Lysobacter erysipheiresistens sp. Nov., an antagonist of powdery mildew, isolated from tobacco-cultivated soil

Article *in* International Journal of Systematic and Evolutionary Microbiology · July 2016

DOI: 10.1099/ijsem.0.001303

CITATIONS
7

READS
68

7 authors, including:

Zhiwei Zhao
Yunnan University
54 PUBLICATIONS **2,542** CITATIONS

SEE PROFILE

Tao Li
Yunnan University
39 PUBLICATIONS **1,384** CITATIONS

SEE PROFILE

Lysobacter erysipheiresistens sp. nov., an antagonist of powdery mildew, isolated from tobacco-cultivated soil

Bing Xie,[1,2] Tao Li,[1] Xin Lin,[2] Chao-Jun Wang,[1] Yun-Jiao Chen,[2] Wei-Juan Liu[2] and Zhi-Wei Zhao[1]

Correspondence
Zhi-Wei Zhao
zhaozhw@ynu.edu.cn

[1]State Key Laboratory for Conservation and Utilization of Bio-Resources in Yunnan, Yunnan University, Kunming, 650091 Yunnan, PR China

[2]Yunnan Reascend Tobacco Technology (Group) Co., Ltd., No. 1699 Haiyuanbei Road, Kunming National Hi-technology Industry Development Zone, 650106 Yunnan, PR China

A bacterial strain, RS-LYSO-3^T, was isolated from tobacco-cultivated soil, collected near Chuxiong, Yunnan province, southwestern China. RS-LYSO-3^T could effectively inhibit the invasion of powdery mildew on tobacco. The colonies of RS-LYSO-3^T were pale yellow, and its cells were Gram-stain-negative and rod-shaped, with 68 mol% DNA G+C content. Gene sequence analysis for its 16S rRNA gene revealed the highest similarity (97.78 %) with that of *Lysobacter spongiicola*KMM 329^T. Chemotaxonomic data showed that RS-LYSO-3^T possesses a quinone system with Q-8, and iso-$C_{16:0}$, summed feature 9 and iso-$C_{15:0}$ as the predominant fatty acids, all of which support the affiliation of RS-LYSO-3^T to the genus *Lysobacter*. The results of DNA–DNA hybridization, physiological and biochemical tests clearly proved that RS-LYSO-3^T is a representative of a novel species of the genus *Lysobacter*, for which the name *Lysobacter erysipheresistens* sp. nov. is proposed. The type strain is RS-LYSO-3^T (=CCIC 23922^T=JCM 31042^T).

The genus *Lysobacter* is a member of the family *Xanthomonadaceae* (order *Xanthomonadales*, class *Gammaproteobacteria*), and was proposed by Christensen & Cook (1978). Some species of the genus *Lysobacter* were formerly classified as species of the genera *Polyangium* or *Sorangium* (Reichenbach, 2006), and include rod-shaped cells lacking fruiting bodies but with the ability to move by gliding. They possess a DNA G+C content of 62–70 mol% and form cream, brown or yellow–brown mucoid colonies. At the time of writing this manuscript, about 32 species of the genus *Lysobacter* had been reported from various sources such as the deep sea, soil, anaerobic reactors, ores, freshwater sediments, sewage and municipal solid waste (Bae *et al.*, 2005; Jung *et al.*, 2008; Lyudmila *et al.*, 2008; Muhammad & Im, 2016; Yang *et al.*, 2015; Yassin *et al.*, 2007; Ye *et al.*, 2015).

Numerous members of the genus *Lysobacter* show a broad spectrum of antagonism against various pathogens such as fungi, Gram-negative bacteria, Gram-positive bacteria and nematodes (Hayward *et al.*, 2010; Ji, 2011). Therefore, species of the genus *Lysobacter* have a great potential in biocontrol applications.

Powdery mildew diseases are caused by a number of fungal species belonging to the order Erysiphales (Jiang, 2012). *Erysiphe cichoracearum* is a pathogen of tobacco (*Nicotiana tabacum*) and usually causes sharp deterioration in tobacco quality, usability, and even death of the entire plant.

