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ORIGINAL PAPER

Description of *Algoriphagus taiwanensis* sp. nov., a xylanolytic bacterium isolated from surface seawater, and emended descriptions of *Algoriphagus mannitolivorans*, *Algoriphagus olei, Algoriphagus aquatilis* and *Algoriphagus ratkowskyi*

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Abstract A novel, Gram-stain negative, strictly aerobic, oval or rod-shaped, red-pigmented, non-spore-forming xylanolytic bacterial strain, designated CC-PR-82^T, was isolated from surface seawater of Pingtung coast, Taiwan, and characterized by polyphasic taxonomy. Strain CC-PR-82^T shared highest pairwise 16S rRNA gene sequence similarity to *Algoriphagus mannitolivorans* IMSNU 14012^T (97.0 %) followed by '*A. boseongensis*' BS-R1^T (96.5 %) and *A. olei* CC-Hsuan-617^T (95.6 %), whereas other ($n = 26$) *Algoriphapus* species shared 95.6–92.6 % sequence similarities. The novel strain further established a distinct phyletic lineage tightly associated with *Algoriphagus* species. The DNA–DNA hybridization value obtained between CC-PR-82^T and *A. mannitolivorans* DSM 15301^T was 29.0 % (33.4 % reciprocal using *A. mannitolivorans* DSM 15301^T probe). The major (>5 % of total) fatty acids were identified as iso-$C_{15:0}$, $C_{16:1}$ $\omega 6c$ and/or $C_{16:1}$ $\omega 7c$, iso-$C_{16:0}$, iso-$C_{17:1}$ $\omega 9c$ and/or $C_{16:0}$ 10-methyl, anteiso-$C_{15:0}$ and $C_{17:1}$ $\omega 6c$. Polar lipids included major amounts of an unidentified aminolipid and an unidentified lipid; moderate amounts of phosphatidylethanolamine, phosphatidylserine and an unidentified aminolipid; trace amounts of an unidentified phospholipid, an unidentified lipid and an unidentified glycolipid. The DNA G+C content was determined to be 42.3 mol%. Menaquinone-7 was the sole respiratory quinone. Based on the polyphasic characteristics, that are in line with those of *Algoriphagus* species, in addition to distinguishing phylogenetic and phenotypic features, strain CC-PR-82^T appears to represent a novel species of the genus *Algoriphagus*, for which the name *Algoriphagus taiwanensis* sp. nov. (type strain CC-PR-82^T = JCM 19755^T = BCRC 80746^T) is proposed. In addition, emended descriptions of the species *A. mannitolivorans, A. aquatilis, A. olei* and *A. ratkowskyi* are also proposed.

Keywords *Cyclobacteriaceae* · Xylan-degrading · Phosphatidylserine · Phosphatidylcholine

Introduction

The genus *Algoriphagus*, affiliated to the family *Cyclobacteriaceae* (Nedashkovskaya and Ludwig 2011) of the phylum *Bacteroidetes*, was proposed by

