International Journal of Systematic and Evolutionary Microbiology (2001), **51**, 171–177 Printed in Great Britain

Reclassification of *Desulfobacterium phenolicum* as *Desulfobacula phenolica* comb. nov. and description of strain Sax^T as *Desulfotignum balticum* gen. nov., sp. nov.

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A mesophilic, sulfate-reducing bacterium (strain Sax^T) was isolated from marine coastal sediment in the Baltic Sea and originally described as a '*Desulfoarculus*' sp. It used a large variety of substrates, ranging from simple organic compounds and fatty acids to aromatic compounds as electron donors. Autotrophic growth was possible with H_2, CO_2 and formate in the presence of sulfate. Sulfate, thiosulfate and sulfite were used as electron acceptors. Sulfur and nitrate were not reduced. Fermentative growth was obtained with pyruvate, but not with fumarate or malate. Substrate oxidation was usually complete leading to CO_2, but at high substrate concentrations acetate accumulated. CO dehydrogenase activity was observed, indicating the operation of the CO dehydrogenase pathway (reverse Wood pathway) for CO_2 fixation and complete oxidation of acetyl-CoA. The rod-shaped cells were 0·8–1·0 µm wide and 1·5–2·5 µm long. Spores were not produced and cells stained Gram-negative. The temperature limits for growth were between 10 and 42 °C (optimum growth at 28–32 °C). Growth was observed at salinities ranging from 5 to 110 g NaCl l^{-1}, with an optimum at 10–25 g NaCl l^{-1}. The G+C content of the DNA was 62·4 mol%. Vitamins were required for growth. Based on the 16S rRNA gene sequence, strain Sax^T represents a new genus within the δ-subclass of the *Proteobacteria*. The name *Desulfotignum balticum* gen. nov., sp. nov. is proposed. After the 16S rDNA sequences of all members of the genus *Desulfobacterium* were published (GenBank accession nos. AJ237601–AJ237604, AJ237606, AJ237607), the need to reclassify most members of the genus *Desulfobacterium* became obvious due to their strong phylogenetic affiliation to other genera. Here, we propose to reclassify *Desulfobacterium phenolicum* as *Desulfobacula phenolica* comb. nov. *Desulfotignum balticum*, *Desulfobacterium phenolicum* and *Desulfobacula toluolica* contain cellular fatty acids which have so far only been found in members of the genus *Desulfobacter*.

Keywords: *Desulfobacula*, *Desulfotignum*, marine sulfate-reducing bacterium, complete oxidation, FAME

INTRODUCTION

Among the sulfate-reducing bacteria of the δ-subclass of the *Proteobacteria* several marine isolates are known to grow on a large variety of aromatic compounds, including phenolic compounds and toluene. They were originally classified as members of the genera *Desulfobacterium* and *Desulfobacula* (Bak & Widdel, 1986a, b; Brysch *et al.*, 1987; Rabus *et al.*, 1993, 2000). Besides the use of various aromatic compounds, members of the genus *Desulfobacula* are characteristically restricted to the utilization of short-chain fatty acids and simple organic compounds as electron donors;

Abbreviations: FAME, fatty acid methyl ester; HMN, 2,2,4,4,6,8,8-heptamethylnonane.

The GenBank accession number for the nearly complete 16S rRNA sequences of strain Sax^T (DSM 7044^T) is AF233370.

