Desulfuromonas svalbardensis sp. nov. and *Desulfuromusa ferrireducens* sp. nov., psychrophilic, Fe(III)-reducing bacteria isolated from Arctic sediments, Svalbard

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Two psychrophilic, Gram-negative, rod-shaped, motile bacteria (strains 112^T and 102^T) that conserved energy from dissimilatory Fe(III) reduction concomitant with acetate oxidation were isolated from permanently cold Arctic marine sediments. Both strains grew at temperatures down to −2 °C, with respective temperature optima of 14 °C and 14–17 °C for strains 112^T and 102^T. The isolated strains reduced Fe(III) using common fermentation products such as acetate, lactate, propionate, formate or hydrogen as electron donors, and they also grew with fumarate as the sole substrate. As alternatives to Fe(III), they reduced fumarate, S^0 and Mn(IV). Based on 16S rRNA gene sequence similarity, strain 112^T was most closely related to *Desulfuromonas acetoxidans* (97·0 %) and *Desulfuromonas thiophila* NZ27^T (95·5 %), and strain 102^T to *Malonomonas rubra* Gra Mal 1^T (96·3 %) and *Desulfuromusa succinoxidans* Gylac^T (95·9 %) within the *Deltaproteobacteria*. Strains 112^T and 102^T therefore represent novel species, for which the names *Desulfuromonas svalbardensis* sp. nov. (type strain 112^T = DSM 16958^T = JCM 12927^T) and *Desulfuromusa ferrireducens* sp. nov. (type strain 102^T = DSM 16956^T = JCM 12926^T) are proposed.

The genus *Desulfuromonas* was first described by Pfennig & Biebl (1976), who isolated the marine species *Desulfuromonas acetoxidans*, which reduces elemental sulfur with acetate. The genus contains four further species, which had been isolated with reduction of iron, sulfur or tetrachloroethene from marine and freshwater sediments: *Desulfuromonas palmitatis* (Coates *et al.*, 1995), *Desulfuromonas acetexigens* (Finster *et al.*, 1994), *Desulfuromonas thiophila* (Finster *et al.*, 1997) and *Desulfuromonas chloroethenica* (Krumholz, 1997; Krumholz *et al.*, 1996). The genus *Desulfuromusa* is represented by three species, *Desulfuromusa bakii*, *Desulfuromusa kysingii* and *Desulfuromusa succinoxidans*, isolated by elemental sulfur reduction (Liesack & Finster, 1994). Together with the genera *Pelobacter*, *Malonomonas* and *Geobacter*, *Desulfuromusa* and *Desulfuromonas* form the family *Geobacteraceae* Holmes *et al.* 2004, a monophyletic group within the *Deltaproteobacteria* (Holmes *et al.*, 2004a; Lonergan *et al.*, 1996). An important characteristic of species within this group is the ability to reduce Fe(III) and/or elemental sulfur. Additionally, some species grow by fermentation or syntrophically (Cord-Ruwisch *et al.*, 1998; Schink, 1984; Schink & Pfennig, 1982; Schink & Stieb, 1983). Due to the variety of metabolic pathways performed by isolated species of the *Geobacteraceae*, the *in situ* activity of this group remains unclear, since several constituents in freshwater and marine sediments can usually be utilized by these bacteria.

Strains were obtained from enrichment cultures inoculated with surface sediments of two fjords along the west coast of Svalbard with bottom water temperatures of 2–3 °C. Strains 49, 60, 102^T and 103 originated from Tempelfjorden, Station CD (78° 25·267′ N 17° 08·277′ E; water depth 64 m) and strain 112^T from Smeerenburgfjorden, Station J (79° 42·006′ N 11° 05·199′ E; water depth 212 m). Enrichment and isolation were performed in artificial sea-water medium (Widdel & Bak, 1992) with a reduced $MgSO_4.7H_2O$ concentration of 0·4 mM to avoid growth of sulfate-reducing bacteria. Acetate (20 mM) and synthetically produced poorly crystalline iron oxide (~30 mM) (Lovley, 2000) were added for enrichments at 10 °C. For the isolation in deep-agar dilution technique (Isaksen & Teske, 1996), iron oxide was replaced with soluble ferric citrate (~30 mM). For the determination of alternative substrates and salt, pH and vitamin requirements, growth medium with a lower salt concentration was used (salt-water medium) (Widdel & Bak, 1992). All physiological tests were performed in duplicate at 10 °C. Cultures growing with alternative substrates

The GenBank/EMBL/DDBJ accession numbers for the 16S rRNA gene sequences of strains 112^T, 49, 60, 103 and 102^T are AY835388–AY835392, respectively.

were transferred into fresh test medium for verification. Temperature tolerance of the strains was determined in an aluminium temperature-gradient block at 13 different temperatures between −2 and 30 °C (Sagemann *et al.*, 1998). Salt requirements were determined in media with 12 different NaCl concentrations between 0·05 and 5 % (w/v) and 10 different $MgCl_2.6H_2O$ concentrations between 0·02 and 3·6 % (w/v). The pH optima of the strains were determined in media with 12 different pH values (in triplicate) that covered a range from pH 5·5 to 8·3. For all tests, growth was monitored spectrophotometrically (Shimadzu UV 1202) by measuring the OD at 580 nm for cells grown on fumarate/acetate and by measuring Fe^{2+} accumulation (Stookey, 1970) for cells grown on ferric citrate/acetate. Reduction of ferric citrate was also tested in media with $FeCl_2.4H_2O$ (2–3 mM end concentration) or cysteine (1 mM end concentration) as reducing agents instead of sulfide.

