Archives of Microbiology (2020) 202:191–196
https://doi.org/10.1007/s00203-019-01738-5

ORIGINAL PAPER

Dyadobacter luteus sp. nov., isolated from rose rhizosphere soil

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Received: 27 June 2019 / Revised: 3 September 2019 / Accepted: 24 September 2019 / Published online: 8 October 2019

Abstract

A novel Gram-negative, aerobic, rod-shaped bacterium, RS19^T, was isolated from rose rhizosphere soil. The strain was psychrophilic and showed good growth over a temperature range of 1–37 ℃. Colonies on TSB agar were circular, smooth, mucoid, convex with clear edges and yellow. Phylogenetic analysis based on 16S rRNA gene sequences characterized RS19^T in the genus *Dyadobacter* and showed that strain RS19^T was most closely related to *Dyadobacter psychrophilus* CGMCC 1.8951^T (97.4%) and *Dyadobacter alkalitolerans* CGMCC 1.8973^T (97.1%). The average nucleotide identity values to the closest related species type strains were less than 84.0%. The DNA G + C content was 43.1 mol%, and the predominant respiratory menaquinone was MK-7. The major fatty acids were summed features 3 ($C_{16:1}$ *ω7c* and/or $C_{16:1}$ *ω6c*), iso-$C_{15:0}$, $C_{16:1}$ *ω5c* and iso-$C_{17:0}$ 3-OH. Based on genotypic, phenotypic and chemotaxonomic data, strain RS19^T is different from closely related species of the genus *Dyadobacter*. RS19^T represents a novel species within the genus *Dyadobacter*, for which the name *Dyadobacter luteus* sp. nov. is proposed. The type strain is RS19^T (= CGMCC 1.13719^T = ACCC 60381^T = JCM 32940^T).

Keywords *Dyadobacter luteus* · *Cytophagaceae* · Rose rhizosphere soil

Abbreviations

NCBI	National Center for Biotechnology Information database
NJ	Neighbor joining
ML	Maximum-likelihood
ME	Minimum evolution
ORFs	Open-reading frames
ANI	Average nucleotide identities
TSB	Tryptic soy broth
TSA	Tripticase soy agar
PE	Phosphatidylethanolamine
PL	Unidentified phospholipid
AL	Aminolipids
L	Unidentified lipids
MK-7	Menaquinone-7

Communicated by Erko Stackebrandt.

The GenBank/EMBL/DDBJ accession number for the 16S rRNA gene and genome of *Dyadobacter luteus* sp. nov. strain RS19^T are MH558673 and QNUL00000000. The digital protologue database (DPD) Taxon Number of strain RS19^T is TA01031.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00203-019-01738-5) contains supplementary material, which is available to authorized users.

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Introduction

The genus *Dyadobacter*, a member of the family *Cytophagaceae*, was proposed by Chelius and Triplett (2000) to accommodate Gram-negative, rod-shaped bacteria within the phylum *Bacteroidetes*, occurred in pairs in young cultures but in chains of coccoid cells in old cultures and produced a nondiffusible, yellow-like pigment (Reddy and Garcia-Pichel 2005). At the time of writing, 13 species of this genus have been included in list of prokaryotic names with standing in nomenclature (LPSN, https://www.bacterio.net). The genus *Dyadobacter* has been isolated from various sources, such as soil, plants, freshwater, seawater, desert sand, glacial samples and subterranean sediment samples

(Chelius and Triplett 2000; Reddy and Garcia-Pichel 2005; Chaturvedi et al. 2005; Liu et al. 2006; Baik et al. 2007; Dong et al. 2007; Tang et al. 2009; Zhang et al. 2010; Lee et al. 2010; Chen et al. 2012; Chun et al. 2013; Shen et al. 2013; Wang et al. 2015; Tian et al. 2015; Gao et al. 2016; Dahal and Kim 2018; Song et al. 2019). To investigate the rhizobacteria of roses, a novel strain, designated RS19^T, was obtained.

Materials and methods

Isolation, cultivation, and maintenance

Strain RS19^T was isolated from rose rhizosphere soil in the Mentougou District of Beijing, People's Republic of China (39°57′48″N 116°05′00″E), with Luria–Bertani (LB) agar plates in May 2016. *D. psychrophilus* CGMCC 1.8951^T and *D. alkalitolerans* CGMCC 1.8973^T were obtained from the China General Microbiological Culture Collection Center and were used as related type strains.

