Description of strain 3CB-1, a genomovar of *Thauera aromatica*, capable of degrading 3-chlorobenzoate coupled to nitrate reduction

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A Gram-negative bacterium, strain 3CB-1, isolated from a 3-chlorobenzoate enrichment culture inoculated with a sediment sample is capable of degrading various aromatic compounds and halogenated derivatives with nitrate as electron acceptor. Compounds capable of serving as carbon and energy sources include 3-chlorobenzoate, 3-bromobenzoate, 2-fluorobenzoate, 4-fluorobenzoate, benzoate, 3-hydroxybenzoate, 4-hydroxybenzoate, 3-aminobenzoate, protocatechuate, *m*-cresol and *p*-cresol. Oxygen, nitrate and nitrite were used as electron acceptors for growth. Cells are Gram-negative short rods with peritrichous flagellation. The predominant fatty acids are *cis*-9-hexadecenoic acid (16:1 ω 7c), hexadecanoic acid (16:0), octadecanoic acid (18:0), octadecenoic acid (18:1), 3-hydroxydecanoic acid (10:0 3OH) and dodecanoic acid (12:0). The sequence of the 16S rRNA gene, as well as the fatty acid composition, indicate that the strain is a member of the genus *Thauera* in the β -subclass of the *Proteobacteria* and very close to *Thauera aromatica*. DNA–DNA hybridization and nutrient screening indicate that strain 3CB-1 is a genomovar of *Thauera aromatica* with the proposed name *Thauera aromatica* genomovar *chlorobenzoica*.

Keywords: *Thauera aromatica* genomovar *chlorobenzoica*, nitrate reduction, 3-chlorobenzoate degradation

INTRODUCTION

The anaerobic degradation of chlorobenzoates has been studied under various conditions, with nitrate, iron(III), sulfate or carbonate as terminal electron acceptors (Häggblom *et al.*, 1993; Kazumi *et al.*, 1995). Chlorobenzoates are also degraded anaerobically by phototrophic bacteria *Rhodospseudomonas palustris* strains WS17 and DCP3 in the presence of light (Kamal & Wyndham, 1990; van der Woude *et al.*, 1994). Anaerobic mineralization of 3- and 4-chlorobenzoate has been observed in various sediment and soil samples with concomitant nitrate reduction (Häggblom *et al.*, 1993, 1996). Strain 3CB-1 was isolated from an enrichment culture carried out under these conditions (Häggblom & Young, 1999) and the purpose of this communication is to describe this organism and to determine its phylogenetic relationships to known taxa.

Preliminary studies on strain 3CB-1 suggested that it was related to the *Thauera*–*Azoarcus* group in the β -subclass of the *Proteobacteria*. The type species of the genus *Thauera* is *Thauera selenatis*, which is capable of selenate and nitrate respiration (Macy *et al.*, 1993). Other species of *Thauera* have since been described under the names *Thauera aromatica*, *Thauera linaloolentis* and *Thauera terpenica* (Anders *et al.*, 1995; Foss & Harder, 1998). Studies on *T. aromatica* strains K172^T and T1 suggested modifications of the genus definition, which eventually underwent two amendments, one of which pertained to physiological properties (Anders *et al.*, 1995) and the other to the flagellation of the cells (Song *et al.*, 1998).

Three strains of *T. aromatica* have been extensively studied. These are strain K172^T, the type strain of the species (Anders *et al.*, 1995), strain AR-1, capable of degrading α -resorcyate with nitrate as electron acceptor (Gallus *et al.*, 1997), and strain T1, which, as strain K172^T, was examined for its capacity for toluene degradation coupled to nitrate reduction (Evans *et al.*, 1991; Song *et al.*, 1998). *T. linaloolentis* and

The GenBank accession number for the 16S rDNA sequence of strain 3CB-1 is AF123264.

Fig. 1. (a) Phase-contrast micrograph and (b) flagella preparation (Leifson stain) of cells of strain 3CB-1. Cells were grown on M-R2A for 24 h. Bars, 5 μ m.

T. terpenica are of interest because of their capacity to degrade linalool (strain 47Lol^T) and monoterpenes (strains 21Mol and 58Eu^T), respectively (Foss & Harder, 1998).

We propose to add strain 3CB-1 to *Thauera aromatica* as a genomovar, *Thauera aromatica* genomovar *chlorobenzoica*, on the basis of a polyphasic analysis.

