Photobacterium

Beijerinck 1889[AL]

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Pho.to.bac.te'ri.um. Gr. neut. n. *phôs*, light; Gr. neut. dim. n. *bakterion*, a small rod; N.L. neut. n. *Photobacterium*, light (-producing) bacterium.

The genus *Photobacterium* contains 37 species with validated names and 3 species whose names have not been validated. Cells are short bacilli Gram-stain negative, and nonsporulated. Facultatively anaerobic. Require NaCl for growth (optimal concentration 1 – 3%). Several species present bioluminescence. Some of them are piezophilic and others are psychrophilic. Isolated from marine environment (seawater and sediment), associated with aquatic animals (mutualism relationships), but some are pathogens for poikilothermic and homeothermic animals.

DNA G + C content (mol%): 38.5 – 53.6.

Type species: **Photobacterium phosphoreum** Beijerinck 1889[AL] (basonym: *Micrococcus phosphoreus* Cohn 1878).

Straight rods, **0.4– 2.0 × 1.0– 6.0 μm,** some coccobacilli. **Gram-negative staining, nonendospore-forming**. **Motile by unsheathed polar flagella**, excepting *P. proteolyticum* that present peritrichous flagella, and *P. damselae* subsp. *piscicida and P. carnosum* that are not motile. **Facultatively anaerobic**, but *P. salinisoli* and *P. arenosum* are aerobic. Chemoorganotrophic, possesses **both respiratory and fermentative types of metabolism**. Optimal growth temperature range appears to be 15 – 30°C, except for the psychrophilic species *P. profundum*. **Sodium ions are required for growth**. Nitrate is reduced to nitrite, excepting for *P. angustum*, *P. salinisoli*, and *P. arenosum*. D-Glucose is usually fermented with the production of acid and, in several species, with gas. **Acetoin production (Voges– Proskauer test) is positive.** Oxidase, catalase, lysine decarboxylase, and arginine dihydrolase activities are variable (Table 1). **Ornithine decarboxylase and tryptophan deaminase activities are negative**. **Negative for the production of H_2S**, except *P. indicum*. Several species accumulate poly-β-hydroxybutyrate (PHB) in the early stationary phase of growth. Most species **grow in a minimal medium containing a seawater base, D-glucose, NH_4, or L-methionine**. D-Glucose, D-fructose, glycerol, and D-mannose are usually utilized as sole carbon and energy sources, **but no species utilize D-alanine**. Some species are bioluminescent (Table 1). **Ubiquinone Q-8 represents the predominant isoprenoid quinone**. **All the species are susceptible to O/129 vibriostatic agent.**

DNA G + C content (mol%): 38.5 – 53.6 (Table 1).

Type species: **Photobacterium phosphoreum** Beijerinck 1889[AL] (basonym: *Micrococcus phosphoreus* Cohn 1878).

Number of species with validly published names: 37.

Number of other species: 3.

Family classification: The genus *Photobacterium* is classified within the family *Vibrionaceae*.

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Further descriptive information

Cell morphology and ultrastructure

Photobacterium spp. display morphologic characteristics typical of members of the *Vibrionaceae*, appearing as straight

TABLE 1. Differential characteristics of species of *Photobacterium* (including subspecies of *P. damselae*)

Characteristic	*P. phosphoreum*	*P. leiognathi*	*"P. mandapamensis"*	*P. angustum*	*P. damselae* subsp. *damselae*	*P. damselae* subsp. *piscicida*	*P. iliopiscarium*	*P. profundum*	*P. indicum*	*P. aplysiae*
Luminescence	+	+	+	v	–	–	–	–	–	–
Oxidase	–	–	–	+	+	+	–	+	–	+
Catalase	+	–	+	nd	+	+	+	+	–	+
LDC	–	–	+	–	–	–	+	–	–	nd
ADH	–	–	+	–	+	+	+	+	+	+
Gelatinase	–	–	–	nd	–	–	–	nd	–	+
Acids from										
D-glucose	+	+	+	–	+	+	+	+	+	+
D-fructose	nd	+	+	nd	nd	+	nd	nd	nd	nd
D-galactose	+	+	+	+	nd	+	+	nd	nd	nd
D-lactose	–	–	–	–	–	nd	–	nd	nd	nd
D-cellobiose	–	–	–	–	nd	–	–	nd	nd	nd
D-melibiose	nd	–	nd	–	+	–	–	–	–	nd
D-trehalose	–	–	–	–	–	nd	w	nd	nd	nd
D-mannose	+	+	+	+	+	+	+	nd	nd	nd
D-xylose	–	–	–	nd	nd	–	nd	nd	nd	nd
D-maltose	+	nd	–	nd	nd	–	nd	nd	+	nd
D-mannitol	–	–	–	–	–	–	–	+	nd	nd
L-rhamnose	–	–	–	–	–	–	–	–	nd	nd
L-arabinose	–	–	–	–	–	+	–	–	–	nd
m-inositol	–	–	–	–	nd	nd	nd	nd	–	nd
Sucrose	–	–	–	+	–	w	–	–	+	nd
Raffinose	–	–	–	–	nd	nd	nd	nd	nd	nd
Amygdalin	nd	nd	nd	nd	nd	nd	nd	nd	–	nd
Optimum growth temperature (°C)	15 – 22	30	nd	20 – 25	18 – 20	25	20	8–12	25	25
G + C content (mol%)[a]	39.6	40.9	42.0	39.5	40.6 – 41.4	41.1 – 41.3	38.9	41.4	41.5	*45.0*

TABLE 1. (*continued*)

Characteristic	*P. frigidiphilum*	*P. lipolyticum*	*P. rosenbergii*	*P. ganghwense*	*P. halotolerans*	*P. kishitanii*	*P. lutimaris*	*P. aquimaris*	*P. gaetbulicola*	*P. jeanii*
Luminescence	–	–	–	+	–	+	–	+	–	–
Oxidase	+	+	nd	+	+	–	+	–	+	+
Catalase	+	+	+	+	+	+	–	+	+	+
LDC	nd	–	–	–	–	+	nd	–	–	–
ADH	+	–	+	+	–	+	+	–	–	+
Gelatinase	+	–	–	+	+	–	–	–	–	+
Acids from										
D-glucose	+	+	+	+	+	w	–	–	+	+
D-fructose	nd	+	nd	nd	nd	nd	+	nd	nd	nd
D-galactose	nd	–	+	+	+	+	–	+	+	nd
D-lactose	nd	–	+	–	+	–	–	–	+	nd
D-cellobiose	nd	+	+	+	–	–	+	–	+	nd
D-melibiose	nd	–	+	–	–	–	–	–	+	+
D-trehalose	+	+	+	+	+	–	–	–	+	nd
D-mannose	+	+	+	–	–	+	–	+	+	nd
D-xylose	nd	nd	–	–	+	nd	+	nd	–	nd
D-maltose	nd	+	+	+	+	nd	–	nd	+	nd
D-mannitol	+	–	+	+	+	–	–	–	+	–
L-rhamnose	nd	–	+	+	–	–	–	nd	–	–
L-arabinose	+	–	–	–	+	–	–	–	–	–
m-inositol	nd	–	+	+	–	–	+	nd	+	–
Sucrose	+	+	+	–	+	–	+	–	+	+
Raffinose	nd	–	–	–	–	nd	–	nd	+	nd
Amygdalin	nd	nd	+	+	–	–	+	nd	nd	–
Optimum growth temperature (°C)	14	25 – 28	20 – 30	35	28	15 – 20	25 – 30	10 – 25	30	20 – 35
G + C content (mol%) [a]	41.6	45.9	47.6	50.5	50.9	39.0	47.6	39.3	49.7	45.1

TABLE 1. (*continued*)

Characteristic	*P. aphoticum*	*"P. atrarenae"*	*P. swingsii*	*"P. marinum"*	*P. aestuarii*	*P. aquae*	*P. panuliri*	*P. piscicola*	*P. sanctipauli*	*P. galatheae*
Luminescence	–	nd	nd	–	–	–	–	+	nd	nd
Oxidase	+	+	+	+	+	+	+	–	+	+
Catalase	+	+	+	–	+	+	+	+	+	nd
LDC	nd	nd	–	+	nd	–	–	+	–	nd
ADH	+	–	+	+	+	nd	+	+	+	–
Gelatinase	–	nd	–	nd	+	+	nd	–	–	+
Acids from										
D-glucose	+	+	nd	+	+	+	+	+	+	+
D-fructose	+	+	nd	nd	nd	nd	+	nd	nd	–
D-galactose	+	nd	nd	nd	nd	nd	–	+	nd	nd
D-lactose	nd	nd	nd	nd	nd	nd	–	–	nd	nd
D-cellobiose	–	nd	nd	nd	nd	nd	–	–	nd	nd
D-melibiose	+	nd	nd	nd	nd	nd	–	–	nd	nd
D-trehalose	nd	+	nd	nd	nd	nd	–	+	nd	+
D-mannose	+	nd	nd	nd	nd	nd	+	+	nd	–
D-xylose	+	nd	nd	nd	nd	nd	–	nd	nd	+
D-maltose	+	+	nd	nd	nd	nd	+	nd	nd	–
D-mannitol	+	nd	nd	nd	+	–	–	–	+	+
L-rhamnose	–	nd	nd	nd	nd	–	–	–	–	nd
L-arabinose	–	nd	nd	nd	+	–	–	–	–	nd
m-inositol	–	+	nd	nd	nd	–	–	–	–	nd
Sucrose	–	nd	nd	nd	+	–	–	–	–	+
Raffinose	nd	nd	nd	nd	nd	nd	–	–	nd	nd
Amygdalin	nd	nd	nd	nd	nd	–	–	–	–	nd
Optimum growth temperature (°C)	20 – 30	37	20 – 30	30 – 37	20	30 – 35	28	20	20 – 30	20 – 30
G + C content (mol%) [a]	49.7	*53.6*	43.7	46.2	*44.2*	49.1	*50.5*	39.2	47.9	49.5

TABLE 1. (*continued*)

Characteristic	*P. sanguinicancri*	*P. alginatilyticum*	*P. proteolyticum*	*P. toruni*	*P. andalusiense*	*P. carnosum*	*P. malacitanum*	*P. chitinilyticum*	*P. salinisoli*	*P. lucens*	*P. arenosum*
Luminescence	–	–	–	–	–	–	–	–	–	+	–
Oxidase	+	+	+	+	+	v	+	+	–	+	+
Catalase	+	+	–	+	+	v	+	+	+	+	–
LDC	–	–	nd	+	+	nd	+	–	nd	+	nd
ADH	+	+	nd	+	+	nd	+	+	–	+	–
Gelatinase	+	+	+	–	–	nd	–	+	–	–	–
Acids from											
D-glucose	nd	+	nd	+	+	+	+	+	+	+	+
D-fructose	nd	nd	nd	+	nd	+	nd	nd	+	+	+
D-galactose	nd	nd	–	+	nd	+	nd	nd	nd	+	nd
D-lactose	nd	+	nd	nd	nd	nd	nd	nd	nd	nd	nd
D-cellobiose	nd	nd	+	–	–	nd	–	nd	nd	–	nd
D-melibiose	nd	nd	–	–	–	nd	–	nd	nd	–	nd
D-trehalose	nd	nd	nd	–	–	nd	–	nd	+	–	+
D-mannose	nd	nd	nd	+	nd	+	nd	nd	–	+	nd
D-xylose	nd	nd	nd	nd	nd	nd	nd	nd	+	nd	nd
D-maltose	nd	nd	nd	+	+	+	+	nd	+	–	+
D-mannitol	nd	+	–	–	–	nd	–	+	+	–	+
L-rhamnose	nd	nd	nd	–	–	nd	–	nd	nd	–	nd
L-arabinose	nd	nd	nd	–	–	nd	–	nd	–	–	nd
m-inositol	nd	+	nd	–	–	nd	–	nd	nd	–	nd
Sucrose	nd	+	nd	–	–	nd	–	+	+	nd	nd
Raffinose	nd	nd	–	nd	nd	nd	nd	nd	nd	nd	nd
Amygdalin	nd	+	nd	nd	nd	nd	nd	+	nd	nd	nd
Optimum growth temperature (°C)	20	32	28	20	18 – 22	15	22 – 30	24	25	30	25 – 30
G + C content (mol%) [a]	43.7 – 43.9	48	47.9	38.6	39.3	38.5	39.7	46.45	50.2	41.4	50.1

LDC, lysine decarboxylase; ADH, arginine dihydrolase; v, variable; nd, not determined; w, weak.
[a]DNA G + C content (mol%) genome determination, when data are in italic is based on wet-lab determination (detailed on list of species of *Photobacterium*).

rods; but several species of *Photobacterium* appear as coccobacilli or short rods. Except for *P. damselae* subsp. *piscicida* and *P. carnosum*, all *Photobacterium* species are motile usually by means of one or more unsheathed flagella. Cells are approximately 0.4– 2.0 µm wide and 1.0 – 6.0 µm long.

Colonial and cultural characteristics

The initial isolation from seawater, sediment, or animal tissues on agar media may take 3 – 7 days. The incubation period on agar media of subcultures usually is 18 – 24 h. On Marine agar (MA), colonies are usually small, circular, smooth, convex, translucents with different colors, and nonswarming (see List of species for details). When grown on TCBS agar, colonies are round, 1 – 7 mm after 24 h incubation, and with green and yellow pigmentation. Some species show luminous colonies, such as *P. aquimaris* and *P. kishitanii*, and other present colonial diffusible pigments (*P. aphoticum* and *P. panuliri*).

Nutrition and growth conditions

Species are facultatively anaerobic, except *P. salinisoli* and *P. arenosum*. The temperature ranges for growth are 4 – 40°C with optimum for most species being 18 – 30°C (Table 1), but *P. profundum*, *P. frigidiphilum*, *P. kishitanii*, and *P. carnosum* are moderately psychrophiles (optimal temperature lower than 15°C). *Photobacterium* species are unable to grow in the absence of Na^+ (optimal growth, 160 – 280 mM Na^+). The genus includes the halophilic species *P. halotolerans*. Members of the genus grow at pH 5.0 – 10.5, with optima at pH 7.0 – 8.0. Most *Photobacterium* species have no organic growth factor requirement; some of them, however, require L-methionine, either alone or in combination with other amino acids. Usually, glucose is utilized as the sole carbon source. PHB is only formed when cells are grown in a basal medium with glucose as the sole carbon source, but it is not formed in rich culture media.

The nutritional versatility of *Photobacterium* species is wide, utilizing many compounds (sugars, amino acids, organic acids, and cycle intermediates) as sole sources of carbon and energy. The most utilized compounds being D-maltose, *N*-acetyl-D-glucosamine, α-D-glucose, D-mannose, D-fructose, D-mannitol, glycerol, inosine, L-alanine, L-serine, methyl pyruvate, DL-lactic acid, and succinic acid. On the contrary, none of the species utilize stachyose, D-raffinose, 3-methyl glucose, D-fucose, D-aspartic acid, L-arginine, L-pyroglutamic acid, L-galactonic acid lactone, mucic acid, quinic acid, D-saccharic acid, and D-malic acid. Gentiobiose, D-turanose, β-methyl-D-glucoside, L-fucose, glucuronamide, and acetoacetic acid are used only for *P. chitinilyticum*. *N*-Acetyl-neuraminic acid, D-galacturonic acid, and D-lactic acid methyl ester are used exclusively for *P. proteolyticum*. Furthermore, *P. alginatilyticum* is the only species that utilizes *i*-erythrirol, D-arabitol, and 2,3-butanediol.

Chemotaxonomic characteristics

The major cellular fatty acid profiles of *Photobacterium* species are $C_{16:0}$, $C_{16:1}$, and $C_{18:1}$ (see Table 2 for details). Q-8 is the predominant isoprenoid quinone in *Photobacterium* species, although in some of them, Q-7 is present. The polar lipids have been investigated only in several species ("*P. marinum*," *P. aquae*, *P. panuliri*, *P. alginatilyticum*, *P. proteolyticum*, *P.chitinilyticum*, *P. salinisoli*, and *P. arenosum*), being phosphatidylethanolamine, phosphatidylglycerol, and phosphatidylglycerol the most predominant in the tested species.

Genome features

The *Photobacterium* genomes size, according to Type (Strain) Genome Server (TYGS) (https://tygs.dsmz.de) (Meier-Kolthoff and Göker, 2019), ranged from 4.2 to 6.4 Mb with the smallest being *P. iliopiscarium* (4.262.179 bp) and the largest being *P. proteolyticum* (6.484.429 bp), similar to other *Vibrionaceae* family members (Thompson et al., 2009; Machado and Gram, 2017). The genomic data available in public databases corresponds to 35 out of 40 species, with no data available for *P. aestuarii*, *P. aplysiae*, "*P. atrarenae*," *P. panuliri*, and *P. salinisoli*. The GC content of the genomes of validated species (TYGS values) varied between 38.5 and 50.9, with the lowest and highest being *P. carnosum* and *P. halotolerans*, respectively. On the basis of GC content, the *Photobacterium* species may be clustered in three ranges: species with GC content lower than 43 mol% (16 species with range 38.5 – 41.6), species with GC content between 43.1 and 47.0 mol% (6 species with range 43.7 – 46.5); and species with GC content higher than 47.1 mol% (13 species with range 47.6 – 50.9). These ranges correlate with phylogenetic tree of the 16S rRNA gene (Figure 1).

