Sphaerochaeta globosa gen. nov., sp. nov. and *Sphaerochaeta pleomorpha* sp. nov., free-living, spherical spirochaetes

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Free-living bacteria with spherical cells 0.5–2.5 µm in diameter were isolated from freshwater sediment. 16S rRNA gene sequence analysis placed the new isolates within the phylum *Spirochaetes* ('spirochaetes'). The isolates never displayed a helical morphology or motility. Growth occurred in the presence of 100 mg ampicillin l⁻¹ in complex and defined mineral salts medium amended with vitamins, yeast extract and monosaccharides, disaccharides or soluble starch as fermentable substrates. Two distinct isolates, designated Buddy^T and Grapes^T, exhibited doubling times of 21 ± 2 and 15 ± 1 h in glucose-amended medium and grew at 15–37 and 15–30 °C. Optimum growth was observed between 25 and 30 °C and pH 6.5–7.5, with no growth below pH 5 or above pH 10. Hexose and pentose fermentation yielded ethanol, acetate and formate as major end products. Growth was strictly fermentative and anaerobic, but the isolates tolerated brief oxygen exposure. Nitrate, sulfate, thiosulfate and carbon dioxide were not used as electron acceptors, but soluble Fe(III) was reduced to Fe(II) in glucose-amended medium. The DNA G + C base contents of isolates Buddy^T and Grapes^T were 45.5–46.4 and 47.0–49.2 mol%, respectively. Phospholipid fatty acid (PLFA) profiles contained large proportions of C_{14:0} and C_{16:0} straight-chain saturated fatty acids; C_{16:1ω7c} and C_{16:1ω9c} dominated the mono-unsaturated PLFAs in isolate Grapes^T, whereas isolate Buddy^T also possessed C_{18:1ω5c}, C_{18:1ω7c} and C_{18:1ω9c} fatty acids. Branched monoenoic acids accounted for up to 12.4 and 30 % of the total PLFA in isolates Grapes^T and Buddy^T, respectively. Based on their unique morphological features and the phylogenetic distance from their closest relatives, we propose the new genus, *Sphaerochaeta* gen. nov., to accommodate the new isolates within the novel species *Sphaerochaeta globosa* sp. nov. (type strain Buddy^T = DSM 22777^T = ATCC BAA-1886^T) and *Sphaerochaeta pleomorpha* sp. nov. (type strain Grapes^T = DSM 22778^T = ATCC BAA-1885^T). *Sphaerochaeta globosa* is the type species of the genus.

Abbreviations: PLFA, phospholipid fatty acid; TCE, trichloroethene; TEM, transmission electron microscopy.

The GenBank/EMBL/DDBJ accession numbers for the 16S rRNA gene sequences of strains Buddy^T and Grapes^T are respectively AF357916 and AF357917.

A supplementary figure and table are available with the online version of this paper.

Novel, free-living bacteria with pleomorphic, spherical morphologies form a phylogenetically coherent, monophyletic clade arising from the family *Spirochaetaceae*. Two isolates were obtained from reductively dechlorinating consortia initiated from sediments of the Red Cedar River (Okemos, MI, USA), and were preliminarily described as 'non-spiral spirochaetes' (Ritalahti & Löffler, 2002) and subsequently as free-living, pleomorphic spirochaetes (Ritalahti & Löffler, 2004). The isolates are non-motile

and replicate in round forms, thus breaking with the prevailing dogma of spirochaete biology, wherein 'all spirochetes are helical or spiral shaped microorganisms with internal organelles of motility called periplasmic flagella' (Paster & Canale-Parola, 1980; Paster & Dewhirst, 2000). Such bacteria belong to the class *Spirochaetes*, order *Spirochaetales*, which includes the families *Brachyspiraceae* (genera *Brachyspira* and *Serpulina*), *Leptospiraceae* (genera *Leptonema* and *Leptospira*) and *Spirochaetaceae* (genera *Borrelia*, *Brevinema*, *Cristispira*, *Spirochaeta*, *Treponema* and *Sphaerochaeta*) (Paster & Dewhirst, 2000). Based on taxonomic comparisons with other spirochaete lineages, the new isolates warrant a new genus designation. We assert that strains Grapes^T and Buddy^T are members of a seventh genus, for which we propose the name *Sphaerochaeta* gen. nov., within the *Spirochaetaceae*.