METHODS

Bacterial strains and growth conditions. Strain 3CB-1 was isolated from a 3-chlorobenzoate-degrading denitrifying enrichment culture inoculated with sediment from the Hudson River near Albany, NY, USA. (Häggblom & Young, 1999). Strain 3CB-1 (ATCC 700723), and *T. aromatica* strains K172^T (DSM 6984^T) and T1 (ATCC 700265) were anaerobically cultivated in a minimal salts medium (Tschech & Fuchs, 1987) with succinate as carbon source and nitrate as electron acceptor. *T. selenatis* strain AX^T (ATCC 55363^T) was grown in a vitamin-amended medium (Macy *et al.*, 1993). *Azoarcus toluolyticus* strain Tol4^T (ATCC 51758^T), *Azoarcus evansii* strain KB740^T (DSM 6898^T), *Azoarcus toluclasticus* strain MF63^T (ATCC 700605^T), *Azoarcus toluovorans* strain Td21^T (ATCC 700604^T) and *Azoarcus indigenus* strain VB32^T (LMG 9092^T) were grown on M-R2A medium as described previously (Song *et al.*, 1999).

Morphological and physiological characterization. Cell dimensions and morphology were examined by phase-contrast microscopy. Flagella were stained using the method of Leifson (1951). Flagellation of strains of *T. linaloolentis* (DSM 12138) and *T. terpenica* (DSM 12139 and DSM 12140) was also determined. The presence of catalase and oxidase was tested as described elsewhere by Smibert & Krieg (1994). Growth on nutrient, brain-heart infusion and trypticase soy agar plates was tested at 30 °C under aerobic conditions. Salt tolerance was tested under denitrifying conditions in liquid medium (Tschech & Fuchs, 1987) containing 2 or 5% NaCl at 30 °C. Hydrolysis of gelatin and starch, and the presence of urease were determined by the methods of Smibert & Krieg (1994). The optimum temperature for growth of cells was tested at 4, 10, 30 and 37 °C and the optimum pH for growth was tested at pH 6, 7, 7.5, 8 and 8.5.

The utilization of aromatic compounds (all compounds purchased from Aldrich; minimum 97% purity) was tested by using a dense cell suspension of strain 3CB-1 and substrates at a concentration of 100 μ M under aerobic and denitrifying conditions. Growth on different compounds was also tested with 1 mM substrates on agar plates (Tschech & Fuchs, 1987) under aerobic and denitrifying conditions. Growth of strain 3CB-1 with alternative electron acceptors (10 mM NO₃⁻, NO₂⁻, SO₄²⁻, SO₃²⁻, S₂O₃²⁻, SeO₄²⁻ or SeO₃, or in

Table 1. Characteristics of strain 3CB-1 and members of the genus *Thauera*

Characteristic	Strain 3CB-1	<i>T. aromatica</i> K172 ^{T*}	<i>T. aromatica</i> T1 [†]	<i>T. selenatis</i> AX ^{T‡}	<i>T. linaloolentis</i> 47Lol ^{T§}	<i>T. terpenica</i> 58Eu ^{T§}
Cell morphology	Rods	Coccoid rods	Rods	Rods	Rods	Rods
Cell size (µm)	3.0 ~ 3.7	1.0 ~ 2.5	2.5 ~ 3.0	1.4	1.4 ~ 2.7	1.6 ~ 2.2
Motility	+	+	+	+	—	+
Flagellation	Peritrichous	Peritrichous	Peritrichous	Monotrichous	None	Monotrichous
Catalase and oxidase	+	+	+	+	+	+
G + C content (mol %)	68.6	67	66	66	65.6	64.2
Optimum pH for growth	7.5–8.0	7.0–7.4	7.5–8.0	8.0	7.0–7.3	7.9–8.8
Optimum temperature for growth (°C)	30	28	ND	25–30	32	32
Electron acceptors	NO ₃ [–] , O ₂	NO ₃ [–] , O ₂	NO ₃ [–] , O ₂	NO ₃ [–] , O ₂ , Se(VI), Se(IV)	NO ₃ [–] , O ₂	NO ₃ [–] , O ₂
Sole carbon substrate	Growth under aerobic or denitrifying conditions					
	O ₂ /NO ₃ [–]	O ₂ /NO ₃ [–]	O ₂ /NO ₃ [–]	O ₂	NO ₃ [–]	NO ₃ [–]
Benzoate	+/+	+/+	+/+	+	—	—
Benzyl alcohol	–/+	–/–	–/–	ND	ND	ND
Caproate	–/+	–/–	–/–	ND	ND	ND
Glucose	–/–	–/–	–/–	±	—	—
2-Hydroxybenzoate	–/–	–/±	–/–	ND	ND	ND
3-Hydroxybenzoate	+/+	+/+	+/+	ND	ND	ND
4-Hydroxybenzoate	+/+	+/+	+/+	ND	ND	ND
4-Hydroxyphenylacetate	–/–	+/+	+/+	ND	ND	ND
Phthalate	–/–	–/–	–/–	ND	ND	ND
Propionate	–/–	+/+	+/+	+	+	+
Toluene	–/–	–/+	–/+	ND	—	—

