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ORIGINAL PAPER

Lysobacter prati sp. nov., isolated from a plateau meadow sample

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Abstract A novel proteobacterial strain designated SYSU H10001^T was isolated from a soil sample collected from plateau meadow in Hongyuan county, Sichuan province, south-western China. The taxonomic position of the strain was investigated using a polyphasic approach. On the basis of 16S rRNA gene sequence similarities and phylogenetic analysis, strain SYSU H10001^T was most closely related to *Lysobacter soli* KCTC 22011^T (98.6%, sequence similarity) and *Lysobacter panacisoli* JCM 19212^T (98.2%). The prediction result of secondary metabolites based on genome shown that the strain SYSU H10001^T contained 3 clusters of bacteriocins, 1 cluster of non-ribosomal peptide synthetase, 1 cluster of type 1 polyketide synthase and 1 cluster of arylpolyene. In addition, the major isoprenoid quinone was Q-8 and the major fatty acids were identified as iso-$C_{15:0}$, iso-$C_{17:0}$ and Summed feature 9. The polar lipids contained diphosphatidylglycerol, phosphatidylglycerol, phosphatidylethanolamine, and three unidentified phospholipids. The genomic DNA G + C content of strain SYSU H10001^T was 66.5% (genome). On the basis of phenotypic, genotypic and phylogenetic data, strain SYSU H10001^T represents a novel species of the genus *Lysobacter*, for which the name *Lysobacter prati* sp. nov. is proposed. The type strain is SYSU H10001^T (= KCTC 72062^T = CGMCC 1.16662^T).

Keywords *Lysobacter prati* sp. nov. · Secondary metabolites · Plateau grassland · Polyphasic taxonomy

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Introduction

The genus *Lysobacter* was first proposed by Christensen and Cook (1978) as the type genus of the family *Lysobacteraceae* of the order *Lysobacterales* in the phylum *Proteobacteria* and was subsequently emended by Park et al. (2008). Members of this genus are generally characterized as Gram-staining negative, aerobic, rod-shaped with variable motility and chemoorganotrophic and have high DNA G + C contents (61–70 mol %) (de Bruijn et al. 2015; Hernández and Fernàndez 2017). Colonies are highly

mucoid, cream-coloured, pink, or yellow–brown; many strains produce a brown, water-soluble pigment. The genus *Lysobacter* contains ubiquinone 8 (Q-8) as the major respiratory quinone and shows a predominance of iso-branched fatty acids (Weon et al. 2007; Srinivasan et al. 2010; Wei et al. 2012). Strains of this genus have been isolated from various environmental niches such as soil, sediments, aquatic habitats and rhizosphere (Fukuda et al. 2013; Choi et al. 2014; Lin et al. 2015; Chen et al. 2016; Siddiqi and Im 2016). At the time of writing, the genus *Lysobacter* comprises 56 species with validly published names (https://www.namesforlife.com/10.1601/tx.2240), of which six novel species were published recently (Chhetri et al. 2019; Kim et al. 2019; Luo et al. 2019; Xiao et al. 2019; Zhang et al. 2019). Furthermore, some species from the genus of *Lysobacter* has been seen as a high-efficiency producer of bioactive natural products including new antibiotics from species such as *L. antibioticus* 76, *L. capsici* 55, *L. enzymogenes* C3, *L. antibioticus* ATCC 29479^T that contain more secondary metabolite gene clusters than others in the genus. The secondary metabolites such as cyclodepsipeptides, cyclic lipodepsipeptides, cephem-type b-lactams and polycyclic tetramate macrolactams (PTM) have been reported from members of this genus (Xie et al. 2012; Panthee et al. 2016). During a study of the diversity of bacteria of the plateau grassland environment, strain SYSU H10001^T was isolated from a soil sample and its taxonomic status was investigated using a polyphasic taxonomy approach.

