Thalassomonas agarivorans sp. nov., a marine agarolytic bacterium isolated from shallow coastal water of An-Ping Harbour, Taiwan, and emended description of the genus *Thalassomonas*

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A marine agarolytic bacterium, designated strain TMA1^T, was isolated from a seawater sample collected in a shallow-water region of An-Ping Harbour, Taiwan. It was non-fermentative and Gram-negative. Cells grown in broth cultures were straight or curved rods, non-motile and non-flagellated. The isolate required NaCl for growth and exhibited optimal growth at 25 °C and 3 % NaCl. It grew aerobically and was incapable of anaerobic growth by fermenting glucose or other carbohydrates. Predominant cellular fatty acids were $C_{16:0}$ (17·5 %), $C_{17:1}\omega8c$ (12·8 %), $C_{17:0}$ (11·1 %), $C_{15:0}$ iso 2-OH/$C_{16:1}\omega7c$ (8·6 %) and $C_{13:0}$ (7·3 %). The DNA G+C content was 41·0 mol%. Phylogenetic, phenotypic and chemotaxonomic data accumulated in this study revealed that the isolate could be classified in a novel species of the genus *Thalassomonas* in the family *Colwelliaceae*. The name *Thalassomonas agarivorans* sp. nov. is proposed for the novel species, with TMA1^T (=BCRC 17492^T=JCM 13379^T) as the type strain.

Alteromonas-like bacteria in the class *Gammaproteobacteria* comprise a large group of marine, heterotrophic, polar-flagellated, Gram-negative rods that are mainly non-fermentative aerobes. They are readily isolated from various marine sources and probably represent a major component of the microbial biota in the sea. The similarity of phenotypic characteristics has made it difficult to differentiate these bacteria at the species level or even at the genus level. However, a phylogenetic study based on 16S rRNA gene sequences classified these bacteria into a variety of families and genera, including *Alteromonadaceae* (*Alteromonas* and *Glaciecola*), *Pseudoalteromonadaceae* (*Pseudoalteromonas* and *Algicola*), *Colwelliaceae* (*Colwellia* and *Thalassomonas*), *Ferrimonadaceae* (*Ferrimonas*), *Idiomarinaceae* (*Idiomarina*), *Moritellaceae* (*Moritella*), *Shewanellaceae* (*Shewanella*), *Psychromonadaceae* (*Psychromonas*), *Oceanimonas* and *Oceanisphaera* (Ivanova *et al.*, 2004); taxonomic affiliation of *Oceanimonas* and *Oceanisphaera* at the family level remained undetermined.

Agar, a complex polysaccharide extracted from marine red algae, is widely employed as a gelling agent for microbiological culture media. This refractory material is attacked by relatively few bacterial species (Holt *et al.*, 1994). Agarolytic bacteria are ubiquitous in coastal and estuarine regions; however, they are not exclusively autochthonous in the marine environment, since some reports have shown that they also occur in freshwater, sewage and soil (Agbo & Moss, 1979; van der Meulen *et al.*, 1974; von Hofsten & Malmqvist, 1975). Several marine agarolytic strains of *Vibrio*-like species have been demonstrated to be capable of fixing N_2 for anaerobic growth using agar as the sole source of carbon and energy (Shieh *et al.*, 1988). A *Vibrio* species, *Vibrio agarivorans*, is also reported to be capable of decomposing agar in addition to these unnamed, *Vibrio*-like agarolytic strains (Macián *et al.*, 2001b). *Alterococcus agarolyticus*, the only thermophilic agarolytic species, is a marine, facultatively anaerobic, fermentative, Gram-negative coccus growing between 38 and 58 °C with optimum growth at about 48 °C (Shieh & Jean, 1998). No other agarolytic bacteria have been reported to grow at temperatures of 45 °C or higher. Only a handful of species belonging to the *Alteromonas*-like *Gammaproteobacteria* such as *Pseudoalteromonas atlantica* (Akagawa-Matsushita *et al.*, 1992; Gauthier *et al.*, 1995), *Pseudoalteromonas agarivorans* (Romanenko *et al.*, 2003a), *Glaciecola mesophila* (Romanenko *et al.*, 2003b) and *Shewanella olleyana* (Skerratt *et al.*, 2002) are agarolytic or weakly agarolytic. Recently, strain JAMB-A33, an agarolytic bacterium which produces a novel α-agarase, was isolated from the sediment off Noma Point, Japan (Ohta *et al.*, 2005). Phylogenetic analysis of 16S rRNA gene sequences suggested that this isolate might represent a novel species of *Thalassomonas* in the *Alteromonas*-like *Gammaproteobacteria*.

