



Lysobacter terrigena sp. nov., isolated from a Korean soil sample

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Abstract

A bacterial strain isolated from a soil collected in Jeju Island, designated as 17J7-1^T, was Gram-negative, rod-shaped, yellow colored, and motile by gliding. This strain was able to grow at temperature range from 10 to 42 °C, pH 7–9, and tolerated up to 1% NaCl. Analysis of 16S rRNA sequence identified strain 17J7-1^T as a member of the genus *Lysobacter* with close sequence similarity with *Lysobacter mobilis* 9NM-14^T (97.4%), *Lysobacter xinjiangensis* RCML-52^T (97.0%), and *Lysobacter humi* FJY8^T (96.9%). The genomic DNA G + C content of the isolate was 67.9 mol%. DNA–DNA relatedness between strain 17J7-1^T and *L. mobilis*, *L. humi*, and *L. xinjiangensis* were 42.3%, 39.5%, and 35.8%, respectively, clearly showing that the isolate is distinct from its closest phylogenetic neighbors in the genus *Lysobacter*. Average nucleotide identity (ANI) and digital DNA–DNA hybridization (dDDH) values between strain 17J7-1^T and *L. enzymogenes* ATCC 29487^T, the type species of this genus, and several other close *Lysobacter* species were less than 77% and 22%, respectively. Major fatty acids were C_{16:0} iso (29.8%), summed feature 9 (C_{17:1} iso ω9c/C_{16:0} 10-methyl; 20.1%), and C_{15:0} iso (17.7%). The predominant respiratory quinone was ubiquinone Q-8 and the major polar lipids were phosphatidylethanolamine, phosphatidylglycerol, and diphosphatidylglycerol. In the light of the polyphasic evidence accumulated in this study, strain 17J7-1^T is considered to represent a novel species in the genus *Lysobacter*, for which name *Lysobacter terrigena* sp. nov. is proposed. The type strain is 17J7-1^T (= KCTC 62217^T = JCM 33057^T).

Keywords *Lysobacter* · *Lysobacteraceae* · Soil bacteria

Introduction

The genus *Lysobacter* belonging to the family *Lysobacteraceae* was first described by Christensen and Cook (1978).

Currently (April 2019), the genus comprises 48 validly published species (<https://www.bacterio.net/lysobacter.html>). Members of the genus *Lysobacter* commonly known

to be a Gram-negative, rod-shaped with pink to yellow colonies, and contain high DNA G + C content (61.7–70.1 mol%) (Christensen 2005; Li et al. 2018). The major fatty acids are C_{15:0} iso, C_{16:0} iso, and summed feature 9 (C_{17:1} iso ω9c/C_{16:0} 10-methyl); ubiquinone 8 (Q-8) is the predominant respiratory quinone and phosphatidylethanolamine, diphosphatidylglycerol, and phosphatidylglycerol are the major polar lipids (Christensen 2005; Chen et al. 2016; Wen et al 2016; Lee et al. 2017a). *Lysobacter* species have been isolated from various habitats, including different types of soil such as cave soil (Chen et al. 2016), forest soil (Margesin et al. 2018), cultivated soil (Siddiqi and Im 2016), manganese factory soil (Li et al. 2018), arid area soil (Lee et al. 2017a), and abandoned gold mine (Liu et al. 2011).

While screening for novel bacteria, strain 17J7-1^T was isolated from a soil sample collected in Jeju Island, Republic of Korea. This strain was considered to be *Lysobacter* like based on the results of 16S rRNA gene sequence analysis and was subjected to detailed polyphasic taxonomic investigation, including genotypic, chemotaxonomic, and phenotypic analysis. The results indicated that strain 17J7-1^T

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should be placed in the genus *Lysobacter* as a representative of a novel species.

