Desulfoluna butyratoxydans gen. nov., sp. nov., a novel Gram-negative, butyrate-oxidizing, sulfate-reducing bacterium isolated from an estuarine sediment in Japan

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A strictly anaerobic, mesophilic, sulfate-reducing bacterial strain, designated MSL71^T, was isolated from an estuarine sediment from the Sea of Japan bordering the Japanese islands and was characterized phenotypically and phylogenetically. The cells were found to be Gram-negative, motile, non-spore-forming, slightly curved rods. Catalase and oxidase activities were not detected. The optimum NaCl concentration for growth was 2.0 % (w/v), the optimum temperature was 30 °C and the optimum pH was 6.3. Strain MSL71^T utilized formate, butyrate, pyruvate, lactate, malate, ethanol, propanol, butanol, glycerol and H_2 as electron donors for sulfate reduction. The organic electron donors used were incompletely oxidized, mainly to acetate. The strain did not use acetate, propionate, fumarate, succinate, methanol, glycine, alanine, serine, aspartate or glutamate. Sulfite and thiosulfate were used as electron acceptors with lactate as an electron donor, but fumarate was not utilized. Without electron acceptors, pyruvate and malate, but not lactate or fumarate, were fermented. The genomic DNA G+C content was 62.0 mol%. Menaquinone MK-8(H_4) was the major respiratory quinone. The major cellular fatty acids were $C_{14:0}$, $C_{16:0}$, $C_{16:1}\omega7$, $C_{18:1}\omega9$, $C_{18:1}\omega7$ and $C_{14:0}$ 3-OH. A phylogenetic analysis based on the 16S rRNA gene sequence placed the strain in the class *Deltaproteobacteria*. The closest recognized relative of strain MSL71^T was *Desulfofrigus fragile* (93.9 % sequence similarity) and the next closest recognized species was *Desulfofrigus oceanense* (93.5 %). On the basis of the significant differences in the 16S rRNA gene sequence and phenotypic characteristics between strain MSL71^T and each of the related species, a novel genus and species, *Desulfoluna butyratoxydans* gen. nov., sp. nov., are proposed to accommodate strain MSL71^T. The type strain is MSL71^T (=JCM 14721^T=DSM 19427^T).

Sulfate-reducing bacteria (SRB) are capable of utilizing various compounds, such as H_2, fatty acids, alcohols, amino acids and sugars, as well as aliphatic and aromatic hydrocarbons, as electron donors for sulfate reduction (Hansen, 1993; Castro *et al.*, 2000; Rabus *et al.*, 2000). Major intermediates of anaerobic decomposition of organic matter, such as formate, acetate, propionate, butyrate, lactate and H_2, serve as the most important electron donors for sulfate reduction, and thus SRB contribute significantly to the mineralization of organic matter and the sulfur cycle (Sørensen *et al.*, 1981; Jørgensen, 1982). In the course of an investigation of SRB in an estuarine sediment from the Japanese islands, we isolated various strains of phylogenetically diverse SRB, including several novel lineages. It was shown, from a comprehensive physiological investigation of these isolates, that the SRB group composed of diverse lineages had the ability to oxidize all of the major intermediates of anaerobic decomposition of organic matter, and that each lineage living in the same sediment should occupy its respective, specific niche in the SRB group in relation to the oxidation of electron donors (Suzuki *et al.*, 2007a, b, c).

Of the strains belonging to the novel lineages among our isolates, we have proposed one novel genus and species of SRB, *Desulfopila aestuarii* gen. nov., sp. nov. (Suzuki *et al.*, 2007a), and one novel species of SRB, *Desulfobulbus japonicus* sp. nov. (Suzuki *et al.*, 2007b). In this paper, we describe the characterization of another isolate, designated strain MSL71^T, that oxidizes butyrate as one

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Abbreviations: CFA, whole-cell fatty acid; SRB, sulfate-reducing bacteria.

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of the electron donors for sulfate reduction (Suzuki *et al.*, 2007c). The phylogenetic, physiological and chemotaxonomic characteristics of MSL71^T supported the proposal of a novel genus and species in the class *Deltaproteobacteria* for this strain.

