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Strain 5GH22-11^T, which was isolated from greenhouse soil in the Yangpyeong region, Gyeonogi province, Republic of Korea, was characterized to be an aerobic, Gram-stainnegative, flagellated, rod-shaped bacterium. It could grow at temperatures from 10 to 33 °C (optimum of 28-30 °C), in the pH range of 6.0-10.0 (optimum of pH 7.0) and without NaCl. 16S rRNA gene sequence analysis showed that strain 5GH18-14^T showed the highest sequence similarities with Lysobacter niabensis GH34-4^T (98.6 %), Lysobacter yangpyeongensis GH19-3^T (98.1 %), 'Lysobacter fragariae' THG-DN8.7 (97.9 %), Lysobacter terrae THG-A13^T (97.3 %), 'Lysobacter rhizosphaerae' THG-DN8.3 (97.2 %), 'Lysobacter tyrosinelyticus' THG-DN8.2 (97.2 %) and Lysobacter oryzae YC6269^T (97.2 %), revealing less than 95.5 % sequence similarities with all other species with validly published names. Phylogenetic trees also indicated that strain 5GH18-14^T formed a compact subcluster with L. niabensis GH34-4^T, L. yangpyeongensis GH19-3^T, L. terrae THG-A13^T and L. oryzae YC6269^T within the genus Lysobacter. The predominant quinone of strain 5GH18-14^T was Q-8. The polar lipids were phosphatidylethanolamine, diphosphatidylglycerol, phosphatidylglycerol and phosphatidylmonomethylethanolamine in large amounts, and moderate or small amounts of three unknown phospholipids and two unknown aminophospholipids. DNA-DNA hybridization values with closely related species were below 70 %. The DNA G+C content was 65.9 mol%. Based on the phylogenetic, physiological and chemotaxonomic data, it has been demonstrated that strain 5GH18-14^T represents a novel species of the genus Lysobacter, for which the name Lysobacter terricola sp. nov. is proposed. The type strain is 5GH18-14^T (=KACC 16954^T=JCM 30862^T).

The genus Lysobacter was first proposed for non-fruiting, gliding bacterial strains with a high base ratio (Christensen & Cook, 1978), and later emended to encompass strains containing the polar lipids diphosphatidylglycerol, phosphatidylethanolamine, phosphatidylglycerol, phosphatidyl-N-methylethanolamine and unknown aminogroup-containing lipids. At the time of writing, there are more than 30 species with validly published names listed (http://www.bacterio.net). Recently, three novel species, including 'Lysobacter tyrosinelyticus', 'Lysobacter fragariae' and 'Lysobacter rhizosphaerae' have been proposed but not yet validly published (Du et al., 2015; Singh et al., 2015). Species of the genus Lysobacter have been characterized as Gram-negative, aerobic bacteria with a high DNA G+C content and containing ubiquinone 8 (Q-8) as the major respiratory quinone, showing a predominance of

Cook, 1978; Weon *et al.*, 2006; Choi *et al.*, 2014). They were isolated from soil, water, a sludge blanket reactor or a deep-sea sponge, and were known to produce various extracellular enzymes and antibiotics (Christensen & Cook, 1978; Nakayama *et al.*, 1999; Ahmed *et al.*, 2003; Park *et al.*, 2008).

The soil from a greenhouse located in the Yangpyeong

iso- $C_{15:0}$, iso- $C_{16:0}$ and iso- $C_{17:1}\omega 9c$ (Christensen &

The soil from a greenhouse located in the Yangpyeong region, Gyeonggi province, Republic of Korea, was sampled. The soil samples were serially diluted in 0.85 % saline solution, and plated on R2A agar medium at 28 °C. Among the isolates, 5GH18-14^T was identified as the type strain of a putative novel species of the genus *Lysobacter* on the basis of 16S rRNA gene sequence analysis. The strain was lyophilized using 12 % (w/v) skimmed milk, and then preserved at 4 °C.

The 16S rRNA gene of strain 5GH18-14^T was amplified with the primers 9F and 1512R (Weisburg *et al.*, 1991), and the purified PCR products were sequenced by Solgent (Daejeon, Republic of Korea). An almost complete sequence of 1478 bp was obtained. 16S rRNA gene

The GenBank/EMBL/DDBJ number for the 16S rRNA gene sequence of strain 5GH18-14^T is KR869779.