Materials and methods

Isolation and culture of bacterial strain

Strain 17J7-1^T was isolated from soil sample collected from Jeju Island (33°26'16.4" N, 126°34'43.9" E), Republic of Korea. The sample was serially diluted by taking 1 g of soil to 10 ml distilled water, then 100 µl from each dilution was spread onto Reasoner's 2A (R2A) agar (Difco) plates. Plates were incubated on 25 °C for 1 week. After incubation, a single colony was purified by sub-culturing under the same conditions. For further investigation, the isolate was sub-cultured on R2A agar plates at 30 °C and preserved at −70 °C as glycerol suspension (20%, w/v). Strain 17J7-1^T was deposited in the Korean Collection for Type Culture (KCTC 62217^T) and the Japan Collection of Microorganisms (JCM 33057^T). Closely related strains *Lysobacter xinjiangensis* KCTC 22558^T, *Lysobacter mobilis* KCTC 52627^T, and *Lysobacter humi* KCTC 42810^T were obtained from the Korean Collection for Type Culture.

Phenotypic and biochemical characteristics

Gram-stain reaction was determined according to standard staining method of Smibert and Krieg (1994). Morphological characteristics were studied under light microscope (Olympus, Tokyo, Japan; 1000× magnification) and HT7700 transmission electron microscope (Hitachi, Tokyo, Japan). The motility test was performed using R2A medium supplemented with 0.5% (w/v) agar (Tittsler and Sandholzer 1936) and gliding motility was observed by microscopic hanging-drop technique (Agarwal et al. 1997). The anaerobic growth test was performed as described previously (Ten et al. 2006). The ability to grow on different media was tested using R2A (Difco), nutrient agar (NA, Difco), trypticase soy agar (TSA, Difco), and Luria–Bertani agar (LB, Difco). Growth at different temperatures (4, 10, 15, 25, 30, 37, 42, and 45 °C), pH values (4.0–10.0, in increments of 1 unit), and NaCl concentrations [0, 0.5, 1, 2, 3, 4, 5, and 10% (w/v)] were evaluated in R2A broth for 7 days as described previously (Lee et al. 2017b). Tests for nitrate and nitrite reduction were performed as described by La et al. (2005). Aesculin hydrolysis was tested on R2A agar as reported previously (Aslam et al. 2006). Catalase activity was determined by bubble production in 3% (v/v) H₂O₂ and oxidase activity was examined using 1% (w/v) tetramethyl-*p*-phenylenediamine as described by Cappuccino and Sherman (2010). Enzyme activity, assimilation of carbon sources, and other physiological characteristics of the novel isolate and the three

reference strains were determined using the API 32GN, API ZYM, and API 20NE kits according to manufacturer's instructions (biomérieux, Marcy-l'Etoile, France).

Sequencing of the 16S rRNA gene and phylogenetic analysis

Genomic DNA of strain 17J7-1^T was extracted according to the procedure of Wilson (1997). The 16S rRNA gene was amplified from chromosomal DNA using universal bacterial primers 9F and 1512R as described by Weisburg et al. (1991) and purified PCR products were sequenced by Macrogen (Seoul, Korea). A nearly complete sequence of the 16S rRNA gene was compiled with SeqMan software (DNASTAR). Identification of phylogenetic neighbors and calculation of 16S rRNA gene sequence similarities were performed using EzBioCloud server (<https://www.ezbiocloud.net>) (Yoon et al. 2017a). 16S rRNA gene sequence of related taxa was obtained from GenBank and assembled with BioEdit (Hall 1999). Multiple alignments were performed using Clustal X program (Thompson et al. 1997) and evolutionary distances were calculated according to Tamura three-parameter model (Tamura 1992). The phylogenetic trees were constructed using neighbors-joining (NJ) (Saitou and Nei 1987), maximum-likelihood (ML) (Felsenstein 1981) and maximum-parsimony (MP) (Fitch 1971) algorithms in the program MEGA7 (Kumar et al. 2016). A bootstrap analysis with 1000 replicate was performed to assess the support for clusters.

