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Desulfoluna limicola sp. nov., a sulfate-reducing bacterium isolated from sediment of a brackish lake

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Abstract

A novel sulfate-reducing bacterium, strain ASN36^T, was isolated from sediment of a brackish lake in Japan. Cells of strain ASN36^T were not motile and rod-shaped, with length of 2.4–4.9 µm and width of 0.6–0.9 µm. Growth was observed at 5–35°C with an optimum growth temperature of 28°C. The pH range for growth was 6.6–8.8 with an optimum pH of 7.3. Major fatty acids were $C_{16:1}$ *ω7c* and $C_{16:0}$. Under sulfate-reducing conditions, strain ASN36^T utilized lactate, malate, pyruvate, butyrate, ethanol, butanol, glycerol, yeast extract and H_2/CO_2 as growth substrate. Fermentative growth occurred on malate and pyruvate. The novel isolate used sulfate, sulfite and thiosulfate as electron acceptors. The genome of strain ASN36^T is composed of a chromosome with length of 6.3 Mbp and G + C content of 55.1 mol%. Analyses of the 16S rRNA gene indicated that strain ASN36^T is related to *Desulfoluna* species. Overall genome relatedness indices indicated that strain ASN36^T does not belong to any existing species. In contrast to the closest relatives, strain ASN36^T lacks genes for reductive dehalogenase required for organohalide respiration and does not use halogenated aromatics as electron acceptors. On the basis of its genomic and phenotypic properties, strain ASN36^T (= DSM 111985^T = JCM 39257^T) is proposed as the type strain of a new species, *Desulfoluna limicola* sp. nov.

Introduction

The genus *Desulfoluna* was proposed in 2008, with the type species of *D. butyratoxydans* described as a butyrate-oxidizing sulfate reducer (Suzuki et al., 2008). The type strain of the species is *D. butyratoxydans* MSL71^T, isolated from an estuarine sediment by using lactate and sulfate as electron donor and acceptor, respectively. The second species of the genus, *D. spongiiphila* was described with the type strain AA1^T isolated from marine sponge (Ahn et al., 2009). *D. spongiiphila* AA1^T was isolated via enrichment culture with 2-bromophenol as sole electron acceptor, and can dehalogenate various organohalide compounds by respiratory reduction (Ahn et al., 2003; Ahn et al., 2009). Organohalide respiration by *D. butyratoxydans* MSL71^T was demonstrated in a following study, in which another strain of *D. spongiiphila* (strain DBB) was isolated from an intertidal sediment by using 1,4-dibromobenzene as electron acceptor (Peng et al, 2020). All these organohalide-respiring *Desulfoluna* strains are known to have three distinct *rdhA* genes (referred to as *rdhA1*, *rdhA2* and *rdhA3*) in their respective genomes (Peng et al, 2020). These *rdhA* genes, encoding the catalytic subunit of reductive dehalogenase, are individually located in three *rdh* gene clusters scattered in the genomes (Peng et al, 2020). As for two *D. spongiiphila* strains, the involvement of the *rdh* gene clusters in organohalide respiration was investigated by transcriptomic and proteomic

59 approaches (Peng et al, 2020; Liu et al, 2020), but roles of the multiple gene clusters have
60 not been fully revealed. In addition to these studies on species with validly published
61 names, an enrichment culture-based study suggested organohalide respiration by some
62 *Desulfoluna* species associated with various marine sponges (Horna-Gray et al, 2022).

63 In this study, a novel sulfate-reducing bacterium was isolated and characterized as a
64 representative of a new species in the genus *Desulfoluna*.

