Desulfotomaculum carboxydivorans sp. nov., a novel sulfate-reducing bacterium capable of growth at 100 % CO

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A moderately thermophilic, anaerobic, chemolithoheterotrophic, sulfate-reducing bacterium, strain CO-1-SRB[T], was isolated from sludge from an anaerobic bioreactor treating paper mill wastewater. Cells were Gram-positive, motile, spore-forming rods. The temperature range for growth was 30–68 °C, with an optimum at 55 °C. The NaCl concentration range for growth was 0–17 g l^{-1}; there was no change in growth rate until the NaCl concentration reached 8 g l^{-1}. The pH range for growth was 6·0–8·0, with an optimum of 6·8–7·2. The bacterium could grow with 100 % CO in the gas phase. With sulfate, CO was converted to H_2 and CO_2 and part of the H_2 was used for sulfate reduction; without sulfate, CO was completely converted to H_2 and CO_2. With sulfate, strain CO-1-SRB[T] utilized H_2/CO_2, pyruvate, glucose, fructose, maltose, lactate, serine, alanine, ethanol and glycerol. The strain fermented pyruvate, lactate, glucose and fructose. Yeast extract was necessary for growth. Sulfate, thiosulfate and sulfite were used as electron acceptors, whereas elemental sulfur and nitrate were not. A phylogenetic analysis of 16S rRNA gene sequences placed strain CO-1-SRB[T] in the genus *Desulfotomaculum*, closely resembling *Desulfotomaculum nigrificans* DSM 574[T] and *Desulfotomaculum* sp. RHT-3 (99 and 100 % similarity, respectively). However, the latter strains were completely inhibited above 20 and 50 % CO in the gas phase, respectively, and were unable to ferment CO, lactate or glucose in the absence of sulfate. DNA–DNA hybridization of strain CO-1-SRB[T] with *D. nigrificans* and *Desulfotomaculum* sp. RHT-3 showed 53 and 60 % relatedness, respectively. On the basis of phylogenetic and physiological features, it is suggested that strain CO-1-SRB[T] represents a novel species within the genus *Desulfotomaculum*, for which the name *Desulfotomaculum carboxydivorans* is proposed. This is the first description of a sulfate-reducing micro-organism that is capable of growth under an atmosphere of pure CO with and without sulfate. The type strain is CO-1-SRB[T] (=DSM 14880[T] = VKM B-2319[T]).

Anaerobic conversion of CO has been reported for a large number of micro-organisms, including phototrophs, homo-acetogens, methanogens and sulfate-reducers (Mörsdorf *et al.*, 1992; Davidova *et al.*, 1994). Several anaerobic hydrogenic thermophilic bacteria that were able to convert CO to H_2/CO_2 have been isolated from different natural habitats (Svetlichny *et al.*, 1991, 1994; Sokolova *et al.*, 2001, 2002, 2004a). Recently, the first hyperthermophilic archaeon capable of hydrogenogenic CO conversion was described (Sokolova *et al.*, 2004b). Most of the recently described carboxydotrophic bacteria grow at a high partial pressure of CO, despite the fact that these conditions are never encountered in the environment.

In contrast to the so-called hydrogenogens (Svetlichnyi *et al.*, 2001), most anaerobic micro-organisms metabolizing

CO are sensitive to high levels of CO. Sulfate-reducing bacteria in particular are considered to be very sensitive to CO (Mörsdorf *et al.*, 1992; Davidova *et al.*, 1994). Several sulfate-reducing bacteria are able to convert CO at concentrations of up to 20 %, but higher concentrations completely inhibit growth (Lupton *et al.*, 1984; Klemps *et al.*, 1985; Karpilova *et al.*, 1983; Mörsdorf *et al.*, 1992; Davidova *et al.*, 1994). Our recent experiments with several strains of thermophilic sulfate-reducing bacteria have demonstrated that *Desulfotomaculum kuznetsovii* and *Desulfotomaculum thermobenzoicum* subsp. *thermosyntrophicum* are able to use CO as a sole carbon and energy source at concentrations of up to 50 % CO in the gas phase and are able to reduce sulfate with CO (Parshina *et al.*, 2005). To date, no sulfate-reducing bacterium, growing on pure CO, has been isolated.