Whole genome sequencing, assembly, and annotation

Genomic DNA was extracted, sequenced, and assembled by DNA LINK Inc (Seoul, Korea). In brief, a library was prepared using TruSeq Nano DNA library prep kit (Illumina) and sequenced using Illumina Novaseq 6000. Assembly (de novo) was performed using MaSuRCA ver. 3.2.4 (Zimin et al. 2013). The genomic DNA G + C content of the strain 17J7-1^T was calculated from the whole genome sequence. Average nucleotide identity (ANI) was calculated with ANI calculator (Yoon et al. 2017b) and the digital DNA–DNA hybridization (dDDH) values were calculated using the genome-to-genome distance calculator (GGDC) (Meier-Kolthoff et al. 2013). Functional genes and potential coding regions were predicted by Rapid Annotation using Subsystem Technology (RAST) search tool (Aziz et al. 2008).

Chemotaxonomic analysis

Following the growth conditions that were used for fatty acid analysis of the three reference strains (Liu et al. 2011;

Yang et al. 2015; Lee et al. 2017a), the novel isolate was grown on R2A agar for 3 days at 30 °C. Fatty acid methyl esters (FAMES) were prepared using process of saponification, extraction, and methylation, as described by Sasser (1990). FAMES were then analyzed by gas chromatography using the MIDI TSBA database, version 6 (Sasser 1990). Polar lipids were extracted from frizzed dried cells of strain 17J7-1^T according to protocol of Minnikin et al. (1984) and analyzed by two-dimensional thin layer chromatography. The TLC plates were sprayed with various reagents to detect different polar lipids (Komagata and Suzuki 1987). Isoprenoid quinones were extracted and purified as described previously (Ten et al. 2008) and analyzed by high-performance liquid chromatography (HPLC) according to the method of Hiraishi et al. (1996).

DNA–DNA hybridization

The genomic DNA of strain 17J7-1^T and the three closely related reference strains, *L. mobilis* KCTC 52627^T, *L. xinjiangensis* KCTC 22558^T, and *L. humi* KCTC 42810^T were extracted according the protocol of Wilson (1997). DNA–DNA hybridization experiments were carried out fluorometrically according to method described by Ezaki et al. (1989), with photobiotin-labeled DNA probes and microdilution wells.