Photobacterium genome architecture is characteristic of members of *Vibrionaceae*, presenting larger and smaller chromosomes (chromosome 1 and chromosome 2, respectively) and plasmids of different sizes based on the information of fully closed genomes available (*P. damselae* strains: 9046-81, Phdp Wu-1, RM-71, KC-Na.1, KC-Na-NB1, KC-DI-1, AS-16-0555-7, 91-197, and AS-16-0540-1; *P. damselae* plasmids: plas1, pPHDD1, pPDD-Na-1 with 4 replicons, pFPPDNB1 with 5 replicons, pPDD_KC-DI-1, pPHDP10,

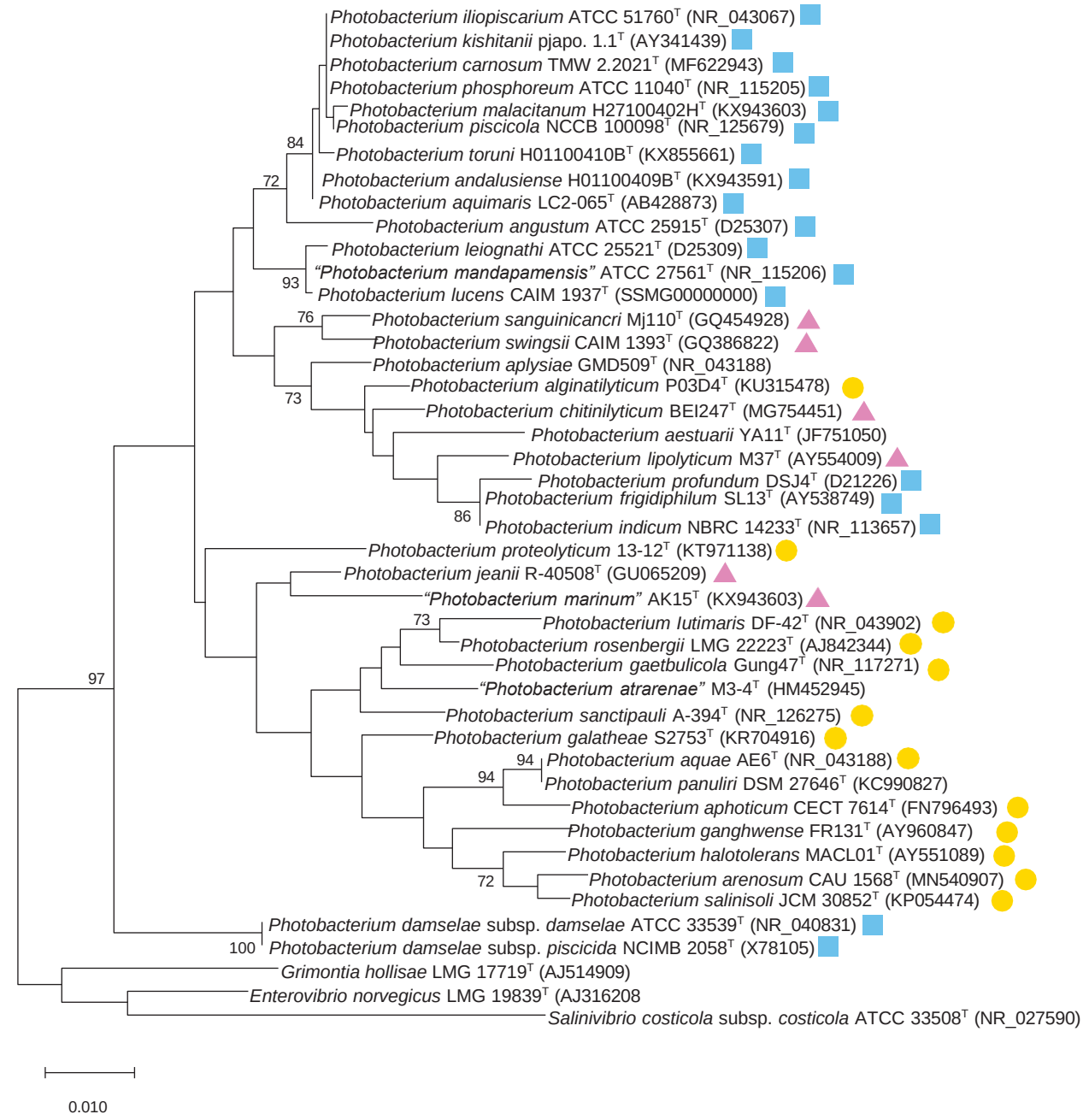
TABLE 2. Fatty acids and drug responses of species of *Photobacterium* (including subspecies of *P. damselae*)

Species	Major fatty acids profiles (>10%)	Resistance to	Sensitivity to
P. phosphoreum	$C_{16:1}$ ω7*c*/$C_{16:1}$ ω6*c*; $C_{18:1}$ ω7*c*/$C_{18:1}$ ω6*c*; $C_{14:0}$; $C_{12:0}$	S-P-CM	SXT-TE-AM-ENR-NA-FLM-OA-PB-C-E-S-OFX
P. leiognathi	$C_{16:1}$; $C_{16:0}$; $C_{18:0}$; $C_{12:0}$; $C_{14:0}$; $C_{12:0}$ 3-OH	P-AMX	C-K-TE-E-NB-F-PB-SXT-AM-FLM-GM-N
"P. mandapamensis"	nd	P	C-S-PB
P. angustum	$C_{16:1}$; $C_{16:0}$; $C_{18:1}$	nd	nd
P. damselae subsp. *damselae*	$C_{16:1}$; $C_{16:0}$; $C_{18:1}$; $C_{12:0}$; $C_{12:0}$ 3-OH	S-E-AM-GM-AMX-P-NB-TE	C-ENR-SXT-FLM-F-NA-K-OA
P. damselae subsp. *piscicida*	$C_{16:1}$ ω7*c*; $C_{16:0}$; $C_{14:0}$	OX-S-E	AMX-SXT-AM-FLM-TE-GM-P
P. iliopiscarium	$C_{18:1}$ ω7*c*; $C_{16:0}$; $C_{16:1}$ ω7*c*/iso $C_{15:0}$ 2-OH	P-E-AM-CM	NB-C-SXT-TE-F-OFX-NA-S-RA-GM-K
P. profundum	$C_{16:1}$; iso $C_{16:0}$; $C_{16:0}$; $C_{20:5}$ ω3*c*	nd	nd
P. indicum	$C_{16:1}$ ω7*c*/$C_{16:1}$ ω6*c*; $C_{16:0}$	E-TE-P	N-K-NB-S
P. aplysiae	$C_{16:1}$; $C_{16:0}$; $C_{18:1}$	nd	nd
P. frigidiphilum	$C_{16:1}$ ω7*c*/$C_{16:1}$ ω6*c*; $C_{16:0}$	nd	nd
P. lipolyticum	$C_{16:1}$ ω7*c*/iso $C_{15:0}$ 2-OH; $C_{16:0}$	nd	nd
P. rosenbergii	$C_{16:1}$ ω7*c*/iso $C_{15:0}$ 2-OH; $C_{18:1}$ ω7*c*; $C_{16:0}$	AM-CF-L-NB-E-OX	PB-P-K-SXT-CB-S
P. ganghwense	$C_{16:1}$ ω7*c*/iso $C_{15:0}$ 2-OH; $C_{16:0}$; $C_{18:1}$ ω7*c*	CB-K-PB	AM-CF-L-NB-P
P. halotolerans	$C_{16:1}$ ω7*c*/iso $C_{15:0}$ 2-OH; $C_{16:0}$; $C_{18:1}$ ω7*c*	SXT-E-AM	CB-P-CF-K-L-NB-PB
P. kishitanii	$C_{16:1}$ ω7*c*/iso $C_{15:0}$ 2-OH; $C_{16:0}$	nd	nd
P. lutimaris	$C_{16:1}$ ω7*c*/iso $C_{15:0}$ 2-OH; $C_{16:0}$; $C_{18:1}$ ω7*c*	TE-OL	AM-CB-CF-K-L-NB-N-P-PB-SXT-E-S-C-GM
P. aquimaris	$C_{16:1}$ ω7*c*/iso $C_{15:0}$ 2-OH; $C_{16:0}$; $C_{18:0}$	AM- S	SXT- TE-ENR-NA-FLM-OA
P. gaetbulicola	$C_{16:1}$ ω7*c*/iso $C_{15:0}$ 2-OH; $C_{16:0}$; $C_{18:1}$ ω7*c*	AM-CF-L-NB-PB	CB-P
P. jeanii	$C_{16:1}$ ω7*c*/iso $C_{15:0}$ 2-OH; $C_{16:0}$; $C_{18:1}$ ω7*c*/$C_{18:1}$ ω6*c*	nd	nd
P. aphoticum	$C_{16:1}$ ω7*c*/$C_{16:1}$ ω6*c*; $C_{18:1}$ ω7*c*/$C_{18:1}$ ω6*c*	OX-P	SXT-S-E-AM
"P. atrarenae"	$C_{16:1}$ ω7*c*/iso $C_{15:0}$ 2-OH; $C_{16:0}$; $C_{18:1}$ ω7*c*	TE-VA	AM-CB-C-E-K-L-NA-N-SXT
P. swingsii	nd	nd	nd
"P. marinum"	$C_{16:0}$; $C_{16:1}$ ω7*c*/iso $C_{15:0}$ 2-OH; $C_{18:1}$ ω7*c*	AMX-AM-G-F-FLM-SXT-TM	B-K-ME-P-VA
P. aestuarii	$C_{16:1}$ ω7*c*/$C_{16:1}$ ω6*c*; $C_{18:0}$	K-OL	AM-L-C-P-S-TE
P. aquae	$C_{16:1}$ ω7*c*/$C_{16:1}$ ω6*c*; $C_{18:1}$ ω7*c*; $C_{16:0}$	OX-P-CM	E-C-GM-SXT-S-AM
P. panuliri	$C_{16:1}$ ω7*c*/$C_{16:1}$ ω6*c*; $C_{16:0}$; $C_{18:1}$ ω7*c*/$C_{18:1}$ ω6*c*; iso $C_{15:0}$; iso $C_{17:0}$	AM-S	SXT-E
P. piscicola	$C_{16:1}$ ω7*c*/iso $C_{15:0}$ 2-OH; $C_{16:0}$; $C_{18:1}$ ω7*c*	AM-S- ENR-NA-FLM-OA	SXT-TE
P. sanctipauli	$C_{16:1}$ ω7*c*/iso $C_{15:0}$ 2-OH; $C_{16:0}$; $C_{18:1}$ ω7*c*	nd	nd
P. galatheae	$C_{16:1}$ ω7*c*/$C_{16:1}$ ω6*c*; $C_{18:1}$ ω7*c*/$C_{18:1}$ ω6*c*	P	C-E-Te
P. sanguinicancri	$C_{16:1}$ ω7*c*/$C_{16:1}$ ω6*c*; $C_{18:1}$ ω7*c*/$C_{18:1}$ ω6*c*	nd	nd
P. alginatilyticum	$C_{16:1}$ ω7*c*/iso $C_{15:0}$ 2-OH; $C_{16:0}$	nd	nd
P. proteolyticum	$C_{16:1}$ ω7*c*/iso $C_{15:0}$ 2-OH; $C_{16:0}$; $C_{18:1}$ ω7*c*	L-TE-VA	C-E-K-NA-N-OFX-P-S-RA-TM-SXT-GM
P. toruni	$C_{16:1}$ ω7*c*/$C_{16:1}$ ω6*c*; $C_{16:0}$	E-S	SXT-TE-AM-ENR-NA-FLM-OA
P. andalusiense	$C_{16:1}$ ω7*c*/$C_{16:1}$ ω6*c*; $C_{16:0}$; $C_{18:1}$ ω6*c*	AM-E-S	SXT-TE- ENR-NA-FLM-OA
P. carnosum	$C_{16:1}$ ω7*c*/iso $C_{15:0}$ 2-OH; $C_{16:0}$; $C_{18:1}$ ω7*c*; $C_{12:1}$ aldehyde and $C_{10:928}$ unknown	CM-P	OFX-NA-AM-SXT-S-RA-GM-K-E-TE
P. malacitanum	$C_{16:1}$ ω7*c*/$C_{16:1}$ ω6*c*; $C_{18:1}$ ω6*c*	AM-E-S-ENR-NA-FLM-OA	SXT-TE
P. chitinilyticum	$C_{16:1}$ ω7*c*/$C_{16:1}$ ω6*c*; $C_{16:0}$	nd	nd
P. salinisoli	$C_{16:1}$ ω7*c*/$C_{16:1}$ ω6*c*; $C_{16:0}$; $C_{18:1}$ ω7*c*/$C_{18:1}$ ω6*c*	nd	nd
P. lucens	nd	nd	nd
P. arenosum	$C_{16:0}$; $C_{16:1}$ ω7*c*/$C_{16:1}$ ω6*c*; $C_{18:1}$ ω7*c*/$C_{18:1}$ ω6*c*	nd	nd

nd, not determined.

AM, ampicillin; AMX, amoxicillin; B, bacitracin; C, chloramphenicol; CB, carbenicillin; CF, cefalotin; CM, clindamycin; E, erythromycin; ENR, enrofloxacin; F, nitrofurantoin; FLM, flumequine; GM, gentamicin; K, kanamycin; L, lincomycin; ME, methicillin; N, neomycin; NA, nalidixic acid; NB, novobiocin; OA, oxolinic acid; OFX, ofloxacin; OL, oleandomycin; OX, oxacillin; P, penicillin G; PB, polymixin B; RA, rifampin; S, streptomycin; SXT, trimethoprim/sulfamethoxazole; TE, tetracycline; TM, tobramycin; VA, vancomycin.

FIGURE 1. Phylogenetic tree of *Photobacterium* based on 16S rRNA gene sequences of all species described (as of January 2022) using the Maximum Likelihood method and Jukes-Cantor model to infer the evolutionary history of this bacterial genus (Jukes and Cantor, 1969; Kumar et al., 2018). *Grimontia hollisae*, *Enterovibrio norvegicus*, and *Salinivibrio costicola* type strain sequences have been added as an outgroup. Sequence accession numbers are given in parentheses. Bootstrap values greater than 70% are shown at branching points (percentage of 1,000 resamplings). Bar indicates number of substitutions per position. DNA G + C (mol%) content range values according to TYGS: blue squares 38.5 – 41.6; pink triangles 43.7 – 46.5; yellow circles 47.6 – 50.9.



pPHDP70, p91-197 with 2 replicons; *P. gaetbulicola* Gung47; *P. ganghwense* C2.2. with plasmid pPGC22; *P. profundum* SS9 with plasmid pPBPR1), being the chromosome 1 more conserved between species than chromosome 2 and plasmids (Machado and Gram, 2017). Core genes are mainly located in the larger chromosome; nonetheless, essential genes are also present in the smaller one, which ensures retention of the small chromosome during cell division, in addition to a predominance of lineage-specific genes. The smaller chromosome and plasmids are highly variable and seem to be responsible for the genetic plasticity of *Photobacterium* species (Egan et al., 2005; Reen et al., 2006; Urbanczyk et al., 2011).

The genomic diversity of *Photobacterium* genus is very high (approximately only 25% of the genes conserved in all strains), with features such as genome size and GC content seem to be associated with different lifestyles adopted by *Photobacterium* species reflected in their ability to colonize different environmental niches (Konstantinidis et al., 2009; Machado and Gram, 2017). However, the distribution of several genetic features, such as virulence factors, bioluminescence determinants, histamine production, secondary metabolism, and CRISPR-Cas operons among *Photobacterium* species appear have do not correlate with their phylogeny. Genomic exchange through prophage infection, presence of genomic islands, and genes coding for transposases are the main driving force for genomic evolution of this genus (Machado and Gram, 2017). In addition, *Photobacterium* genomes often contain plasmids coding for virulence factors (do Vale et al., 2005; Osorio et al., 2015; Rivas et al., 2015a, 2015b) and for drug resistance determinants and its transfer (Balado et al., 2013; Nonaka et al., 2015; Vences et al., 2020).

The genomes of *Photobacterium* species carry multiple rRNA operons with unequal distribution between the large and small chromosomes, and this seems to be related to a better adaptation for changing environmental conditions (Urbanczyk et al., 2011).

Drug resistance

All the species of the genus are sensitive to vibriostatic compound O/129 (2,4-diamino-6,7-diisopropyl-pteridine phosphate). Drug resistance has been reported for many species (Table 2), β-lactams resistance is the most frequently detected (72.2% of the species tested), followed by resistance to macrolides (38.9% of the species tested), and to aminoglycoside (33.3% of the species tested). On the contrary, the highest susceptibility of the species to antimicrobials is to trimethoprim-sulfamethoxazole (61.1% of the species tested) and chloramphenicol (44.4% of the species tested).

Ecology

The members of the genus *Photobacterium* thrive worldwide in oceans, excepting *P. carnosum* that has a terrestrial source (Hilgarth et al., 2018), and they show substantial ecophysiological diversity including free-living, symbiotic, piezophilic, and parasitic lifestyles. The habitats and isolation sources of the species include seawater, marine sediments, saline lake waters, and a variety of marine organisms in which the photobacteria may establish different relationship types, from symbiotic ones, such as commensalism or mutualism, to pathogenic interactions. In the marine environment (seawater and sediment), the species of *Photobacterium* usually are free-living forms, but they may colonize several animal surfaces or the gut of many marine organisms (Martini et al., 2013), developing neutral or negative relationships with the host. These nonspecific or pathogenic associations contrast with the highly specific, mutually beneficial association of certain *Photobacterium* species in bioluminescent symbiosis with aquatic animals (Dunlap, 2009).

There is not a clear discrimination between the *Photobacterium* species regarding their relationship with the isolation source or habitat. Thus, most of the nonluminous photobacteria (lack of *lux* operon genes) have been isolated from marine waters, sediments or in association with diseased or healthy corals, zoanthids, sea hares, mollusks, crustaceans, and fish. Nevertheless, strains of luminous *Photobacterium* species harboring genes for luminescence (*luxCDABEG*) (Dunlap, 2014), have also been isolated from seawater and marine animals. Therefore, luminescence production is not a key to the specific colonization of habitats excepting the light-organs of squids and fish (Labella et al., 2017a). Moreover, an additional gene called *luxF* was also discovered in *lux* operon of some species, such as *P. phosphoreum*, *P. leiognathi*, "*P. mandapamensis*," the luminous strains of *P. angustum*, *P. ganghwense*, *P. kishitanii*, *P. aquimaris*, *P. piscicola*, and *P. lucens*. The *luxF* gene might take part in bioluminescence but is not necessarily required for light formation (Moi et al., 2017). In addition, *Photobacterium* contains additional genes, that is *ribEBHA*, which are involved in the synthesis of riboflavin (Lin et al., 2001). These bioluminescent species may establish symbiosis relationship with marine fish, mollusks, and crustaceans (Zarubin et al., 2012; Naguit et al., 2014), these associations being highly specific at the animal family-bacterial species level (Dunlap and Ast, 2005; Dunlap and Kita-Tsukamoto, 2006; Wada et al., 2006; Ast et al., 2007; Kaeding et al., 2007). The animals accumulate dense populations of luminous bacteria in gland-like tissue complexes called light organs (Dunlap et al., 2008), providing them with

nutrients and oxygen for their growth and light production. Although bioluminescent associations appear to be highly specific, in some cases two *Photobacterium* species may be present within individual light organs of fish (Kaeding et al., 2007), representing a phenomenon named co-symbiosis. Furthermore, different species of the same fish family sometimes harbor different *Photobacterium* species or even bacteria belonging to other bacterial genera, like *Aliivibrio* or *Vibrio* (Dunlap et al., 2008). In addition, distinct strains of a single species may be present with individual light organs of both adult and larval fish (Dunlap et al., 2008). This species- and strain-level variation demonstrates the lack of strict specificity in bioluminescent symbiosis. Some environmental factors, such as the temperature, influence the abundance of the different species of luminous bacteria in the marine environment. Thus, lower temperatures found in deeper waters favor the prevalence of psychrotrophic species such as *P. kishitanii*, which is the main light-organ symbiont in these waters. On the contrary, warmer waters favor the growth of mesophilic *Photobacterium* species, like *P. leiognathi*, and fish larvae in these waters are more receptive to acquire these bacteria as light-organ symbionts. Bioluminescent symbioses appear to represent a paradigm of symbiosis that differs fundamentally from associations involving obligate, intracellularly transferred symbionts (Urbanczyk et al., 2011). While fish and squids are dependent ecologically on luminous bacteria, the bacteria are not obligately dependent on their bioluminescent hosts. The evolutionary adaptations for bioluminescent symbiosis, for example presence of light organs, accessory tissues for controlling, diffusing, and shaping the emission of light, and behavior associated with light emission, all are borne by the animal. No-genetic adaptations have been identified in the bacteria that are necessary for and specific to their existence in light organs compared to the other habitats they colonize. Therefore, luminous bacteria seem to be opportunistic colonizers, able to persist in animal light-organs as well as in several other habitats to which they are adapted (Labella et al., 2017a).

