



Lysobacter segetis sp. nov., Isolated from Soil

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Abstract

A Gram-negative, aerobic, motile by gliding, rod-shaped bacterium, strain 17J68-2^T, was isolated from a soil sample taken from Jeju Island, Republic of Korea. The isolate displayed high 16S rRNA gene sequence similarity to the members of the genus *Lysobacter* in the family *Lysobacteraceae*, with *Lysobacter humi* FJY8^T (98.4% similarity), *Lysobacter xinjiangensis* RCML-52^T (98.3%), and *Lysobacter mobilis* 9NM-14^T (98.1%) as closest phylogenetic neighbors. Growth of strain 17J68-2^T occurred at 15–42 °C, pH 7–8, and in the presence of 0–1.0% NaCl. Draft genome was 2.94 Mb in size with G+C content of 70.5 mol%. The major polar lipids were phosphatidylglycerol, diphosphatidylglycerol, and phosphatidylethanolamine. Ubiquinone Q-8 was the predominant respiratory quinone and the major fatty acids were C_{16:0} iso (39.4%), summed feature 3 (C_{16:1} ω7c/C_{16:1} ω6c) (6.6%), C_{11:0} iso 3-OH (6.4%), C_{15:0} iso (6.4%), and C_{16:1} iso H (6.2%). The DNA–DNA relatedness between strain 17J68-2^T and *L. humi*, *L. xinjiangensis*, and *L. mobilis* were 39.9, 39.4, and 25.3%, respectively. From these results, it is concluded that the novel isolate possesses sufficient characteristics to differentiate it from the most closely affiliated *Lysobacter* species, and strain 17J68-2^T represents a novel species of the genus *Lysobacter*, for which the name *Lysobacter segetis* sp. nov. (=KCTC 62237^T=JCM 33058^T) is proposed.

Introduction

Christensen and Cook [5] proposed the genus *Lysobacter* with *Lysobacter enzymogenes* as the type species. The genus *Lysobacter* belongs to the family *Lysobacteraceae* [38] and currently (October 2019) contains 48 species with validly published names (<https://www.bacterio.net/lysobacter>

[.html](#)). Members of this genus are Gram-stain negative, motile or non-motile, thin rods with a high G+C content (61.7–70.7 mol%) [6, 23, 43]. Predominance of iso-branched fatty acids, ubiquinone Q-8 as respiratory quinone, and phosphatidylglycerol, diphosphatidylglycerol, and phosphatidylethanolamine as the major polar lipids are the typical characteristics of the genus [4, 6, 22, 41, 46]. *Lysobacter* species have been isolated from a wide variety of ecological niches including air [41], lake fresh water from Antarctica [11], seawater [44], stream sediment [36], abandoned lead–zinc ore [43], and ginseng cultivated soil [31].

Herein, we describe bacterial strain 17J68-2^T that was recovered from a soil sample collected on Jeju Island, Republic of Korea. On the basis of 16S rRNA gene sequence analysis, this isolate was assigned to the genus *Lysobacter*. Further genomic, physiological, and chemotaxonomic characterization showed that strain 17J68-2^T represented a novel species of the genus *Lysobacter*, for which we propose the name *Lysobacter segetis* sp. nov.

The 16S rRNA gene sequence of strain 17J68-2^T has been deposited in NCBI GenBank/EMBL/DBJ under the accession number LC434628. The draft genome sequence accession number of the strain in GenBank/EMBL/DBJ is SMRQ00000000. The Digital Protologue Database (DPD) Taxon Number for strain 17J68-2^T is TA00939.

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Materials and Methods

Isolation of the Bacterial Strain and Culture Conditions

Strain 17J68-2^T was isolated from a soil sample collected on Jeju Island (33°26′01.2″N 126°35′04.8″E), Republic of Korea. The soil sample (1 g) was suspended in 10 ml distilled water and serially diluted. Aliquots of 100 µl of each dilution were spread onto Reasoner's 2A agar plates (R2A; Difco) and incubated at 25 °C for 7 days. After incubation, single colony, designated 17J68-2^T, was transferred onto R2A agar plate and incubated under the same condition. Strain 17J68-2^T was cultured on trypticase soy agar plates (TSA; Difco) at 30 °C for further work and it was preserved at −70 °C in a suspension with aqueous glycerol (20% w/v). The isolate was deposited in the Korean Collection for Type Culture (KCTC 62237^T) and the Japan collection of Microorganism (JCM 33058^T). Three reference strains used in this study, *Lysobacter humi* KCTC 42810^T, *Lysobacter xinjiangensis* KCTC 22558^T, and *Lysobacter mobilis* KCTC 52627^T, were obtained from the Korean Collection for Type Culture.

