Photobacterium lutimaris sp. nov., isolated from a tidal flat sediment in Korea

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A Gram-negative, motile, pale-yellow-pigmented, oval-shaped bacterial strain, DF-42^T, was isolated from a tidal flat sediment in Korea. Strain DF-42^T grew optimally at 25–30 °C and in the presence of 2–3 % (w/v) NaCl. It contained Q-8 as the predominant ubiquinone and C_{16:0}, C_{18:1}ω7c and summed feature 3 (C_{16:1}ω7c and/or iso-C_{15:0} 2-OH) as the major fatty acids. The DNA G + C content was 48.3 mol%. Phylogenetic trees based on 16S rRNA gene sequences showed that strain DF-42^T falls within the evolutionary radiation enclosed by the genus *Photobacterium*. Strain DF-42^T exhibited 16S rRNA gene sequence similarity values of 93.8–97.9 % to the type strains of *Photobacterium* species with validly published names. DNA–DNA relatedness data and differential phenotypic properties made it possible to categorize strain DF-42^T as representing a species that is separate from previously described *Photobacterium* species. The name *Photobacterium lutimaris* sp. nov. is proposed, with strain DF-42^T (=KCTC 12723^T = JCM 13586^T) as the type strain.

A member of the *Gammaproteobacteria*, the genus *Photobacterium* was first proposed by Beijerinck (1889). The genus is currently composed of the following species: *Photobacterium phosphoreum* (Beijerinck, 1889; Reichelt & Baumann, 1973), *P. leiognathi* (Boisvert *et al.*, 1967), *P. fischeri* (Beijerinck, 1889; Reichelt & Baumann, 1973), *P. angustum* (Reichelt *et al.*, 1976), *P. damsela* (Smith *et al.*, 1991), *P. iliopiscarium* (Onarheim *et al.*, 1994; Urakawa *et al.*, 1999), *P. profundum* (Nogi *et al.*, 1998), *P. indicum* (Xie & Yokota, 2004), *P. rosenbergii* (Thompson *et al.*, 2005), *P. lipolyticum* (Yoon *et al.*, 2005), *P. frigidophilum* (Seo *et al.*, 2005a), *P. aplysiae* (Seo *et al.*, 2005b), *P. ganghwense* (Park *et al.*, 2006) and *P. halotolerans* (Rivas *et al.*, 2006). Here, we report on the taxonomic characterization of a *Photobacterium*-like bacterial strain, DF-42^T, which was isolated from a tidal flat sediment in Saemankum, Korea.

Strain DF-42^T was isolated by the usual dilution-plating technique on marine agar 2216 (MA; Difco) at 30 °C. Growth at various temperatures from 4 to 45 °C was measured on MA and tolerance of various NaCl concentrations was measured in marine broth 2216 (MB; Difco). Growth in the absence of NaCl was investigated on R2A agar (Difco) and trypticase soy agar prepared according to the formula of the Difco medium except that no NaCl was used. Optimal pH and pH range for growth were determined in MB that was adjusted to various pH values (pH 4.5–9.0 at intervals of 0.5 pH units) after autoclaving. Growth under

anaerobic conditions was determined after incubation in an anaerobic chamber on MA and on MA supplemented with nitrate, both of which had been prepared anaerobically using nitrogen. The cell morphology was examined by light microscopy (Nikon E600) and transmission electron microscopy. The presence of flagella was determined by transmission electron microscopy using cells from exponentially growing cultures. The Gram reaction was determined by using the bioMérieux Gram stain kit according to the manufacturer's instructions. Catalase and oxidase activities and hydrolysis of casein and starch were determined as described by Cowan & Steel (1965). Hydrolysis of hypoxanthine, tyrosine and xanthine was examined on MA with the substrate concentrations described previously (Cowan & Steel, 1965). Hydrolysis of aesculin, gelatin and urea and nitrate reduction were studied as described by Lanyi (1987) with the modification that artificial seawater (containing 23.6 g NaCl, 0.64 g KCl, 4.53 g MgCl₂·6H₂O, 5.94 g MgSO₄·7H₂O and 1.3 g CaCl₂·2H₂O per litre distilled water; Bruns *et al.*, 2001) was used for the preparation of media. Hydrolysis of Tweens 20, 40, 60 and 80 was determined as described by Cowan & Steel (1965) with the modification that artificial seawater was used for the preparation of media. Acid production from carbohydrates was determined as described by Leifson (1963). Utilization of various substrates for growth was determined as described by Yurkov *et al.* (1994). The API ZYM system (bioMérieux) was used to determine enzyme activity. The API 20E system (bioMérieux) was used to examine other physiological and biochemical properties. Antibiotic sensitivity was tested by spreading a bacterial suspension on MA