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Bowman et al. (2003). At the time of writing, present genus comprises 27 species with validly published names (http://www.bacterio.net/uw/Algoriphagus.html; Euzéby 1997) and two species with invalid names. *Algoriphagus ratkowskyi*, the type species of *Algoriphagus* (Bowman et al. 2003) and *A. antarcticus* (Van Trappen et al. 2004) have been isolated from polar habitats. On the other hand, *A. aquimarinus* (Nedashkovskaya et al. 2004) originated from Japanese seawater, *A. marincola* (Yoon et al. 2004; Nedashkovskaya et al. 2007), *A. jejuensis* (Lee et al. 2012) and *A. namhaensis* (Oh et al. 2012) isolated from Korean seawater and '*A. shivajiensis*' (Kumar et al. 2013) was described from a backwater sample collected at India. *A. chordae* and *A. winogradskyi* were isolated and characterized from marine alga in Japan (Nedashkovskaya et al. 2004); *A. vanfongensis* (Nedashkovskaya et al. 2007) was isolated from coral in Vietnam and *A. machipongonensis* (Alegado et al. 2013) was characterized from a colonial choanoflagellate. The species such as *A. yeomjeoni* (Yoon et al. 2005a) and *A. locisalis* (Yoon et al. 2005b) were isolated from Korean marine solar saltern, whereas *A. hitonicola* (Copa-Patiño et al. 2008) was isolated from a Lagoon in Spain. Several *Algoriphagus* species have been isolated from Korean tidal flat/sediment that include *A. lutimaris* (Park et al. 2010), *A. chungangensis* (Kang et al. 2013), '*A. boseongensis*' (Park et al. 2014) and *A. taeanensis* (Kim et al. 2014) and three reclassified species *A. halophilus* (Yi and Chun 2004; Nedashkovskaya et al. 2004), *A. mannitolivorans* and *A. ornithinivorans* (Yi and Chun 2004; Nedashkovskaya et al. 2007). In addition, *A. faecimaris* (Li et al. 2011) and *A. zhangzhouensis* (Yang et al. 2013) have been isolated from coastal and mangrove sediments in China, respectively.

Algoriphagus species have also been found to share non-marine habitats. For example, *A. aquaeductus* (Rau et al. 2012) was isolated from a freshwater pipe in Spain, *A. aquatilis* (Liu et al. 2009) was isolated from a freshwater lake in China, and a reclassified species *A. alkaliphilus* (Tiago et al. 2006; Nedashkovskaya et al. 2007) was isolated from alkaline water collected at Portugal. Species such as *A. terrigena* (Yoon et al. 2006) and *A. olei* (Young et al. 2009) were isolated from soil samples collected at Korea and Taiwan, respectively. In addition, a reclassified species *A. boritolerans* (Ahmed et al. 2007; Nedashkovskaya et al. 2007) was originally isolated from boron-contaminated soil, Turkey. *Algoriphagus* species are Gram-stain negative, motile/non-motile coccobacilli, which produce characteristic non-diffusible pink or red pigments. In this study, we describe polyphasic taxonomic characterization of a xylan-degrading bacterial strain resembling *Algoriphagus*, designated CC-PR-82^T, isolated from coastal surface seawater of Taiwan.

Materials and methods

Isolation, storage, reference strains and culture conditions

Strain CC-PR-82^T was isolated from surface seawater collected at coastal Pingtung, Taiwan. The sample was subjected to a standard dilution-to-extinction plating technique using marine agar 2216 (MA; BD Difco) at 30 °C for 48–96 h. The colony of strain CC-PR-82^T was isolated, purified and preserved in marine broth (MB; BD Difco) supplemented with 20 % (v/v) glycerol at −80 °C. The taxonomic investigations were carried out according to the previously published guidelines (Tindall et al. 2010). Four type strains of *Algoriphagus* species such as *A. mannitolivorans* DSM 15301^T (=IMSNU 14012^T), *A. olei* BCRC 17886^T (=CC-Hsuan-617^T), *A. aquatilis* NBRC 104237^T (=A8-7^T) and *A. ratkowskyi* DSM 22286^T (=LMG 21435^T) were used for direct comparative taxonomic analysis. All strains (except for *A. ratkowskyi* DSM 22286^T, which was cultivated at 25 °C) were cultured by using NA (Himedia) or NB for 48 h at 30 °C, unless specified otherwise.

