Systematic and Applied Microbiology xxx (2012) xxx–xxx

Contents lists available at SciVerse ScienceDirect

Systematic and Applied Microbiology

journal homepage: www.elsevier.de/syapm

Candidatus "Thiodictyon syntrophicum", sp. nov., a new purple sulfur bacterium isolated from the chemocline of Lake Cadagno forming aggregates and specific associations with *Desulfocapsa* sp.☆

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ARTICLE INFO

Article history:
Received 22 July 2011
Received in revised form 11 January 2012
Accepted 15 January 2012

Keywords:
Thiodictyon syntrophicum
Purple bacteria
Meromictic

ABSTRACT

Strain Cad16^T is a small-celled purple sulfur bacterium (PSB) isolated from the chemocline of crenogenic meromictic Lake Cadagno, Switzerland. Long term *in situ* observations showed that Cad16^T regularly grows in very compact clumps of cells in association with bacteria belonging to the genus *Desulfocapsa* in a cell-to-cell three dimensional structure. Previously assigned to the genus *Lamprocystis*, Cad16^T, was here reclassified and assigned to the genus *Thiodictyon*. Based on comparative 16S rRNA gene sequences analysis, isolate Cad16^T was closely related to *Thiodictyon bacillosum* DSM234^T and *Thiodictyon elegans* DSM232^T with sequence similarities of 99.2% and 98.9%, respectively. Moreover, matrix-assisted laser desorption/ionization time of flight mass spectrometry (MALDI-TOF MS) analysis separated Cad16^T from other PSB genera, *Lamprocystis* and *Thiocystis*. Major differences in cell morphology (oval-sphere compared to rod-shaped) and arrangement (no netlike cell aggregates), carotenoid group (presence of okenone instead of rhodopinal), chemolithotrophic growth as well as the ability to form syntrophic associations with a sulfate-reducing bacteria of the genus *Desulfocapsa* suggested a different species within the genus *Thiodictyon*.

This isolate is therefore proposed and described as *Candidatus* "Thiodictyon syntrophicum" sp. nov., a provisionally novel species within the genus *Thiodictyon*.

Introduction

Members of the family Chromatiaceae were previously identified as the most abundant phototrophic sulfur bacteria in the chemocline of meromictic Lake Cadagno, Switzerland (46°33′N, 8°43′E) [1–4]. Molecular analyses of uncultured populations of this family in the chemocline identified all large-celled members as *Chromatium okenii*, while small-celled members were more diverse with populations related to the genus *Lamprocystis*, *i.e.*, *Lamprocystis purpurea* and *Lamprocystis roseopersicina* [2], to the genus *Thiocystis*, *i.e.*, *Thiocystis minor* and *Thiocystis gelatinosa* [3] and now to the genus *Thiodictyon*. Recently two previously uncultured *Thiocystis* populations, *i.e.* population 448 and population H, were isolated and described as novel species: *Thiocystis cadagnonensis* and *Thiocystis chemoclinalis* [5].

The genus *Thiodictyon* was first described by Winogradsky in 1888 [6] and was emended in 1971 by Pfennig and Trueper [7]. Presently, this genus comprises two validly described species, *Thiodictyon elegans* and *Thiodictyon bacillosum* [8]. However, no recent studies were performed on type strains since they are not available from any public culture collection.

Here, we re-evaluate the assignment of strain Cad16^T, isolated from Lake Cadagno [9], to the genus *Lamprocystis* and propose it as a provisionally novel species within the genus *Thiodictyon*, *Candidatus* "Thiodictyon syntrophicum" sp. nov. strain Cad16^T.

☆ The GenBank/EMBL/DDBJ accession number for the 16S rRNA gene sequences of strain Cad16 is AJ511274. The type strain Cad16^T is deposited at the Japan Collection of Microorganisms (JCM 15483) and at the Korean Collection for Type Cultures (KCTC 5955).

