Desulfohalobium utahense sp. nov., a moderately halophilic, sulfate-reducing bacterium isolated from Great Salt Lake

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A novel moderately halophilic, sulfate-reducing bacterium, strain EtOH3^T, was isolated from anoxic hypersaline (270 g NaCl l⁻¹) sediment of the northern arm of the Great Salt Lake, Utah, USA. Cells of strain EtOH3^T were oval to rod-shaped, non-motile, non-sporulating and stained Gram-negative. The strain required sodium and magnesium ions for growth and grew at salinities of up to 240 g NaCl l⁻¹ and 121 g MgCl₂·6H₂O l⁻¹. The optimum NaCl concentration was 80–100 g l⁻¹. Strain EtOH3^T grew at temperatures ranging from 15 to 44 °C (optimum 37 °C). The pH range for growth was 6.5–8.3 (optimum around pH 6.8). Only sulfate and thiosulfate served as electron acceptors for a broad range of electron donors including various short-chain fatty acids and primary (C_{1–5}) alcohols, amino acids, H₂/acetate and H₂/yeast extract. The G + C content of the genomic DNA was 51.4 mol%. Phylogenetic analysis of *dsrAB* [genes encoding the major subunits of dissimilatory (bi)sulfite reductase] and 16S rRNA gene sequence data placed strain EtOH3^T within the deltaproteobacterial family *Desulfohalobiaceae*. Strain EtOH3^T shared 76 and 91 % *dsrAB* and 16S rRNA gene sequence similarity, respectively, with the type strain of the phylogenetically most closely related species with a validly published name, *Desulfohalobium retbaense* DSM 5692^T. High 16S rRNA gene sequence similarity (~97 %) was shared with the recently described strain '*Desulfovermiculus halophilus*' VKM B-2364. Strain EtOH3^T, however, clearly differed from this strain in both genomic G + C content and in several of its phenotypic properties. On the basis of phenotypic and genotypic characteristics, the novel species *Desulfohalobium utahense* sp. nov. is proposed, with strain EtOH3^T (= VKM B-2384^T = DSM 17720^T) as the type strain.

The northern arm of Great Salt Lake (Utah, USA) is a thalassohaline hypersaline environment with salinities of ≥ 270 g NaCl l⁻¹. Despite the extreme salinity, the sediment from this part of the lake was recently shown to harbour active populations of sulfate-reducing micro-organisms (Brandt *et al.*, 2001), although so far the identity of these sulfate reducers has remained unknown. In recent years, growing interest in micro-organisms from hypersaline environments has led to the isolation of a limited number of halophilic sulfate-reducing bacteria (SRB). However, most of these SRB are only weakly halophilic and would hardly be able to proliferate at the elevated salinities in the northern arm of the Great Salt Lake. Thus, members of only

five described SRB species are able to grow *in vitro* at salinities exceeding 200 g NaCl l⁻¹, namely *Desulfohalobium retbaense* DSM 5692^T, which grows at salinities up to 240 g l⁻¹ (Ollivier *et al.*, 1991), '*Desulfovermiculus halophilus*' VKM B-2364 (Belyakova *et al.*, 2006), growing at salinities up to 230 g l⁻¹, and three members of the genus *Desulfovibrio*, growing at salinities up to 217–225 g l⁻¹, '*Desulfovibrio cavernae*' B1T (Sass & Cypionka, 2004), *Desulfovibrio indonesiensis* strains B1M and H3M (Sass & Cypionka, 2004) and *Desulfovibrio oxycliniae* DSM 11498^T (Krekeler *et al.*, 1997).

In the course of a survey of the diversity of SRB inhabiting the sediment of the northern arm of the Great Salt Lake, several novel sulfate-reducing strains were isolated. One strain, designated EtOH3^T, was characterized further and assigned to the deltaproteobacterial genus *Desulfohalobium* as the type strain of a novel species. Strain EtOH3^T and *Desulfohalobium retbaense* represent the most halophilic SRB described to date and together constitute the only recognized members of the genus *Desulfohalobium*, which is

Abbreviation: SRB, sulfate-reducing bacteria.

The GenBank/EMBL/DDBJ accession number for the *dsrAB* and the 16S rRNA gene sequences of strain EtOH3^T are DQ386236 and DQ067421, respectively.