The GenBank/EMBL/DDBJ accession number for the 16S rRNA gene sequence of strain TMA1^T is DQ212914.

However, classification of this isolate on the basis of phenotypic and chemotaxonomic features was not reported (Ohta *et al.*, 2005). Evidence is presented here that an agarolytic bacterium isolated in this laboratory can be classified in a novel species in the genus *Thalassomonas*.

An-Ping Harbour of Tainan is a small harbour located on the south-west coast of Taiwan. A seawater sample collected from the shallow water region of this harbour was decimally diluted with sterile NaCl/Tris buffer (30 g NaCl and 0·24 g Tris in 1 l deionized water, pH 8·0). Aliquots (0·1 ml) of the decimal dilutions (10^2–10^4 times) were spread on PY (Polypepton/yeast extract) plate medium (Shieh *et al.*, 2000). The plates were incubated at 25 °C in the dark for 7 days under aerobic conditions. Strain TMA1^T, appearing as an agarolytic off-white colony, was isolated from one of the plates and subsequently purified by successive streaking on PY plates. Its maintenance in our laboratory was performed repeatedly at an interval of 2–3 months by inoculating early stationary phase cultures grown in PY broth into 7/10-strength seawater at a ratio of 2 : 50 (v/v). Maintenance cultures were kept at 20 °C. The isolate has also been deposited in both JCM and BCRC by lyophilization.

Strain TMA1^T was cultivated aerobically in PY broth at 25 °C in the dark for 3 days. Cells were harvested by centrifugation. Total genomic DNA was extracted and purified from the cells by using a Puregene DNA isolation kit (Gentra Systems) in accordance with the manufacturer's instructions. Hydration solution of the purified DNA sample was prepared at concentrations of 500 μg ml^{-1}. The DNA hydration solution was used for PCR amplification (Jean *et al.*, 2006).

Sequencing of the 16S rRNA gene sample, alignment and comparison of the resulting sequence and reference sequences available in the GenBank database, calculation of distance matrices for the aligned sequences and reconstruction of a phylogenetic tree by the neighbour-joining method were carried out as described by Shieh *et al.* (2004). Phylogenetic trees were also reconstructed by using maximum-parsimony (Fitch, 1971) and maximum-likelihood (Felsenstein, 1981) methods. The accession numbers for the sequences used to reconstruct the phylogenetic tree are shown in Fig. 1. Bootstrap confidence values (Felsenstein, 1985) were obtained with 1000 resamplings with an option of stepwise addition.

Fatty acids in whole cells grown on PY plate medium at 25 °C for 3 days were extracted, saponified and esterified, followed by GC analysis of the fatty acid methyl esters according to the instructions of the MIDI system (Sasser, 1997). This work was performed at the Bioresources Center for Research and Collection (BCRC), Food Industry Research and Development Institute, Taiwan. DNA G+C content was determined by HPLC analysis (Shieh & Liu, 1996), which was also performed at BCRC. DNA–DNA relatedness between strains TMA1^T and *Thalassomonas*