Sediment samples from the Red Cedar River were collected for the purpose of establishing reductively dechlorinating consortia. Microcosms were amended with 0.05–0.1 mM trichloroethene (TCE) as electron acceptor (He *et al.*, 2005). Repeated transfers to defined, completely synthetic, reduced (0.2 mM L-cysteine and 0.2 mM Na₂S · 9H₂O) and bicarbonate-buffered dechlorination medium (Sung *et al.*, 2003) amended with TCE, hydrogen and acetate yielded non-methanogenic, ethene-producing cultures. The enrichment process included six consecutive transfers in dechlorination medium amended with 50 or 100 µg ampicillin ml⁻¹, a peptidoglycan biosynthesis inhibitor. Isolates were obtained from serially diluted culture suspensions in semi-solid (0.6%, w/v, low-melting-point agarose), quarter- or half-strength tryptic soy broth (TSB) medium using the dilution-to-extinction principle (Löffler *et al.*, 2005). This process was repeated before isolated colonies were transferred to Balch tubes with 15 ml half-strength modified TSB (mTSB) medium consisting of 7.4 g TSB l⁻¹ (quarter-strength), 85.6 mM NaCl, 1 g yeast extract l⁻¹, 1.8–5 g D-glucose l⁻¹ (10–30 mM), the Wolin vitamin mixture (Wolin *et al.*, 1963) and 1 mM DTT as reductant. Isolates were maintained (2%, v/v, transfers) in mTSB or the mineral salts dechlorination medium reduced with 1 mM DTT and amended with yeast extract, glucose and vitamins. In semi-solid mTSB, strain Grapes^T formed compact, non-pigmented colonies, 1–1.5 mm in diameter, with irregular, convoluted surfaces after 3 weeks of incubation, which reached 2–4 mm in diameter after 2 months. Strain Buddy^T produced round, loose, pale colonies, 0.2–0.5 mm in diameter after 2 weeks of incubation, which grew into lentil-shaped colonies 0.5–2 mm in diameter and about 0.2 mm thick in the centre of the colonies after extended incubation periods of several months. During exponential growth in liquid medium, individual cells of strain Grapes^T elicited primarily spherical morphologies, 0.5–2.5 µm in diameter, with many cells displaying elongated or crescent shapes and characteristic protrusions (Fig. 1a). Cells also occurred as clusters or aligned along threads like strings of pearls (Fig. 1b). In static mTSB incubations, cells of strain Grapes^T settled and adhered to the glass walls of the culture

Fig. 1. Cells of strain Grapes^T visualized by phase-contrast microscopy (×1000 magnification) (a, b) and TEM (c, d). Protrusions are indicated with arrowheads (a, b). The TEM cross-section (c) shows a single cell. The region inside the rectangle in (c) is magnified in (d) to highlight the cell-wall (CW) architecture. Arrowheads indicate the CW, the periplasmic space (PS) and the outer membrane (OM).

vessels, unlike strain Buddy^T. In growing cultures of strain Buddy^T, one to ten round to oval cells, 0.5–1.2 µm in size, assembled on or within the perimeter of spherical, bubble-like structures, 3–30 µm in diameter (Fig. 2a). Acridine orange staining suggested that only the cells, and not the encapsulating structure, contained DNA (Fig. 2b). Scanning electron microscopy performed with strain Buddy^T corroborated the round cell morphology, and many cells demonstrated the presence of a hook-like feature (Fig. 2c, arrowhead). During transition to stationary phase, cells of the new isolates became smaller and separated into individual cells, and clusters (Grapes^T) or larger encapsulated structures (Buddy^T) were rare. Smaller, individual cells were also common during growth in low-nutrient medium; however, the characteristic aggregates occurred, albeit smaller. The presence of ampicillin (50, 100 and 250 µg ml⁻¹) or rifamycin SV (30 and 60 µg ml⁻¹) had no effect on growth or on colony morphology in liquid or semi-solid media. Additionally, the isolates were resistant to carbenicillin (50 and 250 µg ml⁻¹) and vancomycin (20 and 100 µg ml⁻¹). Sensitivity was observed to kanamycin, erythromycin, chloramphenicol and tetracycline. Growth occurred in full-strength and diluted mTSB medium and was stimulated by monosodium glutamate (2 g l⁻¹) and Casamino acids (10 g l⁻¹). For the two isolates, lag times in D-glucose-amended mineral salts medium ranged from 2–3 (Grapes^T) to 7–14 (Buddy^T) days, and two to three times shorter lag times were observed in mTSB. In half-strength mTSB

Fig. 2. Cells of strain Buddy^T visualized by phase-contrast microscopy (a), confocal microscopy following acridine orange staining (b), critical-point-dried scanning electron microscopy preparation (c) and TEM cross-section (d). In (a), (b) and (d), a membranous structure that encapsulates one to ten cells of strain Buddy^T is highlighted. In (c), a hook-like protrusion is indicated by an arrowhead.