The GenBank/EMBL/DDBJ accession number for the 16S rRNA gene sequence of strain DF-42^T is DQ534014.

Table 1. Differential phenotypic characteristics of *Photobacterium* species

Species: 1, *P. lutimaris* sp. nov. (strain DF-42^T); 2, *P. angustum* (data from Baumann & Baumann, 1984; Nogi *et al.*, 1998); 3, *P. damsela* (Smith *et al.*, 1991; Gauthier *et al.*, 1995; Nogi *et al.*, 1998); 4, *P. iliopiscarium* (Onarheim *et al.*, 1994); 5, *P. leiognathi* (Baumann & Baumann, 1984; Nogi *et al.*, 1998); 6, *P. phosphoreum* (Reichelt & Baumann, 1973; Baumann & Baumann, 1984; Nogi *et al.*, 1998); 7, *P. profundum* (Nogi *et al.*, 1998); 8, *P. indicum* (Johnson & Weisrock, 1969; Xie & Yokota, 2004); 9, *P. lipolyticum* (Yoon *et al.*, 2005); 10, *P. frigidiphilum* (Seo *et al.*, 2005a); 11, *P. aplysiae* (Seo *et al.*, 2005b); 12, *P. rosenbergii* (Thompson *et al.*, 2005); 13, *P. ganghwense* (Park *et al.*, 2006); 14, *P. halotolerans* (Rivas *et al.*, 2006). +, Positive; –, negative; V, variable; W, weak; ND, no data available. Data in parentheses are for type strains.

Characteristic	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Optimum temperature (°C)	25–30	(25)	22–26	20	(26)	(18)	10	25	25–28	14	25	20–30	35	28
Growth at:														
4 °C	+	V	–	+	–	+	+	+	+	–	–	–	–	+
35 °C	+	+	+	–	+	–	–	–	–	–	–	ND	+	+
Motility	+	+	V	+	+	V (+)	+	+	+	+	+	+	+	+
Catalase	w	(–)	+	+	(–)	(+)	+	–	+	+	+	ND	+	+
Oxidase	+	(–)	+	ND	(+)	(+)	+	–	+	+	+	+	+	+
Indole production	+	(–)	(–)	–	(–)	(–)	+	+	+	+	–	–	+	–
H ₂ S production	–	(–)	(–)	–	(–)	(–)	–	+	–	ND	ND	ND	–	–
Nitrate reduction	+	V (–)	V	+	+	+	+	+	+	+	+	+	+	+
Arginine dihydrolase	+	(+)	+	+	(+)	(+)	+	ND	–	+	+	+	+	–
Lysine decarboxylase	–	(–)	(–)	+	(–)	(–)	–	–	–	ND	ND	–	–	–
β-Galactosidase	–	ND	ND	W	+	+	+	ND	–	+	+	+	–	+
Hydrolysis of gelatin	–	V	–	–	–	–	ND	–	–	ND	+	–	+	+
Utilization of:														
D-Fructose	+	+	(+)	+	+	+	V (–)	ND	+	+	+	+	ND	+
D-Galactose	+	+	+	+	+	V (–)	+	ND	–	+	W	+	ND	–
D-Cellobiose	+	–	+	–	–	–	V (–)	ND	–	–	+	+	ND	–
D-Mannose	+	+	+	+	+	+	+	ND	–	+	+	+	W	–
D-Trehalose	+	V (–)	(–)	V	–	–	+	ND	–	+	+	+	ND	+
Sucrose	+	V (+)	(–)	–	–	–	–	+	+	+	+	+	ND	+
Maltose	+	V (+)	(+)	ND	V (+)	+	+	+	+	+	+	+	ND	+
Acetate	–	+	ND	ND	+	–	ND	ND	+	–	ND	+	ND	ND
L-Arabinose	–	–	(–)	–	–	–	–	–	–	+	–	–	ND	–
L-Glutamate	–	–	(–)	ND	V	V	ND	ND	–	+	+	+	ND	ND
Formate	–	–	ND	ND	–	–	ND	ND	–	–	ND	+	ND	ND
Acid production from:														
D-Mannitol	–	–	–	–	–	–	+	ND	–	+	ND	+	+	+
D-Sorbitol	–	–	–	–	–	–	–	ND	–	ND	ND	–	–	–
L-Rhamnose	–	–	–	–	–	–	–	ND	–	ND	ND	V	W	–
Sucrose	+	+	–	–	–	–	–	+	+	+	ND	+	–	+
Melibiose	–	–	+	–	–	–	–	ND	–	ND	ND	+	–	–
L-Arabinose	–	–	–	–	–	–	–	–	–	ND	ND	–	–	+
DNA G + C content (mol%)	48.3	40–42	(42)	38–40	40–44	39–42	42	40	47	43.8	45	47.6–47.9	44	49.8