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doi:10.1016/j.syapm.2012.01.001

Materials and methods

Enrichment and cultivation

Samples from the chemocline of Lake Cadagno were taken at a depth of 12.7 m corresponding to the maximum turbidity and highest bacterial density on August 28, 2001. Water samples were used to fill 0.5 L screw-cap glass bottles that were subsequently stored in the dark at 4 °C for 10 days. PSB accumulating at the neck of the bottle and under the screw-cap were collected with a previously gassed syringe (N_2) and used as inoculums for liquid and deep agar dilutions (1%, v/v) prepared by the Hungate technique [10,11]. Media for enrichments of purple sulfur bacteria were prepared according to Widdel and Bak (1992). For detailed information about medium content and isolation see supplementary material S1. Characteristics of isolate Cad16^T, deposited at the Japan Culture Collection (JCM 15483) and the Korean Collection for Type Cultures (KCTC 5955), were compared to those published for its closest cultured relatives (Table 1).

Pigment analysis

The *in vivo* absorption spectra were determined using the sucrose method and a UV/Vis Spectrometer Lambda 2S (Perkin-Elmer, Waltham, MA) following the procedure described by Pfenning [12]. Pigments were determined by ion pairing, reverse-phase HPLC [13,14].

16S rRNA sequence and G+C content analysis

Nucleic acids were extracted from 1.5 ml of a pure culture at the exponential phase (OD_{650} of 0.6) using the MagNA Pure LC automated extractor (Roche Molecular Biochemicals, Indianapolis, IN, USA) and the DNA isolation extraction kit produced by the same manufacturer.

16S rRNA gene fragments were amplified, purified and sequenced as described previously [2]. The sequence was deposited in the EMBL/GenBank databases with accession number AJ511274.

The G+C content of genomic DNA of isolate Cad16^T was determined at the German Collection of Microorganisms and Cell Cultures (Dr. P. Schumann) by HPLC according to Mesbah et al. [15].

Phyologenetic analysis

The 16S rRNA sequence was aligned with related sequences from Genbank and EMBL searches [16,17] using Sequencher 4.2.2 (Gene Codes Corporation, Ann Arbor, MI), CLUSTAL X and MacClade 4.05 [18,19]. The length of all compared sequences was 1393 bp. Phylogenetic analyses included maximum parsimony (MP), neighbor joining (NJ) and maximum likelihood (ML) methods in PAUP*4.0b10 [20].

MALDI-TOF MS analysis

Two ml of different pure cultures of phototrophic sulfur bacteria (Fig. 3), were centrifuged, the cell pellets resuspended in 15 μl of ddH_2O, and 0.5 μl of this suspension (*Allochromatium vinosum* DSM180^T, *Chlorobium clathratiforme* strain 4DE Lake Cadagno, *Chlorobium pheobacteroides* strain 1VII D7 Lake Cadagno, *Chlorobium tepidum* WT2321^T, *L. purpurea* DSM4197^T, *L. sp.* Population A strain A31 Lake Cadagno, *L. sp.* Population D strain D2V2 Lake Cadagno, *T. cadagnonensis* JCM15111^T, *T. chemoclinalis* JCM15112^T, *T. gelatinosa* DSM215^T, *Thiocystis violascens* DSM198^T and *Candidatus* Thiodictyon syntrophicum strain Cad16^T Lake Cadagno) was transferred to FlexiMass^{TM} target wells using a disposable loop, and overlaid with 1.0 μl alpha-cyano matrix solution (CHCA; 40 mg alpha-cyano in 33% acetonitrile, 33% ethanol, 33% ddH_2O and 1% trifluoroacetic acid). The spotted solution was air-dried for 1–2 min at room temperature, and subsequently analysed with an MALDI-TOF MS Axima^{TM} Confidence spectrometer (Shimadzu-Biotech Corp., Kyoto, Japan) as described in the supplementary material S1.

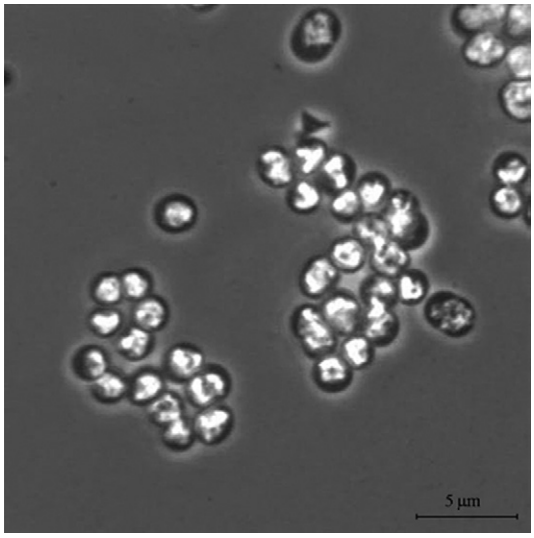

Fig. 1. Phase contrast micrograph of isolate Cad16^T.