In this study, an *Erysiphe cichoracearum*-resistant bacterial strain was isolated from a tobacco field near Chuxiong, Yunnan province, China. Initially, the root exudates of tobacco K326 that were sprayed with 3-acetonyl-3-hydroxyoxindole, a chemical inducer of systemic acquired resistance (Li *et al.*, 2008), were collected as described by Geng (2011). Secondly, 5 g samples of field tobacco soil were collected and suspended in 45 ml of tobacco K326 root exudates at 30 °C at 200 r.p.m. for 3 days. The above soil suspension was then serially diluted 10^{-1}–10^{-7} times in sterile water and was spread on modified LB agar plates [per litre of tobacco root exudates: 20 g LB broth (Beijing Aoboxing Bio-Tech)] and incubated at 30 °C for 3 days. The antagonistic effect of the isolate RS-LYSO-3^T was evaluated by following the methods described in the China National Standards GB/T

The GenBank/EMBL/DDBJ accession number for the 16S rRNA gene sequence of strain RS-LYSO-3^T is KT001243.

Two supplementary figures are available with the online Supplementary Material.

Table 1. Differential phenotypic characteristics of RS-LYSO-3^T with respect to 10 type strains of related species of the genus *Lysobacter*

Strains: 1, RS LYSO-3^T; 2, *L. spongiicola* KMM 329^T; 3, *L. concretionis* Ko07^T (data from Bae *et al.*, 2005); 4, *L. korlensis* ZLD-17^T (Zhang *et al.*, 2011); 5, *L. koreensis* Dae16^T (Lee *et al.*, 2006); 6, *L. arseniciresistens* ZS79^T (Luo *et al.*, 2012); 7, *L. gummosus* KCTC 12132^T (Park *et al.*, 2008); 8, *L. capsici* YC5194^T (Park *et al.*, 2008); 9, *L. soli* DCY21^T (Srinivasan *et al.*, 2010); 10, *L. defluvii* IMMIB APB-9^T (Yassin *et al.*, 2007); 11, *L. antibioticus* DSM 2044^T (Bae *et al.*, 2005; Luo *et al.*, 2012; Srinivasan *et al.*, 2010; Yassin *et al.*, 2007; Zhang *et al.*, 2011). +, Positive; −, negative; W, weakly positive; ND, no data available.

Characteristic	1	2	3	4	5	6	7	8	9	10	11
Indole test	−	−	−	−	−	−	ND	ND	ND	−	−
Nitrate reduction	−	−	−	W	−	−	ND	−	+	−	−
DNA G+C content (mol%)	68.0	69.0	63.8	67.9	68.9	70.7	65.7	65.4	65.4	67.1	69.2
Growth on:											
D-Mannose	−	−	−	−	−	−	ND	W	+	−	+
Inositol	−	−	ND	−	−	+	ND	−	W	−	−
Synanthrin	W	−	ND	ND	ND	ND	ND	ND	ND	−	ND
Glycogen	−	−	+	−	−	−	ND	+	−	−	+
Phenylacetic acid	W	+	ND	−	−	−	ND	ND	ND	−	ND
D-Galactose	W	−	ND	−	ND	+	ND	ND	ND	ND	ND
Salicin	−	−	−	−	−	−	ND	−	−	ND	−
Melibiose	−	−	−	−	−	−	ND	+	−	ND	−
D-Glucose	+	+	−	−	−	−	+	−	+	−	W
L-Arabinose	−	−	−	−	+	−	+	−	+	−	−
Maltose	−	−	−	−	−	−	+	−	W	−	+
Trehalose	−	−	ND	−	ND	−	ND	W	−	ND	+
Starch	−	−	−	+	ND	−	−	−	ND	ND	ND
Sodium citrate	−	−	−	−	+	−	+	+	ND	ND	−
Hydrolysis of:											
Starch	−	−	−	+	ND	−	−	−	ND	−	−
Adenine	−	−	ND	−	ND	−	ND	ND	ND	−	−
Tween 80	+	+	−	ND	ND	−	ND	ND	ND	−	−
Gelatin	+	+	+	−	ND	+	+	+	ND	+	+
Xanthine	−	−	ND	−	ND	−	ND	ND	ND	−	−
Tyrosine	−	−	ND	+	ND	+	ND	ND	ND	−	+
Guanine	−	−	ND	−	ND	−	ND	ND	ND	−	+
Chitin	−	−	−	−	ND	ND	+	+	ND	−	−
Casein	−	+	ND	+	ND	−	+	+	ND	+	+
Enzyme activities											
Urease	−	−	−	−	−	−	ND	ND	ND	−	−
Esterase C4	−	−	ND	+	ND	+	ND	+	+	ND	W
Valine arylamidase	W	−	ND	−	ND	+	−	−	+	ND	−
Acid phosphatase	W	W	ND	+	ND	+	+	+	+	ND	−
β-Glucuronidase	−	−	ND	−	ND	−	ND	−	ND	−	−
α-Mannosidase	−	−	ND	−	ND	−	ND	−	ND	ND	ND
Esterase lipase C8	+	+	ND	+	ND	+	ND	+	+	ND	+
Cystine arylamidase	+	W	ND	−	ND	−	ND	−	+	ND	−
Naphthol-AS-BI-phosphohydrolase	+	W	ND	+	ND	+	ND	+	+	ND	−
α-Glucosidase	−	−	ND	−	ND	+	−	+	+	−	−
β-Fucosidase	−	−	ND	ND	ND	−	ND	−	ND	ND	ND
DNase	−	−	ND	ND	−	ND	ND	ND	ND	ND	ND
Lipase C14	−	−	ND	−	ND	+	+	+	+	ND	−
Trypsin	+	W	ND	+	ND	ND	−	+	−	ND	W
α-Galactosidase	−	−	ND	−	ND	−	−	+	−	−	−
β-Glucosidase	−	−	ND	+	ND	−	+	+	−	−	+
Oxidase	+	+	+	+	−	+	+	+	ND	ND	ND