and applying discs impregnated with the following antibiotics (amount per disc): ampicillin (10 µg), carbenicillin (100 µg), cephalothin (30 µg), chloramphenicol (100 µg), gentamicin (30 µg), lincomycin (15 µg), kanamycin (30 µg), neomycin (30 µg), novobiocin (5 µg), oleandomycin (15 µg), penicillin G (20 U), polymyxin B (100 U), streptomycin (50 µg) and tetracycline (30 µg).

Cell biomass of strain DF-42^T for DNA extraction and for respiratory lipoquinone analysis was obtained by cultivation for 3 days in MB at 30 °C. Chromosomal DNA was isolated

and purified according to the method of Yoon *et al.* (1996). 16S rRNA gene amplification was performed according to a method described previously using two universal primers (Yoon *et al.*, 1998). Sequencing of the amplified 16S rRNA gene was performed as described by Yoon *et al.* (2003). Alignment of sequences was carried out with the CLUSTAL W program (Thompson *et al.*, 1994) and gaps at the 5' and 3' ends of the alignment were omitted from further analysis. Evolutionary distances were calculated using the Kimura two-parameter correction with CLUSTAL W (Thompson *et al.*, 1994). A phylogenetic tree was constructed by using the

Fig. 1. Neighbour-joining tree showing the phylogenetic positions of strain DF-42^T and other related taxa, based on 16S rRNA gene sequences. Bootstrap values are expressed as percentages of 1000 replications; only values greater than 50% are shown. *Escherichia coli* ATCC 11775^T (GenBank accession no. X80725) was used as an outgroup (not shown). Bar, 0.01 substitutions per nucleotide position.

neighbour-joining method (Saitou & Nei, 1987) on the basis of distance matrix data. The reliability of groupings was assessed by 1000 bootstrap resamplings of the neighbour-joining dataset by using CLUSTAL W. DNA–DNA hybridization was determined by the microplate hybridization method (Ezaki *et al.*, 1989) using photobiotin-labelled DNA probes. *P. rosenbergii* LMG 22223^T was used as a reference strain for DNA–DNA hybridization and was obtained from the Laboratorium voor Microbiologie, Universiteit Gent (LMG), Brussels, Belgium. Isoprenoid quinones were extracted according to the method of Komagata & Suzuki (1987) and analysed using reversed-phase HPLC and a YMC ODS-A (250 × 4.6 mm) column. For fatty acid methyl ester analysis, cell mass of strain DF-42^T was harvested from MA plates after incubation for 3 days at 30 °C. Fatty acid methyl esters were extracted and prepared according to the standard protocol of the MIDI/Hewlett Packard Microbial Identification System (Sasser, 1990). The DNA G+C content was determined by the method of Tamaoka & Komagata (1984) with the modification that the DNA was hydrolysed and the resultant nucleotides were analysed by reversed-phase HPLC.