65

66 **Materials and methods**

67

68 Enrichment and isolation

69

70 The novel isolate, strain ASN36^T was isolated from a sample of sediment
71 collected in a brackish lake, Lake Akkeshi in Japan (43.05° N 144.89° E). The sample
72 was that used in a previous study (Takahashi et al., 2022). To establish the first enrichment,
73 0.2 g of the sediment was inoculated into a bicarbonate-buffered medium for marine
74 sulfate-reducing bacteria, supplemented with 5 mM butyrate. The medium (hereafter
75 referred to as a basal medium) was prepared as described previously, to contain the
76 following constituents (l^{-1}): 20.0 g NaCl; 4.0 g Na_2SO_4; 3.0 g $MgCl_2 \cdot 6H_2O$; 0.2 g
77 KH_2PO_4; 0.25 g NH_4Cl; 0.5 g KCl; 0.15 g $CaCl_2 \cdot 2H_2O$; 1 ml trace element solution; 1 ml

78 selenite-tungstate solution; 1 ml vitamin mixture solution; 1 ml vitamin B_{12} solution; 1
79 ml thiamine solution; 30 ml 1 M $NaHCO_3$ solution; and 1.5 ml 1 M Na_2S solution (Widdel
80 & Bak, 1992). The culture was incubated at 18°C in the dark, after filling the headspace
81 with N_2 /CO_2 (80 : 20, v/v). The grown culture was transferred to the same medium three
82 times (with 3-5 weeks intervals), and then subjected to agar shake dilution as described
83 previously (Widdel & Bak, 1992). A colony formed in the agar-solidified medium was
84 picked up in the liquid basal medium, and the isolation procedures were repeated three
85 times in total to obtain pure culture of strain ASN36^T. The purity of the culture was
86 checked by phase-contrast microscopy and 16S rRNA gene sequencing.

87

88 Phenotypic characterization

89 All cultivation experiments were carried out at 28°C in the basal medium
90 supplemented with 5 mM lactate, unless otherwise specified. Temperature range for
91 growth was examined by culturing strain ASN36^T at 0, 5, 8, 10, 13, 15, 18, 22, 25, 28, 32,
92 35, 37, 42 and 45°C. Range of salinity for growth was examined by culturing the strain
93 in media with various NaCI concentrations, 0, 0.5, 1.0, 1.5, 2.0, 2.5, 3.0, 3.5, 4.0, , 5.0 ,
94 6.0, 7.0, 7.5 and 8.0% (w/v). Effect of pH on growth was tested as described previously
95 (Takahashi et al., 2022), by using media buffered with MES, MOPS, or TAPS. The tested

96 pH and buffer were as follows: pH 5.8, 6.0, 6.2, 6.4, 6.6 and 6.8 with MES; pH 6.5, 7.0,
97 7.3, 7.5 and 7.8 with MOPS; 7.8, 8.0, 8.2, 8.4, 8.6, 8.8 and 9.0 with TAPS.

98 Utilization of electron donors was tested in the basal medium supplemented with one
99 of the following (mM, if not indicated differently): formate (5), acetate (5), propionate
100 (2), lactate (5), glycolate (5), butyrate (5), isobutyrate (5), malate (5), succinate (5),
101 fumarate (5), benzoate (2), pyruvate (5), citrate (5), methanol (5), ethanol (5), butanol (5),
102 glycerol (5), glucose (5) and yeast extract (0.05% w/v). Hydrogen-dependent autotrophic
103 growth was tested under a gas mixture of N_2, H_2 and CO_2 (50:40:10 v/v/v, 200 kPa total
104 pressure). Fermentative growth was tested with a modified version of the basal medium
105 which contained no sulfate. The sulfate-free medium was supplemented with ethanol (5),
106 pyruvate (10), lactate (5), succinate (5), malate (5) or fumarate (5). Acetate in grown
107 cultures was quantified with an Acetate Colorimetric Assay Kit (Sigma-Aldrich).
108 Utilization of electron acceptors was tested in the presence of 5 mM lactate, by replacing
109 sulfate in the basal medium with one of the followings; thiosulfate (10), elemental sulfur
110 (0.5 % w/v), sulfite (1 and 5), tetrathionate (5), poorly crystalline Fe(III) oxide (20), 1,4-
111 dibromobenzene (0.1), 2-bromophenol (0.1), 4-bromophenol (0.1), 2,4-dichlorophenol
112 (0.05) and 2,6-dichlorophenol (0.05).

113 The cellular fatty acid profile was analyzed for strain ASN36^T grown on 5 mM

lactate. Fatty acids were identified and quantified with the Sherlock Microbial Identification System (MIDI) version 6.0 (database; MOORE6).