Phenotypic and Biochemical Characteristics

The morphological characteristics of strain 17J68-2^T were investigated after cultivation on R2A agar for 3 days at 30 °C. Cell morphology was observed under a light microscope (Olympus, Tokyo, Japan; ×000 magnification) and a HT7700 transmission electron microscope (Hitachi, Tokyo, Japan). Gram staining of strain 17J68-2^T was performed using standard staining method [32]. Motility was examined by stabbing of semi-solid R2A medium (0.5% agar) tubes with a wire loop of culture. Gliding motility was analyzed by hanging drop technique [1]. An oxidase activity test was carried out using 1% (w/v) tetramethyl-*p*-phenylenediamine and catalase activity was tested by observing air bubble production using 3% (v/v) H₂O₂ [3]. Anaerobic growth test was performed in serum bottles containing R2A broth supplemented with thioglycolate (1 g/L) under a nitrogen atmosphere [19]. Resistance against different concentrations of NaCl [0, 0.5, 1, 2, 3, 4, 5, and 10% (w/v)] and the pH range (4, 5, 6, 7, 8, 9, and 10) for growth were determined in R2A broth (MB Cell) as the basal medium, as described by Lee et al. [21]. The ability to grow on different media was examined on R2A agar, nutrient agar (NA), TSA agar, and Luria–Bertani (LB) agar (all purchased from Difco). Growth at 4, 10, 15, 25, 30, 37, 42, and 45 °C was tested on these four media. Enzyme activities, utilization of carbon sources, and other

biochemical tests were carried out using the API ZYM, API 20NE, and API 32GN systems (bioMerieux, Marcy l'Etoile, France) following the manufacturer's instructions but with increased incubation times. The API 20NE and API 32GN strips were examined after 5 days of incubation at 25 °C. The incubation time for API ZYM was 18 h at 25 °C.

Sequencing of the 16S rRNA Gene and Phylogenetic Analysis

Nearly complete stretch of 16S rRNA gene of strain 17J68-2^T was PCR amplified using universal bacterial primers 9F and 1512R [40], and the purified PCR products were sequenced by Macrogen (Seoul, South Korea). The phylogenetic neighbors were identified and pairwise 16S rRNA gene sequence similarities were calculated using the EzBioCloud server [45]. Multiple alignment with 16S rRNA gene sequences of *Lysobacter* type strains was performed using the Clustal X 2.0 program [18]. Gaps and the 5' and 3' ends of the alignment were edited manually using the program BioEdit [13]. Tree topologies were inferred by neighbor-joining (NJ) [29], maximum-likelihood (ML) [9], and maximum-parsimony (MP) [10] methods using the MEGA 7 program [17]. The NJ and ML phylogenetic trees were constructed using Kimura's two-parameter model [15] and the ML tree was constructed using the nearest neighbor interchange heuristic search method. The MP tree was constructed using subtree pruning and regrafting. The resultant tree topologies were evaluated by bootstrap analyses on basis of 1,000 replicates.

Draft Genome Sequencing

Draft genome sequencing of strain 17J68-2^T was performed by DNA LINK Inc (Seoul, South Korea). A DNA library was generated from extracted DNA using TruSeq Nano DNA library preparation kit (Illumina) and sequenced on an Illumina Novaseq 6000 platform. Genome assembly into contigs was carried out using MaSuRCA genome assembler (version 3.2.4) [47]. Average nucleotide identity (ANI) was calculated with OrthoANI [20] and the digital DNA–DNA hybridization (dDDH) was calculated using the Genome-to-Genome Distance Calculator (GGDC) [25]. The draft genome sequence was annotated using the NCBI prokaryotic Genome Annotation Pipeline (PGAP) [12, 35] and the Rapid Annotation using Subsystem Technology (RAST) annotation server [2].

