Desulfoluna spongiiphila sp. nov., a dehalogenating bacterium in the *Desulfobacteraceae* from the marine sponge *Aplysina aerophoba*

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A reductively dehalogenating, strictly anaerobic, sulfate-reducing bacterium, designated strain AA1^T, was isolated from the marine sponge *Aplysina aerophoba* collected in the Mediterranean Sea and was characterized phenotypically and phylogenetically. Cells of strain AA1^T were Gram-negative, short, curved rods. Growth of strain AA1^T was observed between 20 and 37 °C (optimally at 28 °C) at pH 7–8. NaCl was required for growth; optimum growth occurred in the presence of 25 g NaCl l^{-1}. Growth occurred with lactate, propionate, pyruvate, succinate, benzoate, glucose and sodium citrate as electron donors and carbon sources and either sulfate or 2-bromophenol as electron acceptors, but not with acetate or butyrate. Strain AA1^T was able to dehalogenate several different bromophenols, and 2- and 3-iodophenol, but not monochlorinated or fluorinated phenols. Lactate, pyruvate, fumarate and malate were not utilized without an electron acceptor. The G+C content of the genomic DNA was 58.5 mol%. The predominant cellular fatty acids were $C_{14:0}$, iso-$C_{14:0}$, $C_{14:0}$ 3-OH, anteiso-$C_{15:0}$, $C_{16:0}$, $C_{16:1}\omega7c$ and $C_{18:1}\omega7c$. Phylogenetic analysis based on 16S rRNA gene sequence comparisons placed the novel strain within the class *Deltaproteobacteria*. Strain AA1^T was related most closely to the type strains of *Desulfoluna butyratoxydans* (96 % 16S rRNA gene sequence similarity), *Desulfofrigus oceanense* (95 %) and *Desulfofrigus fragile* (95 %). Based on its phenotypic, physiological and phylogenetic characteristics, strain AA1^T is considered to represent a novel species of the genus *Desulfoluna*, for which the name *Desulfoluna spongiiphila* sp. nov. is proposed. The type strain is AA1^T (=DSM 17682^T =ATCC BAA-1256^T).

The marine environment is a particularly rich source of biogenic organohalides, which are produced by a diversity of marine organisms, including molluscs, algae, polychaetes, jellyfish and sponges (Ashworth & Cormier, 1967; Baker & Duke, 1973; Fielman *et al.*, 1999; Garson *et al.*, 1994; Schmitz & Gopichand, 1978; White & Hager, 1977). A number of sponges (phylum Porifera), such as species of the genus *Aplysina*, have been shown to produce a wide variety of brominated metabolites, including bromoindoles, bromophenols, polybrominated diphenyl ethers and brominated dibenzo-*p*-dioxins (Ebel *et al.*, 1997; Gribble, 1999; Norte & Fernández, 1987; Utkina *et al.*, 2001). Bromine-containing metabolites can account for over 10 % of the sponge dry weight (Turon *et al.*, 2000). These compounds may serve as a chemical defence against predators and may inhibit biofouling (Weiss *et al.*, 1996). In addition, *Aplysina* sponges harbour large amounts of bacteria, which can amount to 40 % of the biomass of the animal, and it has been hypothesized that some of the organobromine compounds may in fact be synthesized by bacteria associated with the sponge (Hentschel *et al.*, 2001, 2003).

As the marine environment is a particularly rich source of biogenic organohalides, it is not surprising that dehalogenating bacteria have been isolated from marine environments. Two dehalogenating bacteria in the genus

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Abbreviations: 2BP, 2-bromophenol; APS, adenosine 5′-phosphosulfate; DGGE, denaturing gradient gel electrophoresis; TRF, terminal restriction fragment; T-RFLP, terminal restriction fragment length polymorphism.

The GenBank/EMBL/DDBJ accession number for the 16S rRNA gene sequence of strain AA1^T is EF187256.

T-RFLP electrophoregrams of sponge enrichments on bromophenols compared with pure culture of strain AA1^T and fatty acid profiles of strain AA1^T and related *Desulfoluna* and *Desulfofrigus* strains are available as supplementary material with the online version of this paper.

