Photobacterium aphoticum sp. nov., isolated from coastal water

Teresa Lucena, María A. Ruvira, Javier Pascual, Esperanza Garay, M. Carmen Macián, David R. Arahál and María J. Pujalte

Correspondence

María J. Pujalte
maria.j.pujalte@uv.es

Departamento de Microbiología y Ecología, Colección Española de Cultivos Tipo (CECT), Universidad de Valencia, Spain

A facultatively anaerobic marine gammaproteobacterium, designated strain M46^T, was isolated from Mediterranean seawater at Malvarrosa beach, Valencia, Spain. The strain was characterized by using a polyphasic approach and was found to be situated within the genus *Photobacterium* in the family *Vibrionaceae*. Phylogenetic analysis based on 16S rRNA gene sequences showed that strain M46^T was closely related to *P. rosenbergii* CECT 7644^T, *P. halotolerans* CECT 5860^T and *P. ganghwense* CECT 7641^T, showing sequence similarities of 96.8, 96.4 and 96.2 %, respectively. According to the results of phylogenetic analyses based on *recA* and *gyrB* gene sequences, the most closely related taxon was *P. ganghwense* CECT 7641^T with 87.4 and 85.0 % sequence similarity, respectively. Regardless of the gene used in phylogenetic analysis, strain M46^T always formed a separate and stable clade containing these three species of the genus *Photobacterium*. Strain M46^T was not luminescent and produced a diffusible brown pigment. It required NaCl to grow, reduced nitrate to nitrite and oxidized a small number of substrates in Biolog GN plates. Strain M46^T was positive for arginine dihydrolase (ADH), β -galactosidase, aesculin hydrolysis and DNase activity. In API ZYM tests, the novel strain was positive for alkaline phosphatase, leucine arylamidase and acidic phosphatase activities. The major cellular fatty acids were unsaturated C₁₈ and C₁₆, as in other members of the genus *Photobacterium*, but their relative amounts and the presence or absence of other fatty acids differentiated strain M46^T from its closest relatives. Based on the results of this polyphasic taxonomic study, strain M46^T represents a novel species of the genus *Photobacterium*, for which the name *Photobacterium aphoticum* is proposed. The type strain is M46^T (=CECT 7614^T =KCTC 23057^T).

At the time of writing, the genus *Photobacterium*, of the family *Vibrionaceae*, contained sixteen species, most of which were isolated from seawater sampled at different depths, others having been isolated from marine animals. Defined as being facultatively anaerobic and weakly halophilic, 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. Only *P.*

phosphoreum, the type species of the genus, *P. leiognathi*, *P. aquimaris*, *P. kishitanii* and *P. ganghwense* have been described as being luminescent. Some of the luminescent species are symbionts of deep-sea fishes that hold them in specialized luminous organs (Ast & Dunlap, 2005; Dunlap & Ast, 2005), while other species, such as *P. damsela*, are pathogenic for marine animals. Phylogenetic positions of other members of the family *Vibrionaceae* showed members of the genus *Photobacterium* grouping with members of the genus *Aliivibrio*, whose earliest named species, *A. fischerii* and *A. logei* were once classified as species of the genus *Photobacterium*. Members of the recently described genera *Grimontia* and *Enterovibrio* also group with *P. damsela* in some phylogenetic analyses using 16S rRNA gene sequences. Intrageneric relationships present between members of the genus *Photobacterium* usually mean that they are distributed into three clades (Jung *et al.*, 2007; Park *et al.*, 2006; Rivas *et al.*, 2006; Yoshizawa *et al.*, 2009); the first containing *P. phosphoreum* along with *P. iliopiscarium*, *P. angustum*, *P. aquimaris* and

Abbreviations: NJ, neighbour-joining; ML, maximum-likelihood; MP, maximum-parsimony.

The GenBank/EMBL/DDBJ accession number of 16S rRNA gene of strain CECT 7614^T is FN796493. Accession numbers of newly reported *gyrB* and *recA* gene sequences of *Photobacterium aphoticum* CECT 7614^T, *Photobacterium angustum* CECT 5690^T, *Photobacterium halotolerans* CECT 5860^T, *Photobacterium ganghwense* CECT 7641^T and *Photobacterium rosenbergii* CECT 7644^T are FN796483–FN796487 and FN796488–FN796492, respectively.

Three supplementary figures and one supplementary table are available with the online version of this paper.