Table 1. cont.

Characteristic	1	2	3	4	5	6	7	8	9	10	11
Arginine dihydrolase	−	−	−	ND	−	−	ND	ND	ND	−	−
Alkaline phosphatase	+	+	ND	ND	ND	+	ND	+	ND	+	+
Leucine aminopeptidase	+	+	ND	+	ND	+	ND	+	ND	−	−
Chymotrypsin	W	+	ND	+	ND	+	ND	−	−	ND	ND
β-Galactosidase	−	−	−	−	−	−	ND	−	ND	−	+
N-Acetylglucosaminidase	−	−	ND	−	ND	−	+	−	+	−	−
Catalase	+	+	+	W	+	+	+	+	ND	ND	+

23222–2008 (Ren *et al.*, 2009). The incidence of powdery mildew declined from 81.33±7.54 % to 16.67±9.70 % (mean±SEM for three independent experiments with more than 60 tobacco seedlings each).

The cell morphology of RS-LYSO-3^T grown on 2216E medium (Qingdao Hope Bio-Technology) at 30 °C for 4 days was observed under compound light (×1000; Olympus B-43) and scanning electron (Hitachi SU8010) microscopes.

Both RS-LYSO-3^T and *Lysobacter spongiicola* KMM 329^T, the most closely related strain, were cultured on 2216E medium. Growth at different temperatures (10, 25, 37 and 42 °C) and pH (5–9) was tested. Salt tolerance was determined in 2216E medium supplemented with 0–6 % NaCl (w/v). Hydrolysis of complex substrates such as adenine, xanthine, tyrosine, guanine, chitin and casein was assessed as described by Gordon (1966, 1967) and Gordon & Smith (1955). Catalase activity was examined by using 3 % H_2O_2 (v/v). Other physiological and biochemical properties of the two strains were assessed with API 20NE, API 50CH and API ZYM kits (BioMérieux) and the *Escherichia coli* Dehydration Biochemical Identification kit (Beijing Land Bridge Technology) as per the manufacturers' instructions.

DNA was extracted with a commercial genomic DNA extraction kit (ChaoShi-Bio) and was quantified using a Nano Drop 2000c spectrophotometer (Thermo Scientific). PCR amplification was performed using the primer pair 27F and 1492R (Lane, 1991). PCR and 16S rRNA gene sequencing were performed as described by Lin *et al.* (2004). Editing and processing of all sequence reads was performed with the Lasergene version 7 software package using the default settings. Using the online BLAST-N (http://www.ncbi. nlm.nih.gov/BLAST/) tool, the sequences were compared against the GenBank database. Multiple alignments were performed with the program CLUSTAL X (Thompson *et al.*, 1997). A phylogenetic tree was reconstructed using the neighbour-joining method with bootstrap analyses based on 1000 replications in the MEGA 5.0 program (Saitou & Nei, 1987). DNA–DNA hybridization was performed by the method developed by Lin (1990).

