**Desulfohalobium retbaense** gen. nov., sp. nov., a Halophilic Sulfate-Reducing Bacterium from Sediments of a Hypersaline Lake in Senegal

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Sulfate-reducing bacterial strain HR100 was isolated from sediments of Retba Lake, a pink hypersaline lake in Senegal. The cells were motile, nonsporulating, and rod shaped with polar flagella and incompletely oxidized a limited range of substrates to acetate and CO₂. Acetate and vitamins were required for growth and could be replaced by Biotrypcase or yeast extract. Sulfate, sulfite, thiosulfate, and elemental sulfur were used as electron acceptors and were reduced to H₂S. Growth occurred at pH values ranging from 5.5 to 8.0. The optimum temperature for growth was 37 to 40°C. NaCl and MgCl₂ were required for growth; the optimum NaCl concentration was near 10%. The guanine-plus-cytosine content of the DNA was 57.1 ± 0.2 mol%. On the basis of the morphological and physiological properties of this strain, we propose that it should be classified in a new genus, *Desulfohalobium*, which includes a single species, *Desulfohalobium retbaense*. The type strain is strain DSM 5692.

Although oxygen availability in hypersaline environments is low because of poor solubility, most studies of life in these ecosystems have been restricted to the aerobic microflora. A few strict anaerobes growing under high salt concentrations were recently described among the fermentative bacteria (22, 25, 26, 32, 42) and methylotrophic methanogens (15, 16, 29, 40, 44). Significant biological sulfate reduction has been reported to occur in various hypersaline ecosystems, such as the Dead Sea (19, 23) and the Great Salt Lake (41). However, none of the sulfate-reducing bacteria involved have been described. The existence of a salt-tolerating strain whose growth was inhibited by 17% NaCl was reported by Tripier (37). Cord-Ruwisch et al. (3) investigated pure mesophilic and moderately thermophilic cultures of sulfate reducers isolated from an oil field which grew at NaCl concentrations up to 19 and 27%, respectively. However, no further characterization of these strains has been performed.

In this paper we describe the isolation of a halophilic hydrogenotrophic sulfate-reducing bacterium from sediments of Retba Lake, a pink hypersaline lake in Senegal, West Africa. The morphological and physiological characteristics of this strain, strain HR100, are consistent with classification in a new genus of sulfate reducers. The name *Desulfohalobium retbaense* gen. nov., sp. nov. is proposed.

**MATERIALS AND METHODS**

**Origin of strain HR100.** Strain HR100 was isolated from Retba Lake surface sediments that were sampled in July 1988 at a depth of 1.50 m. The in situ temperature was about 32°C. The total salt concentration was 340 g/liter, and the pH was 7.15. Retba Lake is a hypersaline African lake (area, about 4 km²) that is located near Dakar 100 m from the Atlantic Ocean. Its level is about 4 m below sea level.

**Culture medium.** Strain HR100 was cultured on medium containing (per liter) 1.0 g of NH₄Cl, 0.3 g of K₂HPO₄, 20.0 g of MgCl₂ · 6H₂O, 2.0 g of CaCl₂, 4.0 g of KCl, 0.3 g of KH₂PO₄, 3.0 g of Na₂SO₄, 100.0 g of NaCl, 1.0 g of sodium acetate, 0.001 g of resazurin, 1 ml of a trace element solution (10), and 1 ml of a sodium selenite solution (30). The medium was boiled under a stream of O₂-free N₂ and cooled to room temperature. Portions (20 ml) of medium were distributed into 60-ml serum bottles that were stoppered with butyl rubber stoppers by using the Hungate anaerobic technique (9). The serum bottles were outgassed with 80% N₂–20% CO₂ and sterilized for 40 min at 110°C. After autoclaving, 0.2 ml of 2% Na₂S · 9H₂O and 1 ml of 10% NaHCO₃ (sterile, anaerobic solutions), as well as 0.2 ml of a vitamin solution (30) and 0.1 ml of a 0.2% sodium dithionite solution (filter-sterilized solutions), were injected into the bottles before inoculation. In the case of roll tubes, 2% agar (Difco Laboratories, Detroit, Mich.) was added to the medium; otherwise, 5-ml portions of medium were distributed into Hungate tubes as described above. A gas mixture containing 80% H₂ and 20% CO₂ was added at a pressure of 200 kPa after the medium was sterilized.