Malonomonas rubra DSM 5091^T, obtained from the Deutsche Sammlung von Mikroorganismen und Zellkulturen (DSMZ, Braunschweig, Germany), was grown in salt-water medium with malonate as substrate. To test the ability of cells to grow by S^0, Fe(III) or Mn(IV) reduction, malonate was replaced with ferric citrate, poorly crystalline iron oxide, manganese oxide or S^0 as electron acceptor and acetate as electron donor.

Fatty acids were analysed by GC and GC-MS (Elvert *et al.*, 2003). Lipoquinones, the G+C content of genomic DNA and DNA–DNA hybridization were determined at the DSMZ.

PCR amplification of 16S rRNA genes was performed with the primers 8F and 1492R and PCR products were amplified for sequence analysis with primers 8F, 341F, 518F, 534R, 1099F and 1492R (Buchholz-Cleven *et al.*, 1997). The ARB program (Ludwig *et al.*, 2004) was used for phylogenetic analysis.

Purity of cultures of strains 49, 60, 103, 112^T and 102^T was checked microscopically and by inoculating the cultures into media with yeast extract, casein, glucose or fructose. Strains 49, 60, 103 and 112^T were all phylogenetically closely related (99·4–99·7 % 16S rRNA gene sequence similarity). The strains were tested for growth with a selection of environmentally important electron acceptors and donors and showed similar substrate spectra (data not shown). Furthermore, the strains all revealed similar optimum growth temperatures around 15 °C and growth at 0 °C (data not shown). Due to the similarities of strains 49, 60, 103 and 112^T, strain 112^T was selected for further detailed characterization. Strain 102^T was also characterized in detail.

Cells of strains 112^T and 102^T grew as thin rods (Fig. 1). Cells of strain 112^T were 0·7 × 2–3·5 μm and those of strain 102^T were 0·7–1 × 3–5 μm in size. Cells of the latter strain formed clumps in liquid culture. Both strains stained Gram-negative and were non-spore-forming and motile. Electron microscopy (Zeiss EM 10 A; conducted at the UFT, University of Bremen) revealed peritrichous flagellation for strain 112^T and monopolar lophotrichous flagellation for strain 102^T (Fig. 1c).

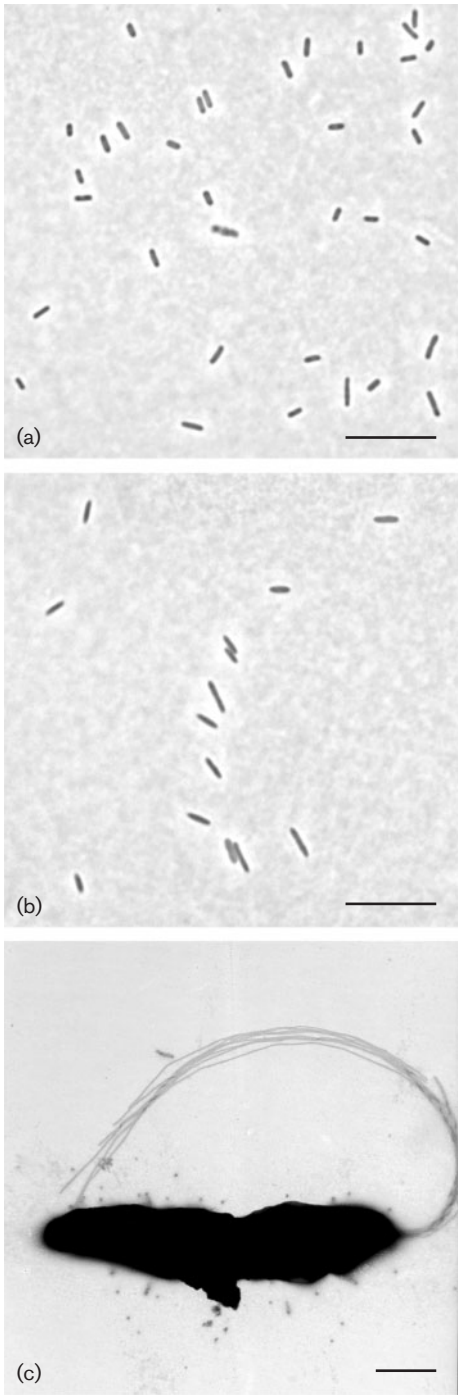

Fig. 1. (a, b) Phase-contrast micrographs of *Desulfuromonas svalbardensis* 112^T (a) and *Desulfuromusa ferrireducens* 102^T (b). (c) Electron micrograph of *Desulfuromusa ferrireducens* 102^T, showing the rod shape and the monopolar lophotrichous flagellation. Bars, 10 μm (a, b) and 1 μm (c).