P. kishitanii; the second containing *P. profundum* together with other psychrophilic species isolated mostly from deep waters, including *P. indicum*, *P. frigidophilum*, *P. aplysiae* and *P. lipolyticum*; and a third containing *P. ganghwense*, *P. rosenbergii*, *P. halotolerans* and *P. lutimaris*. The species *P. damsela* and *P. leiognathi* show an unstable association with the *P. phosphoreum* group. During the writing of this manuscript, two new species of the genus *Photobacterium*, *P. gaetbulicola* (Kim *et al.*, 2010) and *P. jeanii* (Chimetto *et al.*, 2010), were described and as such were included in the analyses. Strain M46^T, isolated from coastal seawater of the Western Mediterranean Sea, was characterized and found to be a new member of the genus *Photobacterium* and grouped with the third intragenetic cluster, showing the highest 16S rRNA sequence similarity to *P. rosenbergii* (96.8 %).

Strain M46^T was isolated from surface seawater collected at Malvarrosa Beach (39° 28' 29" N 0° 19' 23" W), Valencia, Spain, in July 2008. Seawater (25 °C; pH 8) was plated directly on marine agar (MA) and incubated at 26 °C for 4 days, after which isolated colonies were randomly selected and restreaked on the same medium until pure cultures were obtained. Isolates were maintained as cell suspensions in marine broth (MB) supplemented with 20 % (v/v) glycerol at -80 °C. Strain M46^T was routinely grown on MA and MB at 28 °C and all media used for phenotypic characterization were supplemented with half-strength artificial seawater (ASW; 400 mM NaCl, 100 mM MgSO₄·7H₂O, 20 mM KCl, 20 mM CaCl₂·2H₂O) or marine cations supplement (MCS; Farmer & Hickman-Brenner, 2006). For some tests, luminous medium (LM), comprising 5 g yeast extract, 5 g tryptone, 1 g CaCO₃, 20 g agar, 3 g glycerol and 1 l basal medium (BM; 50 mM Tris/HCl, pH 7.5; Baumann & Baumann, 1981), was used. Phenotypic characteristics of the novel strain were tested following previously described methods (Macián *et al.*, 2001) for microscopic observation of cells and for determining colony characteristics on MA and thiosulfate–citrate–bile–sucrose (TCBS) agar, luminescence on MA and LM, oxidase and catalase activities, nitrate reduction, fermentation of D-glucose, D-galactose, sucrose, amygdalin, L-arabinose and melibiose in oxidative–fermentative (OF) medium, activities of arginine dihydrolase (ADH) and lysine and ornithine decarboxylases (LDC, ODC) in Moeller's medium, indole production (in MB), gas production from glucose, Voges–Proskauer reaction, temperature range for growth (4, 15, 28, 37 and 40 °C), hydrolysis of gelatin, casein, starch, alginate, Tween-80 and DNA and the use of 26 carbohydrates, 12 organic acids and 16 amino acids and amines on BM Agar. Ionic requirements and growth in a range of salinities were determined as described by Macián *et al.* (2005). In addition to classical techniques of characterization based on phenotypic traits, tests in the API ZYM, API 20 E, API 50 CHE systems and in Biolog GN microplates were performed in duplicate incubating at 28 °C and using half-strength ASW or MCS as an ionic supplement in cell suspensions used as inocula.

Type strains *P. ganghwense* CECT 7641^T, *P. halotolerans* CECT 5860^T and *P. rosenbergii* CECT 7644^T were included in the phenotypic characterization study for comparison using miniaturized tests.

Cellular fatty acid analysis was performed at the CECT. Strains M46^T, *P. ganghwense* CECT 7641^T, *P. halotolerans* CECT 5860^T and *P. rosenbergii* CECT 7644^T were cultured on MA and incubated at 28 °C for 24 h and fatty acid methyl esters were extracted and prepared according to standard protocols of the MIDI Microbial Identification System (Sasser, 1990). Cellular fatty acids were analysed by GC using an Agilent 6850 chromatograph with the MIDI Microbial Identification System and the TSBA6 method (MIDI, 2008) and identified using the Microbial Identification Sherlock software package. Among other differences, four fatty acids, anteiso-C_{15:0}, anteiso-C_{17:0}, iso-C_{15:1} F and C_{15:1}ω8c, were present as minor components in strain M46^T but were absent (or present in trace amounts) in the other species used for comparison (Table 1).