RS-LYSO-3^T and *L. spongiicola* KMM 329^T were cultured on 2261E medium at 30 °C and cells were then collected in the exponential growth phase for chemotaxonomic testing. The DNA G+C content was determined by HPLC (Thermo Fisher Ultimate 3000 UHPLC), as described by Mesbah *et al.* (1989). Respiratory quinone analysis was performed

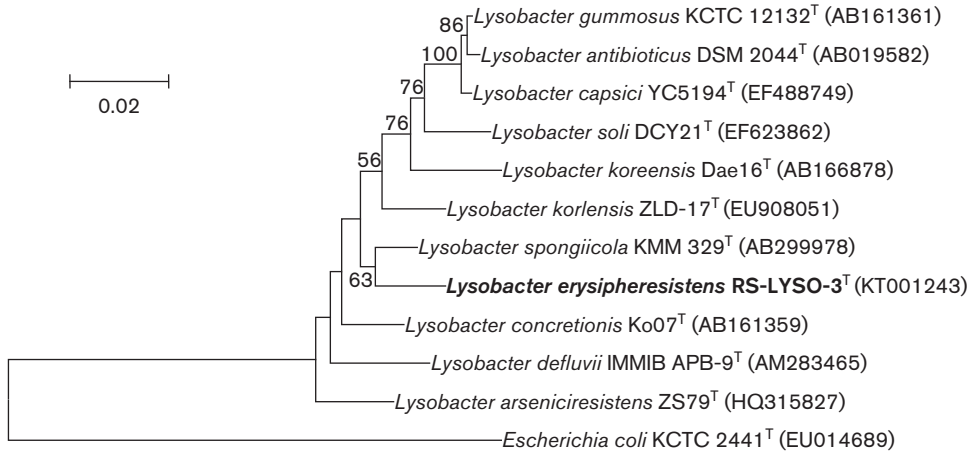

Fig. 1. Phylogenetic relationships of RS-LYSO-3^T with recognized species of the genus *Lysobacter* and other related species. The tree was reconstructed by using the neighbour-joining method. Bootstrap values (expressed as percentages of 1000 replications) greater than 50 % are shown at branch points. Bar, 0.02 substitutions per nucleotide position.

Table 2. Cellular fatty acid contents (percentages) of RS-LYSO-3^T with respect to 10 type strains of related species of the genus *Lysobacter*

Strains: 1, RS LYSO-3^T; 2, *L. spongiicola* KMM 329^T; 3, *L. concretionis* Ko07^T (data from Bae *et al.*, 2005); 4, *L. korlensis* ZLD-17^T (Zhang *et al.*, 2011); 5, *L. koreensis* Dae16^T (Lee *et al.*, 2006); 6, *L. arseniciresistens* ZS79^T (Luo *et al.*, 2012); 7, *L. gummosus* KCTC 12132^T (Park *et al.*, 2008); 8, *L. capsici* YC5194^T (Park *et al.*, 2008); 9, *L. soli* DCY21^T (Srinivasan *et al.*, 2010); 10, *L. defluvii* IMMIB APB-9^T (Yassin *et al.*, 2007); 11, *L. antibioticus* DSM 2044^T (Bae *et al.*, 2005; Luo *et al.*, 2012; Srinivasan *et al.*, 2010; Yassin *et al.*, 2007; Zhang *et al.*, 2011).