Desulfovibrio were isolated by using halophenols as electron acceptors (Boyle *et al.*, 1999, Sun *et al.*, 2000). Sun *et al.* (2000) isolated a halobenzoate-dehalogenating *Desulfomonile limimaris* strain from marine sediments. *Propionigenium maris*, isolated from bromophenol-producing worms, is capable of debrominating 2,4,6-tribromophenol to 4-bromophenol (Steward *et al.*, 1995; Watson *et al.*, 2000).

We have previously demonstrated that the sponge *Aplysina* (synonym *Verongia*) *aerophoba*, which produces a brominated tyrosine derivative, harbours anaerobic, reductively dehalogenating bacteria (Ahn *et al.*, 2003). From *Aplysina* sponge material, we maintained stable anaerobic enrichment cultures by using lactate as an electron donor and bromophenols as electron acceptors. Through metabolic and terminal restriction fragment length polymorphism (T-RFLP) analysis, the enrichments were found to consist of several types of organisms, including dehalogenating organisms. Here, we describe a novel sulfidogenic organism isolated from the sponge *A. aerophoba* that is capable of reductively dehalogenating brominated phenols and is able to couple reductive dehalogenation to growth by using lactate as an electron donor.

Aplysina aerophoba sponges were collected by scuba diving at the Marine Biological Station, Banyuls sur Mer, France, in April 2001. Primary anaerobic enrichment cultures were established with lactate as both electron donor and carbon source and with bromophenols as electron acceptors as described by Ahn *et al.* (2003). Anaerobic medium was prepared as described by Ahn *et al.* (2003). For enrichment of dehalogenating bacteria, we prepared dehalogenating medium by omitting Na_2SO_4 and adding 2.5 mM lactate as electron donor. Periodically, we added 200 μM 2-bromophenol (2BP) as the sole electron acceptor. For preparation of sulfidogenic medium, we added 20 mM sulfate and 2.5 mM lactate. The agar shake tube method (Breznak & Costilow, 1994) was used for isolation. The medium was solidified with Noble agar (10 g l^{-1}; Difco). After three transfers of the original enrichment culture (total dilution of 10^{-9}), a portion of the culture was serially diluted in agar shake culture tubes and incubated in the dark at 28 °C. After 2 weeks, individual colonies were picked and transferred to liquid medium and cultivated to check for dehalogenating activity. We retrieved four cultures showing 2BP-dehalogenating activity. One of these, designated strain AA1^T, was selected for further study, and colonies were re-isolated in agar shake dilution cultures to ensure purity.

T-RFLP analysis and denaturing gradient gel electrophoresis (DGGE) were used to check the make-up of the purified culture. Total DNA was extracted from the cultures and the 16S rRNA gene was amplified by PCR using universal primers (fluorescently labelled 27F and 1525R) (Ahn *et al.*, 2003). The amplified product was digested with restriction enzyme *Mnl*I and the 5′-labelled terminal restriction fragment (TRF) was analysed with an ABI310 sequencer (Applied Biosystems) with GENESCAN software. DGGE was performed with a D gene system (Bio-Rad Laboratories) as described previously (Ahn *et al.*, 2003).

Cells were harvested after growth in anaerobic sulfate-free medium for microscopic observations. Gram staining was performed following the protocols of Murray *et al.* (1994). Cell morphology was observed by using a phase-contrast microscope and epifluorescence microscope (Olympus BX 60) after staining with 0.1 % acridine orange and was visualized with an oil-immersion objective (UPlanF1 100/1.3). Cells were observed by transmission electron microscopy after primary fixing for 3 h in Karnovsky's fixative (combination of low concentration of both formaldehyde and glutaraldehyde in 0.1 M Milloning's phosphate buffer, pH 7.3) (Hayt, 1981). Post-fixation was carried out in 1 % osmium tetroxide buffer for 1 h followed by dehydration in a graded ethanol series and embedding in an Epon/Araldite mixture. Thin sections were prepared by using a diamond knife and LKB-2088 ultramicrotome (LKB – Produkter). Thin sections were stained with 5 % (w/v) uranyl acetate solution in 50 % ethanol for 15 min and then with 0.5 % lead citrate solution in CO_2-free double-distilled water (Reynold's lead citrate stain) for 2 min. Micrographs were taken with a JEM-100CXII electron microscope (JEOL) (Bozzola & Russell, 1992). To prepare samples for scanning electron microscopy, cells were transferred onto a polycarbonate membrane. Primary and post-fixation were carried as described above. After dehydration in a graded ethanol series, filters with cells were critical-point dried (Balzers CPD 020) and sputter coated (Balzers SCD 004). Micrographs were taken with an AMRAY-18301 scanning electron microscope (Bozzola & Russell, 1992).