(without stimulants), doubling times of 15.3 ± 0.6 and 20.9 ± 2.3 h were observed for strains Grapes^T and Buddy^T, respectively. The maximum cell density attained was dependent on the amount of glucose added, rather than the strength of the mTSB medium. In quarter-strength mTSB with 10 mM glucose, strain Buddy^T reached an OD₆₀₀ of ~0.1, whereas cultures of strain Grapes^T reached an OD₆₀₀ of 0.2–0.3. Other hexoses that supported growth included D-galactose and D-fructose, while D-mannose was used by strain Grapes^T but not strain Buddy^T. Other saccharides that supported growth of both isolates included the pentoses D-xylose and L-arabinose, the disaccharide sucrose and the trisaccharides raffinose and melezitose as well as soluble starch. Strain Buddy^T also grew with lactose and maltose, while strain Grapes^T did not. Glucose and xylose fermentation yielded acetate, formate and ethanol, which are characteristic spirochaete carbohydrate fermentation products. H₂–CO₂ homoacetogenic growth was not observed in mineral salts medium with a H₂/CO₂ (80:20, v/v) headspace. Citrate (10 mM), ethanol (1.7 and 170 mM), methanol (2.5 and 250 mM) and glycerol (1.4 and 140 mM) were not used by either isolate, nor was growth observed with the insoluble substrates glycogen, xylan, cellulose, cellobiose or chitin in liquid medium or supplied at 0.1 g l⁻¹ suspended in semi-solid mineral salts medium. Electron acceptors including nitrate (1–5 mM), nitrite (1–5 mM), sulfate (10 mM), fumarate (5 mM) and thiosulfate (10 mM) were not reduced in mineral salts medium amended with glucose, propionate, acetate or hydrogen as electron donors. Soluble Fe(III) (as ferric

citrate; 5 mM) was reduced to Fe(II) in defined medium amended with 10 mM glucose; however, growth with Fe(III) as electron acceptor could not be demonstrated. Neither isolate dechlorinated TCE and the dechlorinating activity in the enrichments was attributed to *Dehalococcoides* sp. strain FL2 (He *et al.*, 2005). The results of substrate utilization experiments were verified in at least two independent experiments. Growth was measured by an increase in OD₆₀₀, microscopic cell counts and analysis of substrate utilization and/or product formation.

In half-strength mTSB with 10 mM glucose, isolates Grapes^T and Buddy^T grew at 15–30 and 20–37 °C, respectively, with optimum growth at 20–25 °C (Grapes^T) and 30 °C (Buddy^T). No growth was observed below 10 °C, but cultures remained viable at 4 °C for at least 3 years, and transfer cultures incubated at 25 °C grew after a 4–6 day lag period. The pH optimum ranged from 6.5 to 7.5, but cultures incubated at pH 5 and pH 10 lost viability (i.e. no growth occurred following transfers to growth medium at pH 7). Both isolates tolerated oxygen (i.e. air) exposure (i.e. shaking of open culture vessels at 200 r.p.m.) for up to 8 h, and resumed growth following transfers; however, the lag times before the onset of growth in mTSB increased to 5–7 days (Grapes^T) or several weeks (Buddy^T), depending on inoculum size and duration of exposure to air. Cultures became non-viable after 24 h of air exposure. Both isolates tested oxidase- and catalase-negative, and growth in mTSB required a reductant, suggesting that both isolates are strict anaerobes.

