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ORIGINAL PAPER

Luteolibacter luteus sp. nov., isolated from stream bank soil

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Abstract

A non-motile, Gram-stain-negative, rod-shaped and yellow-colored bacterium, designated G-1-1-1^T was obtained from soil sampled at Gwanggyo stream bank, Gyeonggi-do, Republic of Korea. Cells were aerobic, catalase positive, grew optimally at 25–30 °C and hydrolysed aesculin and casein. A phylogenetic analysis based on its 16S rRNA gene sequence revealed that strain G-1-1-1^T formed a lineage within the genus *Luteolibacter*. The closest members were *Luteolibacter flavescens* GKX^T (97.7% sequence similarity) and *Luteolibacter arcticus* MC 3726^T (97.3%). The sequence similarities with other members of the genus *Luteolibacter* were ≤ 93.9%. The genome of strain G-1-1-1^T was 6,412,079 bp long with 5176 protein-coding genes. The diagnostic amino acid of cell-wall peptidoglycan of strain G-1-1-1^T was *meso*-diaminopimelic acid. The only respiratory quinone was menaquinone-9 and the principal polar lipids were phosphatidylethanolamine, diphosphatidylglycerol, phosphatidylglycerol and unidentified phospholipids. The predominant cellular fatty acids were iso-$C_{14:0}$, $C_{16:1}$ $\omega 9c$, $C_{16:0}$, $C_{14:0}$ and anteiso-$C_{15:0}$. The DNA G + C content was 61.0 mol%. The anti-SMASH analysis of whole genome showed eight putative biosynthetic gene clusters responsible for various secondary metabolites. Based on genomic, chemotaxonomic, phenotypic and phylogenetic analyses, strain G-1-1-1^T represents a novel species in the genus *Luteobacter*, for which the name *Luteolibacter luteus* sp. nov. is proposed. The type strain is G-1-1-1^T (= KACC 21614^T = NBRC 114341^T).

Keywords *Luteolibacter luteus* · *Verrucomicrobia* · *Verrucomicrobiaceae* · Stream bank soil · *Meso*-diaminopimelic acid

Introduction

The genus *Luteolibacter* was first proposed by Yoon et al. with the type species *Luteolibacter pohnpeiensis* in the family *Verrucomicrobiaceae* within the phylum *Verrucomicrobia* (Yoon et al. 2008). The genus has been subsequently emended by Jiang et al. (Jiang et al. 2012) and Kim et al. (Kim et al. 2015). To date, there are eight species of the genus *Luteolibacter* with validly published names (https://lpsn.dsmz.de/genus/luteolibacter). Representatives of the genus *Luteolibacter* are non-motile, Gram-stain-negative, rod- or coccoid-shaped bacteria that contain MK-9 as predominant isoprenoid quinone, iso-$C_{14:0}$ and $C_{16:0}$ as major fatty acids, with DNA G + C content ranging from 47.2 to 61.0 mol% (Yoon et al. 2008; Jiang et al. 2012; Kim et al. 2015; Zhang et al. 2017). The members of the genus *Luteolibacter* have been isolated from red alga, leech, driftwood, seawater, tundra soil, forest soil and sludge sample (Yoon et al. 2008; Glaeser et al. 2012; Jiang et al. 2012; Park et al. 2013; Kim et al. 2015; Zhang et al. 2017; Pascual et al. 2017). In this study, a novel member of the genus *Luteolibacter*, isolated from soil of Gwanggyo stream bank was described and its taxonomic position was determined during the study of characterization of novel isolates from soil samples.

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Materials and methods

Isolation and ecology

Strain G-1-1-1^T was isolated from forest soil of Gwanggyo stream bank, geographically located at Suwon, Gyeonggi-do, Republic of Korea (37°17′47.7″ N and 127°01′34.5″ E) and subjected to polyphasic approach. Isolation, maintenance and preservation of strain were performed as described in the previous studies (Dahal and Kim 2018a).