Sediment cores were collected to a depth of 10 cm with a core sampler (5 cm in diameter) from sediment at a water depth of 2 m in the Niida River estuary in Sakata Harbour, Japan (Suzuki *et al.*, 2007c). The sediment sample was diluted by consecutive 10-fold dilutions with sterilized seawater bubbled with O_2-free N_2 gas. The diluted samples (0.2 ml) were inoculated into 10 ml seawater agar medium (see below) containing 20 mM sodium lactate; viable colony counts of SRB were determined by using the anaerobic roll-tube method (Hungate, 1966). Several strains of SRB were obtained by picking up black colonies of SRB that appeared on the roll-tube agar after incubation for about 1 month. Strain MSL71^T was finally obtained after several purification procedures through colony isolation using the anaerobic roll-tube method (Suzuki *et al.*, 2007c).

Two basal media (seawater medium and defined medium) were used in this study. Seawater medium contained the following [(l seawater)$^{-1}$]: 0.5 g KH_2PO_4, 0.3 g NH_4Cl, 0.1 g yeast extract, 1 mg sodium resazurin, 10 ml trace element solution [l^{-1}: 10 ml 25 % (v/v) HCl, 1.5 g $FeCl_2.4H_2O$, 0.19 g $CoCl_2.6H_2O$, 0.1 g $MnCl_2.4H_2O$, 0.07 g $ZnCl_2$, 0.062 g H_3BO_3, 0.036 g $Na_2MoO_4.2H_2O$, 0.024 g $NiCl_2.6H_2O$ and 0.017 g $CuCl_2.2H_2O$] (Widdel *et al.*, 1983) and 0.5 g L-cysteine.HCl.H_2O, as well as sodium lactate (20 mM) as an electron donor. The pH was adjusted to 7.2–7.4 with 1 M NaOH. Agar (Difco) (1.5 %, w/v) was added to the medium and used for the anaerobic roll-tube method for isolation and slant cultures. The medium used for the general physiological characterization of the strain (designated 'defined medium' as opposed to 'seawater medium') contained the following (l^{-1}): 0.5 g KH_2PO_4, 1.0 g NH_4Cl, 1.0 g Na_2SO_4, 2.0 g $MgSO_4.7H_2O$, 0.1 g $CaCl_2.2H_2O$, 0.5 g yeast extract, 1 mg sodium resazurin, 10 ml trace element solution, 15 g NaCl and 0.5 g L-cysteine.HCl.H_2O with the appropriate electron donors (Nakamoto *et al.*, 1996; Ueki *et al.*, 1980; Widdel & Bak, 1992). The pH was adjusted to 7.2–7.4 with 1 M NaOH. Cultivation and transfer of the strain were performed under an O_2-free N_2 (100 %) atmosphere. The strain was cultivated at 30 °C. The strain was maintained in slant cultures of seawater medium or defined medium with lactate as an electron donor.

Gram reaction and cellular morphology were confirmed by light microscopy. Motility of the cells was examined by phase-contrast microscopy and staining of flagella was carried out according to Blenden & Goldberg (1965). Growth of the strain under aerobic conditions was examined in the presence of sodium lactate as an electron donor, using the defined medium but without L-cysteine.HCl.H_2O and sodium resazurin. The catalase and oxidase activities of cells were tested as described by Akasaka *et al.* (2003a). The effects of NaCl concentration and pH on growth of the strain were examined in the presence of sodium lactate as an electron donor, using defined medium. The effects of temperature on growth were examined by using seawater medium. Growth of the strain was monitored by measuring the OD_{660} with a spectrophotometer (U-1000; Hitachi).

Utilization of electron donors was determined by using defined medium with each compound at a final concentration of 20 mM. H_2 utilization was determined in the presence of acetate (5 mM) with H_2 in the atmosphere. Utilization of electron acceptors other than sulfate was determined with a sulfate-free medium, i.e. defined medium with chloride instead of sulfate (at the same concentration) and with sodium lactate (20 mM) as an electron donor. Sodium sulfite (3 mM), sodium thiosulfate (15 mM) or disodium fumarate (20 mM) was added to the sulfate-free medium as a possible electron acceptor. Utilization of pyruvate, lactate, fumarate or malate (20 mM each) in the absence of electron acceptors in the medium was also determined by using sulfate-free medium. Fatty acids and amino acids were used in the form of sodium salts and were added to the medium from sterilized stock solutions. Utilization of each electron donor or acceptor was determined by comparing growth in the presence and absence of each compound, and by measuring the concentration of the compound in the medium after cultivation.

