Structure of the Dimeric PufX-containing Core Complex of Rhodobacter blasticus by in Situ Atomic Force Microscopy*

Simon Scheuring‡§, Johan Busselez‡, and Daniel Lévy‡

From the ‡Institut Curie, Unité Mixte de Recherche-CNRS 168 and Laboratoire de Recherche Correspondant-Commissariat à l’Energie Atomique 34V, 11 rue Pierre et Marie Curie, 75231 Paris Cedex 05, France

We have studied photosynthetic membranes of wild type Rhodobacter blasticus, a closely related strain to the well studied Rhodobacter sphaeroides, using atomic force microscopy. High-resolution atomic force microscopy topographs of both cytoplasmic and periplasmic surfaces of LH2 and RC-LH1-PufX (RC, reaction center) complexes were acquired in situ. The LH2 is a nonamer ring inserted into the membrane with the 9-fold axis perpendicular to the plane. The core complex is an S-shaped dimer composed of two RCs, each encircled by 13 LH1 αβ-heterodimers, and two PufXs. The LH1 assembly is an open ellipse with a topography-free gap of ~25 Å. The two PufXs, one of each core, are located at the dimer center. Based on our data, we propose a model of the core complex, which provides explanation for the PufX-induced dimerization of the Rhodobacter core complex. The Qβ site is located facing a ~25 Å wide gap within LH1, explaining the PufX-favored quinone passage in and out of the core complex.

In purple photosynthetic bacteria, highly organized transmembrane pigment-protein complexes perform absorption of light and its conversion into chemical energy. Two light harvesting (LH) complexes, LH2 and LH1, ensure the collection of light. The excitation energy is funneled toward the special pair (P) of bacteriochlorophylls in the reaction center (RC) followed by an electron transfer from P to the ubiquinone (Q) acceptors, QA and QB. After two photoreactions and proton captures, the RC into the membrane. The cytochrome bc1 complex uti-

Simulation of the bacterial photosynthetic apparatus at atomic level is nearly complete. Two RC structures (2–4), two LH2 structures (5, 6), and the structure of the homologue bc1 complex from the respiratory chain (7) are known. However, the structure of the core complex composed of the LH1 and the RC remains undetermined.

Over the last two years, the data of core complexes of Rho-
dospirillum (Rsp.) rubrum (8), Blastochloris viridis (9), and Rhodopseudomonas (Rps.) palustris (10) have been acquired at a resolution sufficient to delineate the LH1 subunit arrangement around the RC. Whereas Rsp. rubrum and B. viridis have monomeric core complexes with 16 LH1 subunits arranged around the RC, Rps. palustris has 15 LH1 subunits plus an unknown polypeptide forming a single trans-membrane helix. The closed architecture of the LH1 assembly raised the question of the quinone exchange through the LH1 assembly between the RC and the cytochrome bc1.

In this context, the structural analysis of Rhodobacter core complexes is of particular interest, because it is the only species in which a small trans-membrane protein named PufX has been identified as crucial for bacterial growth under anaerobic photosynthetic conditions and for the fast exchange of quinones between the RC and the cytochrome bc1 complex (11–20). Biochemical studies have shown that PufX-containing core complexes could be isolated from Rhodobacter sphaeroides membranes as dimeric structures with a 1:1 PufX/RC stoichiometry and a decreased number of LH1-associated bacteriochlorophylls per RC (21). Furthermore, PufX induced a specific orientation of the RC in the LH1 ring as well as the formation of a long range order of LH1-RC core complexes (22). Finally, it has been proposed that PufX containing core complexes of R. sphaeroides are associated in supercomplexes, each one comprising two RCs, one cytochrome bc1, and one cytochrome c2 (23). Taking together, PufX is thought to play a key role in the core complex and in the supramolecular organization of the photosynthetic apparatus of Rhodobacter strains.