Chemotaxonomic Analyses

The analysis of cellular fatty acid methyl esters of strain 17J68-2^T was performed following the same growth

conditions used in previous studies of the three above-mentioned reference strains [22, 24, 43]. As such, strain 17J68-2^T was grown on R2A agar at 30 °C for 3 days. One loopful of bacterial colony was harvested, subjected to saponification, methylation, extraction, and separation by gas chromatography according to protocol of the Sherlock Microbial Identification System (MIDI) [30]. The fatty acid methyl esters were identified and quantified using TSBA6 database (version 6.21) of the Sherlock Microbial Identification System [30]. Isoprenoid quinones were extracted from freeze-dried cells of 17J68-2^T with chloroform/methanol (2: 1, v/v), purified by using Sep-Pak Vac Cartridges Silica (Waters) [37] and analyzed by high-performance liquid chromatography (HPLC) as described by Hiraishi et al. [14] with the following modifications. HPLC analysis was conducted on Agilent 1100 series HPLC (Agilent Technologies, Waldbronn, Germany) equipped with G1315A photodiode array detector and ChemStation software. The chromatographic separation was performed using an Atlantis T3 C₁₈ column (4.6 mm × 250 mm, 5.0 µm; Waters, Milford, USA) and the mobile phase consisting methanol and isopropanol in the proportion of 7:5 (v/v) at a flow rate of 1.2 ml/min. Polar lipids of the isolate were extracted from the freeze-dried cells and analyzed by two-dimensional TLC following protocol established by Minnikin et al. [27] by using four different spray reagents [16].

DNA–DNA Hybridization and Determination of DNA G+C Content

The genomic DNA of strain 17J68-2^T and reference strains *L. humi* KCTC 42810^T, *L. xinjiangensis* KCTC 22558^T, and *L. mobilis* KCTC 52627^T were extracted according to a standard protocol of Wilson [42]. DNA–DNA hybridization was conducted using the microplate method described by Ezaki et al. [8]. The highest and lowest values from five independent repetitions of the same hybridization reaction were excluded, and the mean of the remaining three values was recorded as the DNA–DNA hybridization value. The genomic DNA G+C content of strain 17J68-2^T was calculated from the draft genome sequence.

Results and Discussion

Phylogenetic Analysis

The results of the phylogenetic analysis based on the almost complete 16S rRNA gene sequence of strain 17J68-2^T (1468 bp) revealed that it belongs to the genus *Lysobacter*. The isolate shared highest sequence similarity with *L. humi* FJY8^T (98.4%), *L. xinjiangensis* RCML-52^T (98.3%), and *L. mobilis* 9NM-14^T (98.1%). The sequence similarities

between strain 17J68-2^T and other recognized *Lysobacter* species were less than 96.7%. The phylogenetic position of 17J68-2^T, determined by three tree-making algorithms, revealed that the novel isolate appeared within the genus *Lysobacter* and clustered with the three above-mentioned reference strains in the ML, NJ, and MP trees, with high bootstrap values of 98–100%. A threshold of 97% similarity in 16S rRNA gene sequence was first proposed for bacterial species delineation [33], later, based on a broader dataset, it was re-evaluated to 98.7% by Stackebrandt and Ebers [34] and Chun et al. [7]. Based on the re-evaluated threshold value, the above data indicate that strain 17J68-2^T represents a novel species of the genus *Lysobacter*. To confirm the results of 16S rRNA gene sequence similarity analysis, DNA–DNA hybridizations were performed between the novel isolate and the three above-mentioned closest relatives (Fig. 1).