DPD taxon number and nucleotide sequence accession numbers

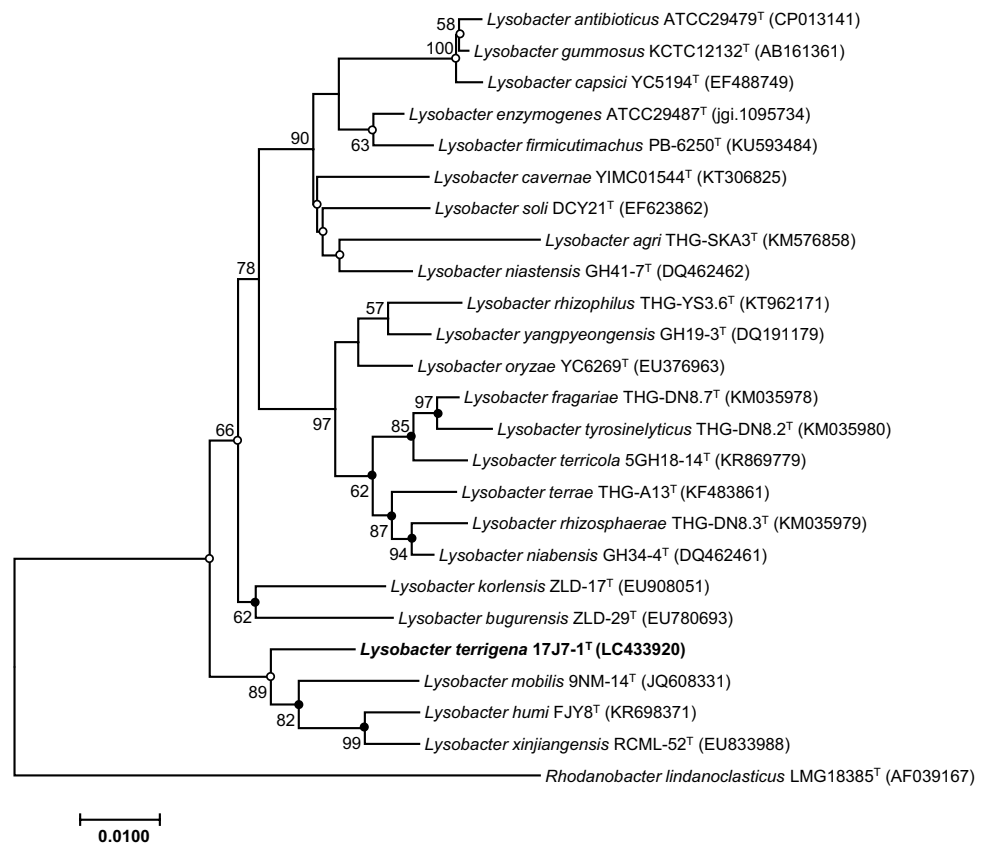
The Digital Protologue Database (DPD) Taxon Number for strain 17J7-1^T is TA00815. The 16S rRNA gene obtained in this study was deposited in NCBI GeneBank/EMBL/DBJ under the accession number LC433920. The GeneBank accession number for the whole genome sequence for strain 17J7-1^T is SELT00000000. The accession numbers of the 16S rRNA gene sequences of the reference strains closely related to strain 17J7-1^T are shown in Fig. 1.

Results and discussion

Phylogenetic analysis

The nearly complete 16S rRNA gene sequence of strain 17J7-1^T was a continuous stretch of 1473 bp. Based on 16S rRNA gene sequence similarity, the closest relatives of the isolate were identified to be *Lysobacter mobilis* 9NM-14^T (97.4%), *L. xinjiangensis* RCML-52^T (97.0%), and *L. humi* FJY8^T (96.9%). The phylogenetic position of the novel isolate, determined using various tree-making algorithms, confirmed that strain 17J7-1^T is a member of the genus *Lysobacter*, forming a coherent cluster with the three

Fig. 1 Neighbor joining phylogenetic tree, based on 16S rRNA gene sequences, showing the position of strain 17J7-1^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* LMG18385^T was used as an outgroup. Bar, 0.01 substitutions per nucleotide position



abovementioned members of this genus in the NJ and ML trees with high bootstrap values of 89% and 85%, respectively (Fig. 1). On the basis of phylogenetic analysis, the three closely related *Lysobacter* species were chosen as reference strains in this study. DNA–DNA hybridization tests were made with *L. mobilis* KCTC 52627^T, *L. xinjiangensis* KCTC 22558^T, and *L. humi* KCTC 42810^T as the similarity of 17J7-1^T with these strains exceeded or approached the recommended threshold of 97% for delineation of bacterial species (Stackebrandt and Goebel 1994). Values of DNA–DNA relatedness for strain 17J7-1^T with *L. mobilis* KCTC 52627^T (42.3%), *L. humi* KCTC 42810^T (39.5%), and *L. xinjiangensis* KCTC 22558^T (35.8%) were less than 70% which is the threshold value for recognition of separate species (Wayne et al. 1987).