Members of the genus *Photobacterium* are common inhabitants of ocean or marine sediments, including *P. phosphoreum*, *P. profundum*, *P. indicum*, *P. frigidiphilum*, *P. lipolyticum*, *P. lutimaris*, "*P. marinum*," *P. proteolyticum*, *P. chitinilyticum*, and *P. arenosum*. From them, *P. phosphoreum*, *P. profundum*, *P. indicum*, and *P. frigidiphilum* may be considered as piezophilic (formerly barophilic) bacteria, because these species possess enhanced growth at pressures above 1 atmosphere, by mean of several adaptation mechanisms (at high hydrostatic pressure, low temperatures, and low organic carbon) (Bartlett and Welch, 1995; Kato and Bartlett, 1997; Allen and Bartlett, 2000; Seo et al., 2005b). The adaptative traits include those related to growth, macromolecules and storage lipids, membrane and soluble proteins, the respiratory-chain compounds, replication, transcription, and translation (Yayanos, 1995; Nogi et al., 1998; Bartlett et al., 2008; Martini et al., 2013; Lauro et al., 2014). The proteins of these bacteria change under different pressure regimes; thus, proteins belonging to the glycolysis/glyconeogenesis pathways were up-regulated at high pressure, whereas several proteins involved in the oxidative phosphorylation pathway were up-regulated at atmospheric pressure (Le Bihan et al., 2013). In addition, the expression of some proteins involved in nutrient transport or assimilation was also directly regulated by pressure (El-Hajj et al., 2009; Tamburini et al., 2013).

Pathogenicity

Most species of *Photobacterium* are nonpathogenic. However, some nonluminous species including *P. rosenbergii*, *P. jeanii*, and *P. sanctipauli* have been reported to be isolated from several species of bleached and healthy corals. On the other hand, the two subspecies of *P. damselae*, *P. toruni*, *P. andalusiense*, and *P. malacitanum* have been reported to produce several pathologies on several hosts, mainly fish and mammals (Romalde, 2002; Yamane et al., 2004; Aigbivhalu and Maraqa, 2009; Labella et al., 2011, 2017b, 2018a, 2020; Rivas et al., 2013).

P. damselae subsp. *damselae* is considered a bacterial pathogen of humans and many aquatic organisms comprising fish, mollusks, crustaceans, reptiles, and other mammals (Rivas et al., 2013). The subspecies is capable of producing extracellular products (ECPs), which include several enzymatic activities involved in the bacterial colonization, invasiveness, and dissemination within its host (Labella et al., 2010). In addition, this subspecies also showed cytotoxin activity for several fish and mammalian cell lines. The main virulence factor detected in this subspecies is the damselysin (Dly), a thermostable phospholipase D extracellular cytotoxin that possesses a hemolytic function against several types of fish erythrocytes. This hemolytic activity may be harbored by the plasmid pPHDD1, which contains the genes *dly* and $hlyA_{pl}$, the last one encodes a small pore-forming toxin (PFT) with hemolysin activity, named phobalysin P (PhlyP) (Rivas et al., 2015a, 2015b). In addition, a chromosome-encoded HlyA ($HlyA_{ch}$) is present in all of the hemolytic *P. damselae* subsp. *damselae* strains. It has been described that $HlyA_{pl}$ is more active against sheep erythrocytes than $HlyA_{ch}$. Additive virulence effects were observed when the two hemolysins

were present. Moreover, synergistic effects against erythrocytes was observed by the interaction of Dly with any of the two HlyA, being responsible for maximum virulence for mice and fish (Rivas et al., 2013). The secretion of Dly, $HlyA_{pl}$, and $HlyA_{ch}$ is regulated by *epsL* (T2SS) and *pilD*, playing a major role in the virulence for mice (Rivas et al., 2015a). In addition, *P*. *damselae* subsp. *damselae* presents an iron-uptake system, the vibrioferrin-like which includes the production of iron-sequestering compounds named siderophores, as well as the use of heme group as an iron source. This heme uptake system includes a TonB-dependent outer membrane receptor (HutA) to transport the heme group into the periplasm. HutA contains a conserved phenylalanine residue at the C-terminal region involved in the incorporation of the protein into the outer membrane. The promoter region of *hutA* contains a putative binding site for the Fur protein (called Fur box) and is iron-regulated through the binding of the Fur repressor. A periplasmic binding protein and an ATP-binding cassette (ABC) (HutB) to drive heme across the cytoplasmic membrane are also present (Rio et al., 2005; Labella et al., 2017a; Puentes et al., 2017). In addition, citrate can be used by *Photobacterium damselae* subsp. *damselae* to facilitate iron uptake. FecB, a periplasmic transporter part of the ferric-citrate transport system, has been identified as a protein expressed under low iron conditions (Balado et al., 2017).

P. *damselae* subsp. *piscicida* is responsible for causing fish pasteurellosis or pseudotuberculosis, which is one of the most threatening bacterial diseases in marine culture worldwide (Romalde, 2002). Several virulence mechanisms of this subspecies have been illustrated, including the synthesis of a polysaccharide capsular material (Andreoni and Magnani, 2014); phospholipase, cytotoxic, and hemolytic activities of its ECPs (Elgendy et al., 2015); use of heme (Rio et al., 2005), secreted citrate (Balado et al., 2017), and a siderophore-based mechanism, named piscibactin (encoded by a pathogenicity island in the plasmid pPHDP70), for iron uptake (Osorio et al., 2015). FrpA is the outer membrane receptor of piscibactin (Osorio et al., 2006). HutA has also been identified in some strains of this subspecies (98% identity to the subspecies *P*. *damselae* subsp. *damseale*) and was suggested to constitute the heme receptor of *P*. *damselae* subsp. *piscicida*, although the complete gene was only found in four Japanese isolates. In other isolates, *hutA* pseudogene with a putative transposase downstream of the *hutA* stop codon has been described (Rio et al., 2005). Regarding the siderophore mechanism of *P*. *damselae* subsp. *piscicida*, a cluster of *irp* genes present in a pathogenicity island (PI) like structure has been implicated in piscibactin synthesis. This PI is related to the Yersinia HPI, which is found in several *Enterobacteriaceae* genera (Bach et al., 2000). This HPI-like cluster is contained in the plasmid pPHDP70, and its transmission relied on plasmid pPHDP60 that encodes a type IV secretion system (Osorio et al., 2015). Gene clusters homologous to pPHDP70 *irp* cluster are present in several species of *Vibrio*, but none is plasmid borne. Horizontal gene transfer of pPHDP70 has been described to a *V*. *alginolyticus* strain deficient in siderophore synthesis (Osorio et al., 2015). However, the major virulence factor of *P*. *damselae* subsp. *piscicida* is a plasmid-encoded apoptosis-inducing protein (AIP56) responsible for apoptogenic activity against fish phagocytes (do Vale et al., 2005). AIP56 is a type II secreted effector. The destruction of phagocytes contributes to severity of infections by facilitating survival and extracellular multiplication of the pathogen. In addition, the destruction of macrophages provokes the lysis of apoptotic cells and the release of cytotoxic intracellular compounds that cause tissue damage and lead to the genesis of the characteristic cytopathology of *P*. *damselae* subsp. *piscicida* (do Vale et al., 2017). Recently, it has been described that Hsp90 and cyclophilin A/D are involved in macrophage intoxications by the toxin AIP56 (Rodrigues et al., 2019).

In the case of the other three fish-pathogenic species, *P*. *toruni*, *P*. *malacitanum*, and *P*. *andalusiense* associated with diseases of cultured redbanded seabream (*Pagrus auriga*), Labella et al. (2020) concluded that the exoenzymatic activities, adherence, and cytotoxic capabilities were the most important virulence factors in these species and responsible for the histopathological damages observed in the diseased or dead fish. *P*. *toruni* strains showed higher hemolytic activity than those of *P*. *malacitanum* and *P*. *andalusiense* on different fish species and sheep erythrocytes. In silico genome analysis of these species also showed the absence of homologues to *dly* and $hlyA_{ch}$ genes from *P*. *damselae* subsp. *damselae*. However, the genome of *P*. *toruni* shows a filamentous hemagglutinin N-terminal domain-containing protein (accession number WP_080176293.1) that could explain the higher hemolytic activity of this species (Labella et al., 2020). Regarding the iron-uptake mechanisms, all the species were able to grow under iron-limiting conditions, and produced high amounts of extracellular citrate that could be used as iron carrier. *P*. *malacitanum* and *P*. *andalusiense* use heme as iron source; however, all *P*. *toruni* strains failed to use heme since they harbor a large deletion that affects not only the heme utilization system but also the TonB1 energy transduction system (Labella et al., 2020).

Isolation and enrichment procedures

Photobacterium strains can be isolated from marine environments, sediments, or animals using a wide range of media. One of the most used is Marine Agar (MA) with the following composition (g/l): peptone, 5.0; yeast extract, 1.0; iron citrate, 0.1; sodium chloride, 19.45; sodium sulfate, 3.24; sodium silicate, 0.004; sodium fluoride, 0.0024; disodium fluoride, 0.008; calcium chloride, 1.8; magnesium chloride, 8.8; potassium chloride, 0.55; potassium bromide, 0.08; strontium chloride, 0.034; ammonium nitrate, 0.0016; boric acid, 0.022; and agar, 15.0. Dunlap and Urbanczyk (2013) recommended the use of LSW-70 medium for growth of luminous bacteria. LSW-70 has the following composition (g/l): tryptone, 10; yeast extract, 5; 35% (v/v) of double-strength artificial seawater; and agar, 15. Several *Photobacterium* species have been isolated using thiosulfate– citrate– bile salts– sucrose (TCBS) agar (g/l): peptone, 10; sodium thiosulfate, 10; sodium citrate, 10; ox gall, 5; sodium cholate, 10; sucrose, 20; sodium chloride, 10; ferric citrate, 1; bromothymol blue, 0.04; thymol blue, 0.04; and agar, 15. Other species of this genus have been isolated from seawater or animals using saline tryptic soy agar (sTSA), with the following composition (g/l): pancreatic digest of casein, 15; peptic digest of soybean meal, 5; sodium chloride, 15; and agar, 15; and MNB agar (400 mM NaCl; 9 mM KCl; 27.5 mM Na_2SO_4; 2.25 mM $NaHCO_3$; 28.5 mM $MgCl_2$; 5 g peptone; 1 g asparagine; and 20 g agar). For the isolation of halophilic strains, the YED agar supplemented with NaCl is usually used, with the following composition (g/l): yeast extract, 4; glucose, 7; sodium chloride, 25; and agar, 20. SM medium supplemented with casein and gelatin has been used for the isolation of *P. proteolyticum*. In addition, MA 2216-E medium supplemented with 1% (v/v) of tributyrin and Luria-Bertani (LB) agar supplemented with 10% tricaprylin have been used for the isolation of lipolytic species.

Enrichment from marine animals can be performed following the procedure described by Dunlap and Urbanczyk (2013). An animal tissue sample is submerged in sterilized seawater or artificial seawater and incubated at temperatures of 10–25°C for several days. Bacteria growing in the broth are then streaked on MA, LSW-70, or TCBS agar plates.

Maintenance procedures

Storage on agar slants is recommended only for a few days. For long-term storage, it is recommended to use cryopreservation at –80°C using cryoprotective media, such as DFM (deep freezer medium) which has the following composition: 1% (w/v) yeast extract; 10% (v/v) dimethyl sulfoxide (DMSO); 10% (v/v) glycerol; and 20% (v/v) 1 M K_2HPO_4/NaH_2PO_4 (pH 7.0). For cryopreservation, equal volumes of liquid culture of the bacterial strain and 2 × DFM medium are mixed through a brief vortexing and placed at ultralow temperature. Other maintenance procedure consists of the use of Marine Broth (MB) supplemented with 15 – 25% (v/v) glycerol.

Procedures for testing special characteristics

Luminescence of strains can be observed on colonies growing on MA or LSW-70 agar. Luminous colonies can usually be observed after 18 – 24 h growth in a dark- room or chamber. Factors affecting the luminescence intensity and luciferase synthesis are described by Rodicheva et al. (1993). Anaerobic growth can be assessed on MA under anaerobic conditions (atmosphere of 4 – 10% CO_2 or with 0.1% of $NaNO_3$). Several *Photobacterium* species have the ability to accumulate PHB as an intracellular reserve product, coupled with the inability to utilize the exogenous monomer, β-hydroxybutyrate, as a sole source of carbon and energy. Accumulation of refractile PHB granules can be readily detected by phase microscopy in early stationary-phase cultures grown in basal medium containing 0.2% (w/v) D-glucose and 0.05 – 0.1% (w/v) yeast extract.

Differentiation of the genus *Photobacterium* from other genera

Photobacterium can be differentiated from other genera in *Vibrionaceae* based on the following characteristics: utilization of D-alanine as sole carbon source, Voges– Proskauer test, and sensitivity to O/129. Species in the genus do not utilize D-alanine, unlike most *Vibrio*, *Salinivibrio*, and *Grimontia*. *Photobacterium* and can be distinguished from *Aliivibrio* and *Enterovibrio* species based on negative result of Voges– Proskauer test. *Photobacterium* species are sensitive to vibriostatic agent O/129, unlike most *Enterovibrio* species.

Taxonomy and phylogeny comments

The genus *Photobacterium* (Greek, photos= "light") was defined based on the criterion of light production by several bacterial strains isolated from fish slime during the late 1800s and early 1900s (Beijerinck, 1889). Since its creation in 1889, a variety of Gram-negative, facultatively anaerobic, PHB-producing bacteria have been included in the genus. Originally, the genus was composed of three species: *P. phosphoreum*, *P. leiognathi*, and *P. angustum*. The taxonomy of

this genus has been controversial in its first stages due to distinct traits exhibited by the newly isolated luminous bacteria and the proximity to the genus *Vibrio* (Beijerinck, 1916; Hendrie et al., 1970). The genus *Photobacterium* was established as a lineage distinct from *Vibrio* based on analysis of the 16S rRNA gene (Haygood and Distel, 1993). *Photobacterium* was found to be paraphyletic with respect to *Vibrio*. All subsequent descriptions of new *Photobacterium* species have included 16S rRNA gene sequence analysis, even to include unknown environmental strains into *Photobacterium* (Süss et al., 2008). The genus *Photobacterium* is the second largest genus of the family *Vibrionaceae*, currently comprising 40 species, but only 37 species have validly published names under the International Code of Nomenclature of Prokaryotes (ICNP). However, *Photobacterium* species have multiple copies of the rRNA operon, including 16S rRNA gene, which potentially complicates phylogenetic analysis based on this single locus (Machado and Gram, 2017).

To overcome this limitation, multi-locus sequence analysis (MLSA) using genes coding for housekeeping proteins, including 16S rRNA gene, is at present used when evaluating *Vibrionaceae* phylogenetic relationships (Thompson et al., 2005; Sawabe et al., 2007, 2013; Pascual et al., 2010; Gabriel et al., 2014), and this has allowed establishing a robust separation of *Photobacterium* from *Aliivibrio* and *Vibrio* (Urbanczyk et al., 2007; Ast et al., 2009). The genes more frequently used to perform phylogenetic studies within the genus *Photobacterium* are *recA* (protein RecA, recombinase A), *rpoA* (RNA polymerase α-subunit), *gyrB* (DNA gyrase subunit B), *pyrH* (uridylate kinase, uridine monophosphate kinase), *gapA* (glyceraldehyde-3-phosphate dehydrogenase, NAD-dependent glyceraldehyde-3-phosphate dehydrogenase), *ftsZ* (cell division protein FstZ), *topA* (DNA topoisomerase I), and *mreB* (rod shape determining protein MreB). This approach has been particularly useful for resolving taxonomic ambiguity and describing new species of *Photobacterium* (Ast and Dunlap, 2004, 2005; Dunlap et al., 2004; Dunlap and Ast, 2005; Ast et al., 2007; Kaeding et al., 2007; Yoshizawa et al., 2009; Chimetto et al., 2010; Lucena et al., 2011; Srinivas et al., 2013; Figge et al., 2014; Moreira et al., 2014; Machado et al., 2015; Gomez-Gil et al., 2016; Labella et al., 2017b, 2018a; Hilgarth et al., 2018; Li et al., 2019; Wang et al., 2019; Enciso-Ibarra et al., 2020).

The division of the *Photobacterium* genus into clades using MLSA has been suggested based on the creation of luminous/symbiotic and nonluminous/nonsymbiotic clusters (Urbanczyk et al., 2011). However, this classification includes species that do not share bioluminescence properties, such as *P. angustum*, *P. damselae*, and *P. ganghwense* (Machado and Gram, 2017); therefore, the generic division of luminous versus nonluminous clades should be avoided.

More recently, MLSA also has been shown to be an appropriate technique to elucidate phylogenetic relationships among *P. damselae* strains and between *P. damselae* and other species of the genus. These analyses have discriminated 22 species into 5 clades, named Clade Damselae, Clade Phosphoreum, Clade Profundum, Clade Ganghwense, and Clade Leiognathi (Labella et al., 2018b).

The ferric up-take regulator (*fur*) gene has been applied as a new marker of evolution within the *Vibrionaceae* family (Machado and Gram, 2015). Based on correlation studies between the average nucleotide identity (ANI) and the different methodologies used (DNA– DNA hybridization, *fur* gene, and MLSA) to study phylogenetic relationships within the genus *Photobacterium*, it has been shown that the *fur* gene presents the highest correlation index, becoming a target gene in the classification of new strains in the family *Vibrionaceae*. Nevertheless, the use of MLSA is still useful to evaluate the evolutionary relationships within this bacterial genus.

As new species of *Photobacterium* have been described in recent years, this type of analysis needs to be re-evaluated to obtain a more complete phylogenetic information of this genus. In this direction, and due to the lack of sequence information of other housekeeping genes in all *Photobacterium* species described (as of January 2022), a phylogenetic analysis of 16S rRNA gene with type strains of all the species of the genus has been performed in the present study (Figure 1).

List of species of the genus *Photobacterium*

The differential characteristics of the species of the genus *Photobacterium* are shown in Table 1.

Photobacterium aestuarii Lo et al. 2014[VP]

a.es.tu.a'ri.i.L.gen.neut.n. *aestuarii*, of a tidal flat, from where the organism was isolated.