Low-resolution (20–30 Å) negative stain projection maps of native crystalline tubular membranes of LH2-deleted R. sphaeroides have revealed dimeric core complexes with S-shaped LH1 assemblies housing the two RCs (24, 25). In both of the negative stain maps, the LH1 assembly of each core covered approximately 75% of a full ellipse corresponding to 12 ± 1 LH1 subunits/core (24, 25). To get further information on this particular core complex and to localize the PufX subunit, structural studies of two-dimensional crystals of RH1-PufX core complexes purified from R. sphaeroides have been performed. First, a cryoelectron microscopy projection map revealing the trans-membrane protein portions showed an S-shaped core complex dimer with an ~30-Å wide protein-free gap in each LH1 assembly (26). A maximum density was found at the dimer junction, leading the authors to propose a localization of the two PufX proteins at the dimer junction. Second, an analysis of purified complexes by negative stain electron microscopy and AFM study showed monomeric core complexes with closed LH1-PufX rings (25). The discrepancies between the two studies in the results and corresponding conclusions are most prob-
ably due to different sample preparations, i.e. solubilization, purification, and reconstitution. To unambiguously localize the different subunits of *Rhodobacter* core complexes, the acquisition of data at molecular resolution under close to native conditions, avoiding preparation artifacts, is required. In this context, a very recent AFM analysis of LH2-containing *R. sphaeroides* native membranes has visualized dimeric core complexes but the resolution was insufficient to analyze their molecular architecture (27).

Here, we present a structural study by high-resolution AFM of the core complex of *R. blasticus*, a strain closely related to *R. sphaeroides* (20, 28). The AFM topographs have been acquired on fused native photosynthetic membranes of *R. blasticus*. Due to the fusion of membranes in “up” and “down” orientations, the topographs revealed the periplasmic and cytoplasmic surfaces of LH2 and core complexes. The LH2 complexes are nonameric rings inserted with their 9-fold axis perpendicular to the membrane plane. Importantly, we have acquired high-resolution topographs of PuX-containing core complexes in situ. AFM topographs at a 15-Å resolution revealed that core complexes assemble in S-shaped dimeric complexes. Each core complex is composed of a clearly open LH1 assembly with a gap of ~25-Å width housing one reaction center. The PuX proteins are identified at the dimer center holding the two cores together. Based on our data, we propose a structural model for the subunit organization of the dimeric S-shaped *Rhodobacter* core complex. This model provides an explanation for the double function of PuX inducing core complex dimerization and indirectly favoring quinol/quinone passage.

**EXPERIMENTAL PROCEDURES**

**Bacterial Culture and Membrane Preparation—** *R. blasticus* (DSM 2131) was photosynthetically grown. Cells were harvested, washed, and broken by two passages through a French pressure cell. Membranes were purified on sucrose gradients and fused by two freeze and thaw cycles for AFM analysis.

**Atomic Force Microscopy—** Mica prepared as described previously (29) was freshly cleaved and used as the support. The mica was immediately covered by 40 μl of adsorption buffer containing 10 mM Tris-HCl, pH 7.3, 150 mM KCl, and 20 mM MgCl2. Subsequently, 3 μl of membrane solution were injected into the adsorption buffer drop on the mica surface. After 10 min, the sample was rinsed with 10 volumes of recording buffer containing 10 mM Tris-HCl, pH 7.3, and 150 mM KCl. Imaging was performed with a commercial Nanoscope-E contact-mode AFM (from Digital Instruments, Santa Barbara, CA) equipped with a low-noise laser and a 160-μm scanner (J-scanner) using oxide-sharpened Si3N4 cantilevers with a length of 100 μm (k = 0.09 Newton/m; Olympus Ltd., Tokyo, Japan). For high-resolution imaging, minimal loading forces of ~100 picoNewton were applied. The piezo precision was determined on protein two-dimensional crystals at scan ranges between 100 and 300 nm, and errors in x- and y- dimensions smaller than 2% were found.