Genomic characterization

Whole genome sequencing was performed using the platforms of Illumina NextSeq and Nanopore GridION. The resulting reads from the platforms were subjected to hybrid assembly using Unicycler (Ver 0.4.7). The assembled genome sequence was annotated with DFAST (Tanizawa et al., 2018).

As genome relatedness indices between strain ASN36^{T} and its closest relatives, values of average nucleotide identity (ANI), average amino acid identity (AAI) and digital DNA–DNA hybridization (dDDH) were calculated by using online tools. The values of ANI and AAI were computed with tools provided by Kostas lab (http://enve-omics.ce.gatech.edu/). The dDDH was calculated with the formula 2 (Meier-Kolthoff et al., 2013), by using Genome-to-Genome Distance Calculator provided by DSMZ.

The key gene for organohalide respiration, the *rdhA* gene was searched for in the genome of strain ASN36^{T}, by BLASTp analysis. All nine proteins encoded by three *rdhA* genes (*rdhA1*, *rdhA2* and *rdhA3*) of three *Desulfoluna* strains (*D. butyratoxydans* MSL71^{T}, *D. spongiiphila* AA1^{T} and *D. spongiiphila* DBB) were used as queries for

BLASTp search against all proteins encoded in the genome of strain ASN36^T. The *rdhA* genes of three strains were identified in a previous study (Peng et al, 2020).

Phylogenetic analysis based on the 16S rRNA gene

Phylogenetic analysis was conducted using MEGA version 11 (Tamura et al., 2021). The 16S rRNA gene sequence of strain ASN36^T was aligned with reference sequences, obtained from LPSN (accessed on 31 May 2022). With the alignment obtained with the MUSCLE algorithm, the best substitution model was selected by the model selection tool, with default settings. The selected best model with the lowest Bayesian Information Criterion (BIC) score was used to construct phylogenic tree.

Results and Discussion

Physiological and chemotaxonomic characteristics

The characteristics of strain ASN36^T are presented in the species description. Cells of strain ASN36^T were non-motile, rod-shaped, 0.6–0.9 μm in width and 2.0–4.9 μm in length. Strain ASN36^T grew at 5–37°C with optimum growth at 25–30°C. Its pH range for growth was 6.0–8.8 with the optimum pH of 7.3. The NaCl range for growth was 0.5–7.0 %.

151 Under the sulfate-reducing conditions, growth of strain ASN36^T was supported
152 with lactate, malate, pyruvate, butyrate, ethanol, butanol, glycerol and east extract. In
153 the sulfate-reducing cultures grown on lactate, production of acetate was observed. The
154 molar amount of the generated acetate was nearly equal to that of lactate consumed by
155 sulfate reduction. These results suggest that strain ASN36^T is an incomplete oxidizer,
156 which oxidizes lactate to acetate and CO_2. Chemolithoautotrophic growth was observed
157 in the presence of H_2 gas and CO_2. In the absence of sulfate, fermentative growth was
158 supported by malate and pyruvate. During the fermentative growth, strain ASN36^T
159 generated 2.2 mM acetate from 5 mM pyruvate. Among the alternative electron
160 acceptors tested, only sulfite and thiosulfate were used. None of the tested
161 organohalides supported growth of strain ASN36^T as electron acceptor, in the presence
162 of lactate.

163 In the cellular fatty acid profile, $C_{16:1}$ $\omega 7c$ and $C_{16:0}$ were predominant,
164 accounting for 27.5% and 25.9% of total, respectively. The other major components
165 (>10% of total) were summed feature 10 ($C_{18:1}\omega 7c$ and/or unknown 17.834; 11.9%)
166 and $C_{18:1}\omega 9c$ (11.5%). The full cellular fatty acid profile is shown in Table S1.
167
168 Genomic and phylogenetic properties

169 The complete genome of strain ASN36^T was reconstructed as a single circular
170 chromosome, with size 6,263,790 bp and G+C content of 55.1%. In the genome, 4971
171 protein-coding sequences, 12 rRNA genes and 83 tRNA genes were predicted.

