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Photobacterium chitinilyticum sp. nov., a marine bacterium isolated from seawater at the bottom of the East China Sea

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Abstract

A Gram-stain-negative, facultative aerobic, motile by a polar flagellum, rod-shaped strain, designated BEI247^T, was isolated from seawater at the bottom of the East China Sea. Phylogenetic analysis of the 16S rRNA gene and whole genome data affiliated it with the genus *Photobacterium*. It was most closely related to *Photobacterium alginatilyticum* P03D4^T (97.36 % 16S rRNA gene similarity). Multi-locus sequence analysis (MLSA) revealed a distinct lineage with *P. alginatilyticum* P03D4^T as its closest relative. Strain BEI247^T was found to have lower than 86.0 % similarities to the type strains of its most closely related species in MLSA, less than 82.3 % using genome average nucleotide identities, and less than 25.3 % in DNA–DNA relatedness studies. Growth occurred at 10–37 °C (optimum, 24 °C), pH 5.0–8.0 (pH 7.0) and in the presence of 1–5 % (w/v) NaCl (3 %). The dominant fatty acids were summed feature 3 ($C_{16:1}\omega7c$ and/or $C_{16:1}\omega6c$) and $C_{16:0}$. The polar lipids of strain BEI247^T comprised phosphatidylglycerol, phosphatidylcholine, phosphatidylethanolamine, two phospholipids and one unknown lipid. The major respiratory quinone was ubiquinone-8 (Q-8). The DNA G+C content of strain BEI247^T was 46.45 mol%. On the basis of the polyphasic evidence, strain BEI247^T is proposed as representing a novel species of the genus *Photobacterium*, for which the name *Photobacterium chitinilyticum* sp. nov. is proposed. The type strain is BEI247^T (=JCM 32689^T=MCCC 1K03517^T=KCTC 62619^T).

The genus *Photobacterium*, belonging to the family *Vibrionaceae* of the class *Gammaproteobacteria*, was first reported by Beijerinck [1] and is composed of 29 species and two subspecies with validly published names (www.bacterio.net). *Photobacterium* has a worldwide distribution, including seawater, marine sediments, saline lakes and a variety of marine organisms [2–6]. Several species are able to grow not only on standard media, but also on selective media, such as thiosulphate–citrate–bile salts–sucrose (TCBS), which has been widely used for vibrios isolation [2, 3]. Members of the genus *Photobacterium* are Gram-stain-negative, facultative aerobic, non-sporulating, motile by means of one to three unsheathed polar flagella, plump and straight rod-shaped bacteria that require NaCl for growth [7]. Q-8 is the predominant respiratory quinone, and $C_{16:1}$ and $C_{16:0}$ are the major fatty acids [8]. Species of the genus *Photobacterium* were originally thought to be mostly luminescent, but more than half of the recognized species in the genus do not display this ecologically important character. Six species within the genus *Photobacterium* have luminescent ability, i.e. *Photobacterium phosphoreum* [9] (the type species of the genus), *Photobacterium leiognathi* [10], *Photobacterium aquimaris* [3], *Photobacterium angustum* [11], *Photobacterium ganghwense* [12] and *Photobacterium kishitanii* [13]. In addition, the latest described species is *Photobacterium carnosum*, which was isolated from spoiled modified atmosphere packaged poultry meat [14]. Here, we report the taxonomic characterization of a novel species belonging to the genus *Photobacterium* that exhibits mesophilic and facultative aerobic properties, designated BEI247^T, for which the name *Photobacterium chitinilyticum* sp. nov. is proposed. A polyphasic approach was used for investigating its taxonomy.