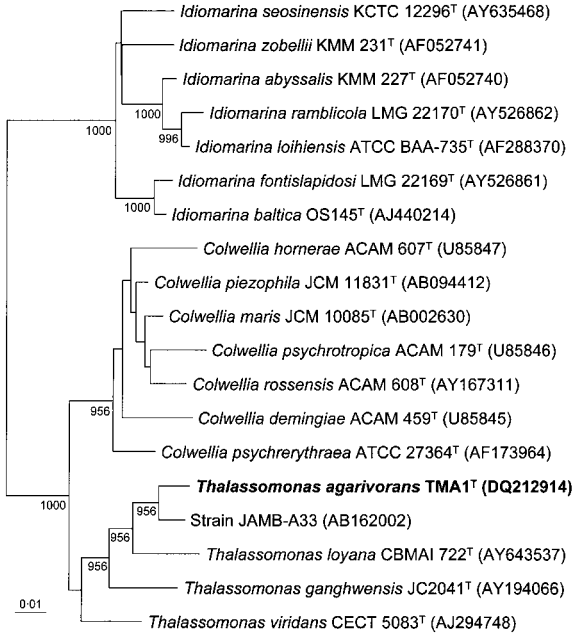

Fig. 1. Unrooted phylogenetic tree derived from neighbour-joining analysis of the 16S rRNA gene sequences of strain TMA1^T and related members of the *Gammaproteobacteria*. GenBank accession numbers are given in parentheses. Numbers above branch nodes are bootstrap values obtained with 1000 resamplings. Bar, 0·01 nucleotide substitutions per position.

loyana CBMAI 722^T was determined as described by Shieh *et al.* (2003a).

Growth and other phenotypic characteristics of strain TMA1^T were examined by the methods of Shieh *et al.* (2000) with modifications and additional tests as described below. Growth at different temperatures was determined in PY broth and recorded daily for up to 5 days at 20, 25, 30, 35, 37 and 40 °C and for 20 days at 4, 10, 13 and 15 °C, unless significant growth had been observed. Growth at various NaCl levels was determined in PY broth containing 0, 0·5, 1, 2, 3, 4, 5, 6, 7 or 8 % NaCl. Anaerobic growth in PY, PYG (Polypepton/yeast extract/glucose) and PYN (Polypepton/yeast extract/nitrate) broth media under argon gas was examined as described by Shieh *et al.* (2004). Utilization of various carbohydrates and other compounds as sole carbon and energy sources for growth was determined in CM (carbohydrate/mineral) media (Shieh *et al.*, 2004) or modifications containing 0·2 % of any one of the test organic acids or amino acids used in place of the carbohydrates. The test compounds included glucose, D-arabinose, L-arabinose, cellobiose, fructose, galactose, lactose, maltose, mannose, melibiose, sucrose, trehalose, xylose, glycerol, dulcitol, inositol, mannitol, acetate, citrate, fumarate, β-hydroxybutyrate, malonate, tartrate, L-alanine, arginine, aspartate, gluconate, glutamine, glutamate, leucine, lysine, tryptophan and L-aconitate. H_2S production from thiosulphate was tested as described by Shieh *et al.* (2004). Urease, arginine