Two supplementary figures and one supplementary table are available with the online Supplementary Material.

sequences of related taxa were obtained from the GenBank database and EzTaxon-e server (http://eztaxon-e.ezbiocloud. net/; Kim et al., 2012). The sequence similarities among strain 5GH18-14^T and closely related species were calculated through the GenBank database and EzTaxon-e server. Sequence alignments were performed using the ARB software package (version December 2007; Ludwig et al., 2004). Trees were reconstructed in MEGA version 6 (Tamura et al., 2013) using the neighbour-joining (Saitou & Nei, 1987), maximum-likelihood (Felsenstein, 1981) and maximum-parsimony algorithms (Fitch, 1971). A neighbour-joining tree was reconstructed with Kimura's two-parameter model (Kimura, 1980). A maximum-likelihood tree was reconstructed using the nearest neighbour interchange as the maximum-likelihood heuristic search method. The maximum-parsimony tree was inferred using the min-mini heuristic algorithm (search level 3). The strength of each topology was checked using 1000 bootstrap replications.

The 16S rRNA gene sequence of strain 5GH18-14^T showed highest sequence similarities with *Lysobacter niabensis* GH34-4^T (98.6 %), *Lysobacter yangpyeongensis* GH19-3^T (98.1 %), '*Lysobacter fragariae*' THG-DN8.7 (97.9 %), *Lysobacter terrae* THG-A13^T (97.3 %), '*Lysobacter rhizosphaerae*' THG-DN8.3 (97.2 %), '*Lysobacter tyrosinelyticus*' THG-DN8.2 (97.2 %) and *Lysobacter oryzae* YC6269^T (97.2 %), revealing less than 95.5 % sequence similarities with all the other species with validly published names. The neighbour-joining phylogenetic tree indicated that strain 5GH18-14^T formed a compact subcluster with '*L. fragariae*' THG-DN8.7, '*L. tyrosinelyticus*' THG-DN8.2, *L. terrae* THG-A13^T, *L. niabensis* GH34-4^T, '*L. rhizosphaerae*' THG-DN8.3, *L. oryzae* YC6269^T and *L. yangpyeongensis* GH19-3^T within the cluster of the genus *Lysobacter* (Fig. 1). The maximum-likelihood and maximum-parsimony trees also showed a similar result (Fig. 1).

The cell morphology of strain 5GH18-14^T was observed by transmission electron microscopy (LEO; model 912AB). Gram-staining was tested with the Difco Gram staining kit according to the manufacturer's instructions. Oxidase activity was tested by bubble production in 3 % (v/v) hydrogen peroxide solution and catalase was checked from the colour change in 1 % (w/v) tetramethyl-pphenylenediamine (bioMérieux). Flexirubin-type pigment production was checked from the reversible colour shift from yellow or orange colonies to red, purple or brown using aqueous 20 % (w/v) KOH solution (Fautz & Reichenbach, 1980). The growth of strain 5GH18-14^T was tested on different media: R2A (Difco), trypticase soy agar (TSA; Difco), nutrient agar (NA; Difco) and MacConkey agar (Difco) at 28 °C. Casein (5 %, w/v), chitin (1 %, w/v), CM-cellulose (1 %, w/v), hypoxanthine (0.5 %, w/v), starch (1 %, w/v), Tween 80 (1 %, w/v), tyrosine (0.1 %, w/v) or xanthine (0.5 %, w/v) were added in R2A medium, and the hydrolysis of these substrates determined after 14 days of incubation at 28 °C. A DNase test was conducted with DNase test agar (Difco). The temperature

range for growth was observed after the incubation period (up to 7 days) on R2A broth at temperatures of 4, 10, 15, 20, 25, 28, 30, 33, 35, 37 and 40 °C. The pH range for growth was tested in R2A broth at 28 °C by adjusting the final pH to 5.0, 6.0, 7.0, 8.0, 9.0 10.0 and 11.0 with appropriate buffers (Na₂HPO₄/NaH₂PO₄ for pH 5.0-7.0 and Na₂CO₃/NaHCO₃ for pH 8.0-11.0). NaCl tolerance was checked in R2A broth containing 0, 1, 2, 3 and 5 % NaCl (w/v). Other phenotypic and enzymic characterizations of strain 5GH18-14^T were determined using API 20NE, API ID 32GN and API ZYM kits (bioMérieux) according to the manufacturer's instructions. The reference strains, 'L. fragariae' KACC 18545, L. niabensis KACC 11587^T, L. oryzae KACC 14553^T, 'L. rhizosphaerae' KACC 18544, L. terrae KACC 17646^T, 'L. tyrosinelyticus' KACC 18543 and L. yangpyeongensis KACC 11407^T, were studied for comparisons.

