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Polyphasic Characterization of *Lysobacter maris* sp. nov., a Bacterium Isolated from Seawater

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Abstract A strictly aerobic, Gram-negative, apricot-pigmented, non-motile, rod-shaped strain designated KMU-14^T was isolated from seawater collected from the coastal zone of Yokji Island, Gyeongsangnam-do, Republic of Korea. Phylogenetic analysis based on the 16S rRNA gene sequence revealed that the novel isolate was affiliated with the genus *Lysobacter* within the class *Gammaproteobacteria* and that it showed the highest sequence similarity (97.1 %) to *Lysobacter concretionis* Ko07^T. The hybridization value for DNA–DNA relatedness between the strains of KMU-14^T and *L. concretionis* Ko07^T was 34.8 %, which was lower than 70 %, the recommended delineation value for differentiation of species. The DNA G+C content of strain KMU-14^T was 64.9 mol%. The major respiratory quinone was ubiquinone 8 (Q-8), and iso-C15:0, iso-C16:0, and 10-methyl C16:0 and/or iso-C17:1 ω9c were the major (>10 %) cellular fatty acids. A polar lipid profile was present consisting of diphosphatidylglycerol, phosphatidylethanolamine, an unidentified phosphoglycolipid, two unidentified aminophospholipids, and two unidentified phospholipids. From the distinct phylogenetic position and combination of genotypic and phenotypic characteristics, the strain is considered to represent a novel species for which the name *Lysobacter maris* sp. nov. is proposed. The type strain of *L. maris* sp. nov. is KMU-14^T (=KCTC 42381^T =NBRC 110750^T).

Introduction

Phylogenetic studies based on the 16S rRNA gene sequences revealed that species of class *Gammaproteobacteria* are abundant in diverse ecosystems including deep and intertidal sediments, seawater, and saline soil [10]. In addition, the members of this phylogenetic group are predominant among the marine bacterioplankton, together with members of the class *Alphaproteobacteria* and the phylum *Bacteroidetes* [8]. Halophilic and chemoheterotrophic representatives are considered to represent a large portion of the marine bacteria that are able to associate with decomposition of complex organic macromolecules [20]. The genus *Lysobacter* was first proposed by Christensen and Cook [4] for gliding bacteria with high DNA G+C content that do not have fruiting-body. At the time of writing, the genus *Lysobacter* includes 29 species, which have been isolated from various natural environments (http://www.bacterio.net/lysobacter.html).

In 2014, in the course of our study on the diversity of culturable marine bacteria in seawater, a bacterium designated KMU-14^T was isolated from the samples collected from the coastal zone of Yokji Island. Phylogenetic analysis based on the 16S rRNA gene sequences revealed that the novel strain belonged to the genus *Lysobacter* of class *Gammaproteobacteria*. In this study, we characterized a marine *Lysobacter* strain, KMU-14^T, isolated from seawater by means of polyphasic taxonomic methods, including 16S rRNA gene sequence analysis, physiological, biochemical, and chemotaxonomic analyses. Based on

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the polyphasic taxonomic data, we suggest that the isolate represents a novel species of the genus *Lysobacter* within the class *Gammaproteobacteria*.

Materials and Methods

Isolation of the Bacterial Strain and Culture Conditions

The seawater sample was collected from the coastal zone of Yokji Island, Gyeongsangnam-do, Republic of Korea in July 2014 in a 1.5-L sterile polyethylene bottle. A 50 μL of the sample was plated onto 1/2 strength R2A agar (Difco) containing 75 % artificial seawater [16]. Several colonies that developed at 25 °C were picked and restreaked onto new 1/2 strength R2A agar plates, and the procedure was repeated twice. A colony with an apricot color was picked up as being representative of several similar colonies, named KMU-14^T, and was used for further investigation.

The strain was routinely subcultured on marine agar 2216 (Difco) at 30 °C and maintained in marine broth 2216 (Difco) supplemented with 20 % (v/v) glycerol at −70 °C.