**Isolation.** Pure cultures were obtained by repeated application of the agar shake dilution method in anaerobic Hungate tubes as described previously (21). Purity was tested on a complex sulfate-free medium containing 0.1% Biotrypcase (Biomérieux, Craponne, France), 0.1% yeast extract (Difco), and 20 mM glucose, as well as on a complex rich NaCl-free medium.

**Analytical techniques.** Volatile fatty acids and alcohols were analyzed as described previously (4). H₂S was determined photometrically as colloidal CuS after reaction with a mixture containing 50 mM HCl and 5 mM CuSO₄ (2). Bacterial growth was quantified by measuring optical density at 580 nm.

**Cell fractionation and isolation of the sulfite reductase.** The cells (6 g) from a 10-liter culture in lactate-sulfate medium were suspended in 20 ml of 10 mM Tris hydrochloride buffer (pH 7.6), and the soluble protein extract was obtained as described previously (20). Cell extracts were examined for the presence of cytochrome and desulfoviridin by using a Philips model PU8820 recording spectrophotometer. Protein
contents were estimated by using the method of Lowry et al. (14).

The bisulfite reductase of strain HR, was purified from the soluble protein extract in four purification steps by using a previously described procedure (8) with the modifications described below. After dialysis of the soluble protein extract, which had a high salt content, the suspension (25 ml) was applied to a DEAE-cellulose (type DE 52; Whatman) column (2 by 5 cm) previously equilibrated with 20 mM Tris hydrochloride (pH 7.6). The adsorbed proteins were eluted by using a discontinuous gradient of 100 to 500 mM Tris buffer (pH 7.6). The bisulfite reductase-containing fraction was eluted with 340 mM Tris hydrochloride and was further purified by filtration on Ultrogel AcA 34 (IBF) and chromatography on hydroxyapatite (HTP Bio-Rad) and DEAE-cellulose. At this stage, the protein was judged to be pure on the basis of both polyacrylamide gel analysis results and its absorption spectrum.

Lipid analysis. Lipid extraction, fatty acid purification, and quantification by capillary gas chromatography were performed as previously described (38). Briefly, a modified Bligh-Dyer chloroform-methanol lipid extraction method was used. The total extractable lipids were fractionated by silicic column chromatography. The fatty acid esters linked to the phospholipids were methylated by mild alkaline methanolysis, and the resulting fatty acid methyl esters were purified by thin-layer chromatography before gas chromatography analysis.

The origin of the thin-layer chromatography plate was scraped. The ether lipids were eluted with CHCl₃-methanol (1/2, vol/vol) and dried under a stream of nitrogen. Glycerol ethers were then formed by acidic hydrolysis of this fraction and were extracted by using hexane and water. The presence of glycerol ether was determined by using thin-layer chromatography.

Fatty acid methyl esters were identified and the position of methyl branching and the degree of unsaturation were checked by gas chromatography-mass spectrometry. Monounsaturation positions and geometry were chemically determined by using dimethyl disulfide derivatization (7).

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added. The doubling time of the isolate cultivated on lactate-containing medium in the presence of 1 g of Biotypecase per liter, 1 g of yeast extract per liter, and 100 g of NaCl per liter was about 5 h. Strain HR100 required NaCl (Fig. 4) and MgCl2 (Fig. 5) for growth. Growth occurred in the presence of NaCl concentrations up to 24%; optimum growth occurred at an NaCl concentration near 10%. The presence of 20% NaCl in the medium greatly diminished the activity of strain HR100 (Fig. 4). The optimum pH for growth was 6.5 to 7.0. Growth was detected between pH 5.5 and 8.0. Strain HR100 grew optimally at temperatures near 40°C (37 to 40°C) (Fig. 6); 45°C was the upper temperature limit for growth. The first replication from an inoculum incubated at 37°C grew at temperatures up to 52°C; however, after several replications at the same temperature, the strain no longer grew at temperatures between 45 and 52°C.

Metabolic properties. Nutritional studies were performed at 35°C. Strain HR100 grew on H2 when we used vitamins, acetate as the carbon source, and sulfate as the electron acceptor. In the absence of sulfate, the isolate incompletely oxidized ethanol, pyruvate, and lactate to acetate and presumably CO2 (Table 1). Fumarate, malate, and succinate were not used. In the absence of sulfate, slight growth occurred on pyruvate. Elemental sulfur, sulfate, thiosulfate, and sulfite were used as electron acceptors.