dihydrolase, lysine decarboxylase, ornithine decarboxylase and hydrolysis of aesculin, alginate and lecithin were tested by methods similar to those of Smibert & Krieg (1994): the urease test was carried out with Christensen urea agar (Smibert & Krieg, 1994) containing 25 g NaCl l^{-1} instead of the original 5 g l^{-1}. A modified PY plate medium containing egg-yolk emulsion (100 ml l^{-1}) was used to test the hydrolysis of lecithin. Modified plate media containing aesculin (1 g l^{-1}) and alginate (10 g l^{-1}), respectively, were used to test hydrolysis of these substrates. Tests for arginine dihydrolase, lysine decarboxylase and ornithine decarboxylase were performed in broth media containing Bacto decarboxylase base Moeller (Difco), NaCl (25 g l^{-1}), $MgCl_2.6H_2O$ (2 g l^{-1}) and the appropriate L-amino acid (10 g l^{-1}). Other constitutive enzyme activities were detected by using the API ZYM system (bioMérieux Vitek). Cell suspensions used for these tests were prepared by suspending the cells in a mineral medium containing 0·54 g NH_4Cl, 30 g NaCl, 3 g $MgCl_2.6H_2O$, 2 g K_2SO_4, 0·2 g K_2HPO_4, 0·01 g $CaCl_2$, 0·006 g $FeCl_3.6H_2O$, 0·005 g $Na_2MoO_4.7H_2O$, 0·004 g $CuCl_2.2H_2O$ and 6 g Tris base dissolved in 1000 ml deionized water and adjusted to pH 8·0. Antibiotic susceptibility tests were performed by disc-diffusion methods as described in our previous reports (Shieh *et al.*, 2003a, b). All test cultures were incubated aerobically at 25 °C in the dark for 7 days, unless stated otherwise.

An almost-complete 16S rRNA gene sequence of strain TMA1^T (1465 bp) was determined. The sequence was aligned and compared with all bacterial sequences available in the GenBank database. Phylogenetic analysis of the 16S rRNA gene sequences revealed that strain TMA1^T was a member of the *Alteromonas*-like bacteria in the *Gammaproteobacteria*. The strain showed highest sequence similarities to strain JAMB-A33 (98·2 %), *T. loyana* CBMAI 722^T (97·0 %), *Thalassomonas ganghwensis* JC2041^T (95·2 %) and *Thalassomonas viridans* CECT 5083^T (94·7 %); strain JAMB-A33 has not been classified on the basis of phenotypic and chemotaxonomic features. Besides members of *Thalassomonas*, species of *Colwellia* were the closest relatives of strain TMA1^T (93·2–93·8 % sequence similarity). No other known bacteria shared more than 91 % sequence similarity with strain TMA1^T. The phylogenetic tree derived from neighbour-joining analysis indicated that strains TMA1^T and JAMB-A33 formed a separate taxon in the genus *Thalassomonas*, which was supported by a bootstrap value of 100 % (Fig. 1). Similar results were obtained from maximum-likelihood and maximum-parsimony algorithms (not shown).

Strain TMA1^T contained $C_{16:0}$ as the most abundant fatty acid (17·5 %). Other major fatty acids present at levels greater than 5 % included $C_{17:1}\omega8c$ (12·8 %), $C_{17:0}$ (11·1 %), $C_{15:0}$ iso 2-OH/$C_{16:1}\omega7c$ (8·6 %; the MIDI system could not differentiate these two fatty acids) and $C_{13:0}$ (7·3 %). *T. ganghwensis* (Yi *et al.*, 2004) and *T. viridans* (Macián *et al.*, 2001a) were also found to contain abundant $C_{15:0}$ iso 2-OH/$C_{16:1}\omega7c$ (20·6–28·4 %) and $C_{16:0}$ (13·7–22·3 %). However, $C_{17:0}$ and $C_{13:0}$ were present at low levels (0–4·7 %) or were not detectable in these species. Strain TMA1^T was rather different from *T. loyana* (Thompson *et al.*, 2006) in the proportions of $C_{13:0}$ (7·3 vs 1·2 %), $C_{14:0}$ (4·7 vs 13·1 %), $C_{15:0}$ iso 2-OH/$C_{16:1}\omega7c$ (8·6 vs 31·3 %), $C_{16:0}$ (17·5 vs 4·6 %) and $C_{17:0}$ (11·1 vs 0 %). Other differences in cellular fatty acids between strain TMA1^T and *Thalassomonas* species are shown in Table 1.

Strain TMA1^T had a DNA G+C content of 41·0 mol%, similar to *T. ganghwensis* (42·0 mol%) and *T. loyana* (39·3 mol%) but significantly lower than *T. viridans* (48·4 mol%). The DNA–DNA relatedness value of strains TMA1^T and *T. loyana* CBMAI 722^T was 24·6 %, when genomic DNA of the former strain was used as a probe. The two strains could be classified as two different genomic species according to this result.