Morphological, Physiological, and Biochemical Analyses

Cell morphology was observed via transmission electron microscopy (TEM) and motility was measured via phase contrast microscopy (Primo Star; ZEISS). For TEM observation, cells were mounted on Formvar-coated copper grids and negatively stained with 1 % (w/v) aqueous uranyl acetate. Grids were observed using a Hitachi H-7100 microscope operated at 75 kV at a magnification of ×30,000.

The temperature range (4, 10, 15, 20, 30, 37, 40 and 45 °C) and pH range (5.5–9.5) for growth were determined by incubating the isolate for 2 weeks on marine agar 2216. The following buffers were used for pH tests: MES (pH 5.5), ACES (pH 6.5 and 7.0), TAPSO (pH 7.6), TAPS (pH 8.5), and CHES (pH 9.0 and 9.5). The NaCl concentration range for growth was determined on TY agar medium [0.2 % tryptone, 0.1 % yeast extract and 1.5 % agar (w/v) with 0–10 % (w/v) NaCl] and the cells were grown at 30 °C. Gram staining was performed using the BD Gram Staining Kit (Becton, Dickinson and Company, USA). Anaerobic growth was tested for up to 2 weeks on marine agar 2216 in a jar containing AnaeroPack-Anaero (Mitsubishi Gas Chemical Co, Inc). Catalase activity was detected by the formation of bubbles in 3 % (v/v) H_2O_2 solution. Oxidase activity test was performed using commercial dropper oxidase reagent (Becton, Dickinson and Co). Degradation of DNA was tested using DNase agar (Scharlau Chemie). The ability to hydrolyze casein, Tween 20, Tween 80, and tyrosine was determined according to Hansen and Sørheim [9]. API 20E, API 50CH, and API ZYM strips (bioMérieux) were used to determine the physiological, and biochemical characteristics. All suspension media for the API test strips were supplemented with 0.85 % (w/v) NaCl solution (final concentration). API 20E, API 50CH, and API ZYM test strips were read after 72 h incubation at 30 °C.

Determination of DNA G+C Content, 16S rRNA Gene Sequencing and Phylogenetic Analyses

Genomic DNA was prepared according to the method of Marmur [17] and the DNA base composition was determined by the HPLC method of Mesbah et al. [18].

Approximately 1500 bp fragment of the 16S rRNA gene was amplified using bacterial universal primers: 27F and 1492R [25]. The 16S rRNA gene sequence of strain KMU-14^T was compared with the sequences obtained from NCBI GenBank (http://www.ncbi.nlm.nih.gov). The EzTaxon-e database [12] was used to identify the nearest taxa. Multiple alignments of the sequences were performed using CLUSTAL_X (version 1.83) [24]. Alignment gaps and ambiguous bases were not taken into consideration when 1388 bases of the 16S rRNA genes were compared. Evolutionary distances (Kimura's two-parameter model; [11]) were calculated and clustering was performed with the neighbor-joining method [22] using MEGA5 software [23]. The topology of the phylogenetic tree was evaluated by the bootstrap resampling method of Felsenstein [7] with 1000 replicates.

DNA–DNA Hybridization Test

DNA–DNA hybridization was performed by the membrane filter method [1]. Each mixture of labeled and unlabeled DNAs was incubated at 37 °C for 12 h. Reciprocal hybridization test was performed in triplicate.

Chemotaxonomic Analysis

The fatty acid methyl esters were extracted and prepared from culture grown on marine agar 2216 at 30 °C for 3 days according to standard protocols provided by the MIDI/Hewlett Packard Microbial Identification system Sherlock Version 3.10/TSBA 50. Polar lipids were extracted according to the procedures described by Minnikin et al. [19] and they were identified by the previously described methods [6, 13, 19, 26]. Determination of the respiratory quinone system was carried out as per the method described by Collins and Jones [5].