Morphological and phenotypic characteristics

Cells of strain 17J7-1^T are Gram-negative, motile by gliding rods that are 0.4–0.6 µm wide and 1.2–1.7 µm long (Supplementary Fig. S1). Colonies are circular, yellow, and translucent on R2A agar. Growth occurred at temperatures 10–42 °C, but not at 4 °C or 45 °C. The isolate grew at a pH range between 7.0 and 9.0, with the optimum being pH 8.0. The strain was found to tolerate 1% (w/v) NaCl, but not 2%. Cells grew on R2A, NA, and TSA, but not on LB agar. The isolate was positive for catalase and oxidase. All other physiological and biochemical properties of strain 17J7-1^T are summarized in the species description. The phenotypic and biochemical characteristics that differentiate the isolate from its closest neighbors in the genus *Lysobacter* are listed in Table 1. In particular, it could readily be differentiated from phylogenetically closest relatives based on its ability to grow at 10 °C, to produce arginine dihydrolase, α-glucosidase, and urease, to assimilate citrate and DL-3-hydroxybutyrate, and its inability to grow at pH 6.

Chemotaxonomic characteristics

The cellular fatty acids profile of strain 17J7-1^T was characterized by the presence of C_{16:0} iso (29.8%), summed feature 9 (C_{17:1} iso ω9c/C_{16:0} 10-methyl; 20.1%), and C_{15:0} iso (17.7%) as major fatty acids. The FAME profile obtained corresponds to those of the members of the genus *Lysobacter*, including the three closest reference strains (Liu et al. 2011; Yang et al. 2015; Lee et al. 2017a) (Table 2). However, strain 17J7-1^T differed from *L. mobilis* 9NM-14^T, *L. xinjiangensis* RCML-52^T, and *L. humi* FJY8^T in terms of proportions of the major fatty acids and some minor fatty acids. In particular, the isolate differed from the reference strains by the presence of C_{18:0} and higher content of C_{15:0} anteiso, and C_{17:0} anteiso. Major polar lipids detected in strain 17J7-1^T were

Table 1 Differential phenotypic characteristic of strain 17J7-1^T and its phylogenetically closest relatives in the genus *Lysobacter*

Characteristic	1	2	3	4
Growth on/at/in				
NA agar	+	–	+	+
TSA	+	–	+	–
LB	–	–	+	–
10 °C	+	–	–	–
42 °C	+	–	+	+
pH 6	–	+ ^a	+ ^b	+ ^c
pH 9	w	– ^a	+ ^b	+ ^c
1% NaCl (w/v)	+	–	+	–
Motility	+	+ ^a	– ^b	– ^c
Oxidase	+	– ^a	+ ^b	+ ^c
Nitrate reduction	–	+	–	–
Aesculin hydrolysis	+	–	+	+
Arginine dihydrolase	+	–	–	–
Urease	+	–	–	–
Enzyme activities (API ZYM)				
α-Chymotrypsin	w	–	+	w (+) ^c
Cystine arylamidase	+	+	+	–
α-Glucosidase	+	–	–	–
β-Glucuronidase	–	+	–	–
Lipase (C14)	–	w (–) ^c	+	+
Trypsin	+	+	+ (–) ^b	+
Assimilation of (API 20NE, API 32GN)				
N-Acetyl-D-glucosamine	–	–	+ (–) ^b	–
L-Arabinose, D-melibiose	–	+ (–) ^a	–	–
Citrate	w	–	–	–
Glycogen, 3-hydroxybenzoate, DL-lactate	–	+	–	–
L-Histidine	–	w	–	–
4-Hydroxybenzoate	–	+	w	–
DL-3-Hydroxybutyrate	+	–	–	–
L-Proline	–	+ (–) ^a	+	–
D-Ribose	–	+	+	–
G+C content (mol%)	67.9	70.7 ^a	69.7 ^b	68.0 ^c

Strains: 1, 17J7-1^T; 2, *L. mobilis* KCTC 52627^T; 3, *L. xinjiangensis* KCTC 22558^T; 4, *L. humi* KCTC 42810^T