Differential characteristics from the phenotypic characterization of strain M46^T and other phylogenetically related species of the genus *Photobacterium* are given in the species description and Table 2. Colonies growing on MA or on LM agar were beige with entire edges and produced a diffusible brown pigment that was visible on the first streak after 24 h of incubation and extended to the entire culture after 48 h. Growth on LM agar was more opaque and the pigment was darker than on MA. Using the same media, *P. ganghwense* CECT 7641^T produced a pink pigment on LM agar that was not displayed on MA. Pigment production of the four type strains used in the comparative study is shown in Supplementary Fig. S1, available in IJSEM Online. Strain M46^T grew on TCBS as green colonies, thus being unable to ferment sucrose. Other carbohydrates (glucose, galactose and melibiose) were fermented in OF medium. Luminescence was not observed on either MA or LM medium after 24 h of incubation. Strain M46^T was shown to have growth factor requirements as it was unable to grow on BM agar [50 mM Tris/HCl, pH 7.5; 19 mM NH₄Cl; 0.33 mM K₂HPO₄·3H₂O; 0.1 mM FeSO₄·7H₂O; 1.3 % (w/v) purified agar (Oxoid) in half-strength ASW; Baumann & Baumann, 1981] with any of the carbohydrates, organic acids or amino acids tested as carbon sources, but grew easily on BM agar with 5 g l⁻¹ yeast extract. Strain M46^T was mesophilic and slightly halophilic and its extracellular hydrolytic abilities were limited to DNase activity, as is true of most species of the genus *Photobacterium*.

The results of tests on strain M46^T using API 20 E, API 50 CHE, API ZYM and Biolog GN microplate systems are reported in the species description. Strain M46^T was unable to oxidize most of the substrates in Biolog GN microplates, which was in sharp contrast to closely related species which were able to metabolize a large number of substrates (Supplementary Table S1).

The 16S rRNA gene sequence of strain M46^T and the *recA* and *gyrB* gene sequences of strains M46^T, *P. angustum*

Table 1. Cellular fatty acid compositions of strain M46^T and closely related members of the genus *Photobacterium*

Taxa: 1, strain M46^T; 2, *P. halotolerans* CECT 5860^T; 3, *P. ganghwense* CECT 7641^T; 4, *P. rosenbergii* CECT 7644^T; 5, *P. lutimaris* KCTC 12723^T; 6, *P. jeanii* LMG 25436^T; 7, *P. gaetbulicola* KCTC 22804^T. Values are the mean percentages of at least three replicas. All data from this study except for 5 (data from Jung *et al.*, 2007), 6 (Chimetto *et al.*, 2010) and 7 (Kim *et al.*, 2010). –, Not detected; tr, trace amount (<1 %).

Fatty acid	1	2	3	4	5	6	7
Hydroxy							
C _{11:0} 2-OH	–	–	–	–	–	–	2.8
C _{12:0} 3-OH	2.5	6.8	3.9	3.2	2.6	3.2	2.8
iso-C _{15:0} 3-OH	1.0	tr	tr	1.1	–	–	–
Saturated							
C _{12:0}	2.3	5.6	4.5	2.6	2.4	3.2	1.7
iso-C _{13:0}	1.8	tr	tr	1.2	–	–	–
C _{14:0}	3.3	1.0	4.2	2.6	2.4	4.0	4.2
iso-C _{15:0}	2.6	tr	tr	3.0	5.0	1.0	6.9
anteiso-C _{15:0}	1.5	–	–	tr	–	–	–
C _{15:0}	–	–	–	–	2.1	–	2.9
iso-C _{16:0}	1.7	1.9	tr	1.3	–	2.7	tr
C _{16:0}	10.1	16.5	14.7	10.4	13.1	20.7	14.0
iso-C _{17:0}	1.5	tr	tr	3.8	1.8	–	3.5
anteiso-C _{17:0}	2.4	tr	–	tr	–	–	–
C _{17:0}	1.1	2.7	1.2	1.5	–	–	1.0
Unsaturated							
iso-C _{15:1} F	1.6	–	–	tr	–	–	–
C _{15:1} ω8c	2.5	tr	tr	tr	–	–	–
C _{16:1} ω7c alcohol	–	–	tr	–	1.2	–	tr
C _{17:1} ω8c	1.4	2.8	tr	1.3	–	–	tr
Summed features*							
1	1.1	1.0	tr	tr	–	–	–
2	3.2	4.9	5.0	3.6	3.0	3.0	3.7
3	37.2	31.6	38.3	38.0	43.0	41.1	33.6
8	13.4	18.2	20.5	19.7	13.0	–	13.4†
9	2.2	–	tr	1.3	1.8†	–	1.4†

