The Primary Structures of the Core Antenna Polypeptides from *Rhodopseudomonas marina*

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Dedicated to Professor Achim Trebst on the occasion of his 60th birthday

B880 Antenna Complex, Light-Harvesting Polypeptide, Purple Non-Sulfur Bacterium, Amino Acid Sequence, *Rhodopseudomonas marina*

The antenna complex B880 of *Rp. marina* has been isolated by applying ion-exchange chromatography on Whatman DE-52 resin and sucrose density centrifugation of LDAO-solubilized photosynthetic membranes. The antenna polypeptides B880-α and B880-β were prepared by organic solvent extraction of extensively dialyzed and freeze-dried B880 antenna complex material or photosynthetic membranes. Gel filtration on Sephadex LH-60 and ion-exchange chromatography on Whatman DE-32 resin in the presence of organic solvents and an additional step on a C-8 reversed phase column yielded pure α- and β-apoproteins. Their complete primary structures have been elucidated using automated Edman degradation and carboxypeptidase digestion. According to quantitative Edman degradation the ratio of B880-α and B880-β has been determined as 1:1 in the isolated antenna complex as well as in the photosynthetic membrane. B880-α of *Rp. marina*, presumably N-formylated, consists of 52 amino acid residues and is 75, 56, 52 and 44% homologous to the corresponding core antenna polypeptides of *Rs. rubrum*, *Rp. viridis*, *Rb. capsulatus* and *Rb. sphaeroides*. In contrast, B880-β (56 amino acid residues) is less homologous to the corresponding core β-antenna polypeptides of the same strains (57, 51, 41 and 42%). It shows an extended N-terminal domain as compared to the B880-α polypeptide. Apart from the typical structural features of bacterial membrane-bound antenna polypeptides (three domain structure, His-residue in the hydrophobic stretch) the antenna polypeptides of *Rp. marina* are structurally related to polypeptides of core antenna complexes with strong near infrared circular dichroism signals.

Introduction

The primary processes of photosynthesis involve two different pigment-protein complexes: A light-harvesting system and the reaction center complex. In purple non-sulfur bacteria absorption of light between 800 and 1020 nm and the transfer of excitation energy are efficiently performed by peripheral antenna complexes (*e.g.* B800–850 or B800–820) and a core antenna (*e.g.* B880); the latter is located next to the reaction center. In general 1–3 carotenoids, 2–3 bacteriochlorophylls and a pair of polypeptides (α and β), form the smallest compositional unit, which aggregates to an oligomeric functional antenna complex [1, 2]. As a result of being bound specifically to intramembrane antenna polypeptides, optimal spatial distances and orientations between light-harvesting pigments are obtained, providing an optimized energy trapping and transfer system. The monomeric BChl molecules (Qy at around 800 nm) most likely are located at the cytosolic side with their tetrapyrrolic system arranged parallel to the membrane plane rather than perpendicular, as observed for the dimeric BChl's absorbing at either 820, 850 and 880 nm [3]. Based on comparative primary structure analyses [4–8] and from experiments probing the orientations of the antenna polypeptides [9, 10], the dimeric pigments have been proposed to be liganded to conserved His residues which are located in the half-bilayer exposed to the periplasmic side. In addition, the amino acid sequence studies focussed on antenna specific structural elements of the relatively small α- and β-polypeptides (*ca.* 40–65 amino acid residues); for example, it has been proposed that antenna typical aromatic amino acids may account

Abbreviations: B880, antenna complex with an absorption maximum (Qy-band) at approx. 880 nm; B880-α(β), α(β)-polypeptide of the B880 antenna complex; MeOH, methanol; NH_4OAc, ammonium acetate; CP, carboxypeptidase; PTH, phenylthiohydantoin; NIR, near infra-red; CD, circular dichroism; LDAO, lauryl-N,N-dimethylamine-N-oxide; BChl, bacteriochlorophyll; *Rp., Rhodopseudomonas; Rs., Rhodospirillum; Rc., Rhodocyclus; Rb., Rhodobacter.*

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for the absorption properties (Qy-band) of the bacterial antenna complexes [5, 11, 12].

Furthermore, the structural data obtained so far suggest specific amino acids (amino acid segments) as a possible molecular basis [11, 12] for the formation of core antenna complexes with strong near infra-red circular dichroism signals as found in *Rs. rubrum, Rp. viridis* and *Rp. acidophila* [13]. In contrast, the core antenna of *Rb. sphaeroides, Rb. capsulatus* and *Rc. gelatinosus* with relatively weak NIR-CD signals [13] synthesize core antenna polypeptides lacking these primary structural features [1, 11].