Table 1 Differential characteristics of strain KMU-14^T and other closely related taxa

Characteristics	1	2	3	4	5	6	7	8	9	10
O_2 requirement	Strictly aerobic	Aerobic	Strictly aerobic	Aerobic	Aerobic	Aerobic	Aerobic	Aerobic	Aerobic	Strictly aerobic
Pigmentation	Apricot	Yellow	Yellow	Yellow	Yellow	Yellow	Yellow	Yellow	Yellow	Pale yellow
Cell size (μm)										
Length	1.3–1.5	1.0–13.5	1.5–2.2	1–2	1.3–1.5	1.0–2.5	1.1–1.5	ND	ND	30–35
Width	0.4–0.5	0.7–1.0	0.3–0.5	ND	0.5–0.6	0.3–0.4	0.6–0.7	ND	ND	0.4–0.5
Temperature range for growth (°C)	20–40	25–30	4–37	22–37	5–41	10–37	10–37	37–55	18–42	10–35
Highest NaCl tolerance (%, w/v)	5	ND	4	6	6	4	11	1	2	3
Catalase	+	+	+	+	+	W	W	+	+	+
Oxidase	–	+	+	+	+	+	+	+	+	+
Hydrolysis of										
Casein	–	ND	–	+	+	+	+	–	+	+
Gelatin	+	+	+	+	+	–	+	+	+	+
Starch	–	–	–	–	–	+	+	–	–	+
Urea	+	–	–	–	–	–	–	–	–	+
Acid production from										
Aesculin	+	–	–	–	–	+	+	+	+	+
Galactose	–	–	+	–	–	–	–	ND	ND	–
Mannose	+	–	+	–	–	–	–	+	–	–
Salicin	+	–	–	ND	–	–	–	ND	ND	–
Polar lipids	DPG, PE, UPGL, 2UAPL, 2UPL	DPG, PE, PG, UGL, UL	DPG, PE, PG, UPL	ND	DPG, PE, PG	DPG, PE, PG, 5UPL, UAL	DPG, PE, PG, 6UPL, UAL	DPG, PE, PG, UPL, UAPL	ND	DPG, PE, PG, UPL, UL
DNA G+C content (mol%)	64.9	63.8	70.7	67.1	69	67.9	68.2	66.9	69.7	68.5

PE phosphatidylethanolamine, *PG* phosphatidylglycerol, *DPG* diphosphatidylglycerol, *SGL* sphingoglycolipid, *UAL* unidentified aminolipid, *UAPL* unidentified aminophospholipid, *UL* unidentified lipid, *UPL* unidentified phospholipid, + positive, − negative, *W* weakly positive, *ND* no data, Strains *1* KMU-14^T (*Lysobacter maris* sp. nov.; present study), *2 Lysobacter concretionis* Ko07^T [3, 21], *3 Lysobacter arseniciresistens* ZS79^T [15], *4 Lysobacter defluvii* IMMIB APB-9^T [27], *5 Lysobacter spongiicola* KMM 329^T [21], *6 Lysobacter korlensis* ZLD-17^T [28], *7 Lysobacter bugurensis* ZLD-29^T [28], *8 Lysobacter oryzae* YC6269^T [2], *9 Lysobacter xinjiangensis* RCML-52^T [14], *10 Lysobacter enzymogenes* KCTC 12131^T (data from this study)

Results and Discussion

Morphological, Physiological, and Biochemical Characteristics

Cells of strain KMU-14^T grown on marine agar 2216 were observed to be straight rods with 0.4–0.5 μm in width and 1.3–1.5 μm in length, devoid of flagella or cell appendages (Supplementary Fig. 1), and produce an apricot-coloring pigment. Gliding motility was not observed via light microscopy. Flexirubin-type pigments were not produced.

The strain showed distinct phenotypic, physiological, and biochemical features that discriminated it from the closely related members in the genus *Lysobacter* as shown in Table 1.

Phylogenetic Analysis and DNA–DNA Hybridization Test

Almost complete 16S rRNA gene sequences of KMU-14^T were determined (GenBank/EMBL/DDBJ accession number LC021525). An evolutionary tree based on the neighbor-joining method generated a comparison of the 16S rRNA gene sequences and showed that strain KMU-14^T was phylogenetically affiliated with species of *Lysobacter*, a genus belonging to the class *Gammaproteobacteria* (Fig. 1). Strain KMU-14^T showed the highest sequence similarity (97.1 %) to *Lysobacter concretionis* Ko07^T, followed by *L. arseniciresistens* ZS79^T (96.6 %) and *L. defluvii* IMMIB APB-9^T (96.2 %). All other validly named species of the genus *Lysobacter* were more distantly