16S rRNA phylogeny

Genomic DNA of strains was extracted using the InstaGene Matrix kit (Bio-Rad) as described by the manufacturer's instructions. Amplification of 16S rRNA gene was done by PCR using forward 27F and reverse 1492R primers (Frank et al. 2008). Sequencing of strain G-1-1-14^T was done using an Applied Biosystems 3770XL DNA analyser with a Big-Dye Terminator cycle sequencing Kit v.3.1 (Applied Biosystems, USA). The nearly complete sequence (1449 bp) of 16S rRNA genes was assembled with SeqMan software (DNASTAR Inc., USA) and deposited to NCBI GenBank under the accession MN685323. The closest phylogenetic neighbors were identified using the EzBioCloud database (Yoon et al. 2017). All the 16S rRNA gene sequences of the closest phylogenetic members were retrieved from the GenBank database and aligned using SILVA alignment (Pruesse et al. 2012). Phylogenetic trees were reconstructed using the three tree making algorithms: neighbor-joining (Saitou and Nei 1987), maximum-likelihood (Felsenstein 1981) and maximum-parsimony (Fitch 1971) with MEGA7 (Kumar et al. 2016). The evolutionary distances were calculated according to Kimura two-parameter model (Kimura 1980) and bootstrap analysis was based on 1000 replications (Felsenstein 1985).

Reference strains

Based on the 16S rRNA gene sequences and phylogenetic analyses, *Luteolibacter flavescens* KCTC 52361^T and *Luteolibacter arcticus* DSM 102244^T were chosen as the reference strains and used for comparative analyses.

Genome features

Whole genome-based approaches were used to affirm the taxonomic status of strain G-1-1-1^T. For whole-genome sequencing, genomic DNA was extracted using DNeasy Blood and Tissue kits (Qiagen, Germany). The whole-genome shotgun sequencing of strain G-1-1-1^T was performed by Macrogen (Republic of Korea) using the Illumina MiSeq platform and assembled by SPAdes VERSION 3.14 (Bankevich et al. 2012). The authenticity of the genome assembly was checked by comparing 16S rRNA gene sequence using NCBI Align Sequences Nucleotide BLAST tool (Zhang et al. 2000) and the potential contamination was checked by ContEst16S algorithm (Lee et al. 2017). After analysis, the genome sequence was annotated using NCBI Prokaryotic Genome Annotation Pipeline (Tatusova et al. 2016) and Rapid Annotation using Subsystem Technology (RAST) server (Aziz et al. 2008). DNA–DNA hybridization was also measured fluorometrically using photobiotin-labeled DNA probes and microdilution plates according to the method developed by Ezaki et al. (Ezaki et al. 1989). In addition, anti-SMASH server was used to identify the biosynthetic gene clusters (BGCs) for various secondary metabolites (Blin et al. 2019).

Morphology, physiology and chemotaxonomy

The cell morphology of strain G-1-1-1^T, grown on R2A agar for 5–6 days at 28 °C were examined by transmission electron microscopy (Talos L120C; FEI)). The colony morphology was observed using a Zoom Stereo Microscope (SZ61; Olympus, Japan). Gram staining was performed as described previously (Doetsch 1981). Motility was observed in R2A medium containing 0.4% (w/v) agar. Catalase activity was observed using 3% (v/v) hydrogen peroxide (H_2O_2). Oxidase activity was determined using 1% (w/v) tetra-methyl-*p*-phenylenediamine dihydrochloride. Growth at various temperatures 4, 10, 15, 20, 25, 28, 30, 32, 35 and 37 °C on R2A agar plates was monitored for 10 days. Growth was determined on various media including R2A agar (MB cell; KisanBio), nutrient agar (NA; Oxoid), tryptone soya agar (TSA; Oxoid), sorbitol MacConkey agar (MA; Oxoid), potato dextrose agar (PDA; Becton), marine agar 2216 (Becton), veal infusion agar (VIA; Becton) and Luria–Bertani agar (LBA; Oxoid). Salt tolerance was examined in R2A broth supplemented with NaCl (0–5%, w/v, at 0.5% subsequent changes). The pH range for growth was determined at 28 °C in R2A broth adjusted to pH 4–12 (in increments of 0.5 pH units) using citrate/NaH_2PO_4 buffer (for pH 4.0–5.5), phosphate buffer (for pH 6–7.5), Tris buffer (for pH 8–10) and 5 M NaOH (for pH 10.5–12.0) (Breznak and Costilow 2007). Hydrolysis of Tween 40, Tween 60 and Tween 80 was assessed using method of Smibert & Krieg (Smibert and Krieg 1994). Anaerobic growth was examined on R2A agar at 28 °C for 10 days using the BD GasPak EZ Gas Generating Pouch System using nitrate as a final electron acceptor. Hydrolysis of starch, CM-cellulose, tyrosine and casein was examined as previously described (Dahal and Kim 2018b). A DNase activity assay was performed with DNase agar (Oxoid). Production of hydrogen sulfide and indole was determined using