*Summed features are groups of two or three fatty acids that cannot be separated by GLC using the MIDI system. Summed feature 1 comprises iso-C_{15:1} H and/or C_{13:0} 3-OH, summed feature 2 comprises C_{14:0} 3-OH and/or iso-C_{16:1} I, summed feature 3 comprises C_{16:1} ω7c and/or C_{16:1} ω6c, summed feature 8 comprises C_{18:1} ω7c and/or C_{18:1} ω6c and summed feature 9 comprises C_{16:0} 10-methyl and/or iso-C_{17:1} ω9c.

†Values correspond to the sum of the proportions of each component of the summed feature when detected individually.

CECT 5690^T, *P. halotolerans* CECT 5860^T, *P. ganghwense* CECT 7641^T and *P. rosenbergii* CECT 7644^T were obtained in this study. Cell pellets of each strain were collected and DNA was extracted using a microbial DNA isolation kit (Ultra Clean; MO BIO Laboratories). Amplification and partial sequencing of 16S rRNA, *recA* and *gyrB* genes were performed as described previously (Lucena *et al.*, 2010; Pascual *et al.*, 2010). The new sequences were compared with those available in gene databases using the NCBI BLAST

Table 2. Differential characteristics of strain M46^T and closely related members of the genus *Photobacterium*

Taxa: 1, Strain M46^T; 2, *P. halotolerans* CECT 5860^T; 3, *P. ganghwense* CECT 7641^T; 4, *P. rosenbergii* CECT 7644^T; 5, *P. lutimaris* KCTC 12723^T; 6, *P. jeanii* LMG 25436^T and 7, *P. gaetbulicola* KCTC 22804^T. All data from this study except for 5 (data from Jung *et al.*, 2007), 6 (Chimetto *et al.*, 2010) and 7 (Kim *et al.*, 2010). +, Positive; –, negative; NA, data not available.

Characteristic	1	2	3	4	5	6	7
Growth at 4 °C	–	+	–	–	+	–	–
Growth at 40 °C	–	–	+	–	+	–	+
API 20 E tests:							
Arginine dihydrolase	+	–	+	+	+	+	–
Indole production	–	–	+	+	+	–	–
Gelatinase	–	+	+	–	–	+	–
Acid production from (API 20 E):							
myo-Inositol	–	–	+	+	+	–	+
Rhamnose	–	–	+	+	–	–	–
Sucrose	–	+	–	+	+	–	+
Arabinose	–	+	–	–	–	–	–
Melibiose	+	–	–	+	–	+	+
Mannitol	+	+	+	+	–	–	+
Fermentation of (API 50 CHE):							
D-Xylose	+	+	–	–	+	NA	NA
Aesculin	+	–	–	+	NA	NA	NA
Salicin	–	–	+	+	NA	NA	NA
Cellobiose	–	–	–	+	+	NA	NA
Enzymic activities (API ZYM)							
Esterase lipase (C8)	–	–	+	+	+	+	+
Cystine arylamidase	–	–	–	–	+	–	–
Oxidization of (Biolog GN):							
Tweens 40 and 80, maltose, D-mannitol, trehalose, citric acid, succinic acid, glycerol, D-alanine, L-alanine, L-alanyl glycine, L-asparagine, L-glutamic acid, L-proline, L-serine, inosine, thymidine	–	+	+	+	+	NA	NA

program (<http://blast.ncbi.nlm.nih.gov/Blast.cgi>). Related sequences were further analysed using the ARB program package (Ludwig *et al.*, 2004) (<http://www.wzw.tum.de/mikrobiologie/>). Automated sequence alignments were corrected manually using the ARB_EDIT sequence editor. Phylogenetic analysis using alternative treeing methods (maximum-parsimony, maximum-likelihood and distance matrix) and data subsets was performed using the appropriate ARB tools (Ludwig *et al.*, 2004). Phylogenetic analysis of the individual and concatenated sequences of 16S rRNA, *recA* and *gyrB* genes confirmed that strain M46^T belonged to the genus *Photobacterium*, always grouping

closely with *P. ganghwense* CECT 7641^T and *P. halotolerans* CECT 5860^T.