Strain BEI247^T, isolated from seawater at the bottom of the East China Sea, was picked as a single colony on TCBS agar

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Keywords: *Photobacterium chitinilyticum*; bottom seawater; East China Sea.
Abbreviations: ANI, average nucleotide identity; DDH, DNA–DNA hybridization; HPLC, high-performance liquid chromatography; JCM, Japan Collection of Microorganisms; MB, marine broth; ML, maximum-likelihood; MLSA, multi-locus sequence analysis; MP, maximum-parsimony; NJ, neighbour-joining; TCBS, thiosulphate-citrate-bile salts-sucrose; WGS, whole genome sequence.
The Whole Genome Shotgun project of strain BEI247^T has been deposited at DDBJ/ENA/GenBank under the accession number RJLM00000000. The version described in this paper is version RJLM01000000. The GenBank accession number for the 16S rRNA gene sequence of BEI247^T is MG754451.
Four supplementary figures and two supplementary tables are available with the online version of this article.

after 2 days of incubation at 28 °C and purified by streaking three times on marine agar 2216E (MA; Becton Dickinson). The sample was collected in March 2017 from site ME4 (42.2 m depth; 19.2 °C; pH 8.04; salinity, 34.4 %; 28.5880° N 122.2404° E) using a Sealogger CTD (SBE25, Electronic Inc.) rosette water sampler. The most closely related strain *Photobacterium alginatilyticum* P03D4^T, obtained from our laboratory, and the type species *P. phosphoreum* JCM 21184^T, obtained from the Japan Collection of Microoorganisms (JCM), were chosen as reference strains in this study. The two reference species were cultured under the same experimental conditions as those used for BEI247^T [MA/marine broth 2216 (MB; BD); 28 °C].

The genomic DNA of strain BEI247^T was extracted according to the procedure of Moore *et al.* [15], and the DNA G+C content was determined by whole genome sequencing, which was performed on the Illumina HiSeq platform. SOAPdenovo assembler software was applied to assemble the reads [16] (http://sourceforge.net/projects/soapdenovo2/files/SOAPdenovo2/). PCR amplification, cloning and sequencing of the 16S rRNA gene were performed according to Zhang *et al.* [17]. The almost-complete 16S rRNA gene sequence (1517 nt) was manually checked and submitted to the GenBank database. Pairwise similarity values between strain BEI247^T and closely related type strains were calculated using the EzBioCloud server (www.ezbiocloud.net/; [18]). The 16S rRNA gene sequences of the related strains were retrieved from the NCBI database (www.ncbi.nlm.nih.gov) and aligned by using the CLUSTAL_X program [19]. Phylogenetic trees based on the neighbour-joining (NJ; Fig. 1), maximum-likelihood (ML; Fig. S1, available in the online version of this article) and maximum-parsimony (MP; Fig. S2) algorithms were reconstructed by the software package MEGA version 7.0 [20]. The genetic distance matrices were calculated by Kimura's two-parameter model [21] for the NJ and ML trees. The topologies of phylogenetic trees were evaluated based on the bootstrap resampling method with 1000 replicates. The relationship between strain BEI247^T and other type strains of species of the genus *Photobacterium* was also evaluated through Multi-locus sequence analysis (MLSA; [22]; Fig. 2). The MLSA was performed by using eight gene sequences (*ftsZ*, *gapA*, *gyrB*, *mreB*, *pyrH*, *recA*, *topA* and the 16S rRNA gene) and all the gene sequences of strain BEI247^T were extracted from its genome sequences (Table S1) [23].

According to the nearly complete 16S rRNA gene sequence (1517 nt) of strain BEI247^T, pairwise alignment showed the highest sequence similarity of 97.36 % to *P. alginatilyticum* P03D4^T [24]. Phylogenetic analysis based on the NJ (Fig. 1), ML (Fig. S1) and MP (Fig. S2) algorithms showed that strain BEI247^T formed a distinct cluster within the genus *Photobacterium*. However, there were a relatively low level of sequence similarities to the type strains in recognized species of the genus*Photobacterium*. Furthermore, in the MLSA, strain BEI247^T showed the highest similarity (86.0 %) to *P. alginatilyticum* P03D4^T (Fig. 2), which indicted that strain BEI247^T belonged to the genus *Photobacterium* and implied that strain BEI247^T may represent a novel species [25].