Here we report on the isolation and the primary structure analyses of the α- and β-polypeptides of the core antenna complex (apparently the only light-harvesting complex) from *Rp. marina*. This organism is unusually thermotolerant (growth up to 44 °C) as compared with typical non-sulfur purple bacteria and requires 1–5% sodium chloride for optimal growth [14].

Material and Methods

Organism and culture conditions

Cells of *Rhodopseudomonas marina* (Deutsche Sammlung für Mikroorganismen, DSM 2698) were grown photosynthetically with succinate as the main carbon source (growth medium DSM 27, plus 3% NaCl [14]). The cells were harvested by centrifugation and immediately used or stored as a frozen pellet at about −20 °C until required.

Isolation of the B880 antenna complex

Cells were broken by ultrasonication (15 × 45 sec intervals) in the presence of a little DNAse. Disrupted membranes were collected by differential centrifugation at 10,000 rpm for 10 min in a Sorvall centrifuge (SS-34 rotor) and at 45,000 rpm in a Titan TFT 70.38 rotor on a Centricon (Kontron) centrifuge for 2 h at 4 °C. The isolation of a RC-depleted B880 antenna complex was performed essentially as described in [15] using LDAO as a detergent. Photosynthetic membranes were solubilized in 0.1 M KH_2PO_4, pH 7.5. LDAO was added up to a concentration of 0.5% (w/v), and incubation was carried out for 4 h at room temperature in the dark. Subsequent centrifugation for 30 min at 45,000 rpm (TFT 70.38 rotor, Centricon) yielded solubilized membranes in the supernatant. The B880 antenna complex was further purified by passage over a Whatman DE-52 column (equilibrated with 20 mM Tris-HCl, pH 8.0) and stepwise elution with 25, 50, 100 and 200 mM NaCl (in 20 mM Tris-HCl, pH 8.0, 0.5% LDAO). In some cases sucrose gradient centrifugation was performed (0.3, 0.6 and 1.2 M sucrose steps, in 20 mM Tris-HCl, pH 8.0) in a fixed angle rotor (TFT 70.38, Centricon) for *ca.* 20 h at 4 °C.

Isolation of the antenna polypeptides

The antenna polypeptides were prepared from freeze-dried membranes (approx. 100–300 mg) by using an extraction mixture of methylene chloride/methanol (1:1, v/v)/0.1 M ammonium acetate. In a first step, organic solvent soluble polypeptides were fractionated according to their size on a Sephadex LH-60 (Pharmacia) column (2.5 × 130 cm) in the same solvent [4–7]. Pooled fractions were then applied in a second step to a DE-32 column (1 × 10 cm) equilibrated in the same organic solvent mixture [4, 6, 7]. The polypeptides were eluted from the column in two steps: one of CH_2Cl_2/MeOH/NH_4OAc; the second of CH_2Cl_2/MeOH/NH_4OAc and 10% acetic acid (v/v).

Column fractions from the Sephadex LH-60 gel-filtration chromatography (or from the ion-exchange chromatography step on DE-32) were applied to a reversed-phase column (C-8, 300 Å, 5 or 15 μm, 1 × 10 cm), either prepacked by Pharmacia (ProRPC HR 10/10) or self-packed, material from Serva according to [16]. Polypeptides were eluted with a linear gradient from 30% to 100% acetonitrile (or a mixture of acetonitrile/isopropanol/tetrahydrofuran = 7:2:1) at a constant concentration of trifluoroacetic acid (= 0.1%). The flow rate was 1.3 ml min^{-1}. Fractions containing polypeptide material were dried in a speed vac concentrator at about 50 mTorr.

Analytical methods

Absorption spectra were recorded on a Perkin Elmer Lambda 5 or a Perkin Elmer Lambda Array 3840 UV/VIS spectrophotometer equipped with a Perkin Elmer microcomputer 7700.

N-Terminal sequence analyses were performed on a liquid-phase Beckman 890 C sequencer and on an Applied Biosystem 470 A gas-phase sequencer. The identification of the PTH-amino acids was carried out as described in [17]. Deblocking of B880-α was essentially as described in [4] by incubating in 2.5% HCl in MeOH for about 3 h at room temperature.