The morphological, physiological and biochemical characteristics of strain 5GH18-14^T are given in Table 1 and in the species description. Strain 5GH18-14^T can be differentiated from closely related species within the genus *Lysobacter* on the basis of its morphological, physiological and biochemical properties such as cell size, flagellum or motility, temperature range for growth, catalase activity, hydrolysis of some substrates, assimilation of carbon sources and enzyme activities (Table 1). Cells were 0.4–0.5 \times 1.5–2.0 μm (Fig. S1, available in the online Supplementary Material).

For cellular fatty acid analysis, strain 5GH18-14^T and the reference strains were grown on R2A agar at 28 °C for 2 days, where the bacterial communities reached the lateexponential stage of growth, according to the four quadrants steak method (Sasser, 1990). Fatty acid methyl esters were prepared and analysed according to the standard protocol of MIDI (Sherlock Microbial Identification System, version 5.0) and identified by the TSBA 50 database of the Microbial Identification System (Sasser, 1990). Cell biomass for polar lipids and respiratory quinones was obtained by centrifugation after shaking at 28 °C in R2A broth for 3 days. Quinones and polar lipids were extracted and analysed using the method of Minnikin et al. (1984). For the detection of polar lipids, molybdophosphoric acid (for total lipids), phosphomolybdic acid (for phospholipids), ninhydrin (for aminolipids) and α-naphthol/sulfuric acid reagent (for glycolipids) were sprayed. The respiratory quinones were separated by TLC and identified by HPLC. The DNA G+C content was determined with the fluorometric method (Gonzalez & Saiz-Jimenez, 2002) using SYBR Green 1 and a real-time PCR thermocycler (Bio-Rad). Genomic DNA samples from Bacillus amyloliquefaciens subsp. plantarum DSM 23117^T, Pseudomonas stutzeri ATCC 17588^T and Micrococcus luteus ATCC 4698^T were calibration references.

The fatty acids of strain 5GH18-14^T consisted of predominantly iso- $C_{16:0}$ (21.6 %), iso- $C_{15:0}$ (19.1 %) and iso- $C_{17:1}\omega 9c$ (11.6 %), with moderate amounts of iso- $C_{11:0}$ 3-OH (7.1 %), anteiso- $C_{15:0}$ (6.8 %), $C_{16:1}\omega 7c$ alcohol

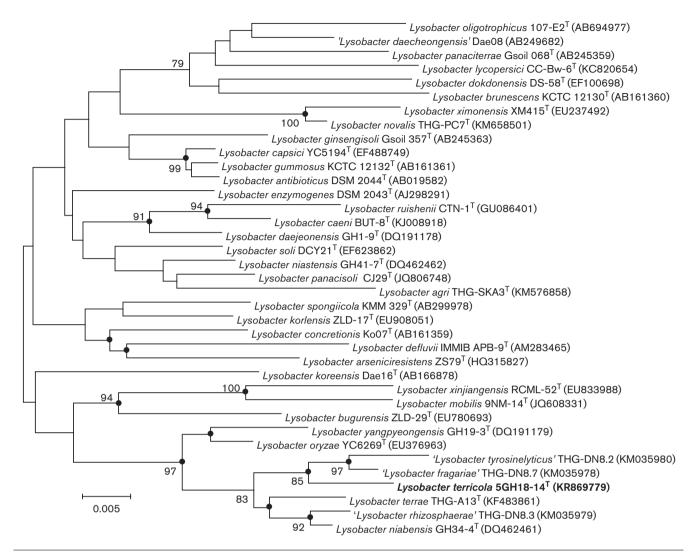


Fig. 1. Neighbour-joining tree, based on 16S rRNA gene sequences, showing the phylogenetic position of strain 5GH18-14^T and related species of the genus *Lysobacter*. Bootstrap values (expressed as percentages of 1000 replications; >70 %) are shown at branch points. Filled circles indicate branches that were also recovered in both maximum-likelihood and maximum-parsimony trees. Bar. 0.005 substitutions per nucleotide position.