Morphology

The purified colonies were observed on LB medium. The cellular morphology was observed by scanning electron microscopy. Gram stain was performed using the bioMérieux Gram stain kit according to the manufacturer's instructions.

Phylogenetic analysis

DNA was extracted and purified using a commercial kit (TaKaRa MiniBEST Bacteria Genomic DNA Extraction Kit Ver. 3.0). The 16S rRNA gene was amplified by PCR with the universal primers 27F and 1492R. The 16S rRNA gene sequence of strain RS19^T was submitted to GenBank and the EzBioCloud server (EzTaxon-e database) to search for similar sequences. The 16S rRNA gene sequence of *Dyadobacter luteus* RS19^T was compared with the sequences available in the National Center for Biotechnology Information (NCBI) GenBank database and EzTaxon-e database. Multiple alignments were performed using CLUSTAL_X software (Thompson et al. 1997). The phylogenetic trees were reconstructed using the neighbor-joining (NJ), maximum likelihood (ML) and minimum-evolution (ME) analysis with the MEGA 7 program (Kumar et al. 2016). The evolutionary distances were calculated using the Maximum Composite Likelihood Method (Tamura et al. 2004). Bootstrap values were calculated based on 1000 replications in each case.

Physiological and biochemical tests

The growth temperature range and optimal growth temperature were tested in tryptic soy broth (TSB) liquid medium at 1, 4, 15, 20, 25, 30, 37, and 45 ℃. Bacterial growth was measured by an increase in turbidity at 600 nm using a spectrophotometer. The bacterium was grown in TSB liquid medium at pH 3, 4, 5, 6, 7, 8, 9, and 10 and at 0, 1, 2, 3, 5, 7, and 10% (w/v) NaCl to determine the pH range and NaCl tolerance for bacterial growth.

Oxidase activity was tested using 1% (w/v) tetra-methyl-p-phenylene diamine. Catalase activity was measured by bubble production in 3% (v/v) H_2O_2. Carbon source utilization tests, enzyme activity tests, and additional physiological and biochemical tests were performed using Biolog GEN III microplates, API ZYM and API 20NE kits (bioMérieux) according to the manufacturer's instructions.

Chemotaxonomic characterization

For measurement of cellular fatty acid composition, *D. luteus* RS19^T, *D. psychrophilus* CGMCC 1.8951^T and *D. alkalitolerans* CGMCC 1.8973^T were incubated on trypticase soy agar (TSA) at 28 ℃ for 2–3 days. The fatty acids were analyzed by a 6890N gas chromatograph (Agilent) using the Sherlock Microbial Identification System with standard MIS Library Generation Software (version 6.0 and date 4; Microbial ID Inc., Newark, DE, USA) (Sasser 2001).

Polar lipids of strain RS19^T and related strains were extracted from 200 mg of freeze-dried cell material according to the method of Minnikin et al. (1977, 1984) and separated by two-dimensional silica gel thin-layer chromatography (Macherey-Nagel Art. No. 818 135). It was developed in chloroform:methanol:water (65:25:4, v/v/v) for the first direction and in chloroform:methanol:acetic acid:water (80:12:15:4, v/v/v/v) for the second direction. Total lipid material was detected using staining reagents (ninhydrin, molybdenum blue and molybdophosphoric acid) specific for defined functional groups. The polar lipid analysis was performed by the identification service of the Agricultural Culture Collection of China.

Respiratory quinones were extracted from lyophilized cells according to the method of Collins et al. (1977), purified by TLC and analyzed by means of HPLC as reported by Xie and Yokota (2003).

Genome sequencing and genotypic characterization

For genome sequencing of strain RS19^T, Illumina MiSeq sequencing was performed at Shanghai Personal Biotechnology Co., Ltd., China. The raw data were filtered and

trimmed by PRINSEQ v0.20.4 (Schmieder and Edwards 2011). The trimmed reads were assembled using A5-miseq v20150522 with default parameters (Coil et al. 2015). CheckM v1.0.3 was used to estimate the completeness of the genome. Protein-coding open-reading frames (ORFs) were predicted by Glimmer v3.02 (Delcher et al. 2007).

The relatedness of the genome sequence of *Dyadobacter luteus* RS19^T to the whole genome sequences of related type strains was determined based on the average nucleotide identities (ANI) (Goris et al. 2007; Meier-Kolthoff et al. 2014; Richter and Rossello-Mora 2009). Genome sequences in a pairwise comparison were split into 1000 bp windows and aligned with nucmer in MUMmer v3.23 (ANIm) (Kurtz et al. 2004). ANI were calculated using JSpecies v1.2.1 (Meier-Kolthoff et al. 2014).