C-Terminal amino acid sequence analyses were performed by using digestion with the carboxypep-

tidases A and B (Boehringer), essentially as described in [6] in the presence of 0.2% SDS. The amino acids released were quantified on a Biotronic LC-6000E amino acid analyser with a routine program.

Amino acid compositions were determined from polypeptide samples, obtained from the reversed phase chromatography steps. Hydrolysis of about 1 nmol of this polypeptide preparation was performed in freshly-distilled 6 N HCl for 24, 72 and 120 h in vacuum-sealed tubes at 110 °C. For accurate values of the branched hydrophobic residues valine, isoleucine and leucine only the 120 h hydrolysis was used.

The stoichiometry of the B880 antenna polypeptides α and β have been determined by comparing the amount of PTH amino acids released after Edman degradation of a freeze-dried B880 antenna complex extracted with organic solvent and chromatographed on a Sephadex LH-60 column.

Results

Isolation of the core antenna complex B880 of Rp. marina

Reaction center-depleted core antenna complex B880 was obtained with a DE-52 ion-exchange chromatography step upon elution with approx. 25–50 mM NaCl. The absorption spectrum (250–900 nm) of this antenna complex fraction is depicted in Fig. 1. It is essentially free of reaction center and is still in its native, 875 nm absorbing form (5 nm blue-shift apparently due to 0.5% LDAO). Furthermore, the ratio of A_{280}/A_{875} being approx. 0.5 is indicative of an antenna complex preparation free of reaction centre polypeptides (see also stoichiometry of B880-α/B880-β).

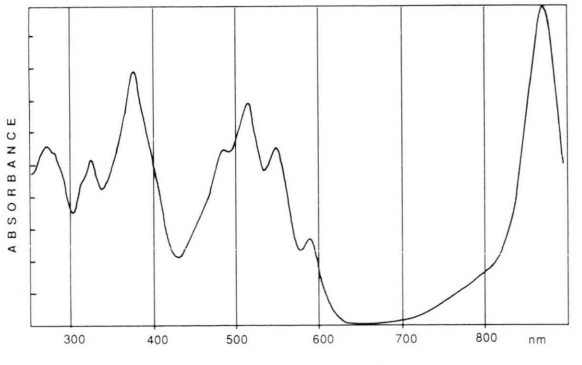

Fig. 1. Absorption spectrum (250–900 nm) of the isolated B 880 antenna pigment-protein complex from *Rhodopseudomonas marina*.

Isolation of the B880-α and B880-β antenna polypeptides

In analogy to previous structural studies on bacterial antenna polypeptides [4–7], organic solvent extraction of photosynthetic membranes has been applied to isolate the light-harvesting polypeptides B880-α and B880-β from *Rp. marina*. As shown in Fig. 2A, subsequent fractionation according to size on a Sephadex LH-60 column yielded 3 major peaks. Peak I, presumably comprised of reaction center polypeptides, represents the void volume fraction (M_r > 14 kDa). Peak II contained B880-α and B880-β in an apparent ratio of 1:1, as determined by Edman degradation. This fraction was further chromatographed on DE-32 in CH_2Cl_2/MeOH/0.1 M NH_4OAc revealing a "break-through" fraction and an additional fraction when 10% (v/v) acetic acid was added to the organic solvent mixture (Fig. 2B). The results of the Edman degradation indicated the "break-through" fraction as being composed of the α-apoprotein, slightly contaminated with the β-polypeptide (approx. 10%). The fraction eluted with 10% acetic acid (Fig. 2B, peak II) was identified as pure β-polypeptide. An alternative separation method is given by the application of reversed phase chromatography of the light-harvesting polypeptide fraction of the Sephadex LH-60 step [16]. As shown in Fig. 2C the α (peak II) and β-polypeptides (peak I) were clearly baseline separated. This procedure allowed the preparation of sufficient amounts (2–5 nmol per run) of highly pure polypeptides, well suited for amino acid sequence determination on the gas-phase sequencer as well as for accurate amino acid analyses (Table IA and IB).

Amino acid sequence determination

B880-α: The amino terminus of B880-α is blocked. For amino acid sequence determination, incubation in 2.5% HCl in methanol was necessary. Thus, the N-terminal amino acid is likely to be formylated (Fig. 3A, N-formyl-methionine), as reported earlier for the core α-antenna polypeptides from *Rs. rubrum, Rb. sphaeroides* and *Rb. capsulatus* [4, 5, 7].