Both strains grew at −2 °C, the freezing point of sea water. Strain 112^T grew fastest at 14 °C and did not grow above 20 °C. The temperature optimum of strain 102^T was between 14 and 17 °C and the maximum temperature was 23 °C. According to their temperature ranges for growth, both strains were defined as psychrophiles. Strain 112^T had an optimum for NaCl at 2·6 %, growing between 0·7 and 4·5 %. The optimum concentration for $MgCl_2.6H_2O$ was between 0·02 and 0·8 %, and growth was inhibited at concentrations above 1·9 %. For strain 102^T, the optimum for NaCl was 2·6–4 %, with growth ranging from 1·5 to 4·5 %. The strain grew equally well over the range of 0·4 to 3·6 % $MgCl_2.6H_2O$. Thus, both strains grew at sea-water concentrations of NaCl and $MgCl_2.6H_2O$, which are 2·5 % for NaCl and 1·1 % for $MgCl_2.6H_2O$. Strain 112^T grew at pH 6·5–7·5, with an optimum at pH 7·3. Strain 102^T showed a similar growth range of pH 6·5–7·9 and an optimum at pH 7·0–7·3.

Strain 112^T grew in the presence of ferric citrate with acetate, propionate, pyruvate, ethanol, propanol, butanol, proline and choline chloride as electron donors and strain 102^T with acetate, lactate, formate, H_2 (H_2/CO_2; 80 : 20, v/v), succinate, pyruvate, fumarate, ethanol, propanol, butanol and proline. Electron donors not used by either strain were butyrate, hexanoate, malate, succinate, citrate, fructose, glucose, glycerol, glycine, glutarate, alanine, serine, proline, betaine, sorbitol, nicotinate, yeast extract and casein; substrates not used by strain 112^T were lactate, formate, fumarate, succinate and H_2, and strain 102^T did not use propionate or choline chloride. Both strains grew by reduction of Fe(III) compounds (ferric citrate and iron oxide tested) and fumarate in the presence of acetate. Additionally, the strains slowly reduced elemental sulfur and manganese oxide. Neither strain reduced sulfate, thiosulfate, sulfite, nitrate, nitrite, oxygen or malate. Ferric citrate was also reduced in media with $FeCl_2$ or cysteine as reducing agents instead of sulfide. No reduction of Fe(III) in the presence of oxygen was observed for either strain. Disproportionation of sulfur or thiosulfate was not observed. Both strains grew with fumarate as the sole substrate, but not with lactate, malate, malonate, pyruvate, glucose or fructose. The major end product of fumarate disproportionation was succinate. Strain 102^T did not require vitamins for growth, whereas strain 112^T required biotin.

The phospholipid-derived ester-linked fatty acid composition of strains 112^T and 102^T is listed in Table 1. $C_{16:1}\omega7c$ and $C_{16:0}$ were dominant as fatty acids in both strains, similar to the fatty acid composition of *Geobacter metallireducens* (Lovley *et al.*, 1993). Cells of strain 112^T contained MK-8 as the major menaquinone and traces of MK-9 (2 %); cells of strain 102^T contained only MK-8. The DNA G+C contents were 50·1 mol% for strain 112^T and 52·3 mol% for strain 102^T.

Comparative analysis of the 16S rRNA gene sequences showed that both strains belong to the *Deltaproteobacteria* (Fig. 2). Strain 112^T was related to *Desulfuromonas acetoxidans* (97·0 % 16S rRNA gene sequence similarity), *Desulfuromonas thiophila* NZ27^T (95·5 %), *Pelobacter venetianus* (93·7 %) and *Desulfuromonas chloroethenica* TT4B^T (93·1 %). Species of the genus *Desulfuromonas* were isolated by reduction of elemental sulfur [*Desulfuromonas acetoxidans* (Pfennig & Biebl, 1976), *Desulfuromonas acetexigens* (Finster *et al.*, 1994) and *Desulfuromonas thiophila* (Finster *et al.*, 1997)], tetrachloroethene [*Desulfuromonas chloroethenica* (Krumholz, 1997; Krumholz *et al.*, 1996) and '*Desulfuromonas michiganensis*' (Sung *et al.*, 2003)] or Fe(III) compounds [*Desulfuromonas palmitatis* (Coates *et al.*, 1995)]. However, all species of this genus were able to reduce iron compounds and sulfur (Table 2). Strain 112^T was most closely related to the marine species *Desulfuromonas acetoxidans*, which, similarly to strain 112^T, was able to reduce elemental sulfur, Fe(III) and Mn(IV) (Pfennig & Biebl, 1976; Roden & Lovley, 1993). The two strains differed mainly in their temperature tolerance, with *Desulfuromonas acetoxidans* being mesophilic, growing between 25 and 35 °C, and strain 112^T being psychrophilic, growing between −2 and 20 °C. Physiological differences between the two strains were the ability of strain 112^T to oxidize propionate and to grow by disproportionation of fumarate and its inability to reduce malate (Table 2). DNA–DNA hybridization determined 22·7 % relatedness between strain 112^T and *Desulfuromonas acetoxidans* DSM 684^T. Therefore, we propose the description of strain 112^T as the type strain of a novel species, *Desulfuromonas svalbardensis* sp. nov.