whereas members of the genus *Desulfobacterium* can also grow chemoautotrophically on H_2 and CO_2 (Bak & Widdel, 1986a, b; Brysch *et al.*, 1987; Rabus *et al.*, 1993; Schnell *et al.*, 1989). In contrast, members of the genera *Desulfococcus*, *Desulfonema* and *Desulfosarcina* only use a limited number of aromatic compounds, mainly benzoic acid derivatives, but also long-chain fatty acids as their sole electron donor and carbon source (Fukui *et al.*, 1999; Widdel, 1980, 1988; Widdel & Bak, 1992; Widdel & Hansen, 1992; Widdel *et al.*, 1983). Recently obtained isolates with interesting degradation capabilities might indicate that in general marine sulfate-reducing bacteria are more versatile than isolates obtained from freshwater habitats (Galushko *et al.*, 1999; Harms *et al.*, 1999; Rueter *et al.*, 1994). However, there are many other sulfate-reducing bacteria (including spore-forming ones) isolated from freshwater habitats which use a large variety of organic compounds as electron donor and are able to grow in marine media (Kuever *et al.*, 1999). Another marine isolate, which was isolated with benzoate and tentatively classified as a '*Desulfoarculus*' (correct spelling should be '*Desulfarculus*') species, can grow slowly on fatty acids with a chain length higher than butyrate (Drzyzga *et al.*, 1993). Therefore, it resembles *Desulfobacterium* and *Desulfobacula* spp. In this paper we describe this species as a new genus within the δ-subclass of the *Proteobacteria*.

The genus *Desulfobacterium* was established by using mainly physiological properties (Brysch *et al.*, 1987). After the 16S rDNA sequences of all members of this genus were published by E. Stackebrandt (GenBank accession nos. AJ237601–AJ237604, AJ237606, AJ237607), the need to reclassify most members of the genus *Desulfobacterium* became obvious due to their strong phylogenetic affiliation to other genera. A comparative analysis using the sequences published by Stackebrandt (see above) indicates that the genus comprises only the type species of the genus, *Desulfobacterium autotrophicum*, and two other species: the non-validly published and as yet undescribed '*Desulfobacterium vacuolatum*' (only listed by Widdel, 1988) and the species originally named *Desulfococcus niacini* (Imhoff & Pfennig, 1983), described as '*Desulfobacterium niacini*'. That both species are members of the genus *Desulfobacterium* had been demonstrated by several phylogenetic analyses (Rabus *et al.*, 1993) and by use of the genus-specific oligonucleotide probe 221 (Devereux *et al.*, 1992; Manz *et al.*, 1998). All other members of the genus have to be reclassified because they belong to other genera or represent new genera. Here we suggest that the former *Desulfobacterium phenolicum* be incorporated within the genus *Desulfobacula* (Rabus *et al.*, 1993, 2000).

METHODS

Source of organism. Strain Sax^T was isolated from a benzoate enrichment culture inoculated with anoxic marine mud from Saxild, Denmark (Drzyzga *et al.*, 1993). Strain Sax^T was deposited in the DSMZ under the accession number DSM 7044^T. *Desulfobacula toluolica* (DSM 7467^T), *Desulfobacterium phenolicum* (DSM 3384^T), *Desulfobacterium autotrophicum* (DSM 3382) and *Desulfobacter postgatei* (DSM 2034) were obtained from the DSMZ.

Media and culture conditions. For enrichment and cultivation the medium was prepared as described previously using benzoate (2·5 mM) as electron donor (Drzyzga *et al.*, 1993). Pure cultures were obtained by repeated use of deep agar dilution series (Widdel & Bak, 1992). Substrate utilization was determined by adding the carbon and energy sources from sterile stock solutions; the cultures were incubated for about 3 weeks. To avoid possible toxic effects of the substances, toluene and xylene isomers were supplied to cultures following adsorption in the deaerated organic solvent 2,2,4,4,6,8,8-heptamethylnonane (HMN; 2%, v/v) (Rabus *et al.*, 1993). A check was made to ensure that HMN did not inhibit growth of strain Sax^T on benzoate.

To test the autotrophic growth capability, cultures were grown under a headspace of H_2/CO_2 (80/20%, v/v) at an overpressure of 101·3 kPa. The temperature range for growth was determined by incubation in a temperature gradient block from 35 to 80 °C in increments of 2–4 °C. The pH range of growth was determined in mineral medium at pH values from 5 to 9. The dependence of growth on the concentration of NaCl was determined in mineral medium with NaCl concentrations from 0 to 130 g NaCl l^{-1}. Strain Sax^T was routinely cultivated in a carbonate-buffered, sulfide-reduced medium for marine sulfate-reducing bacteria supplied with 2·5 mM benzoate as a growth substrate. Salt composition of the medium and incubation conditions were as described by Widdel & Bak (1992).