Materials and methods

Isolation and culture conditions

The soil sample used for isolation of strain SYSU H10001^T was collected from a meadow located in Hongyuan county (32° 82′ N, 105° 58′ E), Sichuan province during a trip in 2017. Sampling was done using a sterile spoon and the sample collected into a sterile sampling bag. It was then transported back to the laboratory under ambient condition and stored at 4 °C. Isolation of *Lysobacter* was done using the standard dilution plate method on Reasoner's 2A agar (Reasoner and Geldreich 1985). The colonies of strain SYSU H10001^T were obtained after incubation for 1 week at 28 °C. Selected colonies were then purified on YIM 38 agar and maintained on YIM 38 agar slants at 4 °C and as glycerol suspensions (20%, w/v) at − 80 °C. The experimental control strains *Lysobacter panacisoli* JCM 19212^T and *Lysobacter soli* KCTC 22011^T were provided by Japan Collection of Microorganisms (JCM) and the Korean Collection for Type Cultures (KCTC), respectively. All the strains were maintained routinely on YIM 38 medium (28 °C, 5 days). Biomass of strain SYSU H10001^T and the experimental control strains for chemotaxonomic and molecular investigations were harvested from cultures grown on YIM 38 medium (28 °C, 5 days).

Phenotypic characterisation

Colony morphology of strain SYSU H10001^T was observed from cultures grown on YIM 38 medium. Cell morphology was observed by transmission electron microscopy (JEM-1400FLASH) with 3-day-old cultures grown on YIM 38 medium. Gram's reaction was determined by Solarbio's Gram staining kit (China) as per the manufacturer's instructions. Growth at various NaCl concentrations (up to 5%, w/v) and at different temperatures (0, 4, 10, 15, 28, 30, 37, 40, 45 °C) were examined on YIM 38 agar plates, while the pH range for growth (4.0–12.0, at intervals of 1 pH unit prepared using the buffer system as described by Xu et al. 2005) were tested for 4 weeks by culturing the strains in YIM 38 broth (Jiang et al. 2016). Activities of oxidase, catalase, and urease, gelatin liquefaction, milk coagulation and peptonisation, nitrate reduction, H_2S production, degradation of Tweens 20, 40, 60 and 80, starch and cellulose hydrolysis were investigated according to the conventional procedures described by Gordon et al. (1974) and Williams et al. (1989). Other enzyme activities and biochemical characteristics were determined by using API ZYM kits (BioMérieux) according to the manufacturer's instructions. Carbon-source utilization tests were performed according to the methods described by Shirling and Gottlieb (1966) and Athalye et al. (1985) Using modified basal medium recommended by Pridham and Gottlieb (1948), sole nitrogen source utilization was observed as described by Nie et al. (2012). Other physiological and biochemical characteristics were assessed by using the media and methods described by Gordon et al. (1974).

Chemotaxonomy

Chemotaxonomic characteristics of strain SYSU H10001^T and the experimental control strain were determined under similar conditions. Menaquinones were extracted from lyophilized cells as described by Collins et al. (1977) and Minnikin et al. (1984), and the extracts were purified and analyzed by HPLC (Kroppenstedt 1982; Tamaoka et al. 1983). For analysis of fatty acids, the three strains were grown on tryptic soy agar for 3 days at 28 °C. The cellular fatty acids were extracted, methylated and analyzed following the instructions of Microbial Identification System (MIDI) (Sherlock Version 6.1; MIDI database: TSBA6) (Sasser 1990). Polar lipids were extracted as the method described by Bligh and Dyer 1959, and the individual polar lipids separated by two-dimensional TLC on silica gel G_{60} plates (Merck; Germany), and the profile was identified using the described procedures (Minnikin et al. 1979; Collins and Jones 1980; Minnikin et al. 1984).

Molecular characterisation

Genomic DNA was extracted, and the 16S rRNA gene PCR-amplified and sequenced as described by Li et al. (2007). The amplicons were purified using a PCR purification kit (Sangon Biotech, China). The 16S rRNA gene sequences obtained were assembled using the SeqMan program (DNAStar software) and compared with the corresponding sequences of cultured species in the EzBioCloud web service (Yoon et al. 2017a) and the NCBI database by using BLAST search (Altschul et al. 1990). To determine the phylogenetic relationships of strain SYSU H10001^T and members of the genus *Lysobacter*, multiple alignments of their 16S rRNA gene sequences were performed using the CLUSTAL_X software package (Thompson et al. 1997). Phylogenetic and molecular evolutionary analyses were performed using the software package MEGA version 7.0 (Kumar et al. 2016). Phylogenetic dendrograms were generated with maximum-likelihood (Felsenstein 1981), neighbour-joining (Saitou and Nei 1987) and maximum-parsimony (Fitch 1971) algorithms. Kimura's two-parameter model (Kimura 1980, 1985) was used to calculate the evolutionary distances in the neighbour-joining and maximum-likelihood phylogenetic dendrograms. Bootstrap analysis was used to evaluate the topology of each tree with 1000 replications (Felsenstein 1985).

