Antonie van Leeuwenhoek
DOI 10.1007/s10482-016-0704-7

ORIGINAL PAPER

Lysobacter cavernae sp. nov., a novel bacterium isolated from a cave sample

Wei Chen · Ying-Liang Zhao · Juan Cheng · Xing-Kui Zhou · Nimaichand Salam · Bao-Zhu Fang · Qing-Qing Li · Wael N. Hozzein · Wen-Jun Li

Received: 27 February 2016 / Accepted: 26 April 2016

Abstract A Gram-staining negative, aerobic, rod-shaped bacterium, designated YIM C01544^T, was isolated from a soil sample collected from Sigangli Cave, Yunnan province, South-West China. The strain was able to grow over a range of temperatures (4–30 °C), pH (6.0–10.0) and NaCl concentration (0–2 %, w/v). Comparative 16S rRNA gene sequence analysis revealed that strain YIM C01544^T should be a member of the genus *Lysobacter*. The strain is closely related to *Lysobacter niastensis* GH41-7^T (97.6 %), *Lysobacter soli* DCY21^T (97.5 %), *Lysobacter enzymogenes* DSM 2043^T (97.3 %), *Lysobacter antibioticus* DSM 2044^T (97.1 %) and *Lysobacter panacisoli* CJ29^T (97.1 %). The genomic DNA relatedness values (<47 %) as indicated by DNA–DNA hybridization studies were below the threshold limit for characterization of new bacterial species. The chemotaxonomic features of the new isolate include diphosphatidylglycerol, phosphatidylglycerol, phosphatidylethanolamine, two unidentified phospholipids and two unidentified polar lipids as its characteristic polar lipids and Q-8 as the only quinone. The major fatty acids detected were iso-$C_{15:0}$ and iso-$C_{17:1}\omega 9c$. The DNA G + C content of the strain was determined to be 64.9 mol %. Based on the data from phenotypic, chemotaxonomic and molecular studies, strain YIM C01544^T merits recognition as

Wei Chen and Ying-Liang Zhao contributed equally to this work.

Electronic supplementary material The online version of this article (doi:10.1007/s10482-016-0704-7) contains supplementary material, which is available to authorized users.

W. Chen · Y.-L. Zhao · X.-K. Zhou
China Tobacco Yunnan Industrial Co. Ltd., Kunming 650231, People's Republic of China

J. Cheng · X.-K. Zhou · W.-J. Li
Key Laboratory of Microbial Diversity in Southwest China, Ministry of Education, Yunnan Institute of Microbiology, Yunnan University, Kunming 650091, People's Republic of China

N. Salam · B.-Z. Fang · W.-J. Li (✉)
State Key Laboratory of Biocontrol and Guangdong Provincial Key Laboratory of Plant Resources, School of Life Sciences, Sun Yat-Sen University, Guangzhou 510275, People's Republic of China
e-mail: liwenjun3@mail.sysu.edu.cn

Q.-Q. Li (✉)
Life Science College, Southwest Forestry University, Kunming 650224, People's Republic of China
e-mail: doublelqq@163.com

W. N. Hozzein
Bioproducts Research Chair, Zoology Department, College of Science, King Saud University, Riyadh 11451, Kingdom of Saudi Arabia

W. N. Hozzein
Botany and Microbiology Department, Faculty of Science, Beni-Suef University, Beni-Suef 62511, Egypt

Published online: 14 May 2016

novel species in the genus *Lysobacter* for which the name *Lysobacter cavernae* sp. nov. is proposed. The type strain of *Lysobacter cavernae* is YIM C01544^T (= KCTC 42875^T = DSM 101561^T = CPCC 100816^T).