During exponential growth, cells stained Gram-negative. Transmission electron microscopy (TEM) of a cross-section of a single cell of strain Grapes^T demonstrated features of a Gram-negative cell wall (Fig. 1c, d). Fig. 1(d) shows the inner cell wall and a double membrane with a periplasmic space between the cell wall and outer membrane. TEM of cross-sections of strain Buddy^T suggested that several cells share a common outer membrane during exponential growth (Fig. 2d). Cell-wall analyses, performed by the DSMZ using chromatographic separation techniques as described previously (MacKenzie, 1987; Rhuland *et al.*, 1955), did not detect diaminopimelic acid in cell hydrolysates; however, only 0.2 mg polymeric substance was obtained from 3.5 g (wet weight) biomass from strain Grapes^T, precluding detailed investigations. GC-MS analysis identified leucine, isoleucine, lysine and other amino acids, but diaminopimelic acid and ornithine were absent. Ornithine is the predominant peptidoglycan cross-link in spirochaetes (Joseph *et al.*, 1973), suggesting that the new isolates lack these structural elements, possibly promoting pleomorphy.

Isolates Buddy^T and Grapes^T grown in half-strength mTSB amended with 10 mM glucose were analysed for phospholipid fatty acid (PLFA) profiles by Microbial Insights (<http://www.microbe.com>; Rockford, TN, USA) using established protocols (White *et al.*, 2005). Similar to other spirochaetes (Franzmann & Rohde, 1992; Kondo & Ueta,

1972; Livermore & Johnson, 1974), both isolates contained large proportions of even-carbon-number, straight-chain saturates, which accounted for 44 % (Grapes^T) and 31 % (Buddy^T) of the total PLFA (Supplementary Table S1, available in IJSEM Online). The major saturated PLFAs were C_{14:0} (26.4 and 13.4 mol% in isolates Grapes^T and Buddy^T, respectively) and C_{16:0} (12.9–16.9 mol%). Mono-unsaturated fatty acids made up 39–42 % of the cellular fatty acids. Of the mono-unsaturated PLFAs, C_{16:1} was the most abundant, and accounted for 90 % of the monoenoic acids in strain Grapes^T, while strain Buddy^T had a slightly smaller total amount of monoenoic acids, and C_{16:1} and C_{18:1} were equally abundant. Branched monoenoic acids (br-C_{15:1}, br-C_{17:1} and br-C_{19:1}) accounted for nearly 30 % and 12.4 % of the total PLFA in Buddy^T and Grapes^T, respectively. These amounts correlated inversely with the abundance of straight-chain mono-unsaturated C_{16:1} fatty acids, which were higher in Grapes^T and lower in Buddy^T (Supplementary Table S1). Odd-carbon-number iso-branched and anteiso-branched PLFAs were not detected.

Motility was not observed during any stage of growth or under non-growth conditions in liquid or semi-solid (0.1–0.6 % low-melting-point agarose) medium under various substrate, pH and temperature regimes. Silver nitrate staining never revealed flagella (i.e. periplasmic flagella) in either isolate. Primers targeting *flaA* (Li *et al.*, 2008) failed to produce amplicons with template DNA from either isolate, whereas DNA from a *Spirochaeta stenostrepta* strain yielded amplicons of the expected size.

The two isolates had distinct rep-PCR profiles (Rademaker *et al.*, 2000), which remained consistent over time, suggesting genome stability. The DNA G+C base contents of strains Buddy^T and Grapes^T were respectively 45.5–46.4 and 47.0–49.2 mol% (determined as described by Mesbah *et al.*, 1989). Phylogenetic analysis based on 1500 positions of the 16S rRNA gene revealed that the sequences of strains Buddy^T and Grapes^T were 95.5 % similar by pairwise alignment performed with Geneious Pro 5.0.2 software and the EzTaxon tool (<http://www.eztaxon.org>; Chun *et al.*, 2007). Additional isolation efforts yielded isolate JEL1 (GenBank accession no. DQ833402; 99.4 % 16S rRNA gene similarity to Grapes^T) from Alaska's King Salmon River. This isolate exhibited a PLFA profile similar to that of strain Grapes^T (Supplementary Table S1). Another isolate, strain TQ1, obtained from sediments of Michigan's Tahquamenon River (DQ833400), shared 95.3 and 95.6 % 16S rRNA gene sequence similarity with strains Grapes^T and Buddy^T, respectively. BLAST analysis revealed that 16S rRNA gene sequences affiliated with strains Grapes^T and Buddy^T have been found in a variety of environments, including a hypersaline, ice-sealed Antarctic lake (GenBank accession no. GQ167322), the microflora of kusawa gravy, a fermented Japanese sauce (AB003448, AB003434; Satomi *et al.*, 1997), an ethylbenzene-utilizing consortium (AB062692–AB062695), oil reservoirs (AY570600, AY570571; Grabowski *et al.*, 2005), dechlorinating enrichment cultures [EU169845 (Chung & Rittmann,