Chemical and biochemical characterization. The presence of desulfoviridin was tested as described by Postgate (1959). The G + C content was determined by thermal denaturation. Analysis of aromatic compounds, identification of cytochromes and measurement of sulfide production was as described previously (Drzyzga *et al.*, 1993).

For fatty acid methyl ester (FAME) analysis strain Sax^T, *Desulfobacula toluolica* and *Desulfobacterium phenolicum* were grown in marine mineral medium with benzoate (2·5 mM) as the only electron donor and carbon source and sulfate (28 mM) as electron acceptor. *Desulfobacterium autotrophicum* and *Desulfobacter postgatei* were grown with butyrate (10 mM) and acetate (20 mM), respectively. Cells from the late exponential growth phase were centrifuged and used for a comparative FAME analysis. The whole-cell fatty acid composition was determined by means of capillary GC and MS analysis. FAME preparation was carried out using a method as described by Sasser (1997).

Preparation of cell extract. Strain Sax^T was grown in 1200 ml bottles containing 1000 ml mineral medium supplied with 2·5 mM benzoate under a gas phase of N_2/CO_2 (80/20%, v/v). Cells from the late exponential growth phase were harvested by centrifugation and washed once in anoxic saline buffer (50 mM potassium phosphate, pH 7·3, containing 26 g NaCl l^{-1}/11·2 g $MgCl_2.6H_2O$ l^{-1}). Collected cells were resuspended in anoxic potassium phosphate buffer (50 mM, pH 7·3) supplied with 2·5 mM $MgCl_2.6H_2O$ and 2·5 mM dithiothreitol and were passed 2–3 times through an anoxic French press cell at 137 MPa. Cell debris and intact cells were removed from the homogenate by centrifugation (30000 ***g***, 20 min). The extract was placed in a small glass vial under N_2 gas phase and stored on ice. Measurements of enzyme activities were done on the day of preparation.

Table 1. Major cellular fatty acids of strain Sax^T and some phylogenetically related species

Percentage of total fatty acids is shown. Fatty acids present in all strains at less than 1 % are not listed. *c*, *cis*; i, iso; cyc, cyclopropane; OH, hydroxy; Me, methyl.

Fatty acid	Sax^T	*Desulfobacula phenolica*	*Desulfobacula toluolica*	*Desulfospira joergensenii**	*Desulfobacterium autotrophicum*	*Desulfobacter postgatei*
14:1	–	1·4	–	–	–	–
14:0	3·7	8·7	8·3	13·9	2·8	15·4
i15:0	–	–	–	1·8	–	0·7
15:1*c*9	0·8	–	–	–	6·5	–
15:0	0·2	2·0	1·6	1·3	5·1	3·1
3-OH 14:0	–	1·3	–	1·6	–	–
16:1*c*9	8·5	16·5†	19·7	38·9	30·7	10·0
16:0	24·2	20·4	31·2	28·4	13·2	20·9
10-Me 16:0	14·0	17·2	17·6	–	7·4	11·2
17:1*c*11	–	–	–	–	10·5	–
17:0cyc	19·5	3·9	2·6	2·4	–	31·5
17:0	0·4	0·7	0·7	0·6	2·9	2·3
3-OH 16:0	–	–	–	2·3	0·5	–
18:1*c*9	3·7	–	–	–	–	–
18:1*c*11	7·4	3·9	6·0	5·3	2·7	1·2
18:0	9·8	2·1	3·1	0·7	1·1	0·5
i19:0	1·7	–	2·5	–	–	–
19:0cyc	1·1	–	–	–	–	–

* Data obtained from Finster *et al.* (1997).

† In addition, 5.6 % of unidentified 16:1 isomers were found.