Keywords *Lysobacter cavernae* sp. nov. · Sigangli Cave · Polyphasic taxonomy

Introduction

Members of the genus *Lysobacter* have been established as potential biocontrol agents (Christensen and Cook 1978; Hashizume et al. 2004). This property has been attributed to their ability to produce a variety of antimicrobial compounds including many extracellular enzymes (Allpress and Mountain 2002; Chohnan et al. 2004; Ogura et al. 2006). A recent study has also indicated that a *Lysobacter* strain XL1 releases an enzyme complex (lysoamidase bacteriolytic complex) in liquid culture that exhibits broad-antimicrobial spectrum (Tishchenko et al. 2016). Genome analysis of a *Lysobacter capsici* strain AZ78 also demonstrated the presence of a gene pool with the capability for production of antibiotics, lytic enzymes and siderophore as well as genes involved in resistance to antibiotics, environmental stressors, fungicides and heavy metals (Puopolo et al. 2016). Their ability to produce a variety of metabolites dictates the importance of searching for new isolates for future industrial applications.

The genus *Lysobacter* belongs to the family *Xanthomonadaceae* (Christensen and Cook 1978) within the class *Gammaproteobacteria*. The distinctive chemotaxonomic features of the genus *Lysobacter* include the presence of Q-8 as predominant quinone and iso-branched cellular fatty acids (Christensen and Cook 1978). The polar lipids are mainly composed of diphosphatidylglycerol (DPG), phosphatidylethanolamine (PE) and phosphatidylglycerol (PG), with genomic G + C content ranging between 61.7 and 70.7 mol % (Christensen and Cook 1978; Saddler and Bradbury 2005; Weon et al. 2006; Luo et al. 2012; Wei et al. 2012; Fukuda et al. 2013). This paper reports the taxonomic characterization of a novel *Gammaproteobacteria* of the genus *Lysobacter* isolated from a cave sample.

Materials and methods

Strain and culture conditions

Strain YIM C01544^T was isolated from a serially diluted soil sample collected from Sigangli Cave (E 103°22.791′, N 25°04.270′), Yunnan province, South-West China, using modified starch casein medium (Soluble starch 1.0 g, Casein 0.3 g, KNO_3 2.0 g, NaCl 2.0 g, K_2HPO_4 2.0 g, $MgSO_4{\cdot}7H_2O$ 0.05 g, $FeSO_4{\cdot}7H_2O$ 0.01 g, $CaCO_3$ 10 g, agar 12 g, Distilled water 1000 mL, pH 8.0) (Hayakawa and Nonomura 1987). The strain was maintained as pure cultures on International *Streptomyces* Project (ISP) 2 agar slants containing 1 % (w/v) $CaCO_3$ at 4 °C and as suspensions in glycerol (20 %, v/v) at −80 °C.

Molecular analysis

Isolation of genomic DNA and sequencing of 16S rRNA gene were performed as reported earlier (Cui et al. 2001; Li et al. 2007). The almost complete 16S rRNA gene sequence (Accession number KT306825) was subjected to BLAST analysis using the EzTaxon-e server (Kim et al. 2012). Multiple alignments with the corresponding closely related sequences (retrieved from the GenBank/EMBL/DDBJ databases) were performed using CLUSTAL_X version 1.83 (Thompson et al. 1997). Phylogenetic trees were constructed with Neighbour-Joining (Saitou and Nei 1987), Maximum-Parsimony (Fitch 1971) and Maximum-Likelihood (Felsenstein 1981) algorithms using the MEGA version 5.0 software packages (Tamura et al. 2011). Kimura's two-parameter model was used to calculate evolutionary distance matrices (Kimura 1980). The topologies of the resultant trees were evaluated by bootstrap resampling method of Felsenstein (1985) with 1000 replicates. The DNA–DNA relatedness values between strain YIM C01544^T and the closely related strains of the genus *Lysobacter* were calculated using fluorometric micro-well-based DNA–DNA hybridization studies (Ezaki et al. 1989; Christensen et al. 2000).