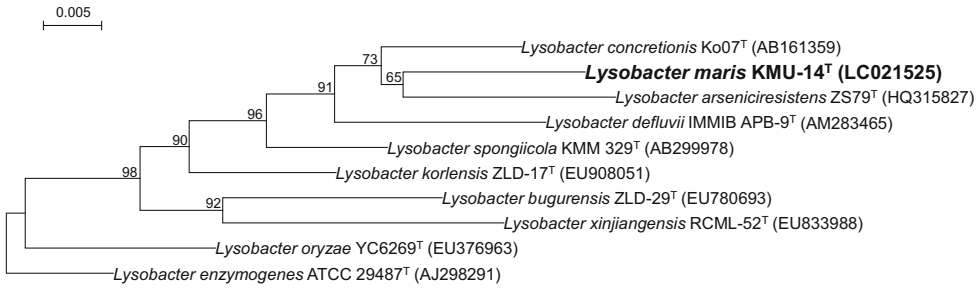

Fig. 1 Neighbor-joining tree based on the 16S rRNA gene sequences showing the phylogenetic position of strain KMU-14^T in the genus *Lysobacter*. The numbers at the nodes indicate the percentages of the occurrence of the strain in 1000 bootstrapped trees. The sequence determined in this study is shown in *bold*. Bootstrap values from neighbor-joining analysis are shown. Bootstrap values are shown at branch nodes. *Bar* 0.5 substitutions per 100 nt

Table 2 Comparison of cellular fatty acids for strain KMU-14^T and other closely related taxa

Fatty acid	1	2	3	4	5	6	7	8	9	10
iso-C11:0	5.6	10.8	12.6	10.9	9.1	4.5	4.9	3.9	9.8	3.7
C10:0 3-OH	1.3	–	–	–	–	–	–	–	–	tr
iso-C11:0 3-OH	5.4	9.8	12.4	8.5	10.8	6.8	6.1	3.2	11.4	6.3
iso-C15:0	13.1	30.6	28.6	28.8	36	5.3	3.6	12.5	19	48
anteiso-C15:0	1	1	–	–	1.3	4.6	–	2.2	–	tr
iso-C16:0	31	15.5	13.6	27.6	16.4	14.2	7.3	8.5	28	tr
C16:0	4.8	1.9	1.5	2.4	–	9.3	13.2	2.7	1.1	4.2
iso-C17:0	4.4	2.7	4.9	5.6	2.8	2.1	3.7	12.3	3.9	3.9
anteiso-C17:0	1.4	–	–	–	–	2.4	–	–	–	tr
C17:0 cyclo	2.2	1.6	–	1	–	–	–	–	–	–
Summed feature 3[a]	8	1.5	1	1.8	–	21.2	28.4	1.1	1.6	18.4
Summed feature 8[b]	2.9	–	–	–	–	–	–	–	–	1.1
Summed feature 9[c]	11.7	–	–	–	–	–	–	–	–	9.6

The data were typically obtained by GLC using the MIDI system

Strains: *1* KMU-14^T (*Lysobacter maris* sp. nov.; present study), *2 Lysobacter concretionis* Ko07^T [3], *3 Lysobacter arseniciresistens* ZS79^T [15], *4 Lysobacter defluvii* IMMIB APB-9^T [27], *5 Lysobacter spongiicola* KMM 329^T [21], *6 Lysobacter korlensis* ZLD-17^T [28], *7 Lysobacter bugurensis* ZLD-29^T [28], *8 Lysobacter oryzae* YC6269^T [2], *9 Lysobacter xinjiangensis* RCML-52^T [14], *10 Lysobacter enzymogenes* KCTC 12131^T (data from this study), *tr* trace (less than 1.0 %), – not detected

[a] Summed feature 3 consists of C16:1 ω7c and/or C16:1 ω6c

[b] Summed feature 8 consists of C18:1 ω7c and/or C18:1 ω6c

[c] Summed feature 9 consists of 10-methyl C16:0 and/or iso-C17:1 ω9c

related, showing a 16S rRNA gene sequence similarity of less than 96 %.