Batch experiments at a moderately elevated temperature (55 °C) with several mesophilic anaerobic sludges have revealed the presence of viable populations of fast-growing hydrogenogenic CO-oxidizing bacteria (Sipma *et al.*, 2003). To date, anaerobic hydrogenogenic CO-converting microorganisms have only been isolated from high-temperature volcanic environments that contain small amounts of CO (Symonds *et al.*, 1994). The presence of hydrogenogenic, moderately thermophilic CO-converting bacteria in anaerobic bioreactors, where *in situ* CO concentrations are presumed to be negligible, is very interesting and has not been observed before. Furthermore, sulfate-reducing activity at high CO concentrations (up to 100 % CO and 180 kPa) has also not been reported previously.

We describe the isolation and characterization of a novel moderately thermophilic, sulfate-reducing bacterium that is able to grow at 100 % CO. Anaerobic granular (methanogenic) sludge samples were obtained from a full-scale anaerobic reactor treating wastewater from several paper mills (Industriewater Eerbeek BV., Eerbeek, The Netherlands). This sludge was originally cultivated at 30–35 °C. CO conversion by this sludge has been described previously (Sipma *et al.*, 2004).

To obtain an enrichment of hydrogenogenic CO-converting bacteria, bottles containing crushed Eerbeek sludge were incubated at 55 °C. A suspension of crushed granules was obtained as reported previously (Sipma *et al.*, 2003) and cultivated in a liquid medium. The medium was prepared as described by Parshina *et al.* (2005). After a few series of dilutions under an atmosphere of 100 % CO (at 120–180 kPa), an enriched culture was obtained that contained at least three morphologically different bacteria. The morphology of one of the strains resembled that of the spore-forming sulfate-reducing bacteria investigated by Parshina *et al.* (2005). The addition of 20 mM sodium sulfate to the dilution series under 100 % CO resulted in a suspension of morphologically identical cells. Roll-tubes containing the same medium supplemented with 5 % agar and pure CO in the gas phase were prepared in order to obtain separate colonies. Some of the colonies obtained

were subsequently inoculated in the liquid medium. One of these cultures, CO-1-SRB[T], was selected for further study.

Desulfotomaculum nigrificans DSM 574[T] was obtained from the Deutsche Sammlung von Mikroorganismen und Zellkulturen (DSMZ), Braunschweig, Germany, and *Desulfotomaculum* sp. RHT-3 (Mori *et al.*, 2000) was kindly provided by Professor K. Takamizawa (Gifu University, Japan). These strains were cultivated in medium supplemented with pyruvate or under an atmosphere of H_2/CO_2 in the presence of sulfate.

CO (purity 99·997 %) was supplied by Hoek Loos. Medium preparation and analytical methods used were as described by Parshina *et al.* (2003, 2005). CO_2 analysis was performed according to Henstra & Stams (2004). Desulfoviridin was analysed using the method of Postgate (1979). In common with *D. nigrificans* DSM 574[T], strain CO-1-SRB[T] did not contain desulfoviridin.

Cells of strain CO-1-SRB[T] were rod-shaped with rounded ends (0·5–1·5 μm thick and 5–15 μm long) and sometimes occurred in pairs. Cells were motile with a 'twisting and tumbling' motion. Strain CO-1-SRB[T] formed oval spores that were terminal or subterminal. After 6 days of growth in agar medium with glucose, rhizoid black colonies with a diameter of 0·5 mm were obtained. The purity of the strain was checked by phase-contrast microscopy after cultivation on CO, H_2/CO_2 and glucose (with and without sulfate).

Unless otherwise stated, experiments were performed in duplicate. Growth was assessed by measuring the OD_{660} and by monitoring substrate consumption and product formation. The temperature, pH and NaCl ranges were determined in stationary cultures with CO. To determine the pH range, medium was prepared with 50 mM phosphate buffer and adjusted by adding 6 M HCl or 6 M NaOH.