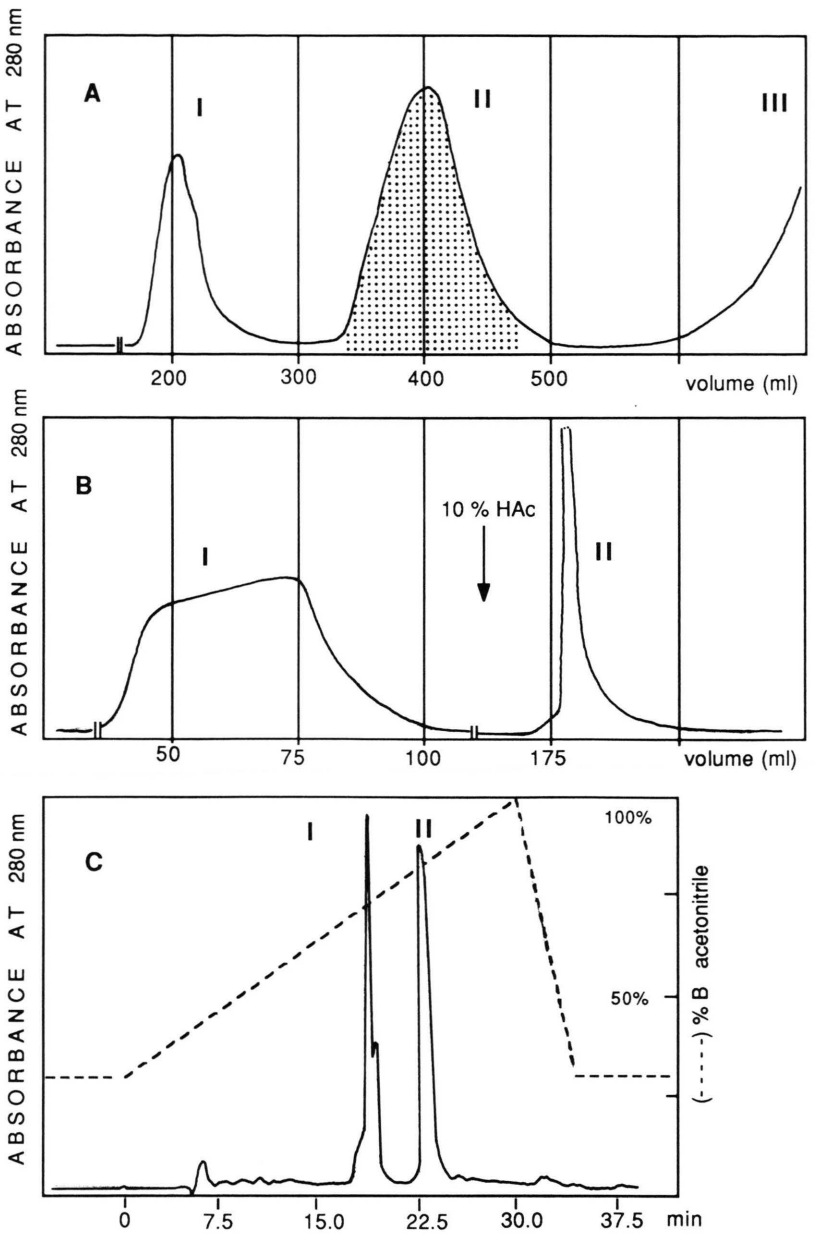

Fig. 2A. Gel-filtration of organic solvent-extracted (freeze-dried) photosynthetic membranes from *Rp. marina* on a Sephadex LH-60 column (2.5 × 130 cm), equilibrated in CH_2Cl_2/MeOH/0.1 M NH_4OAc. Peak I: void volume; presumably reaction-center polypeptides M and L. Peak II: antenna polypeptides B880-α and B880-β in an apparent ratio of 1:1 (see text). Peak III: phospholipids and pigments.

Fig. 2B. Ion-exchange chromatography of peak II (Fig. 1A, pointed area) on a Whatman DE-32 column (1 × 10 cm) equilibrated in CH_2Cl_2/MeOH/0.1 M NH_4OAc. Peak I: mainly B880-α (approx. 10% of B880-β). Peak II: B880-β (start of 10% acetic acid elution is indicated by an arrow).

