MINIREVIEW

Salinibacter: an extremely halophilic bacterium with archaeal properties

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Abstract

The existence of large number of a member of the Bacteroidetes in NaCl-saturated brines in saltern crystallizer ponds was first documented in 1999 based on fluorescence in situ hybridization studies. Isolation of the organism and its description as Salinibacter ruber followed soon. It is a rod-shaped, red-orange pigmented, extreme halophile that grows optimally at 20–30% salt. The genus is distributed worldwide in hypersaline environments. Today, the genus Salinibacter includes three species, and a somewhat less halophilic relative, Salisaeta longa, has also been documented. Although belonging to the Bacteria, Salinibacter shares many features with the Archaea of the family Halobacteriaceae that live in the same habitat. Both groups use KCl for osmotic adjustment of their cytoplasm, both mainly possess salt-requiring enzymes with a large excess of acidic amino acids, and both contain different retinal pigments: light-driven proton pumps, chloride pumps, and light sensors. Salinibacter produces an unusual carotenoid, salinixanthin that forms a light antenna and transfers energy to the retinal group of xanthorhodopsin, a light-driven proton pump. Other unusual features of Salinibacter and Salisaeta include the presence of novel sulfonolipids (halocapnine derivatives). Salinibacter has become an excellent model for metagenomic, biogeographic, ecological, and evolutionary studies.

Introduction

Salt-saturated brines in hypersaline lakes and other hypersaline environments such as saltern crystallizer ponds are characteristically inhabited by dense communities of red halophilic Archaea (family Halobacteriaceae) (Oren, 2013). The unicellular green alga Dunaliella is an integral part of such ecosystems, but the role of the Bacteria at the highest salt concentrations was generally considered negligible.

However, fluorescence in situ hybridization (FISH) analysis of the prokaryotes inhabiting crystallizer ponds in Spain showed an abundance of curved rod-shaped Bacteria besides the flat square archaeon Haloquadratum walsbyi, which dominates this ecosystem (Antón et al., 1999). Sequencing of bacterial 16S rRNA gene recovered showed that the organism, first named ‘Candidatus Salinibacter’, is phylogenetically affiliated with the Bacteroidetes (Antón et al., 2000). While it took nearly a quarter of century from the time Haloquadratum was first recognized to its cultivation (Bolhuis et al., 2004; Burns et al., 2004), isolation of Salinibacter was soon achieved (Antón et al., 2002).

Salinibacter turned out to be a highly unusual organism. Phylogenetically it belongs to the Bacteria, but it shares many properties with halophilic Archaea such as Halo bacterium and Haloquadratum, being very different from all.

Selected aspects of the biology of Salinibacter were earlier reviewed (Oren, 2004; Antón et al., 2005, 2008; Balashov & Lanyi, 2007; Lanyi & Balashov, 2011). This review summarizes all aspects of its biology, comparing its features with those of the halophilic Archaea with which it shares its habitat.

The discovery of Salinibacter and related halophilic Bacteroidetes

After FISH studies showed that rod-shaped Bacteria may constitute 5–25% of the prokaryotes in saltern crystallizer
ponds (Antón et al., 1999), attempts to isolate the organism started immediately. Bacterial 16S rRNA gene sequences recovered were predominantly affiliated with the phylum Bacteroidetes, family Rhodothermaceae. Two groups of sequences were retrieved, designated EHB-1 (numerically dominant) and EHB-2. The closest cultured relative at the time was Rhodothermus, a thermophile from submarine hot springs. To assess the growth demands of the organism, brine samples were enriched in hypersaline media with 0.1% yeast extract, and the density of rod-shaped Bacteria was monitored by FISH. Optimal development occurred at 37 °C and 20–25% salt and up to NaCl saturation (Antón et al., 2000).

Isolation of Salinibacter ruber soon followed. Two approaches independently led to the recovery of similar isolates: (1) hybridization of red colonies with 16S rRNA gene probes directed against the EHB phylotype; and (2) polar lipid analysis by thin-layer chromatography, showing that some red-orange colonies contained not Archaea but Bacteria. The isolates were subjected to a taxonomic description (Antón et al., 2002, 2010; Oren, 2006). Procedures were designed to selectively enrich and isolate Salinibacter and relatives from hypersaline brines, based on the use of antibiotics (anisomycin, bacitracin) that inhibit Halobacteriaceae but do not affect Salinibacter (Elevi Bardavid et al., 2007).