Draft Genome Sequencing Analysis

The raw reads (82,815,012) of strain 17J68-2^T were assembled into 133 contigs with a coverage of 2845.82 × and N50 of 42,536 bp. The draft genome of the isolate was 2,939,468 bp in length with DNA G+C content of 70.5 mol%, which lies within the range observed for recognized members of the genus *Lysobacter* (61.7–70.7 mol%) [6, 23, 43]. Annotation with the NCBI predicted 2913 genes, including 2847 coding DNA sequences (CDSs), 66 RNA genes, and 111 pseudogenes. The draft genome of strain 17J68-2^T analyzed by the RAST server revealed that the most abundant genes can be classified in the following categories: amino acids and derivatives (170 genes), protein metabolism (150 genes), co-factors, vitamins, prosthetic groups, pigments (138 genes), carbohydrates (104 genes), DNA metabolism (91 genes), nucleosides and nucleotides (51 genes) (Supplementary Fig. S1). The ANI and dDDH values between strain 17J68-2^T and *Lysobacter enzymogenes* ATCC 29487^T (FNOG000000000), the type species of the genus, and most closely related strain of *Lysobacter* (95.5% of 16S rRNA gene sequence similarity), whose genome was available at the time of this study, were calculated to be 76.3% and 22.0%, respectively. These values were significantly lower than the accepted threshold values for delineating prokaryotic species using ANI (94–96%) and in silico DDH (70%) [26, 28], providing further evidence for assignment of the strain to a novel species of the genus *Lysobacter*.

Morphological and Phenotypic Characteristics

Cells of strain 17J68-2^T were observed to be Gram-stain negative, aerobic, motile by gliding, yellow pigment-producing rods (0.4–0.6 µm wide and 1.7–3.6 µm long) (Supplementary Fig. S2). The strain grew at 15–42 °C (optimum