The closest relatives of strain 102^T were *Malonomonas rubra* Gra Mal 1^T (96·3 % 16S rRNA gene sequence similarity),

Table 1. Fatty acid abundances of strains 112^T and 102^T

Values are proportions of total fatty acids. tr, Trace (<0·01). Major components are shown in bold.

Fatty acid	112^T	102^T
$C_{13:0}$	0·01	0·01
i-$C_{14:0}$	0	tr
$C_{14:0}$	0·07	0·07
i-$C_{15:0}$	0·02	0
ai-$C_{15:0}$	0	0·01
$C_{15:0}$	0·01	0·01
$C_{16:1}\omega9c$	0·01	0·01
$C_{16:1}\omega7c$	**0·35**	**0·39**
$C_{16:1}\omega7t$	0	0·02
$C_{16:1}\omega5c$	0·04	0·01
$C_{16:0}$	**0·43**	**0·36**
10-Me $C_{16:0}$	0	tr
i-$C_{17:0}$	tr	tr
ai-$C_{17:0}$	tr	tr
$C_{17:0}$	0	0·01
$C_{18:2}$	0	0·02
$C_{18:1}\omega9$	0·01	0·02
$C_{18:1}\omega7$	0·01	0·01
$C_{18:1}\omega5$	tr	0
$C_{18:0}$	0·02	0·06

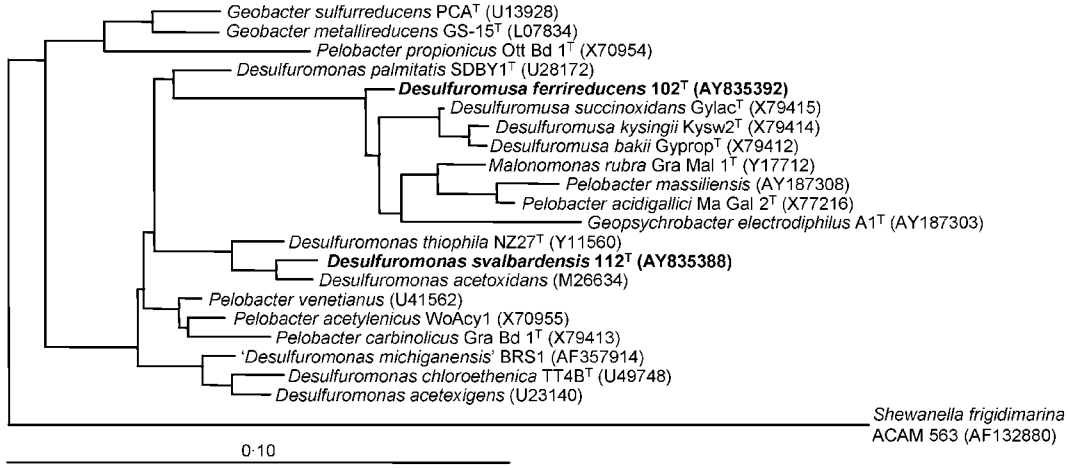

Fig. 2. Phylogenetic tree of 16S rRNA gene sequences based on maximum-likelihood methods with a 50 % filter for *Deltaproteobacteria*, showing the position of *Desulfuromusa ferrireducens* 102^T and *Desulfuromonas svalbardensis* 112^T. Bar, 10 % estimated sequence divergence.

Desulfuromusa succinoxidans Gylac^T (95·9 %), *Desulfuromusa kysingii* Kysw2^T (95·5 %) and *Desulfuromusa bakii* Gyprop^T (95·4 %). *Malonomonas rubra* is so far the only described species of this genus, and the genus was established because of the ability of this species to grow by fermentation of malonate (Dehning & Schink, 1989), but cells did not grow by anaerobic respiration (Kolb *et al.*, 1998). The ability of *Malonomonas rubra* to reduce iron compounds was described recently (Holmes *et al.*, 2004a), and these authors suggested that *Malonomonas rubra* should be renamed as a member of the genus *Desulfuromusa*. This is supported by our results, as *Malonomonas rubra* DSM 5091^T reduced ferric citrate, iron oxide, elemental sulfur and manganese oxide with acetate as electron donor (Table 3). Therefore, we propose strain 102^T as the type strain of a novel species of the genus *Desulfuromusa*, *Desulfuromusa ferrireducens* sp. nov. The newly isolated strain 102^T was psychrophilic, growing between −2 and 23 °C, whereas the other *Desulfuromusa* species do not grow below 4 °C and their optimum temperatures for growth are ⩾25 °C (Finster & Bak, 1993; Liesack & Finster, 1994). The psychrotolerant species *Geopsychrobacter electrodiphilus* is closely related to species of *Desulfuromusa* and *Malonomonas rubra*, but represents a unique phylogenetic cluster (Holmes *et al.*, 2004b). Species of *Desulfuromusa*, *Malonomonas rubra*, strain 102^T and *Geopsychrobacter electrodiphilus* share the

Table 2. Major characteristics of species of the genus *Desulfuromonas* and strain 112^T

Reference species: 1, *Desulfuromonas acetoxidans*; 2, *Desulfuromonas acetexigens*; 3, *Desulfuromonas thiophila*; 4, *Desulfuromonas chloroethenica*; 5, *Desulfuromonas palmitatis*; 6, '*Desulfuromonas michiganensis*'. Data for reference species were taken from Pfennig & Biebl (1976), Finster *et al.* (1994, 1997), Coates *et al.* (1995), Krumholz (1997) and Sung *et al.* (2003). ND, Not determined; +, substrate used for growth; −, substrate not used for growth; (+), substrate reduced but no growth observed. All taxa use sulfur as an electron acceptor. Not all electron donors and acceptors used by the species are listed in this table.