Results and discussion

Morphological and physiological characteristics

Cells are rod-shaped, Gram-stain negative and aerobic. Colonies on TSB agar are circular, smooth, mucoid, convex with clear edges, yellow and 1.0–2.0 mm in diameter after 24 h of incubation at 28 °C.

Phylogenetic analysis

The 16S rRNA gene sequence (1398 bp) of strain RS19^T was deposited in GenBank under the accession number MH558673. The 16S rRNA gene sequences in the GenBank database revealed that strain RS19^T belongs to the genus *Dyadobacter*. Based on the analysis of the EzBioCloud database, the *Dyadobacter psychrophilus* strain showed the highest pairwise similarity of 97.4%. The following highly related species were *Dyadobacter alkalitolerans*, *Dyadobacter sediminis* and *Dyadobacter crusticola,* with pairwise similarities of 97.1%, 96.8% and 96.6%, respectively.

The NJ tree, ME tree and ML tree for the 16S rRNA are presented in Fig. 1, Fig. S1 and Fig. S2. The phylogenetic tree indicated that strain RS19^T was clustered with *D. psychrophilus* CGMCC 1.8951^T and *D. alkalitolerans* CGMCC 1.8973^T.

Chemotaxonomic characteristics

Strain RS19^T grew with D-trehalose, gentiobiose, stachyose, L-fucose, 1% sodium lactate, pectin, D-galacturonic acid, L-galactonic acid lactone and D-glucuronic acid, which are negative for *D. psychrophilus* CGMCC 1.8951^T and *D. alkalitolerans* CGMCC 1.8973^T (Table 1). All strains were positive for utilization of D-glucose. All strains were negative for hydrolysis of gelatin and assimilation of D-mannitol,

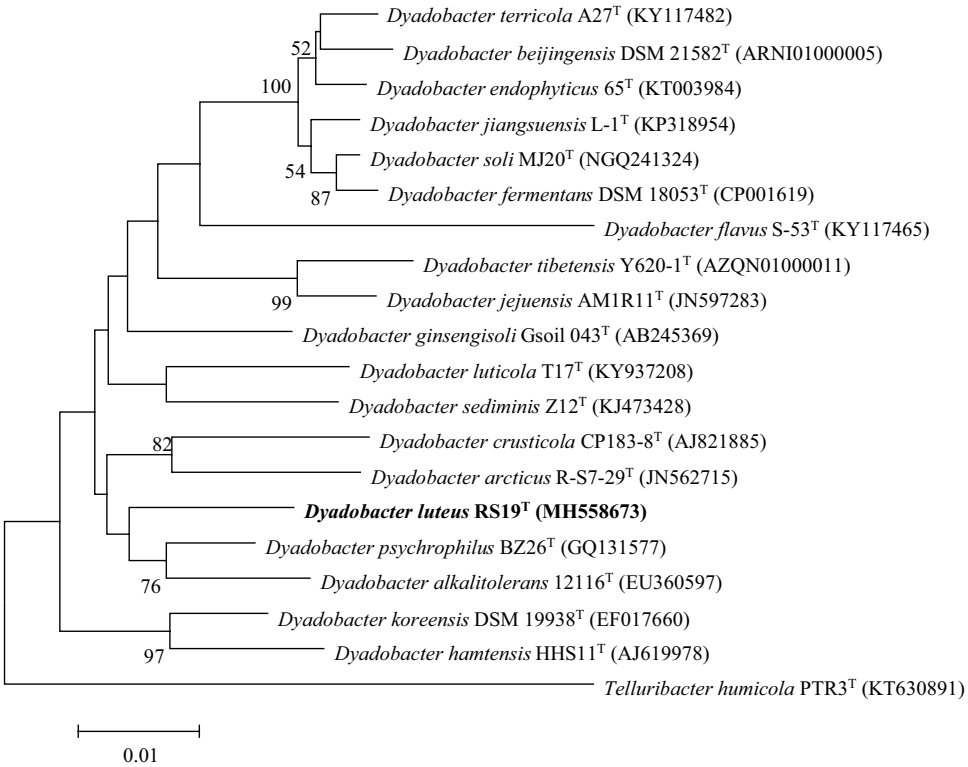

Fig. 1 Neighbor-joining phylogenetic tree based on 16S rRNA gene sequences showing the relationships between strain *Dyadobacter luteus* RS19^T and related taxa. Bootstrap values were determined based on 1000 replications. Only values > 50% are shown. Bar, 0.01 substitutions per nucleotide position. GenBank accession numbers are indicated for each strain