Volatile fatty acids and alcohols were analysed by GC (G-5000 or 263-30; Hitachi), as described previously (Ueki *et al.*, 1986). Non-volatile fatty acids and formate were analysed by HPLC (LC-10AD; Shimadzu) as described by Akasaka *et al.* (2003a) and Ueki *et al.* (2006b). Sulfate, sulfite and thiosulfate were analysed with an ion chromatograph (2000i; Dionex) as described by Nakamoto *et al.* (1996). The genomic DNA extracted was digested with P1 nuclease by using a YAMASA GC kit (Yamasa shoyu) and its G+C content was measured by using HPLC apparatus (L-7400; Hitachi) equipped with a μBondapack C18 column (3.9 × 300 mm; Waters). Isoprenoid quinones were extracted as described by Komagata & Suzuki (1987) and analysed by using a mass spectrometer (JMS-SX102A; JEOL). Whole-cell fatty acids (CFAs) were converted to methyl esters by saponification, methylation and extraction according to the method of Miller (1982). Methyl esters of CFAs were analysed by using a gas chromatograph (Hewlett Packard Hp6890 or Hitachi G-3000) equipped with an HP Ultra 2 column. CFAs were identified from equivalent chain lengths (Miyagawa *et al.*, 1979; Ueki & Suto, 1979) according to the protocol of TechnoSuruga based on the MIDI microbial identification system (Microbial ID) of Moore *et al.* (1994).

Extraction of DNA and PCR amplification of the 16S rRNA gene of the strain were carried out according to the method described by Akasaka *et al.* (2003b) and Ueki *et al.* (2006a).

The 16S rRNA gene, amplified by using PCR with the primer set 27f/1492r, was sequenced by using a Thermo Sequenase primer cycle-sequencing kit (Amersham Biosciences) and a DNA sequencer (4000L; LI-COR). Multiple alignments of the sequence with reference sequences in GenBank were performed with the BLAST program (Altschul *et al.*, 1997). A phylogenetic tree was constructed with the neighbour-joining method (Saitou & Nei, 1987) by using the CLUSTAL W program (Thompson *et al.*, 1994) and the maximum-likelihood program (DNAML) of the PHYLIP 3.66 package (Felsenstein, 2006). All gaps and unidentified base positions in the alignments were excluded before assembly.

Cells of strain MSL71^T were Gram-negative, slightly curved rods with rounded ends and were 0.8–0.9 μm wide and 1.6–3.4 μm long. Cells usually occurred singly or in pairs (Fig. 1) and were motile by means of a single polar flagellum. The strain produced thin, greyish colonies on agar slants of both defined medium and seawater medium. Spore formation was not observed. As cells showed relatively rapid lysis during storage on slants, the cultures were transferred to fresh slant medium every 2 or 3 weeks.

Strain MSL71^T reduced sulfate with lactate as an electron donor and produced acetate at a molar ratio of about 2 : 1 : 2 (lactate : sulfate : acetate) in the defined medium. Thus, the strain showed an incomplete type of oxidation of electron donors. Catalase and oxidase activities were not detected. The strain could not grow in air in the defined liquid medium. Strain MSL71^T showed an absolute requirement for NaCl supplementation to the defined medium; the NaCl concentration for growth was in the range 1.0–6.5 % (w/v), with an optimum at 2.0 % (w/v). The temperature range for growth was 10–35 °C, with an optimum at 30 °C. The pH range for growth was 5.6–8.5, with an optimum at pH 6.3.

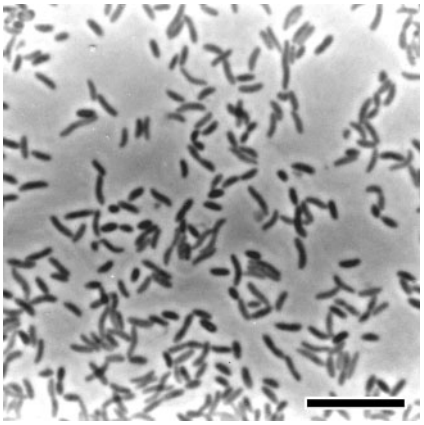

Fig. 1. Phase-contrast photomicrograph of cells of strain MSL71^T grown anaerobically on an agar slant containing seawater medium. Bar, 10 μm.