For the following experiments, 1 % (v/v) inoculum from an actively dehalogenating culture grown on lactate and 2BP was used after washing with anaerobic medium. To test the range of halogenated compounds used as electron acceptors, 3-bromophenol, 4-bromophenol, 2,6-dibromophenol, 2,4,6-tribromophenol, 2-chlorophenol, 3-chlorophenol, 4-chlorophenol, 2-iodophenol, 2-bromobenzoate, 3-bromobenzoate or 4-bromobenzoate (all at a minimum 98 % purity; Sigma-Aldrich) were added at 200 μM to sulfate-free anaerobic medium. Sulfate, sulfite and thiosulfate were tested as electron acceptors at 2.5 mM with lactate as the electron donor. To test the utilization of a range of electron donors, acetate, propionate, fumarate, malate, butyrate, lactate, pyruvate, succinate, benzoate, glucose or sodium citrate were added at 2.5 mM to the medium containing either 2.5 mM sulfate or 200 μM 2BP as the sole electron acceptor. To study the effect of sulfate on dehalogenation of 2BP, 2.5 mM sulfate was added to anaerobic medium containing 200 μM 2BP and electron donors. Before complete consumption of sulfate, the concentration of 2BP was measured to calculate reductive dehalogenation activity. Cultures were monitored periodically for the transformation of electron acceptors by using HPLC and ion chromatography. The optimum temperature for growth of cells was tested at 4, 10, 16,

28, 30 and 37 °C, and the optimum NaCl concentration for growth was tested at 0, 10, 15 and 25 g l^{-1}.

The DNA G+C content was determined by using HPLC as described by Mesbah *et al.* (1989). Nucleosides were analysed by using a model 1100 series chromatograph (Agilent Technologies), with a reversed-phase C18 column (Partisil ODS-3, 4.6 × 250 mm, particle size 5 μm; Whatman) and a solvent of phosphate/methanol (90 : 10), and absorbance was monitored at 254 nm. Phosphate buffer (pH 4.0) was prepared by dissolving KH_2PO_4 (0.049 M) in distilled water and adjusting the pH with 85 % H_3PO_4.

Phenol and halogenated aromatic compounds were analysed by HPLC (1100 series; Agilent) with a C18 column (Spherisorb, 4.6 × 250 mm, particle size 5 μm; Phenomenex), at a flow rate of 1 ml min^{-1}, with an eluent of methanol/water/acetic acid (40 : 58 : 2) and a UV detector set to 280 nm (Ahn *et al.*, 2003). Organic acids were analysed by HPLC (LC-10AS; Shimadzu Corp.) with an HPX-87H column (Bio-Rad) at 60 °C, at a flow rate of 0.6 ml min^{-1}, with an eluent of 0.004 mM sulfuric acid and a UV detector set to 210 nm. Ion chromatography (Dionex DX-120) with an Ion Pac AS9 column was used for measurement of sulfate, sulfite and thiosulfate by using conductivity detection (Boyle *et al.*, 1999; Monserrate & Häggblom, 1997). Protein yield as a cell growth indicator was measured by the Bradford method (Bradford, 1976). Briefly, 10-ml cultures were centrifuged and resuspended in 500 μl phosphate buffer (50 mM, pH 7.0). Cells were lysed in a boiling water bath with 0.1 M NaOH for 10 min and the sample was neutralized with HCl prior to analysis.

Cellular lipids from strain AA1^T grown on sulfate-free medium were saponified, methylated and extracted into hexane/methyl tertiary butyl ether as described by Song *et al.* (2001). Fatty acid methyl esters were analysed via GC by using the SHERLOCK Microbial Identification System (MIDI), and identification was verified by GC-MS with an Agilent series 6890 GC system and 5973 mass-selective detector, equipped with an HP5 MS capillary column (30 m × 0.25 mm inner diameter, film thickness, 0.25 μm) with helium as the carrier gas.