Results

Cad16^T strain characterization

Cells of isolate Cad16^T were spherical to oval shaped with a width of 1.4–2.4 μm (Table 1, Fig. 1). The isolate grew in single cells as well as in compact clumps of cells in liquid media regardless of the age of the culture. Under anoxic autotrophic growth conditions, the generation time was 121 h. After 2 weeks of growth, Cad16^T reached the optical density of 0.7 corresponding to 10^7 cell ml^{-1}. Cells of isolate Cad16^T stained Gram-negative, contained gas vacuoles and had a slime capsule. Bright field microscopy revealed the presence of sulfur globules randomly distributed in the cells. The color of cell suspensions was purple-red, similar to *Lamprocystis* sp. and *Thiocystis* sp. but different from *T. bacillosum* and *T. elegans* that were purple-violet (Table 1). *In vivo* absorption spectra of pigments in cell suspensions of isolate Cad16^T displayed an absorption maximum at 528 nm suggesting the presence of okenone as the predominant carotenoid, while carotenoids of the rhodopinal group, with rhodopinal and rhodopin as major pigment components, were reported for *T. elegans* or *T. bacillosum*, respectively [9,21] (Table 1). The presence of okenone in strain Cad16^T was confirmed by HPLC and genome analysis [22].

Further physiological characterization focused on different combinations of electron donors and acceptors that were aseptically added to the pure cultures of Cad16^T (5 mM final conc.): formate, acetate, pyruvate, propionate, butyrate, lactate, fumarate, succinate, malate, fructose, glucose, ethanol, propanol, and glycerol. Similar to the other *Thiodictyon* species, Cad16^T grew photolithoautotrophically under anaerobic conditions with sulfide and elemental sulfur as electron donors. Growth was also observed with thiosulfate. Globules of sulfur were deposited inside the cells as intermediary oxidation products. In the presence of sulfide and bicarbonate, photoassimilation of acetate was observed for Cad16^T which corresponded to published results for the genus *Thiodictyon* (Table 1). In the presence of carbon dioxide and sulfide, photoassimilation of fructose was also observed. Growth stimulation in

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Table 1
Differentiating characteristics of species of the genus *Thiodictyon* and related genera.

Characteristic	1	2	3	4	5	6	7	8
Shape	Rod	Rod	Sphere-oval	Oval-sphere	Sphere	Sphere	Sphere	Sphere
Size (μm)	1.5–2.0	1.5–2.0	1.4–2.4	1.9–2.3	2.0–3.5	1.2–3.0	2.0–3.0	1.5–2.0
Aggregate formation	Netlike formation	Irregular clumps	Clumps of cells	Clumps of cells	Irregular aggregates	Irregular aggregates	Irregular aggregates	Irregular aggregates
Gas vacuoles	+	+	+	+	+	–	+	+
Sulfur storage	+	+	+	+	nd	+	+	+
Slime capsule	+	+	+	+	–	+	+	+
Color of cell suspension	Purple-violet	Purple-violet	Purple-red	Purple-red	Purple-violet	Pink-rose red	Pink-rose red	Pink-rose red
Motility	–	–	–	–	+	–	–	–
Flagellation	nd	nd	–	nd	+	nd	nd	nd
Carotenoid group	Rhodopinal	Rhodopinal	Okenone	Okenone	Rhodopinal	Spirilloxanthin	Spirilloxanthin	Spirilloxanthin
Chemolithotrophic growth	–	–	+	+	–	+	+	–
mol% G+C of DNA	65.3–66.3	66.3	67.7	63.5	63.8	63.3–66.3	64.3	65.3
pH optimum	6.7–7.3	6.7–7.3	7.0–7.2	7.0–7.3	7.0–7.3	7.3	6.7–7.5	6.7–7.5
Temperature optimum (°C)	20–25	20–30	20–25	23–25	20–30	20–35	20–35	20–35
Photosynthetic electron donors (sulfur compounds)								
Sulfide	+	+	+	+	+	+	+	+
Sulfur	+	+	+	+	+	+	+	+
Thiosulfate	nd	nd	+	+	+	+	+	+
Substrate assimilation in the presence of sulfide and bicarbonate								
Acetate	+	+	+	+	+	+	+	+
Pyruvate	+	+	+	+	+	+	+	+
Formate	nd	nd	–	+	nd	–	–	–
Propionate	nd	nd	–	+	nd	+/–	+	+
Butyrate	nd	nd	–	–	nd	–	–	–
Lactate	nd	nd	–	+	nd	+/–	+	+
Fumarate	nd	nd	–	–	nd	+	–	–
Succinate	nd	nd	–	–	nd	+	–	–
Malate	nd	nd	–	–	nd	+	+/–	+
Fructose	nd	nd	+	–	nd	+	+	–
Glucose	nd	nd	–	+	nd	–	–	+
Ethanol	nd	nd	–	–	nd	–	–	nd
Propanol	nd	nd	–	–	nd	–	–	nd
Glycerol	nd	nd	–	–	nd	–	–	–