Cells are rod-shaped (0.9 – 1.3 × 1.5 – 2.0 μm size). Motile. Facultatively aerobic. Colonies on MA are round, convex, smooth, and yellow. Growth occurs at 10 – 30°C (optimum, 20°C), at pH 6 – 10 (optimum, pH 6.5 – 7.5), and in the presence of 1 – 6% (w/v) NaCl (optimum, 2 – 3%). Nitrate is reduced to nitrite. Oxidase, catalase, and arginine dihydrolase are positive. Tween 80, aesculin, and tyrosine are hydrolyzed, but not Tween 20, urea, casein, and starch. Acid is produced from L-arabinose, D-glucose, D-mannitol, D-sorbitol, and sucrose. Presents the following enzymatic activities:

alkaline phosphatase, leucine arylamidase, acid phosphatase, and *N*-acetyl-β-glucosaminidase. Lipase (C14), cystine arylamidase, α-galactosidase, β-galactosidase, β-glucuronidase, α-glucosidase, β-glucosidase, α-mannosidase, trypsin, α-chymotrypsin, and α-fucosidase activities are absent. The following substrates are utilized as sole carbon source: Tween 80, D-fructose, D-mannitol, D-mannose, trehalose, citric acid, DL-lactic acid, glycerol, succinic acid, L-alanine, L-alanyl-glycine, L-asparagine, L-serine, L-threonine, inosine, and thymidine. D-Glucose, L-arabinose, *N*-acetylglucosamine, maltose, potassium gluconate, adipic acid, trisodium citrate, and phenylacetic acid are not assimilated. The major cellular fatty acids are summed feature 3 ($C_{16:1}$ ω7*c* and/or $C_{16:1}$ ω6*c*), summed feature 8 ($C_{18:1}$ ω7*c* and/or $C_{18:1}$ ω6*c*), and $C_{16:0}$. The only isoprenoid quinone is Q-8. Isolated from a tidal flat of the Yeongam Bay in South Korea.

DNA G + C content of the type strain (mol%): 44.2 (T_m).

Type strain: YA11 (=KACC 16912 =JCM 18592).

GenBank accession number (16S rRNA): JF751050.

Genome size and accession number: not available.

Photobacterium alginatilyticum Wang et al. 2017[VP]

al.gi.na.ti.ly'ti.cum. N.L. neut. n. *alginatum*, alginate; N.L. neut. adj. *lyticum*, (from Gr. neut. adj. *lyticon*) dissolving; N.L. neut. adj. *alginatilyticum*, alginate-dissolving.

Cells are rod-shaped, motile by a polar flagellum (1.2– 1.3 × 2.3 – 3.4 μm cell-size). Colonies are nontransparent, shiny, smooth, circular, and convex on MA after 24 h at 28°C. Facultatively aerobic. No luminescent. Growth occurs at 10 – 50°C (optimum 32°C), in 1 – 7% (w/v) NaCl (optimum 3%), and at a pH ranging 5 – 10 (optimum pH 6). Oxidase and catalase activities are positive. Positive for hydrolysis of DNA, alginate, and Tweens 20 and 40, but negative for gelatin, starch, carboxymethyl cellulose, and chitin. Positive for arginine dihydrolase, indole production, nitrate reduction, β-glucosidase, fermentation of glucose, mannitol, sucrose, and amygdalin, and oxidation of glucose, inositol, sorbitol, and sucrose; negative results were obtained for lysine decarboxylase, ornithine decarboxylase, and tryptophan deaminase activities, citrate utilization, urea hydrolysis, and H_2S production. Acids are produced from methyl-α-D-mannopyranoside, methyl-α-D-glucopyranoside, lactose, xylitol, gentibiose, turanose, D-lyxose, D-tagalose, D-fucose, and potassium 5-ketogluconate. Activities of alkaline phosphatase, esterase (C4), esterase lipase (C8), leucine arylamidase, cystine arylamidase, acid phosphatase, α-galactosidase, α-fucosidase, and *N*-acetyl-β-glucuronidase are present. The following compounds are used as carbon and energy sources: adonitol, D-arabitol, D-mannitol, D-fructose, α-D-glucose, *i*-erythritol, D-mannose, D-psicose, succinic acid monoethyl ester, acetic acid, α-hydroxybutyric acid, β-hydroxybutyric acid, γ-hydroxybutyric acid, DL-lactic acid, bromosuccinic acid, L-alanine, L-asparagine, L-glutamic acid, L-proline, D-serine, urocanic acid, inosine, uridine, thymidine, 2,3-butanediol, and glycerol. The major respiratory quinone is Q-8. The polar lipids are phosphatidylglycerol, phosphatidylcholine, and one unknown lipid. The major cellular fatty acids are summed feature 3 ($C_{16:1}$ ω7*c* and/or iso-$C_{15:0}$ 2-OH) and $C_{16:0}$. Isolated from a bottom seawater sample at East China Sea.

DNA G + C content of the type strain (mol%): 44.3 (HPLC), 48 (genome sequence).

Type strain: P03D4 (=KCTC 52365 =CGMCC 1.15764 =MCCC 1K03200).

GenBank accession number (16S rRNA): KU315478.

Genome size and accession number: 6.5 Mb. ASM991067v1.

Photobacterium andalusiense Labella et al. 2018a, VL185

an.da.lu.si.en'se. N.L. neut. adj. *andalusiense*, pertaining to Andalusia, community located at South of Spain.

Cells are rod-shaped, motile, chemo-organotrophic, and facultatively anaerobic. Optimal growth occurs in the presence of 0.5 – 8% (w/v) NaCl. Growth occurs at 4 – 30°C with at optimum temperature of 18 – 22°C. No diffusible pigment production. Glucose is fermented with the production of gas. Oxidase and catalase are positive. Reduces nitrate to nitrite, but not to N_2. It is positive for arginine dihydrolase, lysine decarboxylase, urease, amylase, acid- and alkaline phosphatases, α-chymotrypsin, phosphohydrolase, esterase, esterase-lipase, leucine-arylamidase, α-galactosidase, and *N*-acetyl-β-glucosaminidase; but negative for indole production, ornithine decarboxylase, trypsin, hydrolysis of gelatine and aesculin, β-galactosidase, α-glucosidase, β-glucosidase, β-glucuronidase, α-maltosidase, α-mannosidase, α-fucosidase, L-aspartic acid arylamidase, valine arylaminase, and cystine arylaminase. Produces acids from D-glucose and D-maltose; however, the reactions of fermentation of L-arabitol, D-arabitol, D-mannitol, adonitol, palatinose, sucrose, melibiose, L-arabinose, D-trehalose, L-rhamnose, inositol, D-cellobiose, D-sorbitol, galacturonate,

and 5-ketoglutarate are negatives. Dextrin, *N*-acetyl-D-galactosamine, *N*-acetyl-D-glucosamine, D-cellobiose, D-fructose, D-galactose, α-D-lactose, lactulose, maltose, D-mannose, D-melibiose, D-psicose, methyl pyruvate, *cis*-aconitic acid, formic acid, α-hydroxybutyric acid, α-keto-butyric acid, α-keto-glutaric acid, DL-lactic acid, succinic acid, bromo succinic acid, L-alaninamide, L-alanine, L-alanylglycine, L-asparagine, L-aspartic acid, L-glutamic acid, glycil-L-aspartic acid, L-serine, L-threonine, inosine, uridine, thymidine, glycerol, DL-α-glycerol phosphate, α-D-glucose-1-phosphate, and D-glucose-6-phosphate are used as sole carbon sources. It is negative for the assimilation of β-methyl-D-glucoside, itaconic acid, and sebacic acid. The major cellular fatty acids are $C_{16:0}$, summed in feature 3 ($C_{16:1}$ ω7*c* and/or $C_{16:1}$ ω6*c*), and $C_{18:1}$ ω6*c*. Isolated from diseased cultured fish (*Pagrus auriga*).

DNA G + C content of the type strain (mol%): 39.5 (T_m), 39.3 (genome).

Genome size and reference: 4.5 Mb. GCA_900185625.1.

Type strain: H01100409B^T (=CECT 9192^T =LMG 29994^T).

GenBank accession number (16S rRNA): KX943591.

Photobacterium angustum Reichelt et al. 1979^{AL}

an.gus'tum. L. neut. adj. *angustum*, limited, with respect to nutritional versatility.

Rods, motile by means of polar flagella. Luminescence variable depending on the strains. The major isoprenoid quinone is Q-8. Optimal growth at 20 – 25°C and in 160 – 280 mM Na^+. No growth in absence of NaCl, or at NaCl concentration higher than 8% (w/v), and at temperatures up to 42°C. No gas production from D-glucose. Nitrate is not reduced. Oxidase and DNase positive. Urease, lysine decarboxylase, and phenylalanine deaminase are not produced. D-Adonitol, L-arabinose, cellobiose, aesculin, *myo*-inositol, α-D-lactose, D-mannitol, raffinose, L-rhamnose, salicin, and D-sorbitol are not fermented. Acetate, DL-glycerate, and pyruvate are utilized as sole carbon sources, but not arginine, citrate, citrulline, ethanol, glycine, leucine, malate, methionine, proline, and putrescine. The major cellular fatty acids are $C_{16:1}$, $C_{16:0}$, and $C_{18:1}$. Isolated from the open ocean and from the light organs of several fish species.

DNA G + C content of the type strain (mol%): 41.0 (T_m), 39.5 (genome).

Genome size and reference: 4.9 Mb. ASM302689v1.

Type strain: ATCC 25915^T (=CAIM 908^T =CCUG 16300^T =CIP 75.10^T =LMG 8455^T).

GenBank accession number (16S rRNA): D25307, X74685.

Photobacterium aphoticum Lucena et al. 2011^{VP}

a.p ho'ti.cum. Gr. pref. *a-*, not; Gr. neut. n. *phôs*, (gen. phôtos), light; L. neut. adj. suff.-*icum*, suffix used with the sense of pertaining to; N.L. neut. adj. *aphoticum*, referring to the non-luminescent character of the species.

Cells are motile bacilli (0.7– 1.1 × 2.2 – 3.3 μm). Grows on MA producing regular colonies 1.5–2.0 mm in diameter with a diffusible light-brown pigment after 24 h of incubation at 28°C. Chemo-organotrophic and facultatively anaerobic. Ferments glucose, galactose, and melibiose without production of gas. Oxidase and catalase are positives. No luminescent. Grows at 15 and 37°C, but not at 4 or 40°C. Grows well in 0.85 – 7% total salts, but no growth in NaCl concentrations lower than 0.35% or in higher than 8%. Reduces nitrate to nitrite, but not to N_2. Positive for arginine dihydrolase, DNase and β-galactosidase activities, and hydrolysis of aesculin; but negative for indole production, urease activity, acetoin production, and hydrolysis of gelatin, casein, starch, alginate, agar, and Tween-80. Produces acid from D-ribose, D-xylose, D-galactose, D-glucose, D-fructose, D-mannose, D-mannitol, *N*-acetyl-D-glucosamine, maltose, melibiose, and starch. Positive for alkaline phosphatase, leucine arylamidase, acid phosphatase, β-galactosidase, and *N*-acetyl-β-glucosaminidase activities. *N*-Acetyl-D-glucosamine, D-fructose, D-glucose, and D-mannose are oxidized. The major cellular fatty acids are summed feature 3 ($C_{16:1}$ ω7*c* and/or $C_{16:1}$ ω6*c*), summed feature 8 ($C_{18:1}$ ω7*c* and/or $C_{18:1}$ ω6*c*), and $C_{16:0}$. Isolated from coastal seawater in Valencia, Spain.

DNA G + C content of the type strain (mol%): 49.7 (genome).

Genome size and reference: 5.3 Mb. ASM102943v1.

The type strain: M46^T (=CECT 7614^T =KCTC 23057^T =DSM 25995^T).

GenBank accession number (16S rRNA): FN796493.

Photobacterium aplysiae Seo et al. 2005a^{VP}

ap.ly'si.ae. L. gen. fem. n. *aplysiae*, of *Aplysia*, a zoological genus, referring to the isolation of the type strain from a sea hare, genus *Aplysia*.

Cells are rod-shaped (0.5 – 0.8 × 1.0 – 4.0 μm). Motile by means of a polar flagellum. Cream-colored, opaque, smooth, circular, convex colonies with entire margins are formed on MA. Facultatively anaerobic. Growth occurs between 10 and 31°C (optimum 25°C). The pH range for growth is 4–9, with an optimum at pH 8. Obligate

requirement of NaCl for growth; grows at concentrations of 1 – 5% (w/v) (optimal at 3% NaCl). Catalase, oxidase, arginine dihydrolase, β-galactosidase, α-glucosidase, alkaline phosphatase, esterase/lipase, lipase, leucine arylamidase, acid phosphatase and naphthol-AS-BI-phosphohydrolase activities and hydrolysis of gelatin are positive. Nitrate is reduced to nitrite. Acid is produced from glucose. Does not utilize β-hydroxybutyrate. The following carbon sources are utilized or are weakly positive: dextrin, glycogen, *N*-acetyl-D-glucosamine, cellobiose, D-fructose, maltose, D-mannitol, D-mannose, sucrose, D-trehalose, DL-lactic acid, L-alanine, methyl pyruvate, glycyl-L-aspartic acid, L-serine, L-threonine, L-alanyl glycine, glutamic acid, inosine, uridine, glycerol, glucose 6-phosphate, Tweens 40 and 80, D-galactose, D-psicose, D-gluconic acid, α-ketoglutaric acid, succinic acid, glycyl-L-glutamic acid, and asparagine. The major fatty acids are $C_{16:1}$, $C_{16:0}$, and $C_{18:1}$. Isolated from the eggs of a sea hare (*Aplysia kurodai*) collected in at depth of 12 m, in Mogiyeo, an uninhabited small island in the South Sea of Korea.

DNA G + C content of the type strain (mol%): 45.0 (HPLC).

Genome size and reference: not available.

Type strain: GMD509^T (=KCTC 12383^T =JCM 12948^T).

GenBank accession number (16S rRNA): NR_043188.

Photobacterium aquae Liu et al. 2014^{VP}

a'quae. L. gen. fem. n. *aquae*, of water.

Cells are short rod- or coccobacillary-shaped (0.7 – 1.0 × 1.0 – 2.0 µm). Motile by a polar flagellum. Colonies on MA are circular, smooth, convex, and cream colored. Oxidase- and catalase-positive. Chemo-organotrophic and facultatively anaerobic. Reduces nitrate to nitrite. Growth occurs at 15 – 40°C (optimum 30 – 35°C), at pH 5.5– 10.0 (optimum at 7.0 – 7.5), and in the presence of 0.5 – 7% (w/v) NaCl (optimum 2 – 3%). NaCl is required for growth. Hydrolyses arginine, gelatin, Tweens 40, 60, and 80 and starch, but not L-tyrosine, aesculin, and casein. Negative for the production of indole, H_2S and acetoin, and for β-galactosidase, urease, lysine decarboxylase, ornithine decarboxylase, and tryptophan deaminase activities and citrate utilization. Acid is produced from glucose, but not from D-mannitol, *myo*-inositol, D-sorbitol, L-rhamnose, sucrose, amygdalin, or L-arabinose. Positive for dextrin, maltose, *N*-acetyl-D-glucosamine, *N*-acetyl-β-D-mannosamine, α-D-glucose, D-mannose, D-fructose, inosine, glycerol, D-glucose 6-phosphate, D-fructose 6-phosphate, glycyl-L-proline, L-aspartic acid, L-glutamic acid, L-serine, methylpyruvate, L-lactic acid, α-ketoglutaric acid, L-malic acid and α-ketobutyric acid; but results negative for utilization of trehalose, cellobiose, gentiobiose, sucrose, turanose, stachyose, raffinose, α-lactose, methyl-β-D-glucoside, D-salicin, *N*-acetyl-D-galactosamine, *N*-acetyl neuraminic acid, D-galactose, 3-methyl-glucose, DL-fucose, L-rhamnose, D-sorbitol, D-mannitol, *myo*-inositol, D-aspartic acid, D-serine, gelatin, L-alanine, L-arginine, L-histidine, L-pyroglutamic acid, pectin, D-galacturonic acid, L-galactonic acid lactone, D-gluconic acid, D-glucuronic acid, glucuronamide, mucic acid, quinic acid, D-saccharic acid, *p*-hydroxyphenylacetic acid, D-lactic acid methyl ester, citric acid, D-malic acid, bromosuccinic acid, γ-aminobutyric acid, α-hydroxybutyric acid, β-hydroxy-DL-butyric acid, acetoacetic acid, propionic acid, acetic acid, and formic acid. Presents the following enzymatic activities: alkaline phosphatase, esterase, leucine arylamidase, acid phosphatase, and *N*-acetyl-β-glucosaminidase. The predominant respiratory quinone is Q-8. The polar lipids are phosphatidylethanolamine, phosphatidylglycerol, diphosphatidylglycerol, two unidentified ninhydrin-positive phospholipids, and an unknown phospholipid. The major cellular fatty acids are summed feature 3 ($C_{16:1}$ ω7*c* and/or $C_{16:1}$ ω6*c*), $C_{18:1}$ ω7*c*, and $C_{16:0}$. Isolated from a recirculating mariculture system in Tianjin, China.

DNA G + C content of the type strain (mol%): 47.1 (T_m), 49.1 (genome).

Genome size and reference: 5.1 Mb. ASM102944v1.

Type strain: AE6^T (=CGMCC 1.12159^T =JCM 18480^T).

GenBank accession number (16S rRNA): JQ948040.

Photobacterium aquimaris Yoshizawa et al. 2009^{VP}

a.q ui.ma'ris. L. fem. n. *aqua*, water; L. gen. neut. n. *maris*, of the sea; N.L. gen. neut. n. *aquimaris*, of water of the sea.

Motile by means of polar flagella. Nonpigmented, translucent, luminescent colonies on MA. Growth occurs in the presence of 0.9 – 3.5% NaCl (w/v), but not in 0.5, 6, 8, or 10% NaCl. Grows at 10 – 25°C, but not at 4, 30, or 37°C. Oxidase-negative and catalase-positive. Alkaline- and acid phosphatases, leucine arylamidase, naphthol-AS-BI-phosphohydrolase, α-galactosidase, β-galactosidase and *N*-acetyl-β-glucosaminidase activities are present, but arginine dihydrolase, lysine decarboxylase, ornithine decarboxylase, urease, tryptophan deaminase, gelatinase, esterase (C4), esterase lipase (C8), lipase (C4), valine arylamidase, cystine arylamidase, trypsin, chymotrypsin, β-glucuronidase, α-glucosidase, β-glucosidase, α-mannosidase, and α-fucosidase are absent. Reduces nitrate to nitrite, but not further to N_2. The predominant cellular fatty acids are summed feature 3

(iso-$C_{15:0}$ 2-OH and/or $C_{16:1}$ ω7*c*), $C_{16:0}$, and $C_{18:0}$. Isolated from seawater of Sagami Bay in Japan.