DNA was extracted as described previously (Ahn *et al.*, 2003) and was used for cloning and sequencing of 16S rRNA genes. The 16S rRNA gene was amplified with universal primers (27F and 1525R) (Lane, 1991) and was cloned by using the TOPO TA cloning kit (Invitrogen). Clones were sequenced with a BigDye fluorescent dye terminator sequencer (Perkin Elmer). Internal primers of conserved regions of the 16S rRNA gene sequence (Lane, 1991) were used for sequencing. The dissimilatory adenosine 5′-phosphosulfate (APS) reductase genes (*aprBA*) were amplified with primers AprA-1-FW (5′-TGGCAGATCATGATYMAYGG), AprA-10-RV (5′-CKG-WAGTAGWARCCRGGRTA) (Meyer & Kuever, 2007), APS7b-F (5′-GGYCTSTCCGCYATCAAY) and APS8-R (5′-GCACATGTCGAGGAAGTCTTC) (Friedrich, 2002) by using the following reaction conditions: 1 min at 95 °C, 40 cycles of 1 min at 95 °C, 1 min at 54 °C and 90 s at 72 °C and a final extension of 10 min at 72 °C. Completed sequences were compiled and compared with entries in GenBank by using BLASTN (Altschul *et al.*, 1997). Sequences were aligned with CLUSTAL X (Thompson *et al.*, 1997) and 1300 bp of unambiguously aligned sequence was used for phylogenetic analysis. A phylogenetic tree was created via the NEIGHBOR program by using the distance matrix (DNADIST) and maximum-likelihood (DNAML) method with programs in the PHYLIP package (Felsenstein, 1993). Bootstrap values were calculated with SEQBOOT and the tree was generated by using the programs NEIGHBOR and CONSENSE (Felsenstein, 1993).

A 2BP-dehalogenating culture was enriched from an *A. aerophoba* sponge sample by using lactate as electron donor and 2BP as electron acceptor. The dehalogenating culture was serially diluted in agar shake tubes and incubated until colonies developed. It took 2 weeks for colonies (diameter <0.5 mm) to appear. Twenty separate colonies were picked and transferred directly into anaerobic medium. Four of these showed 2BP-dehalogenating activity in liquid culture assays. These cultures were serially diluted in agar shake tubes until pure cultures were obtained. T-RFLP analysis showed that the final purified culture contained only one peak with a TRF of 196 bp (see Supplementary Fig. S1 in IJSEM Online). TRF 196 was observed in the original 2BP-dehalogenating enrichment (Ahn *et al.*, 2003) as a major peak. DGGE analysis revealed a single band, the sequence of which exactly matched that of the isolate (data not shown). The 16S rRNA genes of four separate isolates were sequenced and were found to be identical to the PCR product. One of these isolates, designated strain AA1^T, was selected for further study.

Cells of strain AA1^T were Gram-negative, slightly curved rods, approximately 1 × 4 μm (Fig. 1). Motility was not observed. Rod-shaped cells were observed in early phases of growth but were observed less frequently in older cultures. In stationary-phase cultures, long and curved rods were observed. Spores were not detected in 2-week-old cultures. When grown under optimal conditions with 2.5 mM lactate and 200 μM 2BP, subcultures (1 %, v/v, inoculum from an early stationary-phase culture) usually reached stationary phase within 4–5 days. Strain AA1^T grew at temperatures up to 37 °C, with optimum growth occurring at 28 °C.

Propionate, lactate, pyruvate, succinate, citrate, benzoate and glucose (2.5 mM each) were used by strain AA1^T as electron donors with either sulfate or 2BP as electron acceptors (Table 1). Acetate accumulated in the medium during growth with lactate as the electron donor and sulfate or 2BP as electron acceptor. Acetate or butyrate (2.5 mM) were not used by strain AA1^T and utilization of lactate, pyruvate, fumarate or malate was not observed in the absence of an electron acceptor. Sulfate, sulfite and thiosulfate (2.5 mM) as electron acceptors supported