Fig. 2C. Reversed-phase chromatography of peak II (Fig. 2A, pointed area) on a Pro RPC HR (C-8; 15 µm, 1 × 10 cm) column (Pharmacia). Sample preparation as described in [16]. Flow rate was 1.3 ml/min. Solvent A: H_2O, 0.1% Trifluoroacetic acid (TFA). Solvent B: $CNCH_3$, 0.1% TFA. Peak I: B880-β. Peak II: B880-α.

Table I A: Amino acid composition of the B880-α antenna polypeptide from *Rp. marina*. The results are expressed as mol residues per mol polypeptide on the basis of 3 mol Arg per mol polypeptide (bold).
A 24 h; **B** 72 h; **C** 120 h hydrolysis time; **D** integer; **E** according to sequence analysis.

Amino acid	**A**	**B**	**C**	**D**	**E**
Asp	2.45	2.43	2.67	3	2
Asn	–	–	–	–	1
Thr	4.41	4.18	4.07	5*	5
Ser	2.01	1.43	1.26	2*	2
Glu	2.12	2.13	2.13	2	0
Gln	–	–	–	–	2
Pro	2.92	3.25	3.29	3	3
Gly	1.06	0.99	1.03	1	1
Ala	4.16	4.56	4.77	5**	5
Cys	0	0	0	0	0
Val	2.28	2.81	2.88	3**	3
Met	2.25	1.84	1.82	2	2
Ile	1.19	1.63	1.62	2**	2
Leu	7.45	9.39	9.83	10**	10
Tyr	0	0	0	0	0
Phe	4.43	5.61	6.19	6**	6
Lys	1.01	1.01	1.09	1	1
His	0.51	0.91	0.95	1	1
Arg	**3**	**3**	**3**	**3**	**3**
Trp	–	–	–	nd	3
Total					**52**

* According to 24 h; ** according to 120 h; nd = not determined.

Table I B: Amino acid composition of the B880-β antenna polypeptide from *Rp. marina*. The results are expressed as mol residues per mol polypeptide on the basis of 3 mol Arg per mol polypeptide (bold).
A 24 h; **B** 72 h; **C** 120 h hydrolysis time; **D** integer; **E** according to sequence analysis.

Amino acid	**A**	**B**	**C**	**D**	**E**
Asp	1.08	1.09	1.11	1	1
Asn	–	–	–	–	0
Thr	1.72	1.63	1.52	2*	2
Ser	2.52	2.28	2.01	3*	3
Glu	5.01	5.03	5.08	5	5
Gln	–	–	–	–	0
Pro	3.18	3.85	4.23	4	4
Gly	4.62	4.78	4.72	5	5
Ala	5.49	6.65	6.61	7	7
Cys	0	0	0	0	0
Val	3.57	4.56	4.67	5**	5
Met	2.94	2.62	2.65	3	3
Ile	3.72	4.64	4.67	5**	5
Leu	2.91	2.91	2.65	3**	3
Tyr	0.95	0.93	0.94	1	1
Phe	3.05	3.82	4.08	4**	4
Lys	0.13	0.12	0.19	0	0
His	1.67	1.91	1.93	2	2
Arg	**3**	**3**	**3**	**3**	**3**
Trp	–	–	–	nd	3
Total					**56**

* According to 24 h; ** according to 120 h; nd = not determined.

From a long sequencer run structural information was obtained up to position 52 with the PTH-derivatives of Thr_{51} and Ser_{52} appearing only as small, but significant peaks on the HPLC chromatograms. As shown in Table I A the numbers of the individual amino acids obtained by the amino acid analyses agreed with the ones determined by the Edman degradation (Trp amount determined only by sequence analyses). By using carboxypeptidase digestion the C-terminal end was confirmed to be Thr_{51}–Ser_{52} (Fig. 3 A). Characteristic features of the amino acid composition of B880-α are i) lack of cysteine and tyrosine, ii) 10 leucine residues and iii) a large number of aromatic amino acids: 3 Trp and 6 Phe out of 52 residues.