Strain CO-1-SRB[T] grew between 30 and 68 °C, with an optimum temperature of 55 °C. Growth occurred between 0 and 17 g NaCl l^{-1}; at concentrations higher than 8 g NaCl l^{-1}, the growth rate was reduced. Growth occurred between pH 6·0 and 8·0, with an optimum between 6·8 and 7·2. The following possible electron donors for growth were tested (20 mM unless otherwise indicated): pyruvate, lactate, glucose, fructose, sucrose, maltose, galactose, serine, alanine, acetate, formate, butyrate, fumarate, benzoate, ethylene glycol, cellobiose, amorphous cellulose (2 g l^{-1}), methanol, ethanol, propanol, butanol, H_2/CO_2 (80 : 20 %) and CO (100 %) with (20 mM) and without sulfate. Potential electron acceptors that were tested included sulfate (20 mM), thiosulfate (20 mM), sulfite (2 mM), nitrate (10 mM) and sulfur (2 g l^{-1}). Growth in the presence of sulfate was found with CO (100 %), H_2/CO_2, pyruvate, glucose, fructose, maltose, lactate, alanine, serine, ethanol and glycerol. Very weak growth was observed on yeast extract alone (2 g l^{-1}) plus sulfate. Growth in the absence of sulfate was found with CO (100 %), pyruvate,

lactate, glucose and fructose. No growth in the presence of sulfate was observed on acetate, malate, fumarate, benzoate, cellobiose, galactose, maltose, butyrate or ethylene glycol. In the absence of sulfate, no growth was observed on acetate, malate, fumarate, glycerol, alanine, ethanol, methanol, formate, butyrate, benzoate, cellobiose, galactose or ethylene glycol. Growth with sulfate, thiosulfate and sulfite as the electron acceptor was observed using lactate as the electron donor, whereas no growth was found with sulfur and nitrate. Glucose was degraded to hydrogen and acetate. Yeast extract (0.5 g l^{-1}) was necessary for growth.

Fig. 1 shows CO conversion by strain CO-1-SRB^T with 100 % CO, in the absence and presence of sulfate. The CO conversion rates were similar. Pure CO was converted with stoichiometric production of H_2 and CO_2 (CO_2 was not analysed during the course of this experiment and is therefore not shown). The OD_{660} at the end of growth was 0·15. In the medium with sulfate, hydrogen and H_2S (up to 6 mM) were formed and a final OD_{660} of 0·32 was obtained. No other products were formed during CO conversion.

Lipid fatty acids were extracted from dry samples (5 mg). The biomass was methanolysed in 0·4 ml 1·2 M HCl in methanol by heating at 80 °C for 1 h. The resulting fatty acid methyl esters were extracted twice with 0·2 ml hexane and processed using the computer-assisted Microbial Identification System (MIS) (Microbial ID) with a gas chromatograph (5890A; Hewlett Packard) equipped with

an automatic sampler (7673A; Hewlett Packard). The parameters used for chromatography were those recommended in the MIS instruction manual.

Gas chromatography-mass spectrometry (GC-MS) analysis was performed using a GC-MS system (AT-5973B; Agilent Technology) with a cross-linked methyl silicone capillary column (HP-5MS, Hewlett Packard). The oven temperature was programmed for 2 min at 120 °C, rising to 280 °C at 5 °C min^{-1}. Samples (1–2 µl) were injected into the GC at 280 °C. Fatty acids and other lipid components were ionized by electron impact at 70 eV after separation in the GC column and analysed in the scan mode. The quadruple mass spectrometer had a resolution of 0·5 mass units over the whole mass range of 2–550 atomic mass units. The sensitivity of the GC-MS system was 0·01 ng methyl stearate. Each substance was confirmed by its mass spectrum and by a search of the NIST mass spectral database library.