Characteristic	Strain 112^T	1	2	3	4	5	6
Temperature optimum (°C)	14	30	30	26–30	21–31	40	25
Temperature range (°C)	−2 to 20	25–35	ND	10–40	21–31	ND	5–45
Electron donors							
Propionate	+	−	−	−	ND	−	−
Electron acceptors							
Fe(III) compounds	+	+	ND	(+)	+	+	+
Mn(IV) oxide	+	+	ND	ND	ND	+	ND
Fumarate	+	+	+	−	+	+	+
Malate	−	+	+	−	ND	−	+
Disproportionation of fumarate	+	−	ND	−	ND	ND	+

Table 3. Major characteristics of species of the genus *Desulfuromusa*, *Malonomonas rubra*, *Geopsychrobacter electrodiphilus* and strain 102^T

Reference species: 1, *Desulfuromusa succinoxidans*; 2, *Desulfuromusa kysingii*; 3, *Desulfuromusa bakii*; 4, *Malonomonas rubra*; 5, *Geopsychrobacter electrodiphilus*. Data for reference species were taken from Liesack & Finster (1994), Dehning & Schink (1989) and Holmes *et al.* (2004b). ND, Not determined; +, substrate used for growth, −, substrate not used for growth. All taxa use elemental sulfur as an electron acceptor. Not all electron donors and acceptors used by the species are listed in this table.

Characteristic	Strain 102^T	1	2	3	4	5
Temperature optimum (°C)	14–17	30–35	30–35	25–30	28–30	22
Temperature range (°C)	−2 to 23	4–35	4–35	8–32	22–45	4–30
Electron donors:						
Formate	+	−	−	−	ND	−
Propionate	−	+	+	+	ND	−
Alcohols*	+	−	−	−	ND	Ethanol only
Lactate	+	+	+	+	ND	−
Electron acceptors:						
Fe(III) compounds	+	−	+	−	+	+
Mn(IV) oxide	+	ND	ND	ND	+	+
Fumarate	+	+	+	+	ND	−
Malate	−	−	+	−	ND	−
Nitrate	−	−	+	−	ND	ND
Disproportionation of:						
Fumarate	+	+	+	+	+	ND
Malate	−	+	+	+	+	ND
Malonate	−	−	−	−	+	ND

*Alcohols tested were ethanol, propanol and butanol.

ability to reduce elemental sulfur and Mn(IV) and oxidize acetate, succinate and pyruvate, but differ in the usage of other substrates (Table 3).

The *in situ* abundance of members of the family *Geobacteraceae* had been demonstrated for temperate as well as permanently cold marine sediments of the Arctic and Antarctica, as several sequences closely related to strains of the *Geobacteraceae* had been found in 16S rRNA clone libraries of these sediments (Ravenschlag *et al.*, 1999; Bowman & McCuaig, 2003; Purdy *et al.*, 2003; Mußmann *et al.*, 2005). The isolation of strains 102^T and 112^T from marine sediments from Svalbard suggests that this group of bacteria is present in diverse freshwater and marine environments. Yet, the significance and *in situ* activity of the sulfur-/ferric iron-reducing members of the *Geobacteraceae* remains unclear for most habitats. As reviewed by Thamdrup (2000), ferric iron reduction is the second most important anaerobic respiration pathway in a wide range of habitats. In Arctic marine sediments of Svalbard, ferric iron reduction accounted for 0–26 % of the total carbon respiration (Kostka *et al.*, 1999). Marine surface sediments that have a zone of reactive iron and manganese as well as accumulation of elemental sulfur provide optimal conditions for bacteria able to reduce these compounds, such as the strains described here. Such a sediment setting was, for example, described on the Danish coast, where the concentration of sulfur was highest in the zone of iron/manganese reduction (Sørensen & Jørgensen, 1987), due to the rapid reaction of H_2S with Mn(IV) or Fe(III) to form elemental sulfur.

Possible substrates for Fe(III)-reducing bacteria are common fermentation products such as volatile short-chain fatty acids and hydrogen. Strains 112^T and 102^T oxidized important fermentation products such as acetate, lactate, formate or hydrogen concomitant with the reduction of Fe(III). Acetate is an important substrate for sulfate-reducing bacteria in temperate as well as Arctic marine sediments (e.g. Sørensen *et al.*, 1981; Finke, 2003). Turnover rates in Arctic fjord sediments were highest for acetate, followed by lactate and propionate (Finke, 2003).