Pigments. A soluble extract of strain HR100 exhibited the characteristic absorption bands of cytochrome c3, with maxima at 418.5, 522.5, and 552 nm, when it was reduced with sodium dithionite. An oxidized extract had an absorption maximum at 408.5 nm corresponding to the Soret peak. The cytochrome was not reduced by sodium ascorbate, which indicated that it had a low midpoint redox potential. The extract was also examined for the presence of desulfoviridin, the dissimilatory sulfite reductase present in most species of the genus Desulfovibrio (6). The absorption spectrum (no absorption band at 628 nm) and the results of a fluorescence test on cell suspensions (31) showed that strain HR100 was devoid of desulfoviridin; however, the spectrum had two other broad absorption bands at about 540 and 580 nm (Fig. 7).

As other types of dissimilatory sulfite reductases have been isolated from sulfate-reducing bacteria (8, 12, 36), the bisulfite reductase of this halophilic microorganism was purified in order to identify this enzyme. Disc electrophoresis of the purified protein (100 μg) revealed the presence of two closely migrating reddish brown bands which appeared to be the only proteins in the preparation after it was stained with Coomassie blue. The protein bands in the gels directly catalyzed the sulfite-dependent oxidation of reduced methyl viologen (8).

The absorption spectrum of the oxidized bisulfite reductase isolated from strain HR100 had major peaks at 544, 396, and 279 nm and a shoulder at about 580 nm. In addition, the spectrum had two weak absorption bands at around 700 and 730 nm. The ratio of A544 to A279 was 0.14. This absorption spectrum is similar in most respects to that of desulfoviridin, the dissimilatory bisulfite reductase isolated previously from Desulfovibrio baculatus (Norway strain) (12). However, the spectrum of strain HR100 bisulfite reductase differed slightly from that of the homologous protein of Desulfovibrio baculatus in that the former had an additional weak absorption band at 700 nm and a more distinguishable shoulder in the 580-nm region.

Lipid analysis. The fatty acid distribution in the membrane phospholipids is shown in Table 2. Branched saturated fatty acids accounted for 30% of the total fatty acids, with branched iso-C15:0 acid predominating. The following monounsaturated fatty acids were also present: C16:1ω9, C16:1ω7, C18:1ω9, C18:1ω7c, and C17:1ω8 fatty acids. The fatty acid profile also contained branched-chain components, such as iso-C17:1ω7c (4%) and branched C18:1ω6.

DNA base composition. The average DNA base composition of strain HR100 was 57.1 ± 0.2 mol% guanine plus cytosine.
DISCUSSION

Retba Lake is a hypersaline African lake (total salt concentration, 340 g/liter) near Dakar, Senegal. Preliminary work revealed the existence of methanogenic, cellulytic, and sulfate-reducing bacteria in its sediments (17). Biological sulfate reduction has been observed in similar ecosystems (19, 41), and a limited range of substrates have been found to be involved in this process (24, 41). Strain HR100, which was isolated from the sediment of Retba Lake, incompletely oxidizes a few substrates, including ethanol and pyruvate, to acetate and CO2. It uses lactate; in contrast, the addition of this organic compound did not enhance the sulfate-reducing activity in sediments from the Dead Sea (24), which suggests that there are sulfate-reducing bacteria with different metabolic activities in halophilic environments.

Strain HR100 is a moderately halophilic, sulfate-reducing bacterium which has to grow in the presence of salt concentrations that are greater than its optimum salt concentration in hypersaline Retba Lake, since salt concentrations greater than 18% reduce its growth. High salt concentrations have also been reported to decrease metabolic activity toward H2 and volatile fatty acids, as indicated by the significant amounts of these compounds present in sediments (11, 41). The latter results indicate that the reduction of sulfate in hypersaline ecosystems may be due to the activity of moderately halophilic strains, such as strain HR100.

Our isolate is the first hydrogenotrophic anaerobe that has been reported to grow in the presence of NaCl concentrations greater than 10%. At such NaCl concentrations, no methanogenic bacteria were isolated by using H2, and there was no evidence that H2 might be used to reduce CO2 (24). These results suggest that in hypersaline ecosystems there is probably no competition for H2 between sulfate reducers and methanogens, as described in other environments (5, 13), and that SO42- rather than CO2 is probably a high-potential electron acceptor. In the case of strain HR100, the measured growth rate shows that active H2 transfer might occur via sulfate reduction when the NaCl concentration in the medium is 10 to 18%.

No archaeobacterial isoprenyl glycerol ether lipids were detected in strain HR100, which indicates that this isolate is an eubacterium and not an archaeabacterium (39). Since saline environments might be similar to biota which occurred early in the evolution of the Earth, it will be interesting to compare this strain phylogenetically with the sulfate-reducing species described previously, particularly the newly described bacterium Archaeoglobus fulgidus (43).