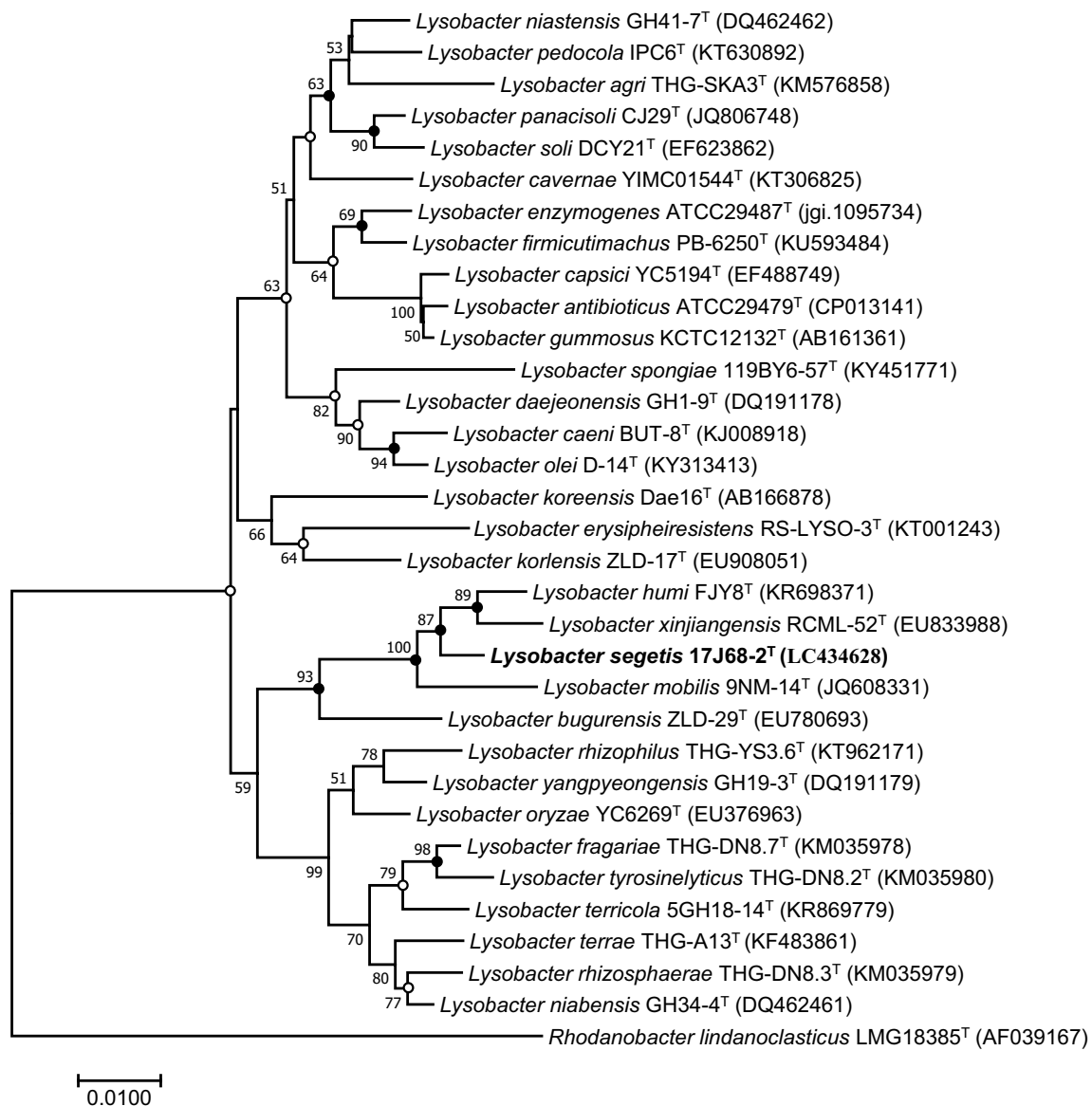


Fig. 1 Neighbor-joining phylogenetic tree, based on 16S rRNA gene sequences, showing the position of strain 17J68-2^T within the genus *Lysobacter*. Bootstrap values (based on 1000 replications) greater than 50% are shown at branch points. Filled circles indicate that the corresponding nodes were also recovered in trees generated using the maximum-likelihood and maximum-parsimony algorithms. Open

circles indicate that the corresponding nodes were also recovered in the trees generated using the maximum-likelihood or maximum-parsimony algorithms. Accession numbers are shown in parenthesis. *Rhodanobacter lindanoclasticus* LMG 18385^T was used as an out-group. Bar = 0.01 substitutions per nucleotide position

30 °C) but not at 10 or 45 °C. The pH range for growth was pH 7–8 (optimum pH 7). The strain was found to grow in the presence of 0–1% NaCl (w/v) but not in 2% NaCl (w/v). Growth occurred on R2A, TSA, and NA but not on LB agar. The results of other physiological and biochemical analyses are summarized in the species description and negative characteristics of strain 17J68-2^T in API ZYM, API 20NE, and API 32GN tests are given in Supplementary Table S1. The morphological, physiological, and biochemical characteristics differentiating the novel strain from *L. humi* KCTC

42810^T, *L. xinjiangensis* KCTC 22558^T, and *L. mobilis* KCTC 52627^T are listed in Table 1.

Chemotaxonomic Characteristics

The major fatty acids of strain 17J68-2^T were identified as C_{16:0} iso (39.4%), summed feature 3 (C_{16:1} ω7c/C_{16:1} ω6c) (6.6%), C_{11:0} iso 3-OH (6.4%), C_{15:0} iso (6.4%), and C_{16:1} iso H (6.2%). These results are similar to the previously described cellular fatty acids profiles of other members

Table 1 Differential phenotypic characteristics of strain 17J68-2^T and its phylogenetically closely related species in the genus *Lysobacter*

Characteristic	1	2	3	4
Cell size (μm)				
Width	0.4–0.6	0.7–1.0 ^a	0.5–0.7 ^b	0.4–0.6 ^c
Length	1.7–3.6	1.3–1.5 ^a	1.1–2.1 ^b	0.8–1.0 ^c
Growth on/at				
15 °C	+	–	–	+
42 °C	+	+	+	–
pH 10	–	+	+	–
1% NaCl	+	–	+	–
Motility	+	–	–	+
Catalase	–	+	+	–
Nitrate reduction	–	–	–	+
Aesculin hydrolysis	–	+	+	–
Enzyme activity (API ZYM)				
α-Chymotrypsin	w	w(+) ^a	+	–
Cystine arylamidase	+	–	+	+
α-Glucosidase	w	–	–	–
β-Glucuronidase	–	–	–	+
Lipase (C14)	–	+	+	w(–) ^a
Trypsin	–	+	+	+
Assimilation of (API 20NE, API 32GN)				
N-Acetyl-D-glucosamine	–	–	+	–
L-Arabinose, D-melibiose	–	–	–	+
L-Histidine	–	–	–	w
4-Hydroxybenzoate	–	–	w	+
L-Proline	–	–	+	+
D-Ribose	–	+	+	–
G+C content (mol%)	70.5	68.0 ^a	69.7 ^b	70.7 ^c