Fatty Acid	1	2	3	4	5	6	7	8	9	10	11
$C_{10:0}$	–	0.19	–	1.1	–	–	ND	ND	ND	ND	0.88
$C_{10:0}$ 3OH	0.16	0.23	ND	–	–	–	ND	–	ND	ND	ND
iso-$C_{11:0}$	4.74	11.54	6.42	4.5	3.5	12.6	ND	2.3	ND	1.78	3.47
iso-$C_{11:0}$ 3OH	6.21	14.86	5.55	6.8	5.6	12.4	ND	3.8	5.8	ND	5.17
iso-$C_{12:0}$	1.79	1.11	ND	1.4	0.7	–	ND	ND	ND	ND	ND
$C_{14:0}$	0.13	0.28	0.82	1.2	–	–	1.3	1.9	ND	0.17	1.67
iso-$C_{14:0}$	4.63	1.14	2.56	–	2.7	–	ND	ND	ND	0.71	2.25
anteiso-$C_{15:0}$	0.49	0.24	1.15	4.6	–	–	ND	ND	ND	–	5.43
iso-$C_{15:0}$	11.38	17.84	36.06	5.3	17.0	28.6	ND	23.3	34.3	40.87	19.87
iso-$C_{15:1}$ AT 5	–	–	ND	–	2.7	–	ND	ND	ND	ND	ND
iso-$C_{15:1}$ F	–	0.95	ND	1.4	ND	1.7	ND	ND	ND	ND	ND
$C_{16:0}$	0.5	1.86	2.43	9.3	2.0	1.5	17.6	10.8	1.4	2.92	10.45
iso-$C_{16:0}$	34.54	18.92	19.92	14.2	33.0	13.6	–	–	7.5	19.25	12.08
iso-$C_{16:1}$ H	5.25	1.31	ND	–	ND	–	ND	ND	ND	ND	ND
$C_{16:1}\omega 11c$	0.1	–	–	–	–	–	–	2.2	ND	–	5.54
$C_{16:1}\omega 7c$ alcohol	6.57	–	–	–	4.1	–	–	ND	ND	ND	3.0
$C_{17:0}$	0.07	0.03	ND	ND	ND	ND	1.5	ND	ND	0.76	ND
anteiso-$C_{17:0}$	0.14	0.11	ND	2.4	ND	–	ND	ND	ND	–	ND
$C_{17:0}$ cyclo	0.54	0.5	2.49	–	–	–	6.9	ND	ND	3.2	8.06
iso-$C_{17:0}$	0.86	3.78	2.93	2.1	2.5	4.9	–	3.7	17.2	11.14	1.86
iso-$C_{17:1}\omega 9c$	–	–	13.9	16	19.9	19.9	–	–	19.5	5.84	4.53
iso-$C_{18:0}$	0.27	0.13	ND	ND	0.9	ND	ND	ND	ND	–	–
Summed feature 3*	1.78	1.46	ND	21.2	ND	1.0	14.4	20.4	ND	ND	ND
Summed feature 4*	–	–	0.91	ND	2.1	ND	1.3	ND	ND	ND	11.16
Summed feature 9*	13.87	20.35	ND	ND	ND	ND	ND	ND	ND	ND	ND

*Summed feature 3 contained $C_{16:1}\omega 7c$ and/or $C_{16:1}\omega 6c$; summed feature 4 contained iso-$C_{15:0}$ 2-OH and/or $C_{16:1}\omega 7c$; summed feature 9 contained $C_{16:0}$ 10-methyl and/or iso-$C_{17:1}\omega 9c$.

by HPLC (SHIMADZU LC-20A) according to the method described by Xie & Yokota (2003). Whole-cell fatty acid analysis was performed according to the instructions of the Sherlock Microbial Identification System (MIDI Sherlock version 4.5, MIDI database TSBA40 4.10). Polar lipids were extracted and analysed by TLC (Merck TLC Silica gel60 F254), as described by Tindall (1990).

Strain RS-LYSO-3^T was Gram-stain-negative, rod-shaped (0.2–0.5×1.0–2.0 μm) and appeared either singly or in pairs (Fig. S1, available in the online Supplementary Material). Colonies grown on 2216E medium for 4 days were circular, pale yellow, glossy, semi-transparent and smaller than 0.5 mm in diameter. Strain RS-LYSO-3^T was found to assimilate D-glucose as the sole carbon source, and was catalase- and oxidase-positive. Tests for esterase lipase (C8), cystine arylamidase, naphthol-AS-BI-phosphohydrolase, trypsin, alkaline phosphatase and leucine aminopeptidase also yielded positive results. It only hydrolysed Tween 80 and gelatin. The physiological characteristics of strain RS-LYSO-3^T are summarized in the species description, and a comparison with the related type strains is shown in Table 1.