Whole-genome sequencing of strain SYSU H10001^T and experimental control strain (*L. panacisoli* JCM 19212^T) were performed using paired-end sequencing method with Hiseq X platform (Illumina, San Diego, CA, USA) at Beijing Genomics Institute (Beijing, China). Reads of each data set were filtered, and high-quality paired-end reads assembled using Spades (Harrison and Strulo 2000). Contigs, with length greater than 500 bp, were kept for gene prediction by applying Prodigal (Hyatt et al. 2010). The predicted coding sequences of each genome were translated and annotated using the KEGG, COG and Pfam databases. For generation of phylogenomic tree, 16 syntenic genes that have been shown to undergo limited lateral gene transfer (*rpL*2, *rpL*3, *rpL*4, *rpL*5, *rpL*6, *rpL*14, *rpL*15, *rpL*16, *rpL*18, *rpL*22, *rpL*24, *rpS*3, *rpS*8, *rpS*10, *rpS*17, and *rpS*19) of the selected genomes of the genus *Lysobacter* in the NCBI database were extracted using AMPHORA2 (Wu and Scott 2012). Sequences of each of the marker genes were aligned separately using MUSCLE (Edgar 2004). Alignments were concatenated by using perl script (https://github.com/nylander/catfasta2phyml), prior to the generation of the tree. Poorly aligned regions were removed from the datasets using Gblocks (Castresana 2000). The phylogenomic tree was generated with software program RAxML (Stamatakis 2014) using the default parameters and visualized using the online Interactive Tree of Life program v.4.2 (Letunic and Bork 2019). The presence of gene clusters encoding secondary metabolites was predicted by using the antiSMASH 5.0 database (Blin et al. 2019). Furthermore, values of average nucleotide identity (ANI) were calculated by using the ANI Calculator (Yoon et al. 2017b).

Results and discussion

Phenotypic characteristics

Cells of strain SYSU H10001^T stained Gram-negative and were aerobic, non-motile, and rod-shaped (Supplementary Fig. S1). Colonies on YIM 38 medium were observed to be circular, convex, opaque and yellow in colour. No soluble pigments and melanin production were observed on the above tested media.

Detailed physiological and biochemical characteristics of strain SYSU H10001^T are summarised in the species description, and characteristics that differentiate strain SYSU H10001^T from its closely related type strains are listed in Table 1.

Molecular characteristics

Pairwise comparison of the 16S rRNA gene sequence of strain SYSU H10001^T (GenBank accession number MN181427) with the corresponding 16S rRNA gene sequences in the EzBioCloud database indicated that the strain shared 16S rRNA gene sequence similarities of 98.6% and 98.2% with *L. soli* KCTC 22011^T and *L. panacisoli* JCM 19212^T, respectively. In the maximum-likelihood phylogenetic tree based on 16S rRNA gene sequences, strain SYSU H10001^T formed a close clade with the above two strains (Fig. 1). This relationship was also supported in the phylogenetic trees generated with maximum-parsimony and neighbour-joining methods (Supplementary Figs. S3 and S4).

The genome of strain SYSU H10001^T generated 2.58 Gb raw data of which 2.36 Gb was clean data following quality-filtering. The de novo read assembly produced 48 contigs with an N_{50} size of 420,681 bp. The high-quality assembled draft genome sequence consisted of 4,127,215 bp with a DNA G + C content of 66.5% which is within the reported range of DNA G + C contents for species of the genus *Lysobacter*.