sulfide indole motility medium (SIM; Oxoid). Presence of spore was examined by staining with malachite green. Other physiological and biochemical tests were performed using API 20NE and API ID 32GN test kits (bioMérieux). Enzyme activities were determined using an API ZYM kit (bioMérieux) as recommended by the manufacturer's instructions.

For fatty acid analysis, cells of isolated strains and reference strains were harvested from the same culture condition (on R2A agar plate at 28 °C for 4 days). Fatty acids were extracted using the standard MIDI protocol (Sherlock Microbial Identification System, version 6.0B), analyzed with a gas chromatograph (Agilent 6890 Series GC System; Hewlett Packard) and identified using the TSBA6 database of the Microbial Identification System (Sasser 1990). Diagnostic cell-wall amino acid was extracted from freeze dried cells and analyzed as described previously (Dahal et al. 2017). Polar lipids and isoprenoid quinones were extracted from freeze-dried cells according to the procedures described by Minnikin et al. (Minnikin et al. 1984). Appropriate detection reagents were used to identify the spots (Komagata and Suzuki 1988).

Results and discussions

16S rRNA phylogeny

GenBank/EMBL/DDBJ accession of the 16S rRNA gene sequences for strain G-1-1-1^T is MN685323. The phylogenetic analysis based on its 16S rRNA gene sequence revealed that strain G-1-1-1^T formed a lineage within the genus *Luteolibacter*. The closest members were *Luteolibacter flavescens* GKX^T (97.7% sequence similarity) and *Luteolibacter arcticus* MC 3726^T (97.3%). The sequence similarities with other members of the genus *Luteolibacter* were ≤ 93.9%. The 16S rRNA gene sequence similarity of strain G-1-1-1^T with other members of the genus *Luteolibacter* was ≤ 97.7%, which is lower than 98.65% of species demarcation threshold recommended for species delineation (Kim et al. 2014). In addition, the phylogenetic trees: neighbor-joining (NJ), maximum-likelihood (ML) and maximum-parsimony (MP) formed strong bootstrap for strain G-1-1-1^T with *Luteolibacter arcticus* and *Luteolibacter flavescens* which strongly supported for a novel species within the genus *Luteolibacter* (Figs. 1, S1 and S2).

Genome analysis

Whole Genome Shotgun project has been deposited at DDBJ/ENA/GenBank under the accession CP051774. The genome of strain G-1-1-1^T was 6,412,079 bp. The genome consists 5176 coding genes, 32 pseudogenes, one scaffold and genome coverage of 180.0×. The RAST analysis showed the presence of 249 subsystems (Table 1). RAST analyses revealed various metabolic genes for various metabolism such as auxin biosynthesis, sulfur metabolism, RNA metabolism, protein metabolism, nitrogen metabolism, phosphorus metabolism and other metabolisms (Fig. S3). The antiSMASH analyses of BGCs showed strain G-1-1-1^T consists 8 putative BGCs responsible for secondary metabolites such as NRPS, arypolyene, T1PKS, T3PKS, terpene and bacteriocin (Table S1). DNA G + C content of strains G-1-1-1^T was 61.0 mol%, which was calculated based on genome sequences. The ANI (average nucleotide identity) and dDDH (digital DNA–DNA hybridization) have not been performed as there were no available genome sequences for the other members of the genus *Luteolibacter*.