172 The genome harbors four copies of the 16S rRNA gene with an identical
173 sequence. This sequence indicated the highest sequence identities to the 16S rRNA gene
174 sequences of *Desulfoluna* species (Table 1). By constructing phylogenetic tree of the
175 16S rRNA gene, it was confirmed that strain ASN36^T is closely related to *Desulfoluna*
176 species (Fig. 1). The genome of strain ASN36^T was compared with those of type strains
177 in the genus *Desulfoluna*, by calculating values of ANI, AAI and dDDH (Table 1). All
178 values calculated are lower than threshold for species delineation, suggesting that strain
179 ASN36^T represents a novel species.

180 In the BLASTp searches with the RdhA sequences from the *Desulfoluna*
181 strains, there was no hit with alignment length greater than 43% of query length. This
182 indicated that none of the genes possessed by strain ASN36^T can be regarded as
183 homologous with the *rdhA1*, *rdhA2* or *rdhA3*. In other words, strain ASN36^T lacks the
184 *rdhA* genes conserved in the other *Desulfoluna* strains.

185

Conclusion

The analysis of 16S rRNA gene suggested that strain ASN36^T represents a novel species in the genus *Desulfoluna*. The values of ANI, AAI and dDDH between strain ASN36^T and the type strains of *Desulfoluna* species supported the creation of a new species (Table 1). In addition, genomic G + C content of strain ASN36^T is distinct from those of other type strains of *Desulfoluna* species, with differences greater than 2% (Table 1). The differences between strains of same species are 1% or smaller in general (Meier-Kolthoff et al., 2014). Strain ASN36^T also has some phenotypic characteristics, distinct from representatives of existing *Desulfoluna* species (Table 1). On the basis of these results, strain ASN36^T is proposed to be assigned to a new species of the genus *Desulfoluna*, with the name *Desulfoluna limicola* sp. nov., as the first *Desulfoluna* species that does not reduce organohalides.

Description of *Desulfoluna limicola* sp. nov.

Desulfoluna limicola (li.mi'co.la. L. masc. n. *limus*, mud; L. masc. fem. suff. -*cola*, dweller; from L. masc. fem. n. *incola*, dweller; N.L. masc./fem. n. *limicol*, mud-dweller).

Cells are not motile, rod shaped, 2.0–4.9 μm in length and 0.6–0.9 μm in width. Growth

occurs at 5–35°C with an optimum growth at 25–30°C. The pH range for growth is 6.0–8.8, with an optimum pH of 7.3. Predominant fatty acids are $C_{16:1}$ *ω7c* and $C_{16:0}$. Under sulfate-reducing conditions, grows on lactate, malate, pyruvate, butyrate, ethanol, butanol, glycerol and yeast extract. Formate, acetate, propionate, glycolate, isobutyrate, succinate, fumarate, benzoate, citrate, methanol and glucose are not utilized as growth substrate. Ferments pyruvate and malate. Does not ferment lactate, succinate and ethanol. Grows chemolithoautotrophically on H_2 and CO_2. Uses sulfate, sulfite and thiosulfate as electron acceptor. Elemental sulfur, tetrathionate, poorly crystalline Fe(III) oxide, 1,4-dibromobenzene, 2-bromophenol, 4-bromophenol, 2,4-dichlorophenol and 2,6-dichlorophenol are not used as electron acceptors. G + C content of genomic DNA of the type strain is 55.1 mol%.

The type strain ASN36^T (= DSM 111985^T = JCM 39257^T) was isolated from sediment of a brackish lake in Japan.

The GenBank/EMBL/DDBJ accession numbers for the 16S rRNA gene and complete genome of strain ASN36^T are LC726356 and AP024488, respectively.

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Statements and Declarations

The authors declare that authors have no relevant financial or non-financial interests to disclose.

Figure legend

Fig. 1. Phylogenetic position of strain ASN36^{T}, based on the 16S rRNA gene sequences. This maximum likelihood tree was constructed based on Kimura 2-parameter model. A discrete gamma distribution was used to model differences in evolutionary rates among sites (5 categories). The rate variation model allowed for some sites to be invariable (53.53% sites). All positions containing gaps and missing data were eliminated, leaving a total of 1,345 positions in the final dataset. Numbers on nodes represent percentage values of 1,000 bootstrap resampling.