The 16S rRNA gene sequence of RS-LYSO-3^T is 1410 bp in length. A phylogenetic tree revealed that RS-LYSO-3^T formed a distinct subclade within the genus *Lysobacter* (Fig. 1) and its closest relative is *L. spongiicola* KMM 329^T with 97.78 % sequence similarity, followed by *Lysobacter concretionis* Ko07^T (96.85 %), *L. korlensis* ZLD-17^T (96.48 %), *L. koreensis* Dae16^T (96.42 %), *L. arseniciresistens* ZS79^T (95.99 %), *L. gummosus* KCTC 12132^T (95.56 %), *L. capsici* YC5194^T (95.49 %), *L. soli* DCY21^T (95.27 %), *L. defluvii* IMMIB APB-9^T (95.20 %) and *L. antibioticus* DSM 2044^T (95.19 %).

The DNA G+C content of RS-LYSO-3^T was 68.0 mol%. The respiratory quinone was Q-8 (100 %). The major

cellular fatty acids (>10 %) in RS-LYSO-3^T included iso-$C_{16:0}$ (34.54 %), summed feature 9 (13.87 %) and iso-$C_{15:0}$ (11.38 %). Although similar fatty acids to those of type strains of members of the genus *Lysobacter* were found, the predominant fatty acids were different among the various species (Table 2). The major polar lipids of RS-LYSO-3^T included diphosphatidylglycerol, phosphatidylethanolamine, phosphatidylglycerol and unidentified phospholipids (Fig. S2).

Data on DNA G+C content, 16S rRNA gene sequence similarity, and Q-8 as the major respiratory quinone clearly indicate that RS-LYSO-3^T belongs to the genus *Lysobacter*. However, some of its distinct physiological and biochemical characteristics are significantly different from those of the other type strains of members of the genus *Lysobacter*, as described in Tables 1 and 2. In addition, clear evidence is also indicated by the low DNA–DNA relatedness (43.6 ±9.1 %, mean±SEM, N=3) between RS-LYSO-3^T and its closest phylogenetic relative, *L. spongiicola* KMM 329^T. To the best of our knowledge, RS-LYSO-3^T is the first member of the genus *Lysobacter* to show antifungal activity against *Erysiphe cichoracearum*. On the basis of the above evidence, RS-LYSO-3^T represents a novel species of the genus *Lysobacter*, which is named as *Lysobacter erysipheiresistens* sp. nov.

Description of *Lysobacter erysipheiresistens* sp. nov.

Lysobacter erysipheiresistens [e.ry.si.phe.i.re.sis′tens. N. L. n. *erysiphe* powdery mildew (*Erysiphe cichoracearum*); L. pres. part. *resistens* resisting; N. L. part. adj. *erysipheiresistens* resisting of powdery mildew].

Cells are Gram-stain-negative, rod-shaped (0.2–0.5×1.0–2.0 μm), occurring singly or in pairs. Colonies grown on 2216E medium for 4 days are circular, pale yellow, glossy, semi-transparent and smaller than 0.5 mm in diameter. In contrast to growth inhibition on LB agar, the bacterium grows well on 2216E medium and on LB containing tobacco root exudates. Growth occurs at a range of 10–35 °C, 0–5 % NaCl (w/v) and pH 6–8. The major cellular fatty acids (>10 %) include iso-$C_{16:0}$, summed feature 9 and iso-$C_{15:0}$. The bacterium hydrolyses Tween 80 and gelatin, but not starch, adenine, xanthine, tyrosine, guanine, chitin or casein. Among the 50 carbon sources tested for assimilation, RS-LYSO-3^T shows positive assimilation for only D-glucose as the sole carbon source, and is weakly positive for synanthrin, phenylacetic acid, sucrose and D-galactose. RS-LYSO-3^T cannot assimilate the following carbon sources: glycerol, D-ribose, β-methyl-D-xyloside, D-mannose, inositol, α-methyl-D-glucoside, aesculin, lactose, glycogen, D-lyxose, D-arabitol, 5-ketogluconate, erthritol, D-xylose, L-sorbose, mannitol, *N*-acetylglucosamine, salicin, melibiose, melicitose, xylitol, D-tagatose, L-arabitol, decanoic acid, D-arabinose, L-xylose, L-rhamnose, sorbitol, amygdalin, cellobiose, raffinose, gentiobiose, D-fucose, potassium gluconate, hexanedioic acid, L-arabinose, adonitol, D-fructose, dulcitol, α-methyl-D-mannitol glycosides, arbutin, maltose, trehalose, starch, turanose, L-fucose, 2-ketogluconate and sodium citrate. Enzyme activities for esterase lipase (C8), cystine arylamidase, naphthol-AS-BI-phosphohydrolase, trypsin, oxidase, alkaline phosphatase, leucine aminopeptidase and catalase are present, but urease, esterase (C4), β-glucuronidase, α-mannosidase, α-glucosidase, β-fucosidase, DNase, lipase (C14), α-galactosidase, β-glucosidase, arginine dihydrolase, β-galactosidase and *N*-acetylglucosaminidase activities are absent. Activities of valine arylamidase, acid phosphatase and chymotrypsin are weakly positive. Tests for nitrate reduction and indole yield negative results. Q-8 is the sole respiratory quinone.