Two additional Salinibacter species were recently described: S. iranicus and S. luteus from Aran-Bidgol salt lake, Iran. In their salt requirement and tolerance, they resemble S. ruber (Makhdoumi-Kahki et al., 2012). Another related red-orange halophile is Salisaeta longa. It was obtained from a mesocosm containing a mixture of Dead Sea and Red Sea water. Its cells are extremely long (15–30 μm), and it is markedly less halophilic than Salinibacter: it grows between 5% and 20% salt with optimal growth at 10% NaCl + 5% MgCl₂·6H₂O. Further properties such as fatty acid content, DNA G+C percentage and pigmentation are similar to those of Salinibacter (Vaisman & Oren, 2009).

Metabolism

Salinibacter ruber is a motile, Gram-negative aerobic heterotroph that grows in hypersaline media with a low concentration (1 g L⁻¹) of yeast extract (Fig. 1). Studies using microautoradiography combined with FISH in Mallorca saltern crystallizer brine surprisingly did not show incorporation of amino acids or glycerol (Rosselló-Mora et al., 2003), substrates used in pure culture. Glucose and some other sugars stimulate growth. Glucose consumption starts after other substrates are depleted. Activities of a constitutive, salt-inhibited hexokinase and a constitutive, salt-dependent NADP-linked glucose-6-phosphate dehydrogenase were found, but fructose-1, 6-bisphosphate aldolase activity was not detected. Glucose degradation by the Entner–Doudoroff pathway was therefore suggested, but no activity of 2-keto-3-deoxy-6-phosphogluconate aldolase was found (Oren & Mana, 2003). Genomic analysis later showed genes for a complete Embden–Meyerhof glycolytic pathway (Mongodin et al., 2005).

Salinibacter ruber cultures take up glycerol. Part is respired, and part is incorporated into cell material, but up to 20% is converted to another compound and excreted: dihydroxyacetone, formed by incomplete glycerol oxidation (Sher et al., 2004; Elevi Bardavid & Oren, 2008a). Dihydroxyacetone can be further metabolized by Haloquadratum. Degradation of glycerol, produced as an osmotic solute by Dunaliella, may thus involve dihydroxyacetone as an intermediate (Elevi Bardavid et al., 2008).

Intracellular ionic concentrations

Aerobic halophilic Bacteria characteristically use organic ‘compatible’ solutes to provide osmotic pressure of their cytoplasm. Therefore, it came as a surprise that S. ruber maintains high intracellular potassium concentrations, the ratio K⁺/protein being similar to that of the Halobacteriaceae. X-ray microanalysis in the electron microscope confirmed the presence of high intracellular K⁺ and Cl⁻ concentrations (Oren et al., 2002). A search for organic osmotic solutes, using ³¹C-NMR and HPLC, showed very low concentrations of glutamate, glycine...
betaine, and N\textsubscript{2}-acetyllysine, contributing little to osmotic balance. *Salinibacter* thus uses a similar mode of haloadaptation to that of the aerobic halophilic Archaea (Oren et al., 2002) and *Halorhodospira halophila* (Deole et al., 2013). In accordance with the high intracellular KCl concentrations, hydrolysates of the *S. ruber* bulk protein showed a high content of acidic amino acids (Asp/Asn, Glu/Gln) and low abundance of basic and hydrophobic amino acids (Oren & Mana, 2002). Analysis of the *S. ruber* genome confirmed the presence of an acidic proteome with a median pI of 5.2 for the predicted proteins, slightly higher than the value of 4.6 for *Halobacterium salinarum* and *Haloarcula marismortui* (Mongodin et al., 2005).

The behavior of individual enzymes toward salt varies considerably (Oren & Mana, 2002). NAD-dependent isocitrate dehydrogenase functions optimally at 0.5–2 M KCl, with rates of 60% of the optimum at 3.3 M. NADP-dependent isocitrate activity increases with increasing KCl concentration. However, NAD-dependent malate dehydrogenase is most active in the absence of salt, but 25% of the optimal activity was measured in 3–3.5 M KCl or NaCl, observations confirmed in an in-depth study of this nonhalophilic enzyme (Madern & Zaccai, 2004). The salt relationships of the NAD-dependent glutamate dehydrogenase activity are complex (Oren & Mana, 2002), explained by the presence of two enzymes: GDH depends on high salt for stability but not for activity, displaying maximal activity in the absence of salts; GDHII requires high salt concentrations for both activity and stability (Bonete et al., 2003).