A transmission electron micrograph of a cell of strain EtOH3^T is available as supplementary material in IJSEM Online.

the type genus of the family *Desulfohalobiaceae* (Kuever *et al.*, 2005). In addition to these taxa, other species affiliated with this family include *Desulfonatovibrio hydrogenovorans* (Zhilina *et al.*, 1997), *Desulfothermus naphthae* (Kuever *et al.*, 2006), *Desulfonauticus submarinus* (Audiffren *et al.*, 2003) and '*Desulfovermiculus halophilus*' (Belyakova *et al.*, 2006).

Strain EtOH3^T was isolated from an anoxic hypersaline (270 g NaCl l⁻¹) sediment sample, obtained from Station 27 (Brandt *et al.*, 2001). Strain EtOH3^T was enriched, isolated and routinely cultivated in an anoxic basal medium (BM) consisting of (l⁻¹ Milli-Q water): NaCl, 100 g; MgSO₄·7H₂O, 10 g; KCl, 6·0 g; CaCl₂·2H₂O, 0·4 g; NH₄Cl, 1·0 g; KH₂PO₄, 0·1 g; yeast extract, 0·5 g; trace element solution, 1·0 ml (Widdel & Bak, 1992); 20 g l⁻¹ resazurin solution, 50 µl; selenite tungstate solution, 1·0 ml (Widdel & Bak, 1992). The medium was prepared as described by Brandt & Ingvorsen (1997). NaHCO₃ (30 mM final concentration) was used as the buffer and the pH was 7·0–7·2. Unless otherwise noted, all incubations were carried out at 30 °C in the dark using a 1 % (v/v) inoculum. Strain EtOH3^T was enriched and isolated using ethanol (10 mM) as the electron donor. The isolation was performed by repeated application of the roll-tube technique (Hungate, 1969) using BM solidified by 20 g washed agar l⁻¹. The purity of cultures was checked by phase-contrast microscopy and by performing growth tests in BM containing yeast extract (1 g l⁻¹), glucose (10 mM), fumarate (10 mM), pyruvate (10 mM), lactate (10 mM) and succinate (10 mM) at 10 or 100 g NaCl l⁻¹.

Unless stated otherwise, all growth experiments were performed in triplicate in BM dispensed into 16 × 125 mm Hungate anaerobic culture tubes (Bellco Glass) with a 3 ml gas phase (90:10 N₂:CO₂, by vol.) using lactate (10 mM) as the electron donor and sulfate as the electron acceptor (lactate subsequently proved to be a better growth substrate than ethanol). Cell growth was quantified by measuring optical density at 600 nm, by phase-contrast microscopy combined with photometric measurement of sulfide by the method of Cline (1969) or, for pH experiments only, by total counts of SYBR Gold-stained cells as described by Mogensen *et al.* (2005). The effect of temperature on growth rate was investigated simultaneously at 14 different temperatures between 10 and 45 °C using a temperature gradient block (Elsgaard *et al.*, 1994). The pH range for growth was investigated by titrating a modified BM with sterile, anoxic 1 M HCl or NaOH solution. This medium, in which NaHCO₃ was replaced by 10 g MOPS (pK_a 7·2) l⁻¹ and 11 g CAPSO (pK_a 9·6) l⁻¹, buffered effectively within a pH range of 6·0–10·0 and did not interfere with the ability of strain EtOH3^T to grow (results not shown). Growth was tested at 11 different pH values ranging from 6·2 to 9·3; the pH was monitored regularly during these incubations and adjusted if necessary. Because of the development of precipitates in the modified BM at pH values of >7·5, growth was quantified by total

counts of cells stained with SYBR Gold (see above). Strain EtOH3^T was tested for growth at 15 different concentrations of NaCl (ranging from 0 to 300 g l⁻¹) in BM with and without 0·5 g yeast extract l⁻¹. Furthermore, the effect of Mg²⁺ on growth was tested at 21 different concentrations in modified BM (100 g NaCl l⁻¹) in which MgSO₄·7H₂O was replaced by Na₂SO₄ (5·76 g l⁻¹) and 0–200 g MgCl₂·6H₂O l⁻¹. Substrate utilization was tested by substituting either lactate or sulfate with potential electron donors or electron acceptors (Table 1). Transmission electron microscopy was performed as described previously (Mogensen *et al.*, 2005). The Gram-staining reaction was determined using standard procedures.