DNA G + C content of the type strain (mol%): 42.2 (T_m), 39.3 (genome).

Genome size and reference: 4.3 Mb. GCA_900185565.1.

Type strain: LC2-0065^T (=KCTC 22356^T =NBRC 104633^T =CAIM 1844^T =DSM 23343^T).

GenBank accession number (16S rRNA): AB428873.

Photobacterium arenosum Weerawongwiwat et al. 2021^{VP}

a.r e.no'sum L. neut. adj. *arenosum*, sandy, dwelling in sand.

Cells are short rod-shaped (0.8–0.9 × 1.2–1.3 µm size). Aerobic and motile by a single flagellum. Growth occurs at 4–37°C (optimum 25–30°C), pH 6.0–10.5 (optimum pH 6.5 – 8.5), and 0 – 6% (optimum 0 – 4%) NaCl (w/v). Colonies on MA are circular, light-yellow-colored, convex, rough, and opaque. Positive for oxidase activity, glucose fermentation, and aesculin; catalase, nitrate reduction, indole production, arginine dihydrolase, urease, gelatinase activities, and starch and casein hydrolysis are absent. Positive activities for alkaline phosphatase, leucine arylamidase, valine arylamidase, and naphthol-AS-BI-phosphohydrolase. Can ferment glucose, fructose, mannitol, *N*-acetyl-glucosamine, maltose, and trehalose. Ubiquinone Q-8 is the predominant respiratory quinone. The dominant polar lipids are diphosphatidylglycerol, phosphatidylglycerol, phosphatidylcholine, and phosphatidylethanolamine. The major fatty acids are $C_{16:0}$, summed feature 3 ($C_{16:1}$ ω6*c* and/or $C_{16:1}$ ω7*c*), and summed feature 8 ($C_{18:1}$ ω7*c* and/or $C_{18:1}$ ω6*c*). Isolated from marine sediment sand collected from the Sido Island coast, Incheon, Republic of Korea.

DNA G + C content of the type strain (mol%): 50.1 (genome).

Genome size and reference: 4.7 Mb. ASM1484111v1.

Type strain: CAU 1568^T (=KCTC 82404^T = MCCC 1K05668 ^{T}).

GenBank accession number (16S rRNA): MN540907.

Photobacterium carnosum Hilgarth et al. 2018, VL181

car.no'sum. L. neut. adj. *carnosum*, pertaining to flesh.

Cells are coccoid to rod shaped, nonmotile, and non-luminescent. Facultatively anaerobic. Quinone Q-8 is the sole respiratory ubiquinone. Growth at 0 – 20°C (optimum, 10 – 15°C), within pH 5.0–8.5 (optimum, pH 6 – 8), and in the presence of 0.5 – 3% (w/v) NaCl (optimum, 1%). Acid is produced from starch, glycogen, D-glucose, and D-ribose. It presents naphthol-AS-BI-phosphohydrolase, oxidase, and α-glucosidase activities. The major cellular fatty acids are summed feature 3 ($C_{15:1}$ ω7*c* and/or iso-$C_{15:1}$ 3-OH), $C_{16:0}$, $C_{18:1}$ ω7*c*, and summed feature 2 ($C_{12:0}$ aldehyde and/or $C_{10.928}$ unknown). Isolated from spoiled retail modified-atmosphere packaged poultry meat.

DNA G + C content of the type strain (mol%): 38.5 (genome).

Genome size and reference: 4.6 Mb. ASM284960v1.

Type strain: TMW 2.2021^T (=DSM 105454^T =CECT 9394^T).

GenBank accession number (16S rRNA): MF622943.

Photobacterium chitinilyticum Wang et al. 2019^{VP}

chi.ti.ni.ly'ti.cum. N.L. neut. n. *chitinum*, chitin; N.L. masc. adj. *lyticus*, able to loosen, able to dissolve; N.L. neut. adj., *chitinilyticum* chitin-dissolving.

Cells are rod-shaped (1.2 – 2.7 × 0.5 – 0.9 µm size). Facultatively aerobic. Motile by a polar flagellum. Nonluminescent. Colonies on MA are nontransparent, shiny, smooth circular, and convex. Growth occurs at 10 – 37°C (optimum, 24°C). The salinity range for growth is 1 – 5% (w/v) NaCl (optimum, 3%) and the pH range is pH 5 – 8 (optimum at pH 7). Oxidase and catalase activities are positives. Positive reactions for the hydrolysis of DNA, gelatin, chitin, starch, cellulose, and Tweens 20, 40, and 80, but negative for the hydrolysis of casein and alginate. Positive results are obtained for arginine dihydrolase, indole production and gelatinase, fermentation of glucose, mannitol, sucrose and amygdalin, and oxidation of glucose, inositol, and sucrose; negative results are obtained for lysine decarboxylase, ornithine decarboxylase and tryptophan deaminase activities, urea hydrolysis, and H_2S production. Acids are produced from methyl α-D-mannopyranoside, methyl-α-D-glucopyranoside, lactose, xylitol, gentiobiose, turanose, D-lyxose, D-tagatose, D-fucose, and potassium 5-ketogluconate. Esterase (C4 and C8), lipase (C14), valine arylamidase, cystine arylamidase, trypsin, α-chymotrypsin, α-galactosidase, β-galactosidase, β-glucuronidase, α-glucosidase, β-glucosidase, α-fucosidase, α-arylamidase, acid phosphatase, and naphthol-AS-BI-phosphohydrolase are absent. Cellobiose, gentiobiose, turanose, melibiose, methyl-β-D-glucoside, *N*-acetyl-D-glucosamine, *N*-acetyl-β-D-mannosamine, D-mannose, D-fructose, L-fucose, L-rhamnose, D-sorbitol, D-mannitol, D-fructose-6-phosphate, L-alanine, L-histidine, D-glucuronic acid, glucuronamide, citric acid, L-malic acid, Tween 40, acetoacetic acid, propionic acid, acetic acid, and sodium lactate are utilized as sole carbon sources. The predominant respiratory quinone

is Q-8. The major polar lipids are phosphatidylglycerol, phosphatidylcholine, phosphatidylethanolamine, two phospholipids, and one unknown lipid. The dominant fatty acids are summed feature 3 ($C_{16:1}$ ω7*c* and/or $C_{16:1}$ ω6*c*) and $C_{16:0}$. Isolated from seawater sample collected at the bottom of the East China Sea.

DNA G + C content of the type strain (mol%): 46.45 (genome).

Genome size and reference: 5.9 Mb. ASM410435v1.

Type strain: BEI247^T (=JCM 32689^T =MCCC 1K03517^T =KCTC 62619^T).

GenBank accession number (16S rRNA): MG754451.

Photobacterium damselae Smith et al. 1991^{VP} (basonym: *Vibrio damsela* Love et al. 1981, VL8)

dam.se' la.e. N. L. fem. n. *damselae*, of damselfish.

Gram-negative, straight rods, motile by one or more unsheathed polar flagella. Facultatively anaerobic with weak gas production. Grows better at 25°C than at 37°C. Grows on thiosulfate citrate bile salts agar as 2- to 3-mm green colonies. Inhibited by 0/129 disks (22-mm zone). Positive deoxyribonuclease production, and nitrate reduction to nitrite. Accumulate PHB when grown with glucose, but unable to utilize DL-β-hydroxybutyrate. Arginine dihydrolase and urease are strongly positive. Oxidase, Voges– Proskauer, and extracellular lipase are weakly positive. Not luminescent. Na^+ required for growth (1, 3.5, and 6% NaCl). Phenylalanine deaminase, ornithine decarboxylase, alginase, amylase, and gelatinase activities are absent, but catalase is present. H_2S is not produced. Pyruvate, lactate, glutamate, mannose, galactose, glucose, cellobiose, and glycerate are used as carbon and energy sources. Serine and α-ketoglutarate utilization are variable. No utilization of L-arabinose, D-gluconate, L-rhamnose, salicin, D-xylose, caprate, caproate, butyrate, caprylate, heptanoate, isobutyrate, isovalerate, pelargonate, propionate, valerate, DL-β-hydroxybutyrate, aconitate, citrate, betaine, hippurate, sarcosine, glutarate, malonate, lactose, melibiose, trehalose, mannitol, sorbitol, ethanol, *n*-propanol, benzoate, *p*-hydroxybenzoate, quinate, tyrosine, D-α-alanine, β-alanine, γ-aminobutyrate, δ-aminovalerate, arginine, citrulline, glycine, L-leucine, L-ornithine, putrescine, and spermine. Includes the subspecies *P. damselae* subsp. *damselae* and *P. damselae* subsp. *piscicida*.

DNA G + C content of the type strain (mol%): 42 – 43.6 (Bd).

Genome size and reference: 4.6 Mb. ASM170803v2.

Type strain: ATCC 33539^T (=DSM 7482^T =CAIM 331^T =CCUG 13626^T =CDC 2588-80^T =CIP 102761^T =IFO 15633^T =LMG 7892^T =NBRC 15633^T =NCTC 11647^T).

GenBank accession number (16S rRNA): X74700.

Photobacterium damselae subsp. *damselae* Gauthier et al. 1995^{VP} emend. Kimura et al. 2000

Motile. The major isoprenoid quinone is Q-8 (90%), and a minor quinone is Q-7 (10%). Able to grow at 1 – 6% (w/v) NaCl, with an optimum of 3% NaCl. Produces urease, phosphatase, and DNase, but not gelatinase. Citrate, acetate, and DL-glycerate are not used as sole source of carbon and energy. Gas production from D-glucose. Utilizes *N*-acetyl-D-galactosamine, *N*-acetyl-D-glucosamine, cellobiose, D-fructose, D-galactose, glycogen, glycerol, DL-lactate, maltose, D-mannose, D-ribose, and turanose; but not D-adonitol, L-arabinose, D-arabitol, dulcitol, erythritol, D-gluconate, *myo*-inositol, α-D-lactose, D-mannitol, raffinose, L-rhamnose, salicin, D-sorbitol, or sucrose. The fatty acid profile contains high concentrations of $C_{16:1}$, $C_{16:0}$, $C_{18:1}$, $C_{12:0}$, and $C_{12:0}$ 3-OH. Isolated from several marine fish (damselfish, yellowtail, seabream, brown shark, lemon shark, etc.), mammals (dolphin), reptiles (turtle), and mollusks (octopus). Wound infections in humans have also been described.

DNA G + C content (mol%): 40.6 – 41.4 (genome).

Genome size and reference: 4.6 Mb. ASM170803v2.

Type strain: ATCC 33539^T (=DSM 7482^T =CAIM 331^T =CCUG 13626^T =CDC 2588-80^T =CIP 102761^T =IFO 15633^T =LMG 7892^T =NBRC 15633^T =NCTC 11647^T).

GenBank accession number (16S rRNA): X74700.

Photobacterium damselae subsp. *piscicida* Gauthier et al. 1995^{VP} (synonym: "Pasteurella piscicida" Janssen and Surgalla 1968)

pis.ci.ci' da. L. gen. masc. n. *piscis*, a fish; L. masc. n. suff. – *cida*, from L. v. *caedo*, to cut or to kill; N.L. masc. n. *piscicida*, fish killer.

Nonmotile, straight rods with bipolar staining (1.0 × 1.5 μm), changing from coccoidal to long rods under different culture conditions. Capsules may be produced. Cells are not able to grow at NaCl concentrations lower than 0.02 M (optimal growth at 0.3 M NaCl). Grows at 25°C, but not at 4°C, the growth at 37°C is variable. Cells are able to grow at pH 6 – 9 (optimum pH 6.8). Oxidase positive. Lecithinase and lipase positives. Does not produce urease, elastinase, caseinase, phospholipase, and lysine decarboxylase. Glutamate, adipate, and L-proline are utilized as sole carbon and energy sources. Fructose, D-galactose, and D-mannose are fermented. L-Rhamnose, D-glucitol, D-xylose, maltose, glycerol, galactitol, and cellobiose are not fermented. Gas is not produced from D-glucose. Fatty acid analysis has revealed

that saturated and unsaturated fatty acids of 16 carbon atoms are the predominant fatty acids. Isolated from diseased fish (mainly *Seriola quinqueradiata*, *Sparus aurata*, and *Dicentrarchus labrax*).

DNA G + C content (mol%): 41.1 – 41.3 (genome).

Genome size and reference: 4.6 Mb. ASM1477569v1.

Type strain: NCIMB 2058^T (=ATCC 51736^T =CIP 104404^T).

GenBank accession number (16S rRNA): X78105.

Photobacterium frigidiphilum Seo et al. 2005b^{VP}

fri.gi.di.phi'lum. L. masc. adj. *frigidus*, cold; N.L. masc. adj. suff. *philus -a -um* from Gr. masc. adj. *philos*, friendly to, loving; N.L. neut. adj. *frigidiphilum*, cold-loving.

Cells are rods (0.8 – 1.5 × 2.3 – 3.8 µm). Motile by a polar flagellum. Colonies are cream-colored, opaque, smooth, circular, and convex with entire margins. Facultatively anaerobic. Nonluminescent. Psychrophilic. Growth occurs between 6 and 20°C (optimum 14°C). The pH range for growth is 5.0– 8.5 (optimum pH 6.0). Requires NaCl for growth (1.0 – 3.5% w/v of NaCl), with an optimum at 1.5% (w/v). Catalase, oxidase, arginine dihydrolase, β-glucosidase, protease, β-galactosidase and lipase are present. Reduces nitrate to nitrite, and indole is produced. Utilizes as sole carbon source dextrin, glycogen, Tweens 40 and 80, *N*-acetyl-D-glucosamine, *N*-acetyl-D-galactosamine, D-fructose, D-galactose, α-D-glucose, *myo*-inositol, maltose, D-mannitol, D-mannose, sucrose, D-trehalose, D-glucuronic acid, DL-lactic acid, propionic acid, succinic acid, L-alanine, L-asparagine, L-aspartic acid, L-glutamic acid, glycyl-L-aspartic acid, glycyl-L-glutamic acid, L-serine, inosine, glycerol, and D-glucose-6-phosphate. Does not utilize β-hydroxybutuyrate. The major cellular fatty acids are summed feature 3 ($C_{16:1}$ ω7*c* and/or $C_{16:1}$ ω6*c*) and $C_{16:0}$. Isolated from sediments at Edison Seamount (1,500 m depth) in the Western Pacific Ocean.

DNA G + C content of the type strain (mol%): 43.8 (T_m), 41.6 (genome).

Genome size and reference: 6.4 Mb. ASM302561v1.

Type strain: SL13^T (=KCTC 12384^T =JCM 12947^T).

GenBank accession number (16S rRNA): AY538749.

Photobacterium gaetbulicola Kim et al. 2010^{VP}

gaet.bu.li.co'la. N.L. neut. n. *gaetbulum*, gaetbul, the Korean name for a tidal flat; L. masc./fem. n. suff. *-cola* (from L. n. *incola*), a dweller, inhabitant; N.L. masc./fem. n. *gaetbulicola*, a dweller of a tidal flat.

Cells are rod- or oval-shaped (0.4– 1.0 × 1.0 – 5.0 µm). Motile. Colonies on MA are circular to irregular, flat, smooth, glistening, and greyish-yellow in color. Growth occurs at 10 and 40°C (optimum 30°C), but not at 4 or 45°C, and at pH 5.0 (optimum pH 7 – 8), but not at pH 4.5. Growth occurs with 0 – 8% (w/v) NaCl (optimum 2 – 5%). Mg^{2+} ions are required in absence of NaCl. Catalase- and oxidase-positive. Nitrate reduction is positive. Arginine dihydrolase, lysine decarboxylase, ornithine decarboxylase, and tryptophan deaminase are absent. Hydrolyze aesculin and starch. Acids are formed from cellobiose, D-galactose, D-glucose, *myo*-inositol, lactose, maltose, D-mannitol, D-mannose, melibiose, raffinose, sucrose, and trehalose. Uses as sole carbon source cellobiose, D-mannose, sucrose and acetate. The predominant ubiquinone is Q-8. The major cellular fatty acids are summed feature 3 ($C_{16:1}$ ω7*c* and/or iso-$C_{15:0}$ 2-OH), $C_{16:0}$, and $C_{18:1}$ ω7*c*. Isolated from a tidal flat of Gung harbor on the west coast of Korea.

DNA G + C content of the type strain (mol%): 50.6 (HPLC), 49.7 (genome).

Genome size and reference: 5.9 Mb. ASM94099v1.

Type strain: Gung47^T (=KCTC 22804^T =CCUG 58399^T =DSM 26887^T).

GenBank accession number (16S rRNA): NR_117271.

Photobacterium galatheae Machado et al. 2015^{VP}

ga.la.the'ae. N.L. gen. fem. n. *galatheae*, referring to the research expedition on which the type strain was first isolated.

Cells are motile rods (0.74 – 1.2 × 1.6 – 3.0 µm), with polar flagella. Facultatively anaerobic. Growth occurs from 15 to 40°C and in NaCl concentrations of 0.5 – 9% (w/v). It reduces nitrate to nitrite and hydrolyses gelatin, but not aesculin. Negative for indole production, urease, arginine dihydrolase, and β-galactosidase activities. Utilizes dextrin, glycogen, Tweens 40 and 80, *N*-acetyl-D-galactosamine, *N*-acetyl-D-glucosamine, D-fructose, α-D-glucose, maltose, D-mannitol, D-psicose, trehalose, pyruvic acid methyl ester, acetic acid, citric acid, β-hydroxybutyric acid, DL-lactic acid, succinic acid, bromo-succinic acid, L-alanine, L-alanyl-glycine, L-aparagine, L-aspartic acid, L-glutamic acid, L-histidine, L-proline, L-serine, L-threonine, urocanic acid, inosine, uridine, thymidine, putrescine, glycerol, adipic acid, malic acid, and trisodium citrate as sole carbon sources. It does not utilize L-arabinose, D-mannose, potassium gluconate, capric

acid, D-galactose, β-methyl-D-glucoside, sucrose, *cis*-aconitic acid, D-gluconic acids, L-pyroglutamic acid, and phenylacetic acid. The major cellular fatty acids are summed feature 3 ($C_{16:1}$ ω7*c* and/or $C_{16:1}$ ω6*c*), $C_{16:0}$, and summed feature 8 ($C_{18:1}$ ω7*c* and/or $C_{18:1}$ ω6*c*). Isolated from the surface of a mussel in the Solomon Sea, Solomon Islands.

DNA G + C content of the type strain (mol%): 49.5 (genome).

Genome size and reference: 4.5 Mb. GCA_000695255.1.

Type strain: S2753^T (=LMG 28894^T =DSM 100496^T).

GenBank accession number (16S rRNA): KR704916.

Photobacterium ganghwense Park et al. 2006^{VP}

gang.hwen'se. N.L. neut. adj. *ganghwense*, pertaining to Ganghwa Island, Korea, the geographical origin of the type strain of the species.