Strains: 1, 17J68-2^T; 2, *L. humi* KCTC 42810^T; 3, *L. xinjiangensis* KCTC 22558^T; 4, *L. mobilis* KCTC 52627^T

All data obtained in this study, unless otherwise noted

All strains were positive for gelatin hydrolysis, oxidase, acid phosphatase, alkaline phosphatase, esterase (C4), esterase (C8), leucine arylamidase, naphthol-AS-BI-phosphohydrolase, and valine arylamidase, but negative for acid production from glucose, indole production, N-acetyl-β-glucosaminidase, arginine dihydrolase, α-fucosidase, α-galactosidase, β-galactosidase, β-glucosidase, α-mannosidase, and assimilation of acetate, adipate, L-alanine, caprate, citrate, L-fucose, gluconate, D-glucose, glycogen, 3-hydroxybenzoate, DL-3-hydroxybutyrate, inositol, itaconate, 2-ketogluconate, 5-ketogluconate, DL-lactate, L-malate, malonate, D-maltose, D-mannitol, D-mannose, phenylacetate, propionate, L-rhamnose, L-serine, salicin, D-sorbitol, D-sucrose, suberate, and n-valerate

+ positive reaction, – negative reaction, w weak positive reaction

Results deviating from published data are shown within parentheses

^aData from Ref [22]

^bData from Ref [24]

^cData from Ref [43]

Table 2 Fatty acids composition of strain 17J68-2^T and closely related *Lysobacter* species

Fatty acids	1	2	3	4
Saturated				
C _{10:0} iso	2.1	1.1	2.3	–
C _{11:0} iso	4.0	5.3	12.4	7.0
C _{12:0} iso	3.1	tr	1.7	–
C _{14:0} iso	3.4	–	–	–
C _{15:0} iso	6.4	13.7	11.0	18.2
C _{15:0} anteiso	2.3	tr	tr	tr
C _{16:0}	3.9	2.1	2.3	3.3
C _{16:0} iso	39.4	26.9	24.3	7.9
C _{17:0} iso	tr	3.4	4.3	7.9
C _{18:0}	1.6	–	–	–
Hydroxy				
C _{11:0} iso 3–OH	6.4	4.8	7.7	10.0
C _{12:0} 3–OH	1.5	–	–	–
C _{16:0} N alcohol	–	tr	tr	2.1
C _{17:0} 3–OH	–	tr	tr	4.9
Unsaturated				
C _{14:1} ω5c	tr	tr	tr	5.8
C _{16:1} iso H	6.2	1.3	tr	–
Summed feature 3 ^a				
(C _{16:1} ω7c/C _{16:1} ω6c)	6.6	6.3	3.3	2.3
Summed feature 9 ^a				
(C _{17:1} iso ω9c/C _{16:0} 10-methyl)	4.8	26.2	19.9	27.8

Strains: 1, 17J68-2^T; 2, *L. humi* FJY8^T [22]; 3, *L. xinjiangensis* RCML-52^T [24]; 4, *L. mobilis* 9NM-14^T [43]

All strains were grown on R2A agar for 3 days at 30 °C. Values are percentage of total fatty acids, and only fatty acids accounting for more than 1.0% in at least one strain of the strains are indicated

– not detected, tr trace (<1.0%)