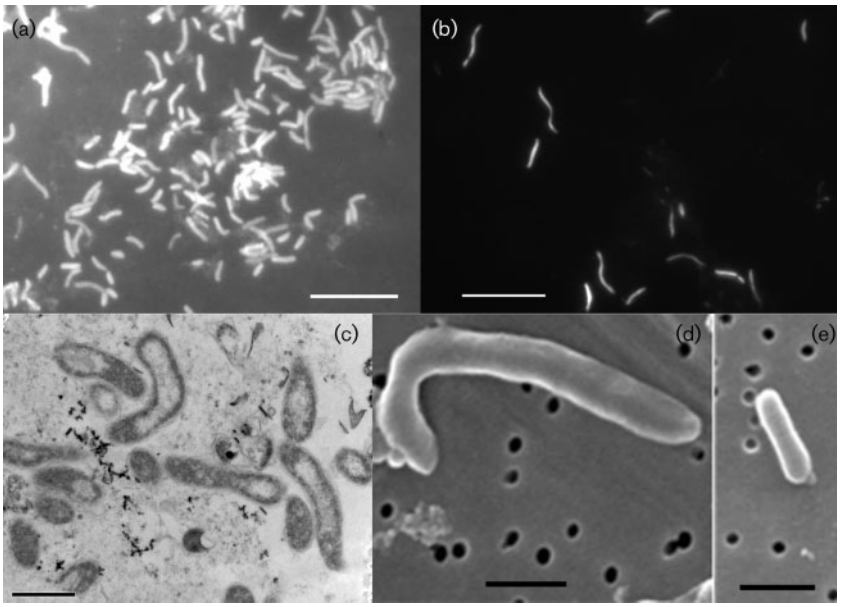

Fig. 1. Micrographs of cells of strain AA1^T. (a, b) Photomicrographs of cells grown with 2-bromophenol and lactate; (c) transmission electron micrograph of young cells; (d, e) scanning electron micrographs of old (10 days) (d) and young (1–2 days) (e) cells. Bars, 10 μm (a, b) and 1 μm (c–e).

Table 1. Characteristics of strain AA1^T and type strains of related *Desulfoluna* and *Desulfofrigus* species

Strains: 1, strain AA1^T; 2, *Desulfoluna butyratoxydans* MSL71^T (data from this study unless indicated); 3, *Desulfofrigus oceanense* ASv26^T (data from Knoblauch *et al.*, 1999); 4, *Desulfofrigus fragile* LSv21^T (Knoblauch *et al.*, 1999). The *Desulfofrigus* strains were cultivated at 4 or 10 °C. ND, Not determined/no data available. All strains stained Gram-negative. Desulfoviridins were not detected. Utilization of electron donors was tested with sulfate as electron acceptor (and, for strain AA1^T, also with 2BP). All strains utilized lactate, pyruvate and malate. None of the strains utilized propionate or succinate. Sulfate was used by all strains as electron acceptor.

Characteristic	1	2	3	4
Source	Marine sponge	Estuarine sediment*	Arctic marine sediment	Arctic marine sediment
Cell morphology	Curved rods	Curved rods*	Thick rods	Slightly curved rods
Cell size (μm)				
Width	1	0.8–0.9*	2.1	0.8
Length	2–4	1.6–3.4*	4.2–6.1	3.2–4.2
Optimum NaCl concentration for growth (%)	2.5	2.0*	1.5–2.5	1.0–2.0
Temperature optimum/range (°C)	28/10–36	30/ND*	10/1.8–16	18/1.8–27
Utilization of electron donors (2.5 mM)				
Acetate	−	−	+	−
Fumarate	−	−	−	+
Butyrate	−	+	+	+
Formate	+	+	ND	ND
Citrate	+	−	ND	ND
Glucose	+	−	ND	ND
Utilization of electron acceptors				
2,6-Dibromophenol (200 μM)	+	−	ND	ND
Thiosulfate (2.5 mM)	+	+	+	−
Sulfite (2.5 mM)	+	+	+	−
DNA G+C content (mol%)	58.5	62*	52.8	52.1
Isoprenoid quinone	ND	MK-8(H_4)*	MK-9	MK-9

*Data from Suzuki *et al.* (2008).

grow in oxidized medium. The DNA G+C content of strain AA1^T was 58.5 mol% (Table 1).