All data obtained in this study, unless otherwise noted. All strains were positive for gelatin hydrolysis, acid phosphatase, alkaline phosphatase, catalase, esterase (C4), esterase (C8), leucine arylamidase, naphthol-AS-BI-phosphohydrolase, and valine arylamidase, but negative for indole production, acid production from glucose, N-acetyl-β-glucosaminidase, α-fucosidase, α-galactosidase, β-galactosidase, β-glucosidase, and α-mannosidase, and assimilation of acetate, adipate, L-alanine, caprate, L-fucose, gluconate, D-glucose, inositol, itaconate, 2-ketogluconate, 5-ketogluconate, 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; (–), negative; (w), weak reaction

Deviating results from published data are shown in parenthesis

^aData from Yang et al. (2015)

^bData from Liu et al. (2011)

^cData from Lee et al. (2017a)

Table 2 Fatty acids compositions of strain 17J7-1^T and its closely related species of the genus *Lysobacter*

Fatty acids	1	2	3	4
Saturated				
C _{10:0} iso	tr	—	2.3	1.1
C _{11:0} iso	4.7	7.0	12.4	5.3
C _{12:0} iso	tr	—	1.7	tr
C _{15:0} iso	17.7	18.2	11.0	13.7
C _{15:0} anteiso	1.7	tr	tr	tr
C _{16:0}	3.2	3.3	2.3	2.1
C _{16:0} iso	29.8	7.9	24.3	26.9
C _{17:0} iso	3.0	7.9	4.3	3.4
C _{17:0} anteiso	2.0	—	tr	tr
C _{18:0}	1.1	—	—	—
Hydroxy				
C _{11:0} iso 3-OH	5.6	10.0	7.7	4.8
C _{16:0} N alcohol	—	2.1	tr	tr
C _{17:0} 3-OH	—	4.9	tr	tr
Unsaturated				
C _{14:1} ω5c	tr	5.8	tr	tr
C _{16:1} iso H	1.4	—	tr	1.3
Summed feature^a				
3 (C _{16:1} ω7c/C _{16:1} ω6c)	3.9	2.3	3.3	6.3
9 (C _{17:1} iso ω9c/C _{16:0} 10-methyl)	20.1	27.8	19.9	26.2

Strains: 1, 17J7-1^T; 2, *L. mobilis* 9NM-14^T (Yang et al. 2015); 3, *L. xinjiangensis* RCML-52^T (Liu et al. 2011); 4, *L. humi* FJY8^T (Lee et al. 2017a)

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

phosphatidylethanolamine (PE), phosphatidylglycerol (PG), and diphosphatidylglycerol (DPG), which are similar to members of the genus *Lysobacter* (Yang et al. 2015; Lee et al. 2017a; Li et al. 2018). In addition, polar lipid profile of the isolate included minor quantities of three unidentified aminophospholipids (APL₁–APL₃), three unidentified lipids (L₁–L₃), and two unidentified aminolipids (AL₁ and AL₂) (Supplementary Fig. S2). The predominant respiratory quinone detected was (Q-8), which is consistent with genus *Lysobacter* (Christensen 2005; Chen et al. 2016; Siddiqi and Im 2016; Wen et al. 2016).

Whole genome sequencing analysis

The raw reads (88,512,606 bp) of strain 17J7-1^T were assembled into 88 contigs with a coverage of 2,774.7 and N50 of 104,852 bp. The whole genome sequence of the

isolate contains 3,221,864 bp (GenBank accession no. SELT00000000). The DNA G + C content of strain 17J7-1^T was 67.9 mol%, which lies within the range observed for recognized members of the genus *Lysobacter* (61.7–70.1 mol%) (Christensen 2005; Li et al. 2018). RAST analysis of strain 17J7-1^T shows that > 8% of the major categories contained genes required for metabolism of “protein metabolism” (184 genes), “amino acids and derivatives” (178 genes), “co-factors, vitamins, prosthetic groups, pigments” (139 genes), and “carbohydrates” (106 genes) (Supplementary Fig. S3). The ANI and dDDH values between strain 17J7-1^T and *L. enzymogenes* ATCC 29487^T (96.1% of 16S rRNA gene sequence similarity), *L. soli* KCTC 22011^T (95.7%), *L. antibioticus* ATCC 29479^T (94.5%), and several other close *Lysobacter* species were less than 77% and 22%, respectively (Supplementary Table S1). These values were significantly lower than the accepted threshold values for delineating prokaryotic species using ANI (94–96%) and in silico DDH (70%) (Konstantinidis and Tiedje 2005; Meier-Kolthoff et al. 2013), providing further evidence for assignment of the strain to a novel species of the genus *Lysobacter*.