Sequence analysis performed with the 16S rRNA gene showed that strain M46^T had the highest sequence similarity (96.8 %) to *P. rosenbergii* CECT 7644^T but showed maximum sequence similarities to *P. ganghwense* CECT 7641^T when *gyrB* and *recA* gene sequences were analysed (85.0 % and 87.4 %, respectively).

Phylogenetic trees obtained with the neighbour-joining (NJ) algorithm and respective distance matrices based on almost complete 16S rRNA, partial *recA*, partial *gyrB* and concatenated gene sequences of strain M46^T and closely related species are shown in Fig. 1. Trees based on the 16S rRNA gene that were reconstructed using the maximum-parsimony (MP) and maximum-likelihood (ML) algorithms (Supplementary Fig. S2 and S3) did not display the same topology as that obtained when using the NJ method. In NJ analysis, the genus *Photobacterium* was organized into three clades. The relative branching order within each clade was almost identical between phylogenetic trees reconstructed using different gene sequences; however, the positioning of species *P. jeanii*, *P. leiognathi* and *P. damsela* subsp. *damsela* differed between them. The joint position of the genera *Aliivibrio* and *Vibrio* (represented by the type strain of the type species of each genus) also varied between the trees, whereas other representatives of the family *Vibrionaceae*, *Grimontia*, *Enterovibrio* and *Salinivibrio*, always maintained an outgroup position. In all NJ trees, strain M46^T was always the sister species of *P. halotolerans* and *P. ganghwense*.

The NJ phylogenetic trees obtained using *recA* and *gyrB* gene sequences (Fig. 1) also positioned strain M46^T in the proximity of *P. ganghwense* and *P. halotolerans*. Likewise, the NJ tree based on the concatenated gene sequences (only species for which all three gene sequences were available were included) shows the same relative position of strain M46^T with its closest phylogenetic neighbours.

Strain M46^T showed highest 16S rRNA sequence similarity with *P. rosenbergii* (96.8 %), which is below the value of 97 % recommended by Stackebrandt & Goebel (1994) as the threshold for the delineation of bacterial species. The classification of strain M46^T as a novel species is also supported by the *recA* and *gyrB* gene sequence analyses. Based on *recA* gene sequences, the maximum similarity value was 87.4 % between strain M46^T and *P. ganghwense* CECT 7641^T, which is within the range of values seen between other species of the genus *Photobacterium* with validly published names (78.3 % between *P. rosenbergii* and *P. damsela* subsp. *damsela* and 95.5 % between *P. phosphoreum* and *P. illiipiscarium*). Based on *gyrB* gene sequences the maximum similarity value was 85 % between strain M46^T and *P. ganghwense* CECT 7641^T, which was lower than those obtained for other species pairs; *P. kishitanii* and *P. frigidophilum* share 98 % sequence similarity and 11 other species pairs share between 85 and 91 % sequence similarity. These results confirm that strain M46^T represents a novel species of the genus *Photobacterium*.

Although no luminescence was observed, the genome of strain M46^T was tested for the presence of *lux* genes. Amplification and sequencing of the *luxA* gene was performed according to Wimpee *et al.* (1991) with the modified PCR primers *luxAD* (5'-CTWYTRGATCAAA-TGTCAAAAGGWCGT-3') and *luxAR* (5'-CTTGGTTTY-GAAGCRAAYGGTTCWGA-3'). Reference strains *P. phosphoreum* CECT 4192^T, *P. leiognathi* CECT 4191^T, *P. halotolerans* CECT 5860^T and *P. ganghwense* CECT 7641^T were used as controls. Strain M46^T yielded a PCR product of 700 bp, *P. phosphoreum* CECT 4192^T gave an amplicon of 750 bp and *P. ganghwense* gave a product of 650 bp; two unspecific PCR products (500 and 1300 bp) were always obtained for *P. leiognathi* CECT 4191^T and no amplicon was obtained for *P. halotolerans* CECT 5860^T.