For the comparison of genome relatedness, genome data for *P. phosphoreum* JCM 21184^T and other 25 species were obtained from the GenBank database. Genome data for *P. alginatilyticum* P03D4^T was sequenced by our laboratory. The level of pairwise genome-based similarity was evaluated based on both the average nucleotide identity (ANI) value determined by using orthoANI (www.ezbiocloud.net/tools/orthoani) described by Yoon *et al.* [18] and a genome-to-genome distance calculation performed by using the Genome-to-Genome Distance Calculator software version 2.1 (http://ggdc.dsmz.de/distcalc2.php). Formula 2 was used as recommended for the calculation of DNA–DNA hybridization (DDH) for incomplete genomes.

The genome of strain BEI247^T was 5.93 Mbp including 295 contigs with N50 as 473 535, 5160 coding sequences. The ANI values of strain BEI247^T and its reference species *P. phosphoreum* JCM 21184^T and *P. alginatilyticum* P03D4^T were 72.1 and 82.3 %, respectively, which were much lower than the cut-off value of 95–96 %. The digital DDH values between strain BEI247^T and *P. phosphoreum* JCM 21184^T and *P. alginatilyticum* P03D4^T were 19.9 and 25.3 %, respectively, which were lower than the cut-off point of 70 % for the delineation of a novel species.

Gram-staining and flagellum-staining were investigated using standard methods [26]. The presence of gliding motility was investigated using the methods described by Bernardet *et al.* [27]. The cellular morphology of strain BEI247^T was determined by transmission electron microscopy (JEM–1200EX; JEOL) after cells were stained negatively with 1 % (w/v) phosphotungstic acid. To test for anaerobic growth, bacterial strains were cultured on MA with resazurin (0.02 %, w/v) as an indicator of anaerobic conditions in an anaerobic jar filled with nitrogen and a packet of AneroPack-Anaero (Mitsubishi Gas Chemical) at 28 °C for 1 month. The temperature range for growth was determined on MA plates by incubating at 10–44 °C (10, 16, 24, 28, 30, 37 and 44 °C) for 5 days, and at 0 and 4 °C on MA for at least 30 days. Luminescence was observed in the dark on an MA plate. In addition, luminous medium (LM) was also used to detect luminescence of strain BEI247^T as described by Trick [28]. In the salinity experiment, distilled water was used to prepare synthetic marine ZoBell broth (per litre: 5 g peptone, 1 g yeast extract and 0.1 g $FePO_4$). NaCl concentrations were adjusted to 0, 0.5 and 1–15 % (w/v, at intervals of 1.0 %). Salinity tolerance and pH ranges for growth were investigated in test tubes. The pH range from pH 5.5 to 11.0 at intervals of 0.5 pH unit for growth was determined in MB, using the following buffer systems: MES (pH 5.0–6.0), MOPS (pH 7.0), Tricine (pH 8.0), TAPS (pH 9.0), CAPS (pH 10.0) and Na_2CO_3/$NaHCO_3$ (pH 11.0). Various phenotypic properties of strain BEI247^T and two reference strains were tested according to standard approaches [29] except that sterile seawater (pH 7.0, 3 % NaCl) was substituted for