Morphological, cultural, physiological and biochemical characteristics of strain DF-42^T are given in the species description or are shown in Table 1. The almost-complete 16S rRNA gene sequence of strain DF-42^T determined in this study comprised 1508 nucleotides. Comparative 16S rRNA gene sequence analysis revealed that strain DF-42^T was phylogenetically most closely affiliated to the genus *Photobacterium* (Fig. 1). In the phylogenetic tree based on the neighbour-joining algorithm, strain DF-42^T fell within the radiation of the cluster comprising *Photobacterium* species, joining *P. rosenbergii* LMG 22223^T at a bootstrap

Table 2. Comparison of cellular fatty acid compositions of strain DF-42^T and some other *Photobacterium* species

Species/strains: 1, *P. lutimaris* sp. nov. DF-42^T; 2, *P. rosenbergii* (data from Thompson *et al.*, 2005); 3, *P. lipolyticum* M37^T (Yoon *et al.*, 2005); 4, *P. ganghwense* KCTC 12328^T (Park *et al.*, 2006); 5, *P. halotolerans* LMG 22194^T (Rivas *et al.*, 2006). Values are percentage of total fatty acids. –, Not detected or not described. ECL, Equivalent chain-length.

Fatty acid	1	2	3	4	5
Straight-chain fatty acids					
C _{12:0}	2.4	2	–	3.4	5.9
C _{14:0}	2.4	3–4	3.8	3.6	1.0
C _{15:0}	2.1	1–2	–	–	–
C _{16:0}	13.1	10–15	25.9	21.1	21.2
C _{17:0}	–	1	–	–	–
Branched fatty acids					
iso-C _{13:0}	–	1	–	–	–
iso-C _{15:0}	5.0	2–4	–	–	–
iso-C _{17:0}	1.8	3–6	–	–	–
iso-C _{17:1} ω ₉ c	1.8	1–2	–	–	–
iso-C _{16:0}	–	–	–	–	1.0
Unsaturated fatty acids					
C _{16:1} ω ₉ c	–	–	–	–	2.5
C _{17:1} ω ₈ c	–	1	–	–	–
C _{18:1} ω ₇ c	13.0	17–19	5.9	29.6	19.9
C _{16:1} ω ₇ c alcohol	1.2	1	–	–	–
Hydroxy fatty acids					
C _{12:0} 3-OH	2.6	2–3	4.0	2.1	6.6
iso-C _{15:0} 3-OH	–	1	–	–	–
Unknown ECL 12.484	–	–	–	–	1.0
Summed features*					
2	3.0	2–3	–	2.7	3.0
3	43.3	41–44	51.3	27.8	32.6

*Summed features represent groups of two or three fatty acids that could not be separated by GLC with the MIDI system. Summed feature 2 contained C_{14:0} 3-OH, iso-C_{16:1} I, an unidentified fatty acid with an equivalent chain-length of 10.928 and/or C_{12:0} ALDE. Summed feature 3 contained C_{16:1}ω₇c and/or iso-C_{15:0} 2-OH.

resampling value of 97.6% (Fig. 1). Strain DF-42^T exhibited 16S rRNA gene sequence similarity values of 97.9% to *P. rosenbergii* LMG 22223^T and 93.8–96.0% with respect to the type strains of the other *Photobacterium* species (Fig. 1). The mean DNA–DNA relatedness level between strain DF-42^T and *P. rosenbergii* LMG 22223^T was 21.6% when their DNAs were used individually as labelled DNA probes for cross-hybridization. The results obtained from chemotaxonomic analyses were consistent with the phylogenetic affiliation of strain DF-42^T to the genus *Photobacterium*. Strain DF-42^T contained Q-8 as the predominant ubiquinone at a peak area ratio of approximately 90%. The cellular fatty acid profile of strain DF-42^T is shown in Table 2, together with those of phylogenetically related *Photobacterium* species. The fatty acid profile was characterized by the presence of

large amounts of straight-chain, branched, unsaturated and hydroxy fatty acids; the major components were C_{16:0}, C_{18:1}ω7c and summed feature 3 (C_{16:1}ω7c and/or iso-C_{15:0} 2-OH). This fatty acid profile is similar to those of other *Photobacterium* species, although there were differences in the proportions of some fatty acids (Table 2). Some fatty acids that were detected in amounts of more than 1 % in *P. rosenbergii* strains, including C_{17:0}, iso-C_{13:0}, C_{17:1}ω8c and iso-C_{15:0} 3-OH, were not found in strain DF-42^T.