Taxa: 1, *Thiodictyon elegans* DSM232^T; 2, *Thiodictyon bacillosum* DSM234^T; 3, strain Cad16^T; 4, *Lamprocystis purpurea* DSM4197^T; 5, *Lamprocystis roseopersicina* DSM229; 6, *Thiocapsa roseopersicina* DSM217^T; 7, *Thiocapsa rosea* DSM235^T; 8, *Thiocapsa pendens* DSM236^T. Data for taxa 1–2 and 4–8 are from Imhoff (2005) and Pfennig and Trueper (1989). Sulfide and elemental sulfur were utilized as photosynthetic electron donors by all strains, pyruvate and acetate were photoassimilated by all strains. No salt requirement was reported for taxa 1–8 except for marine strains of *L. rosepersicina* which may tolerate low concentrations of NaCl. +, substrate utilized or present; –, substrate not utilized or absent; +/–, variable depending on the strain; nd, not determined.

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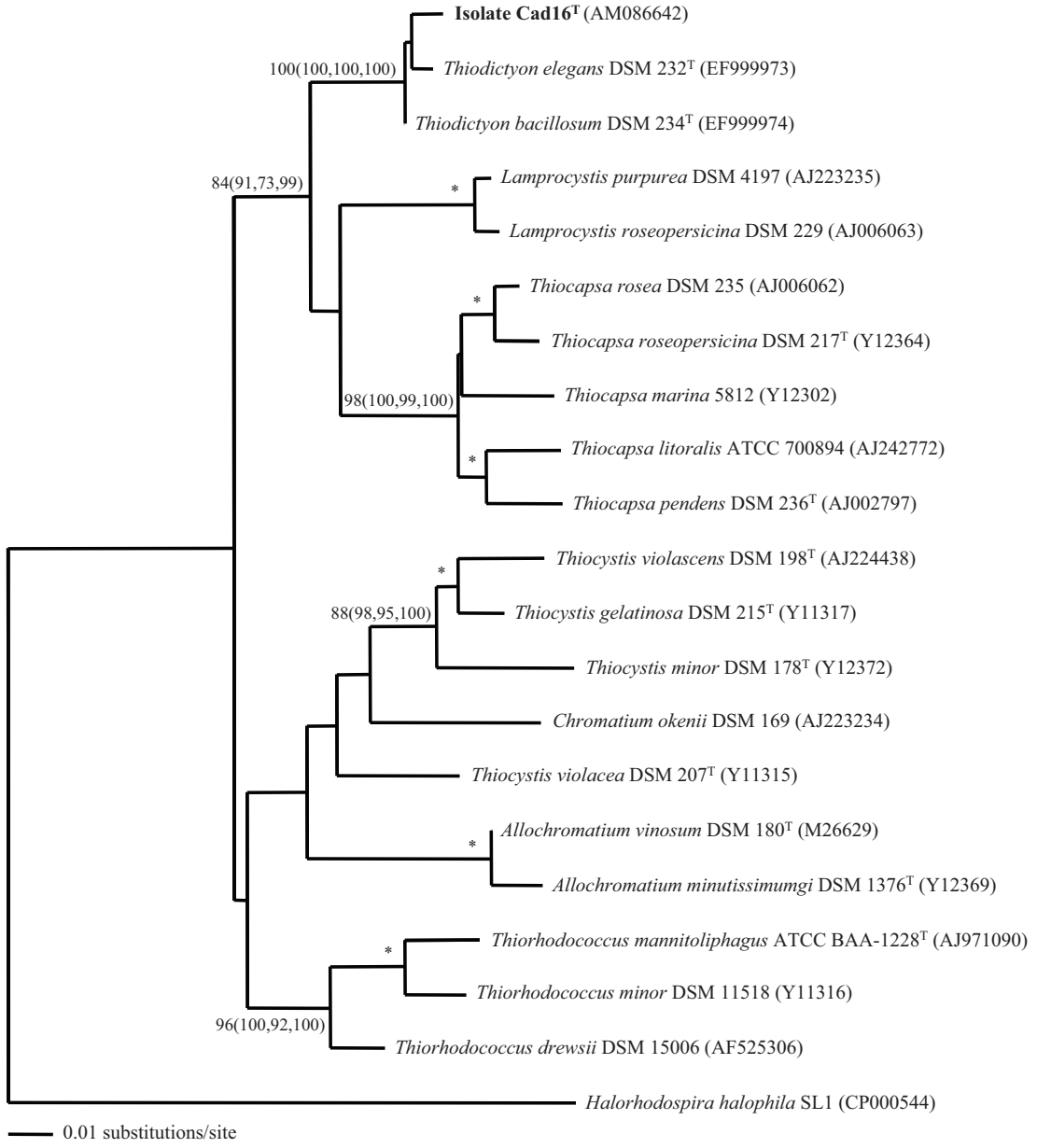

Fig. 2. Maximum likelihood tree topology from 16S rRNA gene sequences for isolate Cad16^T and other closely related species of the family Chromatiaceae created using PAUP*4.0b10 and a GTR model of sequence evolution [20]. Numbers reflect bootstrap support (BS) measures generated in PAUP and only include those measures over 70%. Numbers in parentheses reflect BS measures from neighbor joining and maximum parsimony analyses in PAUP and Bayesian posterior probabilities (PP) created using MRBAYES version 3.0 [27], respectively. The outgroup was specified as strain *H. halophila* (CP000544). T: type strain.