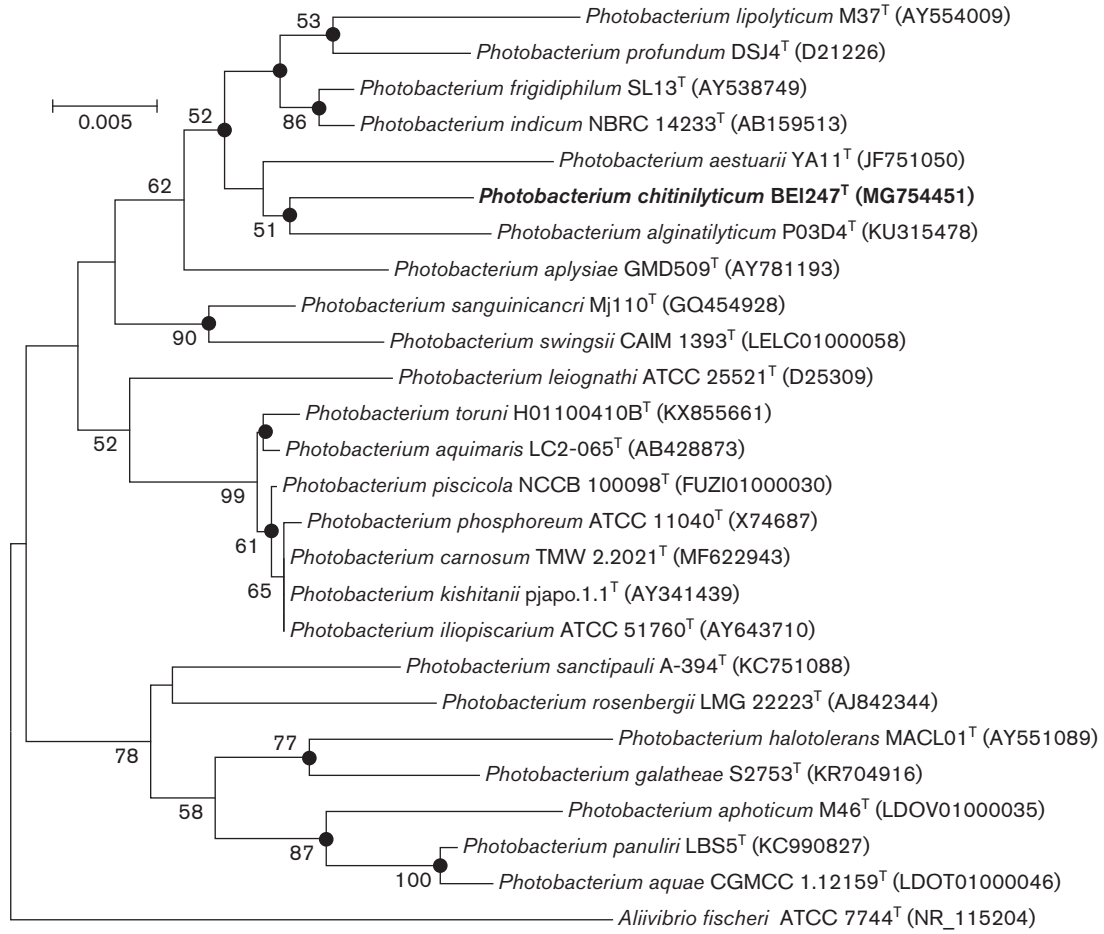

Fig. 1. Neighbour-joining phylogenetic tree based on 16S rRNA gene sequences (1517 nt) showing the phylogenetic positions of strain BEI247^T and other closely related species. Percent bootstrap values ≥50 (1000 replicates) are shown at branch nodes. Closed circles indicate that the corresponding nodes were also recovered in the tree generated with the maximum-likelihood and maximum-parsimony algorithms. *Aliivibrio fischeri* ATCC 7744^T (GenBank accession no. NR_115204) was used as an outgroup. Bar, 0.005 substitutions per nucleotide position.

distilled water, including activities of catalase, oxidase and hydrolysis of starch, casein, gelatin and Tweens 20, 40 and 80. Chitin (1.0 %, w/v) and sodium alginate (2.0 %, w/v) were added to MA plates to determine the degradation by the formation of clear zones around colonies directly or after flooding with appropriate solutions [30]. DNase agar (Qingdao 96 Hope Bio-technology) prepared with sterile water was used to detect the DNase activity according to the manufacturer's instructions. Activities of constitutive enzymes and other physiological properties were determined after growth on MA at 28 °C for 2 days by using API 20E, API 50CH and API ZYM strips (bioMérieux) and GN3 MicroPlates (Biolog) according to the manufacturers' instructions, except that the strips were inoculated with sterile seawater [31]. The morphological, physiological and biochemical characteristics of strain BEI247^T are shown in Table 1, Fig. S3 and the species description.