The type strain, RS-LYSO-3^T (=CCIC 23922^T=JCM 31042^T), was isolated from tobacco-cultivated soil at Chuxiong, Yunnan province, China. The DNA G+C content of the type strain is 68.0 %.

Acknowledgements

This research was supported by grant 2013FA001 from Key Project of Applied Basic Research of Yunnan.

References

Bae, H.-S., Im, W.-T. & Lee, S.-T. (2005). *Lysobacter concretionis* sp. nov., isolated from anaerobic granules in an upflow anaerobic sludge blanket reactor. *Int J Syst Evol Microbiol* **55**, 1155–1161.

Christensen, P. & Cook, F. D. (1978). *Lysobacter*, a new genus of nonhiting, gliding bacteria with a high base Ratio. *Int J Syst Evol Microbiol* **28**, 367–393.

Geng, G. (2011). Effect of crop root exudates on carbon and nitrogen contents, microorganisms quatity and enzyme activities in soil. In Soil and Environment College. (Shengyang: Shengyang Agricultural University).

Gordon, R. E. & Smith, M. M. (1955). Proposed group of characters for the separation of *Streptomyces* and *nocardia*. *J Bacteriol* **69**, 147–150.

Gordon, R. E. (1966). Some criteria for the recognition of Nocardia madurae (Vincent) Blanchard. *J Gen Microbiol* **45**, 355–364.

Gordon, R. E. (1967). The taxonomy of soil bacteria. In *The Ecology of Soil Bacteria*, pp. 293–321. Edited by T. R. G. Gray & B. Parkinson. Liverpool: Liverpool University Press.

Hayward, A. C., Fegan, N., Fegan, M. & Stirling, G. R. (2010). *Stenotrophomonas* and *Lysobacter*: ubiquitous plant-associated gamma-proteobacteria of developing significance in applied microbiology. *J Appl Microbiol* **108**, 756–770.

Ji, G.-H. (2011). Advancesin the study on *Lysobacter* spp. bacteria andtheir effects on biological control of plant diseases. *J Yunnan Agric Univ* **26**, 124–130.

Jiang, W.-T. (2012). *Taxonomyand flora of powdery mildews (Erysiphaceae) in Jilin Province. In Agricultural College.* (Jilin: Jilin Agricultural University).

Jung, H.-M., Leonid, N.-T., Im, W.-T., Yoo, S.-A. & Lee, S.-T. (2008). *Lysobacter ginsengisoli* sp. nov., a novel species isolated from soil in Pocheon Province, South Korea. *J Microbiol Biotechnol* **18**, 1496–1499.

Lane, D. J. (1991). 16S/23SrRNA sequencing. In *Nucleic Acid Techniques in Bacterial Systematics*, pp. 115–175. Edited by E. Stackebrandt & M. Goodfellow. Chichester: Wiley.

Lin, W.-M. (1990). *Moleculargenetic Classification and Identification of Bacteria*. Shanghai: Shanghai Science and Technology Press.

Lee, J.-W., Im, W.-T., Myung, K.-K. & Yang, D.-C. (2006). *Lysobacter koreensis* sp. nov., isolated from a ginseng field. *Int J Syst Evol Microbiol* **56**, 231–235.

Li, Y.-M., Zhang, Z.-K., Jia, Y.-T., Shen, Y.-M., He, H.-P., Fang, R.-X., Chen, X.-Y. & Hao, X.-J. & Hao, X.-J. (2008). 3-Acetonyl-3-hydroxyoxindole: a new inducer of systemic acquired resistance in plants. *Plant Biotechnol J* **6**, 301–308.