Table 1 Differential phenotypic characteristics between strain SYSU H10001^T and its closely related type strains of the genus *Lysobacter*

Characteristic	1	2	3
Cell morphology	Short rods	Rods, cocci	Short rods
Temperature range for growth (°C)	4–37	4–40	4–40
NaCl tolerance (% w/v)	0–1.5	0–1.5	0–2
Hydrolysis of			
Tween 40	+	−	−
Tween 60	+	−	−
Tween 80	+	−	−
Starch	−	−	+
Assimilation as sources of carbon and nitrogen			
D-Arabinose	−	−	+
Gentiobiose	−	−	+
D-Cellobiose	+	−	−
D-Maltose	+	−	+
D-Sorbitol	−	−	+
D-Trehalose	−	−	+
D-Xylose	−	−	+
L-Arginine	+	−	−
L-Cystine	+	−	−
L-Glutamic	+	−	−
L-Histidine	+	−	−
L-Lysine	+	+	−
L-Phenylalanine	+	−	−
API ZYM			
Chymotrypsin	+	+	−
Esterase lipase (C8)	+	+	−
Valine arylamidase	+	+	−
Chymotrypsin	+	+	−
α-Glucosidase	+	−	−
Major polar lipids	DPG, PE, PG	DPG, PE, PG	DPG, PE, PME, PG

Strains: (1) SYSU H10001^T; (2) *L. panacisoli* JCM 19212^T; (3) *L. soli* KCTC 22011^T. All data are from this study unless indicated otherwise