Colonies of strain EtOH3^T (in roll-tube cultures) were brown and disc-shaped with a diameter of approximately 1 mm. The cells were oval to rod-shaped and non-motile (transmission electron microscopy did not reveal the presence of flagella; see Supplementary Fig. S1 available in IJSEM Online), often growing in pairs. Cells were 1·0–1·2 µm wide and 2·5–3·0 µm long when grown under optimal conditions (see below). Under suboptimal growth conditions (low salinity, high pH or high temperature), cells were longer (up to 15 µm) and had a tendency to form filaments. Cells stained Gram-negative and endospores were never observed. When grown on lactate in BM at 30 °C, the doubling time of strain EtOH3^T was 2·5 days. Notably, under the same conditions the doubling time increased to 4·0 days when yeast extract (0·5 g l⁻¹) was omitted from the medium. Strain EtOH3^T required NaCl and Mg²⁺ for growth. Growth occurred in the presence of NaCl concentrations up to 240 g l⁻¹ in BM containing 0·5 g yeast extract l⁻¹ and up to 200 g l⁻¹ in BM devoid of yeast extract. Thus, strain EtOH3^T and *Desulfohalobium retbaense*, which have identical upper salinity limits for growth (Ollivier *et al.*, 1991), represent the most halotolerant SRB described to date. Optimum growth occurred at 80–100 g NaCl l⁻¹ independent of the presence of yeast extract. This NaCl optimum classifies strain EtOH3^T as a moderate halophile according to Larsen (1986). The highest MgCl₂·6H₂O concentration tolerated by strain EtOH3^T was 121 g l⁻¹, with an optimum ranging from 2 to 51 g l⁻¹. Despite the high NaCl tolerance of strain EtOH3^T compared with most other known SRB, the observed upper NaCl limit for growth for this strain nevertheless indicates that it must be challenged by severe salt stress in its natural habitat, i.e. hypersaline sediment of Great Salt Lake, which contained 270 g NaCl l⁻¹. The moderately halophilic SRB *Desulfovibrio halophilus* DSM 5663^T was shown previously to profit from the uptake of compatible solutes for osmoadaptation (Welsh *et al.*, 1996). The effect of compatible solutes on the growth of strain EtOH3^T was tested by adding a mixture consisting of (final concentrations) glycine betaine (5 mM), trehalose (2·6 mM), sucrose (5 mM) and choline (5 mM) to BM containing 100 g NaCl l⁻¹ and lactate as the electron donor. The aforementioned test had shown that strain EtOH3^T was unable to utilize any of these compatible solutes as growth substrates (Table 1).

Table 1. Phenotypic and genotypic characteristics of strains affiliated to the family *Desulfohalobiaceae*

Strains: 1, strain EtOH₃^T; 2, *Desulfohalobium retbaense* DSM 5692^T (data from Ollivier *et al.*, 1991); 3, '*Desulfovermiculus halophilus*' VKM B-2364 (Belyakova *et al.*, 2006); 4, *Desulfonatovibrio hydrogenovorans* DSM 9292^T (Zhilina *et al.*, 1997); 5, *Desulfonauticus submarinus* DSM 15269^T (Audiffrin *et al.*, 2003); 6, *Desulfothermus naphthae* DSM 13418^T (Kuever *et al.*, 2006). All the strains utilize sulfate and thiosulfate as electron acceptors. The following compounds did not support growth of strain EtOH₃^T. (a) Electron donors (with sulfate as the electron acceptor): benzoate (10 mM), sucrose (10 mM), trehalose (6 mM), fructose (10 mM), rhamnose (10 mM), xylose (10 mM), arabinose (10 mM), mannose (10 mM), glucose (10 mM), galactose (5 mM), glycine betaine (10 mM), choline (10 mM), acetone (10 mM) and H₂/CO₂. (b) Fermentation: formate (10 mM), lactate (10 mM), pyruvate (10 mM), fumarate (10 mM) and ethanol (10 mM). (c) Electron acceptors (with lactate as the electron donor): fumarate (10 mM), nitrite (5 mM), nitrate (10 mM), iron(III) citrate (5 mM), iron(III) chloride (6 mM) and oxygen. NR, Not reported; (+), weak growth.