DNA–DNA hybridization value between strain KMU-14^T and *Lysobacter concretionis* Ko07^T was 34.8 %. These results strongly suggest that strain KMU-14^T could be classified as a separate species.

Chemotaxonomic Characteristics

The predominant cellular fatty acids (>10 %) of strain KMU-14^T were iso-C15:0 (13.1 %), iso-C16:0 (31 %), and summed feature 9 (10-methyl C16:0 and/or iso-C17:1 ω9c) (11.7 %) as identified by the MIDI system (Table 2). On the basis of the fatty acid composition, strain KMU-14^T could easily be differentiated from the phylogenetically closest taxon *Lysobacter concretionis* Ko07^T (Table 2). Moreover, strain KMU-14^T could be distinguished from the other members of the genus *Lysobacter* by a different proportion of C10:0 3-OH, anteiso-C17:0, summed feature 8 (C18:1 ω7c and/or C18:1 ω6c), and summed feature 9 (10-methyl C16:0 and/or iso-C17:1 ω9c), indicating that strain KMU-14^T probably represents an independent species of the genus *Lysobacter* (Table 2).

The polar lipids of strain KMU-14^T were determined to be composed of diphosphatidylglycerol, phosphatidylethanolamine, an unidentified phosphoglycolipid,

two unidentified aminophospholipids, and two unidentified phospholipids (Supplementary Fig. 2). The unidentified components distinguished strain KMU-14^T from other species in the genus *Lysobacter* (Table 1). From these results, it is suggested that strain KMU-14^T represents an independent species of the genus *Lysobacter*, for which the name *Lysobacter maris* sp. nov. is proposed.

Description of *Lysobacter maris* sp. nov

Lysobacter maris (ma'ris. L. gen. n. *maris* of the sea).

Cells are straight rods of 0.4–0.5 μm in width and 1.3–1.5 μm in length. Cells lack flagella and are non-motile. Gliding motility is not observed. Colonies grown on marine agar 2216 are circular and apricot-pigmented after 3 days of incubation at 30 °C. The temperature range for growth is 20–40 °C; the optimal temperature is around 30 °C but no growth occurs at 4 or 45 °C. The pH range for growth is 6–8 (optimum, pH 7), while no growth was observed below 5 or above 9. NaCl is required for growth and can be tolerated at a concentration of up to 5 % (w/v) but no growth occurs above 6 % (w/v) NaCl. Oxidase activity is negative. Gelatin and urea are hydrolyzed, but agar, casein, DNA, starch, tyrosine, Tween 20 and Tween 80 are not. The reactions for *o*-nitrophenyl-β-D-galactopyranoside (ONPG), arginine dihydrolase, ornithine decarboxylase, citrate utilization, Voges-Proskauer test are positive (API 20E). Acid is produced from mannose, *N*-acetylglucosamine, amygdalin, esculin ferric citrate, salicin, cellobiose, L-fucose, and D-arabitol (API 50CH). Alkaline phosphatase, esterase (C4), acid phosphatase, naphthol-AS-BI-phosphohydrolase, and α-glucosidase are present (API ZYM). All negative results from the API 20E, API 50CH, and API ZYM strips are indicated in Supplementary Fig. 3. The major fatty acids (>10 %) of strain KMU-14^T were identified as iso-C15:0 (13.1 %), iso-C16:0 (31 %), and summed feature 9 (10-methyl C16:0 and/or iso-C17:1 ω9c) (11.7 %). The major polar lipids are diphosphatidylglycerol, phosphatidylethanolamine, an unidentified phosphoglycolipid, two unidentified aminophospholipids, and two unidentified phospholipids. The G+C of the genomic DNA of the type strain is 64.9 mol%.

The type strain is KMU-14^T (=KCTC 42381^T =NBRC 110750^T), which was isolated from seawater collected from the coastal zone of Yokji Island, Gyeongsangnam-do, Republic of Korea. The GenBank/EMBL/DDBJ accession number of the 16S rRNA gene sequence of strain KMU-14^T is LC021525.

Compliance with Ethical Standards

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

Research involving human participants and/or animals This article does not contain any studies with human participants or animals performed by any of the authors.

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