+ positive; − negative; *w* weakly positive. *ND* not determined

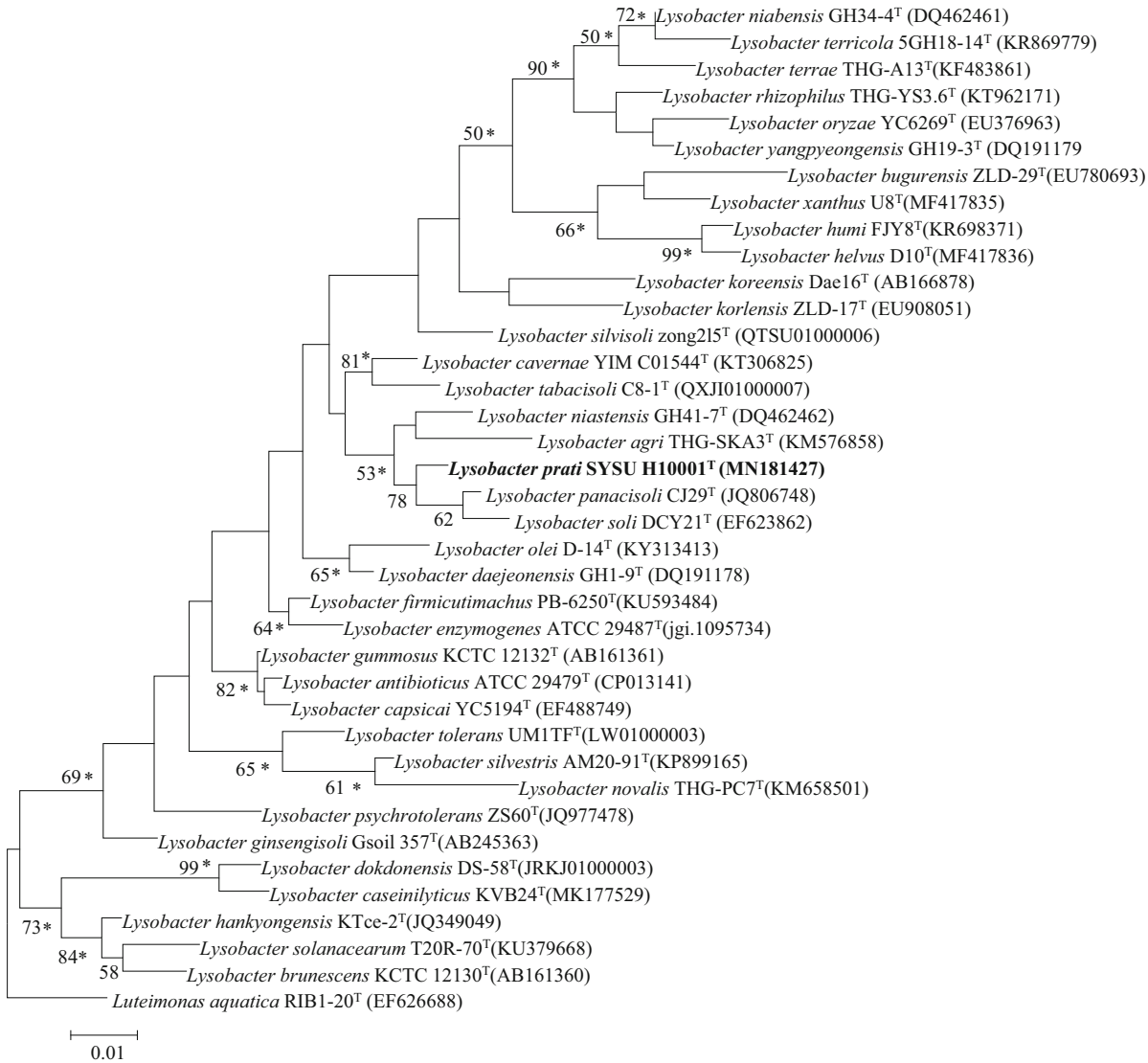


Fig. 1 Maximum-likelihood phylogenetic tree showing the relationship between strain SYSU H10001^T and its closest relatives. Asterisks indicate branches that were also recovered using the maximum-parsimony and neighbour-joining methods. Bootstrap values (expressed as percentages of 1000 replications) of above 50% are shown at the branch points. *Luteimonas aquatica* RIB1-20T was used as an outgroup. Bar: 0.01 substitutions per nucleotide position

No contamination was detected for the 16S rRNA gene. The genome had a total of 3787 genes, including 3728 protein-coding genes, 53 tRNA genes, 6 rRNA genes (one 5S, three 16S and two 23S rRNA genes). The ANI values between the strain SYSU H10001^T and the type strains of the species *L. panacisoli* JCM 19212^T and *L. soli* KCTC 22011^T were 84.6% and 83.8%, respectively, which were lower than the threshold value recommended for distinguishing novel species (Goris et al. 2007; Richter and Rosselló-Móra 2009). The general features of the genomes of *L. prati* SYSU H10001^T and *L. panacisoli* JCM 19212^T and *L. soli* KCTC 22011^T are shown in Table 2.

The analysis of secondary metabolic gene clusters revealed that strain SYSU H10001^T harboured fewer gene clusters than other species in the genus. This gene clusters include 3 clusters of bacteriocins, 1 cluster of non-ribosomal peptide synthetase, 1 cluster of type 1

polyketide synthase and 1 cluster of arylpolyene (Supplementary Data 1). Based on the genome analysis and the phylogenomic tree, strains in the genus of *Lysobacter* could be divided into two groups, Group I that contains the species *L. capsici*, *L. antibioticus* ATCC 29479^T and *L. enzymogenes* ATCC 29487^T with higher secondary metabolic genes cluster, and Group II the other species. Strain SYSU H10001^T form a subclade with the Group II members in the phylogenomic tree (Fig. 2 and Supplementary Data 2). Similar to certain members in Group II with high gene clusters such as *Lysobacter* sp. ZS60, *Lysobacter daejeonensis* GH1-9^T and *Lysobacter maris* HZ9B^T, the genome of strain SYSU H10001^T yielded 29 secondary metabolic genes (0.78%, secondary metabolic gene numbers/predicted gene numbers).

Chemotaxonomical characteristics

The ubiquinone Q-8 was detected as the predominant respiratory ubiquinone in strain SYSU H10001^T. The polar lipid profile consists of diphosphatidylglycerol, phosphatidylglycerol, phosphatidylethanolamine and three unidentified phospholipids (Supplementary Fig. S2). The major fatty acids (> 10%) are iso-$C_{15:0}$, iso-$C_{17:0}$ and Summed Feature 9 (10-methyl $C_{16:0}$ and/or iso-$C_{17:1}$ $\omega 9c$). While the main fatty acids types between strains SYSU H10001^T and the related type strains remain the same, the observed difference is at the proportion of these fatty acids, particularly the Summed Feature 9. The detailed fatty acid compositions are listed in Supplementary Table S1.

