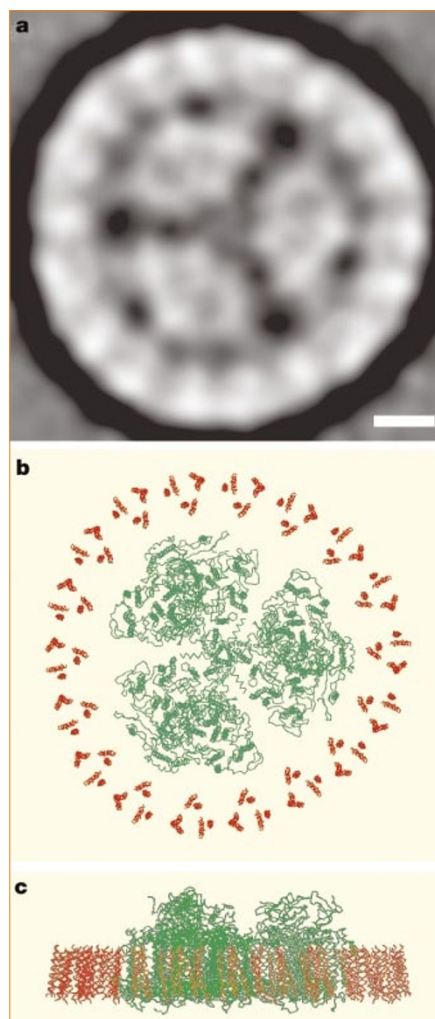


Oxyphotobacteria

# Antenna ring around photosystem I

The oceanic picoplankton *Prochlorococcus* — probably the most abundant photosynthetic organism on our planet<sup>1,2</sup> — can grow at great depths where light intensity is very low<sup>3</sup>. We have found that the chlorophyll-binding proteins in a deep-living strain of this oxyphotobacterium form a ring around a trimer of the photosystem I (PS I) photosynthetic reaction centre, a clever arrangement that maximizes the capture of light energy in such dim conditions.

Many types of oxyphotobacterium collect light for photosynthesis by means of



**Figure 1** The Pcb-photosystem I (Pcb-PS I) supercomplex of *Prochlorococcus*. **a**, Projection of the top view of the Pcb-PS I supercomplex isolated from *Prochlorococcus marinus*, strain SS120. This map is derived from the initial analyses of 3,500 negatively stained particles viewed under electron microscopy at room temperature (scale bar, 5 nm). **b**, **c**, Top view from the stromal side (**b**), and side view showing the extrinsic domains on the stromal side (**c**) of a three-dimensional model of the Pcb-PS I supercomplex; the model is based on X-ray data from cyanobacterial PS I trimers<sup>10</sup> (green) and CP43 transmembrane helices of cyanobacterial photosystem II (ref. 8; red).

water-soluble phycobilisomes, but *Prochlorococcus*, *Prochloron* and *Prochlorothrix* all use intrinsic light-collecting proteins that bind to chlorophyll *a* or *b*. Consequently, it was thought that the chloroplasts of green algae and higher plants, which also contain chlorophyll *a/b*-binding proteins, were derived by endosymbiosis from an ancestral prokaryote phylogenetically related to one of these three atypical oxyphotobacteria<sup>4</sup>.

Gene sequencing has shown, however, that the *pcb* genes that encode the principal light-collecting proteins are not closely related to the *cab* genes that encode the chlorophyll *a/b*-binding proteins of green plastids<sup>5</sup>, but instead are similar to the iron-stress-induced *isiA* gene of cyanobacteria<sup>5</sup>. Both encode proteins predicted to have six transmembrane helices that share homology with the six transmembrane helices of CP43, a protein that binds to chlorophyll *a* in photosystem II (PS II).

We investigated how the chlorophyll *a/b*-binding Pcb proteins structurally interact with the PS I reaction centre in *Prochlorococcus*. Figure 1a shows a projection map derived from electron microscopy and single-particle analysis of a large PS I complex isolated from *Prochlorococcus* strain SS120 by centrifugation through a density gradient of sucrose. The central region of the image has threefold symmetry and is surrounded by 18 separate subunits, as inferred from their densities.

This structure is remarkably similar to that of the PS I complex isolated from the cyanobacterium *Synechocystis* PCC6803 after iron deprivation<sup>6</sup>. In this case, the central region consists of a trimer of the PS I reaction centre surrounded by 18 copies of the *isiA* gene product. Given the sequence similarity between the *isiA* and *pcb* genes, the structure shown in Fig. 1a might also represent a trimer of PS I surrounded by 18 copies of one or more of the 7 chlorophyll *a/b*-binding Pcb proteins found in this *Prochlorococcus* strain<sup>7</sup>.

Chlorophyll fluorescence and protein analysis confirmed that this new complex contained PS I and Pcb proteins, and that efficient energy transfer occurs from the Pcb antenna ring to the core of the reaction centre. Furthermore, optical absorption spectra indicated that chlorophyll *a* and *b* are contained within the antenna ring and also within the PS I trimer. Figure 1b, c shows the three-dimensional structure of this Pcb-PS I supercomplex. This was modelled using the X-ray structures of the PS I trimer and CP43 transmembrane helices<sup>8,9</sup> of the cyanobacterium *Synechococcus elongatus*.

The *Prochlorococcus* strain used here was originally collected from the Sargasso Sea<sup>2,10</sup>, where it grows at considerable depths and would benefit from an antenna

system of the type reported here in order to increase the collecting capacity of PS I. The ring of Pcb proteins contributes a further 270 light-collecting chlorophyll molecules to the 300 predicted to be associated with the PS I reaction-centre trimer, assuming that the Pcb subunits each bind to 15 chlorophyll molecules.

The antenna ring therefore represents an increase of 90% in light-collecting capacity by the Pcb-PS I supercomplex over that of PS I in cyanobacteria such as *Synechocystis*, when growing in the absence of iron stress. In this latter case, the cyanobacterial PS I/PS II ratio is about 3:1, compared with 1:1 in *Prochlorococcus*. Under iron-stress conditions, however, when the IsiA antenna ring forms around PS I, the PS I/PS II ratio drops to about 1:1 in cyanobacteria as well. The formation of these Pcb and IsiA rings around PS I may therefore represent a mechanism for increasing the efficiency of this photosystem when its level is close to that of PS II.

It is not clear whether the PS I antenna ring is present in other types of chlorophyll *b*-containing oxyphotobacteria, as the number of *pcb* genes differs in *Prochloron*, *Prochlorothrix* and *Prochlorococcus*, as well as among different strains of *Prochlorococcus*<sup>5,7</sup>. Although the relationship between gene number and structural features in other strains of *Prochlorococcus* remains to be investigated, our discovery of an antenna ring around PS I in both *Prochlorococcus* and iron-deficient cyanobacteria<sup>6</sup> opens up discussion on the regulation of light-collection systems in oxyphotobacteria, as well as having implications for the evolution of these photosynthetic prokaryotes. The structures give functional significance to the trimerization of PS I in oxyphotobacteria, as well as providing new systems for studying energy transfer in light-collecting antennae during photosynthesis.

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