For cellular fatty acid analysis, strain BEI247^T and the related reference strains were grown on MA at 28 °C for 12 h until the bacterial communities reached the late-exponential stage of growth according to the four quadrant streak method [32]. Fatty acid methyl esters were prepared and analysed according to the standard protocol of MIDI (Sherlock Microbial Identification System, version 6.10), and identified by using the TSBA6.0 database of the Microbial Identification System [32]. For analyses of polar lipids and the respiratory quinone, cell biomass of strain BEI247^T and the related reference strains were harvested from MB after shaking at 28 °C for 48 h and freeze-dried. Polar lipids of strains BEI247^T, *P. phosphoreum* JCM 21184^T and *P. alginatilyticum* P03D4^T were extracted according to the procedures described by Minnikin *et al.* [33] and separated by two-dimensional TLC on silica gel 60 F254 plates (Merck) [34]. The identification of individual lipids was conducted by spraying with the appropriate detection reagents [35].

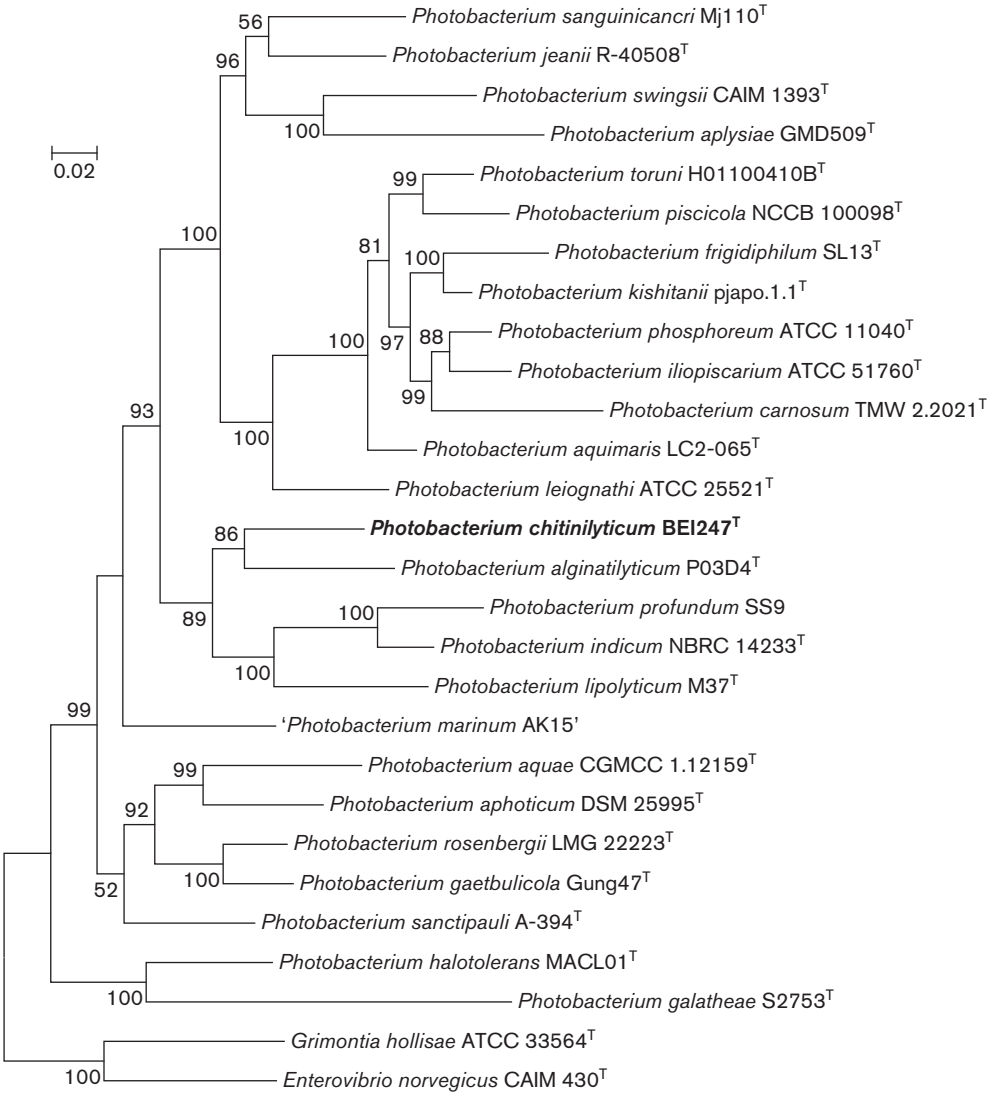

Fig. 2. Phylogenetic tree based on concatenated sequences of the *ftsZ* (1216 bp), *gapA* (849 bp), *gyrB* (2269 bp), *mreB* (773 bp), *pyrH* (741 bp), *recA* (1064 bp), *topA* (2654 bp) and 16S rRNA (1458 bp) genes, reconstructed by using the neighbour-joining method. Two strains, *Enterovibrio norvegicus* CAIM 430^T and *Grimontia hollisae* ATCC 33564^T, were used as outgroups. Bootstrap values were expressed based on 1000 replications; only values 50 % or above are shown at the nodes. Bar, 0.02 nucleotide substitutions per 100 nucleotides.

The respiratory quinone of strain BEI247^T and other two reference strains were extracted with chloroform/methanol (2 : 1, v/v), separated by TLC and identified by HPLC as described by Xie and Yokota [36].