### Genomics and metagenomics

*Salinibacter ruber* M31\textsuperscript{T} possesses a 3.5-Mbp chromosome (66.3 mol% G+C) and a 35-kbp plasmid (57.9 mol% G+C). Genes annotated include all activities of the glycolysis pathway, a complete tricarboxylic acid cycle, two putative cellulases, chitinase, amylase, pectinase, proteases, and lipases. There is a ‘hypersalinity island’ – a cluster containing different K\textsuperscript{+} uptake/efflux systems and cationic amino acid transporters important for a halophilic lifestyle. Four retinal proteins are encoded: a proton pump (xanthorhodopsin), a putative halorhodopsin-like chloride pump, and two sensory rhodopsins (Mongodin et al., 2005).

*Salinibacter ruber* strains from different locations worldwide are markedly similar. A collection of 17 strains from Mallorca, Alicante, the Ebro Delta, Canary Islands, and Peru was subjected to a phenotypic characterization, including analysis of polar lipids, fatty acids, quinones, substrate utilization, DNA G+C content, and the sequence of the spacer separating the 16S and 23S rRNA genes. Differences were slight, but populations from different sites could be discriminated by genomic fingerprints (Peña et al., 2005). Genomic and metabolomic analyses of two strains, M8 and M31\textsuperscript{T}, isolated from the same Mediterranean saltern at the same time, showed a mosaic structure with conserved and hypervariable regions (HVRs). The HVRs or genomic islands are enriched in transposases and genes related to surface properties. Overall, 10% of the genes present in M8 are absent from M31\textsuperscript{T} and could be recent acquisitions. At least 40 genes are candidates of interdomain lateral gene transfer (closest relatives for most: *Halobacterium*, *Haloarcula*, *Natronomonas*). Most are located outside the HVRs in the M8 genome. Metabolomic analyses, phage susceptibility, and competition experiments indicate that avoidance of competition by microniche adaptation and response to viral predation may be major forces that drive *Salinibacter* microevolution (Peña et al., 2010, 2011). No genetic system is yet available for *Salinibacter* to test whether genes from haloarchaea could be functional in *Salinibacter*.

To assess genetic diversity of *Salinibacter* in natural populations, the genomic sequence of strain M31\textsuperscript{T} was compared to metagenomic fragments recovered from the San Diego, CA, saltern crystallizers. Presence of highly variable ‘metagenomic islands’ varies greatly among the different lineages in the population. Three DNA regions of the type strain were scarcely represented in the metagencode. The metagenomic islands show an atypically low GC content, low coding density, and many pseudogenes and short hypothetical proteins. Many of the genes in these metagenomic islands code for enzymes involved in biosynthesis of cell wall polysaccharide components or DNA-related enzymes (Pašić et al., 2009).

### Lipids

Two early isolates of *S. ruber* were recognized as Bacteria based on polar lipid thin-layer chromatography. *Salinibacter* and *Salisaeta* both possess lipids typical for the Bacteria, including phosphatidylserine, *N,N*-dimethylphosphatidylethanolamine, bisphosphatidylglycerol (cardiolipin), and a glycolipid. The major acyl chains are iso-C15:0, C16:1 \(\Delta 9\)cis, and C18:1 \(\Delta 9\)cis (Lattanzio et al., 2009; Antón et al., 2010; Baronio et al., 2010). Cardiolipin represents ~20% of the polar lipids. This may be an adaptation to high salinity, to support and optimize the functioning of the membranal bioenergetic systems (Lattanzio et al., 2009). Presence of phosphatidylcholine and phosphatidylglycerol was not confirmed in all studies (Peña et al., 2005).

*Salinibacter* and *Salisaeta* both contain unusual sulfonolipids, named acylhalocapnines (Fig. 2). ESI-MS
(electrospray ionization mass spectrometry-negative ion) analyses of the lipid extract show a peak at m/z 660.6. The compound was purified and its structure elucidated. Sulfonolipid SL1 represents about 10% of the *Salinibacter* lipids (Corcelli et al., 2004). It is a structural variant of the sulfonolipids earlier identified in *Cytophaga* and relatives. A variant with an additional hydroxyl group (SL2, Fig. 2) is present in *Salisaeta* (Baronio et al., 2010). The name halocapnine was proposed for the sulfonate sphingoid base of these lipids.

The peak at m/z 660.6 can be used as a chemotaxonomic marker to detect *Salinibacter* and relatives in hypersaline environments. It is present in the ESI-MS profile and in MALDI-TOF/MS of lipid extracts from the biomass of crystallizer ponds in Italy, together with peaks belonging to archaeal phospholipids, sulfolipids, and glycolipids (Corcelli et al., 2004; Lopalco et al., 2011).