The fatty acid profile contains components that are associated with sulfate-reducing bacterial species. Iso-C17:0 7c fatty acid is present in significant amounts in the genus Desulfovibrio and has been recognized as a good biomarker of these microorganisms in marine sediments (28, 35), and
C17:1ω8 fatty acid has been suggested for use as a biomarker of the genus *Desulfobulbus* (27). However, further analyses will be required in order to determine the influence of both nutritional and external parameters on the fatty acid distribution in the membrane of strain HR100.

Strain HR100 clearly belongs to the group of sulfate-reducing bacteria which incompletely oxidize organic substrates (30). It differs from *Desulfovibrio pigra* in morphology and from species of the genus *Desulfotomaculum* in its lack of spores. In contrast to *Desulfobulbus* species, strain HR100 does not oxidize propionate, and it cannot belong to the genus *Thermodesulfobacterium* because of its growth temperature range.

Recent studies of *Desulfovibrio thermophilus* and *Desulfovibrio baculatus* have shown that these two organisms belong to the genera *Thermodesulfobacterium* (34) and *Desulfomicrobium* (33), respectively, and all of the incomplete oxidizers belonging to *Desulfovibrio* species are vibriolike forms containing only desulfoviridin (6). The cells of strain HR100 are mainly straight rods and contain desulfurubidin. This halophilic strain cannot be affiliated with the genus *Thermodesulfobacterium* because of its growth temperature range.

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Chemooorganotroph; respiratory metabolism; strictly anaerobic. Incompletely oxidizes organic substrates. Sulfate and other oxidized sulfur compounds serve as electron acceptors and are reduced to H2S.

NaCl and MgCl2 are required for growth. Vitamins and acetate as a carbon source are necessary for growth on H2 and can be replaced by adding Biotryptase or yeast extract. The optimum temperature for growth is 37 to 40°C. The cells contain desulfurubidin.

**Description of Desulfohalobium gen. nov.** *Desulfohalobium* (De.sul.fo.hal.o'bi.um. L. pref. de, from; L. n. sulfur, sulfur; Gr. n. hals, the sea, salt; Gr. n. bios, life; M. L. adj. halobius, living on salt; M. L. masc. n. Desulfohalobium, a sulfate-reducing salt-requiring rod-shaped bacterium).

Rod-shaped eubacteria with cells that are 0.7 to 0.9 by 1 to 3 μm, have rounded ends, and occur singly or in pairs when H2 is the energy source. Longer cells up to 20 μm long occur in medium containing lactate. Motile by means of one or rarely two polar flagella. Spores are not formed. Gram negative.

**Description of Desulfohalobium retbaense sp. nov.** *Desulfohalobium retbaense* (ret.ba.en'se. N. L. adj. retbaense, pertaining to Retba Lake in Senegal). Straight to slightly...
FIG. 6. Effect of temperature on the growth rate of strain \( HR_{100} \) cultivated on lactate-containing medium supplemented with 100 g of NaCl per liter.

curved rods that are 0.7 to 0.9 by 1 to 3 \( \mu m \), have rounded ends, and occur singly or in pairs. When the organism is grown on \( H_2 \) as an energy source, longer cells up to 20 \( \mu m \) long occur in lactate-containing medium. Motile by means of one or rarely two polar flagella. No spore formation. Gram negative.

Strictly anaerobic chemoorganotroph. Incompletely oxidizes lactate, ethanol, and pyruvate to acetate and \( CO_2 \). Ferments pyruvate slowly. Does not use glycerol, fructose, glucose, fumarate, malate, succinate, choline, yeast extract, and Biotrypcase.

The optimum temperature for growth is 37 to 40\( ^\circ \)C. NaCl

FIG. 7. Absorption spectrum of strain \( HR_{100} \) bisulfite reductase. The spectrum of the bisulfite reductase (0.34 mg/ml) in 20 mM Tris hydrochloride buffer (pH 7.6) was recorded by using a cuvette with a 1-cm light path. The inset shows the spectrum from 480 to 800 nm in greater detail; this spectrum was obtained by using a concentrated sample of bisulfite reductase (1.89 mg/ml).