Table 1 Differential characteristics of *Dyadobacter luteus* RS19^T and the type strains of closely related species

	1	2	3
Temperature range (°C)	4–37	1–30	4–30
P-nitroso-D-methyl galactose	−	+	+
Assimilation			
L-Arabinose	+	−	−
N-Acetyl glucosamine	W	−	+
D-Maltose	+	−	+
Carbon resources (Biolog GENIII)			
D-Maltose	+	W	+
D-Trehalose/gentiobiose/sucrose/stachyose	+	−	−
D-Cellobiose/D-turanose	+	−	W
1% sodium lactate/pectin/L-galactonic acid lactone	+	−	−
N-Acetyl-D-glucosamine	+	−	+
D-Galactose	+	+	W
L-Fucose	W	−	−
L-Rhamnose	+	W	−
Myo-inositol/lincomycin	−	+	−
D-Galacturonic acid/D-glucuronic acid	+	−	−
Vancomycin	+	+	−
Tetrazolium violet	+	+	W
Tween 40	−	−	W
Enzyme production (API ZYM)			
Esterase/esterase lipase	+	W	W
Valine arylamidase	W	+	+
Trypsin	−	W	W
Acid phosphomonoesterase/naphthol-AS-BI-phosphoric acid	+	+	W
β-Glucuronidase	−	+	−
β-Glucosidase/α-mannosidase	W	+	+
DNA G+C content (mol%)	43.1	48.9[a]	46.3[b]

All data are from this study unless indicated. 1, *Dyadobacter luteus* RS19^T; 2, *Dyadobacter psychrophilus* CGMCC 1.8951^T; 3, *Dyadobacter alkalitolerans* CGMCC 1.8973^T

+, positive; −, negative; W, weakly positive reaction

[a]Data from Zhang et al. (2010)

[b]Data from Tang et al. (2009)

potassium gluconate, decanoic acid, adipic acid, malic acid, citric acid and phenylacetic acid.

The fatty acid analysis revealed that all strains contained iso-$C_{15:1}$, iso-$C_{15:0}$, $C_{16:1}$ *ω5c*, $C_{16:0}$, iso-$C_{15:0}$ 3-OH, iso-$C_{17:0}$ 3-OH and summed feature 3 ($C_{16:1}$ *ω7c* and/or $C_{16:1}$ *ω6c*) as the major components. The major cellular fatty acid profile (> 5% of total) of strain RS19^T was summed feature 3 ($C_{16:1}$ *ω7c* and/or $C_{16:1}$ *ω6c*), iso-$C_{15:0}$, $C_{16:1}$ *ω5c*, iso-$C_{17:0}$ 3-OH and iso-$C_{15:0}$ 3-OH (Table 2).

The polar lipids of RS19^T contained phosphatidylethanolamine (PE), unidentified phospholipid (PL), two aminolipids (AL), and eleven unidentified lipids (L) (Fig. S3). For the closely related species, the polar lipids were PE, PL, two AL, and nine L for *D. psychrophilus* CGMCC 1.8951^T, and PE, PL, two AL, and seven L for *D. alkalitolerans* CGMCC 1.8973^T.

Genotypic characteristics

The total genome sequence length of RS19^T was 6.95 Mbp. 5857 ORFs, 38 tRNAs, 4 rRNAs and 14 ncRNAs were predicted in the genome sequence of RS19^T. The G+C content was 43.1 mol%, which was lower than that of *D. psychrophilus* CGMCC 1.8951^T (48.9 mol%) and *D. alkalitolerans* CGMCC 1.8973^T (46.3 mol%). The ANIm values of *D. psychrophilus* CGMCC 1.8951^T and *D. alkalitolerans* CGMCC 1.8973^T versus *D. luteus* RS19^T were 83.82% and 83.6%, respectively. Based on comparative analysis of the ANI values, the ANI threshold range for species demarcation was 95–96%, as suggested by Miller et al. (2016), Kim et al. (2014) and Richter and Rossello-Mora (2009). The ANIm values of *Dyadobacter luteus* RS19^T to closely related type strains were lower than 84%, providing strong evidence in

Table 2 Cellular fatty acid compositions of strain RS19^T and the type strains of closely related species