**Image Analysis—** Averages were calculated after the alignment of handpicked particles from trace and retrace images acquired at different magnifications using the Xmipp single particle analysis program package; LH2 cytoplasmic surface, *n* = 388; LH2 periplasmic surface, *n* = 235; and the core complex cytoplasmic surface, *n* = 51. The spectral signal-to-noise ration resolution criterion was used to evaluate the average resolution (30, 31).

**RESULTS**

**Fusion of Chromatophores of *R. blasticus*—** Purified native photosynthetic chromatophores of *R. blasticus* are uniformly small in size with a diameter of ~50 nm as determined by electron microscopy (EM). These membranes are too small for AFM analysis. We fused the small vesicles by freeze-thawing cycles (see “Experimental Procedures”). This led to the formation of vesicular membranes with sizes of up to 1 μm amenable to AFM analysis (Fig. 1).

**High-resolution Topographs of Fused Native Membranes of *R. blasticus*—** A topograph on a fused vesicle is shown in Fig. 1.

Although the fused membranes are not completely flat, we have been able to acquire high-resolution topographs allowing the identification of the different components within the membrane. Two types of complexes can be visualized and identified by comparison with previous AFM, EM, and x-ray data of LH2 and LH1-RC-PuX complexes. Small rings at ~50 Å in diameter with no central density are LH2 complexes, and large S-shaped complexes of ~10 × ~20 nm in size encircling protruding central proteins are dimeric RC-LH1-PuX complexes. For both complexes, two surfaces with different heights and appearances were observed. These differences in the protrusion heights of the two surfaces of LH2 and of core complexes have already been reported and attributed to their sidedness. For LH2, the weakly and the strongly protruding surfaces represent the cytoplasmic and the periplasmic surfaces, respectively (32, 33). For the core complex, the strongly protruding LH1 housed a central protruding topography corresponding to the H subunit and representing the cytoplasmic surface (34). Because in the native membrane both LH2 and core complexes have the same orientation, the existence of two differently protruding surfaces of the two types of complexes can only be interpreted assuming that native chromatophores have fused in up and down orientations during the freeze-thaw process.

Although the up and down membrane fusion precludes a detailed interpretation of the position and association of the photosynthetic complexes in the native membrane, regions corresponding to one orientation show that the complexes are in physical contact with neighboring complexes. The distance between the LH2s (Fig. 1, top left) are similar to LH2-LH2 distances found in two-dimensional crystals with a hexagonal lattice (32). In addition, many LH2 rings are in direct contact with the PuX-containing core complexes, facilitating the transfer of excitation energy from LH2 to LH1 and hence to the RC. Such physical contact among the different photosynthetic complexes, as recently reported by AFM in other native membranes (27, 35), would represent the basic requirement for the efficient harvesting, transmission, and trapping of light energy in photosynthetic bacteria. The arrangement does ensure the absence of single isolated complexes unconnected from the light-harvesting system. A LH2 complex lacking physical contact to other LH2 or LH1 complexes is not functional, i.e. its excitation energy upon photon capture will be lost.

On the other hand, the fusion process, which leads to membranes with complexes in up and down orientations, turns into an important advantage because it allows the analysis of both
the cytoplasmic and the periplasmic surfaces of the different components by AFM (Figs. 2, 3, and 5). Indeed, the strongly protruding H-subunit of the RC on the cytoplasmic face makes the acquisition of highly resolved information regarding the LH1 arrangement impossible (27). Only high-resolution imaging of the periplasmic surface of the core complexes allowed us to determine the PuF localization and delineate the presence of a ~25 Å gap within the LH1 topography.

The LH2 Complexes—In the case of LH2, two surfaces with different heights and appearance were observed, a weaker protruding ring with a larger apparent diameter (Fig. 2A) and a stronger protruding ring with a narrower apparent diameter (Fig. 2B). Differences in the protrusion heights of the two surfaces of LH2 have already been reported, and their sidedness assignment has been established (32, 33). The weakly and the strongly protruding surface represent the cytoplasmic and the periplasmic surface, respectively (32, 33). In the case of R. blasticus, the cytoplasmic surface protrudes weakly by 6 ± 1 Å (n = 20) and has a top ring diameter of 55 Å (Fig. 2A and C, left), whereas the periplasmic surface of the LH2 complex protrudes strongly by 17 ± 3 Å (n = 20) and has a top ring diameter of 45 Å (Fig. 2B and C, right). The averaging of the complexes using reference-free alignment allowed us to determine the imaging resolution to 15 Å (30, 31). Rotational power spectrum analysis of the complexes indicated a nonameric assembly of the LH2 complexes from R. blasticus.