2007), AF349763 (Gu *et al.*, 2004), AJ249227 and AF349763], a methanogenic, glucose-fed bioreactor with highly abundant 'spirochaetal' 16S rRNA gene sequences, but with a predominance of round cells (Fernandez *et al.*, 2000), and a cellulose- and methanol-utilizing digester (EF586024, EF559111) (Supplementary Fig. S1). Phylogenetic affiliation with the spirochaetes was determined by BLAST analysis against the GenBank nr database and the RDP (Cole *et al.*, 2005). Unrooted phylogenetic trees of 16S rRNA gene sequences of spirochaete type strains (Fig. 3, Supplementary Fig. S1) were generated using the Geneious software and the PhyML tree plugin (Drummond *et al.*, 2009; Guindon & Gascuel, 2003). Alignment algorithms utilized MUSCLE with the neighbour-joining or UPGMA clustering method and CLUSTAL W weighting scheme (1352 aligned bases). All approaches yielded similar results, with isolates Buddy^T, Grapes^T, JEL1 and TQ1 forming a distinct cluster within the family *Spirochaetaceae* (Fig. 3). Supplementary Fig. S1 highlights 16S rRNA gene clone sequences related to those of the new isolates and aligned with representative *Spirochaeta* and *Treponema* sequences.

Organisms with <98.5 % 16S rRNA gene sequence similarity have been found to share less than 95 % average nucleotide identity and therefore would not belong to the same species (Cole *et al.*, 2010; Stackebrandt *et al.*, 2002). The closest relative with confirmed spirochaete-characteristic motility and spiral morphology is *Spirochaeta smaragdinae* DSM 11293^T (GenBank accession no. U80597), a free-living, anaerobic, mesophilic, carbohydrate-fermenter (Magot *et al.*, 1997), which exhibits 85.1 and 85.2 % 16S rRNA gene sequence similarity to Buddy^T and Grapes^T, respectively. Phylogenetic analysis based on the comparison of sequences with >1200 16S rRNA gene nucleotide positions available in the RDP (Cole *et al.*, 2005) demonstrated that the new isolates, along with a number of environmental clone sequences, formed a monophyletic cluster arising from the genus *Spirochaeta* (Fig. 3). The genus *Spirochaeta* comprises facultatively or obligately anaerobic, free-living spirochaetes that are often isolated from aquatic or marine environments, including deep-sea sediments (Canale-Parola, 1984). Only two isolates, *Spirochaeta coccoides* SPN1^T (GenBank accession no. AJ698092; about 11 % 16S rRNA gene sequence divergence from the novel isolates) obtained from the termite hindgut (Dröge *et al.*, 2006) and *Spirochaeta* sp. ACE-P (M87055; 13.3 % sequence divergence), an unusual, obligately psychrophilic, wall-less spirochaete from Ace Lake, Antarctica (Franzmann & Dobson, 1992), have been described with round rather than spiral morphology. As shown in Fig. 3 and Supplementary Fig. S1, the new isolates share a common line of descent with *Spirochaeta* but exhibit >10 % 16S rRNA gene sequence divergence. Based on the unique taxonomic features, we propose that the new isolates belong to a new genus, *Sphaerochaeta* gen. nov., as the type strains of two novel species, *Sphaerochaeta pleomorpha* sp. nov. and *Sphaerochaeta globosa* sp. nov. As non-motile spirochaetes with round cells have been described as members of the

Fig. 3. Phylogeny of isolates Grapes^T, Buddy^T, JEL1 and TQ1 among related species of the family Spirochaetaceae based on a maximum-likelihood analysis of nearly complete 16S rRNA gene sequences. No culture or sequence is available for *Spirochaeta plicatilis*, the type species of the genus *Spirochaeta*; a request to replace this species with *Spirochaeta stenostrepta* as the type species (Canale-Parola, 1981) was denied (Wayne, 1982). An unrooted tree of the Spirochaetaceae is shown, with bootstrap values greater than 50 % expressed as percentages of 1000 replications. Bar, 9 substitutions per 100 sequence positions.

genera *Spirochaeta* and *Sphaerochaeta*, future comparative analyses that include more isolates may justify reclassification of *Spirochaeta coccoides* SPN1^T and *Spirochaeta* sp. ACE-P as members of the genus *Sphaerochaeta*.