The cellular fatty acid profile of strain BEI247^T and the reference strains are given in Table S2. The major cellular fatty acids of strain BEI247^T (>10 % of the total fatty acids) were summed feature 3 ($C_{16:1}\omega7c$ and/or iso-$C_{15:0}$ 2-OH; 52.5 %) and $C_{16:0}$ (23.3 %). The overall fatty acid profile of strain BEI247^T was similar to those of the reference strains, although there were some differences in the respective proportions of some components. Moreover, compared to the two reference strains, strain BEI247^T had higher amounts of $C_{14:0}$ and $C_{18:0}$, but less $C_{12:0}$ 3-OH and summed feature 2 [any combination of an unknown fatty acid (equivalent chain length 10.928), $C_{12:0}$ aldehyde, $C_{14:0}$ 3-OH and/or iso-$C_{16:1}$ I] (Table S2). The major polar lipids (Fig. S4) detected in strain BEI247^T were phosphatidylglycerol, phosphatidylcholine, phosphatidylethanolamine, two phospholipids and one unknown lipid, which were identical to the two reference strains. The predominant respiratory quinone detected in strain BEI247^T was ubiquinone-8 (Q-8), which was consistent with other members of the genus *Photobacterium*. The DNA G+C content of strain BEI247^T was

Table 1. Differential characteristics between strain BEI247^T and the reference strains of phylogenetically related species of genus *Photobacterium*

Strains: 1. *Photobacterium chitinilyticum* BEI247^T (this study); 2. *Photobacterium alginatilyticum* P03D4^T (this study; [24]); 3, *Photobacterium phosphoreum* JCM 21184^T (this study; [5, 8, 9]); 4. *Photobacterium frigidiphilum* SL13^T [38]; 5, *Photobacterium aestuarii* YA11^T [7]; 6, *Photobacterium aplysiae* GMD509^T [39]; 7, *Photobacterium lipolyticum* M13^T [40]; 8, *Photobacterium profundum* DSJ4 [8]; 9, *Photobacterium indicum* NBRC 14233^T [41, 42]. All the strains are positive for nitrate reduction, acid production from glucose and require NaCl for growth. All strains have Q-8 as a respiratory quinone. +, Positive reaction; –, negative reaction; ND, no data available.