**Pigments and their functions**

*Salinibacter* is pigmented orange-red. A number of pigmented molecules were identified: salinixanthin – a novel carotenoid (Fig. 2), xanthorhodopsin – a retinal-proton pump that interacts with salinixanthin, and sensory rhodopsin(s).

Salinixanthin, the principal carotenoid of *S. ruber* (~96% of total carotenoids), is a C40-carotenoid acyl glycoside. It contains iso-C15:0 as esterifying fatty acid (Lutnæs et al., 2002). In organic solvents, its absorption maximum is at 478 nm with a shoulder at 506–510 nm. A procedure for the efficient extraction of salinixanthin from *Salinibacter* was described (de Lourdes Moreno et al., 2012). Salinixanthin can be used as a biomarker for the characterization of microbial communities inhabiting hypersaline environments as it can be identified and quantified by HPLC (Oren & Rodríguez-Valera, 2001). The Raman resonance frequencies of salinixanthin were documented in a study that also included archaeal bacterioruberin carotenoids (Jehlicka et al., 2013).

Following the identification of genes encoding four retinal pigments in *Salinibacter* (Mongodin et al., 2005), an in-depth study was made of xanthorhodopsin, a light-driven proton pump resembling the action of bacteriorhodopsin (Balashov et al., 2005; Balashov & Lanyi, 2007; Lanyi & Balashov, 2011). Its absorption maximum at 560 nm. The sequence of reactions includes formation of the K-, L-, M-, N-, and O-like intermediates. The xanthorhodopsin photocycle resembles that of bacteriorhodopsin more than bacteriorhodopsin, with proton uptake occurring first, and proton release at the end of the photocycle.

When the action spectrum of xanthorhodopsin proton pumping was determined by measuring light-induced pH changes in membrane vesicles or by quantification of the photoinhibition of respiration by different wavelengths, it became clear that xanthorhodopsin acts as a dual chromophore system with one retinal and one carotenoid. Salinixanthin is found in close proximity to the retinal, acting as an antenna pigment to collect light for proton pumping by xanthorhodopsin. The antenna carotenoid extends the wavelength range of light collection for transmembrane proton transport (Balashov et al., 2005, 2006; Boichenko et al., 2006; Balashov & Lanyi, 2007; Slouf et al., 2011). Light energy absorbed by the carotenoid is transferred to the retinal with a quantum efficiency of ~40–45% (Polivka et al., 2009). In the *Halobacteriaceae*, the bacterioruberin carotenoids do not act as antenna pigments to transfer light energy to bacteriorhodopsin; their function is restricted to photo-protection or a possible structural role. The carotenoid can be removed from the xanthorhodopsin complex by ammonium persulfate oxidation, leaving a functional xanthorhodopsin with a slightly slower photocycle. Salinixanthin addition enables reconstitution of the native complex (Imasheva et al., 2011). Interactions between the retinal of xanthorhodopsin and salinixanthin were characterized using circular dichroism spectroscopy of artificial pigments derived from synthetic retinal analogues with different absorption maxima (Smolensky & Sheves, 2009). The structure of the xanthorhodopsin–salinixanthin complex was determined by X-ray diffraction to 1.9 Å resolution. The close approach of the two polyenes at their ring ends explains the high efficiency of the excited-state energy transfer, the chromophore location being a compromise between optimal capture of light of all polarization angles and excited-state energy transfer (Luecke et al., 2008). The xanthorhodopsin–salinixanthin complex is the simplest known biological excited-state donor-acceptor system for collecting light (Balashov et al., 2008; Luecke et al., 2008).

Sensory rhodopsin I of *Salinibacter* (SrSRI) was studied as the first eubacterial SRI known as a functional protein. The protein has an all-trans retinal and shows a slow photocycle. It is a dual photoreceptor that regulates both negative and positive phototaxis. In contrast to *Halobacterium salinarum* SRI, the protein is stable in the absence of salt. Chloride binding shifts the absorption maximum from 542 to 556 nm (Kitajima-Ihara et al., 2008; Suzuki et al., 2008, 2009; Inoue et al., 2011; Sudo et al., 2011). Anion binding is important for color tuning and for controlling the photocycle kinetics (Reissig et al., 2012). SrSRI together with its transducer protein SrtHrI was cloned and expressed in *Escherichia coli* as a fusion construct (Sudo et al., 2009).