Characteristic	1*	2	3	4	5	6
Cell shape	Oval-rod-shaped	Curved rod	Curved rod	Vibrio	Curved rod	Curved rod
Cell size (µm)	1.0–1.2 × 2.5–3.0 (15†)	0.7–0.9 × 1.0–3.0	0.5–0.6 × 1.0–1.5	0.5 × 1.5–2.0	5.0–6.0 × 0.35–0.5	0.8 × 2.0
Motility	–	+	+	+	+	+
NaCl range (optimum) (g l ⁻¹)	20–240 (80–100)	>0–240 (100)	30–230 (80–100)	10–120 (30)	0–50 (20)	NR (20)
MgCl ₂ ·6H ₂ O range (optimum) (g l ⁻¹)‡	>0–121 (2–51)	>0–142 (51)	NR (3)	NR	NR	NR
pH range (optimum)	6.5–8.3 (6.8)	5.5–8.0 (6.5–7.0)	6.0–8.5 (7.2)	8.0–10.2 (9.5–9.7)	NR (7.0)	6.1–7.1 (6.5–6.8)
Temperature range (optimum) (°C)	15–44 (37)	25–43 (37–40)	25–47 (37)	15–43 (37)	30–60 (45)	50–69 (60–65)
Yeast extract requirement	–	+	–	+	NR	–
G+C content of DNA (mol%)	51.4	57.1	55.2	48.6	34.4	37
Utilization of electron donors (with sulfate)						
H ₂ /CO ₂	–	–	+	–	–	–
H ₂ /acetate	+	+	+	+	+	–
Formate	+	+	+	+	+	–
Acetate	–§	–	–	–	–	NR
Propionate	+	–	+	–	–	NR
Lactate	+	+	+	–	–	–
Pyruvate	+	+	+	–	NR	–
Butyrate	+	–	+	–	–	NR
Succinate	+	–	+	–	–	–
Malate	+	–	+	–	–	–
Fumarate	+	–	+	–	–	–
Methanol	+	NR	–	–	–	–
Ethanol	+	+	+	–	–	–
1-Propanol	+	NR	–	NR	NR	–
1-Butanol	+	NR	–	NR	NR	–
1-Pentanol	+	NR	NR	NR	NR	NR
Casamino acids	+ (15 mM)	–	NR	–	–	–
Yeast extract	+ (1.0 g l ⁻¹)	–	–	–	–	–

Table 1. cont.

Characteristic	1*	2	3	4	5	6
Fermentation of pyruvate	–	(+)	+	–	NR	NR
Utilization of electron acceptors						
Sulfite	–	+	+	+	+	NR
Sulfur	–	+	+	–	+	NR
Complete oxidation of organic compounds	NR	–	+	NR	NR	+

*Electron donors were tested at 10 mM unless otherwise indicated.

†When grown under suboptimal conditions.

‡Tested in the presence of 100 g NaCl l⁻¹.§Acetate was not consumed during long-term incubation as determined by HPLC analysis (Kjeldsen *et al.*, 2005).|| Addition of H₂ stimulated growth slightly.

In the presence of yeast extract (0.5 g l⁻¹), the addition of compatible solutes increased the final cell densities and the growth rate of strain EtOH3^T by 17 and 13 %, respectively. In the absence of yeast extract, the addition of compatible solutes increased the same two values by 22 and 21 %, respectively. Each of these increments was significant according to a one-way analysis of variance (results not shown). Although the observed effects were minor, the presence of compatible solutes in the surrounding medium thus seems to enhance the growth of strain EtOH3^T. In this respect, it is worth mentioning that yeast extract may contain the compatible solute glycine betaine in relatively large amounts (Galinski & Trüper, 1994) in addition to other possible growth-stimulating compounds. The availability of the tested or other more potent osmolytes in the Great Salt Lake sediment may help to explain the above-mentioned discrepancy between the NaCl tolerance of strain EtOH3^T *in vitro* and the salinity of the sediment *in situ*. The optimum pH for growth of strain EtOH3^T was 6.8 and growth was detected between pH 6.5 and 8.3. The strain was mesophilic, growing within a temperature range of 15.0–43.6 °C with an optimum at 37 °C. Unlike other members of the family *Desulfohalobiaceae*, and other halophilic SRB, strain EtOH3^T utilized a broad range of different electron donors (Table 1). For instance, strain EtOH3^T grew on propionate, methanol and Casamino acids, which, respectively, are only utilized by the weakly to moderately halophilic SRB *Desulfacinum hydrothermale* DSM 13146^T (Sievert & Kuever, 2000), as well as ‘*Desulfovermiculus halophilus*’ (Belyakova *et al.*, 2006), ‘*Desulfovibrio cavernae*’ HIM (Sass & Cypionka, 2004) and ‘*Desulfovibrio brasiliensis*’ DSM 15816 (Warthmann *et al.*, 2005). In contrast to other members of the family *Desulfohalobiaceae*, strain EtOH3^T was unable to use sulfite as a terminal electron acceptor (Table 1). This finding was unexpected, as the strain harboured genes (*dsrAB*) encoding the alpha and beta subunits of the dissimilatory (bi)sulfite reductase enzyme (EC number 1.8.99.3) (Fig. 1b). It may be argued that the concentrations of sulfite tested (2.5 and 5.0 mM) were toxic to strain EtOH3^T. However, the strain was able to grow when the same concentrations of sulfite were added to BM containing sulfate and, furthermore, sulfite had no effect on the morphology of the cells as evaluated by phase-contrast microscopy (results not shown). These findings indicated that the sulfite concentrations applied were not toxic to strain EtOH3^T. It is therefore possible that the strain lacks a transport mechanism for the uptake of sulfite.