The authenticity and contamination assessment based on 16S rRNA gene sequences confirmed that the genomes belonged to strain G-1-1-1^T. The DNA–DNA relatedness

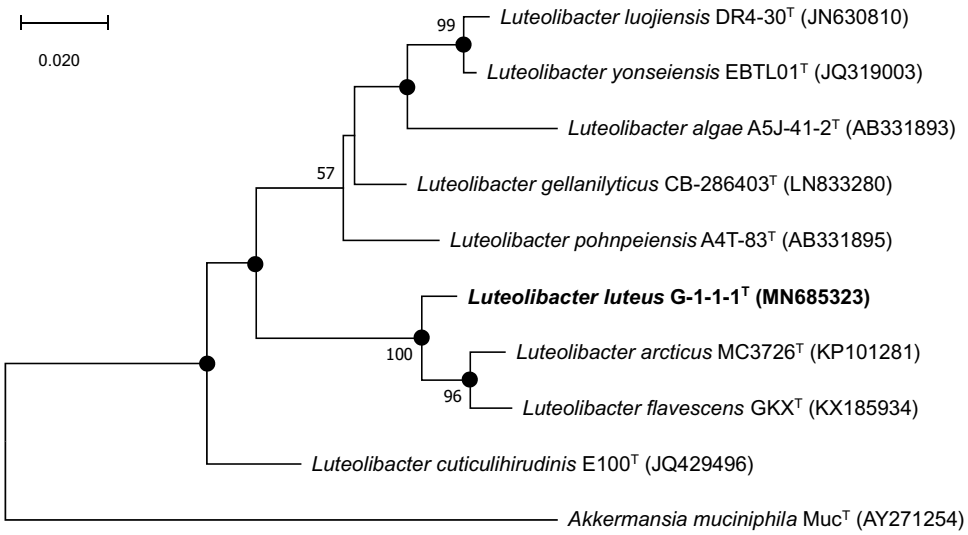

Fig. 1 Maximum-likelihood tree based on 16S rRNA gene sequences showing the phylogenetic position of strain G-1-1-1^T among members of the genus *Luteolibacter*. Filled circles indicate nodes recovered by treeing methods (neighbor-joining, maximum-likelihood and maximum-parsimony). The numbers at the nodes indicate the percentage of 1000 bootstrap replicates yielding this topology; only values > 50% are shown. *Akkermansia muciniphila* Muc^T was used as an out-group. GenBank accession numbers are given in parentheses. Bar, 0.020 substitutions per nucleotide position

Table 1 General genomic feature of strain G-1-1-1^T

Genome features	Value
Genome size (bp)	6412,079
G + C content (mol%)	61.0
No. of scaffold	1
N50	6412,079
No. of subsystem	249
Total genes	5268
CDSs (total)	5208
Protein-coding genes	5176
Genes (RNA)	60
Complete rRNAs (5S, 16S, 23S)	6 (2, 2, 2)
tRNAs	51
ncRNA	3
Pseudo Genes (total)	32
CDSs (without protein)	32
CRISPR repeats	6
Cas cluster	1
Genome coverage	180.0×

between strain G-1-1-1^T, *Luteolibacter flavescens* KCTC 52361^T and *Luteolibacter arcticus* DSM 102244^T were 26.6 ± 2.1 and 24.1 ± 1.9%, respectively. These results demonstrated that strain G-1-1-1^T differ genetically from other species of the genus *Luteolibacter* at the species level (Wayne et al. 1987).

Morphology, physiology and chemotaxonomy

Cell of strain G-1-1-1^T was rod shaped (Fig. S4), Gram-stain negative, strictly aerobic, non-motile and non-sporulating. Cells of strain G-1-1-1^T hydrolysed casein and aesculin but unable to hydrolyse DNA, urea, starch, chitin, CM-cellulose, tyrosine and Tweens. The highest growth temperature was 35 °C. The cells of strain G-1-1-1^T were able to grow at wide range of pH (6.5–10.5) and could tolerate NaCl up to 2% (w/v). On the basis of salt tolerance, hydrolysis and pH growth range G-1-1-1^T were different from the reference strains of the genus *Luteolibacter*. Additional physiological and biochemical differential characteristics are presented in Table 2. All the negative traits from API ZYM, API 20NE and API ID32GN are presented in supplementary table (Table S2).