Phenotypic characterisation

Gram staining was performed using standard Gram's reaction and confirmed by KOH lysis test (Cerny 1978). Morphology was examined by light microscopy

(BH-2; Olympus) and scanning electron microscopy (QUANTA200; FEI). Growth at various temperatures (4–50 °C) and NaCl tolerance (0–15 %, w/v) were tested on ISP 2 plates (7 days, 28 °C). The pH range (pH 4.0–11.0, at intervals of 1.0 pH unit) for growth was tested in ISP 2 medium (28 °C, 7 days) using the buffer system described by Xu et al. (2005). Anaerobic growth was checked in a Whitley A35 anaerobic workstation containing CO_2, N_2 and H_2 gas mixture. Catalase activity was determined by assessing the production of bubbles on addition of a drop of 3 % (v/v) H_2O_2 on the bacterial cell. Oxidase activity was determined based on oxidation of tetramethyl-p-phenylenediamine (Kovacs 1956). Hydrolysis of starch and Tweens 20, 40, 60 and 80 were determined as described by Collins et al. (1977). Other phenotypic and enzyme activities were tested using the API 20NE (bioMérieux), API 50CH (bioMérieux) and Biolog GN III Micro Plate assays according to manufacturer's instructions.

Chemotaxonomy

Polar lipids were extracted as described by Minnikin et al. (1979) and identified by two-dimensional TLC (Collins and Jones 1980). Quinones were extracted (Collins et al. 1977) and analyzed using HPLC (Kroppenstedt 1982). Cellular fatty acid analysis was performed by using the Microbial Identification System (Sherlock Version 6.1; MIDI database: TSBA6; Sasser 1990). Biomass for fatty acid analysis was obtained from cells grown on tryptose soy agar (TSA; Difco) at 28 °C for 4 days. The G + C content of genomic DNA of strain YIM C01544^T was determined according to the method of Mesbah et al. (1989).

Results

Molecular analysis

The strain YIM C01544^T showed high 16S rRNA gene sequence similarities with *Lysobacter niastensis* GH41-7^T (97.6 %), *L. soli* DCY21^T (97.5 %), *L. enzymogenes* DSM 2043^T (97.3 %), *L. antibioticus* DSM 2044^T (97.1 %) and *L. panacisoli* CJ29^T (97.1 %), and had low levels of similarities (<97.0 %) with other members of the genus *Lysobacter*. Based on the sequence analysis data and neighbour-joining phylogenetic tree (Fig. 1), strains *L. niastensis* KACC 11588^T, *L. soli* KCTC 22011^T, *L. enzymogenes* BCRC 11654^T and *L. antibioticus* BCRC 11653^T were considered for DNA–DNA hybridization studies with strain YIM C01544^T to determine its taxonomic position within the genus *Lysobacter*. In addition, comparative studies were also done with *L. panacisoli* CJ29^T, *L. gummosus* KCTC 12132^T and *L. capsici* YC 5194^T as they formed a cluster with strain YIM C01544^T but have low 16S rRNA gene sequence similarities. Strain YIM C01544^T exhibited relatively low levels of DNA–DNA relatedness (Supplementary Table S1) with *L. niastensis* KACC 11588^T (46.9 %), *L. soli* KCTC 22011^T (42.3 %), *L. enzymogenes* BCRC 11654^T (26.8 %) and *L. antibioticus* BCRC 11653^T (19.2 %), which were well below the threshold point (70 %) for distinguishing novel prokaryotic species (Stackebrandt and Goebel 1994).

Phenotypic characteristics

Cells of strain YIM C01544^T were observed to be Gram-staining negative, aerobic and rod-shaped (1.0-1.8 × 0.3 μm) (Fig. S1). The strain was able to grow over a wide range of temperature (4–30 °C) and pH (6.0-10.0) on ISP 2 agar, and could tolerate up to 2 % NaCl (w/v). Optimal growth was observed at 22–28 °C, 0–1 % NaCl (w/v) and pH 7.0–8.0. The strain was found to be positive for catalase test but negative for oxidase activity. It can hydrolyse Tween 60, but not starch and Tweens 20, 40 and 80. The differential phenotypic characteristics of strain YIM C01544^T and related type strains of the genus *Lysobacter* are summarized in Table 1. Detailed biochemical features as indicated by the API 20NE (bioMérieux), API 50CH (bioMérieux) and Biolog GN III Micro Plate assays are listed in Supplementary Table S2.