Molecular systematics

The genomic DNA of strain CC-PR-82^T was isolated by using UltraClean^{TM} Microbial Genomic DNA Isolation Kit (MO BIO, USA) according to manufacturer's instructions. The partial 16S rRNA gene was amplified via PCR as described in Shahina et al. (2013). Gene sequencing was performed by using a Bigdye terminator kit (Heiner et al. 1998) and an automatic DNA sequencer (ABI PRISM 310, Applied Biosystems, CA, USA) (Watts and MacBeath 2001). Sequence fragments were then assembled using the Fragment Assembly System program from the Wisconsin Package (GCG 1995). Sequence similarity

values were computed using the BLAST search (Altschul et al. 1990) program of EzTaxon-e (Kim et al. 2012). Sequence data were analyzed by MEGA 5 (Molecular Evolutionary Genetics Analysis, version 5.0; Tamura et al. 2011), after multiple alignment by Clustal_X (Thompson et al. 1997). The distance matrix method (distance options according to the Kimura two-parameter model; Kimura 1980) including clustering by neighbor–joining (Saitou and Nei 1987), a discrete character-based maximum-parsimony (Fitch 1971) and maximum-likelihood (Felsenstein 1981) methods were used. The topologies of the trees were evaluated by using bootstrap resampling method based on 1,000 replications (Felsenstein 1985).

Phenotypic, physiological and biochemical analysis

The following phenotypic tests were carried out exclusively on novel strain. Colonies were examined for morphological features such as colony appearance, size, shape, texture and pigmentation. Presence of endospore was assessed by phase-contrast microscopy (model A3000, Zeiss) after malachite-green staining (Smibert and Krieg 1994) of the cells grown on MA for 7 days. Cell morphology including presence of flagella was determined by placing the cells (1–2 days old) on a carbon-coated copper grid followed by staining with 0.2 % uranyl acetate for 5–10 s, brief air-drying and observation under a transmission electron microscope (JEOL JEM-1400). Gram staining was performed according to Murray et al. (1994). The requirement for NaCl was tested on R2A agar (BD Difco) supplemented with 0–10 % (w/v) NaCl (at 1 % intervals). The pH range (4.0–10.0, at 1.0 pH unit intervals) for growth was determined in MB that was prepared using 100 mM acetate (pH 4–5), 100 mM NaH_2PO_4/Na_2HPO_4 (pH 6–8) and 100 mM $NaHCO_3/Na_2CO_3$ (pH 9–10) buffers. Growth at 10, 20, 25, 30, 37, 40, 45, 50 and 55 °C was tested in MB after 72 h of incubation. Anaerobic growth was tested using MA or MA supplemented with 0.1 % (w/v) KNO_3 by incubating the culture plates in an anaerobic chamber (COY, USA). Saline suspension of strain was inoculated in API 50 CH strip (bioMérieux) and Biolog GN2 MicroPlate according to the manufacturers' instructions.

The following phenotypic tests were carried out on all five strains. Growth was tested on nutrient agar (NA, Himedia), tryptic soy agar (TSA, BD difco) and R2A (BD difco) agar. Activity of catalase and oxidase, and hydrolysis of starch, egg yolk, Tweens 20 and 80, casein (skim milk), colloidal chitin, carboxymethylcellulose and xylan were tested as described previously (Hameed et al. 2013) using NA as basal media. DNase activity was assessed using DNase test agar (HiMedia). Bacterial saline suspensions were inoculated in API 20 NE and API ZYM according to the manufacturers' instructions. Results were recorded after 48 h of incubation at 30 °C.

Chemotaxonomic analyses

For chemotaxonomic purpose, all strains (except for *A. ratkowskyi* DSM 22286^T, which was cultivated at 25 °C) were cultivated on NA at 30 °C for 2–3 days. For whole-cell fatty acid analysis, samples were harvested during exponential growth phase, and subjected to saponification, methylation and extraction as described previously (Kämpfer and Kroppenstedt 1996) followed by gas chromatography (model 7890A, Agilent). Peaks were automatically integrated, and fatty acid names and percentages were determined using the microbial identification standard software package MIDI (version 6) (Sasser 1990) and the database RTSBA6. Respiratory quinones of strain CC-PR-82^T were extracted according to Minnikin et al. (1984) and analyzed by RP-HPLC according to Collins (1985) with minor modifications (Shahina et al. 2013). Polar lipids of all five strains were extracted and analyzed by two-dimensional TLC with appropriate detection reagents for aminolipids, glycolipids and phospholipids (Embley and Wait 1994). Authentic phosphatidylcholine and phosphatidylseine standards were purchased from Sigma-Aldrich. The spot of phosphatidylcholine was confirmed by spraying the TLC plates with Dragendorff's reagent. Genomic DNA of strain CC-PR-82^T was subjected to thermal denaturation followed by enzymatic digestion into nucleosides as described previously (Mesbah et al. 1989). The resultant nucleoside mixture was separated and quantified by RP-HPLC according to Mesbah et al. (1989) with minor modifications (Shahina et al. 2013).