B880-β: Automated Edman degradation allowed the unequivocal identification of 55 amino acids (Fig. 3 B). Based on the sequence results, the amino

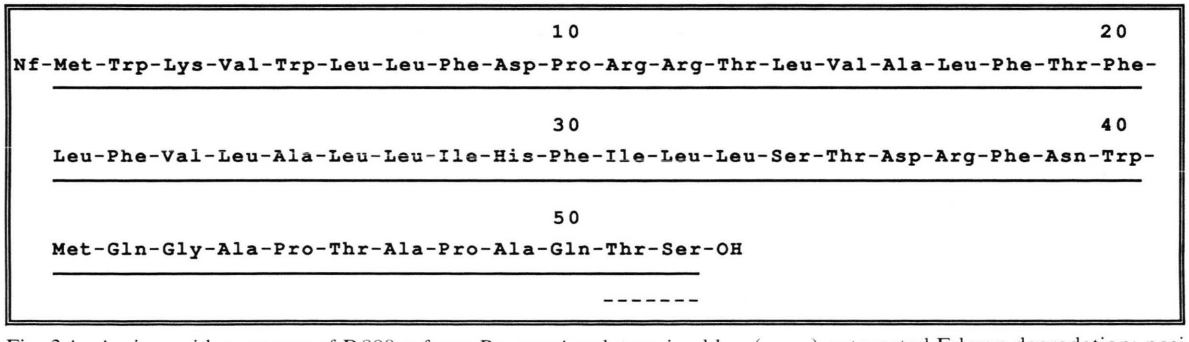

Fig. 3 A. Amino acid sequence of B880-α from *Rp. marina* determined by: (____) automated Edman degradation: position 1 to position 52; (-------) amino acids released by CP A and B: positions 51 and 52.

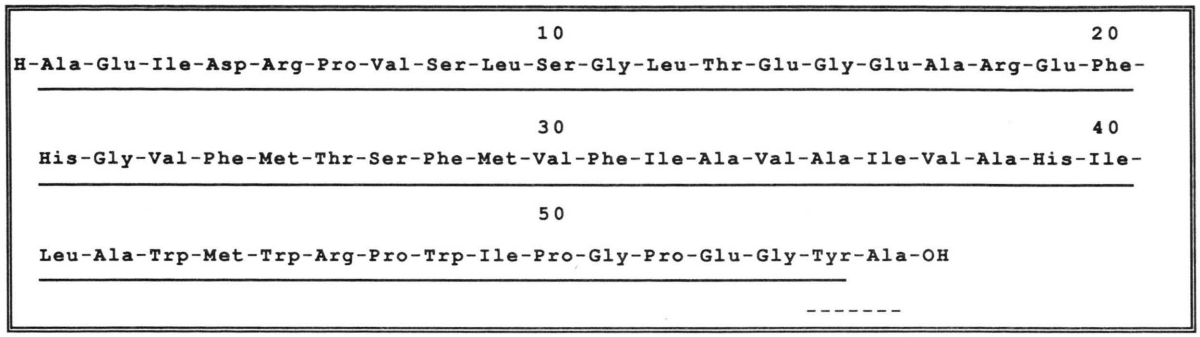

Fig. 3B. Amino acid sequence of B880-β from *Rp. marina* determined by: (____) automated Edman degradation: position 1 to position 55; (-------) amino acids released by CP A and B: positions 55 and 56.

acid composition (Table 1B) and the carboxypeptidase digestion experiments (Fig. 3B), B880-β was shown to consist of 56 amino acid residues. In contrast to the β-core antenna polypeptide from *Rb. sphaeroides* and *Rb. capsulatus*, B880-β of *Rp. marina* exhibits an extended C-terminal domain with Pro–Gly–Pro–Glu–Gly–Tyr–Ala_{56}–COOH like those of *Rs. rubrum* and *Rp. viridis* as shown in Fig. 4B. A possible structural and functional role of this specific domain will be discussed below. The characteristic compositional features of B880-β of *Rp. marina* are i) devoid of Asn, Gln, Lys and Cys, ii) 6 negatively charged amino acids (1 Asp and 5 Glu), iii) an additional His residue (β-polypeptide specific [1, 2]) and iiii) a large number of aromatic amino acids (3 Trp, 1 Tyr and 4 Phe out of 56 residues).