The principal cellular fatty acids of strain G-1-1-1^T were iso-$C_{14:0}$ (34.9%), $C_{16:1}$ *ω9c* (22.2%), $C_{16:0}$ (16.2%), $C_{14:0}$ (8.8%), and anteiso-$C_{15:0}$ (6.2%) and are in agreement with those of other members of the genus *Luteolibacter* (Table 3). Differences in major and minor fatty acids and the presence of certain trace amounts of minor fatty acids differentiate strain G-1-1-1^T from other members of the genus *Luteolibacter* (Table 3). The diagnostic amino acid of cell-wall peptidoglycan was *meso*-diaminopimelic acid. The only respiratory quinone was menaquinone-9 (MK-9) and the major polar lipids were phosphatidylethanolamine (PE), diphosphatidylglycerol (DPG), phosphatidylglycerol (PG), and unidentified phospholipid (PL4) (Fig. S5). The presence of three unidentified phospholipids, an unidentified aminophospholipid and four unidentified glycolipids, and two unidentified polar lipids differentiate strain G-1-1-1^T from other species (Fig. S5) (Kim et al. 2015; Zhang et al. 2017).

Table 2 Phenotypic characteristics of strain G-1-1-1^T that differentiates with phylogenetically related type species of the genus *Luteolibacter*

Characteristic	1	2	3
Maximum growth temperature (°C)	35	35	37
Highest salt tolerance (%, w/v)	2.0	4.0	0.5
pH range	6.5–10.5	5.5–9.5	5.0–9.0
Nitrate reduction	–	+	–
Hydrolysis of			
Casein	+	+	–
Starch	–	+	+
Urea	–	+	+
Tween 40	–	+	–
Tween 60	–	+	–
Tween 80	–	+	+
Enzyme activity:			
Esterase (C4)	w	w	+
Esterase lipase (C8)	w	w	+
Leucine arylamidase	+	+	–
N-acetyl-*β*-glucosaminidase	+	–	–
Valine arylamidase	–	w	–
α-galactosidase	+	–	–
α-glucosidase	–	w	–
α-mannosidase	+	–	–
β-glucosidase	–	–	+
Assimilation of:			
D-glucose	+	+	–
D-maltose	+	+	–
D-mannitol	+	w	–
D-mannose	+	w	–
D-melibiose	+	+	–
D-saccharose (sucrose)	+	+	–
D-sorbitol	+	–	–
L-arabinose	–	w	–
L-fucose	w	–	+
L-rhamnose	+	–	+
Salicin	+	–	–
DNA G + C content (mol%)	61.0	59.5[a]	60.7[b]

Strains: 1, G-1-1-1^T; 2, *Luteolibacter flavescens* KCTC 52361^T; 3, *Luteolibacter arcticus* DSM 102244^T. All data were obtained from this study except G + C mol%. +, positive; w, weak; –, negative

Data from [a](Zhang et al. 2017) and [b](Kim et al. 2015)

Table 3 Cellular fatty acid profiles (% of totals) of strain G-1-1-1^T and closely related reference strains

Fatty acid	1	2	3
Saturated			
$C_{14:0}$	8.8	12.1	10.3
$C_{15:0}$	–	2.0	–
$C_{16:0}$	16.2	18.6	17.6
Unsaturated			
$C_{16:1}$ *ω9c*	22.2	16.2	24.3
$C_{18:1}$ *ω9c*	TR	1.6	TR
Hydroxy			
$C_{12:0}$ 3-OH	1.3	0.7	TR
$C_{16:0}$ 3-OH	2.7	3.0	–
iso-$C_{14:0}$ 3-OH	1.2	2.0	2.9
Branched saturated			
iso-$C_{14:0}$	34.9	31.3	35.0
iso-$C_{16:0}$	2.0	0.6	2.2
anteiso-$C_{15:0}$	6.2	6.8	3.9
Summed features[a]			
2	1.4	2.9	0.6