Strain DF-42^T was distinguished from other *Photobacterium* species by differences in some phenotypic properties, as shown in Table 1. Particularly, strain DF-42^T differed from its closest phylogenetic neighbour, *P. rosenbergii*, in several phenotypic properties, including growth at 4 °C, indole production, β-galactosidase activity, utilization of some substrates and acid production from some substrates. The phylogenetic distinctiveness and DNA–DNA relatedness data, together with differential phenotypic properties, show that strain DF-42^T is distinct from recognized *Photobacterium* species (Wayne *et al.*, 1987; Stackebrandt & Goebel, 1994). Therefore, on the basis of the data presented, strain DF-42^T should be classified in the genus *Photobacterium* as the type strain of a novel species, for which the name *Photobacterium lutimaris* sp. nov. is proposed.

Description of *Photobacterium lutimaris* sp. nov.

Photobacterium lutimaris (lu.ti.ma'ris. L. n. *lutum* mud; L. gen. n. *maris* of the sea; N.L. gen. n. *lutimaris* of mud of the sea).

Cells are Gram-negative, oval-shaped and 0.9–1.3 × 1.5–2.1 µm. Motile by means of a single polar flagellum. Colonies on MA are circular to slightly irregular, flat, smooth, glistening, pale yellow in colour and 2.0–4.0 mm in diameter after 3 days incubation at 30 °C. Not bioluminescent. Growth occurs under anaerobic conditions on MA and on MA with nitrate. Growth occurs at 4 and 41 °C with an optimum temperature of 25–30 °C. Optimal pH for growth is 7.5–8.5; growth occurs weakly at pH 5.0, but not at pH 4.5. Optimal growth occurs in the presence of 2–3 % (w/v) NaCl; growth occurs in the presence of 6 % (w/v) NaCl, but no growth occurs without NaCl or in the presence of >7 % NaCl. Aesculin, starch and Tweens 20, 40, 60 and 80 are hydrolysed. Tyrosine is hydrolysed weakly. Urea, hypoxanthine, xanthine and casein are not hydrolysed. Ornithine decarboxylase and tryptophan deaminase are absent. Using the API ZYM system (bioMérieux), alkaline phosphatase, esterase (C4), esterase lipase (C8), leucine arylamidase, cystine arylamidase, acid phosphatase and naphthol-AS-BI-phosphohydrolase are present, but lipase (C14), valine arylamidase, trypsin, α-chymotrypsin, α-galactosidase, β-glucuronidase, α-glucosidase, β-glucosidase, N-acetyl-β-glucosaminidase, α-mannosidase and α-fucosidase are absent. D-Glucose, D-xylose, citrate, succinate, L-malate, salicin and pyruvate are utilized as sole carbon and energy sources, but benzoate is not. Acid is produced from *myo*-inositol, D-xylose, D-ribose, D-fructose

and D-cellobiose, but not from D-melezitose, D-glucose, D-galactose, D-mannose, lactose, maltose, D-trehalose or D-raffinose. Susceptible to polymyxin B, streptomycin, penicillin G, chloramphenicol, ampicillin, cephalothin, gentamicin, novobiocin, kanamycin, lincomycin, neomycin and carbenicillin, but not to oleandomycin or tetracycline. The major cellular fatty acids are C_{16:0}, C_{18:1}ω7c and summed feature 3 (C_{16:1}ω7c and/or iso-C_{15:0} 2-OH). The predominant ubiquinone is Q-8. The DNA G + C content of the type strain is 48.3 mol%.

The type strain, DF-42^T (=KCTC 12723^T=JCM 13586^T), was isolated from a tidal flat sediment at Saemankum, Korea.

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