the presence of pyruvate was clearly observed at 2.5 mM, however, growth was only slightly promoted at 5 mM and not at all at 1 mM.

Chemolithoautotrophic growth was obtained both with hydrogen sulfide (0.02%) and thiosulfate (0.07%) or with sulfide alone (0.07%) in the dark, with a micro-oxic headspace atmosphere (5% O_2, 10% CO_2 and 85% N_2) as suggested by Kämpf and Pfennig [23] in deep agar shake cultures. Unlike Cad16^T both *T. bacillosum* and *T. elegans* were not able to grow under chemolithoautotrophic conditions (Table 1.)

Phylogenetic analysis

A representative ML tree with BS support values for ML, NJ, and MP analyses and posterior probability values (PP) for Bayesian analysis shows that isolate Cad16^T clustered with high support with representative strains of the genus *Thiodictyon* within the γ-subdivision of Proteobacteria (Fig. 2). Tree topologies were identical for each of the phylogenetic methods employed. Isolate Cad16^T had 100.0% and 99.9% 16S rRNA gene sequence identity (1393 bp), to clone 371 (AJ006061) and clone 335 (AJ006059), respectively [2,3]. The closest relatives of isolate Cad16^T were *T. bacillosum* DSM234^T with 99.2% and *T. elegans* DSM232^T with 98.9% sequence similarity (Fig. 2). 16S rRNA gene sequence similarity between *T. bacillosum* and *T. elegans* was found to be higher (99.4%). 16S rRNA gene sequences of *T. elegans* (EF999973) and *T. bacillosum* (EF999974) were deposited in the EMBL/GenBank databases in 2007, and were thus not included in the recent reclassification of species belonging to the Chromatiaceae.