A comparison of the fatty acid profiles of strains CO-1-SRB^T, *D. nigrificans* DSM 574^T and *Desulfotomaculum* sp. RHT-3 is presented in Table 1. All three strains were cultivated in the same medium with pyruvate plus sulfate. Strain CO-1-SRB^T contained saturated and unsaturated fatty acids as well as hydroxylated fatty acids. All strains contained fatty acids common for *Desulfotomaculum* species (Ueki & Suto, 1979; Hagenauer *et al.*, 1997; Liu *et al.*, 1997; Love *et al.*, 1993). The strains showed some quantitative differences in the fatty acid content. Fatty acids iso 14 : 0, iso 15 : 1, anteiso 16 : 1 and iso 16 : 0 aldehyde were absent in *D. nigrificans* and present only in trace amounts in strain RHT-3 (Table 1). Fatty acids from iso 18 : 0 aldehyde up to anteiso 19 : 0 were absent in *D. nigrificans* DSM 574^T but present in strain RHT-3. Fatty acids 17 : 1 aldehyde and 17 : 0 aldehyde were found only in strain RHT-3.

DNA isolation and G+C content analyses were performed by the identification service of the DSMZ and at the Institute of Microbiology (INMI, Russian Academy of Sciences, Moscow, Russia). At DSMZ, DNA was isolated according to the procedure of Cashion *et al.* (1977). DNA was hydrolysed with P1 nuclease and the nucleotides were dephosphorylated with bovine alkaline phosphatase (Mesbah *et al.*, 1989). The resulting deoxyribonucleotides were analysed by HPLC (Shimadzu) using a method adapted from Tamaoka & Komagata (1984). Calibration was performed with non-methylated lambda DNA (Sigma), G+C content 49·858 mol% (Mesbah *et al.*, 1989). The DNA G+C content was calculated from the ratio of deoxyguanosine (dG) and thymidine (dT) according to Mesbah *et al.* (1989). At INMI, DNA isolation and DNA G+C content of strain CO-1-SRB^T were performed by previously described methods (Parshina *et al.*, 2003).

Analysis of the 16S rRNA gene sequence of the isolate was performed by the DSMZ Identification Service, as described previously (Parshina *et al.*, 2003).
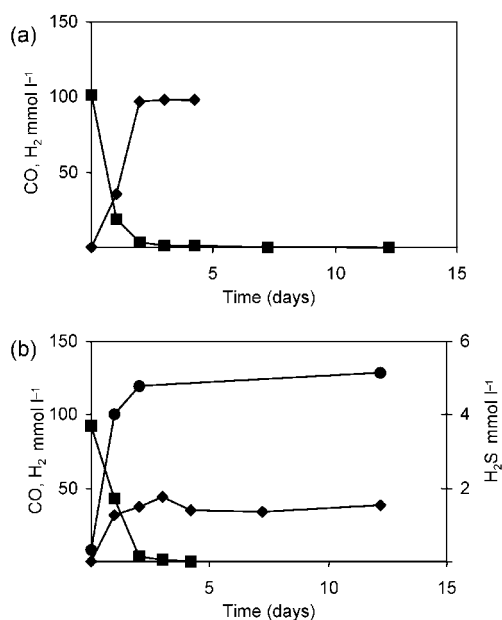

Fig. 1. CO (■) conversion and H_2 (◆) and H_2S (●) formation by strain CO-1-SRB^T under an atmosphere of 100 % CO in the absence (a) and presence (b) of sulfate.
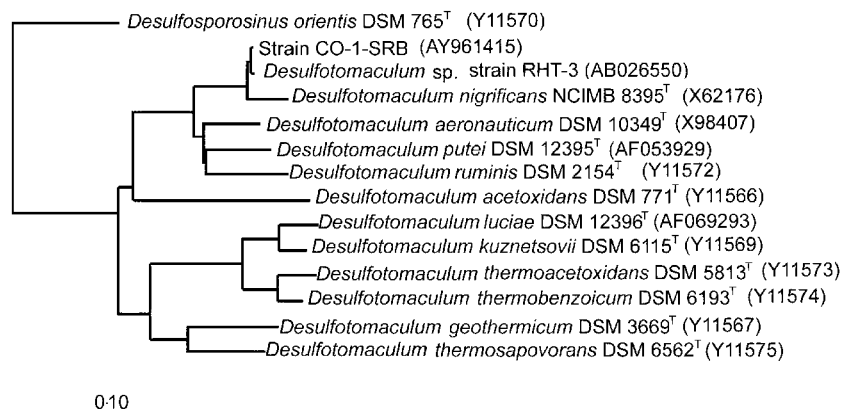
Fig. 2. 16S rRNA gene sequence-based phylogenetic tree constructed by the neighbour-joining method (Saitou & Nei, 1987) as implemented in the ARB software package (Ludwig *et al.*, 2004) using *E. coli* positions 49 to 1387 and showing the position of strain CO-1-SRB^T in relation to members of the genus *Desulfotomaculum*. GenBank accession numbers are given in parentheses. Bar, 10 % divergence.