The *dsrAB* and 16S rRNA gene sequences of strain EtOH3^T were retrieved, aligned and compiled as described previously (Abildgaard *et al.*, 2006). Phylogenetic 16S rRNA gene sequence-based trees were inferred from neighbour-joining (with Jukes–Cantor distance correction), maximum-parsimony and maximum-likelihood analyses of a sequence dataset consisting of sequences of > 1300 nt and including a broad range of proteobacterial taxa. Analyses were performed using the respective algorithms of the ARB program

Fig. 1. Consensus trees based on comparative analyses of 16S rRNA gene (a) and DsrAB amino acid sequences (b) showing the inferred phylogenetic position of strain EtOH3^T among members of the class *Deltaproteobacteria*. Numbers at nodes indicate neighbour-joining (16S rRNA) or distance-matrix (DsrAB)-based bootstrap values (100 replications). 16S rRNA gene sequence taxa affiliated with the family *Desulfohalobiaceae* are shaded. Broken lines indicate partial sequences subsequently added to the trees without changing their overall topology using parsimony criteria. Numbers in square brackets indicate the number of taxa contained in the respective groupings. Bars, 10% sequence divergence as estimated by neighbour-joining (16S rRNA) and distance-matrix (DsrAB) analysis. Details of the construction of the trees are given in the text.

package (Ludwig *et al.*, 2004). Two different filters [the deltaproteobacterial 50% conservation filter of the ssu_jan04_corr_opt ARB database (available at <http://www.arb-home.de>) and a custom-made 50% conservation filter calculated for the *Desulfohalobiaceae*-affiliated taxa shown in Fig. 1a] were used to select sequence positions for the analyses. Neighbour-joining-based bootstrap analysis was performed in PAUP*, version 4.0b10 (Swofford, 2003). Phylogenetic analyses of DsrAB amino acid sequence (deduced from nucleotide sequences) datasets including 530 unambiguously aligned positions were performed as described previously (Abildgaard *et al.*, 2006). The phylogenetic consensus trees shown in Fig. 1 were constructed as recommended by Ludwig *et al.* (1998). A range of outgroup taxa were removed from the presented phylogenetic consensus trees; complete trees are available from the corresponding author on request. The genomic G+C content of strain EtOH3^T was determined by HPLC analysis at the Identification Service of DSMZ (Deutsche Sammlung von Mikroorganismen und Zellkulturen GmbH, Braunschweig, Germany).

Phylogenetic analyses of the *dsrAB* and 16S rRNA gene sequences of strain EtOH3^T consistently grouped the strain within the deltaproteobacterial family *Desulfohalobiaceae* (Fig. 1). The phylogenetically closest relative of strain EtOH3^T with a validly published name was *Desulfohalobium retbaense* (Ollivier *et al.*, 1991), sharing 76.0 and 90.5% *dsrAB* and 16S rRNA gene sequence similarity,

respectively, with strain EtOH3^T (Fig. 1). Recently the isolation of a novel moderately halophilic SRB, 'Desulfovermiculus halophilus' strain 11, was reported (Belyakova *et al.*, 2006). No *dsrAB* data are currently available for 'Desulfovermiculus halophilus' strain 11, but the 16S rRNA gene sequence of this strain differs by only 3.1% (1413 nt included) from that of strain EtOH3^T (Fig. 1a). The 16S rRNA gene sequence of strain EtOH3^T contained a unique 97 nt insert from positions 186 to 191 (*Escherichia coli* numbering), which is absent in the 16S rRNA gene sequences of all other species affiliated with the family *Desulfohalobiaceae*. This region was not included in phylogenetic analyses. The DNA of strain EtOH3^T differed in G+C content by 5.7 and 3.8 mol% from *Desulfohalobium retbaense* and 'Desulfovermiculus halophilus', respectively (Table 1). This is around the threshold of 5 mol% difference in genomic G+C content empirically observed generally to constitute the common range within a species (Rosselló-Mora & Amann, 2001). In contrast to the comparison of the available genotypic data, strain EtOH3^T differed significantly from 'Desulfovermiculus halophilus' when comparing their phenotypic characteristics (Table 1). Most notably, 'Desulfovermiculus halophilus' differed from strain EtOH3^T in its capacity for autotrophic growth, its low Mg²⁺ tolerance and its limited ability to grow using alcohols (Table 1). Similarly, several phenotypic characteristics differentiated strain EtOH3^T from *Desulfohalobium retbaense* as well as the other species affiliated with the family *Desulfohalobiaceae* (Table 1). The cellular fatty acid profile