A gene for photoactive yellow protein (PYP), a blue light photoreceptor, was found in the *S. ruber* genome.
To determine whether it encodes a functional protein, it was cloned in *E. coli* along with the genes for chromophore biosynthesis from *Rhodobacter capsulatus*. SrPYP has an absorption maximum at 431 nm (compare 446 nm for the prototypical *H. halophila* PYP). SrPYP is a halophilic protein that requires KCl to stabilize its tertiary structure (Memmi et al., 2008).

**Biogeography**

*Salinibacter* is found worldwide. Isolates and/or related 16S rRNA gene sequences were found in salterns around the Mediterranean Sea (Antón et al., 2002; Benlloch et al., 2002; Øvreás et al., 2003; Baati et al., 2008) and near the Red Sea (Sørensen et al., 2005; E elevi Bardavid et al., 2007), a salt lake in Turkey (Mutlu et al., 2008), hypersaline coastal lagoons in Brazil and in Mexico (Spear et al., 2003; Clementino et al., 2008; Sabet et al., 2009), salterns in India (Manikandan et al., 2009), inland hypersaline sites and salterns in the USA (E elevi Bardavid et al., 2007; Pasić et al., 2009), Lake Tebenquiche in the Salar de Atacama, Chile (Demergasso et al., 2008), and salterns in the Peruvian Andes (Maturrano et al., 2006). This list is not exhaustive; for more information, see Antón et al. (2005, 2008). Except by cultivation and 16S rRNA gene-based techniques such as clone libraries, FISH, and metagenomics, *Salinibacter* and relatives can also be detected using specific chemotaxonomic markers: the carotenoid salini-xanthin (Oren & Rodríguez-Valera, 2001) and the unique sulfonolipid (Corcelli et al., 2004; Lopalco et al., 2011).

To selectively grow *Salinibacter* in liquid cultures and on agar plates, anisomycin and bacitracin can be used to inhibit the growth of *Halobacteriaceae* (Elevi Bardavid et al., 2007).

In the early 1990s, attempts were made to differentiate between archaeal and bacterial heterotrophic activities in saltern ponds using antibiotics; at the highest salinities, amino acid incorporation activity was abolished by anisomycin, while little inhibition was found by chloramphenicol (Oren, 1990). At the time, *Salinibacter* was yet unknown and *Haloquadratum* had not yet been brought into culture. A re-evaluation of the data was therefore necessary based on the behavior of cultures of these organisms toward different inhibitors. Amino acids uptake per cell was two orders of magnitude lower in *Salinibacter* than in *Haloquadratum* under the same

**Fig. 2.** The structures of salinixanthin – the C₄₀-carotenoid acyl glycoside pigment of *Salinibacter* (Lutnæs et al., 2002) and of the unusual membrane sulfonolipids SL1 (*Salinibacter, Salisaeta*) and SL2 (*Salisaeta*) (Corcelli et al., 2004; Baronio et al., 2010).
conditions. Erythromycin (inhibiting protein synthesis in Bacteria) and taurocholate (causing lysis of halophilic Archaea) proved most valuable to differentiate between archaeal and bacterial activities in saltern brines (Elevi Bardavid & Oren, 2008b). The contribution of Salinibacter to the heterotrophic activity in its environment and the ways it may compete or collaborate with the archaeal community are still largely unknown.

In a study of the response of S. ruber to environmental changes during the transition from exponential to stationary growth phase and to different forms of environmental stress (dilution; temperature decrease), changes in culturability, ribosomal content (by FISH), and metabolic changes were observed. There was an important decrease in cultivability not accompanied by a decrease in FISH counts, pointing to a transition to a viable but noncultivable state (Brito-Echeverría et al., 2011). To what extent Salinibacter may occur in its natural environment in such a state remains to be assessed.

The global distribution of Salinibacter in geographically isolated hypersaline niches provides unique opportunities for biogeographic studies. Using a metabolomic approach based on ultrahigh-resolution Fourier transform ion cyclotron resonance mass spectrometry, with 28 strains of S. ruber isolated from salterns in Mallorca, Alicante, Tarragona, Ibiza, Canary Islands (Spain), Eilat (Israel), and Peru, subtle differences could be distinguished that were correlated to the geographical distances. However, the discriminative metabolite patterns were quantitative rather than qualitative (Rosselló-Mora et al., 2008).