Strain TMA1^T grew significantly over a pH range of 7–9, with better growth at pH 8–9. No growth could be observed below pH 6. It grew over a temperature range of 20–35 °C and most rapidly at 25 °C. Growth was relatively slow and weak at 15 and 37 °C and absent at 4, 13 and 40 °C. The strain was halophilic, growing in 1–5 % NaCl, with optimal

Table 1. Cellular fatty acids (%) of strain TMA1^T, *T. viridans*, *T. ganghwensis* and *T. loyana*

Strains: 1, strain TMA1^T (data from this study); 2, *T. viridans* CECT 5083^T and CECT 5082 (Macián *et al.*, 2001a); 3, *T. ganghwensis* JC2041^T (Yi *et al.*, 2004); 4, *T. loyana* CBMAI 722^T (Thompson *et al.*, 2006). −, Not detected; tr, trace amount detected (<1 %).

Fatty acid	1	2	3	4
$C_{10:0}$	1·1	tr	4·9	−
$C_{11:0}$	2·2	tr–1·1	−	−
$C_{12:0}$	4·8	1·6–2·0	−	2·3
$C_{11:0}$ 3-OH	1·4	3·0–4·2	−	2·5
$C_{13:0}$ iso	1·3	−	−	−
$C_{13:0}$	7·3	tr	−	1·2
$C_{12:0}$ 3-OH	2·2	5·0–6·1	−	6·3
$C_{14:0}$ iso	1·2	−	−	−
$C_{14:0}$	4·7	2·3–3·1	−	13·1
$C_{15:1}$ iso H/$C_{13:0}$ 3-OH	2·8	tr–1·3	−	−
$C_{15:1}\omega8c$	2·7	4·5–5·8	−	3·1
$C_{14:0}$ 3-OH/$C_{16:1}$ iso I	2·0	−	−	−
$C_{16:0}$ iso	tr	tr	7·1	−
$C_{16:1}\omega9c$	2·9	−	4·7	5·7
$C_{15:0}$ iso 2-OH/$C_{16:1}\omega7c$	8·6	21·2–28·4	20·6	31·3
$C_{15:0}$	−	6·0–11·1	1·2	−
$C_{16:0}$	17·5	11·2–13·7	22·3	4·6
$C_{17:1}\omega8c$	12·8	14·1–19·7	4·4	11·7
$C_{17:0}$	11·1	3·1–4·7	−	−
$C_{18:1}\omega9c$	2·3	tr	−	1·9
$C_{18:1}\omega7c$	4·8	3·2–6·1	11·3	6·6
$C_{18:0}$	1·7	tr	−	−

growth at 3 % NaCl; no growth was observed at 0 or 6–8 % NaCl. Substitution of KCl (1–5 %) for NaCl did not support growth, indicating that the strain required Na^+ for growth and that the Na^+ requirement was not for osmotic function. Strain TMA1^T exhibited good growth in PY, PYN and PYG broth media under aerobic conditions (maximal OD_{600} >0·6), whereas no growth was observed in these media under anaerobic conditions. This indicated that the strain was a strict aerobe that could not achieve anaerobic growth by either nitrate reduction or glucose fermentation. Various marine bacteria have been reported to grow in CM media and their modifications containing carbohydrates, organic acids or amino acids as sole carbon and energy sources (Shieh *et al.*, 2000, 2003a, b, 2004). Strain TMA1^T might require organic growth factors, since it did not grow in any of these media, nor did it grow significantly in any of these media supplemented with Bacto yeast extract at 0·1 g l^{-1} (maximal OD_{600} <0·05).