Phylogenetic analysis of the 16S rRNA gene sequence placed strain AA1^T as a member of the class *Deltaproteobacteria* (Fig. 2). Strain AA1^T was related most closely to *Desulfoluna butyratoxydans* MSL71^T (96 % 16S rRNA gene sequence similarity of 1489 bp compared), *Desulfofrigus oceanense* ASv26^T (95 % of 1522 bp compared) and *Desulfofrigus fragile* LSv21^T (95 % of 1520 bp compared). The phylogeny predicted from the dissimilatory APS reductase genes (*aprBA*) was generally in agreement with that predicted from 16S rRNA gene sequences (data not shown). The *aprBA* gene sequence of strain AA1^T was related closely to those of *Desulfofrigus* sp. HRS-La3x (GenBank accession no. EF442924; 93 % similarity of 1545 bp compared) (Meyer & Kuever, 2007) and *Desulfofrigus oceanense* DSM 12341^T (AF418145; 92 % of 891 bp compared) (Friedrich, 2002). The *aprBA* gene sequence of *Desulfoluna butyratoxydans* MSL71^T was not available and could not be included in the comparison. Based on this phylogenetic analysis, strain AA1^T is considered to represent a novel species of the genus *Desulfoluna*.

Strain AA1^T was able to dehalogenate a wide range of brominated phenolic compounds (Table 2), namely 2BP, 3-bromophenol, 4-bromophenol, 2,6-dibromophenol, 2,4,6-tribromophenol, 3,5-dibromo-4-hydroxybenzoate, 2-iodophenol and 2-bromo-4-fluorophenol. Transformation of 3-bromophenol to phenol took much longer than for 2BP and for 4-bromophenol. During dehalogenation of 2BP, stoichiometric amounts of phenol accumulated (data not shown). Phenol was not utilized even after prolonged incubation. No transformation of 2BP occurred without lactate as electron donor, and lactate alone was not converted to acetate. These data indicate that strain AA1^T was able to respire and to grow via reductive dehalogenation of bromophenols. Strain AA1^T was able to dehalogenate 2BP in the presence of sulfate, and sulfate reduction occurred simultaneously, contributing to an increase in cell mass over that observed when 2BP was added as the only electron acceptor (data not shown). No bromobenzoate, monochlorophenol or fluorophenol isomers were dehalogenated. Interestingly, 2- and 3-iodophenol were also dehalogenated by strain AA1^T. Dehalogenation of iodophenols has previously been observed in co-cultures (Fennell *et al.*, 2004) and sediment enrichment cultures (Häggblom & Young, 1995). Similar to brominated compounds, iodinated organic compounds are also produced naturally by marine organisms (Faulkner, 1977; King, 1986). Reductive dehalogenation of organoiodine compounds is more likely than dehalogenation of organobromine or organochlorine compounds, because of the lower electron negativity of iodine. Bromophenol-dehalogenating micro-organisms in the marine environment appear to have cross-activity against iodinated compounds.

Strain AA1^T contained mainly even-numbered fatty acids, which is an indication of the use of acetyl CoA as a precursor for chain elongation during the synthesis of fatty acids (Taylor & Parkes, 1983). The dominant cellular fatty acids were $C_{14:0}$ (6.1±0.3 % of the total; mean±SD of three determinations), iso-$C_{14:0}$ (10.5±2.8 %), $C_{14:0}$ 3-OH (14.9±2.7), iso-$C_{15:0}$ (1.9±0.2 %), anteiso-$C_{15:0}$ (11.6±0.5 %) $C_{16:0}$ (9.8±1.2 %), iso-$C_{16:0}$ (2.3±0.1 %)