Strains: 1, G-1-1-1^T; 2, *Luteolibacter flavescens* KCTC 52361^T; 3, *Luteolibacter arcticus* DSM 102244^T. All data were obtained from this study. TR, trace amount (< 0.5%); –, not detected

[a]Summed features are groups of two or three fatty acids that are treated together for the purpose of evaluation in the MIDI system and include both peaks with discrete ECLs as well as those where the ECLs are not reported separately. Summed feature 2 comprised $C_{14:0}$ 3-OH and/or iso-$C_{16:1}$

Based on the phenotypic, chemotaxonomic, genotypic, phylogenetic and genomic analyses, strain G-1-1-1^T represents novel species in the genus *Luteolibacter* for which the name *Luteolibacter luteus* sp. nov. is proposed.

Description of *Luteolibacter luteus* sp. nov.

Luteolibacter luteus (lu′te.us. L. masc. adj. *luteus* golden yellow, reflecting the color of colonies).

Cells (1.6–2.1 μm long and 0.6–0.8 μm wide) are aerobic, rod shaped, Gram-stain negative and non-motile. Cells grow well only on R2A agar and no growth is observed on Luria–Bertani agar, potato dextrose agar, veal infusion agar, sorbitol MacConkey agar and marine agar 2216. Colonies on R2A are yellow coloured, entire, convex and circular. Colony size is 0.5–1 mm on R2A agar for 6 days at 28 °C. Cells grow at 20–35 °C (optimum, 25–30 °C) and pH 6.5–10.5 (optimum pH, 7.0–8.0). Cells grow optimally in the absence of NaCl but tolerate 2% (w/v) of NaCl. Catalase is positive and oxidase is negative. Hydrogen sulfide is not produced. Glucose is not fermented. Casein and aesculin are hydrolysed but DNA, CM-cellulose, tyrosine, chitin, gelatin, urea, Tween 80, Tween 60 and Tween 40 are not. Nitrate and nitrite are not reduced. The type strain shows the following enzyme activities: positive for alkaline phosphatase, leucine arylamidase, acid phosphatase, naphthol-AS-BI-phosphohydrolase, *α*-galactosidase, *β*-galactosidase, *N*-acetyl-*β*-glucosaminidase and *α*-mannosidase; weakly positive for esterase (C4) and esterase lipase (C8). D-glucose, D-maltose, D-mannitol, D-mannose, D-melibiose, D-saccharose, D-sorbitol, L-rhamnose, *N*-acetyl-glucosamine and salicin are assimilated and L-fucose is weakly assimilated. The only respiratory quinone is MK-9. The principal cellular fatty acids are iso-$C_{14:0}$, $C_{16:1}$ *ω9c*, $C_{16:0}$, $C_{14:0}$ and anteiso-$C_{15:0}$. The major polar lipids are phosphatidylethanolamine, diphosphatidylglycerol, phosphatidylglycerol and unidentified phospholipid. The diagnostic amino acid of cell-wall peptidoglycan is *meso*-diaminopimelic acid. The DNA G+C content of the type strain is 61.0 mol%.

The type strain, G-1-1-1^T (= KACC 21614^T = NBRC 114341^T), was isolated from Gwanggyo stream bank soil, geographically located at Suwon, Gyeonggi-do, Republic of Korea (37°17′47.7″ N and 127°01′34.5″ E). The GenBank/EMBL/DDBJ accession numbers for the 16S rRNA gene sequence and the whole genome sequence of strain G-1-1-1^T are MN685323 and CP051774, respectively.

Author contributions RHD prepared the draft manuscript, DKC and DUK analyzed the data and revised the manuscript, JK supervised the whole study and finalized the manuscript. All authors read and approved the final version of the manuscript.

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Availability of data and materials GenBank/EMBL/DDBJ accessions of the 16S rRNA gene sequences for strain G-1-1-1^T is MN685323 and Whole Genome Shotgun project has been deposited at DDBJ/ENA/GenBank under the accession CP051774. Supplementary materials are available with the online version of this manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that there are no conflicts of interest regarding the publication of this manuscript.

Ethical statement This study does not describe any experimental work related to human.

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