The phylogenetic analyses, morphological and chemotaxonomic characteristics support the characterisation of strain SYSU H10001^T as a member of the genus *Lysobacter*. The differences in biochemical characteristics and fatty acid compositions distinguish strain SYSU H10001^T from its closely related strains. Based on the above characteristics, strain SYSU H10001^T is considered to represent a novel species of the genus *Lysobacter*, for which the name *Lysobacter parti* is proposed.

Fig. 2 RAxML phylogenomic tree using genomes of selected members of the genus *Lysobacter* to determine the phylogenetic position of strain SYSU H10001^T The phylogenomic tree was generated with the RAxML method using the default parameters. *Luteimonas rhizosphaerae* 4-12 (NRQR00000000) was used as an outgroup. Bar, 0.1 substitutions per nucleotide position. *Note* The heatmap showed the percentage of the secondary metabolic genes of each genome, the value was calculated by secondary metabolic genes/prediction genes

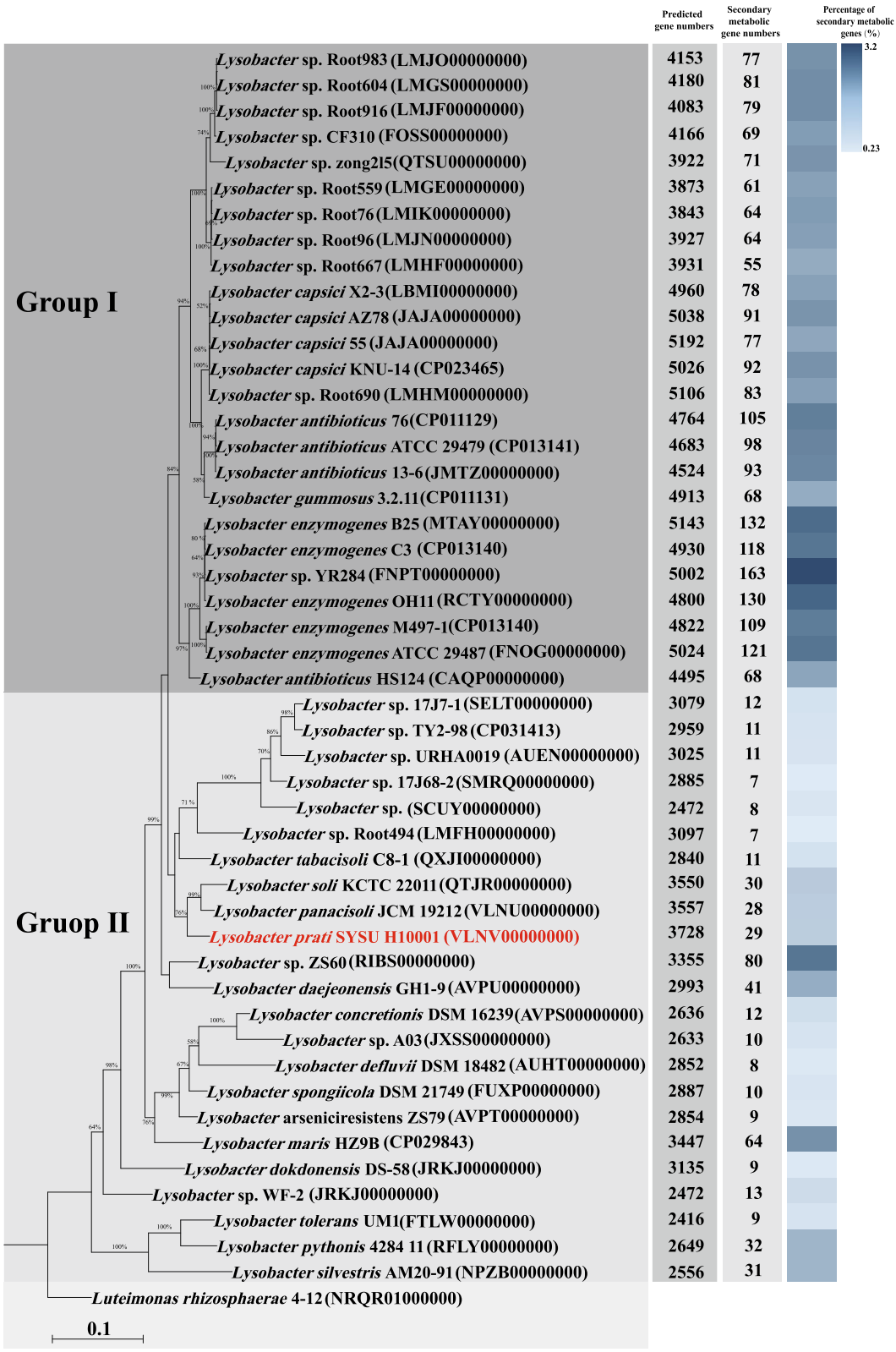
Description of *Lysobacter prati* sp. nov