Sequence similarity searches were performed using the BLAST algorithm (http://www.ncbi.nih.gov/blast/; Altschul *et al.*, 1990). Phylogenetic analysis and tree construction (Fig. 2) were performed with programs from the ARB software package (Ludwig *et al.*, 2004). The phylogenetic tree was constructed using the neighbour-joining method (Saitou & Nei, 1987) and was based on the results of distance matrix analysis including only those nucleotides between *Escherichia coli* positions 49 to 1387 that are conserved in at least 50 % of sequences from relevant members of Gram-positive bacteria. The topology of the tree was confirmed using maximum-parsimony and maximum-likelihood methods as implemented in the ARB program package.

The DNA G+C content of strain CO-1-SRB^T, determined by two different methods, was similar, 45·6 mol% (DSMZ) and 46·9 mol% (INMI). The DNA G+C content of *D. nigrificans* DSM 574^T and *Desulfotomaculum* sp. strain RHT-3 was 51·1 and 46·1 mol% (INMI), respectively.

Phylogenetic analysis revealed that strain CO-1-SRB^T is highly related to *D. nigrificans* (99 %), based on their 16S rRNA gene sequences. Comparisons of the 16S rRNA gene sequences of CO-1-SRB^T with close relatives revealed the following similarities: *D. acetoxidans* (88·2 %), *D. ruminis* (93·1 %), *D. putei* (93·7 %), *D. aeronauticum* (93·9 %), *D. nigrificans* (99 %) and *Desulfotomaculum* sp. RHT-3 (100 %). DNA–DNA hybridization of strain CO-1-SRB^T with *D. nigrificans* DSM 574^T showed 70·5 % relatedness (DSMZ analysis) and 53 % (INMI). The DNA–DNA relatedness of CO-1-SRB^T to strain RHT-3 was 60 % (INMI analysis). For *D. nigrificans* DSM 574^T, DNA–DNA relatedness to strain RHT-3 was 61 % (DSMZ) and 52 % (INMI). The DNA G+C content of *D. nigrificans* DSM 574^T was higher than that of strain CO-1-SRB^T and strain RHT-3. The DNA–DNA hybridization values of all three strains were lower than 70 %, the value suggested for species discrimination (Wayne *et al.*, 1987).

A morphological and physiological comparison of the phylogenetically related strains is presented in Table 2. *D.*

Table 1. Cellular fatty acid composition (%) of the related strains CO-1-SRB^T, *Desulfotomaculum* sp. RHT-3 and *D. nigrificans* DSM 574^T