Description of *Sphaerochaeta* gen. nov.

Sphaerochaeta [Sphae.ro.chae'ta. Gr. n. *sphaira* (Latin transliteration *sphaera*), a sphere; Gr. fem. n. *chaitê* (Latin transliteration *chaeta*), long flowing hair; N.L. fem. n. *Sphaerochaeta* round cells along threads of hair, indicative of a round morphology with a derivation from spirochaetal ancestry].

Spherical cells, 0.4–2.5 µm in diameter. Pleomorphic; cells of different sizes and shapes are observed during growth. Spiral morphology not observed. Cells are non-motile, without flagella, periplasmic or otherwise. Cells stain Gram-negative and do not have ornithine or lysine peptidoglycan cross-links. Mesophilic. Neutrophilic. Chemoheterotrophic anaerobes; fermentative growth is observed with carbohydrates including pentose and hexose monosaccharides, disaccharides and soluble starch. End products of glucose fermentation include acetate, formate and ethanol. Growth is stimulated by yeast extract, Casamino acids and vitamins. DNA G + C content is 45–48 mol%. Oxidase- and catalase-negative. Phylogenetic position is in the family Spirochaetaceae, order Spirochaetales, class Spirochaetes of the phylum Spirochaetes. *Sphaerochaeta globosa* is the type species.

Description of *Sphaerochaeta globosa* sp. nov.

Sphaerochaeta globosa (glo.bo'sa. L. fem. adj. *globosa* sphere-shaped, reflecting the characteristic morphology, wherein round cells form on spherical 'bubbles' during exponential growth).

Has the following properties in addition to those described for the genus. Cells in exponential growth phase occur as spherical aggregates, 3–25 µm in diameter, comprising one to ten cells. A membranous structure surrounds cell aggregates. Cells carry a single, hook-like protrusion. Prefers low-nutrient conditions. Fermentable substrates include D-galactose, D-glucose, D-fructose, D-xylose, sucrose, maltose, lactose, raffinose, melezitose and soluble starch. L-Arabinose is used poorly; D-mannose is not used for growth, nor are glycogen, cellulose, chitin or xylan. Major cellular fatty acids are C_{14:0}, C_{16:0}, C_{16:1ω7c}, C_{18:1ω7c}, C_{18:1ω9c} and br-C_{17:1ω7c} (Supplementary Table S1). Grows at 20–35 °C, with irreversible inactivation above 40 °C. The DNA G + C content of the type strain is 46.5 ± 0.4 mol%.

The type strain, Buddy^T (=ATCC BAA-1886^T =DSM 22777^T), was isolated from black, anoxic sediments of the Red Cedar River in Okemos, MI, USA (42° 41' 49.72" N 84° 22' 43.67" W).

Description of *Sphaerochaeta pleomorpha* sp. nov.

Sphaerochaeta pleomorpha (ple'o.mor'pha. Gr. adv. *pleon* more; Gr. n. *morphe* shape, form; N.L. adj. *pleomorpha* having many shapes and sizes, pleomorphic, reflecting the characteristic morphological progression during phases of growth).

Has the following properties in addition to those described for the genus. Chains of cells, 0.8–2 µm in size, predominate during exponential growth. Cells carry a single, hook-like protrusion. Fermentable substrates

include D-galactose, D-glucose, D-fructose, D-mannose, D-xylose, sucrose, raffinose, melezitose and soluble starch. L-Arabinose is used poorly; maltose, lactose, glycogen, cellulose, chitin and xylan are not utilized as growth substrates. Major cellular fatty acids are C_{14:0}, C_{16:0}, C_{16:1 ω 7c} and br-C_{17:1 ω 7c} (Supplementary Table S1). Grows at 15–30 °C, with irreversible inactivation above 35 °C. Exhibits biofilm formation on glass surfaces. The DNA G+C content of the type strain is 48.1 ± 1.1 mol%.

The type strain, Grapes^T (=ATCC BAA-1885^T =DSM 22778^T), was isolated from black, anoxic sediments of the Red Cedar River in Okemos, MI, USA (42° 41' 49.72" N 84° 22' 43.67" W).

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