Different types of peripheral LH2 antenna complexes have been isolated from various species of purple bacteria, and their structures have been analyzed. McDermott et al. (5) first studied the structure of LH2 from Rhodopseudomonas acidophila by x-ray crystallography, revealing a membrane-spanning cylinder (5) formed by nine subunits. The atomic structure from three-dimensional crystals of Rhodospirillum molischianum LH2 revealed an octameric arrangement (6). In addition, electron crystallography and AFM data in both cases at a resolution sufficient to at least resolve the number of α/β-heterodimer subunits were also acquired on two-dimensional crystals of LH2s from Rhodovalum sulfidophilum, R. sphaeroides, and Rubrivivax gelatinosus, all exhibiting a nonameric organization (32, 33, 36–38). For R. sphaeroides LH2, a tilted membrane insertion of ~6° was measured in two-dimensional crystals (33, 37) but was attributed to crystal contacts (39). We cannot confirm such a tilt of the LH2 complexes in the non-crystalline native membrane R. blasticus.

The Two Surfaces of the Dimeric Core Complex—The general appearance of the core complex is an S-shaped molecule of ~10 × ~20 nm in size, in agreement with our previous EM studies of dimeric core complexes of R. sphaeroides in native crystalline tubes and in two-dimensional crystals of purified proteins (24, 26). Because of the chromatophore fusion process, two types of core complex topographies corresponding to its two surfaces were found: 1) one weaker protruding (7 Å) S-shaped and 2) the other stronger protruding (15 Å) Z-shaped. The sidedness assignment of the core complex has been established on the core complex of Rsp. rubrum where the strongly protruding LH1 housed the RC, exposing its H-subunit on the cytoplasmic side, and the weakly protruding LH1 surrounded the periplasmic surface of the RC, exhibiting the flat surfaces of the L- and M-subunits (34). Indeed, the H-subunit, characteristic for the cytoplasmic side, can be scratched away by the AFM tip in contact mode, revealing the underlying L- and M-subunits (25, 34). In agreement, the weakly protruding S-shaped dimeric core complex exposes a weakly protruding RC and hence corresponds to the periplasmic surface. On the other hand, the strongly protruding LH1 is rather Z-shaped and houses a stronger protruding RC topography on the cytoplasmic surface.

The Periplasmic Surface of the Dimeric Core Complex—We have analyzed individual dimeric LH1-RC-PufX core complexes
(Fig. 3, A and B). High-resolution raw data topographs of the periplasmic face are shown in the left panel, and the corresponding 2-fold symmetrized complexes are shown in the right panel. The LH1-PufX assembly forms a continuous S with a height of 7 ± 1 Å (n = 20) and housing two RCs. As revealed by single molecule imaging, both RCs have one unique and identical orientation in the LH1 assembly, i.e. the same orientation with respect to the dimer center (Fig. 3B, arrows). Consistently, the major protrusions of the RCs are located at the same positions in both the raw data topographies (Fig. 3, A and B, left panel) and the 2-fold symmetrized complexes (Fig. 3, A and B, right panel). Averaging enhances the signal to noise ratio and allows to compute the topography resolution to 15 Å (Fig. 3C, left) (30, 31). The LH1 assembly clearly covers "only" 290°, housing 13 LH1 α/β-heterodimers (Fig. 3C, middle). Furthermore, the LH1 assembly of each core is elliptical, i.e. the S is skewed. Ellipse dimensions measured on top of LH1 of the long and the short axes are 100 and 90 Å, respectively.