Chemotaxonomy

The polar lipids of strain YIM C01544^T consisted of DPG, PG, PE, two unidentified phospholipids (PLs) and two unidentified polar lipids (Ls) (Supplementary Fig. S2). Ubiquinone-8 (Q-8) was the only quinone detected. The cellular fatty acids detected were iso-$C_{15:0}$ (47.8 %), iso-$C_{17:1}\omega 9c$ (10.3 %), iso-$C_{11:0}$ 3OH (7 %), Summed Feature 4 (iso-$C_{17:1}$ I and/or anteiso B)

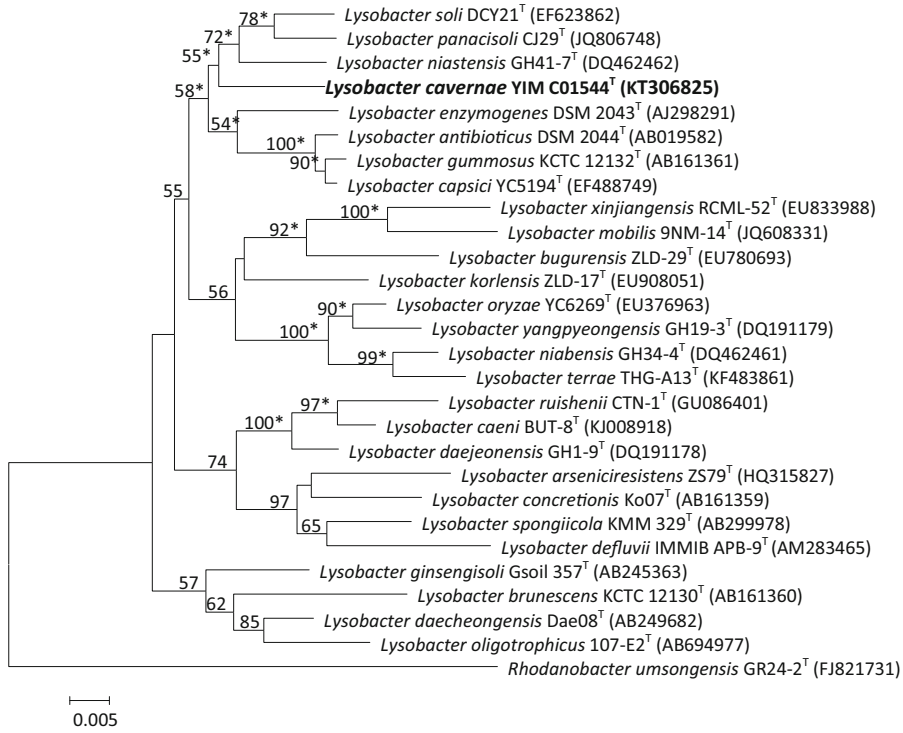

Fig. 1 Neighbour-joining phylogenetic tree based on 16S rRNA gene sequences of strain YIM C01544^T and members of the genus *Lysobacter*. Bootstrap values (expressed as percentages of 1000 replications) of above 50 % are shown at the branch points. *Asterisks* at nodes, denotes branches recovered using the maximum-parsimony and maximum-likelihood methods. *Rhodanobacter umsongensis* GR24-2^T was used as outgroup. Bar 0.005 substitutions per nucleotide position

(6.7 %), Summed Feature 3 ($C_{16:1}\omega6c$ and/or $C_{16:1}\omega7c$) (4.3 %), iso-$C_{11:0}$ (4.3 %), iso-$C_{17:0}$ (3.9 %), anteiso-$C_{15:0}$ (3.5 %), iso-$C_{16:0}$ (2.6 %), $C_{16:0}$ (1.9 %), $C_{17:0}$ cyclo (1.2 %), iso-$C_{15:0}\omega9c$ (0.7 %), iso-$C_{14:0}$ (0.7 %) and Summed Feature 1 ($C_{13:0}$ 3OH and/or $C_{15:1}$ i H) (0.6 %). The genomic G + C content was determined to be 64.9 mol %.