### Conclusions

In hindsight, it is surprising that Salinibacter was discovered only recently. The organism is easy to grow and readily forms colonies on media with > 15–20% salt and low concentrations of yeast extract, media used since long for isolation of halophilic heterotrophs. In colony shape and color, it resembles the Halobacteriaceae, and this may explain why Salinibacter was not recognized earlier.

Table 1 compares the properties of S. ruber with those of H. salinarum, one of the best studied halophilic Archaea. Halococcus, often the dominant archaeal component in ecosystems with Salinibacter, has an atypically low DNA G+C content and, being nonmotile, lacks sensory rhodopsins. Phylogenetically, Salinibacter is unrelated to the Halobacteriaceae. This appears not only from the 16S rRNA gene sequences but also from the sequences of many other genes. A phylogenetic analysis was performed for 22 genes from the S. ruber M31 genome. Although single genes supported different topologies, the topology of the concatenated data sets was found identical to that based on 16S rRNA gene analysis (Soria-Carrasco et al., 2007).

Phenotypically, Salinibacter is remarkably similar to Halobacterium. Genomic analysis suggests that this resemblance has arisen through convergence at the physiological level (different genes producing similar overall phenotype) and the molecular level (independent mutations yielding similar sequences or structures). Some genes and gene clusters may have been derived from the Halobacteriaceae by lateral transfer (Oren, 2004; Oren et al., 2004; Mongodin

### Table 1. A comparison between selected properties of Salinibacter ruber and Halobacterium salinarum

<table>
<thead>
<tr>
<th>Property</th>
<th>Salinibacter ruber</th>
<th>Halobacterium salinarum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phylogenetic affiliation</td>
<td>Bacteria – Bacteroidetes – Sphingobacteriales</td>
<td>Archaea – Euryarchaeota – Halobacteriales</td>
</tr>
<tr>
<td>NaCl range for growth and optimum (%)</td>
<td>15–30 (20–30)</td>
<td>18–30 (20–25)</td>
</tr>
<tr>
<td>G+C content of the DNA</td>
<td>66.3</td>
<td>67.9 (chromosome)</td>
</tr>
<tr>
<td>Genome size (Mbp)</td>
<td>3.5</td>
<td>65.9 (including plasmids)</td>
</tr>
<tr>
<td>Median pI of predicted proteins</td>
<td>5.2</td>
<td>2.01 (chromosome)</td>
</tr>
<tr>
<td>Osmotic solute</td>
<td>KCl</td>
<td>2.57 (including plasmids)</td>
</tr>
<tr>
<td>Salt dependence of enzymes</td>
<td>Salt-requiring or salt-tolerant</td>
<td>Mainly salt-requiring</td>
</tr>
<tr>
<td>Lipids</td>
<td>Bacterial ester lipids including bisphosphatidylglycerol, phosphatidylglycerol (?), phosphatidylserine, N,N-dimethylphosphatidylethanolamine, phosphatidylcholine (?), an unusual sulfolipid, and unidentified glycolipids and other lipids</td>
<td>Phytanyl ether derivatives of phosphatidylglycerol, phosphatidyl glycerophosphate methyl ester, phosphatidylglycerol sulfate, different triglycerol, and tetraglycosyl glycolipids</td>
</tr>
<tr>
<td>Carotenoids</td>
<td>Salininxanthin (a C40 carotenoid acyl glycoside)</td>
<td>C50 carotenoids: α-bacterioruberin and derivatives</td>
</tr>
<tr>
<td>Carotenoid function</td>
<td>Light harvesting antenna; radiation protection (?)</td>
<td>Radiation protection</td>
</tr>
<tr>
<td>Retinal pigments</td>
<td>Xantherebacter (light-driven proton pump)</td>
<td>Bacteriorhodopsin (light-driven proton pump)</td>
</tr>
<tr>
<td></td>
<td>A putative light-driven chloride pump</td>
<td>Halorhodopsin (light-driven chloride pump)</td>
</tr>
<tr>
<td></td>
<td>Two sensory rhodopsins</td>
<td>Two sensory rhodopsins</td>
</tr>
</tbody>
</table>

Information on Halobacterium salinarum (mainly based on strain NRC-1) was derived from Oren, 2013.
et al., 2005). The impact of these modular adaptive elements on the cell biology and ecology of *S. ruber* is substantial, affecting salt adaptation, bioenergetics, and photobiology. *Salinibacter* is thus a prokaryote with a ‘split personality’: phylogenetically, it belongs to the Bacteroidetes, but physiologically, it behaves like the extremely halophilic Archaea.

References


Salinibacter: an extremely halophilic bacterium