Enzyme assays. All enzyme assays were done under strictly anoxic conditions at 30 °C in 1·5 ml glass cuvettes sealed with butyl rubber stoppers. Assays were performed in 1 ml potassium phosphate buffer (50 mM, pH 7·3) which was slightly reduced by addition of several microlitres of 0·05 % dithionite solution. All additions were done from anoxic stock solutions with microlitre syringes. One unit of enzyme activity was defined as 1 μmol min^{-1} (mg $\text{protein})^{-1}$.

The presence of 2-oxoglutarate:electron acceptor oxidoreductase was checked by following the reduction of benzyl viologen (2 mM) at 578 nm in the presence of 2-oxoglutarate (3 mM) and CoA (0·2 mM).

Activity of CO dehydrogenase was determined by following the reduction of benzyl viologen (5 mM) in the presence of CO. To perform the assay, cuvettes were flushed with CO until the assay buffer was saturated with CO.

Protein content in cell-free extract was determined with bichinchoninic acid as a reagent by following a standard protocol assay (BCA protein assay kit; Pierce) and with bovine serum albumin fraction V (Pierce) as a standard for calibration. Gases were purchased from Messer-Griesheim and Sauerstoffwerke Friedrichshafen.

PCR amplification and sequencing of the 16S rRNA gene. To amplify the almost complete 16S rRNA-encoding gene (1500 bp) of strain Sax^T, primers GM3F and GM4R were used in a 35-cycle PCR with an annealing temperature of 40 °C (Muyzer *et al.*, 1995). PCR products were purified by using the QIAquick Spin PCR purification kit (Qiagen) as described by the manufacturer. The *Taq* DyeDeoxy Terminator Cycle Sequencing kit (Applied Biosystems) was used to directly sequence the PCR products, according to the manufacturer's protocol. The sequencing primers were described by Buchholz-Cleven *et al.* (1997). The sequence reaction mixtures were electrophoresed on an Applied Biosystems 373S DNA sequencer.

Phylogenetic analyses of 16S rRNA gene sequence data. The sequences were loaded into the 16S rRNA sequence database of the Technical University of Munich, Germany, using the ARB program package (http://www.mikro.biologie.tu-muenchen.de). The tool ARB_ALIGN was used for sequence alignment. The alignment was visually inspected and corrected manually. Tree topologies were evaluated by performing maximum-parsimony, neighbour-joining and maximum-likelihood analyses with different sets of filters. Only sequences with at least 1200 nt were used for the calculation of different trees. The partial sequence of strain Sax^T (1462 nt) was added to the reconstructed tree by applying parsimony criteria without allowing changes in the overall tree topology. The strain designations and nucleotide sequence accession numbers which were not included in the ARB database are as follows: *Desulfobacula toluolica* DSM 7467^T, X70593; *Desulfobacterium phenolicum* DSM 3384^T, AJ237606 (submitted by E. Stackebrandt); *Desulfospira joergensenii*, DSM 10085^T; X99637; *Desulfotignum balticum* (strain Sax^T), DSM 7044^T, AF 233370; clone SB-9, AF029042; clone Sva0605, AF230098.

RESULTS

FAME analysis

The fatty acid composition of strain Sax^T and its phylogenetically closest relatives are listed in Table 1. Significant amounts of unidentified fatty acids (ECL16.07, ECL18.09) were found in *Desulfobacula*

Table 2. Comparison of selected characteristics of *Desulfobacula toluolica*, *Desulfobacula phenolica*, *Desulfospira joergensenii* and strain Sax^{T}

NR, Not reported; +, good growth; (+), poor growth; −, no growth; [a], autotrophic growth; sp, single polar flagellum. Data obtained from Bak & Widdel (1986a), Drzyzga *et al.* (1993), Finster *et al.* (1997) and Rabus *et al.* (1993). All strains were negative for desulfoviridin and for growth on isobutyrate, 2-methylbutyrate and 3-methylbutyrate and could use sulfate as electron acceptor. Substrate oxidation was complete for all strains.