Discussion

The chemotaxonomic features of strain YIM C01544^T including the presence of Q-8 as quinone, iso-$C_{15:0}$ and iso-$C_{17:1}\omega9c$ as major fatty acids and DPG, PG and PE as major polar lipids are consistent with the characteristics of the genus *Lysobacter* (Christensen and Cook 1978; Saddler and Bradbury 2005; Weon et al. 2006; Luo et al. 2012; Wei et al. 2012; Fukuda et al. 2013). However, strain YIM C01544^T could be differentiated from the related type strains of the genus *Lysobacter* by many physiological characteristics. For example, the temperature range for growth of strain YIM C01544^T is low compared to those of reference type strains (Table 1). Salt tolerance is consistent with that of *L. gummosus* KCTC 12132^T and *L. capsici* YC 5194^T (Christensen and Cook 1978; Park et al. 2008) but differs from the other type strains (Weon et al. 2006; Srinivasan et al. 2010; Choi et al. 2014). Strain YIM C01544^T was found to be negative for oxidase reaction unlike strains *L. niastensis* KACC 11588^T, *L. soli* KCTC 22011^T,*L. antibioticus* BCRC 11653^T, *L. gummosus* KCTC 12132^T and *L. capsici* YC 5194^T (Weon et al. 2006; Srinivasan et al. 2010; Christensen and Cook 1978; Park et al. 2008) and was found to be positive for nitrate reduction unlike *L. antibioticus* BCRC 11653^T, *L. panacisoli* CJ 29^T, *L. gummosus* KCTC 12132^T and *L. capsici* YC 5194^T (Christensen and Cook 1978; Choi et al. 2014; Park et al. 2008). In addition, the major fatty acids were similar to the type strain *L. niastensis* KACC 11588^T, *L. soli* KCTC

Table 1 Differential characteristics of strain YIM C01544^T and closely related species of the genus *Lysobacter*. 1, YIM C01544^T; 2, *L. niastensis* KACC 11588^T; 3, *L. soli* KCTC 22011^T; 4, *L. enzymogenes* BCRC 11654^T; 5, *L. antibioticus* BCRC 11653^T; 6, *L. panacisoli* CJ 29^T; 7, *L. gummosus* LMG 8763^T; 8, *L. capsici* YC 5194^T

	1	2	3	4	5	6[£]	7[§]	8[∓]
Cell size (μm)	1.0–1.8 × 0.3	2.0–4.0 × 0.5-0.6	0.6–0.9 × 0.2-0.5	38.0 × 0.5	6.5 × 0.4	0.4–0.45 × 1.0–2.0	0.4 × 2.0	0.3–0.5 × 2.0–20
Gliding motility	−	−	+	+	+	−	+	−
NaCl tolerance (w/v, %)	0-2	0-1	0-1	0-1	0-1	0-1	0-2	0-2
pH range for growth	6-10	4-9	5-10	4-10	5-9	5-11	4-9	5.5-8.5
Temperature range for growth (°C)	4-30	10-40	4-42	10-40	4-40	10-40	10-40	15-37
Oxidase activity	−	+	+	+	+	−	+	+
Aesculin hydrolysis	+	−	+	+	+	+	+	+
β-galactosidase	+	−	−	+	+	+	+	−
Nitrate reduction	+	+	w	−	−	−	−	−
Urease activity	−	−	+	−	−	−	−	−
Assimilation of								
Cellobiose	−	−	−	−	+	−	−	−
D-fucose	−	−	+	−	−	−	−	w
D-glucose	−	w	+	+	−	−	+	−
D-lyxose	−	−	+	−	−	−	−	−
D-maltose	−	+	+	+	+	+	+	+
D-mannitol	−	+	−	−	−	−	−	−
D-mannose	+	−	+	+	+	+	+	+
D-ribose	+	−	−	−	−	−	−	+
D-xylose	−	w	−	+	+	+	−	−
Gentiobiose	−	−	−	w	+	−	−	−
L-arabinose	−	−	+	+	+	−	−	−
Methyl α-D-glucoside	+	−	−	+	+	−	−	w
N-acetyl glucosamine	+	+	+	+	−	−	+	−
Sucrose	−	−	−	w	w	+	−	−
Trehalose	−	+	−	+	+	−	+	w
DNA G + C content (mol %)	64.9	66.6[¥]	65.4[*]	69[§]	69.2[§]	65.6	65.7	65.4