(5.8 %) and iso- $C_{11:0}$ (5.4 %). The fatty acid compositions of strain $5GH18-14^T$ and closely related species were quite similar, containing iso- $C_{15:0}$, iso- $C_{16:0}$ and iso- $C_{17:1}\omega 9c$ as the major fatty acids. The quantitative differences between the fatty acids among the species compared is shown in Table S1. The predominant quinone of strain $5GH18-14^T$ was ubiquinone 8 (Q-8), which is also the major quinone of the genus *Lysobacter*. The polar lipids of strain $5GH18-14^T$ were large amounts of phosphatidylethanolamine (PE), diphosphatidylglycerol (DPG), phosphatidylglycerol (PG) and phosphatidylmonomethylethanolamine (PME), and moderate or small amounts of three unknown phospholipids and two unknown aminophospholipids (Fig. S2). Among closely related species, the polar lipids of strain $5GH18-14^T$ were similar to those of *L. terrae* THG-A13^T, *L. oryzae* KACC 14553^T

and *L. yangpyeongensis* KACC 11407^T, which contained PE, DPG, PG and PME, but quite different from those of *L. niabensis* KACC 11587^T, which lacked PG and PME (Ngo *et al.*, 2015).

DNA–DNA hybridization was conducted using the filter hybridization method described by Seldin & Dubnau (1985). Probe labelling was conducted by using a non-radioactive DIG High Prime system and hybridized DNA was visualized using a DIG luminescent detection kit (Roche). DNA–DNA relatedness was quantified by using a densitometer (Bio-Rad).

Strain 5GH18-14^T revealed DNA–DNA hybridization values of 45 ± 4 % (reciprocal value of 47 ± 5 %), 38 ± 5 %, 45 ± 5 %, 47 ± 3 %, 46 ± 4 %, 38 ± 6 % and 32 ± 5 %, respectively, with *L. niabensis* KACC 11587^T, *L. yangpyeongensis*

Table 1. Differential characteristics between strain $5GH18-14^{T}$ and closely related species of the genus *Lysobacter*

Strains: 1, 5GH18-14^T; 2, 'L. fragariae' KACC 18545; 3, L. niabensis KACC 11587^T; 4, L. oryzae KACC 14553^T; 5, 'L. rhizosphaerae' KACC 18544; 6, L. terrae KACC 17646^T; 7, 'L. tyrosinelyticus' KACC 18543; 8, L. yangpyeongensis KACC 11407^T. Data were obtained in this study unless otherwise indicated. +, Positive; w, weakly positive; -, negative; ND, not determined; DPG, diphosphatidylglycerol; PE, phosphatidylethanolamine; PG, phosphatidylglycerol; PME, phosphatidylmonomethylethanolamine.

Characteristic	1	2	ю	4	5	9	7	8
Isolation source	Greenhouse soil	Rhizosphere of strawberry plant	Greenhouse Soil	Rhizosphere of rice	Rhizosphere of strawberry plant	Rhizosphere of Aglaia odorata	Soil	Greenhouse soil
Cell size	$0.4 - 0.5 \times 1.5 - 2.0$	$0.7-0.9 \times 3.4-4.7^{a_{\star}}$	$0.5 \times 2.0 - 5.0^{b}$	$0.3-0.5 \times 1.8-2.0^c$		$0.40-0.45 \times 1.5-5.1^d$	$0.2-0.5 \times 1.5-2.5^e$	$0.4-0.6 \times 3.0-4.0^{f}$
Flagellum or motility	+	_ a	ND	_ c	_ a	+ 4	- e	+
Temperature range for	10–33	$10-28^{a}$	$5-37^{b}$	$15-42^{c}$	$18-28^{a}$	4-37 ^d	$18-28^{e}$	$15-40^{f}$
growth (°C)								
Growth at 1 % (w/v)	I	+ a	+ 6	- c	_ a	<i>p</i> —	+	<i>f</i> _
NaCl								
Catalse/oxidase	+/-	+/+a	+/+ _p	+/+	+/-a	$\mathbf{W}' + \mathbf{d}$	+/+e	-/+ _f
Hydrolysis of:								
Aesculin	+	I	+	I	I	+	+	+
Starch	ı	_ a	+	- c	+a	<i>p</i> —	+	+
Assimilation of:								
D-Glucose	I	I	+	I	+	I	I	+
N-Acetylglucosamine	1	I	+	I	ı	ı	I	+
Maltose	I	I	+	I	+	I	I	+
L-Serine	I		I	+	I	I	+	I
Propionic acid	+	I	I	+	+	+	I	I
Valeric acid	I	I	+	+	+	I	I	+
Enzyme activity								
Esterase (C4)	+	W	I	I	W	+	W	I
α -Chymotrypsin	ı	ı	+	ı	I	I	ı	I
β -Galactosidase	+	I	I	I	I	I	I	I
α -Glucosidase	+	W	I	I	+	+	W	I
N-Acetyl-	+	Ι	+	Ι	+	+	I	+
β -glucosaminidase								
Major polar lipids	DPG, PE, PG, PMF	DPG, PE, PG, PME a	$\mathrm{DPG},\mathrm{PE}^d$	PG, PE, PME^d	DPG, PE, PG, PMF a	DPG, PE, PG§	DPG, PE, PG, PMF e	DPG, PE, PG, PMF d
DNA G+C content	62.9	66.9^{a}	62.5^{b}	67.4^{c}	67.8^{a}	66.3^{d}	66.0^e	67.3
(mol%)								

