 1104
53. Tani, K. *et al.* (2022) A Ca^{2+}-binding motif underlies the unusual properties of certain photosynthetic bacterial core light-harvesting complexes. *J. Biol. Chem.* 298, 101967
54. Niedzwiedzki, D.M. *et al.* (2010) Spectroscopic studies of carotenoid-to-bacteriochlorophyll energy transfer in LHRC photosynthetic complex from *Roseiflexus castenholzii*. *J. Phys. Chem. B* 114, 8723–8734
55. Jackson, P.J. *et al.* (1859) (2018) Identification of protein W, the elusive sixth subunit of the *Rhodopseudomonas palustris* reaction center-light harvesting 1 core complex. *Biochim. Biophys. Acta Bioenerg.* 2, 119–128
56. Lilburn, T.G. *et al.* (1992) Pleiotropic effects of pufX gene deletion on the structure and function of the photosynthetic apparatus of *Rhodobacter capsulatus*. *Biochim. Biophys. Acta* 1100, 160–170
57. Semchonok, D.A. *et al.* (2012) Structure of the dimeric RC-LH1-PufX complex from *Rhodobaca bogoriensis* investigated by electron microscopy. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 367, 3412–3419
58. Niwa, S. *et al.* (2014) Structure of the LH1-RC complex from *Thermochromatium tepidum* at 3.0 Å. *Nature* 508, 228–232
59. Kimura, Y. *et al.* (2009) Calcium ions are required for the enhanced thermal stability of the light-harvesting-reaction center core complex from thermophilic purple sulfur bacterium *Thermochromatium tepidum*. *J. Biol. Chem.* 284, 93–99
60. Imanishi, M. *et al.* (2019) A dual role for Ca^{2+} in expanding the spectral diversity and stability of light-harvesting 1 reaction center photocomplexes of purple phototrophic bacteria. *Biochemistry* 58, 2844–2852
61. Crouch, L.I. and Jones, M.R. (2012) Cross-species investigation of the functions of the *Rhodobacter* PufX polypeptide and the composition of the RC-LH1 core complex. *Biochim. Biophys. Acta* 1817, 336–352
62. Ratcliffe, E.C. *et al.* (2011) Experimental evidence that the membrane-spanning helix of PufX adopts a bent conformation that facilitates dimerisation of the *Rhodobacter sphaeroides* RC-LH1 complex through N-terminal interactions. *Biochim. Biophys. Acta* 1807, 95–107
63. Francia, F. *et al.* (2002) Role of the N- and C-terminal regions of the PufX protein in the structural organization of the photosynthetic core complex of *Rhodobacter sphaeroides*. *Eur. J. Biochem.* 269, 1877–1885
64. Qian, P. *et al.* (2008) Three-dimensional reconstruction of a membrane-bending complex: the RC-LH1-PufX core dimer of *Rhodobacter sphaeroides*. *J. Biol. Chem.* 283, 14002–14011
65. Busselez, J. *et al.* (2007) Structural basis for the PufX-mediated dimerization of bacterial photosynthetic core complexes. *Structure* 15, 1674–1683
66. Qian, P. *et al.* (2005) The 8.5 Å projection structure of the core RC-LH1-PufX dimer of *Rhodobacter sphaeroides*. *J. Mol. Biol.* 349, 948–960
67. Tani, K. *et al.* (2023) *Rhodobacter capsulatus* forms a compact crescent-shaped LH1-RC photocomplex. *Nat. Commun.* 14, 846