Strain TMA1^T was Gram-negative. It produced circular, off-white, opaque and non-luminescent colonies surrounded by distinct depressions on PY agar plates after incubation for 2–5 days. Clear yellow haloes formed around the colonies in contrast to the purple–brown background when the plates were flooded with iodine/potassium iodide solution. This indicated diffusion of agarase out from the colonies and release of reducing compounds during agar hydrolysis. Cells grown in PY broth were straight or curved rods, non-motile and non-flagellated during the late exponential to early stationary phase of growth. Carbohydrate fermentation tests in PYC (Polypepton/yeast extract/carbohydrate) stab media (Shieh *et al.*, 2000) indicated that the strain did not ferment any of the test carbohydrates D-arabinose, L-arabinose, cellobiose, galactose, glucose, lactose, mannose, melibiose, sucrose, trehalose and xylose. Oxidase and catalase tests were both positive. Indole was not produced from tryptophan. Aesculin, alginate, casein, DNA, gelatin and starch were hydrolysed, but lecithin and Tween 80 were not. Nitrate was reduced to nitrite but not further to N_2O or N_2. Additional phenotypic characterization data are given below in the species description.

Strain TMA1^T was phenotypically distinguished from *T. ganghwensis* (Yi *et al.*, 2004), *T. viridans* (Macián *et al.*, 2001a) and *T. loyana* (Thompson *et al.*, 2006) in that it was a non-motile, non-flagellated bacterium capable of decomposing agar. Other characteristics useful for differentiating strain TMA1^T from these *Thalassomonas* species are summarized in Table 2.

Phylogenetic, chemotaxonomic and phenotypic data accumulated in this study support the establishment of a novel species in the genus *Thalassomonas*. The name *Thalassomonas agarivorans* is proposed for this novel species, with TMA1^T as the type strain. Establishment of this novel species requires an emended description of the genus *Thalassomonas*, since the genus is currently defined as including only motile, polar-flagellated species that are incapable of nitrate reduction and hydrolysis of agar and alginate.

Table 2. Characteristics that differentiate strain TMA1^T from *T. viridans*, *T. ganghwensis* and *T. loyana*

Strains: 1, strain TMA1^T (data from this study); 2, *T. viridans* CECT 5083^T and CECT 5082 (Macián *et al.*, 2001a); 3, *T. ganghwensis* JC2041^T (Yi *et al.*, 2004); 4, *T. loyana* CBMAI 722^T (Thompson *et al.*, 2006). +, Positive; −, negative; W, weakly positive; ND, no data available. All species grow at 16–36 °C and in 2–5 % NaCl, are positive for catalase and are negative for arginine dihydrolase, lysine decarboxylase and ornithine decarboxylase.

Characteristic	1	2	3	4
Colony colour	Off-white	Green	Yellow	Cream
Motility	−	+	+	+
Monotrichous flagellation	−	+	+	+
Oxidase	+	+	+	−
Growth in/at:				
1 % NaCl	+	−	+	+
6 % NaCl	−	+	+	+
8 % NaCl	−	−	+	+
13 °C	−	+	−	−
40 °C	−	−	+	−
Hydrolysis of:				
Aesculin	+	ND	+	+
Agar	+	−	−	−
Alginate	+	−	−	+
Lecithin	−	+	−	ND
Starch	+	+	−	+
Tween 80	−	−	+	−
Nitrate reduction	+	−	+	W
API ZYM tests:				
Esterase lipase (C8)	+	ND	−	ND
Valine arylamidase	−	ND	+	ND
α-Chymotrypsin	+	ND	−	ND
α-Glucosidase	+	ND	−	ND
N-Acetyl-β-glucosaminidase	+	ND	−	ND
DNA G+C content (mol%)	41·0	48·4	42·0	39·3

Emended description of the genus *Thalassomonas* Macián *et al.* 2001

Thalassomonas (Tha.las′so.mo.nas. Gr. fem. n. *thalassa* the sea; Gr. n. *monas* a unit; N.L. fem. n. *Thalassomonas* a monad from the sea).