Data from other studies are as indicated: [¥] Weon et al. (2006); [*] Srinivasan et al. (2010); [§] Christensen and Cook (1978); [£] Choi et al. (2014); [∓] Park et al. (2008)

22011^T, *L. enzymogenes* BCRC 11654^T and *L. antibioticus* BCRC 11653^T but the presence of $C_{17:0}$ cyclo was seen only in strain YIM C01544^T.

Strain YIM C01544^T and type species of the genus, *L. enzymogenes*, formed separate sub-clades in the phylogenetic dendrogram (Fig. 1). The two shared a DNA relatedness value of 26.8 % clearly distinguishing them as separate species. Apart from the molecular characteristics, the proposed new strain can be distinguished from the type species by many phenotypic characters (Table 1). The type species exhibited gliding motility, and was found to be positive for oxidase activity unlike strain YIM C01544^T. The two also differed in the assimilation of several key carbon sources including L-arabinose, D-glucose, D-maltose, D-ribose and trehalose. Strain YIM C01544^T could reduce nitrate and tolerate 2 % NaCl (w/v) in the growth medium but not the type species. *L. enzymogenes* could grow at pH 4 and 40 °C unlike the new strain. Morphologically, cell size of the type species (38.0 × 0.5 μm) is much larger and longer than the proposed new taxon (1–1.8 × 0.3 μm) under similar conditions of growth. Based on the phenotypic, chemotaxonomic and molecular characteristics, strain YIM C01544^T is determined to represent a novel species within the genus *Lysobacter*, for which the name *Lysobacter cavernae* sp. nov. is proposed.

Description of *Lysobacter cavernae* sp. nov

Lysobacter cavernae (ca.ver'nae. L. gen. n. *cavernae*, of a cave; referring to the source of the organism)

Cells are Gram-staining negative, aerobic, rod-shaped (1.0–1.8 × 0.3 μm) and non-motile. Colonies are yellow and circular on ISP 2 agar medium. Growth occurs at temperature range 4–30 °C, pH 6.0–10.0 and 0–2 % NaCl (w/v). Positive for catalase and nitrate reduction tests, but negative for oxidase activity. Cells can hydrolyse casein, gelatin, aesculin and Tween 60, but not starch and Tweens 20, 40 and 80. The polar lipids detected include diphosphatidylglycerol, phosphatidylglycerol, phosphatidylethanolamine, two unidentified phospholipids and two unidentified polar lipids. The predominant quinone is Q-8. The major components of fatty acid are iso-$C_{15:0}$ and iso-$C_{17:1}\omega 9c$. The G + C content of the genomic DNA of the type strain is 64.9 mol %.

The type strain YIM C01544^T (= KCTC 42875^T = DSM 101561^T = CPCC 100816^T) was isolated from a soil sample of Sigangli Cave, Yunnan province, South-West China.

Acknowledgments The authors are grateful to Soon-Wo Kwon (KACC, Korea), Miss Sang-Mi Lee (KCTC, Korea) and Dr. Tamura Tomohiko (NBRC, Japan) for providing the reference type strains. This work was funded by projects from China Tobacco Yunnan International Co. Ltd. (Nos. 2015CP01), Key Laboratory of Cigarette Perfumery Industry (2014-334) and Key Discipline Construction Project of Biology in Yunnan province (50097505), Doctoral Scientific Research Foundation of Southwest Forestry University (111441) and the Deanship of Scientific Research at King Saud University through the research group no. PRG-1436-27. Wen-Jun Li was also supported by Guangdong Province Higher Vocational Colleges & Schools Pearl River Scholar Funded Scheme (2014).