Cells are oval or rod-shaped (0.8 – 1.2 × 1.3 – 2.0 μm in size). Motility by means of a polar flagellum. Colonies on MA are circular, smooth, convex with entire margins, and slightly cream-colored. Facultatively anaerobic. Oxidase- and catalase-positive. Growth occurs in 1–7% (w/v) NaCl (optimum 2%). Grows at pH 5 – 11 (optimum pH 8 – 9) and at 10–45°C (optimum at 35°C). Bioluminescence is observed. No gas is produced from D-glucose under aerobic conditions. Acid is formed from D-glucose without gas production. Does not present lysine decarboxylase, ornithine decarboxylase, urease, or tryptophan deaminase activities. Arginine dihydrolase and gelatinase activities are present. Aesculin is not hydrolyzed. Ferments glucose, D-mannitol, D-inositol, and amygdalin. Positive for assimilation of glucose, mannitol, *N*-acetyl-D-glucosamine, gluconate, malate, citrate, and phenylacetate. Produces alkaline phosphatase, esterase (C4), esterase lipase (C8), leucine arylamidase, acid phosphatase, naphthol-AS-BI-phosphohydrolase, and α-glucosidase, but not lipase (C14), valine arylamidase, cystine arylamidase, trypsin, α-chymotrypsin, α-galactosidase, β-galactosidase, β-glucuronidase, β-glucosidase, *N*-acetyl-β-glucosaminidase, α-mannosidase or β-fucosidase. Major fatty acids are $C_{18:1}$ ω7*c*, summed feature 3 ($C_{16:1}$ ω7*c* and/or iso-$C_{15:0}$ 2-OH), and $C_{16:0}$. Isolated from sea water from Ganghwa Island, South Korea.

DNA G + C content of the type strain (mol%): 44 (T_m), 50.5 (genome).

Genome size and reference: 5.7 Mb. ASM1732954v1.

Type strain: FR1311^T (=IMSNU 60287^T =KCTC 12328^T= JCM 12487^T =DSM 22954^T).

GenBank accession number (16S rRNA): AY960847.

Photobacterium halotolerans Rivas et al. 2006^{VP}

ha.lo.to'le.rans. Gr. masc. n. hals (gen. halos), salt; L. pres. part. *tolerans*, tolerating; N.L. part. adj. *halotolerans*, referring to the ability to tolerate high salt concentrations.

Cells are rod-shaped, motile by means of polar flagella. Colonies on TSA supplemented with 1.5% (w/v) NaCl are circular, smooth, white to cream in color, and opaque. Oxidase- and catalase-positive. Aerobic or facultatively anaerobic, chemo-organotrophic, mesophilic, and halotolerant. Grows in the presence of NaCl concentrations up to 8% (w/v) and optimally in the presence of 1.5% (w/v) NaCl at 28°C. Growth occurs at 4–37°C (optimum 28°C), and at pH 5 – 8.5 (optimum at pH 7). Luminescence is negative. Indole, acetoine, and H_2S are not produced. Positive for reduction of nitrate to nitrite. Does not produce arginine dihydrolase, lysine decarboxylase, ornithine decarboxylase, caseinase, urease, esterase, esterase lipase, valine arylamidase, cystine arylamidase, trypsin, chymotrypsin, phosphohydrolase, or glucuronidase, but produces amylases, β-galactosidase, acid- and alkaline phosphatases, leucine arylamidase, and β-glucosaminidase. Gelatin is hydrolyzed. Ferments glucose, mannitol, sucrose and L-arabinose. Uses *N*-acetyl-glucosamine, citrate, adipate, glucose, malate, maltose, mannitol, phenylacetate, sucrose, fructose, and trehalose as sole carbon sources. Does not use amygdalin, caproate, D-arabinose, L-xylose, L-rhamnose, galactose, sorbose, D-mannose, melibiose, cellobiose, lactose, melezitose, raffinose, turanose, lyxose, tagatose, D-fucose, L-fucose, methyl-α-D-xyloside, methyl-α-D-mannoside, methyl-α-D-glucoside, arbutin, salicin, inulin, adonitol, inositol, sorbitol, dulcitol, erythritol, xylitol, arabinitol, glycerol, 2-ketogluconate, and 5-ketogluconate as carbon sources. The most abundant fatty acids are summed feature 3 ($C_{16:1}$ ω7*c* and/or iso-$C_{15:0}$ 2-OH), $C_{16:0}$, and $C_{18:1}$ ω7*c*. Isolated from Lake Martel, Mallorca, Spain.

DNA G + C content of the type strain (mol%): 49.8 (T_m), 50.9 (genome).

Genome size and reference: 4.6 Mb. ASM990467v1.

Type strain: MACL01^T (=LMG 22194^T =CECT 5860^T =DSM 18316^T).

GenBank accession number (16S rRNA): AY551089.

Photobacterium iliopiscarium Urakawa et al. 1999[VP] (basonym: *Vibrio iliopiscarius* Onarheim et al. 1994, VL53)

i.li.o.pis.ca'ri.um. L. neut. n. ilium, intestines, guts; *ilio*, pertaining to intestines; L. masc. adj. *piscarius*, belonging to fish; *iliopiscarium*, belonging to intestines of fish.

Cells are pleomorphic depending on the salt levels, presence of glucose, temperature, and age of the culture. At NaCl concentration of 2% (w/v) without glucose, cells tend to aggregate and the dominant cell morphology is rods and curved rods. Motile. Not luminescent. Growth is better under aerobic conditions. At least 0.5% NaCl is required for growth (optimum 2% NaCl), but no growth occurs at NaCl concentrations of 5% or higher. No growth is observed at 30°C (optimum 20°C) but can grow at 4 or 37°C. Produces gas from glucose. Positive for catalase, lysine decarboxylase, and arginine dihydrolase, but negative for urease, gelatinase, amylase, ornithine decarboxylase, and tryptophan deaminase activities. Citrate, D-mannitol, *myo*-inositol, D-sorbitol, adonitol, dulcitol, L-arabinose, L-rhamnose, sucrose, melibiose, raffinose, amygdalin, erythritol, D-xylose, L-xylose, β-methylxyloside, L-sorbose, α-methyl-D-mannoside, α-methyl-D-glucoside, arbutin, salicin, inulin, melezitose, xylitol, D-turanose, D-lyxose, D-tagatose, D-fucose, L-fucose, L-arabitol, 2-ketogluconate and 5-ketogluconate are not utilized. Isolated from the intestines of fish (herring, coal fish, cod, and salmon) living in cold seawater.

DNA G + C content of the type strain (mol%): 38.9 (genome).

Genome size and reference: 4.3 Mb. ASM302545v1.

Type strain: PS1^T (=ATCC 51760^T =DSM 9896^T =CAIM 909^T =CIP 104755^T =LMG 19543^T).

GenBank accession number (16S rRNA): AB000278.

Photobacterium indicum Ivanova et al. 2004[VP] (basonym: *Hyphomicrobium indicum* Johnson and Weisrock 1969[AL])

in'di.cum. N.L. neut. adj. *indicum*, named after the bacterium isolated from the Indian Ocean.

Cells appear rod- or coccus-shaped (0.7–1.0 × 2.0–6.0 µm). Motile by a polar monotrichous flagellum. Growth occurs at 4–25°C and at pH 4.5 – 9.5. Acid is produced from glucose, and the cells can use glucose, sucrose, and maltose but not lactose, arabinose, gelatin, casein, or starch. Produces indole and H_2S, and reduces nitrate to nitrite. Negative reactions for the enzymatic activities: urease, catalase, oxidase, and lysine decarboxylase; but positive for phenylalanine deaminase. The major cellular fatty acids are summed feature 3 ($C_{16:1}$ ω7*c* and/or $C_{16:1}$ ω6*c*) and $C_{16:0}$ (Jung et al., 2007). The major quinone system is ubiquinone Q-8. Isolated from sea mud at a depth of 400 m.

DNA G + C content of the type strain (mol%): 40.0 (T_m), 41.5 (genome).

Genome size and reference: 5.9 Mb. ASM302621v1.

Type strain: NBRC 14233^T (=ATCC 19614^T =DSM 5151^T =MBIC 3157^T =LMG 22857^T =KCTC 12355^T =IFO 14233^T =NCIMB 2221^T).

GenBank accession number (16S rRNA): NR_113657.

Photobacterium jeanii Chimetto et al. 2010[VP]

jea'ni.i. N.L. gen. masc. n. *jeanii*, of Jean, after the Belgian microbiologist Jean Swings.

Cells are small coccobacilli (1–2 × 2–2.5 µm size), motile, and catalase- and oxidase-positive. Colonies on MA are convex, round, beige, and opaque with entire and smooth margins. Growth occurs between 20 and 35°C and in NaCl concentrations of 0.5 – 2% (w/v). No growth appears at 4, 7, or 42°C, or in 0% or 6% NaCl. All strains are positive for alkaline phosphatase, esterase (C4), esterase lipase (C8), lipase (C14), leucine arylamidase, trypsin, acid phosphatase, naphthol-AS-BI-phosphohydrolase, α-glucosidase, arginine dihydrolase, and gelatinase. Ferments glucose and melibiose and reduces nitrate to nitrite. Inositol, sorbitol, rhamnose, amygdalin, and arabinose are not fermented. Cystine arylamidase, α-chymotrypsin, α-galactosidase, β-glucuronidase, β-glucosidase, α-mannosidase, α-fucosidase, lysine decarboxylase, ornithine decarboxylase, urease, and tryptophan deaminase activities are absent. Citrate is not utilized and H_2S and indole are not produced. The most abundant cellular fatty acids are summed feature 3 (iso-$C_{15:0}$ 2-OH and/or $C_{16:1}$ ω7*c*), $C_{16:0}$, and summed feature 8 ($C_{18:1}$ ω7*c* and/or $C_{18:1}$ ω6*c*). Isolated from mucus of the zoanthid *Palythoa caribaeorum* in the Sao Sebastiao channel, Brazil.

DNA G + C content of the type strain (mol%): 44.5 (HPLC), 45.1 (genome).

Genome size and reference: 5.1 Mb. ASM302549v1.

Type strain: R-40508^T (=LMG 25436^T =CAIM 1817^T =DSM 100339^T).

GenBank accession number (16S rRNA): GU065209.

Photobacterium kishitanii Ast et al. 2007[VP]

ki.shi.tan'i.i. N.L. gen. masc. n. *kishitanii*, of Kishitani, in honor the deceased Japanese scientist Teijito Kishitani, who first isolated luminous bacteria from the light organ of *Physiculus japonicus*.

Cells are coccoid or coccoid rods (0.9 × 1.2 – 3.0 μm). Motile. Colonies grown on LSW-70 are small, round, white, and strongly luminous. Catalase positive. Presents luminescence. Nitrate reduction to nitrite is positive. Arginine dihydrolase and lysine decarboxylase are positive; ornithine decarboxylase, tryptophan deaminase, urease, gelatinase, and β-galactosidase activities are absent. It does produce acids from amygdalin, arabinose, inositol, mannitol, melibiose, rhamnose, and sorbitol. Does not use as sole carbon source arabinose, mannitol, *N*-acetyl-glucosamine, capric acid, malate, trisodium citrate, and phenylacetic acid. The predominant ubiquinone is Q-8. The major cellular fatty acids are summed feature 3 (iso-$C_{15:1}$ 2-OH and/or $C_{16:1}$ ω7*c*) and $C_{16:0}$. Isolated from seawater, surface of fish and as light-organ symbiont of many fish species.

DNA G + C content of the type strain (mol%): 40.2 (HPLC), 39.0 (genome).

Genome size and reference: 5.1 Mb. BDW_PRJEB5262.

Type strain: pjapo.1.1^T (=ATCC BAA-11944^T =LMG 23890^T).

GenBank accession number (16S rRNA): AY341439.

Photobacterium leiognathi Boisvert et al. 1967^{AL} (synonym: *Photobacterium mandapamensis* Reichelt and Baumann 1975^{VP})

lei.o.gna'thi. N.L. gen. masc. n. *leiognathi*, of Leiognathus, named after fish of the genus *Leiognathus* (family *Leiognathidae*).

Coccobacilli (approximately 1.6 × 3.2 μm). Motile. Luminescent. The isoprenoid quinones are Q-8 (90%) and Q-7 (10%). Requires L-methionine for optimal growth. The optimal temperature is 30°C, it can grow at 37°C, but not at 4°C. Cells can grow at a salt concentration of 0.5– 6% (optimal NaCl concentration is 1.5%, w/v). Negative for the production of oxidase, tryptophan deaminase, lysine decarboxylase, ornithine decarboxylase, gelatinase, lipase, amylase, and alginase. Aesculin is not hydrolyzed. Fermentation occurs without gas production from D-fructose, D-glucose, D-galactose, glycerol, glycogen, D-mannose, D-ribose, *N*-acetyl-D-glucosamine, *N*-acetyl-D-galactosamine, and turanose. Cells are not able to ferment adonitol, L-arabinose, cellobiose, D-gluconate, dulcitol, *myo*-inositol, α-D-lactose, D-mannitol, raffinose, L-rhamnose, D-sorbitol, sucrose, trehalose, or D-xylose. Citrate, citrulline, glucuronate, leucine, malonate, methionine, putrescine, and tartrate are not utilized. The major cellular fatty acids are $C_{16:1}$, $C_{16:0}$, $C_{18:0}$, $C_{12:0}$, $C_{12:0}$ 3-OH, and $C_{14:0}$. Isolated from the light organs of fish belonging to *Leiognathidae* and *Apogonidae* families.

DNA G + C content of the type strain (mol%): 41.6 (T_m), 40.9 (genome).

Genome size and reference: 4.6 Mb. ASM21149v1.

Type strain: ATCC 25521^T (=CAIM 327^T =CCUG 16229^T =DSM 21260^T =LMG 4228^T =CIP 66.5^T).

GenBank accession number (16S rRNA): D25309, X74686.

Photobacterium lipolyticum Yoon et al. 2005^{VP}

li.po.ly'ti.cum. Gr. neut. n. *lipos*, fat; Gr. neut. adj. *lytikos*, dissolving; N.L. neut. adj. *lipolyticum*, dissolving fat or lipid.

Cells are pleomorphic. Motile by means of a single polar flagellum. Colonies on MA are circular, smooth, glistening, low-convex, and cream-colored. Optimum growth occurs between 25 and 28°C (range 4– 34°C, but not at 35°C). Growth pH is between 5.0 and 8.0 (optimum at pH 7 – 8). No growth occurs without NaCl or in the presence of more than 6% (w/v) NaCl (optimum in 1 – 2%). Oxidase and catalase are positive, but lysine decarboxylase and arginine dihydrolase are negative. Nitrate is reduced to nitrite. Aesculin, starch, and Tweens 20, 40, 60, and 80 are hydrolyzed, but not hypoxanthine, tyrosine, gelatin, urea, and xanthine. Alkaline phosphatase, esterase (C4), esterase lipase (C8), leucine arylamidase, acid phosphatase, and naphthol-AS-BI-phosphohydrolase activities are present, but valine arylamidase, cystine arylamidase, trypsin, α-chymotrypsin, α-galactosidase, β-galactosidase, β-glucuronidase, α-glucosidase, β-glucosidase, *N*-acetyl-β-glucosaminidase, α-mannosidase, and α-fucosidase are absent. D-Fructose, sucrose, maltose, malate, acetate, pyruvate, and succinate are utilized for growth, while D-galactose, D-cellobiose, D-mannose, D-trehalose, D-xylose, benzoate, butyrate, citrate, glutamate, lactate, formate, ethanol, and methanol are not utilized as sole carbon sources. Acid is produced from D-cellobiose, D-glucose, D-fructose, maltose, D-mannose, D-ribose, sucrose and D-trehalose. Acid is not produced from adonitol, *myo*-inositol, D-mannitol, D-sorbitol, L-arabinose, D-galactose, lactose, D-melezitose, melibiose, D-raffinose or L-rhamnose. The predominant respiratory quinone is Q-8. The major fatty acids are summed feature 3 ($C_{16:1}$ ω7*c* and/or iso-$C_{15:0}$ 2-OH) and $C_{16:0}$. Isolated from an intertidal sediment from the Yellow Sea of Korea.

DNA G + C content of the type strain (mol%): 47.0(HPLC), 45.9(genome).

Genome size and reference: 4.9 Mb. ASM302647v1.

Type strain: M37^T (=KCTC 10562BP^T =DSM 16190^T).

GenBank accession number (16S rRNA): AY554009.

Photobacterium lucens Enciso-Ibarra et al. 2020, VL195

lu'cens. L. part. adj. *lucens*, shining, referring to the strong luminescence of the strains.

Luminescent. Growth occurs in the salinity range of 0 – 9% (w/v) NaCl at 30°C and at pH range 4.5– 10. Green and luminescent colonies on TCBS medium. Positive for catalase, oxidase, lysine decarboxylase, arginine dihydrolase, β-galactosidase, and *N*-acetyl-D-glucosaminidase. Acids are produced from D-glucose, D-fructose, D-galactose, D-mannose, glycerol, and *N*-acetyl-glucosamine. No fermentation was observed for L-arabitol, D-arabitol, maltose, D-mannitol, adonitol, D-melibiose, L-arabinose, D-trehalose, L-rhamnose, inositol, D-cellobiose, D-sorbitol and 5-ketoglutarate. Isolated from a cultured shrimp (*Penaeus vannanei*) in Sinaloa, Mexico.

DNA G + C content of the type strain (mol%): 42 (T_m), 41.4 (genome).

Genome size and reference: 4.5 Mb. ASM987433v1.

Type strain: M09-03a^T (=CAIM 1937^T =CECT 9699^T).

GenBank accession number (16S rRNA): SSMG00000000.

Photobacterium lutimaris Jung et al. 2007^{VP}

lu.ti.ma'ris. L. neut. n. *lutum*, mud; L. gen. neut. n. *maris*, of the sea; N.L. gen. neut. n. *lutimaris*, of mud of the sea.

Cells are oval-shaped (0.9– 1.3 × 1.5 – 2.1 μm). Motile by means of a single polar flagellum. Not bioluminescent. Colonies on MA are circular to slightly irregular, flat, smooth, glistening, and pale yellow in color. Growth occurs under anaerobic conditions 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; but not in 0 or 7% NaCl. Aesculin, starch, and Tweens 20, 40, 60, and 80 are hydrolyzed. Urea, hypoxanthine, xanthine, and casein are not hydrolyzed. Ornithine decarboxylase and tryptophan deaminase are absent. Presents alkaline phosphatase, esterase (C4), esterase lipase (C8), leucine arylamidase, cystine arylamidase, acid phosphatase, and naphthol-AS-BI-phosphohydrolase, 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 not benzoate. 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. The predominant ubiquinone is Q-8. The major cellular fatty acids are summed feature 3 (iso-$C_{15:0}$ 2-OH and/or $C_{16:1}$ ω7*c*), $C_{16:0}$, and $C_{18:1}$ ω7*c*. Isolated from a tidal flat sediment at Saemankum, Korea.