Members are Gram-negative rods belonging to the *Gammaproteobacteria*. Catalase-positive. Oxidase is usually present. Non-motile or motile by means of a single polar flagellum. Halophilic, growing in 2–4 % NaCl but not in the absence of NaCl. Mesophilic, growing at 20–35 °C but not at 4 or 45 °C. Chemo-organotrophs capable of respiratory but not fermentative metabolism. Arginine dihydrolase, lysine decarboxylase and ornithine decarboxylase are absent. Cells contain either $C_{15:0}$ iso 2-OH/$C_{16:1}\omega7c$ or $C_{16:0}$ as the most abundant fatty acid(s). The DNA G+C content is 39·3–48·5 mol%. The type species is *Thalassomonas viridans*.

Description of *Thalassomonas agarivorans* sp. nov.

Thalassomonas agarivorans (a.ga.ri.vo′rans. N.L. n. *agarum* agar; L. part. adj. *vorans* devouring, destroying; N.L. part. adj. *agarivorans* agar-devouring).

In addition to the characteristics included in the emended description of the genus, the following characteristics are observed. Cells during late exponential to early stationary phase of growth in broth cultures are non-motile, straight or curved rods that measure approximately 1·4–2·2 by 0·4–0·7 μm. Colonies produced on agar plates are circular, off-white, opaque, non-luminescent and agarolytic; distinct depressions are formed by these colonies in a few days and much of the agar in the plate medium is liquefied after incubation for several weeks. Growth occurs between 15 and 37 °C with optimal growth at 25 °C; no growth at 4–13 or 40 °C. Growth occurs in 1–5 % NaCl with optimal growth at 3 %; no growth at 0 or 6 % NaCl. Able to grow over a pH range of 7–9 but not at pH 6. Nitrate is reduced to nitrite but not further to N_2O or N_2. H_2S is not produced from thiosulphate. Indole is not produced from tryptophan. Aesculin, alginate, casein, DNA, gelatin and starch are hydrolysed but lecithin, Tween 80 and urea are not. The following constitutive enzyme activities are detected in API ZYM tests: α-chymotrypsin, esterase (C4), esterase lipase (C8), *N*-acetyl-β-glucosaminidase, α-glucosidase, leucine arylamidase, naphthol-AS-BI-phosphohydrolase, acid phosphatase and alkaline phosphatase. Organic growth factors are probably required since growth does not occur on the following compounds as sole carbon sources: glucose, D-arabinose, L-arabinose, cellobiose, fructose, galactose, lactose, maltose, mannose, melibiose, sucrose, trehalose, xylose, glycerol, dulcitol, inositol, mannitol, acetate, citrate, fumarate, β-hydroxybutyrate, malonate, tartrate, L-alanine, arginine, aspartate, gluconate, glutamine, glutamate, leucine, lysine, tryptophan and L-aconitate. Cellular fatty acids present at levels greater than 5 % include $C_{16:0}$, $C_{17:1}\omega8c$, $C_{17:0}$, $C_{15:0}$ iso 2-OH/$C_{16:1}\omega7c$ and $C_{13:0}$. Susceptible to ampicillin (10 μg), colistin (10 μg), erythromycin (15 μg), gentamicin (10 μg), kanamycin (30 μg), neomycin (30 μg), novobiocin (30 μg), penicillin G (10 U), polymyxin B (300 U) and tetracycline (30 μg); intermediate susceptibility to nalidixic acid (30 μg); resistant to carbenicillin (100 μg), cephalothin (30 μg), chloramphenicol (30 μg), clindamycin (2 μg), lincomycin (2 μg), oxacillin (1 μg), streptomycin (10 μg) and vancomycin (30 μg).

The type strain, TMA1^T (=BCRC 17492^T=JCM 13379^T), was isolated from shallow seawater of An-Ping Harbour, Tainan, Taiwan. It has a DNA G+C content of 41·0 mol%.

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