ND, Not determined.

* Data obtained from Anders *et al.* (1995).

† Data obtained from Song *et al.* (1999).

‡ Data obtained from Macy *et al.* (1993).

§ Data obtained from Foss & Harder (1998).

|| +, Growth; –, no growth.

the presence of oxygen) was tested using succinate as carbon source.

Determination of cellular fatty acids. Strain 3CB-1, strains of the genera *Azoarcus* and *Thauera*, and *Pseudomonas stutzeri* type strain ATCC 17588^T were grown with 10 mM succinate and 30 mM nitrate under anaerobic conditions for 24 h as described previously (Song *et al.*, 1999). *T. selenatis* AX^T was cultivated with the same medium with the addition of a fivefold higher concentration of vitamins. Cells were harvested by centrifugation and the cellular fatty acid composition was determined by GC following the procedures of the Sherlock Microbial Identification System (MIDI Inc.).

To observe changes in the fatty acid profile of strain 3CB-1 during growth, cells were cultivated with 10 mM succinate and 30 mM nitrate in liquid medium and harvested after different incubation periods.

Isolation of genomic DNA and determination of DNA base composition. Genomic DNA was isolated and purified as

described previously (Song *et al.*, 1998). The DNA base composition of strain 3CB-1 was determined by HPLC (Mesbah *et al.*, 1989).

16S rRNA gene amplification, sequencing and phylogenetic analysis. PCR amplification of the 16S rRNA gene of strain 3CB-1 was performed with a GeneAmp PCR system 2400 as described previously (Song *et al.*, 1998). The complete sequence of the 16S rRNA gene was obtained by using internal 16S rRNA oligonucleotide sequencing primers 27F, 357F, 704F, 1242F, 1522R, 907R, 685R and 321R (Johnson, 1994b) and automated sequencer model ABI 373A (Perkin Elmer).

The rRNA gene sequences of strains in the genera *Thauera* and *Azoarcus* were obtained from the GenBank database and were aligned by using the PILEUP program of the Genetics Computer Group (GCG) software package (Devereux *et al.*, 1984).

Phylogenetic analysis was carried out according to Kimura's two-parameter method (Kimura, 1980) and neighbour-

Table 2. Degradation of aromatic compounds by strain 3CB-1 under aerobic and denitrifying conditions

A dense cell suspension was incubated at 30 °C for 3 d after feeding 100 µM substrate. +, Complete loss of substrate; —, < 10% loss of substrate; ND, not determined.

Substrate	Aerobic conditions	Denitrifying conditions
Benzoate	+	+
2-Hydroxybenzoate	—	—
3-Hydroxybenzoate	+	+
4-Hydroxybenzoate	+	+
2-Fluorobenzoate	+	+
3-Fluorobenzoate	+	—
4-Fluorobenzoate	+	+
2-Chlorobenzoate	—	—
3-Chlorobenzoate	—	+
4-Chlorobenzoate	—	—
2-Bromobenzoate	—	—
3-Bromobenzoate	—	+
4-Bromobenzoate	—	—
3-Aminobenzoate	—	+
4-Aminobenzoate	—	—
Protocatechuate	ND	+
Phthalate	—	—
Phenol	—	—
2-Methylphenol	—	—
3-Methylphenol	—	+
4-Methylphenol	ND	+

joining topology (Saitou & Nei, 1987). The SEQBOOT program was used to obtain the confidence level for neighbour-joining analysis using a 100 bootstrapped data set (Felsenstein, 1985).