Fatty acid	1	2	3
Iso-$C_{15:1}$ G	5.0	2.7	1.3
Iso-$C_{15:0}$	18.5	16.6	26.6
Anteiso-$C_{15:0}$	1.5	–	–
$C_{16:1}$ *ω5*c	14.5	13.3	5.7
$C_{16:0}$	4.5	8.5	5.2
Iso-$C_{15:0}$ 3-OH	5.7	2.8	3.8
$C_{16:0}$ 3-OH	–	3.2	2.0
Iso-$C_{17:0}$ 3-OH	9.2	8.6	9.2
Summed feature 3[a]	36.1	38.1	38.1

All data are from this study. 1, *Dyadobacter luteus* RS19^T; 2, *Dyadobacter psychrophilus* CGMCC 1.8951^T; 3, *Dyadobacter alkalitolerans* CGMCC 1.8973^T. Values are percentages of the total fatty acids; –, not detected

[a]Summed features represent groups of two or three fatty acids that cannot be separated by GLC with the MIDI system. Summed feature 3 contains $C_{16:1}$ *ω6c* and/or $C_{16:1}$ *ω7c*

favor of recognizing RS19^T as a novel species in the genus *Dyadobacter*.

Based on the genomic evidence, chemotaxonomic and physiological data, strain RS19^T represents a novel species within the genus *Dyadobacter*, for which the name *Dyadobacter luteus* sp. nov. is proposed.

Description of *Dyadobacter luteus* sp. nov.

Dyadobacter luteus (lu'te.us. L. masc. adj. *luteus* yellow).

Cells are Gram stain negative, aerobic, nonmotile, and rod shaped with a length between 1.4 and 2.3 μm and a width between 0.5 and 0.6 μm. Cells occur in pairs in young cultures, but in chains of short rod shaped to coccoid cells in older cultures. Colonies on TSB agar are circular, smooth, yellow and 1.0–2.0 mm in diameter after 24-h incubation at 28 ℃. Growth occurs in liquid TSB medium at 1–37 ℃ (optimum at 15–30 ℃), at pH 6–8 and in the presence of up to 1% NaCl. *Dyadobacter luteus* sp. nov. is positive for catalase and oxidase. Esculin but not gelatin is hydrolyzed. Positive for nitrate reduction. Positive for assimilation of D-glucose, L-arabinose, D-mannose, *N*-acetyl glucosamine and D-maltose. The following substrates are utilized as sole carbon and energy sources: D-maltose, D-trehalose, D-cellobiose, gentiobiose, sucrose, D-turanose, stachyose, D-raffinose, α-D-lactose, D-melibiose, β-methyl-D-glucoside, D-salicin, *N*-acetyl-D-glucosamine, *α*-D-glucose, D-mannose, D-fructose, D-galactose, L-fucose, L-rhamnose, 1% sodium lactate, pectin, D-galacturonic acid, L-galactonic acid lactone and D-glucuronic acid. Positive for alkaline phosphatase, esterase (C4), esterase lipase (C8), leucine-arylamidase, valine arylamidase, cystine arylamidase, acid phosphomonoesterase, naphthol-AS-BI-phosphoric acid, α-galactosidase, β-galactosidase, α-glucosidase, β-glucosidase, *N*-acetyl-β-glucosaminase, and *α*-mannosidase, but negative for *P*-nitroso-D-methyl galactose, lipase (C14), trypsin, chymotrypsin, β-glucuronidase, and β-fucosidase. The polar lipids are phosphatidylethanolamine (PE), unidentified phospholipid (PL), two aminolipids (AL), and eleven unidentified lipids (L). The major fatty acids are summed features 3 ($C_{16:1}$ *ω7c* and/or $C_{16:1}$ *ω6c*), iso-$C_{15:0}$, $C_{16:1}$ *ω5c* and iso-$C_{17:0}$ 3-OH. The predominant respiratory quinone is menaquinone-7 (MK-7). The DNA G + C content of the type strain is 43.1 mol%.

The type strain RS19^T (= CGMCC 1.13719^T = ACCC 60381^T = JCM 32940^T) was isolated from rose rhizosphere soil in Mentougou District of Beijing, People's Republic of China.

Acknowledgements We would like to thank Prof. Aharon Oren for very valuable help in naming the organism. We thank Yu Luo for the help with acquisition of the SEM images of the strain.

Funding This work was supported by the Fundamental Research Funds for the Central Non-profit Research Institution of the Chinese Academy of Forestry (CAFYBB2017MA020, CAFYBB2017MA017) and National Natural Science Foundation of China (31700548, 31700571).

Compliance with ethical standards

Conflict of interest The authors declare that there are no conflicts of interest.

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