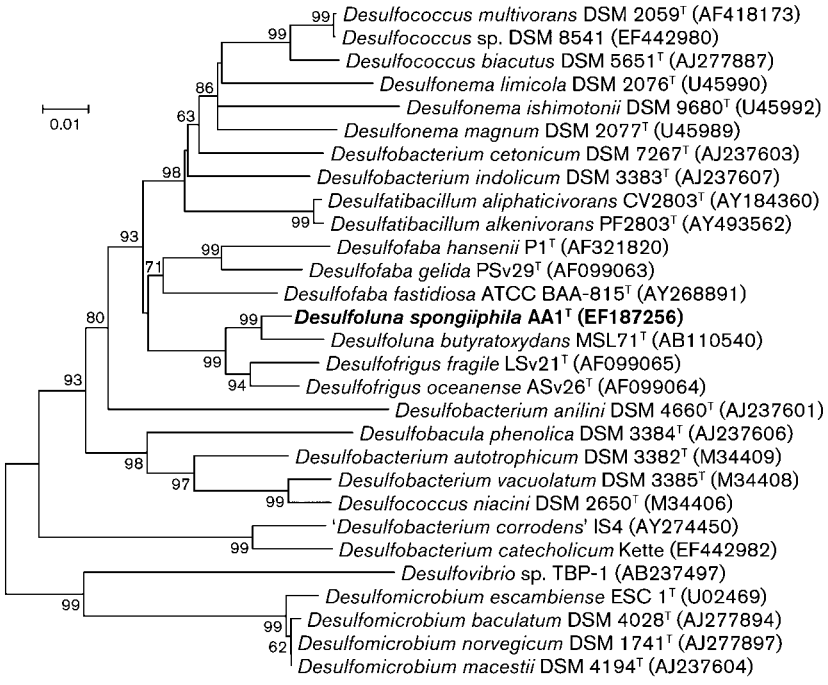

Fig. 2. Phylogenetic tree based on 16S rRNA gene sequences showing the position of strain AA1^T among related species in the *Desulfobacteraceae*. Bootstrap values above 50 % are shown at nodes. Bar, 0.01 substitutions per 100 positions.

Table 2. Dehalogenation of halogenated phenols and benzoates by strain AA1^T

Strain AA1^T was supplied with lactate and assayed after 30 days incubation at 28 °C. Bromobenzoate, monochlorophenol and fluorophenol isomers were not dehalogenated.

Dehalogenation observed	End product
2-Bromophenol	Phenol
3-Bromophenol	Phenol
4-Bromophenol	Phenol
2,4-Dibromophenol	Phenol
2,6-Dibromophenol	Phenol
2,4,6-Tribromophenol	4-Bromophenol, phenol
2-Iodophenol	Phenol
3-Iodophenol	Phenol
2-Bromo-4-fluorophenol	4-Fluorophenol
3,5-Dibromo-4-hydroxybenzoate	4-Hydroxybenzoate

$C_{16:1}\omega7c$ (17.0±2.6 %) and $C_{18:1}\omega7c$ (23.8±0.9 %). The fatty acid profiles of *Desulfoluna butyratoxydans* MSL71^T, *Desulfofrigus oceanense* ASv26^T and *Desulfofrigus fragile* LSv21^T, the closest phylogenetic relatives of strain AA1^T, were distinctly different (Supplementary Table S1). In particular, two of the major fatty acids in strain AA1^T, iso-$C_{14:0}$ and anteiso-$C_{15:0}$, were not reported in the above *Desulfoluna* and *Desulfofrigus* species.

Desulfofrigus species have been isolated from cold environments (Sahm *et al.*, 1999; Knoblauch *et al.*, 1999), whereas strain AA1^T was from a subtropical area. *Desulfoluna butyratoxydans* MSL71^T was isolated from estuarine sediment and the optimum growth temperature is 30 °C (Suzuki *et al.*, 2008). In addition, *Desulfoluna butyratoxydans* MSL71^T is not able to dehalogenate 2,6-dibromophenol or to utilize citrate or glucose as electron donor, in contrast to strain AA1^T. On the basis of the phylogenetic, physiological and chemotaxonomic characteristics described here, strain AA1^T is considered to represent a novel species of the genus *Desulfoluna*, for which the name *Desulfoluna spongiiphila* sp. nov. is proposed.

Description of *Desulfoluna spongiiphila* sp. nov.

Desulfoluna spongiiphila (spon.gi.i.phi′la. L. fem. n. *spongia* sponge; N.L. fem. adj. *phila* from Gr. *philos* friendly, loving; N.L. fem. adj. *spongiiphila* friendly to/living within a sponge).

Anaerobic, reductively dehalogenating, Gram-negative, short, curved rods. Uses sulfate, sulfite and thiosulfate as electron acceptors, in addition to halophenols. Propionate, lactate, pyruvate, succinate, citrate, benzoate and glucose are used as electron donors for dehalogenation of brominated phenolic compounds. The G+C content of the genomic DNA of the type strain is 58.5 mol%. The predominant cellular fatty acids are $C_{14:0}$, iso-$C_{14:0}$, $C_{14:0}$ 3-OH, anteiso-$C_{15:0}$, $C_{16:0}$, $C_{16:1}\omega7c$ and $C_{18:1}\omega7c$.

The type strain, AA1^T (=DSM 17682^T =ATCC BAA-1256^T), was isolated from a marine sponge from the Mediterranean Sea.

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