DNA–DNA hybridization. DNA–DNA hybridization was performed with ³H-TTP-labelled genomic DNAs of strains 3CB-1 and K172^T by using the S1 nuclease method at a reannealing temperature of 68.7 °C (Johnson, 1994a). DNA

similarities of strain 3CB-1 were estimated with strains T1, K172^T, AX^T, VB32^T, Tol4^T and KB740^T. Each DNA–DNA hybridization reaction was performed in duplicate and the mean value was taken as the DNA similarity value.

RESULTS AND DISCUSSION

Morphological and phenotypic characterization

Strain 3CB-1 was isolated from a river sediment after enrichment with 3-chlorobenzoate as carbon source and nitrate as electron acceptor (Häggblom & Young, 1999). Cells are short rods of 3–3.75 µm by 1–1.25 µm (Fig. 1) and motile during early stages of growth. The flagella stain preparations show peritrichous insertion of the flagella (Fig. 1), a property in common with *T. aromatica*.

A phenotypic characterization of strain 3CB-1 in comparison with those of other strains in the genus *Thauera* is shown in Table 1. Strain 3CB-1 is catalase- and oxidase-positive and grows well on nutrient, brain-heart infusion and trypticase soy agar plates. It can tolerate 2% but not 5% NaCl under denitrifying conditions. It grows best at 30 °C and at pH 7.5–8. It cannot hydrolyse gelatin, starch or urea. The cells can grow with O₂, NO₃[−] or NO₂[−] as electron acceptors in the presence of succinate, but not with SO₄^{2−}, SO₃^{2−}, S₂O₃^{2−}, SeO₄^{2−} nor SeO₃^{2−}.

Strain 3CB-1 can utilize 3-chlorobenzoate, 3-bromobenzoate and 3-iodobenzoate as growth substrate with nitrate as terminal electron acceptor (Häggblom & Young, 1999). Additional growth substrates are listed in Table 1. The degradation of aromatic compounds by strain 3CB-1 under denitrifying or aerobic conditions is also listed in Table 2. Benzoate, benzyl alcohol, 3- and 4-hydroxybenzoate and caproate were used under denitrifying conditions, but in contrast to *T. aromatica* strains K172^T and T1, 4-hydroxyphenylacetate, propionate and toluene were not used as carbon sources.

Table 3. 16S rRNA gene sequence similarities and genetic distances

	1	2	3	4	5	6	7	8	9	10	11	12
1. Strain 3CB-1 (AF123264)		1:36	1:51	3:37	3:44	2:98	6:57	6:65	6:90	6:24	6:73	6:32
2. <i>T. aromatica</i> T1 (U95176)	98:5		0:15	3:06	4:23	2:44	6:57	6:65	6:58	6:24	6:41	5:76
3. <i>T. aromatica</i> K172 ^T (X77118)	98:5	99:7		3:22	4:39	2:59	6:73	6:81	6:74	6:41	6:57	5:92
4. <i>T. linaloolentis</i> 47Lol ^T (AJ005816)	97:1	97:0	97:0		4:40	4:72	7:14	7:22	6:73	6:40	7:47	5:59
5. <i>T. terpenica</i> 58Eu ^T (AJ005817)	97:1	96:0	96:0	96:0		4:88	6:35	6:26	6:28	5:79	6:60	5:86
6. <i>T. selenatis</i> AX ^T (X68491)	97:2	97:5	97:4	95:4	95:2		6:58	6:58	6:83	6:33	6:34	6:01
7. <i>A. tolulyticus</i> Tol4 ^T (L33687)	94:2	94:0	94:0	93:4	94:0	93:6		0:60	1:89	1:36	3:21	4:95
8. <i>A. toluclasticus</i> MF63 ^T (AF123077)	93:6	93:4	93:3	93:2	93:8	93:6	99:5		1:97	1:51	3:13	5:19
9. <i>A. toluovorans</i> Td21 ^T (L33692)	94:0	94:0	94:0	93:8	94:1	93:3	98:3	98:2		0:68	4:2	5:60
10. <i>A. evansii</i> KB740 ^T (X77679)	94:4	94:0	94:4	94:4	94:7	93:9	98:8	97:9	99:4		3:68	5:03
11. <i>A. anaerobius</i> LuFRes1 ^T (Y14701)	94:0	94:2	94:2	93:5	94:0	93:9	97:1	96:4	96:2	96:4		5:60
12. <i>A. indigenus</i> VB32 ^T (AF011345)	92:6	94:3	92:8	93:0	92:7	94:2	95:5	93:5	94:9	94:3	94:5

Fig. 2. Phylogenetic relationship of strain 3CB-1 with species of the genera *Azoarcus* and *Thauera* of the β -subclass of *Proteobacteria*. To build the tree 1500 bases were used. Scale bar represents 5 nt substitutions per 100 nt.