Fatty acid	CO-1-SRB^T	RHT-3	DSM 574^T
iso 14:0	1·19	0·10	0
14:0	3·63	4·50	1·09
iso 15:1	1·50	0·70	0
14:0 OH	0·10	0	0·72
iso 15:0	1·38	15·87	12·27
anteiso 15:0	4·93	5·62	4·06
15:0	0·54	0·64	0·45
iso 15:0 aldehyde	0·99	0	0·33
iso 16:1	0·98	0·22	0
anteiso 16:1	1·39	0·37	0
iso 16:0	9·29	2·35	3·02
16:1ω9	0·94	1·11	0·73
16:1ω7	1·71	2·46	1·20
16:0	15·28	22·42	17·37
iso 16:0 aldehyde	1·81	0	0·35
16:1 aldehyde	0·68	0	0·45
16:0 OH	0	0	0·25
iso 17:1	5·64	4·20	4·01
anteiso 17:1	0	0·43	0
16:0 aldehyde	4·22	6·07	7·27
iso 17:0	7·91	11·11	14·13
anteiso 17:0	1·49	3·88	5·28
iso 17:1 aldehyde	2·94	0·49	2·43
anteiso 17:1 aldehyde	0·46	0·47	0·56
17:0	0·42	0·55	0·48
iso 17:0 aldehyde	2·39	0·60	8·20
anteiso 17:0 aldehyde	1·13	0·51	2·48
iso 18:1	0·60	0	0
17:1 aldehyde	0	1·03	0
17:0 aldehyde	0	2·21	0
18:1ω9	1·61	1·17	1·70
18:1ω7	0·64	1·27	1·41
18:0	6·53	9·18	6·66

Table 2. Comparison of morphological and physiological characteristics of strain CO-1-SRB[T] and its phylogenetic neighbours

Data from reference taxa were obtained from Mori *et al.* (2000), Akagi & Jackson (1967), Hagenauer *et al.* (1997), Liu *et al.* (1997), Campbell & Postgate (1965), Campbell & Singleton (1986), Daumas *et al.* (1988), Holt *et al.* (1994), Klemps *et al.* (1985), Widdel & Pfennig (1977, 1981) unless indicated. Species/strain: 1, strain CO-SRB[T]; 2, *Desulfotomaculum* sp. RHT-3; 3, *D. nigrificans*; 4, *D. aeronauticum*; 5, *D. putei*; 6, *D. ruminis*; 7, *D. acetoxidans*. +/−, Variable; (+), weakly positive; NR, not reported.

Characteristic	1	2	3	4	5	6	7
Cell diameter (μm)	0·5–1·5	0·8–1·0	1·0–1·2	0·5–0·8	1·0–1·1	0·5–0·7	1·0–1·5
Cell length (μm)	5·0–15·0	3·0–3·3	3·0–6·0	2·2–5·5	2·0–5·0	3·0–6·0	3·5–9·0
Salinity:							
Range (g l^{-1})	0–16	NR	<20	0–25	<20	NR	10–20
Optimum (g l^{-1})	0–8	NR	0	NR	NR	NR	NR
Temperature:							
Range (°C)	30–68	45–60	30–70	20–42	22–65	NR	20–40
Optimum (°C)	55	55	55	37	64	37	36
pH:							
Range	6·0–8·0	6·0–7·5	6·0–8·0	6·0–9·0	6·0–7·8	NR	6·6–6·7
Optimum	6·8–7·2	NR	7·0–7·9	7·0	7·0–7·9	NR	7·1
DNA G+C content (mol%)	46·9	46·1*	49·9 (51·1*)	43·8	47·1	48·5–49·9	37·5
Electron donors:							
Acetate	−	NR	−	−	−	−	+
Alanine	+	NR	+	(+)	NR	+	NR
CO (%)	+ (100 %)	+* (⩽50 %)	+* (⩽20 %)†	NR	NR	NR	NR
Ethanol	+	−	+	(+)	+	(+)	+
Fructose	+	NR	+	−	−	−	−
Glucose	+	NR	+/−	−	−	−	−
H$_2$	+	+	+	+	+	+	−
Lactate	+	+	+	−	+	+	−
Methanol	−	NR	−	NR	(+)	−	NR
Pyruvate	+	+	+	+	+	+	−
Serine	+	NR	NR	−	NR	NR	NR
Fermentation:							
CO	+	−*	−*	NR	NR	NR	NR
Fructose	+	NR	−/+	NR	−	NR	−
Glucose	+	NR	−	NR	−	−	−
Lactate	+	NR	−	NR	−	+	−
Pyruvate	+	NR	+	NR	+	+	−
Electron acceptors:							
Na$_2$SO$_4$	+	+	+	−	+	+	+
Na$_2$SO$_3$ (2 mM)	+	+	+	+	+	+	−
Na$_2$S$_2$O$_3$	+	+	+	+	+	+	−
S^0	−	NR	−	(+)	−	−	−