^aSummed feature contained two or three fatty acids that could not be separated by gas liquid chromatography (GLC) using the Sherlock Microbial Identification (MIDI) System

of the genus *Lysobacter*, which are known to contain iso-branched chain fatty acids as major components [22, 46]. However, strain 17J68-2^T can be clearly differentiated from the three reference strains by the presence of C_{14:0} iso, C_{18:0}, and C_{12:0} 3–OH, higher content of C_{16:1} iso H, lower content of summed feature 9 (C_{17:1} iso ω9c/C_{16:0} 10-methyl), and the absence of C_{16:0} N alcohol and C_{17:0} 3–OH, as shown in Table 2. The quinone analysis showed that strain 17J68-2^T contained ubiquinone Q-8 as the predominant quinone, which is the major respiratory quinone found in other members of the genus *Lysobacter* [4, 6, 41]. The major polar lipids in strain 17J68-2^T were observed to be phosphatidylglycerol (PG), diphosphatidylglycerol (DPG), and phosphatidylethanolamine (PE) (Supplementary Fig. S3), which have been identified as the main polar lipids in other *Lysobacter* species [23, 37, 43]. In addition, the polar lipid profile of the

isolate included two unidentified aminophospholipids (APL₁ and APL₂), four unidentified phospholipids (PL₁–PL₄), and five unidentified lipids (L₁–L₅).

DNA–DNA Hybridization Results

DNA–DNA hybridization values for strain 17J68-2^T with *L. humi* KCTC 42810^T, *L. xinjiangensis* KCTC 22558^T, and *L. mobilis* KCTC 52627^T were 39.9, 39.4, and 25.3%, respectively. All DNA–DNA pairing values are below the threshold value of 70% recommended for the delineation of novel bacterial species [39]. Thus, the results of 16S rRNA gene sequence similarity analysis and DNA–DNA hybridization data are consistent with the contention that strain 17J68-2^T forms a new species not currently recognized within the genus *Lysobacter*.

Taxonomic Conclusion

The combined results obtained in the current study demonstrate that it is reasonable to classify strain 17J68-2^T as a member of the genus *Lysobacter*. However, based on its phylogenetic distance from currently recognized species within the genus *Lysobacter*, low levels of DNA relatedness shared with closely related species, and its specific combination of phenotypic and chemotaxonomic characteristics (Table 1), it is clear that strain 17J68-2^T is not affiliated with any recognized species in the genus *Lysobacter*. Therefore, strain 17J68-2^T should be classified as a representative of a novel species within the genus *Lysobacter*, for which the name *Lysobacter segetis* sp. nov. is proposed.

Description of *Lysobacter segetis* sp. nov.

Lysobacter segetis (se.ge'tis. L. n. *seges* soil; L. gen. n. *segetis* of the soil).

Cells are Gram-negative, motile by gliding, aerobic rods, 0.4–0.6 µm wide and 1.7–3.6 µm long. Colonies grown on TSA agar after 48 h of incubation are circular, convex, yellow in color with a mean diameter of 1–2 mm. Optimum temperature for growth is 30 °C; growth occurs at 15–42 °C on TSA, NA, and R2A agar. Cells grow at pH 7–8 and with 0–1% NaCl. No growth is observed under anaerobic conditions. Tests for oxidase activity and gelatin hydrolysis are positive. Catalase is absent, indole is not produced, and nitrate is not reduced. Negative results in tests for arginine dihydrolase, urease, hydrolysis of aesculin, and acid production from glucose. In API ZYM tests, the strain is positive for acid phosphatase, alkaline phosphatase, α-chymotrypsin (weakly, w), cystine arylamidase, esterase (C4), esterase (C8), α-glucosidase (w), leucine arylamidase, naphthol-AS-BI-phosphohydrolase (w), and valine arylamidase activities. In API 32GN and API 20NE tests, all substrates are not

utilized. The fatty acid profile consists predominantly of iso-branched acids with the major components C_{16:0} iso, C_{11:0} iso 3-OH, C_{15:0} iso, and C_{16:1} iso H. Phosphatidylglycerol, diphosphatidylglycerol, and phosphatidylethanolamine are major polar lipids. Two unidentified aminophospholipids, four unidentified phospholipids, and five unidentified lipids are present in moderate to minor amounts. The predominant respiratory isoprenoid quinone is ubiquinone Q-8.

The type strain 17J68-2^T (=KCTC 62237^T = JCM 33058^T) was isolated from a soil sample collected on Jeju Island (33°26'01.2"N 126°35'04.8"E), Republic of Korea. The genomic DNA G+C content of the type strain is 70.5 mol%.

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