Characteristic	*Desulfobacula toluolica*	*Desulfobacula phenolica*	*Desulfospira joergensenii*	Sax^{T}
Morphology	Oval	Oval to curved rod	Vibrioid	Rod
Width × length (μm)	1·2–1·4 × 1·2–2·0	1–1·5 × 2–3	0·7–0·8 × 1–2	0·5–0·7 × 1·5–3·0
Motility	+*	+(sp)	−	+(sp)
G+C content (mol%)	42	41	50	62
Major menaquinone	NR	MK-7(H_2)	MK-7 and MK-7(H_2)	NR
Optimum salinity (g NaCl l^{-1})	20	20	12–20	20
Optimum temperature (°C)	28	28	26–30	28–32
Compounds used as electron donor and carbon source:				
H_2 + CO_2	−	−	+	(+[a])
Formate	−	(+)	+[a]	(+[a])
Acetate	−	(+)	−	(+)
Fatty acid (no. of C atoms)	4	(4)	4, 8, 12, 14	4 (10, 12, 16, 18)
Ethanol	+	(+)	−	−
Lactate	−	−	+	+
Pyruvate	+	+	+	+
Fumarate	+	(+)	+	+
Succinate	+	(+)	+	(+)
Malate	+	(+)	−	+
Benzoate	+	+	−	+
4-Hydroxybenzoate	+	+	−	+
Phenol	−	+	−	(+)
Phenylacetate	−	+	−	(+)
Toluene	+	(+)	−	−
Others	Propanol, butanol, *p*-cresol, glutarate	Propanol, butanol, 2-hydroxybenzoate, *p*-cresol, glutarate	Crotonate, glutarate, maleinate, glycolate, glycerol, betaine, proline, yeast extract	Crotonate, maleinate
Fermentative growth	NR	NR	−	+ (on pyruvate)
Electron acceptors:				
Sulfite	NR	−	+	+
Sulfur	NR	−	+	NR
Thiosulfate	NR	+	+	+
Nitrate	NR	−	−	−
Growth factor requirement	Vitamins	−	Biotin	Vitamins

* Cells are motile during early exponential growth phase, but motility can rapidly decline during growth.

toluolica (7·5%) and *Desulfobacula phenolica* (16·6%), and also in trace amounts in strain Sax^{T}. The FAME analysis for *Desulfobacula toluolica* grown on ethanol (van der Maarel *et al.*, 1996) was very similar to our results.

Enzyme activities

In cell-free extracts of strain Sax^{T} active CO dehydrogenase was found [2·6 U (mg protein^{-1})], whereas 2-oxoglutarate dehydrogenase (a key enzyme of the citric acid cycle) was not detected. This finding indicated the presence of the CO dehydrogenase pathway for the oxidation of acetyl-CoA (Thauer, 1988).

Physiological and morphological properties

All physiological and morphological properties of strain Sax^{T}, *Desulfobacterium phenolicum* and *Desulfobacula toluolica* are listed in Table 2 and compared to