Strain MSL71^T grew even when electron donors were absent from the medium: it reduced sulfate with the concomitant production of acetate, suggesting that the yeast extract or L-cysteine . HCl . H_2O added to the medium was used as an electron donor. The strain utilized formate, butyrate, pyruvate, malate, ethanol, propanol, butanol, glycerol and H_2, as well as lactate, as electron donors for sulfate reduction. Almost all of the organic electron donors used were oxidized mainly to acetate. Of the electron donors used, highest growth rates were produced with lactate, pyruvate and glycerol (μ=0.175, 0.197 and 0.157 h^{-1}, respectively). Although the growth rate with butyrate was significantly lower (μ=0.081 h^{-1}) than those obtained with these preferred electron donors and the molar ratio (butyrate : sulfate : acetate) was slightly different from the theoretical ratio (2 : 1 : 4), a substantial amount of butyrate (18.8 mM) was oxidized to acetate (34.6 mM) with sulfate reduction (10.8 mM) after cultivation for about 4 days. Propanol was oxidized to propionate, whilst butanol (5.7 mM) was oxidized to acetate (6.1 mM) with a trace amount of butyrate (0.3 mM). Butyrate produced through the oxidation of butanol might be further converted to acetate. The strain did not utilize acetate, propionate, fumarate, succinate, methanol, glycine, alanine, serine, aspartate or glutamate as electron donors.

Strain MSL71^T utilized sulfite and thiosulfate, in addition to sulfate, as electron acceptors, with lactate as an electron donor. The strain did not utilize fumarate as an electron acceptor. In the absence of electron acceptors, strain MSL71^T oxidized pyruvate (18.8 mM) and produced acetate (18.2 mM) and butyrate (1.8 mM). The strain also oxidized a small amount of malate and produced acetate. The strain did not use lactate or fumarate in the absence of electron acceptors.

The G+C content of genomic DNA from strain MSL71^T was 62.0 ± 0.7 mol%. The major respiratory quinone was MK-8(H_4). Almost all of the CFAs of strain MSL71^T were even-numbered, straight-chain fatty acids, the predominant ones being $C_{14:0}$ (11.4 %), $C_{16:0}$ (27.0 %), $C_{16:1}\omega7$ (12.9 %), $C_{18:1}\omega9$ (7.5 %), $C_{18:1}\omega7$ (17.8 %) and $C_{14:0}$ 3-OH (8.9 %).

On the basis of the almost-complete 16S rRNA gene sequence (1498 bp) obtained for MSL71^T, the strain is affiliated with the class *Deltaproteobacteria*. The closest relative of MSL71^T in GenBank was strain Delta proteobacterium LacK5 (AY771930; isolated from marine subsurface sediment), with a sequence similarity of 96.2 % (sequence length compared, 1399 bp). The closest known relative of strain MSL71^T was *Desulfofrigus fragile* (a member of the SRB), with a sequence similarity of 93.9 % (Knoblauch *et al.*, 1999) (sequence length compared, 1475 bp). The next most closely related recognized species was *Desulfofrigus oceanense*, with a sequence similarity of 93.5 % (sequence length compared, 1477 bp) (Knoblauch *et al.*, 1999). Strain MSL71^T formed a separate branch in the phylogenetic tree with respect to these related species (Fig. 2).