Characteristic	1	2	3	4	5	6	7	8	9
Flagellum (polar)	1	1	1–3	1	1	1	1	1	1
Luminensence	–	–	+	–	–	–	–	–	–
Oxidase	+	+	–	+	+	+	+	+	–
Optimum growth temperature (°C)	24	32	18	14	20	25	25–28	10	25
Growth with/at:									
4 °C	–	–	+	–	–	–	+	+	+
35 °C	+	+	–	–	–	–	–	–	–
6 % NaCl	–	+	–	+	+	–	–	+	ND
Hydrolysis of:									
DNA	+	+	+	–	ND	ND	ND	ND	ND
Gelatin	+	–	–	+	+	+	–	ND	–
Alginate	–	+	–	–	ND	ND	ND	ND	ND
Starch	+	–	+	–	–	ND	+	ND	–
Utilization of (Biolog GN–III):									
Cellobiose	+	–	–	–	–	+	+	–	ND
L-Rhamnose	+	–	–	–	–	–	–	ND	ND
D-Sorbitol	+	–	–	–	–	–	–	ND	ND
D-Fructose	+	+	+	+	+	+	+	–	ND
α-D-Glucose	–	+	+	+	–	–	+	+	+
D-Mannitol	+	+	–	+	+	+	–	+	ND
D-Mannose	+	+	+	+	+	+	+	+	ND
D-Galactose	–	–	–	+	+	+	–	+	ND
N-Acetyl-D-glucosamine	+	–	+	+	–	+	–	–	+
myo-Inositol	–	–	–	+	–	–	–	–	ND
Maltose	–	–	+	+	–	+	+	+	+
Propionic acid	+	–	–	+	–	–	ND	ND	ND
Sucrose	–	–	–	+	–	+	+	–	+
Trehalose	–	–	–	+	–	+	+	+	+
D-Glucuronic acid	+	–	–	+	–	–	+	ND	ND
Turanose	+	–	–	+	–	–	ND	–	ND
L-Alanine	+	+	–	+	+	+	–	+	ND
L-Glutamic acid	–	+	–	+	–	+	–	ND	ND
Glycerol	–	+	–	+	+	+	ND	+	ND
API 20E and 20NE:									
Arginine dihydrolase	+	+	–	+	+	+	–	+	+
Indole production	+	+	–	+	–	–	+	+	+
Gelatinase	+	+	–	+	+	+	–	ND	–
β-Galactosidase	–	–	+	+	+	+	–	+	+
DNA G+C content (mol%)	46.5	47.9	39.1	43.8	44.2	45.0	47.0	42.0	40.0

46.45 mol%, which was within the range (40.2–50.6 mol%) for the genus *Photobacterium* [37].

The major features of strain BEI247^T, including major respiratory quinone, hydrolysis of Tweens 20 and 40, the presence of catalase and DNase activities, utilization of D-fructose, D-mannose and D-mannitol, nitrate reduction, glucose fermentation, the predominant cellular fatty acids (Table S2), and polar lipid profile were similar to the reference strains, which showed a close phylogenetic relationship (Table 1). In addition, the results based on 16S rRNA gene sequences and MLSA showed that strain BEI247^T formed a distinct cluster with *P. alginatilyticum* P03D4^T. All the above characteristics demonstrated that the strain BEI247^T belonged to the genus *Photobacterium*. However, the ANI values and digital DDH values were much lower than the

cut-off values, and the relatively low level of 16S rRNA gene sequence similarity to *P. alginatilyticum* P03D4^T implied that strain BEI247^T represented a novel species in genus *Photobacterium*. Moreover, strain BEI247^T could be clearly differentiated from the reference strains based on some features including cell morphology, the temperature and NaCl ranges that support growth, indole production, hydrolysis of starch, alginate and gelatin, and numerous enzyme activities (Table 1) and differences in the proportion of some fatty acids (Table S2). On the basis of phenotypic characteristics and phylogenetic inferences, strain BEI247^T is considered to represent a novel species of the genus *Photobacterium*, for which the name *Photobacterium chitinilyticum* sp. nov. is proposed.