Table 4. Genomic DNA similarities between strain 3CB-1 and strains of *Azoarcus* and *Thauera*

Strain	Similarity (%)
<i>T. aromatica</i> K172 ^T	48.6
<i>T. aromatica</i> T1	47.5
<i>T. selenatis</i> AX ^T	21.9
<i>A. tolulyticus</i> Tol4 ^T	3.1
<i>A. evansii</i> KB740 ^T	2.9
<i>A. indigens</i> VB32 ^T	2.7

16S rRNA gene sequence analysis and phylogenetic analysis

16S rRNA gene sequence analysis data and comparison with other strains of the genera *Thauera* and *Azoarcus* are listed in Table 3. Strain 3CB-1 is closely related to *T. aromatica* K172^T and T1 with 98.5% sequence homology, and has 97.1% sequence similarity with *T. linaloolentis* and *T. terpenica*, and 97.2% similarity with type species *T. selenatis*. The phylogenetic analysis shows that strain 3CB-1 is located in the cluster of the genus *Thauera* as an individual taxon (Fig. 2).

DNA–DNA hybridization

Strain 3CB-1 has a G+C content of 68.6 mol%. This value was used for the calculation of the proper reannealing temperature during DNA–DNA hybridization.

The genomic DNA homology values of strain 3CB-1 with members of the genera *Thauera* and *Azoarcus* are listed in Table 4. Strain 3CB-1 has about 48% DNA homology with strains K172^T and T1 of *T. aromatica* and 21.9% genomic DNA homology with *T. selenatis* strain AX^T, but it does not have significant DNA homology with two species of the genus *Azoarcus*. In summary, on the basis of 16S rRNA gene sequence analysis and DNA–DNA hybridization, it can be concluded that strain 3CB-1 represents a new strain of the genus *Thauera* and may be considered a genomovar of *T. aromatica*.

Determination of cellular fatty acid profiles

The predominant fatty acids of the genera *Thauera* and *Azoarcus* are 10:0 3OH (5–8%), 12:0 (4–8%), 16:1 ω 7c (42–53%), 16:0 (24–32%) and 18:1 (6–18%) after growth under denitrifying conditions. The cellular fatty acid profile of strain 3CB-1 compared with members of the genera *Thauera* and *Azoarcus* is shown in Table 5.

A dendrogram of *Azoarcus* and *Thauera* strains based on their fatty acid profiles is shown in Fig. 3. *Thauera* and *Azoarcus* are well differentiated at a Euclidian distance of 8 units, with the exception of *T. selenatis* which clusters separately from other *Thauera* spp. One main difference is the presence of 12:0 3OH in *T. selenatis* and the absence of this fatty acid in other strains (Table 5). Strain 3CB-1 is included in the *T. aromatica* group, but not with *T. selenatis*. Thus, strain 3CB-1 can be considered as closely related to *T. aromatica* on the basis of the cellular fatty acid analysis.

Table 5. Fatty acid composition of strains of *Thauera* and *Azoarcus*

Cells were cultivated with 10 mM succinate and 30 mM nitrate under anaerobic conditions for 24 h at 30 °C. *T. selenatis* was cultivated in the same denitrifying medium with addition of fivefold vitamin solution.