of strain EtOH3^T was determined at the Identification Service of the DSMZ. Cells used for the analysis were cultivated in BM containing 100 g NaCl l⁻¹ and 10 mM lactate, harvested by centrifugation (16 000 g), washed with 20 g NaCl l⁻¹ solution and freeze-dried. The major fatty acids of strain EtOH3^T were (calculation method TSBA50): iso-C_{15:0} (68.47%), iso-C_{17:0} (11.61%), iso-C_{17:1}ω9c (5.92%), iso-C_{15:0} 3-OH (3.19%), C_{16:0} (2.15%), C_{18:0} (2.98%), 10-methyl C_{18:0} (tuberculostearic acid) (1.15%), iso-C_{17:0} 3-OH (0.89%) and iso-C_{16:0} (0.79%). No substantial similarities in the fatty acid profiles of strain EtOH3^T and *Desulfohalobium retbaense* (Ollivier *et al.*, 1991) were evident. Unfortunately, fatty acid profiles have not been published for '*Desulfovermiculus halophilus*'.

Several physiological characteristics of *Desulfohalobium retbaense*, '*Desulfovermiculus halophilus*' and strain EtOH3^T, such as the NaCl, temperature and pH ranges for growth, were very similar (Table 1). This is in agreement with their strong phylogenetic coherence demonstrated by the *dsrAB* and 16S rRNA gene sequence analyses (Fig. 1). Based on the phenotypic and genotypic data discussed above, it is proposed that strain EtOH3^T represents a novel species within the genus *Desulfohalobium*, *Desulfohalobium utahense* sp. nov. As the name '*Desulfovermiculus halophilus*' has not yet been validly published, strain EtOH3^T cannot be assigned to its genus, although this might seem justifiable from the available phylogenetic data avoiding making the genus *Desulfohalobium* paraphyletic (Fig. 1a). In fact, according to its genotypic and phenotypic characteristics (Fig. 1a; Table 1), it may even be warranted to reclassify '*Desulfovermiculus halophilus*' as a novel member of the genus *Desulfohalobium*. Future research resulting in the description of additional members of the family *Desulfohalobiaceae* and in particular the genus *Desulfohalobium* will allow this issue to be addressed in further detail.

Description of *Desulfohalobium utahense* sp. nov.

Desulfohalobium utahense (u'tah.en'se. N.L. neut. adj. *utahense* pertaining to the state of Utah, USA, where the type strain was first isolated).

Cells are non-motile, oval to rod-shaped (1.0–1.2 × 2.5–3.0 µm) and occur singly or in pairs. Under suboptimal conditions, cell elongation (up to 15 µm) and/or filamentous growth may occur. Cells stain Gram-negative and do not contain endospores. Anaerobic and chemo-organotrophic. Utilizes (with sulfate as the electron acceptor): formate, propionate, lactate, pyruvate, butyrate, succinate, malate, fumarate, methanol, ethanol, 1-propanol, 1-butanol, 1-pentanol, yeast extract, Casamino acids, H₂/acetate and H₂/yeast extract. Acetate is not oxidized during long-term incubation. Sulfate and thiosulfate are used as electron acceptors with lactate as the electron donor. Sulfur and sulfite are not reduced. Yeast extract improves, but is not required for, growth. Temperature range is 15.0–43.6 °C with an optimum of 37 °C. Sodium and magnesium ions are

required for growth, the NaCl and MgCl₂·6H₂O growth ranges being 20–240 and >0–121 g l⁻¹, respectively. The optimum NaCl and MgCl₂·6H₂O concentrations are 80–100 and 2–51 g l⁻¹, respectively. The optimum pH is 6.8–7.5. Growth occurs between pH 6.5 and 8.3. The G + C content of the DNA is 51.4 mol%.

The type strain, EtOH3^T (= VKM B-2384^T = DSM 17720^T), was isolated from the hypersaline northern arm of Great Salt Lake, Utah, USA.

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