G+C content

The genomic G+C content of isolate Cad16^T was 67.7% which is notably different but in the same range as values reported for *T. bacillosum* and *T. elegans* (66.3% and 65.3%, respectively), and

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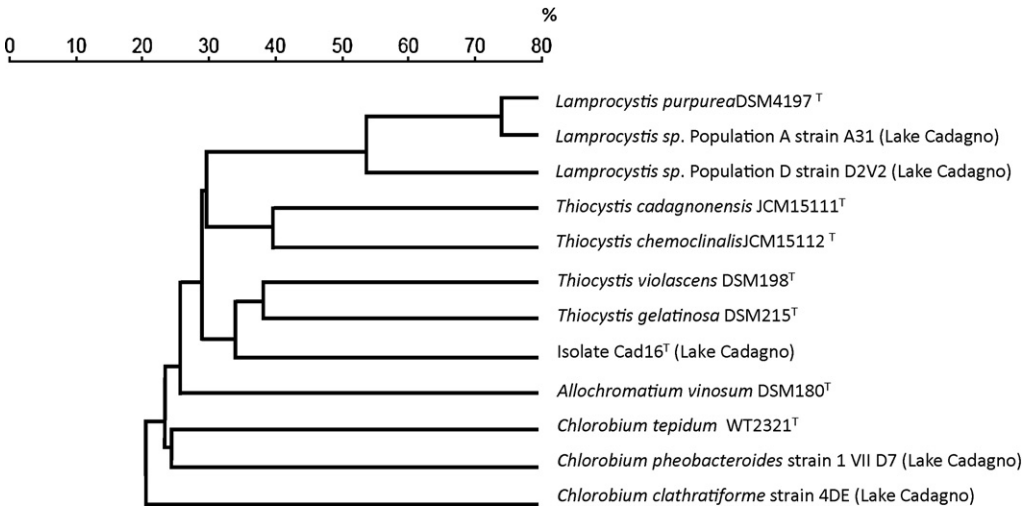

Fig. 3. MALDI-TOF MS dendrogram of 12 strains of phototrophic sulfur bacteria, resulting from single-link clustering analysis (SARAMIS^{TM} database software). Error 0.08%; range of m/y from 2000–20,000. T: type strain.

more distant to values for the genera *Lamprocystis* (63.4–64.1%) and *Thiocapsa* (63.3–66.3%).

MALDI-TOF MS analysis

All available strains of phototrophic sulfur bacteria, including 7 strains previously isolated from Lake Cadagno, were analyzed by MALDI-TOF MS (Fig. 3). Unfortunately, no other *Thiodictyon* strains were available. All *Lamprocystis* species, including *L. purpurea* DSM4450^T and *L.* sp. population D strain D2V2, clustered together and distant from Cad16^T.

Discussion

The 16S rRNA sequence similarity of Cad16^T to the genus *Thiodictyon* and the clear separation from the genus *Lamprocystis* by MALDI-TOF MS analysis, as well as others molecular and physiological differences confirm the classification of strain Cad16^T as a member of the genus *Thiodictyon*, and support the description of a new *Thiodictyon* species, *i.e. Candidatus* "Thiodictyon syntrophicum" sp. nov. strain Cad16^T. Moreover, our data support the morphology-based classification proposed by Pfennig and Trüper [8], and the phylogenetic position of the genus *Thiodictyon* related to the genera *Lamprocystis*, *Thiocystis* and *Thiocapsa* (Imhoff, 2005) was confirmed in this study.