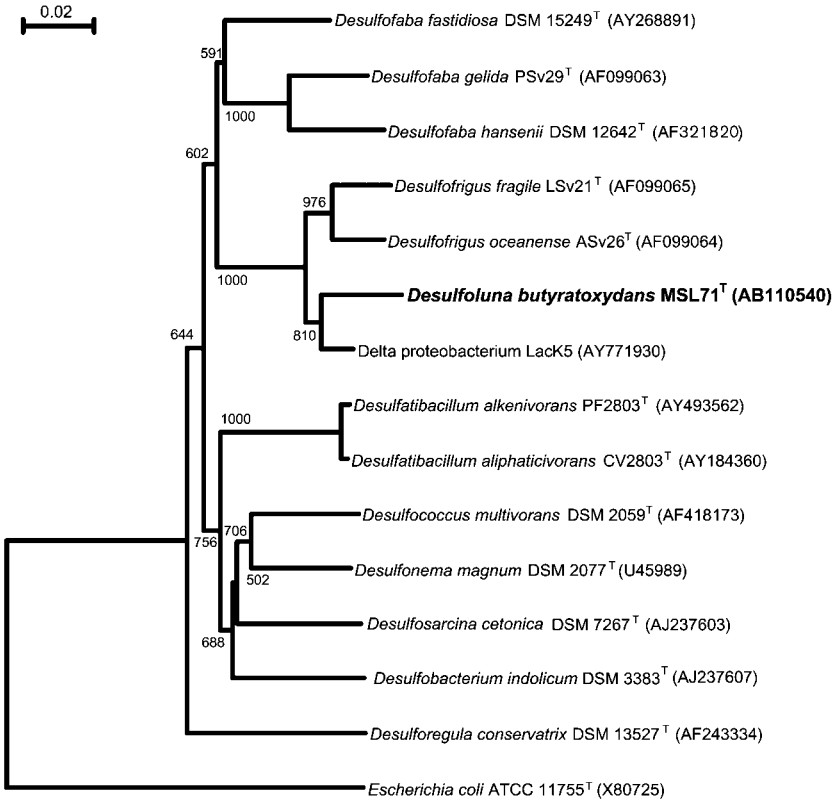

Fig. 2. Neighbour-joining phylogenetic tree, based on 16S rRNA gene sequences, showing the relationships of strain MSL71^T and related species in the class *Deltaproteobacteria*. Bootstrap values (out of 1000 replicates) are shown at branch points. *Escherichia coli* ATCC 11755^T was used as the outgroup. The tree topology evaluated by using the maximum-likelihood method was almost the same as that obtained with the neighbour-joining method. Bar, 2 % estimated difference in nucleotide sequence positions.

Some physiological and chemotaxonomic characteristics of strain MSL71^T and the two most closely related species (*Desulfofrigus* spp.) are compared in Table 1. Cells of strain MSL71^T and *Desulfofrigus fragile* are slightly curved rods, whereas those of *Desulfofrigus oceanense* are thick rods. Cells of *Desulfofrigus fragile* are reported to show rapid lysis

Table 1. Characteristics useful for differentiating strain MSL71^T from related species

Strains: 1, MSL71^T; 2, *Desulfofrigus fragile* LSv21^T (Knoblauch *et al.*, 1999); 3, *Desulfofrigus oceanense* ASv26^T (Knoblauch *et al.*, 1999).

Characteristic	1	2	3
Source	Estuarine sediment	Arctic marine sediment	Arctic marine sediment
Cell shape	Curved rods	Curved rods	Rods
Optimum growth conditions			
NaCl (%, w/v)	2.0	1.0–2.5	1.5–2.5
Temperature (°C)	30	18	10
pH	6.3	7.0–7.4	7.0–7.5
Utilization of electron donors			
Acetate	−	−	+
Fumarate	−	+	−
Glycine	−	−	+
Alanine	−	+	−
Serine	−	+	+
H_2	+	−	+
Utilization of electron acceptors			
Sulfite	+	−	+
Thiosulfate	+	−	+
Utilization of lactate in the absence of an electron acceptor	−	−	+
DNA G+C content (mol%)	62.0	52.1	52.8
Isoprenoid quinone	MK-8(H_4)	MK-9	MK-9

in the stationary phase of growth (Knoblauch *et al.*, 1999); those of strain MSL71^T have a similar property.

Both *Desulfofrigus* species were isolated from permanently cold Arctic marine sediments. The optimum growth temperatures of *Desulfofrigus fragile* and *Desulfofrigus oceanense* are 18 and 10 °C, respectively, and the temperature ranges for growth are −1.8 to 27 °C and −1.8 to 16 °C, respectively (Knoblauch *et al.*, 1999). In contrast, the optimum growth temperature of strain MSL71^T, which was isolated from temperate estuarine sediment, is 30 °C and the range is 10–35 °C. Both *Desulfofrigus* species have pH optima in the neutral range, but that of MSL71^T is slightly acidic.