*Data from a, Singh et al. (2015); b, Weon et al. (2007); c, Aslam et al. (2009); d, Ngo et al. (2015); e, Du et al. (2015); f, Weon et al. (2006).

KACC 11407^T, 'L. fragariae' KACC 18545, L. terrae KACC 17646^T, 'L. rhizosphaerae' KACC 18544, 'L. tyrosinelyticus' KACC 18543, and L. oryzae KACC 14553^T.

On the basis of the phylogenetic analysis, phenotypic characteristics and DNA–DNA hybridization values, strain 5GH18-14^T is considered to represent a novel species of the genus *Lysobacter*, for which the name *Lysobacter terricola* sp. nov. is proposed.

Description of Lysobacter terricola sp. nov.

Lysobacter terricola (ter.ri'co.la. L. n. terra earth, soil; L. suff. -cola inhabitant, dweller; N.L. n. terricola a dweller upon earth, soil-dweller, referring to the isolation of the type strain from soil).

Cells are aerobic, non-spore-forming, flagellated, Gramstain-negative rods $(0.4-0.5 \times 1.5-2.0 \,\mu\text{m})$. Grows at temperatures from 10-33 °C with optimum growth at 28–30 °C, and in the pH range of 6.0–10.0, with optimum growth at pH 7.0. Grows only at 0 % NaCl (w/v) with no growth at even 1 % NaCl (w/v). Grows on R2A and NA, but does not grow on TSA or MacConkey agar. Colonies on R2A agar plates are irregular and yellow. Catalasenegative and oxidase-positive. Flexirubin-type pigments are absent. Hydrolyses casein and tyrosine, but does not hydrolyse starch, DNA, xanthine, hypoxanthine, Tween 80, chitin or cellulose. Positive for aesculin hydrolysis and gelatin hydrolysis, but negative for nitrate reduction, indole production, glucose fermentation, arginine dihydrolase and urease. Assimilates sodium acetate, glycogen, propionic acid and 3-hydroxybutyric acid, but does not assimilate D-glucose, L-arabinose, D-mannitol, N-acetylglucosamine, maltose, potassium gluconate, capric acid, adipic acid, malic acid, trisodium citrate, phenylacetic acid, L-rhamnose, D-ribose, inositol, sucrose, itaconic acid, suberic acid, sodium malonate, lactic acid, L-alanine, potassium 5-ketogluconate, 3-hydroxybenzoic L-serine, salicin, melibiose, L-fucose, D-sorbitol, valeric acid, L-histidine, potassium 2-ketogluconate, 4-hydroxybenzoic acid or L-proline. Positive for alkaline phosphatase, esterase (C4), leucine arylamidase, acid phosphatase, naphthol-AS-BI-phosphohydrolase, β -galactosidase, α -glucosidase and *N*-acetyl- β -glucosaminidase, but negative for esterase lipase (C8), lipase (C14), valine arylamidase, cystine arylatrypsin, α-chymotrypsin, α-galactosidase, β -glucuronidase, β -glucosidase, α -mannosidase and α -fucosidase. The major fatty acids are iso- $C_{16:0}$, iso- $C_{15:0}$ and iso- $C_{17:1}\omega 9c$. The predominant quionone is Q-8. The polar lipids are large amounts of phosphatidylethanolamine, diphosphatidylglycerol, phosphatidylglycerol and phosphatidylmonomethylethanolamine, and moderate or small amounts of three unknown phospholipids and two unknown aminophospholipids.

The type strain, 5GH18-14^T (=KACC 16954^T=JCM 30862^T), was isolated from greenhouse soil, from the Yangpyeong

region, Gyeonggi province in the Republic of Korea. The DNA G+C content of the type strain is 65.9 mol%.

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