Further characterization using the criteria recommended by Imhoff and Caumette [24] showed new characteristics within this genus: chemolithoautotrophic growth under micro-oxic conditions in the dark and the presence of okenone was not found in the other two *Thiodictyon* species from which Cad16^T differed in cell morphology and cell arrangement. Unfortunately, only a limited data set was available for the 2 described *Thiodictyon* species, and thus some specific characteristics of isolate Cad16^T could not be compared to those of the described species (*e.g.* its ability to grow on thiosulfate which has not been assessed for the described species so far) (Table 1). Because *T. elegans* DSM232^T and *T. bacillosum* DSM234^T were not available from any official culture collection, characteristics of isolate Cad16^T could only be compared to data retrieved from previous publications [6,25] and to other type strains belonging to the genera *Lamprocystis* and *Thiocapsa* [25,26]. Another characteristic of Cad16^T is that in its natural habitat it is frequently observed in association with sulfate-reducing bacteria related to *Desulfocapsa thiozymogenes* in a cell-to-cell contact three dimensional structure [9].

Our data based on morphological and physiological traits as well as the ecological relevance of the isolated strain Cad16^T support the description of a provisionally novel species within the genus *Thiodictyon*. Our isolate is therefore proposed and described as *Candidatus* "Thiodictyon syntrophicum" sp. nov. strain Cad16^T, a provisionally novel species within the genus *Thiodictyon* (*syn.tro'phi.cum*. Gr. pref. *syn*, together with; Gr. adj. *trophikos*, nursing, tending or feeding; N.L. neut. adj. *syntrophicum*, syntrophic). Due to the syntrophic association and cell-to-cell aggregation with a sulfate-reducing and sulfur disproportionating bacteria, *Desulfocapsa* sp., observed in mixed culture and in natural environment [3,9], see also the supplementary material S2.

Acknowledgements

The authors wish to thank N. Ruggeri, A. Caminada, C. Benagli and S. De Respinis. This work was supported by grants from the Swiss National Science Foundation (NF31-46855.96), the US National Science Foundation (NSF GK-12 grant 0742306), the canton of Ticino and the Alpine Biology Center Foundation (Switzerland). We acknowledge Dr. P. Schumann (DSMZ, Braunschweig) for the analysis of the mol% G+C content of the DNA, Dr. A. Lami (CNR Istituto Italiano di Idrobiologia) for ion pairing reversed-phase HPLC analysis, and Dr. J. Euzéby for help on the nomenclature.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.syapm.2012.01.001.

References

[1] Decristophoris, P.M.A., et al. (2009) Fine scale analysis of shifts in bacterial community structure in the chemocline of meromictic Lake Cadagno, Switzerland. J. Limnol. 68 (1), 16–24.
[2] Tonolla, M., et al. (1999) In situ analysis of phototrophic sulfur bacteria in the chemocline of meromictic Lake Cadagno (Switzerland). Appl. Environ. Microbiol. 65 (3), 1325–1330.
[3] Tonolla, M., Peduzzi, R., Hahn, D. (2005) Long-term population dynamics of phototrophic sulfur bacteria in the chemocline of Lake Cadagno, Switzerland. Appl. Environ. Microbiol. 71 (7), 3544–3550.
[4] Tonolla, M., et al. (1998) Microscopic and molecular in situ characterization of bacterial populations in the meromictic lake Cadagno. Doc. Istit. Ital. Idrobiol. 63, 31–44.
[5] Peduzzi, S., et al. (2011) *Thiocystis chemoclinalis* sp. nov. and *Thiocystis cadagnonensis* sp. nov., two new motile purple sulfur bacteria isolated from