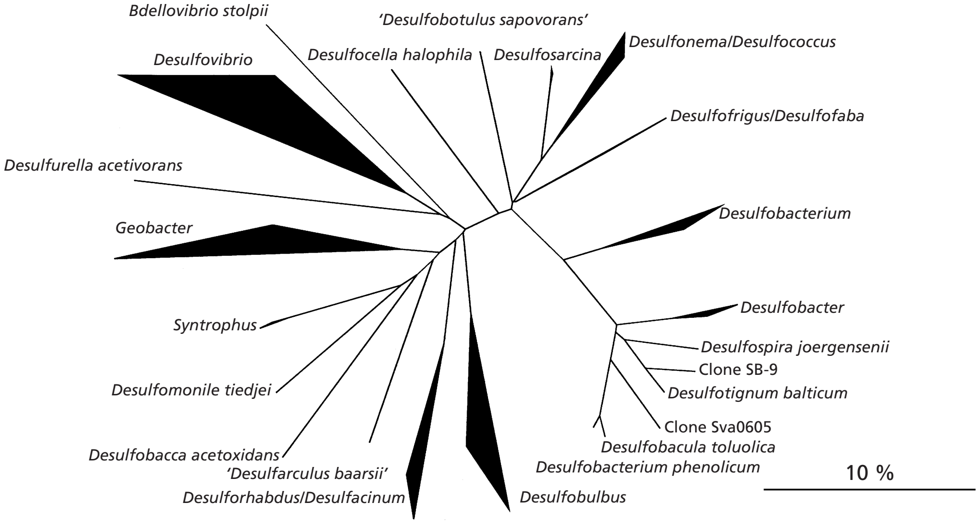

Fig. 1. Phylogenetic tree showing the affiliations of 16S rDNA sequences from *Desulfobacula phenolica* and *Desulfotignum balticum* to selected reference sequences of the δ-subclass of the *Proteobacteria*. The tree was calculated by neighbour-joining analysis and corrected with filters which considered only 50 % conserved regions of the 16S rRNA of δ-*Proteobacteria*. The sequence of *Desulfurella acetivorans* was used as outgroup. The bar represents 10 % estimated sequence divergence.

the closely related species *Desulfospira joergensenii*. For a more detailed description the original publications should be consulted (Bak & Widdel, 1986a; Drzyzga *et al.*, 1993; Finster *et al.*, 1997; Rabus *et al.*, 1993).

Strain Sax^T did not grow on toluene, nor on *o*-, *m*- and *p*-xylenes supplied adsorbed in HMN; nor did this organic solvent inhibit growth of the bacterium on benzoate.

Phylogenetic analyses

The 16S rRNA gene sequence of strain Sax^T shares less than 94·1 % identity with the 16S rRNA gene sequences of other sulfate reducers of the δ-subclass of the *Proteobacteria* (data not shown). The phylogenetic position of strain Sax^T and its closest relatives is shown in Fig. 1. The closest affiliation was found to clone SB-9 (Phelps *et al.*, 1998) with a similarity value of 96·6 %, followed by *Desulfospira joergensenii* (94·1 %) (Finster *et al.*, 1997) and *Desulfobacterium phenolicum* (93·9). As can be seen in Fig. 1 the sequence of clone Sva0605, obtained from permanently cold sediments at Svalbard, is in close proximity to these organisms (Ravenschlag *et al.*, 1999). Clearly, they are all members of the δ-subclass of the *Proteobacteria*. Furthermore, the comparative phylogenetic analyses indicated *Desulfobacterium phenolicum* to be a member of the genus *Desulfobacula*. It was closely related to *Desulfobacula toluolica* (98·8 % similarity of their 16S rRNA sequence), which is the only species of this genus described so far (Fig. 1). Based on the sequence of the 16S rRNA, strain Sax^T could not be affiliated with any of the other genera and was therefore proposed as a new genus in its own right.

DISCUSSION

The physiological and morphological properties (Table 2) in combination with the comparative 16S rDNA and FAME analyses (Fig. 1 and Table 1) clearly demonstrate that *Desulfobacterium phenolicum* is a member of the genus *Desulfobacula*. It can be clearly distinguished from *Desulfobacula toluolica* by its motility, morphology, missing vitamin requirement and use of different electron donors for sulfate reduction. Therefore, we propose to rename it as *Desulfobacula phenolica*.

In view of the 16S rRNA gene sequence analyses presented in this study strain Sax^T should be regarded as belonging to a new genus, since it was not closely related to other genera (a maximum of 94·1 % 16S rRNA sequence identity). The distinct morphological and physiological properties (Table 2) in accordance with the FAME analysis (Table 1) argue in the same direction. Both *Desulfobacula* species and strain Sax^T contain relatively high amounts of the fatty acid 10-Me 16:0, whereas this fatty acid is completely absent in *Desulfospira joergensenii* (Finster *et al.*, 1997). The finding of this fatty acid in *Desulfobacula toluolica* is consistent with the results obtained by van der Maarel *et al.* (1996). Strain Sax^T can be distinguished from both *Desulfobacula* species by the high amount of the cyclopropane fatty acid 17:0cyc, which is also a dominant fatty acid in *Desulfobacter* spp. Therefore, the designation *Desulfotignum balticum* gen. nov., sp. nov. is proposed for strain Sax^T.