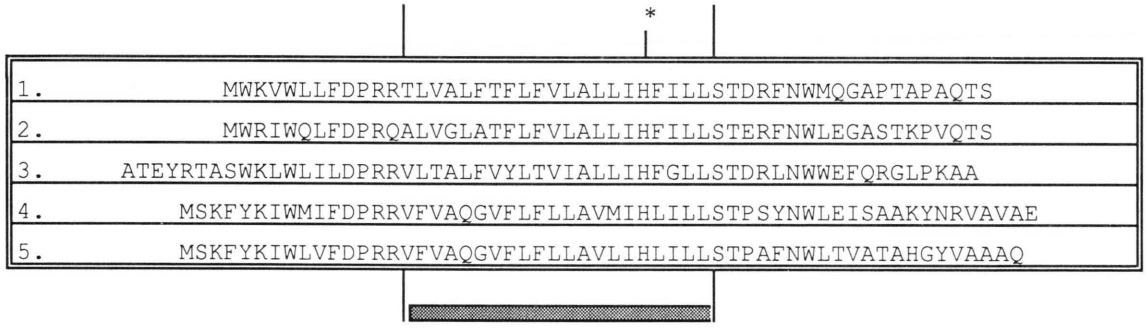

Fig. 4A. Amino acid sequence comparison of the α-polypeptides of the core antenna complexes from: 1. *Rp. marina* 2. *Rs. rubrum* 3. *Rp. viridis* 4. *Rb. sphaeroides* 5. *Rb. capsulatus*. * Transmembrane located histidine. | = Border between hydrophobic stretch ▬ and N/C-terminal polar domains.

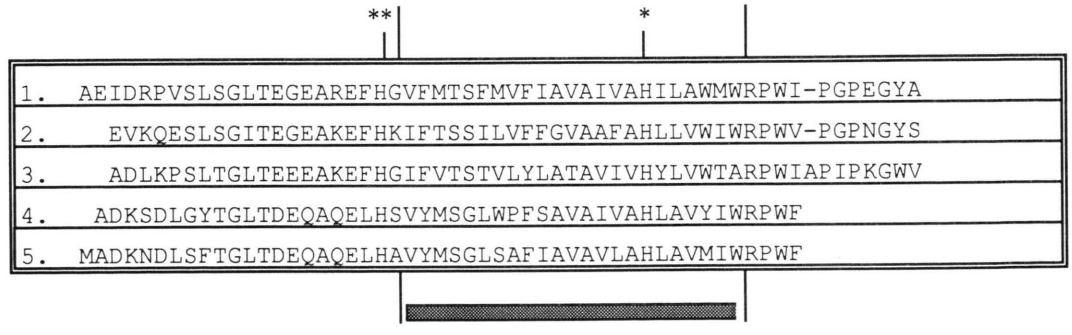

Fig. 4B. Amino acid sequence comparison of the β-polypeptides of the core antenna complexes from: 1. *Rp. marina* 2. *Rs. rubrum* 3. *Rp. viridis* 4. *Rb. sphaeroides* 5. *Rb. capsulatus*. * Transmembrane located histidine; ** β-specific histidine, located in the N-terminal part. | = Border between hydrophobic stretch ▬ and N/C-terminal polar domains. – = Amino acid deletion.

Stoichiometry of B880-α and B880-β

The elution profile of the reversed phase chromatographed antenna polypeptides B880-α and B880-β of *Rp. marina* (Fig. 2C, recorded at 280 nm; see Table IA and B: similar amount of aromatic amino acids) suggests a 1:1 stoichiometry within the photosynthetic membrane. Sephadex LH-60 fractionation of the isolated B880 antenna (results not shown) and subsequent Edman degradation indeed revealed the PTH-derivatives Met_1 (α-polypeptide) and Ala_1 (β-polypeptide) in an apparent ratio of 1:1. Furthermore, this B880 antenna chromatographed on LH-60 was free of any reaction center polypeptides eluting in the void volume ($M_r > 14$ kDa) when organic solvent extracts of photosynthetic membranes were applied (see Fig. 2C).

Discussion

Fractionation of LDAO solubilized photosynthetic membranes on DE-52 gives evidence of only one type of antenna complex synthesized in the purple non-sulfur bacterium *Rp. marina; i.e.*, the core antenna complex with its Qy-band at around 875 to 880 nm (Fig. 1). The position of the red-most absorbing band depends largely on the LDAO concentration. Its absorption spectrum is very similar to that of *Rs. rubrum* [15], indicating that the smallest compositional unit of the B880 antenna of *Rp. marina* is also comprised of two bacteriochlorophyll a molecules and one carotenoid molecule (most likely of the spirilloxanthin serie [14]). In agreement with structural studies on light-harvesting polypeptides from other strains of Rhodospirillaceae [1, 2, 5, 7], the elementary unit of the B880 antenna of *Rp. marina* consists, besides the pigments, of an α/β polypeptide heterodimer, designated as B880-α and B880-β.