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the chemocline of meromictic lake Cadagno, Switzerland. Int. J. Syst. Evol. Microbiol. 61 (7), 1682–1687.
[6] Winogradsky, S. (1888) Beitrage zur Morphologie und Physiologie der Bakterien. Zur Morphologie and Physiologie der Schwefelbakterien. A. Felix, Leipzig. Microbiologie du sol. Massonet Cie, Paris, vol. 1.
[7] Pfennig, N., Truper, H.G. (1971) Higher taxa of the phototrophic bacteria. Int. J. Syst. Evol. Microbiol. 21 (1), 17–18.
[8] Pfennig, N., Trüper, H.G. 1989 Anoxygenic phototrophic bacteria Bergey's Manual of Systematic Bacteriology, vol. 3, pp. 1635–1709.
[9] Peduzzi, S., Tonolla, M., Hahn, D. (2003) Isolation and characterization of aggregate-forming sulfate-reducing and purple sulfur bacteria from the chemocline of meromictic Lake Cadagno, Switzerland. FEMS Microbiol. Ecol. 45 (1), 29–37.
[10] Widdel, F., Bak, F. (1992) Gram-negative mesophilic sulfate-reducing bacteria. Prokaryotes 4, 3352–3378.
[11] Pfennig, N. (1978) *Rhodocyclus purpureus gen.* nov. and sp. nov., a ring-shaped, vitamin B12-requiring member of the family Rhodospirillaceae. Int. J. Syst. Evol. Microbiol. 28 (2), 283–288.
[12] Pfennig, N. (1974) *Rhodopseudomonas globiformis*, sp. n., a new species of the Rhodospirillaceae. Arch. Microbiol. 100 (1), 197–206.
[13] Mantoura, R.F.C., Llewellyn, C.A. (1983) The rapid determination of algal chlorophyll and carotenoid pigments and their breakdown products in natural waters by reverse-phase high-performance liquid chromatography. Anal. Chim. Acta 151, 297–314.
[14] Hurley, J.P. (1988) Analysis of aquatic pigments by high performance liquid chromatography. J. Anal. Purif. 3, 12–16.
[15] Mesbah, M., Premachandran, U., Whitman, W.B. (1989) Precise measurement of the G+C content of deoxyribonucleic acid by high-performance liquid chromatography. Int. J. Syst. Evol. Microbiol. 39 (2), 159–167.
[16] Altschul, S., et al. (1997) Gapped BLAST and PSI-BLAST: a new generation of protein database search programs. Nucleic Acids Res. 25 (17), 3389–3402.
[17] Pearson, W.R., Lipman, D.J. (1988) Improved tools for biological sequence comparison. Proc. Natl. Acad. Sci. USA 85 (8), 2444–2448.
[18] Maddison, W.P., Maddison, D.R. 1992 MacClade: Analysis of Phylogeny and Character Evolution, Version 3.0, Sinauer, Sunderland, MA.
[19] Thompson, J.D., et al. (1997) The CLUSTAL_X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acids Res. 25 (24), 4876.
[20] Swofford, D.L. 2003 PAUP*. Phylogenetic Analysis Using Parsimony (* and other methods). Version 4, Sinauer Associates, Sunderland, MA.
[21] Pfennig, N., Markham, M.C., Liaaen-Jensen, S. (1968) Carotenoids of Thiorhodaceae. Arch. Microbiol. 62 (2), 178–191.
[22] Vogl, K., Bryant, D.A. (2011) Elucidation of the biosynthetic pathway for Okenone in *Thiodictyon* sp. Cad16 leads to the discovery of two novel carotene ketolases. J. Biol. Chem. 286 (44), 38521–38532.
[23] Kämpf, C., Pfennig, N. (1980) Capacity of Chromatiaceae for chemotrophic growth. Specific respiration rates of *Thiocystis violacea* and *Chromatium vinosum*. Arch. Microbiol. 127 (2), 125–135.
[24] Imhoff, J.F., Caumette, P. (2004) Recommended standards for the description of new species of anoxygenic phototrophic bacteria. Int. J. Syst. Evol. Microbiol. 54 (4), 1415–1421.
[25] Brenner, D.J., et al. 2005 Anoxygenic phototrophic purple bacteria. In: Bergey's Manual® of Systematic Bacteriology, Springer, US, pp. 119–132.
[26] Eichler, B., Pfennig, N. (1988) A new purple sulfur bacterium from stratified freshwater lakes. *Amoebobacter purpureus* sp. nov. Arch. Microbiol. 149 (5), 395–400.
[27] Huelsenbeck, J.P., Ronquist, F. (2001) MRBAYES: Bayesian inference of phylogenetic trees. Bioinformatics 17 (8), 754–755.

Please cite this article in press as: S. Peduzzi, et al., *Candidatus* "Thiodictyon syntrophicum", sp. nov., a new purple sulfur bacterium isolated from the chemocline of Lake Cadagno forming aggregates and specific associations with *Desulfocapsa* sp. Syst. Appl. Microbiol. (2012), doi:10.1016/j.syapm.2012.01.001