Psychrophilic sulfate-reducing bacteria isolated from Svalbard sediments showed constant growth yields between −2 °C and their optimum growth temperature (Knoblauch & Jørgensen, 1999). Among the Fe(III)-reducing bacteria, psychrophiles of the genus *Shewanella* have been isolated from the Antarctic, the Alboran Sea and deep-sea sediments of the Pacific Ocean, including *Shewanella frigidimarina*, *Shewanella gelidimarina*, *Shewanella woodyi* and *Shewanella violacea* (Bowman *et al.*, 1997; Makemson *et al.*, 1997; Nogi *et al.*, 1998). The strains isolated by Fe(III) reduction in the present study grew at *in situ* temperatures just above the freezing point of sea water and were accordingly well adapted to the permanently low temperatures of the Arctic Ocean.

Recently, the first psychrophilic and psychrotolerant species within the family *Geobacteraceae* have been isolated, *Geopsychrobacter electrodiphilus* and *Geobacter psychrophilus* (Holmes *et al.*, 2004b; Nevin *et al.*, 2005). Our isolates extend the group of psychrophiles within the *Geobacteraceae*.

In summary, the isolated strains were well suited to life in anoxic, permanently cold sediments of Svalbard. The abundance and diversity of Fe(III)- and sulfur-reducing bacteria in this environment have, however, not been investigated. More studies on the microbial communities and their *in situ* activities are needed to understand fully the importance of sulfur and Fe(III) reduction in marine sediments.

Description of *Desulfuromonas svalbardensis* sp. nov.

Desulfuromonas svalbardensis (sval.bard.en′sis. N.L. fem. adj. *svalbardensis* from Svalbard, a group of islands in the northern Barents Sea, from where the type strain was isolated).

Cells are rod-shaped, 0·7 × 2·5–3 μm, motile by peritrichous flagella. Gram-negative, strictly anaerobic and chemo-organotrophic. Biotin is required for growth. Grows by oxidation of acetate, propionate, ethanol, propanol, butanol, choline chloride or pyruvate with concomitant reduction of Fe(III). Fe(III) compounds, manganese oxide, elemental sulfur and fumarate serve as electron acceptors. Disproportionation of fumarate is observed. The pH range for growth is pH 6·5–7·5; optimum pH is 7·3. Psychrophilic, with an optimum growth temperature of 14 °C and a temperature range for growth of −2 to 20 °C. The DNA G+C content of the type strain is 50·1 mol%.

The type strain, strain 112^T (= DSM 16958^T = JCM 12927^T), was isolated from a permanently cold fjord sediment of the west coast of Svalbard.

Description of *Desulfuromusa ferrireducens* sp. nov.

Desulfuromusa ferrireducens [fer.ri.re.du′cens. L. n. *ferrum* iron; L. part. adj. *reducens* leading back, bringing back and, in chemistry, converting to a reduced oxidation state; N.L. part. adj. *ferrireducens* reducing Fe(III) to Fe(II)].

Cells are rod-shaped, 0·7–1 × 3–5 μm, motile by monopolar lophotrichous flagella. Gram-negative, strictly anaerobic and chemo-organotrophic. No vitamins are required for growth. Oxidizes acetate, lactate, succinate, fumarate, pyruvate, proline, ethanol, propanol, butanol, formate or H_2 with the reduction of Fe(III). Fe(III) compounds, elemental sulfur, manganese oxide and fumarate serve as electron acceptors. Disproportionation of fumarate is observed. The pH range for growth is pH 6·5–7·9; optimum is pH 7·0–7·3. Psychrophilic, with an optimum growth temperature of 14–17 °C and a temperature range for growth of −2 to 23 °C. The DNA G+C content of the type strain is 52·3 mol%.

The type strain, strain 102^T (= DSM 16956^T = JCM 12926^T), was isolated from a permanently cold fjord sediment of the west coast of Svalbard.

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References

Bowman, J. P. & McCuaig, R. D. (2003). Biodiversity, community structural shifts, and biogeography of prokaryotes within Antarctic continental shelf sediment. *Appl Environ Microbiol* **69**, 2463–2483.

Bowman, J. P., McCammon, S. A., Nichols, D. S., Skerratt, J. H., Rea, S. M., Nichols, P. D. & McMeekin, T. A. (1997). *Shewanella gelidimarina* sp. nov. and *Shewanella frigidimarina* sp. nov., novel Antarctic species with the ability to produce eicosapentaenoic acid (20 : 5ω3) and grow anaerobically by dissimilatory Fe(III) reduction. *Int J Syst Bacteriol* **47**, 1040–1047.

Buchholz-Cleven, B. E. E., Rattunde, B. & Straub, K. L. (1997). Screening for genetic diversity of isolates of anaerobic Fe(II)-oxidizing bacteria using DGGE and whole-cell hybridization. *Syst Appl Microbiol* **20**, 301–309.

Coates, J. D., Lonergan, D. J., Phillips, E. J. P., Jenter, H. & Lovley, D. R. (1995). *Desulfuromonas palmitatis* sp. nov., a marine dissimilatory Fe(III) reducer that can oxidize long-chain fatty acids. *Arch Microbiol* **164**, 406–413.