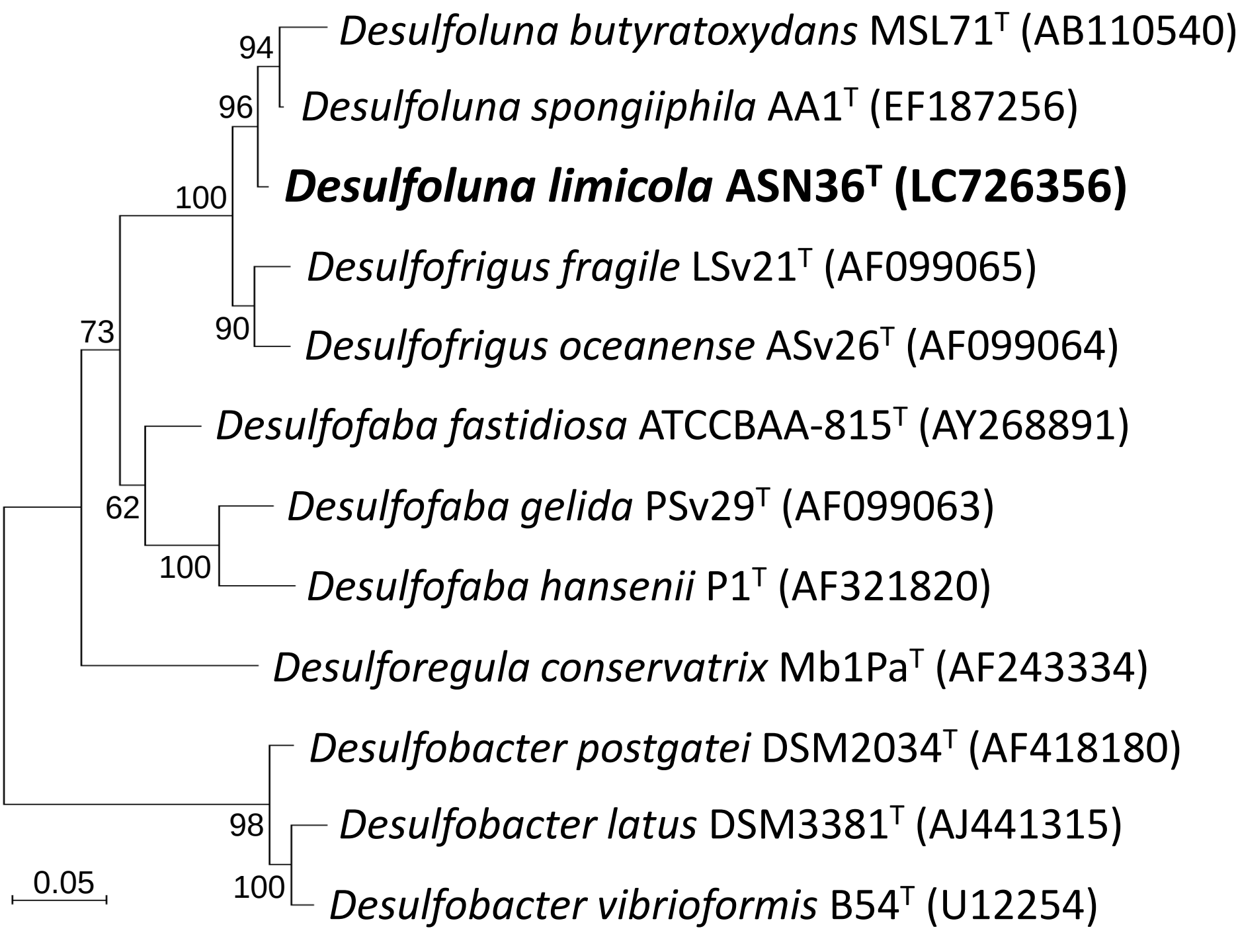
Table 1 Differential properties between strain ASN36^T and type strains of species in the genus *Desulfoluna.* Strains: 1, ASN36^T (this study); 2, *Desulfoluna butyratoxydans* MSL71^T (Suzuki et al., 2008); 3, *Desulfoluna spongiiphila* AA1^T (Ahn et al., 2009). All strains grow on lactate, malate and pyruvate. All strains reduce sulfate, sulfite and thiosulfate. Genome size and G+C content were cited from descriptions in the public database. Organohalide respiration by strain 2 was investigated by Peng et al, 2020.