PCR amplicons of M46^T and *P. phosphoreum* CECT 4192^T were purified using an UltraClean PCR clean-up kit (MO BIO Laboratories). Subsequent sequencing reactions were done on an Abi Prism 3730 automated sequencer using a Big Dye Terminator v3.1 cycle sequencing kit in premixed format. Sequencing primers were the same ones used in the amplification reaction but diluted ten fold (5 pmol). Further analysis with BLAST revealed that the nucleotide and the amino acid sequence of strain M46^T had no significant sequence similarity to the *luxA* gene of other species of the genus *Photobacterium*, whereas *P. phosphoreum* CECT 4192^T, as expected, contained the *luxA* gene, as previously published for this species (Wimpee *et al.*, 1991). The deduced amino acid sequence of M46^T showed similarity to a putative acriflavin resistance protein and other membrane transporters of several species of the genera *Vibrio*, *Aliivibrio* and *Photobacterium*. A similar result was observed in *P. iliopiscarium* (Ast & Dunlap, 2005), a non-luminescent species of *Photobacterium*. The absence of the *luxA* gene product is consistent with the absence of luminescence for strain M46^T.

Based on the phenotypic, chemotaxonomic and phylogenetic evidence presented here, strain M46^T represents a novel species of the genus *Photobacterium*, for which the name *Photobacterium aphoticum* sp. nov. is proposed.

Description of *Photobacterium aphoticum* sp. nov.

Photobacterium aphoticum (a.pho'ti.cum. Gr. pref. *a* not; Gr. n. *phos*, *photos* light; L. neut. 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 Gram-reaction-negative, motile bacilli, 0.7–1.1 × 2.2–3.3 µm. Chemo-organotrophic and facultatively anaerobic. Ferments glucose, galactose and melibiose without production of gas. Oxidase- and catalase-positive. 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. No luminescence was observed on MA or LM. Grows on TCBS agar producing green (sucrose-negative) colonies. Grows at 15 and 37 °C but

Fig. 1. Neighbour-joining phylogenetic trees based on the almost complete 16S rRNA (a), partial *recA* (b), partial *gyrB* (c) and concatenated (d) gene sequences of strain M46^T and closely related species of the genus *Photobacterium*. Bootstrap values greater than 70 % (based on 1000 resamplings) are shown at branch points. Nodes that were also obtained in the MP and ML trees are indicated by a circle and a filled circle, respectively. Bars represent number of substitutions per nucleotide position.

not at 4 or 40 °C. No growth is observed in the absence of NaCl. Grows well on 0.85–7 % total salts but no growth is observed at 0.35 % or less or in 8 % salinity or greater. Reduces nitrate to nitrite but not to N₂. Positive for arginine dihydrolase (ADH) and β -galactosidase (ONPG) activities, aesculin hydrolysis and DNase activities but negative for indole production from tryptophan, urease activity, Voges–Proskauer reaction and hydrolysis of gelatin, casein, starch, alginate, agar and Tween-80. Produces acid from the following carbohydrates (API 20 E and API 50 CHE): D-ribose, D-xylose, D-galactose, D-glucose, D-fructose, D-mannose, D-mannitol, N-acetyl D-glucosamine, maltose, melibiose and starch. In the API ZYM system, positive for alkaline phosphatase, leucine arylamidase, acid phosphatase, β -galactosidase and N-acetyl- β -glucosaminidase activities. α -Glucosidase activity is variable. Does not assimilate any of the substrates included in the API 20 NE system and is unable to grow on any of the carbon sources tested on BM agar, including 26 carbohydrates, 12 organic acids and 16 amino acids, suggesting a nutritional requirement that is covered by yeast extract. N-Acetyl-D-glucosamine, D-fructose, D-glucose and D-mannose are oxidized in Biolog GN microplates after 24 h incubation. Other substrates give variable responses (D-galactose and dextrin) or negative reactions. The major cellular fatty acids are C_{16:1} ω 7c/ ω 6c (37.2 %), C_{16:0} (10.1 %) and C_{18:1} ω 7c/ ω 6c (13.4 %). C_{12:0} 3-OH, C_{12:0}, C_{14:0}, C_{15:1} ω 8c, iso-C_{15:0}, anteiso-C_{17:0} and summed features 2 (C_{14:0} 3-OH and/or iso-C_{16:1} I) and 9 (C_{16:0} 10-methyl and/or iso-C_{17:1} ω 9c) are also present in minor amounts (2–4 %).

The type strain, M46^T (=CECT 7614^T =KCTC 23057^T), was isolated from coastal seawater in Valencia, Spain.

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