Ecological relevance of members of the genera *Desulfobacula* and *Desulfotignum*

The cellular fatty acid composition of strain Sax^T shows the highest similarity to that of *Desulfobacter postgatei*. It is distinguished from the composition of *Desulfobacula toluolica* and *Desulfobacula phenolica* by the presence of 17:0cyc. Nevertheless, strain Sax^T, *Desulfobacula phenolica* and *Desulfobacula toluolica* contain significant amounts of 10-Me 16:0 which was previously described as a biomarker for *Desulfobacter* spp. (Dowling *et al*., 1986) and was also found in lesser amounts ($< 10\%$) in *Desulfobacterium autotrophicum* (Vainshtein *et al*., 1992). Therefore, the use of this fatty acid as a specific biomarker for micro-organisms belonging to the genus *Desulfobacter* should no longer be considered reliable. The presence of this fatty acid in marine sediment could also account for sulfate-reducing bacteria belonging to the aforementioned genera.

Emended description of the genus *Desulfobacula* (Rabus *et al.* 1993).

The description of the genus *Desulfobacula* is the same as that given by Rabus *et al.* (1993) except that the oval cells may be motile or non-motile.

Description of *Desulfotignum* gen. nov.

Desulfotignum (De.sul.fo.tig′num. L. pref. *de* from, L. n. *sulfur* sulfur; M.L. n. *tignum* stick; M.L. neut. n. *Desulfotignum* sulfate-reducing stick).

Cells are straight, sometimes slightly curved rods that are motile. They are strict anaerobes, using sulfate as the terminal electron acceptor that is reduced to sulfide. Aromatic compounds, fatty acids and a number of low-molecular-mass aliphatic acids may be utilized as electron donor. Autotrophic growth on H_2 plus CO_2 and formate. Electron donors are completely oxidized to CO_2 via the CO dehydrogenase pathway. *Desulfotignum* belongs to the δ-subclass of the *Proteobacteria*; the closest relatives are *Desulfobacula* and *Desulfospira* spp. The type species is *Desulfotignum balticum* DSM 7044^T.

Description of *Desulfotignum balticum* sp. nov.

Desulfotignum balticum (bal.ti′cum. M.L. neut. adj. *balticum* from the Baltic Sea, pertaining to location of the sampling site).

Cells are short rods, 0·5–0·7 × 1·5–3·0 μm. Spore formation is absent. Cells are motile. Gram stain reaction of cells is negative. Strict anaerobe. Growth on H_2/CO_2, formate, acetate, butyrate, crotonate, straight long-chain fatty acids up to C_{18}, lactate, pyruvate, fumarate, succinate, maleinate, malate, benzoate, 4-hydroxybenzoate, phenol, phenylalanine and phenylacetate. Substrate oxidation is usually complete leading to CO_2, but at high substrate concentrations acetate can accumulate. Electron acceptors used are sulfate, sulfite and thiosulfate. Nitrate and nitrite are not used. Slow fermentative growth on pyruvate. Addition of at least 10 g NaCl l^{-1} is necessary; optimum NaCl concentration for growth is 20 g l^{-1}, but NaCl is tolerated up to 110 g l^{-1}. Vitamins are required for growth. Temperature requirements: T_{min}, 10 °C; T_{opt}, 28–32 °C; T_{max}, 42 °C. The pH range for growth is 6·5–8·2; optimum 7·3. The G+C content of the DNA is 62·4 mol% (T_m). The type strain is Sax^T (= DSM 7044^T).

ACKNOWLEDGEMENTS

We thank Ingrid Kunze for technical assistance, Hans-Georg Trüper, Karl-Heinz Blotevogel for advice and help, and Geoff Mattison for linguistic improvements to the manuscript. This work was in part funded by the Max-Planck Society, Munich, Germany.

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