Cord-Ruwisch, R., Lovley, D. R. & Schink, B. (1998). Growth of *Geobacter sulfurreducens* with acetate in syntrophic cooperation with hydrogen-oxidizing anaerobic partners. *Appl Environ Microbiol* **64**, 2232–2236.

Dehning, I. & Schink, B. (1989). *Malonomonas rubra* gen. nov., sp. nov., a microaerotolerant anaerobic bacterium growing by decarboxylation of malonate. *Arch Microbiol* **151**, 427–433.

Elvert, M., Boetius, A., Knittel, K. & Jørgensen, B. B. (2003). Characterization of specific membrane fatty acids as chemotaxonomic markers for sulfate-reducing bacteria involved in anaerobic oxidation of methane. *Geomicrobiol J* **20**, 403–419.

Finke, N. (2003). *The role of volatile fatty acids and hydrogen in the degradation of organic matter in marine sediments.* PhD thesis, University of Bremen, Germany.

Finster, K. & Bak, F. (1993). Complete oxidation of propionate, valerate, succinate, and other organic compounds by newly isolated types of marine, anaerobic, mesophilic, gram-negative, sulfur-reducing eubacteria. *Appl Environ Microbiol* **59**, 1452–1460.

Finster, K., Bak, F. & Pfennig, N. (1994). *Desulfuromonas acetexigens* sp. nov., a dissimilatory sulfur-reducing eubacterium from anoxic freshwater sediments. *Arch Microbiol* **161**, 328–332.

Finster, K., Coates, J. D., Liesack, W. & Pfennig, N. (1997). *Desulfuromonas thiophila* sp. nov., a new obligately sulfur-reducing

bacterium from anoxic freshwater sediment. *Int J Syst Bacteriol* **47**, 754–758.

Holmes, D. E., Nevin, K. P. & Lovley, D. R. (2004a). Comparison of 16S rRNA, *nifD*, *recA*, *gyrB*, *rpoB* and *fusA* genes within the family *Geobacteraceae* fam. nov. *Int J Syst Evol Microbiol* **54**, 1591–1599.

Holmes, D. E., Nicoll, J. S., Bond, D. R. & Lovley, D. R. (2004b). Potential role of a novel psychrotolerant member of the family *Geobacteraceae*, *Geopsychrobacter electrodiphilus* gen. nov., sp. nov., in electricity production by a marine sediment fuel cell. *Appl Environ Microbiol* **70**, 6023–6030.

Isaksen, M. F. & Teske, A. (1996). *Desulforhopalus vacuolatus* gen. nov., sp. nov., a new moderately psychrophilic sulfate-reducing bacterium with gas vacuoles isolated from a temperate estuary. *Arch Microbiol* **166**, 160–168.

Knoblauch, C. & Jørgensen, B. B. (1999). Effect of temperature on sulphate reduction, growth rate and growth yield in five psychrophilic sulphate-reducing bacteria from Arctic sediments. *Environ Microbiol* **1**, 457–467.

Kolb, S., Seelinger, S., Springer, N., Ludwig, W. & Schink, B. (1998). The fermenting bacterium *Malonomonas rubra* is phylogenetically related to sulfur-reducing bacteria and contains a c-type cytochrome similar to those of sulfur and sulfate reducers. *Syst Appl Microbiol* **21**, 340–345.

Kostka, J. E., Thamdrup, B., Glud, R. N. & Canfield, D. E. (1999). Rates and pathways of carbon oxidation in permanently cold Arctic sediments. *Mar Ecol Prog Ser* **180**, 7–21.

Krumholz, L. R. (1997). *Desulfuromonas chloroethenica* sp. nov. uses tetrachloroethylene and trichloroethylene as electron acceptors. *Int J Syst Bacteriol* **47**, 1262–1263.

Krumholz, L. R., Sharp, R. & Fishbain, S. S. (1996). A freshwater anaerobe coupling acetate oxidation to tetrachloroethylene dehalogenation. *Appl Environ Microbiol* **62**, 4108–4113.

Liesack, W. & Finster, K. (1994). Phylogenetic analysis of five strains of gram-negative, obligately anaerobic, sulfur-reducing bacteria and description of *Desulfuromusa* gen. nov., including *Desulfuromusa kysingii* sp. nov., *Desulfuromusa bakii* sp. nov., and *Desulfuromusa succinoxidans* sp. nov. *Int J Syst Bacteriol* **44**, 753–758.

Lonergan, D. J., Jenter, H. L., Coates, J. D., Phillips, E. J. P., Schmidt, T. M. & Lovley, D. R. (1996). Phylogenetic analysis of dissimilatory Fe(III)-reducing bacteria. *J Bacteriol* **178**, 2402–2408.

Lovley, D. (2000). Dissimilatory Fe(III)- and Mn(IV)-reducing prokaryotes. In *The Prokaryotes. An Evolving Electronic Resource for the Microbiological Community*. Edited by M. Dworkin, S. Falkow, E. Rosenberg, K. H. Schleifer & E. Stackebrandt. http://141.150.157.117:8080/prokPUB/index.htm

Lovley, D. R., Giovannoni, S. J., White, D. C., Champine, J. E., Phillips, E. J. P., Gorby, Y. A. & Goodwin, S. (1993). *Geobacter metallireducens* gen. nov. sp. nov, a microorganism capable of coupling the complete oxidation of organic compounds to the reduction of iron and other metals. *Arch Microbiol* **159**, 336–344.