The oxidation type of the electron donors is heterogeneous for the *Desulfofrigus* species, i.e. *Desulfofrigus fragile* has an incomplete type, whereas *Desulfofrigus oceanense* has a complete type (Knoblauch *et al.*, 1999). Thus, the oxidation type of strain MSL71^T is consistent with that of *Desulfofrigus fragile*. Strain MSL71^T and the two *Desulfofrigus* species commonly utilize butyrate as an electron donor, but the range of electron donors utilized by strain MSL71^T is different from that of any of the *Desulfofrigus* species. Strain MSL71^T utilizes H_2, but not fumarate, whereas *Desulfofrigus fragile* utilizes fumarate, but not H_2. Both *Desulfofrigus* species utilize amino acids, unlike strain MSL71^T.

The range of electron acceptors used by strain MSL71^T is similar to that of *Desulfofrigus oceanense*, but different from that of *Desulfofrigus fragile*. Strain MSL71^T utilizes both sulfite and thiosulfate, but *Desulfofrigus fragile* does not. In the absence of electron acceptors, strain MSL71^T and *Desulfofrigus fragile* do not utilize lactate, unlike *Desulfofrigus oceanense*. Strain MSL71^T produces a small amount of butyrate together with acetate from pyruvate in the absence of electron acceptors. To our knowledge, strain MSL71^T is the first species of SRB to be described as producing butyrate by the fermentation of pyruvate.

The G+C content of the genomic DNA of strain MSL71^T (62.0 mol%) is significantly different from those of *Desulfofrigus fragile* LSv21^T and *Desulfofrigus oceanense* ASv26^T (52.1 and 52.8 mol%, respectively). Strain MSL71^T has MK-8(H_4) as a respiratory quinone, whereas both *Desulfofrigus* species have MK-9. The presence of menaquinones such as MK-5(H_2) (*Desulfobulbus* spp.), MK-6 or MK-6(H_2) (*Desulfovibrio* spp. and *Desulfotalea* spp.) and MK-7 or MK-7(H_2) (some species in the family *Desulfobacteraceae*) are relatively common in SRB species belonging to the class *Deltaproteobacteria* (Kuever *et al.*, 2005). Although MK-8 and MK-8(H_4) have been found in *Desulfofaba gelida* in the family *Desulfobacteraceae*, in a psychrophilic species in the SRB (Knoblauch *et al.*, 1999) and also in *Desulfopila aestuarii* in the family *Desulfobulbaceae* (Suzuki *et al.*, 2007a), respectively, the presence of MK-8 (including the hydrogenated types) is rather rare among species of the SRB.

The CFA profiles of strain MSL71^T and both *Desulfofrigus* species are compared in Table 2. The overall CFA profile of strain MSL71^T is similar to those of both of the *Desulfofrigus* species, but the percentages of even-numbered, unsaturated fatty acids in the latter species are much higher (about 62–74 %) than that in strain MSL71^T (about 38 %). One of the major fatty acids in strain MSL71^T is $C_{14:0}$ 3-OH, which is not detected in the *Desulfofrigus* species.

Of the known butyrate-oxidizing SRB isolated from marine environments, many species in genera such as *Desulfobacterium*, *Desulfosarcina*, *Desulfobacula*, *Desulfotignum*, *Desulfonema*, *Desulfothermus*, *Thermodesulforhabdus* and *Desulfacinum* oxidize butyrate completely to CO_2 (Kuever *et al.*, 2005). In contrast, incomplete oxidization is restricted to a few species, such as *Desulforhopalus singaporensis*, *Desulfofaba gelida* and *Desulfofrigus fragile* (Kuever *et al.*, 2005). Thus, strain MSL71^T is valuable as a novel SRB isolated from marine environments that shows incomplete oxidization of butyrate. Furthermore, it is noteworthy that, although almost all known butyrate-oxidizing SRB species have been isolated by using enrichment cultures with various electron donors (Kuever *et al.*, 2005), strain MSL71^T was isolated directly by picking up a colony using the agar roll-tube method with lactate as an electron donor (Suzuki *et al.*, 2007c).