References

Allpress JD, Mountain Gowland PC (2002) Production, purification and characterization of an extracellular keratinase from *Lysobacter* NCIMB 9497. Lett Appl Microbiol 34:337–342

Cerny G (1978) Studies on aminopeptidase for the distinction of Gram-negative from Gram-positive bacteria. Appl Microbiol Biotechnol 5:113–122

Chohnan S, Shiraki K, Yokota K, Ohshima M, Kuroiwa N, Ahmed K, Masaki T, Sakiyama F (2004) A second lysine-specific serine protease from *Lysobacter* sp. strain IB-9374. J Bacteriol 186:5093–5100

Choi JH, Seok JH, Cha JH, Cha CJ (2014) *Lysobacter panacioli* sp. nov., isolated from ginseng soil. Int J Syst Evol Microbiol 64:2193–2197

Christensen P, Cook FD (1978) *Lysobacter*, a new genus of nonfruiting gliding bacteria with a high base ratio. Int J Syst Bacteriol 28:367–393

Christensen H, Angen O, Mutters R, Olsen JE, Bisgaard M (2000) DNA–DNA hybridization determined in microwells using covalent attachment of DNA. Int J Syst Evol Microbiol 50:1095–1102

Collins MD, Jones D (1980) Lipids in the classification and identification of coryneform bacteria containing peptidoglycan based on 2,4-diaminobutyric acid. Appl Bacteriol 48:459–470

Collins MD, Pirouz T, Goodfellow M, Minnikin DE (1977) Distribution of menaquinones in actinomycetes and corynebacteria. J Gen Microbiol 100:221–230

Cui XL, Mao PH, Zeng M, Li WJ, Zhang LP, Xu LH, Jiang CL (2001) *Streptomonospora salina* gen. nov., sp. nov., a new member of the family *Nocardiopsaceae*. Int J Syst Evol Microbiol 51:357–363

Ezaki T, Hashimoto Y, Yabuuchi E (1989) Fluorometric deoxyribonucleic acid-deoxyribonucleic acid

hybridization in microdilution wells as an alternative to membrane filter hybridization in which radioisotopes are used to determine genetic relatedness among bacterial strains. Int J Syst Evol Microbiol 39:224–229

Felsenstein J (1981) Evolutionary trees from DNA sequences: a maximum likelihood approach. J Mol Evol 17:368–376

Felsenstein J (1985) Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39:783–791

Fitch WM (1971) Toward defining the course of evolution: minimum change for a specific tree topology. Syst Zool 20:406–416

Fukuda W, Kimura T, Araki S, Miyoshi Y, Atomi H, Imanaka T (2013) *Lysobacter oligotrophicus* sp. nov., isolated from an Antarctic freshwater lake in Antarctica. Int J Syst Evol Microbiol 63:3313–3318

Hashizume H, Hattori S, Igarashi M, Akamatsu Y (2004) Tripropeptin E, a new tripropeptin group antibiotic produced by *Lysobacter* sp. BMK333–48F3. J Antibiot (Tokyo) 57:394–399

Hayakawa M, Nonomura H (1987) Humic acid-vitamin agar, a new medium for the selective isolation of soil actinomycetes. J Ferment Technol 65:501–509

Kim OS, Cho YJ, Lee K, Yoon SH, Kim M, Na H, Park SC, Jeon YS, Lee JH, Yi H, Won S, Chun J (2012) Introducing EzTaxon-e: a prokaryotic 16S rRNA gene sequence database with phylotypes that represent uncultured species. Int J Syst Evol Microbiol 62:716–721

Kimura M (1980) A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. J Mol Evol 16:111–120

Kovacs N (1956) Identification of *Pseudomonas pyocyanea* by the oxidase reaction. Nature 178:703

Kroppenstedt RM (1982) Separation of bacterial menaquinones by HPLC using reverse phase (RP 18) and a silver loaded ion exchanger as stationary phases. J Liq Chromatograph 5:2359–2387