### TABLE 1. Substrates used as energy sources by strain \( HR_{100} \) in the presence and absence of sulfate

<table>
<thead>
<tr>
<th>Substrate(^a)</th>
<th>Use as an energy source</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>In the presence of ( SO_4^{2-} )</td>
</tr>
<tr>
<td>( H_2 )</td>
<td>+ (^b)</td>
</tr>
<tr>
<td>Formate</td>
<td>+</td>
</tr>
<tr>
<td>Ethanol</td>
<td>+</td>
</tr>
<tr>
<td>Pyruvate</td>
<td>+</td>
</tr>
<tr>
<td>Lactate</td>
<td>+</td>
</tr>
</tbody>
</table>

\(^a\) Most substrates were tested at concentrations of 20 mM. Casamino Acids, yeast extract, and Biotrypcase were tested at concentrations of 2 g/liter. The growth medium contained 1 g of Biotrypcase per liter and 1 g of yeast extract per liter. We tested the following compounds which did not support sulfide production: acetate, propionate, butyrate, fumarate, malate, succinate, glycerol, glucose, fructose, choline, Casamino Acids, yeast extract, and Biotrypcase. Growth was measured by determining \( H_2S \) production and absorbancy after 7 days at 35\( ^\circ \)C.

\(^b\) +, Substrate used as electron donor (turbidity increased); -, substrate not used as electron donor; (+), substrate used as electron donor but growth was slow.

### TABLE 2. Fatty acid distribution in membrane phospholipids of strain \( HR_{100} \)

<table>
<thead>
<tr>
<th>Fatty acids</th>
<th>% of total fatty acids</th>
</tr>
</thead>
<tbody>
<tr>
<td>( C_{13:0} )</td>
<td>0.11</td>
</tr>
<tr>
<td>( C_{14:0} )</td>
<td>1.68 ± 0.1</td>
</tr>
<tr>
<td>( C_{15:0} )</td>
<td>0.95</td>
</tr>
<tr>
<td>( C_{16:0} )</td>
<td>15.28 ± 2.3</td>
</tr>
<tr>
<td>( C_{17:0} )</td>
<td>3.61 ± 0.3</td>
</tr>
<tr>
<td>( C_{18:0} )</td>
<td>0.23</td>
</tr>
<tr>
<td>( C_{19:0} )</td>
<td>3.93 ± 0.4</td>
</tr>
<tr>
<td>( C_{18:1} )</td>
<td>5.34 ± 0.5</td>
</tr>
<tr>
<td>( C_{19:1} )</td>
<td>0.58</td>
</tr>
<tr>
<td>( C_{20:0} )</td>
<td>4.10 ± 0.7</td>
</tr>
<tr>
<td>( C_{21:0} )</td>
<td>13.33 ± 2.8</td>
</tr>
<tr>
<td>( C_{24:0} )</td>
<td>3.88 ± 0.1</td>
</tr>
<tr>
<td>( C_{25:0} )</td>
<td>1.90 ± 0.4</td>
</tr>
<tr>
<td>( C_{17:0} )</td>
<td>2.24 ± 1.1</td>
</tr>
<tr>
<td>( C_{18:0} )</td>
<td>8.05 ± 1.5</td>
</tr>
<tr>
<td>( C_{19:0} )</td>
<td>0.71 ± 0.6</td>
</tr>
<tr>
<td>( C_{18:1} )</td>
<td>3.33 ± 0.8</td>
</tr>
<tr>
<td>Branched-( C_{16:0} )</td>
<td>0.36</td>
</tr>
<tr>
<td>( C_{18:0} )</td>
<td>3.86 ± 1.4</td>
</tr>
<tr>
<td>( C_{18:1} )</td>
<td>6.53 ± 2.2</td>
</tr>
<tr>
<td>( C_{19:0} )</td>
<td>0.23</td>
</tr>
<tr>
<td>( C_{18:0} )</td>
<td>15.97 ± 5.2</td>
</tr>
<tr>
<td>( C_{18:1} )</td>
<td>0.43</td>
</tr>
</tbody>
</table>

Unidentified       | 3.37                   |
and MgCl₂ are required for growth. The optimum NaCl concentration is near 10%. Grows in media containing NaCl at concentrations up to 24%. The pH range for growth is 5.5 to 8.0; the optimum pH is 6.5 to 7.0.

Cells contain cytochrome c₃ and desulforubidin. The guanine-plus-cytosine content of the DNA is 57.1 ± 0.2 mol%.

Isolated from sediments of a hypersaline African lake, Retba Lake, near Dakar, Senegal.

The type strain is strain DSM 5692.

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REFERENCES


30. Pfennig, N., F. Widdel, and H. G. Trüper. 1981. The dissimila-


32. Rengpipat, S., T. A. Langworthy, and J. G. Zeikus. 1988. Halobacteroides acetocrrophicus sp. nov., a new obligately an-


biologija) 57:85-89.