*This study.
†Plus 1 mM acetate.

acetoxidans, *D. ruminis* and *D. aeronauticum* are mesophilic, with a temperature optimum of 36–37 °C (Table 2). *D. putei* is thermophilic, but does not grow on glucose or fructose plus sulfate and does not ferment lactate, glucose or fructose. *D. nigrificans* does not grow on glycerol plus sulfate and does not ferment lactate. *Desulfotomaculum* sp. RHT-3 does not utilize ethanol in the presence of sulfate. Unfortunately, only a few substrates have been tested for strain RHT-3 (Mori *et al.*, 2000); therefore, we tested the strain in CO in the presence and absence of sulfate. Isolate CO-1-SRB[T] was able to grow on ethanol plus sulfate and grew weakly on glycerol plus sulfate. Furthermore, strain CO-1-SRB[T] could actively ferment lactate, glucose and fructose. The most remarkable difference was the ability to oxidize CO. In a direct comparison with strain CO-1-SRB[T], both *D. nigrificans* DSM 574[T] and strain RHT-3 were unable to oxidize CO without sulfate. In the presence of sulfate, *D. nigrificans* DSM 574[T] could grow at a CO concentration of 5–20 %, but

not higher, confirming the data of Klemps *et al.* (1985). Moreover, we found that *Desulfotomaculum* sp. RHT-3 was not able to grow at a CO concentration exceeding 50 %. Strain CO-1-SRB[T] could grow on CO both in the presence and in the absence of sulfate. During the growth of *D. nigrificans* DSM 574[T] and *Desulfotomaculum* sp. RHT-3 in CO, hydrogen was never detected in the gas phase. This suggests that these strains use CO directly for sulfate reduction without the intermediate formation of hydrogen, as has been also reported recently for *D. kuznetsovii* and *D. thermobenzoicum* subsp. *thermosyntrophicum* (Parshina *et al.*, 2005). During the growth of strain CO-1-SRB[T] at all studied CO concentrations (5–100 %) with sulfate, hydrogen was always an intermediate. During growth in CO without sulfate, hydrogen and CO_2 were the only products of CO conversion.

Based on a combination of 16S rRNA gene sequence and chemotaxonomic and physiological data, we propose that strain CO-1-SRB[T] represents a novel species within the genus *Desulfotomaculum*. We propose the name *Desulfotomaculum carboxydivorans* sp. nov. with the type strain CO-1-SRB[T].

Description of *Desulfotomaculum carboxydivorans* sp. nov.

Desulfotomaculum carboxydivorans (car.bo.xy.di.vor′ans. N.L. n. *carboxydum* carbon monoxide; L. part. adj. *vorans* devouring; N.L. part. adj. *carboxydivorans* carbon monoxide digesting).

Cells are rod-shaped with rounded ends, $0 \cdot 5$–$1 \cdot 5 \times 5$–15 μm, single or sometimes paired. Cells are motile with 'twisting and tumbling' movements. Cells form oval spores, terminal or subterminal. CO (100 % in the gas phase) can serve as a sole electron donor both in the presence and absence of sulfate. Other substrates utilized with sulfate are H_2/CO_2, pyruvate, lactate, glucose, fructose, maltose, ethanol, glycerol, alanine and serine. The bacterium ferments pyruvate, lactate, glucose and fructose. The optimum pH is $6 \cdot 8$–$7 \cdot 2$; the optimum temperature is $55\,^{\circ}C$. The optimum NaCl concentration is 0–8 g l^{-1}. The DNA G + C content is $45 \cdot 6$ mol%.

The type strain, CO-1-SRB[T] (=DSM 14880[T] =VKM B-2319[T]), was isolated from sludge from an anaerobic bioreactor treating paper mill wastewater.

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