Taxonomic conclusion

The phenotypic and phylogenetic characteristics of strain 17J7-1^T indicated that it is a member of the genus *Lysobacter*. However, on bases of its phylogenetic distance from established *Lysobacter* species, DNA–DNA relatedness level of less than 45% with respect to the three closest phylogenetic neighbors, and its specific phenotypic characteristics (Table 1), it is clear that strain 17J7-1^T is not affiliated with any recognized species in the genus *Lysobacter*. Therefore, based on the data presented in this study, strain 17J7-1^T should be placed in the genus *Lysobacter* as a novel species, for which name *Lysobacter terrigena* sp. nov. is proposed.

Description of *Lysobacter terrigena* sp. nov.

Lysobacter terrigena (ter.ri'ge.na. L. masc. or fem. n. *ter-rigena* child of the earth, referring to the isolation of the type strain from soil).

Cells are Gram-negative, motile by gliding, aerobic rods that are 0.4–0.6 μm wide and 1.2–1.7 μm long. After 3 days of incubation at 30 °C on R2A agar, colonies are yellow, circular, and translucent. Cells grow on R2A, NA, and TSA, but not on LB agar. Growth is supported at temperatures 10–42 °C (optimum 30 °C) and at pH 7–9 (optimum 8). Cells tolerate 1% NaCl, but could not tolerate 2%. No growth is observed under anaerobic conditions. Cells are positive for catalase, oxidase, aesculin and gelatin hydrolysis, arginine dihydrolase, and urease, but negative for acid production from glucose, nitrate reduction, and indole production. In the API ZYM test, cells are positive for acid phosphatase,

alkaline phosphatase, α -chymotrypsin (w, weak), cystine arylamidase, esterase C4 (w), esterase C8, α -glucosidase, leucine arylamidase, naphthol-AS-BI-phosphohydrolase, trypsin, and valine arylamidase, but negative for *N*-acetyl- β -glucosaminidase, α -fucosidase, α -galactosidase, β -galactosidase, β -glucosidase, β -glucuronidase, lipase C14, and α -mannosidase. In API 32GN and API 20NE tests, cells assimilate citrate (w) and DL-3-hydroxybutyrate, but not acetate, *N*-acetyl-D-glucosamine, adipate, L-alanine, L-arabinose, caprate, L-fucose, gluconate, D-glucose, glycogen, L-histidine, 3-hydroxybenzoate, 4-hydroxybenzoate, inositol, itaconate, 2-ketogluconate, 5-ketogluconate, DL-lactate, L-malate, malonate, D-maltose, D-mannitol, D-mannose, D-melibiose, phenylacetate, L-proline, propionate, L-rhamnose, D-ribose, salicin, L-serine, D-sorbitol, suberate, D-sucrose, or n-valerate. The major cellular fatty acids are C_{16:0} iso, summed feature 9 (C_{17:1} iso ω 9c/C_{16:0} 10-methyl), and C_{15:0} iso. Major polar lipids are phosphatidylethanolamine, phosphatidylglycerol, and diphosphatidylglycerol, predominant respiratory quinone is ubiquinone 8 (Q-8). The whole genome sequence of the isolate contains 3,221,864 bp with G+C content of 67.9 mol%.

The type strain 17J7-1^T (= KCTC 62217^T = JCM 33057^T) was isolated from a soil sample collected from Jeju Island (33°26'16.4"N, 126°34'43.9"E), Republic of Korea.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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