DNA G + C content of the type strain (mol%): 48.3 (HPLC), 47.6 (genome).

Genome size and reference: 6.0 Mb. ASM302555v1.

Type strain: DF-42^T (=KCTC 12723^T =JCM 13586^T =DSM 21778^T).

GenBank accession number (16S rRNA): NR_043902.

Photobacterium malacitanum Labella et al. 2018a, VL185

ma.la.ci.ta'num. N. L. neut. adj. *malacitanum*, pertaining to the city of Malaga, South of Spain.

Cells are rods, motile, chemo-organotrophic, and facultatively anaerobic. Na^+ required for growth (0.5 – 8% NaCl). Growth occurs at 4 – 45°C with an optimum temperature of 22 – 30°C. No diffusible pigment production. Glucose is fermented with weak production of gas. Oxidase and catalase are positives. Reduces nitrate to nitrite, but not to N_2. It is positive for arginine dihydrolase, lysine decarboxylase, urease, amylase, acid- and alkaline phosphatases, α-chymotrypsin, phosphohydrolase, esterase, esterase-lipase, leucine-arylamidase, α-galactosidase, β-galactosidase, and *N*-acetyl-β-glucosaminidase; but negative for indole production from tryptophan, ornithine decarboxylase, trypsin, hydrolysis of gelatine and aesculin, α-glucosidase, β-glucosidase, β-glucuronidase, α-maltosidase, α-mannosidase, α-fucosidase, L-aspartic acid arylamidase, valine aryalminase, and cystine arylaminase. It produces acids from D-glucose and D-maltose, but not from L- and D-arabitol, D-mannitol, adonitol, palatinose, sucrose, melibiose, L-arabinose, D-trehalose, L-rhamnose, inositol, D-cellobiose, and D-sorbitol. Dextrin, *N*-acetyl-D-galactosamine, *N*-acetyl-D-glucosamine, D-cellobiose, D-fructose, D-galactose, α-D-lactose, lactulose, maltose, D-mannose, D-melibiose, D-psicose, methylpyruvate, *cis*-aconitic acid, formic acid, α-ketobutyric acid, α-ketoglutaricacid, dl-lactic acid, succinic acid, bromo succinic acid, L-alaninamide, L-asparagine, L-aspartic acid, glycil-L-aspartic acid, L-serine, inosine, uridine, thymidine, glycerol, DL-α-glycerol phosphate, α-D-glucose-1-phosphate, and D-glucose-6-phosphate are used as sole carbon sources. On the contrary, it is negative for the

assimilation of L-arabinose, *i*-erythritol, β-methyl-D-glucoside, xylitol, D-galactonic acid lactone, γ-hydroxybutiric acid, *p*-hydroxyphenylacetic acid, itaconic acid, α-ketovaleric acid, sebacic acid, and urocanic acid. The major cellular fatty acids are $C_{16:0}$, summed in feature 3 ($C_{16:1}$ ω7*c* and/or $C_{16:1}$ ω6*c*), and $C_{18:1}$ ω6*c*. Isolated during one episode of mortality of cultured redbanded seabream fish.

DNA G + C content of the type strain (mol%): 39.8 (T_m), 39.7 (genome).

Genome size and reference: 4.4 Mb. GCA_900185615.1.

Type strain: H27100402H^T (=CECT 9190^T =LMG 29992^T).

GenBank accession number (16S rRNA): KX943603.

Photobacterium panuliri Deep et al. 2014, VL165

pa.nu'li.ri. N.L. gen. masc. n. *panuliri*, of *Panulirus*, isolated from the spiny lobster (*P. penicillatus*) in Andaman Sea.

Cells are short rods (0.5– 0.8 × 1–3 μm), nonluminescent, and facultatively anaerobic. Colonies on MA are circular to slightly irregular, slightly elevated, and light brown in color. Temperature and pH range for growth are 15–38°C and 5.5–11, respectively. Optimum growth occurs at 28°C and pH 7.5. Na^+ ions are required for growth. Growth occurs in 0.5 – 7% (w/v) NaCl, but not in 8% NaCl (optimum 2 – 4% NaCl). Positive for catalase, oxidase, and arginine dihydrolase; negative for indole, acetoine production, lysine decarboxylase, ornithine decarboxylase, tryptophan deaminase, β-glucosidase, and β-galactosidase activities. Hydrolyses cellulose and DNA, but not starch, aesculin, gelatin, and casein. It is positive for utilization of D-mannose and D-fructose as sole source of carbon and energy. Acid production from D-glucose, D-mannose, D-fructose, *N*-acetyl-D-glucosamine, D-maltose and negative for glycerol, erythritol, D-arabinose, L-arabinose, D-ribose, D-xylose, L-xylose, D-adonitol, methyl-β-D-xylopyranoside, D-galactose, L-sorbose, L-rhamnose, dulcitol, inositol, D-mannitol, D-sorbitol, methyl-α-D-mannopyranoside, methyl-α-D-glucopyranoside, amygdalin, arbutin, salicin, D-cellobiose, D-lactose, D-melibiose, D-sucrose, D-trehalose, inulin, D-melezitose, D-raffinose, starch, glycogen, xylitol, gentiobiose, D-turanose, D-lyxose, D-tagatose, D-fucose, L-fucose, D-arabitol, L-arabitol, potassium gluconate, potassium 2-keto gluconate, and potassium 5-keto gluconate. Alkaline phosphatase, esterase (C4), esterase lipase (C8), leucine arylamidase, valine arylamidase, acid phosphatase, napthol-AS-BI-phosphohydrolase, α-glucosidase, and *N*-acetyl-β-glucosaminidase activities are positive, but negative for lipase (C14), cystine arylamidase, trypsin, α-chymotrypsin, α-galactosidase, β-galactosidase, β-glucuronidase, β-glucosidase, α-mannosidase, and α-fucosidase. Polar lipids include phosphatidylglycerol, diphosphatidylglycerol, phosphatidylethanolamine, and one unidentified lipid (L1). The major cellular fatty acids are summed feature 3 ($C_{16:1}$ ω7*c* and/or $C_{16:1}$ ω6*c*), summed feature 8 ($C_{18:1}$ ω6*c* and/or $C_{18:1}$ ω7*c*), $C_{16:0}$, iso-$C_{15:0}$, $C_{16:0}$ 10-methyl, and/or iso-$C_{17:1}$ ω9*c* and iso-$C_{17:0}$. Isolated from eggs of spiny lobster *P. penicillatus* collected from Andaman Sea, Northeastern Indian Ocean.

DNA G + C content of the type strain (mol%): 50.5 (T_m).

Genome size and reference: not available.

Type strain: LBS5^T (=DSM 27646^T =LMG 27617^T =JCM 19199^T).

GenBank accession number (16S rRNA): KC990827.

Photobacterium phosphoreum Beijerinck 1889^{AL} (*Micrococcus phosphoreus* Cohn 1878)

phos.pho're.um. Gr. masc./fem. adj. *phôsphoros*, bringing light; N.L. neut. adj. *phosphoreum*, light-bearing.

Straight rods. Motile by means of unsheathed polar flagella. Luminescent. Ubiquinone Q-8 represents 100% of the total isoprenoid quinones. May require L-methionine for optimal growth. It grows at 4°C, but not at 35 or 40°C. Optimum growth occurs at 160 – 280 mM Na^+ and 20 – 25°C. Gas production from D-glucose. Oxidase, caseinase, gelatinase, and lipase are not produced. Adonitol, L-arabinose, cellobiose, *myo*-inositol, α-D-lactose, D-mannitol, raffinose, L-rhamnose, salicin, D-sorbitol, sucrose, trehalose, and D-xylose are not fermented. Acetate, alanine, arginine, citrate, ethanol, glycine, leucine, putrescine, L-proline, pyruvate, and threonine are not used as sole carbon sources. The major cellular fatty acids are summed in feature 3 ($C_{16:1}$ ω7*c* and/or $C_{16:1}$ ω6*c*), $C_{16:0}$, summed in feature 8 ($C_{18:1}$ ω7*c* and/or $C_{18:1}$ ω6*c*), $C_{14:0}$, $C_{12:0}$, and $C_{12:0}$ 3-OH (Labella et al., 2017b). Isolated from the light organs of several fish families, such as *Macrouridae*, *Merluccidae*, *Opisthoproctidae*, *Trachichthydae*, and *Moridae*, which are usually live in deep-cold waters. *P. phosphoreum* is a psychrophilic species found at depths of 50 – 500 m.

DNA G + C content of the type strain (mol%): 40.8 (T_m), 39.6 (genome).

Genome size and reference: 4.6 Mb. ASM295472v1.

Type strain: ATCC 11040^T (=LMG 4233^T =CAIM 328^T =CIP 102511^T =DSM 15556^T =HAMBI 1726^T =JCM 21184^T =NBRC 103031^T).

GenBank accession number (16S rRNA): D25310, X74687, Z19107.

Photobacterium piscicola Figge et al. 2014, VL161

pis.ci'co.la. L. gen. masc. n. *piscis*, fish; L. masc./fem. n suff. *-cola* (from L.n. *incola*), inhabitant, dweller; N.L. masc./fem. n. *piscicola*, fish-dweller.

Cells are rods, motile, and facultatively anaerobic. Colonies are beige, round, entire, and 2 – 3 mm in diameter after 2 days of aerobic incubation on MWB agar at 20°C. Growth at 6 – 25°C and in the presence of 0.5 – 6% (w/v) NaCl. Bioluminescence after 2 – 3 days of incubation at 20°C on media supplemented with 3% NaCl. Positive results for the following activities: catalase, lysine decarboxylase, glucose oxidation, nitrate reduction, assimilation of glucose, mannose, *N*-acetyl-glucosamine, maltose, malate, production of alkaline phosphatase, leucine arylamidase, acid phosphatase, *N*-acetyl-β-glucosaminidase, reduction of triphenyl tetrazolium chloride, hydrolysis of *p-n-p*-phosphate, proline nitroanilide, *p-n-p*-bis-phosphate, and *p-n-p-N*-acetyl-glucosamidine. Negative for cytochrome oxidase production, β-galactosidase, ornithine decarboxylase, citrate utilization, H_2S production, production of urease, tryptophan deaminase, indole, acetoin, gelatin hydrolysis, oxidation of mannitol, inositol, sorbitol, rhamnose, sucrose, melibiose, amygdalin, arabinose, glucose acidification, hydrolysis of aesculin, assimilation of arabinose, mannitol, gluconate, caprate, adipate, citrate, phenyl-acetate, production of lipase, valine arylamidase, cysteine arylamidase, trypsin, α-chymotrypsin, α-galactosidase, β-galactosidase, β-glucuronidase, α-glucosidase, β-glucosidase, α-mannosidase, α-fucosidase, hydrolysis of γ-L-glutamyl *p*-nitroanilide, *p*-nitro-DL-phenylalanine, *p-n-p*-β-galactoside, *p-n-p*-xyloside, *p-n-p*-α-arabinoside, degradation of glycine and utilization of malonic acid, and adonitol. The major cellular fatty acids are summed feature 3 (iso-$C_{15:0}$ 2-OH and/or $C_{16:1}$ ω7*c*), $C_{16:0}$, and $C_{18:1}$ ω7*c*. Isolated from whiting (*Merlangius merlangus*) from the North Sea.

DNA G + C content of the type strain (mol%): 38.9 (HPLC), 39.2 (genome).

Genome size and reference: 4.5 Mb. GCA_900166965.1.

Type strain: W3^T (=NCCB 10009^T =LMG 27681^T).

GenBank accession number (16S rRNA): NR_125679.

Photobacterium profundum Nogi et al. 1998, VL66

pro.fun'dum. L. neut. adj. *profundum*, deep, living within the depth of the oceans.

Cells are rod shaped (0.8– 1.0 × 2–4 μm size). Motile by means of an unsheathed polar flagellum. Nonluminescent. The major isoprenoid quinone is Q-8. Growth occurs between 4 and 18°C at atmospheric pressure, with optimum growth displayed between 8 and 12°C. No growth occurs at 0 or 20°C. Moderately psychrophilic, growth occurs at pressures between 0.1 MPa and 70 MPa at 10°C (optimum at 10 MPa). No growth occurs in the absence of NaCl (optimum 3% NaCl, w/v). Acid is produced from D-glucose, but gas is not produced. Positive for indole production, nitrate reduction, oxidase, catalase, and arginine dihydrolase. D-Galactose, glycogen, glycerol, maltose, D-mannitol, D-mannose, trehalose, and turanose can be utilized as a sole carbon and energy sources, but not *N*-acetyl-D-galactosamine, *N*-acetyl-D-glucosamine, adonitol, L-arabinose, cellobiose, D-fructose, *myo*-inositol, α-D-lactose, raffinose, L-rhamnose, D-sorbitol or sucrose. The predominant cellular fatty acids are $C_{16:1}$, iso-$C_{16:0}$, $C_{16:0}$, $C_{18:1}$, and $C_{20:5}$ ω3*c*. Isolated from sediment at a depth of 5,110 m.

DNA G + C content of the type strain (mol%): 42.0 (HPLC), 41.4 (genome).

Genome size and reference: 6.2 Mb. ASM15342v1.

Type strain: DSJ4^T (=CIP 106289^T =JCM 10084^T).

GenBank accession number (16S rRNA): D21226.

Photobacterium proteolyticum Li et al. 2017^{VP}

pro.te.o.ly'ti.cum. N.L. neut. adj. *proteolyticum*, proteolytic.

Cells are motile rods with peritrichous flagella (1.0– 2.0 × 2.0 – 2.5 μm size). Colonies on MA are round, convex, smooth, and yellow in color. Facultatively anaerobic. Grows at 4–45°C, pH 6.0–9.5 and 1–7% (w/v) NaCl, with optimum growth occurring at 28°C, pH 6.5 – 7.0 and 2 – 3% (w/v) NaCl. Nitrate reduction and oxidase are positive. Amylase, agarase, and β-galactosidase activities are present. Produces serine protease. Catalase, cellulase and esterase are negative. Acids are produced from cellobiose, but not from D-galactose, D-mannitol, melibiose, and inulin. The following compounds are used as carbon and energy sources: *N*-acetyl-β-D-mannosamine, *N*-acetyl-neuraminic acid, *myo*-inositol, D-serine, D-galacturonic acid, D-lactic acid methyl ester, γ-aminobutyric acid, β-hydroxy-D,L-butyric acid, and citric acid; but D-galactose, melibiose, raffinose, gelatin, bromo-succinic acid, formic acid, D-saccharic acid, and sodium lactate are not used. The major menaquinone is Q-8. The polar lipids are phosphatidylethanolamine, phosphoaminolipid, and phospholipid. The major cellular fatty acids are summed feature 3 ($C_{16:1}$ ω7*c* and/or iso-$C_{15:0}$ 2-OH), $C_{16:0}$,

and $C_{18:1}$ ω5*c*. Isolated from ocean sediment from Laizhou Bay, Bohai Sea, P.R. China.

DNA G + C content of the type strain (mol%): 47.9 (genome).

Genome size and reference: 6.5 Mb. ASM193973v1.

Type strain: 13-12^T (=KCTC 42764^T =CGMCC 1.14970^T).

GenBank accession number (16S rRNA): KT971138.

Photobacterium rosenbergii Thompson et al. 2005^{VP}

ro.sen.ber'gi.i. N.L. gen. masc. n. *rosenbergii*, of Rosenberg, after the Israeli microbiologist Eugene Rosenberg.

Cells are motile with a size of 1 – 2 × 2–4 µm. Oxidase positive. Growth occurs between 20 and 30°C and in NaCl concentrations (w/v) of 2 – 6%. No growth is observed at 4 or 40°C or in 0 or 8% NaCl. Nitrate is reduced to nitrite. Negative for acetoin and indole production. Utilizes the following carbon compounds are sole energy sources: dextrin, glycogen, Tweens 40 and 80, *N*-acetyl-D-glucosamine, cellobiose, D-fructose, D-galactose, α-D-glucose, maltose, D-mannitol, D-mannose, D-melibiose, D-raffinose, methyl-β-D-glucoside, psicose, sucrose, D-trehalose, methyl pyruvate, monomethyl succinate, acetic acid, *cis*-aconitic acid, citric acid, formic acid, *p*-hydroxyphenylacetic acid, α-ketobutyric acid, α-ketoglutaric acid, DL-lactic acid, propionic acid, succinic acid, bromosuccinic acid, alaninamide, L-alanine, L-alanyl glycine, L-asparagine, L-aspartic acid, L-glutamic acid, glycyl-L-aspartic acid, glycyl-L-glutamic acid, L-histidine, L-ornithine, L-serine, L-threonine, inosine, uridine, thymidine, glycerol, DL-α-glycerol phosphate, glucose 1-phosphate, and glucose 6-phosphate. Does not utilize adonitol, L-arabinose, D-arabitol, α-D-lactose lactulose, xylitol, D-galactonic acid, γ-hydroxybutyric acid, itaconic acid, α-ketovaleric acid, malonic acid, D-saccharic acid, sebacic acid, D-alanine, hydroxyl-L-proline, L-leucine, D-serine, DL-carnitine, γ-aminobutyric acid, urocanic acid, phenylethylamine, 2-aminoethanol or 2,3-butanediol. It ferments glucose, D-mannitol, sucrose, melibiose, and amygdalin, but not sorbitol or arabinose. Presents the following enzymatic activities: arginine dihydrolase, β-galactosidase, alkaline phosphatase, esterase, esterase lipase, leucine arylamidase, valine arylamidase, acid phosphatase, naphthol-AS-BI-phosphohydrolase, and *N*-acetyl-β-glucosaminidase. Lysine and ornithine decarboxylase, urease, tryptophan deaminase, gelatinase, cystine arylamidase, trypsin, α-chymotrypsin, β-glucuronidase, β-glucosidase, α-mannosidase, and α-fucosidase activities are absent. The major fatty acids are summed feature 3 ($C_{16:1}$ ω7*c* and/or iso-$C_{15:0}$ 2-OH), $C_{18:1}$ ω7*c*, and $C_{16:0}$. Isolated from different species of bleached and healthy corals in Magnetic Island, Australia.

DNA G + C content (mol%): 47.6 (HPLC).

Genome size and reference: 6.4 Mb. ASM302645v1.

Type strain: CC1^T (=CBMAI 622^T =LGM 22223^T =DSM 19138^T).

GenBank accession number (16S rRNA): AJ842344.

Photobacterium salinisoli Li et al. 2019^{VP}

sa.li.ni.so'li. N.L. masc. adj. *salinus*, salty; L. neut. n. *solum*, soil; N.L. gen. neut. n. *salinisoli*, of salty soil, referring to the source of sampling for enrichment.