Lin, Y.-C., Uemori, K., de Briel, D. A., Arunpairojana, V. & Yokota, A. (2004). *Zimmermannella helvola* gen. nov., sp. nov., *Zimmermannella alba* sp. nov., *Zimmermannella bifida* sp. nov., *Zimmermannella faecalis* sp. nov. and *Leucobacter albus* sp. nov., novel members of the family Microbacteriaceae. *Int J Syst Evol Microbiol* **54**, 1669–1676.

Luo, G.-S., Shi, Z.-J. & Wang, G.-J. (2012). *Lysobacter arseniciresistens* sp. nov., an arsenite-resistant bacterium isolated from iron-mined soil. *Int J Syst Evol Microbiol* **62**, 1659–1665.

Lyudmila, A. R., Masataka, U., Naoto, T., Galina, M. F. & Valery, V. M. (2008). *Lysobacter spongiicola* sp. nov., isolated from a deep-sea sponge. *Int J Syst Evol Microbiol* **58**, 370–374.

Muhammad, Z. S. & Im, W.-T. (2016). *Lysobacter hankyongensis* sp. nov., isolated from activated sludge and *Lysobacter Sediminicola* sp. nov., isolated from fresh water sediment. *Int J Syst Evol Microbiol* **66**, 212–218.

Mesbah, M., Premachandran, U. & Whitman, W. B. (1989). Precise measurement of the G+C content of deoxyribonucleic acid byhigh-performance liquid chromatography. *Int J Syst Bacteriol* **39**, 159–167.

Park, J. H., Kim, R., Aslam, Z., Jeon, C. O. & Chung, Y. R. (2008). *Lysobacter capsici* sp. nov., with antimicrobial activity, isolated from the rhizosphere of pepper, and emended description of the genus *Lysobacter*. *Int J Syst Evol Microbiol* **58**, 387–392.

Reichenbach, H. (2006). The genus *Lysobacter*. *Prokaryotes* **6**, 939–957.

Ren, G.-W., Kong, F.-Y. & Wang, F.-L. (2009). *GB/T23222-2008 Grade and invetigation method of tobacco diseases and insect pests*. Beijing: Standards Press of China.

Saitou, N. & Nei, M. (1987). The neighbor-joining method: a new method for reconstructing phylogenetic trees. *Mol Biol Evol* **4**, 406–425.

Srinivasan, S., Kim, M. K., Sathiyaraj, G., Kim, H.-B., Kim, Y.-J. & Yang, D.-C. (2010). *Lysobacter soli* sp. nov., isolated from soil of a ginseng field. *Int J Syst Evol Microbiol* **60**, 1543–1547.

Tindall, B. J. (1990). Lipid composition of *Halobacterium lacusprofundi*. *FEMS Microbiol Lett* **66**, 199–202.

Thompson, J. D., Gibson, T. J., Plewniak, F., Jeanmougin, F. & Higgins, D. G. (1997). The CLUSTAL_X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Res* **25**, 4876–4882.

Xie, C. H. & Yokota, A. (2003). Phylogenetic analyses of *Lampropedia hyalina* based on the 16S rRNA gene sequence. *J Gen Appl Microbiol* **49**, 345–349.

Yang, S.-Z., Feng, G.-D., Zhu, H.-H. & Wang, Y.-H. (2015). *Lysobacter mobilis* sp. nov., isolated from abandoned lead-zinc ore. *Int J Syst Evol Microbiol* **65**, 833–837.

Yassin, A. F., Chen, W.-M., Hupfer, H., Siering, C., Kroppenstedt, R. M., Arun, A. B., Lai, W.-A., Shen, F.-T., Rekha, P. D. & Young, C. C. (2007). *Lysobacter defluvii* sp. nov., isolated from municipal solid waste. *Int J Syst Evol Microbiol* **57**, 1131–1136.

Ye, X.-M., Chu, C.-W., Shi, C., Zhu, J.-C., He, Q. & He, J. (2015). *Lysobacter caeni* sp. nov., isolated from the sludge of a pesticide manufacturing factory. *Int J Syst Evol Microbiol* **65**, 845–850.

Zhang, L., Bai, J., Wang, Y., Wu, G.-L., Dai, J. & Fang, C.-X. (2011). *Lysobacter korlensis* sp. nov. and *Lysobacter bugurensis* sp. nov., isolated from soil. *Int J Syst Evol Microbiol* **61**, 2259–2265.