At the dimer center, the LH1 assembly shows particular features such as an enlarged and depressed topography in which two tiny protrusions are clearly visible (Fig. 3C, middle, arrow 1). Because the LH1 assembly is composed of multiple identical α/β pairs and one PufX polypeptide (21), we identified two PufX peptides, in the particular topology at the dimer center, from the two cores holding the dimer together (see "Discussion").

Besides the major dimeric fraction (75%), a minor fraction (25%) of monomeric core complexes was found. These monomers are probably due to the dissociation of dimers as evidenced by particular complexes, which might represent dissociating dimers (Fig. 4A). In this dimeric complex, which has lost its internal 2-fold symmetry, one of the two monomers is significantly bent over at the dimer center. Furthermore, the monomers are identical to one-half of a dimer with a discontinuous LH1 assembly and a gap of similar size than each monomer in a dimer (Fig. 4B). The monomers could represent a native state in equilibrium with dimeric cores or could result from the sample preparation, i.e. the freeze-thawing cycles. Whatever the final explanation, it should be recalled that such open monomers can reform dimers upon reconstitution (26).

Importantly, we never observed monomeric closed LH1 surrounding the RC. Thus, we cannot confirm the existence of closed LH1-RC-PufX monomeric complexes as Siebert et al. (25) have reported in topographs of purified reconstituted core complexes of *R. sphaeroides*.

**The Cytoplasmic Surface of the Dimeric Core Complex**—On the cytoplasmic surface, the RC exposes its strongly protruding H-subunit. This makes imaging difficult because of its strong corrugation height and hampered so far the elucidation of the subunit architecture of the core complex by AFM (27). Using contact-mode AFM, the strongly protruding H-subunit can be removed by the tip; however, the imaging resolution of the cytoplasmic surface is lower than on the periplasmic surface. Indeed, some dimeric core complexes retain the H-subunits of the reaction centers. Consequently, averaging was impossible because of the strongly different appearance of the cores viewed from the cytoplasmic side. In any case, on some of the core complexes, the Z-shaped protrusion of the LH1 assembly is visible (Fig. 5, particle 1). The LH1 protrudes by 15 ± 3 Å (n = 20) from the lipid bilayer. When the H-subunit is removed, the surface of the L- and M-subunits on the periplasmic surface protrudes equally by −15 Å (see Fig. 5A, particle 1, lower monomer). The H-subunit itself protrudes ~3 nm further from the complex (see Fig. 5A, particle 1, upper monomer). Again, besides the dimers, monomers are found (Fig. 5, particles 3 and 4), which show a discontinuous LH1 assembly with a gap as found for monomers viewed from the cytoplasmic side (Fig. 4).

**DISCUSSION**

This study has directly revealed the structure of the PufX-containing core complex of *R. blasticus* in its native environ-
ment. We have found a dimer consisting of two elliptical C-shaped LH1 assemblies housing one RC each. An elliptical arrangement of LH1 has already been reported for the core complexes of B. viridis, Rsp. rubrum, Rps. palustris, and R. sphaeroides (8–10, 25, 26). In absence of RC, the LH1 is circular (9, 40). Thus, it appears that ellipticity is a general feature resulting from the interactions between the RC and the LH1 assembly. In the case of the core complexes of R. blasticus and R. sphaeroides, the ellipticity is particularly astonishing since one would expect larger flexibility of an open LH1 assembly. Thus, it is likely that the ellipticity results from specific interactions over large parts of the RC. Furthermore, as reported for R. sphaeroides (22), we found a unique orientation of the RC in the dimer of R. blasticus (Fig. 3). Hence, specific interactions with PuFX lock the RC and restrict its mobility within the LH1 ellipse.