	1	2	3
Electron donor			
Formate	-	+	+
Succinate	-	-	+
Butyrate	+	+	-
Citrate	-	-	+
Glucose	-	-	+
Electron acceptor			
1,4-Dibromobenzene	-	-	+
2-Bromophenol	-	+	+
4-Bromophenol	-	-	+
Genome size (Mb)	6.26	6.44	6.53
G+C content (mol %)	55.1	57.9	57.2
Relatedness to strain ASN36^T			
Identity of the 16S rRNA gene sequence (%)	100	94.8	98.2
ANI (%)	100	81.00	81.26
AAI (%)	100	78.44	79.46
dDDH (%)	100	24.50	24.80

Table S1. Cellular fatty acid profiles of strain ASN36^T, *Desulfoluna butyratoxydans* MSL71^T and *Desulfoluna spongiiphila* AA1^T. Data of strains MSL71^T and AA1^T were taken from Suzuki et al., 2008 and Ahn et al., 2009, respectively. Summed features consist of fatty acids that could not be separated, as follows: Summed feature 2, $C_{12:0}$ 3OH and/or $C_{13:0}$ DMA; Summed feature 3, iso-$C_{15:0}$ aldehyde and/or unknown 13.570; ; Summed feature 5, $C_{15:0}$ DMA and/or $C_{14:0}$ 3OH; Summed feature 10, $C_{18:1}\omega$7c and/or unknown 17.834.

Fatty acid (%)	ASN36^T	MSL71^T	AA1^T
$C_{10:0}$	2.1	-	-
$C_{12:0}$	0.5	-	-
iso-$C_{14:0}$	-	-	10.5±2.8
$C_{14:1}$ ω5c	0.5	-	-
$C_{14:0}$	8.2	11.4	6.1±0.3
iso-$C_{15:0}$	-	-	1.9±0.2
anteiso-$C_{15:0}$	-	-	11.6±0.5
$C_{16:1}$ ω9c	1.2	-	-
$C_{16:1}$ ω7c	27.5	12.9	17.0±2.6
$C_{16:1}$ ω5c	0.5	-	-
$C_{16:0}$	25.9	27.0	9.8±1.2
iso-$C_{16:0}$	-	-	2.3±0.1
branched-$C_{17:1}$	-	1.5	-
$C_{18:2}$ ω6,9c	0.7	-	-
$C_{18:1}$ ω9c	11.5	7.5	-
$C_{18:0}$	1.1	2.1	3.7±1.8
$C_{20:0}$	0.1	-	-
Summed feature 2	0.6	-	-
Summed feature 3	0.3	-	-
Summed feature 5	7.3	8.9^a	14.9±2.7^a
Summed feature 10	11.9	17.8^b	23.8±0.9^b

a: Reported as $C_{14:0}$ 3OH. *b*: Reported as $C_{18:1}\omega$7c.


94
96
100
73
90
62
100
98
100
0.05
Desulfoluna butyratoxydans MSL71^{T} (AB110540)
Desulfoluna spongiiphila AA1^{T} (EF187256)
***Desulfoluna limicola* ASN36^{T} (LC726356)**
Desulfofrigus fragile LSv21^{T} (AF099065)
Desulfofrigus oceanense ASv26^{T} (AF099064)
Desulfofaba fastidiosa ATCCBAA-815^{T} (AY268891)
Desulfofaba gelida PSv29^{T} (AF099063)
Desulfofaba hansenii P1^{T} (AF321820)
Desulforegula conservatrix Mb1Pa^{T} (AF243334)
Desulfobacter postgatei DSM2034^{T} (AF418180)
Desulfobacter latus DSM3381^{T} (AJ441315)
Desulfobacter vibrioformis B54^{T} (U12254)