Strain	Percentage of total fatty acids									
	10:0	10:0 3OH	12:0	12:0 3OH	14:0	16:1 ω 7c	16:1 ω 5c	16:0	17:0 cyclo	18:1 ω 7c/ ω 9t/ ω 12t
Strain 3CB-1	0.0	5.5	5.5	0.0	0.0	45.7	0.5	28.7	0.7	13.4
<i>T. aromatica</i> K172 ^T	0.0	5.5	5.7	0.0	0.0	46.2	1.3	25.1	1.7	14.5
<i>T. aromatica</i> T1	0.4	6.3	6.0	0.0	0.8	42.5	0.6	31.5	1.5	10.3
<i>T. selenatis</i> AX ^T	0.0	5.0	7.8	3.6	0.0	40.9	0.0	24.6	0.0	17.6
<i>A. tolulyticus</i> Tol4 ^T	0.6	6.6	7.1	0.0	0.8	52.7	0.5	25.4	0.0	6.8
<i>A. toluvorans</i> Td21 ^T	0.5	3.1	4.7	0.0	0.8	51.0	0.0	29.7	0.0	10.3
<i>A. toluclasticus</i> MF63 ^T	0.5	5.5	5.6	0.0	0.4	51.8	0.8	25.6	0.0	9.3
<i>A. evansii</i> KB740 ^T	0.8	8.0	6.9	0.0	0.8	46.9	0.5	27.4	0.0	8.2

Fig. 3. Dendrogram of *Azoarcus* and *Thauera* strains based on cellular fatty acids analysis with *Pseudomonas stutzeri* as an outgroup. Strains were grown with 10 mM succinate and 30 mM nitrate for 24 h under denitrifying conditions. *T. selenatis* was grown in the same medium with a fivefold greater concentration of vitamins.

During extended incubation of strain 3CB-1, a marked shift in the fatty acid profile was observed. As the cells reached the exponential growth phase, a small amount of 17:0 cyclo fatty acid was produced (Fig. 4). During stationary phase, the amount of 17:0 cyclo increased with a stoichiometric reduction in the amount of 16:1 ω 7c. Similar production of cyclic fatty acids has been observed in other strains of the genus *Thauera* (data not shown) and other bacteria (*Vibrio cholerae*, *Arthrobacter protophormiae*, *Pseudomonas aureofaciens* and *Pseudomonas fluorescens*) during stationary phase or stress conditions (Guckert *et al.*, 1986; Kieft *et al.*, 1994, 1997).

Description of *Thauera aromatica* genomovar *chlorobenzoica*

Thauera aromatica genomovar *chlorobenzoica* (chlor.o.ben.zo'i.ca. M.L. adj. *chloro* pertaining to chlorine, from Gr. adj. *chloros* pale green; M.L. adj. *benzoicus* pertaining to benzoic acid; M.L. fem. adj. *chlorobenzoica* indicating the ability to utilize chlorobenzoic acid).

Gram-negative short rod, 3–3.7 μ m when grown on MR2A aerobically for 24 h at 30 °C. Motile by peritrichous flagella during early stages of growth. Oxidase- and catalase-positive. Optimum temperature

Fig. 4. Growth of strain 3CB-1 (●) and changes in the ratio of methylene-hexadecanoic acid (17:0 cyclo) and *cis*-9-hexadecenoic acid (16:1 ω 7c) (■) during prolonged incubation.

30 °C, optimum pH 7.5–8. Nitrate, nitrite and oxygen used as terminal electron acceptors. 3-Chlorobenzoate, 3-bromobenzoate and 3-iodobenzoate utilized as growth substrates under denitrifying conditions. Benzoate, 3- and 4-hydroxybenzoate, and 2- and 4-fluorobenzoate utilized under both aerobic and anaerobic conditions. Benzyl alcohol, caproate, 3-aminobenzoate, protocatechuate, and 3- and 4-methylphenol used only under denitrifying conditions. Tolerates 2% NaCl under denitrifying conditions. No hydrolysis of gelatin, starch or urea. The predominant fatty acids are *cis*-9-hexadecenoic acid (16:1 ω 7c), hexadecanoic acid (16:0), octadecanoic acid (18:0), octadecenoic acid (18:1), 3-hydroxydecanoic acid (10:0 3OH) and dodecanoic acid (12:0). During prolonged incubation under denitrifying conditions, the relative proportion of methylene-hexadecanoic acid (17:0 cyclo) increases with corresponding decrease in *cis*-9-hexadecenoic acid (16:1 ω 7c). On the basis of the cellular fatty acid analysis, 16S rRNA gene sequence analysis and DNA–DNA hybridization results, strain 3CB-1 belongs to *Thauera aromatica* as a genomovar, *Thauera aromatica* genomovar *chlorobenzoica*. It has been deposited in the American Type Culture Collection as strain ATCC 700723.

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