Lysobacter. prati (pra'ti. L. gen. neut. n. *prati* of a meadow, the place from where the novel strain is isolated).

Cells are Gram-staining negative, aerobic, non-motile, and rod-shaped. Colonies on YIM 38 agar are smooth, circular, opaque and yellow in colour after 3 days of cultivation at 28 °C. Growth occurs at 4–37 °C (optimum 28 °C), pH 6.0–9.0, and in the presence of up to 1.5% (w/v) NaCl. Positive for nitrate reduction, milk coagulation and peptonisation, and catalase and oxidase activities, but not for urease activity. Give positive results in tests for hydrolysis of gelatin, esculin, and tweens 40, 60 and 80, but not in tests for production of H_2S or hydrolysis of cellulose, starch or tween 20. Utilizes D-cellobiose, D-galactose, D-glucose, glycerol, D-maltose, and D-sucrose as sole carbon sources but not L-arabinose, D-fructose, inositol, D-ribose, lactose, D-mannitol, D-mannose, D-

Table 2 General features of the genomes of *L. prati* SYSU H10001^T, *L. panacisoli* JCM 19212^T and *L. soli* KCTC 22011^T

Attribute	*L. prati*	*L. panacisoli*	*L. soli*
Genomic size (bp)	4,127,215	3,879,713	3,953,742
Number of contigs	48	3	27
Mean length (bp)	85,983	1,293,234	146,434
N_{50} length (bp)	420,681	2,610,236	285,382
G + C content (%)	66.5	67.5	67.7
Protein-coding genes	3728	3586	3544
Genes assigned to COGs	1685	2694	3267
Genes assigned to KEGG	1830	3284	1808