Cells are rod-shaped (0.5 – 0.8 × 1.0 – 2.5 µm size), motile, and aerobic. Colonies on MA are circular to slightly irregular and light brown in color. The temperature range for growth is from 10 to 40°C (optimum, 35°C). The pH range for growth is from pH 6.0– 11.0 (optimum, 7.0). Grows in the NaCl range of 0 and 9% (optimum in 2%). Positive for catalase but negative for oxidase, nitrate reduction, indole production, arginine dihydrolase, and urease. Tweens 20, 60, and 80 and starch are hydrolyzed. Negative for hydrolysis of casein, aesculin, and gelatin. Alkaline phosphatase, esterase (C4), esterase lipase (C8), leucine arylamidase, valine arylamidase, acid phosphatase, α-glucosidase, and *N*-acetyl-β-glucosaminidase activities are positives; negatives for trypsin, chymotrypsin, α-galactosidase, β-galactosidase, β-glucosidase, β-glucuronidase, α-mannosidase and α-fucosidase. Positive for fermentation of D-glucose, D-xylose, D-mannitol, *N*-acetyl-glucosamine, D-fructose, sucrose, trehalose, maltose, gluconate, malic acid, and citrate; negative for arabinose, mannose, capric acid, adipic acid, glycogen, and phenylacetic acid. The predominant respiratory quinone is ubiquinone Q-8. The main polar lipids are diphosphatidylglycerol, phosphatidylglycerol, phosphatidylethanolamine, aminophospholipid, and four unidentified lipids. The major fatty acids are summed feature 3 ($C_{16:1}$ ω6*c* and/or $C_{16:1}$ ω7*c*), $C_{16:0}$, and summed feature 8 ($C_{18:1}$ ω7*c* and/or $C_{18:1}$ ω6*c*). Isolated from a sulfonylurea herbicide-degrading consortium enriched with saline soil collected from Lingxian County (Shandong, P.R. China).

DNA G + C content of the type strain (mol%): 50.2 (genome).

Genome size and reference: 4.7 Mb. GCA_003614885.

Type strain: LAM9072^T (=ACCC 19961^T =JCM 30852^T).

GenBank accession number (16S rRNA): KP054474.

Photobacterium sanctipauli Moreira et al. 2014, VL161

sanc.ti.pau.li. N.L. gen. masc. n. *sanctipauli*, of Saint Paul, after the St Peter & St Paul Archipelago.

Cells are small bacilli (2– 3 μm in diameter) and motile. Colonies on MA are small, beige, irregular shaped, with smooth and translucent edge. Facultatively anaerobic. Oxidase and catalase are positive. Grows at 20 and 30°C and pH 6 – 11, but not at 4 and 45°C. Na^+ required for growth (1– 8% NaCl). Positive for alkaline phosphatase, leucine arylamidase, naphtol-AS-BI-phosphohydrolase, *N*-acetyl-β-glucosaminidase, β-galactosidase, and arginine dihydrolase; but negative for lipase, valine arylamidase, cystine arylamidase, trypsin, α-chymotrypsin, acid phosphatase, α-galactosidase, β-glucuronidase, α-glucosidase, β-glucosidase, α-mannosidase, α-fucosidase, lysine decarboxylase, ornithine decarboxylase, H_2S production, urease activity, and gelatinase. Reduces nitrate to nitrite, but not to N_2. Positive for fermentation/oxidation of glucose and mannitol, but negative for inositol, sorbitol, rhamnose, sucrose, amygdalin, and arabinose. D-Salicin, α-D-glucose, D-mannose, and D-galactose are used as sole energy sources. Does not utilize dextrin, D-raffinose, glycerol, *N*-acetyl-D-galactosamine, D-aspartic acid, D-serine, gelatin, glycyl-L-proline, L-alanine, L-arginine, L-aspartic acid, L-glutamic acid, L-pyroglutamic acid, L-serine, pectin, L-galactonic acid lactone, mucic acid, quinic acid, D-saccharic acid, *p*-hydroxy-phenylacetic acid, methyl pyruvate, D-lactic acid methyl ester, citric acid, D-malic acid, bromo-succinic acid, γ-amino-butyric acid, α-hydroxy-butyric acid, β-hydroxy-DL-butyric acid, propionic acid, acetic acid, and formic acid. The major cellular fatty acids are summed feature 3 ($C_{16:1}$ ω7*c* and/or iso-$C_{15:0}$ 2-OH), $C_{16:0}$, and $C_{18:1}$ ω7*c*. Isolated from the tissues of bleached *Madracis decactis* (Scleractinia) in St Peter & St Paul Archipelago, Brazil.

DNA G + C content of the type strain (mol%): 48.2 (T_m), 47.9 (genome).

Genome size and reference: 5.8 Mb. ASM302649v1.

Type strain: A-394^T (=LMG 27910^T =CAIM 1892^T =DSM 100436^T).

GenBank accession number (16S rRNA): NR_126275.

Photobacterium sanguinicancri Gomez-Gil et al. 2016, VL171

san.gui.ni.can'cri. L. masc. n. *sanguis*, *-inis*, blood; L. masc. n. *cancer*, crab; N.L. gen. masc. n. *sanguinicancri*, from the blood, hemolymph, of crabs.

Cells are small bacilli, motile, and nonluminescent. Growth occurs between 4 and 30°C, but not at 35°C. NaCl is required for growth. Positive for arginine dihydrolase and oxidase. Reduces nitrates to nitrites. Catalase positive, produces acetoin and gelatinase. Negative for the production of gas from D-glucose and production of H_2S, indole, or urease. Negative for lysine- and ornithine decarboxylases, and tryptophan deaminase activities. Can utilize D-maltose and glucose, but amygdalin, D-cellobiose, sucrose, D-xylose, lactose, and salicin are not utilized as sole carbon sources. Major fatty acids include summed feature 3 ($C_{16:1}$ ω6*c* and/or $C_{16:1}$ ω7*c*), $C_{16:0}$ and summed feature 8 ($C_{18:1}$ ω6*c* and $C_{18:1}$ ω7*c*). Isolated from the hemolymph of the spider crab *Maja brachydactyla* in Ria A Coruña, Galicia, Spain.

DNA G + C content of the type strain (mol%): 43.7 – 43.9 (genome).

Genome size and reference: 5.5 Mb. ASM226526v1.

Type strain: Mj110^T (=CAIM 1827^T =CECT 7579^T =DSM 24670^T).

GenBank accession number (16S rRNA): GQ454928.

Photobacterium swingsii Gomez-Gil et al. 2011^{VP}

swing'si.i. N.L. gen. masc. n. *swingsii*, of Swings, in honor of the Belgian microbiologist Jean Swings.

Cells are small coccobacilli. On MA after 24 h incubation, colonies were white, smooth, and nonluminescent. Facultatively anaerobic. Positive for oxidase, nitrate reduction, arginine dihydrolase, and acetoine production. Negative for urease, lysine decarboxylase, ornithine decarboxylase, citrate, and production of H_2S and indole. Grows between 3 and 8% NaCl, but not in 0 or 10% NaCl. Optimal growth occurs between 20 and 30°C, but not at 40°C. Utilizes as sole sources of carbon, L-arabinose, cellobiose, D-fructose, D-galactose, D-glucosamine, D-glucose, maltose, D-mannose, D-ribose, D-salicin, trehalose, methanol, glycerol, L-alanine, glycine, L-aspartate, L-glutamate, L-glutamine, L-ornithine, L-threonine, acetate, citrate, fumarate, ketoglutarate, pyruvate, propionate and succinate, but not sucrose, D-xylose, *myo*-inositol, D-sorbitol, L-lysine, L-rhamnose, D-galacturonate, D-glucuronate, malate, or *p*-hydroxybenzoate. Produces acid phosphatase, alkaline phosphatase, esterase lipase (C8), lipase (C14), leucine arylamidase, and naphthol-AS-BI-phosphohydrolase, but not α-chymotrypsin, α-fucosidase, α-galactosidase, β-galactosidase, β-glucuronidase, β-glucosidase, or α-mannosidase. Isolated from the hemolymph of wild spider crabs (*Maja brachydactyla*) from the Canary Islands, Spain. Other strains were isolated from homogenates of cultured Pacific oysters (*Crassostrea gigas*) from Northwestern Mexico.

DNA G + C content of the type strain (mol%): 46.7 (T_m), 43.7 (genome).

Genome size and reference: 5.5 Mb. ASM302643v1.

Type strain: Mj283^T (=CAIM 1393^T =CECT 7576^T =DSM 24669^T).

GenBank accession number (16S rRNA): GQ386822.

Photobacterium toruni Labella et al. 2017b^{VP}

to.ru'ni. N.L. gen. neut. n. *toruni*, from El Toruño, the first centre of investigation on aquaculture established in Andalusia, Spain, referring to the isolation location.

Cells are motile bacilli (0.6–1.1 × 2.3–3.3 µm size). Chemo-organotrophic and facultatively anaerobic. Oxidase and catalase are positive. Grows at 4, 18, and 30°C, but not at 37°C, and in 0 – 8% (w/v) NaCl. Positive for lysine decarboxylase, urease, amylase, acid- and alkaline phosphatases, naphthol-AS-BI-phosphohydrolase, esterase (C4), α-glucosidase and *N*-acetyl-β-glucosaminidase, but negative for indole production, ornithine decarboxylase, trypsin, α-chymotrypsin, hydrolysis of gelatin and aesculin, β-glucosidase, α-galactosidase, β-galactosidase, β-glucuronidase, α-maltosidase, α-mannosidase, α-fucosidase, L-aspartic acid arylamidase, valine arylamidase, and cystine arylamidase. Produces acids from D-glucose, D-galactose, D-mannose, D-fructose, and maltose; but not from L-arabitol, D-arabitol, D-mannitol, adonitol, palatinose, sucrose, melibiose, L-arabinose, trehalose, L-rhamnose, inositol, cellobiose, D-sorbitol, phenol red, galacturonate, and 5-keto-glutarate. It is not able to grow on acyclodextrin, glycogen, Tweens 40 and 80, *N*-acetyl-D-galactosamine, adonitol, D-arabitol, L-fucose, gentiobiose, *myo*-inositol, α-D-lactose, lactulose, L-arabinose, D-mannitol, melibiose, D-sorbitol, sucrose, raffinose, L-rhamnose, trehalose, D-galactonic acid lactone, *i*-erythritol, xylitol, methyl-β-D-glucoside, *p*-hydroxyphenylacetic acid, itaconic acid, α-ketovaleric acid, sebacic acid, urocanic acid, capric acid, adipic acid, and phenylacetic acid. Grows on dextrin, *N*-acetyl-D-glucosamine, cellobiose, D-fructose, D-galactose,α-D-glucose, maltose, D-mannose, D-psicose, methyl pyruvate, methyl succinate, α-ketobutyric acid, α-ketoglutaricacid, DL-lactic acid, succinic acid, bromosuccinic acid, succinamic acid, L-asparagine, L-aspartic acid, L-glutamic acid, glycyl L-aspartic acid, glycyl L-glutamic acid, L-serine, L-threonine, inosine, uridine, thymidine, glycerol, DL-α-glycerol phosphate, α-D-glucose 1-phosphate, and D-glucose 6-phosphate. The major cellular fatty acids are summed feature 3 ($C_{16:1}$ ω7*c* and/or $C_{16:1}$ ω6*c*) and $C_{16:0}$. Isolated from diseased fish-farmed redbanded seabream (*Pagrus auriga*).

DNA G + C content of the type strain (mol%): 38.6 (genome).

Genome size and reference: 4.4 Mb. GCA_900166975.1.

Type strain: H01100410B^T (=CECT 9189^T =LMG 29991^T).

GenBank accession number (16S rRNA): KX855661.

Other species

"Photobacterium atrarenae" Kim et al. 2011

a.tra.re'nae. L. fem. adj. *atra*, black, L. gen. fem. n. *arenae*, of/from sand, N.L. gen fem. n. *atrarenae*, from black sand.

Cells are short rods (0.7– 0.9 × 1.1 – 1.3 µm). Motile by a monotrichous flagellum. Colonies are circular, smooth, raised, and entire, and the colony color is beige and opaque after 1 day at 37°C on MA plates. Facultatively anaerobic. Catalase- and oxidase-positive. Cells grow at 15–40°C and not under 10°C or over 45°C (optimum at 37°C). Cells grow well in the presence of 1 – 4% (w/v) NaCl, but not 0% nor 5% NaCl, and at pH range of 6.5 – 9.5 (optimum at pH 7 – 8). Positive for hydrolysis of casein, starch, gelatin, L-tyrosine, and Tweens 20, 40, 60, and 80; but negative for aesculin hydrolysis. Nitrate is reduced to nitrite. D-Glucose, *N*-acetylglucosamine, D-maltose, malic acid, and trisodium citrate are assimilated; but not L-arabinose, D-mannose, D-mannitol, potassium gluconate, capric acid, adipic acid, and phenylacetic acid. Arginine dihydrolase, urease, and β-galactosidase activities are absent. Positive for alkaline phosphatase, esterase (C4), esterase lipase (C8), and leucine arylamidase, but negative for valine arylamidase, cystine arylamidase, trypsin, α-chymotrypsin, naphthol-AS-BI-phosphohydrolase, α-galactosidase, β-galactosidase, β-glucuronidase, α-glucosidase, β-glucosidase, *N*-acetyl-β-glucosaminidase, α-mannosidase, and α-fucosidase. Acid is produced from glycerol, D-ribose, D-glucose, D-fructose, inositol, *N*-acetylglucosamine, D-maltose, D-trehalose, starch, and glycogen. Utilizes as sole carbon source dextrin, glycogen, Tweens 40 and 80, *N*-acetyl-D-glucosamine, D-fructose, α-D-glucose, *myo*-inositol, maltose, D-trehalose, pyruvic acid methyl ester, *cis*-aconitic acid, β-hydroxybutyric acid, α-keto glutaric acid, DL-lactic acid, succinic acid, bromosuccinic acid, L-alanine, L-alanyl-glycine, L-asparagine, hydroxy-L-proline, L-proline, L-serine, L-threonine, inosine, thymidine, and glycerol. The predominant fatty acids are summed feature 3 ($C_{16:1}$ ω7c and/or iso-$C_{15:1}$ 2-OH), $C_{16:0}$, and $C_{18:1}$ ω7*c*. Isolated from Black Sea sand.

DNA G + C content of the type strain (mol%): 53.6 (HPLC).

Genome size and reference: not available.

Type strain: M3-4^T(=KCTC 23265^T =NCAIM B02414^T).

GenBank accession number (16S rRNA): HM452945.

"*Photobacterium mandapamensis*"
Hendrie et al. 1970 (synonym: *Photobacterium leiognathi* Reichelt and Baumann 1975, homotypic synonym: '*P. leiognathi* subsp. *mandapamensis*' Ast and Dunlap 2004)

man.da.pam.en'sis. N.L. masc./fem. adj. *mandapamensis*, named after the bacterium isolated from seawater in Mandapam.

Short rods or coccobacilli (0.4– 1.0 × 1.0 – 2.5 μm). Motile by polar flagella. Blue luminescence. Grows at 37°C but not at 5°C, and at pH 6 to 9. Growth in 0.5 – 5% NaCl (w/v), but not in 0% or in 7.5% NaCl. Facultatively anaerobic or aerobic. Nitrite is produced from nitrate. Indole and acetoine are not produced. Oxidase negative and catalase positive. Arginine dihydrolase, lysine decarboxylase, and lipase are present, but ornithine decarboxylase is absent. Tweens 20 and 40, and chitin are hydrolyzed, but not Tweens 60 and 80, or starch. Gas from D-glucose negative. Acid from D-glucose, D-fructose, D-galactose, and D-mannose is formed, but negative fermentation is obtained from arabinose, rhamnose, ribose, xylose, fucose, lactose, sucrose, maltose, trehalose, sorbose, cellobiose, raffinose, cellulose, mannitol, dulcitol, sorbitol, glycerol, inositol, salicin, dextrin, inulin, laminarin, starch or glycogen. Utilizes *N*-acetyl-glucosamine, acetate, succinate, fumarate, DL-malate, DL-lactate, DL-glycerate, pyruvate, glycerol, L-α-alanine, L-serine, L-aspartate, L-glutamate, and L-proline. Differs from *P. leiognathi* in the organization of the *luxCDAB(F)E* genes (Ast and Dunlap, 2004). Isolated from seawater in Mandapam, India.

DNA G + C content of the type strain (mol%): 42.0 (genome).

Genome size and reference: 4.6 Mb. ASM21149v1.

Type strain: ATCC 27561^T.

GenBank accession number (16S rRNA): NR_115206.

"*Photobacterium marinum*"
Srinivas et al. 2013

ma.ri'num. L. neut. adj. *marinum*, of the sea, marine.

Cells oval to slightly curved rod shaped (1.0– 1.2 × 1.5 – 2.0 μm size), motile, and facultatively anaerobic. Colonies on MA are circular, smooth, shiny, translucent, and raised with entire margins. Grows at 10 – 37°C with an optimum temperature of 30 – 37°C and at pH 5 – 10 range (optimum 7 – 8). Tolerates up to 8% (w/v) NaCl, requiring NaCl for growth. Oxidase, arginine dihydrolase, and lysine decarboxylase activities are present, but catalase and ornithine decarboxylase activities are absent. Nitrate is reduced to nitrite. H_2S, indole, and acetoine are not produced. Accumulate PHB granules. Bioluminescence is not observed. Tweens 20, 40, and 60 are hydrolyzed. Aesculin, agar, casein, and starch are not hydrolyzed. Positive Ala-PhePro-arylamidases and urease activities, but negative for glutamyl arylamidase, γ-glutamyl-transferase, lipase, tyrosine arylamidase, phosphatase, glycine arylamidase, glu-gly-arg-arylamidases, L-pyrrolidonyl arylamidase, β-*N*-acetylglucosaminidase, β-glucosidase, β-xylosidase, β-alanine arylamidase, L-proline arylamidase, α-glucosidase, β-*N*-acetyl-galactosaminidase, α-galactosidase, β-galactosidase, and β-glucuronidase activities. Fermentation of D-glucose is positive with production of gas. Does not utilize adonitol, L-arabitol, D-cellobiose, citrate, D-maltose, D-mannitol, D-mannose, palatinose, D-sorbitol, sucrose, D-tagatose, D-trehalose, malonate, 5-keto-D-gluconate, L-histidine, courmarate, L-malate and L-lactate. Polar lipids: Phosphatidylethanolamine, two unidentified phospholipids (PL1 and PL2), and three unidentified lipids (L1-L3). Isolated from a sediment sample collected from offshore Rameswaram, Palk Bay, India.

DNA G + C content of the type strain (mol%): 46.8 (T_m), 46.2 (genome).

Genome size and reference: 5.5 Mb. GCA_000331515.1.

Type strain: AK15^T (=MTCC 11066^T =DSM 25368^T).

GenBank accession number (16S rRNA): NR_133050.

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