Amino acid sequence analyses of B880-α (52 amino acids) and B880-β (56 amino acids) from *Rp. marina* revealed the typical three domain structure for both polypeptides, with a central hydrophobic stretch of 21 to 23 amino acids flanked by polar/charged N- and C-terminal segments wich are comprised of 11 to 22 amino acid residues (Fig. 4A and B). Accordingly, the orientation and arrangement of the antenna polypeptides of *Rp. marina* appear to be similar to the ones of *Rs. rubrum* [9, 10]: The hydrophobic stretch crosses the photosynthetic membrane once, most probably in an α-helix with 5 to 6 turns [1, 2, 7], whereas the polar N- and C-terminal domains are located at or near the membrane surface. Within the hydrophobic domain a conserved histidine (Fig. 4A and B, indicated by an asterix), which is located close to the C-terminal part, most likely serves as the bacteriochlorophyll binding site, as has been proposed earlier [1, 2, 5, 7]. The β-specific histidine residue [1, 2], located at the border line of the N-terminal part and the hydrophobic stretch, is also present in B880-β of *Rp. marina* (His_{19}, Fig. 4B, indicated by double asterix). In addition, as shown in Fig. 4B, the β-core polypeptides can be classified into two subgroups: one group (*Rb. sphaeroides* and *Rb. capsulatus*) synthesizes β-polypeptides with short C-terminal ends (Arg–Pro–Trp–Phe–COOH), whereas representatives of the other group (*Rp. marina, Rs. rubrum* and *Rp. viridis*) synthesize β-polypeptides exhibiting an additional, peculiar C-terminal amino acid segment. The consensus sequence with Pro–X–Pro–Gly–X–Tyr(Trp)–X–COOH points to an extreme turn constellation (according to the rules of common secondary structure predictions) with an aromatic amino acid as second last position. In connection with variable intensities or near-infrared circular dichroism signals of the core antenna from different species of Rhodospirillaceae [13], this particular C-terminal end together with a Phe residue next to the conserved His in the α-polypeptide (Fig. 4A) have been proposed as the basis for the strong NIR-CD signals of the core antenna of *Rs. rubrum, Rp. viridis* and *Rp. acidophila* [11, 12]. Thus, it seems likely that the core antenna of *Rp. marina* is a representative of the antenna group with strong NIR-CD signals, as well.

The sequence homologies between the α- (respectively β-)core antenna polypeptides from the species *Rp. marina, Rs. rubrum, Rp. viridis, Rb. capsulatus* and *Rb. sphaeroides* are compiled in Table II. It is seen that the antenna polypeptides of *Rp. marina* exhibit a pronounced structural relatedness to those of *Rs. rubrum* and *Rp. viridis*, with 75 and 56% homology for the α-polypeptides and 57 and 51% homology for the β-polypeptides. In the α-polypeptides identical amino acid positions are located mainly in the vicinity of the conserved histidine (Fig. 4A), whereas the C-terminal part is rather variable (*e.g.* the primary structures of the α-polypeptides from *Rp. marina* and *Rs. rubrum* are identical between position 19 and 35). In contrast, a higher structural variation is observed in the vicinity of the conserved

Table II: Amino acid sequence homologies (in %) between the core antenna polypeptides α and β of *Rp. marina*, *Rs. rubrum*, *Rp. viridis*, *Rb. capsulatus* and *Rb. sphaeroides*.

	α-Polypeptides				
	Rp. marina	*Rs. rubrum*	*Rp. viridis*	*Rb. capsulatus*	*Rb. sphaeroides*
Rp. marina		75	56	52	44
Rs. rubrum	57		44	48	42
Rp. viridis	51	40		37	39
Rb. capsulatus	41	36	32		78
Rb. sphaeroides	42	34	28	76	
	β-Polypeptides				

histidine of the β-polypeptides. However, amino acids at the border line between the hydrophobic stretch and the C-terminal domain, as well as the extended C-terminal ends of the β-antenna polypeptides of *Rp. marina*, *Rs. rubrum*, and *Rp. viridis* are highly conserved (Fig. 4B). They are comprised of the β-specific aromatic amino acid clusters (*e.g.* ...–Trp_{45}–Arg_{46}–Pro_{47}–Trp_{48}–... in B880-β of *Rp. marina*) which have been proposed to form part of the binding pocket of the dimeric bacteriochlorophyll a molecules absorbing at about 880 nm [1, 5, 11, 12].

Acknowledgements

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