Ludwig, W., Strunk, O., Westram, R. & 29 other authors (2004). ARB: a software environment for sequence data. *Nucleic Acids Res* **32**, 1363–1371.

Makemson, J. C., Fulayfil, N. R., Landry, W., van Ert, L. M., Wimpee, C. F., Widder, E. A. & Case, J. F. (1997). *Shewanella woodyi* sp. nov., an exclusively respiratory luminous bacterium isolated from the Alboran Sea. *Int J Syst Bacteriol* **47**, 1034–1039.

Mußmann, M., Ishii, K., Rabus, R. & Amann, R. (2005). Diversity and vertical distribution of cultured and uncultured *Deltaproteobacteria* in an intertidal mud flat of the Wadden Sea. *Environ Microbiol* **7**, 405–418.

Nevin, K. P., Holmes, D. E., Woodard, T. L., Hinlein, E. S., Ostendorf, D. W. & Lovley, D. R. (2005). *Geobacter bemidjiensis* sp. nov. and *Geobacter psychrophilus* sp. nov., two novel Fe(III)-reducing subsurface isolates. *Int J Syst Evol Microbiol* **55**, 1667–1674.

Nogi, Y., Kato, C. & Horikoshi, K. (1998). Taxonomic studies of deep-sea barophilic *Shewanella* strains and description of *Shewanella violacea* sp. nov. *Arch Microbiol* **170**, 331–338.

Pfennig, N. & Biebl, H. (1976). *Desulfuromonas acetoxidans* gen. nov. and sp. nov., a new anaerobic, sulfur-reducing, acetate-oxidizing bacterium. *Arch Microbiol* **110**, 3–12.

Purdy, K. J., Nedwell, D. B. & Embley, T. M. (2003). Analysis of sulfate-reducing bacterial and methanogenic archaeal populations in contrasting Antarctic sediments. *Appl Environ Microbiol* **69**, 3181–3191.

Ravenschlag, K., Sahm, K., Pernthaler, J. & Amann, R. (1999). High bacterial diversity in permanently cold marine sediments. *Appl Environ Microbiol* **65**, 3982–3989.

Roden, E. E. & Lovley, D. R. (1993). Dissimilatory Fe(III) reduction by the marine microorganism *Desulfuromonas acetoxidans*. *Appl Environ Microbiol* **59**, 734–742.

Sagemann, J., Jørgensen, B. B. & Greef, O. (1998). Temperature dependence and rates of sulfate reduction in cold sediments of Svalbard, Arctic Ocean. *Geomicrobiol J* **15**, 85–100.

Schink, B. (1984). Fermentation of 2,3-butanediol by *Pelobacter carbinolicus* sp. nov. and *Pelobacter propionicus* sp. nov., and evidence for propionate formation from C_2 compounds. *Arch Microbiol* **137**, 33–41.

Schink, B. & Pfennig, N. (1982). Fermentation of trihydroxybenzenes by *Pelobacter acidigallici* gen. nov. sp. nov., a new strictly anaerobic, non-spore-forming bacterium. *Arch Microbiol* **133**, 195–201.

Schink, B. & Stieb, M. (1983). Fermentative degradation of polyethylene glycol by a strictly anaerobic, gram-negative, nonsporeforming bacterium, *Pelobacter venetianus* sp. nov. *Appl Environ Microbiol* **45**, 1905–1913.

Sørensen, J. & Jørgensen, B. B. (1987). Early diagenesis in sediments from Danish coastal waters: microbial activity and Mn-Fe-S geochemistry. *Geochim Cosmochim Acta* **51**, 1583–1590.

Sørensen, J., Christensen, D. & Jørgensen, B. B. (1981). Volatile fatty acids and hydrogen as substrates for sulfate-reducing bacteria in anaerobic marine sediment. *Appl Environ Microbiol* **42**, 5–11.

Stookey, L. L. (1970). Ferrozine – a new spectrophotometric reagent for iron. *Anal Chem* **42**, 779–781.

Sung, Y., Ritalahti, K. M., Sanford, R. A., Urbance, J. W., Flynn, S. J., Tiedje, J. M. & Löffler, F. E. (2003). Characterization of two tetrachloroethene-reducing, acetate-oxidizing anaerobic bacteria and their description as *Desulfuromonas michiganensis* sp. nov. *Appl Environ Microbiol* **69**, 2964–2974.

Thamdrup, B. (2000). Bacterial manganese and iron reduction in aquatic sediments. *Adv Microb Ecol* **16**, 41–84.

Widdel, F. & Bak, F. (1992). Gram-negative mesophilic sulfate-reducing bacteria. In *The Prokaryotes*, 2nd edn, pp. 3352–3378. Edited by A. Balows, H. G. Trüper, M. Dworkin, W. Harder & K. H. Schleifer. Berlin: Springer.