DESCRIPTION OF *PHOTOBACTERIUM CHITINILYTICUM* SP. NOV.

Photobacterium chitinilyticum [chi.ti.ni.ly'ti.cum. N.L. n. *chitinum* chitin; N.L. masc. adj. *lyticus* (from Gr. masc. adj. *lytikos*) able to loosen, able to dissolve; N.L. neut. adj. *chitinilyticum* chitin-dissolving].

Cells are Gram-stain-negative, facultative aerobic, motile by means of a polar flagellum and rod–shaped. The cell size is approximately 1.2–2.7 µm long and 0.5–0.9 µm wide after culturing on MA for 6 h at 28 °C. Colonies are non-transparent, shiny, smooth circular (0.5–1.0 mm in diameter) and convex on MA after 24 h at 28 °C. Growth occurs on thiosulphate–citrate–bile salts–sucrose medium (TCBS agar; Oxoid), producing yellow colonies. Non–luminescent is observed on MA and LM plate. 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 5.0–8.0 (optimum, pH 7.0). Oxidase and catalase activities are positive. Positive for hydrolysis of DNA, gelatin, chitin, starch, CM-cellulose and Tweens (20, 40 and 80), but negative for hydrolysis of casein and alginate. In the API 20E strips, 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. In API 50CH strips, acid is produced from methyl α-D-mannopyranoside, methyl α-D-glucopyranoside, lactose, xylitol, gentiobiose, turanose, D-lyxose, D-tagatose, D-fucose and potassium 5-ketogluconate, but not from other substrates. In API ZYM strips, esterase (C4), esterase lipase (C8), lipase (C14), valine arylamidase, cystine arylamidase, trypsin, α-chymotrypsin, α-galactosidase, β-galactosidase, β-glucuronidase, α-glucosidase, β-glucosidase, α-fucosidase, α-mannosidase and *N*-acetyl-β-glucosaminidase activities are present; alkaline phosphatase, leucine arylamidase, acid phosphatase and naphthol-AS-BI-phosphohydrolase are absent. There are positive reactions in the Biolog GN3 MicroPlate system for 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-PO4, L-alanine, L-histidine, D-glucuronic acid, glucuronamide, citric acid, L-malic acid, nalidixic acid, Tween 40, acetoacetic acid, propionic acid, acetic acid, 1 % NaCl, 1 % sodium lactate, troleandomycin, lincomycin, vancomycin and aztreonam. The dominant fatty acids are summed feature 3 ($C_{16:1}\omega7c$ and/or $C_{16:1}\omega6c$) and $C_{16:0}$. The major respiratory quinone is Q-8. The major polar lipids are phosphatidylglycerol, phosphatidylcholine, phosphatidylethanolamine, two phospholipids and one unknown lipid.

The type strain, BEI247^T (=JCM 32689^T=MCCC 1K03517^T =KCTC 62619^T), was isolated from a sample of sea water collected at the bottom of the East China Sea (28.5880° N, 122.2404° E). The DNA G+C content of the type strain is 46.45 mol%. The Whole Genome Shotgun project of strain BEI247^T has been deposited at DDBJ/ENA/GenBank under the accession number RJLM00000000, and the GenBank accession number for the 16S rRNA gene sequence of BEI247^T is MG754451.

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Conflicts of interest
The authors declare that there are no conflicts of interest.

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