The high-resolution AFM images allowed us to delineate the individual LH1 α/β-heterodimers, a particular topography at the dimer junction and a unique orientation of the RCs. The height and the topography of the LH1 subunits along the C-shaped LH1 assemblies are homogeneous, whereas at the dimer center, an enlarged and depressed topography is found in both the raw data (Fig. 3, A and B) and the average images (Fig. 3C). Since the stoichiometry PuFX/RC was found to be 1/1 (21), we attribute the two tiny protrusions at the dimer center (Fig. 3C) to the two PuFXs, one from each core. Thus, in contrast to the general view that PuFX can be located in the gap within the LH1 assembly causing interruption of a closed LH1 ring (22, 25, 41), we show the location of a dimer of PuFX at the dimer junction. Previously, we have found an enhanced protein density at the dimer junction in a cryo-EM projection map (26). Here, we detect a particular depressed topography at the dimer center. Both techniques provide complementary information, the cryo-EM density map the trans-membrane domains, and the AFM topography, the extra-membranous domains. Thus the PuFX-dimer at the dimer junction is structurally different from LH1 α/β-heterodimers, resulting in a different projection density and a different topography.

Based on our data, we generated a model using the only structure of a core complex available, a backbone model of Rps. palustris (10). This core complex is elliptical and monomeric and contains an unidentified PuFX-like peptide termed W, which is interspersed among 15 LH1 subunits. For docking the AFM topograph of the dimeric core complex of R. blasticus (Fig. 3), we have removed two LH1 subunits and built a crystallographic dimer with the two W-peptides (representing PuFX) at the dimer center. No other changes of the Rps. palustris core complex model were undertaken. In particular, the orientation of the RC was unchanged.

The model contains two RCs housed by two C-shaped LH1 assemblies consisting of 13 LH1 subunits and two PuFX subunits at the dimer center (Fig. 6A). A striking result is that the size of the gap is too small for the addition of a 14th LH1 subunit. Indeed, a 14th subunit (shown in red in Fig. 6B) can simply not be present for steric reasons. The trans-membrane helix of the β-polypeptide of the 14th subunit (shown in red) is collapsing with the trans-membrane helix of the β-polypeptide of the second LH1 subunit of the other core within the dimer (Fig. 6B, dashed line). Hence, the existence of the gap in the LH1 fence seems to be a secondary effect of the formation of dimeric core complexes. While waiting for the structural elucidation of a dimeric Rhodobacter core complex by x-ray crystallography, we provide a working model of the role of PuFX in the first steps of Rhodobacter photosynthesis.

The structure of the dimeric open core complex of R. blasticus revealed by in situ AFM is similar to the core complex structure of R. sphaeroides elucidated by electron microscopy (24, 26). This is strong evidence that in all of the Rhodobacter strains, i.e. sphaeroides, blasticus, capsulatus, azonotorhonsmans, and veldkampi, for which a pufX gene has been identified, the dimeric core complex architecture is conserved.

A dimeric arrangement of RCs in Rhodobacter strains is demanded by a supercomplex model containing one bc1 complex per two RCs proposed in R. sphaeroides based on spectroscopy data and thermodynamic considerations (23, 42–44). The supercomplex remains structurally to be shown. The AFM with its high signal to noise ratio and lateral resolution will play a key role for the structural analysis of the supramolecular organization of the photosynthetic apparatus, taking together LH2, the core complex, the bc1 complex, and the ATP synthase in situ.

PuFX is not forming a channel across the LH1 fence but indirectly through core dimerization induces the formation of a gap within the LH1 ring. In conclusion, we could acquire high-resolution topographs of the dimeric core complex of R. blasticus and localize the PuFX proteins at the dimer junction. We show that the PuFX protein is the structural key for the dimerization of core complexes rather than providing a direct pathway for the Q/Q-H2 exchange. Furthermore, we built a model based on our data, which provide an explanation for the dimer formation and the fast Q/Q-H2 transfer from and to the Qb site. Hence, the facilitated diffusion of Q/Q-H2 through a protein-free gap in the LH1 fence seems to be a secondary effect of the formation of dimeric core complexes.
Acknowledgements—We thank Dr. J. L. Rigaud for constant help and careful reading of the paper. We also thank Drs. A. Vermeglio and N. Ginet for fruitful continuous discussions.

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