Li WJ, Xu P, Schumann P, Zhang YQ, Pukall R, Xu LH, Stackebrandt E, Jiang CL (2007) *Georgenia ruanii* sp. nov., a novel actinobacterium isolated from forest soil in Yunnan (China), and emended description of the genus *Georgenia*. Int J Syst Evol Microbiol 57:1424–1428

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

Mesbah M, Premachandran U, Whitman WB (1989) Precise measurement of the G + C content of deoxyribonucleic acid by high-performance liquid chromatography. Int J Syst Bacteriol 39:159–167

Minnikin DE, Collins MD, Goodfellow M (1979) Fatty acid and polar lipid composition in the classification of *Cellulomonas*, *Oerskovia* and related taxa. J Appl Bacteriol 47:87–95

Ogura J, Toyoda A, Kurosawa T, Chong AL, Chohnan S, Masaki T (2006) Purification, characterization, and gene analysis of cellulose (Cel8A) from *Lysobacter* sp. IB-9374. Biosci Biotechnol Biochem 70:2420–2428

Park JH, Kim R, Aslam Z, Jeon CO, Chung YR (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

Puopolo G, Tomada S, Sonego P, Moretto M, Engelen K, Perazzolli M, Pertot I (2016) The *Lysobacter capsici* AZ78 genome has a gene pool enabling it to interact successfully with phytopathogenic microorganisms and environmental factors. Front Microbiol 7:96. doi:10.3389/fmicb.2016.00096

Saddler GS, Bradbury JF (2005) Family I. *Xanthomonadaceae* fam. nov. In: *Bergey's Manual of Systematic Bacteriology*, 2nd edn, vol. 2, pp. 63–122. Edited by DJ Brenner, NR Krieg, JT Staley, GM Garrity. New York: Springer

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

Sasser M (1990) Identification of bacteria by gas chromatography of cellular fatty acids, MIDI Technical Note 101. MIDI Inc, Newark

Srinivasan S, Kim MK, Sathiyaraj G, Kim HB, Kim YJ, Yang DC (2010) *Lysobacter soli* sp. nov., isolated from soil of a ginseng field. Int J Syst Evol Microbiol 60:1543–1547

Stackebrandt E, Goebel BM (1994) Taxonomic note: a place for DNA-DNA reassociation and 16S rRNA sequence analysis in the present species definition in bacteriology. Int J Syst Bacteriol 44:846–849

Tamura K, Peterson D, Peterson N, Stecher G, Nei M, Kumar S (2011) MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. Mol Biol Evol 28:2731–2739

Thompson JD, Gibson TJ, Plewniak F, Jeanmougin F, Higgins DG (1997) The CLUSTAL_X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acids Res 25:4876–4882

Tishchenko S, Gabdulkhakov A, Meinik B, Kudryakova I, Latypov O, Vasilyeva N, Leontievsky A (2016) Structural studies of component of lysoamidase bacteriolytic complex from *Lysobacter* sp. XL1. Protein J 35:44–50

Wei DQ, Yu TT, Yao JC, Zhou EM, Song ZQ, Yin YR, Ming H, Tang SK, Li WJ (2012) *Lysobacter thermophilus* sp. nov., isolated from a geothermal soil sample in Tengchong, south-west China. Antonie Van Leeuwenhoek 102:643–651

Weon HY, Kim BY, Baek YK, Yoo SH, Kwon SW, Stackebrandt E, Go SJ (2006) Two novel species, *Lysobacter daejeonensis* sp. nov. and *Lysobacter yangpyeongensis* sp. nov., isolated from Korean greenhouse soils. Int J Syst Evol Microbiol 56:947–951

Xu P, Li WJ, Tang SK, Zhang YQ, Chen GZ, Chen HH, Xu LH, Jiang CL (2005) *Naxibacter alkalitolerans* gen. nov., sp nov., a novel member of the family '*Oxalobacteraceae*' isolated from China. Int J Syst Evol Microbiol 55:1149–1153