On the basis of physiological and chemotaxonomic characteristics, in addition to the significant differences in the 16S rRNA gene sequences (similarities of 93.5–93.9 %) between strain MSL71^T and the related *Desulfofrigus* species, we propose a novel genus and species,

Table 2. Cellular fatty acid compositions (%) of strain MSL71^T and related species

Strains: 1, MSL71^T; 2, *Desulfofrigus fragile* LSv21^T (Knoblauch *et al.*, 1999); 3, *Desulfofrigus oceanense* ASv26^T (Knoblauch *et al.*, 1999). –, Not detected.

Fatty acid	1	2	3
Saturated straight chain			
$C_{10:0}$	–	2.5	–
$C_{12:0}$	–	0.6	–
$C_{14:0}$	11.4	5.0	6.7
$C_{16:0}$	27.0	21.7	9.3
$C_{18:0}$	2.1	0.7	0.6
Unsaturated straight chain			
$C_{14:1}\omega5$	–	–	0.9
$C_{16:1}\omega9$	–	3.0	0.7
$C_{16:1}\omega7$	12.9	30.6	43.7
$C_{16:1}\omega5$	–	0.5	2.2
$C_{18:1}\omega9$	7.5	8.6	2.8
$C_{18:1}\omega7$	17.8	18.5	23.0
$C_{18:1}\omega5$	–	–	0.4
$C_{20:1}\omega7$	–	0.3	–
Hydroxy			
$C_{14:0}$ 3-OH	8.9	–	–
Unsaturated branched chain			
Branched $C_{17:1}$	1.5	–	–

Desulfoluna butyratoxydans gen. nov., sp. nov., in the class *Deltaproteobacteria* to accommodate strain MSL71^T.

Description of *Desulfoluna* gen. nov.

Desulfoluna (De.sul.fo.lu′na. L. pref. *de* from; L. n. *sulfur* sulfur; L. fem. n. *luna* the figure of a half-moon, a crescent, lune; N.L. fem. n. *Desulfoluna* a sulfate-reducing crescent).

Mesophilic. Strictly anaerobic. Cells are Gram-negative, non-spore-forming, curved rods. Sulfate serves as an electron acceptor. Organic electron donors are incompletely oxidized. The type species is *Desulfoluna butyratoxydans*.

Description of *Desulfoluna butyratoxydans* sp. nov.

Desulfoluna butyratoxydans (bu.ty.rat.o′xy.dans. N.L. n. *butyras*, *-atis* butyrate; N.L. part. adj. *oxydans* oxidizing; N.L. part. adj. *butyratoxydans* butyrate-oxidizing).

Has the following characteristics in addition to those described for the genus. Cells are slightly curved, rod-shaped with rounded ends, 0.8–0.9 μm wide and 1.6–3.4 μm long. Motile by single polar flagella. Catalase and oxidase activities are negative. Colonies are greyish and thin and spread on slant media. The NaCl concentration range for growth is 1.0–6.5 % (w/v), with an optimum at 2.0 % (w/v). The temperature range for growth is 10–35 °C, with an optimum at 30 °C. The pH range for growth is 5.6–8.5, with an optimum at 6.3. Utilizes formate, butyrate, pyruvate, lactate, malate, ethanol, propanol, butanol, glycerol and H_2 as electron donors for sulfate reduction. Organic electron donors are oxidized mainly to acetate. Does not utilize acetate, propionate, fumarate, succinate, methanol, glycine, alanine, serine, aspartate or glutamate. Utilizes sulfite and thiosulfate in addition to sulfate as electron acceptors, but not fumarate. Ferments pyruvate and malate in the absence of electron acceptors. Butyrate, together with acetate, is produced from fermentation of pyruvate. Does not ferment lactate or fumarate. The genomic DNA G+C content is 62.0 mol%. The major respiratory quinone is MK-8(H_4). Major cellular fatty acids are $C_{14:0}$, $C_{16:0}$, $C_{16:1}\omega7$, $C_{18:1}\omega9$, $C_{18:1}\omega7$ and $C_{14:0}$ 3-OH.

The type strain, MSL71^T (=JCM 14721^T=DSM 19427^T), was isolated from an estuarine sediment located in the Sea of Japan bordering the Japanese islands.

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