Predicted gene numbers
Secondary metabolic gene numbers
Percentage of secondary metabolic genes (%)
3.2
0.23
Group I
Gruop II
Lysobacter sp. Root983 (LMJO00000000) 4153 77
Lysobacter sp. Root604 (LMGS00000000) 4180 81
Lysobacter sp. Root916 (LMJF00000000) 4083 79
Lysobacter sp. CF310 (FOSS00000000) 4166 69
Lysobacter sp. zong2l5(QTSU00000000) 3922 71
Lysobacter sp. Root559 (LMGE00000000) 3873 61
Lysobacter sp. Root76 (LMIK00000000) 3843 64
Lysobacter sp. Root96 (LMJN00000000) 3927 64
Lysobacter sp. Root667 (LMHF00000000) 3931 55
Lysobacter capsici X2-3 (LBMI00000000) 4960 78
Lysobacter capsici AZ78 (JAJA00000000) 5038 91
Lysobacter capsici 55 (JAJA00000000) 5192 77
Lysobacter capsici KNU-14 (CP023465) 5026 92
Lysobacter sp. Root690 (LMHM00000000) 5106 83
Lysobacter antibioticus 76(CP011129) 4764 105
Lysobacter antibioticus ATCC 29479 (CP013141) 4683 98
Lysobacter antibioticus 13-6 (JMTZ00000000) 4524 93
Lysobacter gummosus 3.2.11 (CP011131) 4913 68
Lysobacter enzymogenes B25 (MTAY00000000) 5143 132
Lysobacter enzymogenes C3 (CP013140) 4930 118
Lysobacter sp. YR284 (FNPT00000000) 5002 163
Lysobacter enzymogenes OH11 (RCTY00000000) 4800 130
Lysobacter enzymogenes M497-1(CP013140) 4822 109
Lysobacter enzymogenes ATCC 29487 (FNOG00000000) 5024 121
Lysobacter antibioticus HS124 (CAQP00000000) 4495 68
Lysobacter sp. 17J7-1 (SELT00000000) 3079 12
Lysobacter sp. TY2-98 (CP031413) 2959 11
Lysobacter sp. URHA0019 (AUEN00000000) 3025 11
Lysobacter sp. 17J68-2 (SMRQ00000000) 2885 7
Lysobacter sp. (SCUY00000000) 2472 8
Lysobacter sp. Root494 (LMFH00000000) 3097 7
Lysobacter tabacisoli C8-1 (QXJI00000000) 2840 11
Lysobacter soli KCTC 22011 (QTJR00000000) 3550 30
Lysobacter panacisoli JCM 19212 (VLNU00000000) 3557 28
Lysobacter prati SYSU H10001 (VLNV00000000) 3728 29
Lysobacter sp. ZS60 (RIBS00000000) 3355 80
Lysobacter daejeonensis GH1-9 (AVPU00000000) 2993 41
Lysobacter concretionis DSM 16239(AVPS00000000) 2636 12
Lysobacter sp. A03 (JXSS00000000) 2633 10
Lysobacter defluvii DSM 18482 (AUHT00000000) 2852 8
Lysobacter spongiicola DSM 21749 (FUXP00000000) 2887 10
Lysobacter arseniciresistens ZS79 (AVPT00000000) 2854 9
Lysobacter maris HZ9B (CP029843) 3447 64
Lysobacter dokdonensis DS-58 (JRKJ00000000) 3135 9
Lysobacter sp. WF-2 (JRKJ00000000) 2472 13
Lysobacter tolerans UM1(FTLW00000000) 2416 9
Lysobacter pythonis 4284 11 (RFLY00000000) 2649 32
Lysobacter silvestris AM20-91 (NPZB00000000) 2556 31
Luteimonas rhizosphaerae 4-12 (NRQR01000000)
0.1

raffinose, D-ribose, L-rhamnose, D-sorbitol, D-sucrose, xylitol, or D-xylose. Utilizes L-alanine, L-aspartic acid, glycine, L-glutamic acid, L-glutamine, L-histidine, L-methionine, L-phenylalanine and L-serine, L-threonine, L-tyrosine and L-valine as sole nitrogen sources but not L-tyrosine, L-alanine, L-valine, L-tryptophan, L-glutamine, L-ornithine, adenine or hypoxanthine. In the API ZYM tests, positive for activities of acid phosphatase, alkaline phosphatase, cysteine arylamidase, esterase (C4), esterase lipase (C8), naphthol-AS-BI-phosphohydrolase, chymotrypsin, and valine arylamidase, α-glucosidase; and negative for activities of cysteine arylamidase, leucine arylamidase, lipase (C14), β-fucosidase, α-galactosidase, β-galactosidase, β-glucuronidase, *N*-acetyl-β-glucosaminidase, α-mannosidase, and trypsin. The predominant respiratory quinone is Q-8. The cellular polar lipids are diphosphatidylglycerol, phosphatidylglycerol, phosphatidylethanolamine and three unidentified phospholipids. The major fatty acids are iso-$C_{15:0}$, iso-$C_{17:0}$ and Summed Feature 9 (10-methyl $C_{16:0}$ and/or iso-$C_{17:1}$ $\omega 9c$).

The type strain SYSU H10001^T (= KCTC 72062^T = CGMCC 1.16662^T) was isolated using a soil sample collected from a meadow in Hongyuan county, Szechwan province, P. R. China. The DNA G + C content of the type strain is 66.5% (genome). The 16S rRNA gene and genome sequences of strain SYSU H10001^T were submitted to GenBank with accession numbers MN181427 and VLNV00000000, respectively.

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Author's contributions BZF and WJL designed research and project outline. BZF, ZXK, and LL performed isolation, deposition, and identification. YGX, JYJ and XTZ performed genome analysis. BZF, MW and WJL drafted the manuscript. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest All the authors have declared no conflict of interest.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

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