Results and discussion

The amplified 16S rRNA gene of strain CC-PR-82^T contained 1,511 nucleotides, which has been deposited in GenBank/EMBL/DDBJ under the accession number KF732813. The sequence analysis in EzTaxon-e server revealed that strain CC-PR-82^T shared high level of sequence similarity to *Algoriphagus* species and was most-closely related to *A. mannitolivorans* IMSNU 14012^T (97.0 %) followed by '*A. boseongensis*' BS-R1^T (96.5 %), *A. olei* CC-Hsuan-617^T (95.6 %), *A. aquatilis* A8-7^T (95.6 %), *A. marincola* DSM 16067^T (95.5 %), *A. ornithinivorans* IMSNU 14014^T (95.5 %), '*A. shivajiensis*' NIO-S3^T (95.3 %) and *A. aquaeductus* T4^T (95.1 %). Other species of *Algoriphagus* shared 94.9–92.9 % similarities, whereas *A. ratkowskyi* LMG 21435^T (type species of *Algoriphagus*) shared lowest (92.6 %) level of sequence similarity with novel strain. In the neighbor-joining phylogenetic tree, the strain CC-PR-82^T formed a distinct phyletic lineage associated with *A. mannitolivorans* IMSNU 14012^T and '*A. boseongensis*' BS-R1^T (Fig. 1). Similarly, the phylogenetic association between strain CC-PR-82^T and other *Algoriphagus* species was conserved in the trees generated using maximum-parsimony (Fig. S1) and maximum-likelihood (Fig. S2) algorithms.

DNA–DNA hybridization (DDH) assay was performed between strain CC-PR-82^T and *A. mannitolivorans* DSM 15301^T (due to 97 % 16S rRNA gene sequence identity) by using DIG DNA labeling and detection kit (cat. no. 11 093 657 910; Roche Diagnostics) according to the manufacturer's protocol. The obtained DDH values were 29.0 and 33.4 % (reciprocal using *A. mannitolivorans* DSM 15301^T probe). These values were well below 70 % cutoff that has been prescribed for species distinction (Tindall et al. 2010), which clearly indicated that these two strains are not related at species-level.

The morphological characteristics of strain CC-PR-82^T are shown in Fig. 2. Cells of strain CC-PR-82^T were observed to be oval or rod-shaped with varying cell size and devoid of flagella and appendages. Cells were not filamentous. The features that distinguished the isolate from reference *Algoriphagus* strains are given in Table 1.

The major (>5 % of total) fatty acids in strain CC-PR-82^T were identified as iso-$C_{15:0}$ (25.2 %), $C_{16:1}$ $\omega6c$ and/or $C_{16:1}$ $\omega7c$ (summed feature 3, 14.9 %), iso-$C_{16:0}$ (10.1 %), iso-$C_{17:1}$ $\omega9c$ and/or $C_{16:0}$ 10-methyl (summed feature 9, 5.8 %), anteiso-$C_{15:0}$ (5.7 %) and $C_{17:1}$ $\omega6c$ (5.7 %). The fatty acids such as iso-$C_{15:0}$, anteiso-$C_{15:0}$ and summed feature 3 were also found in major amounts in other four

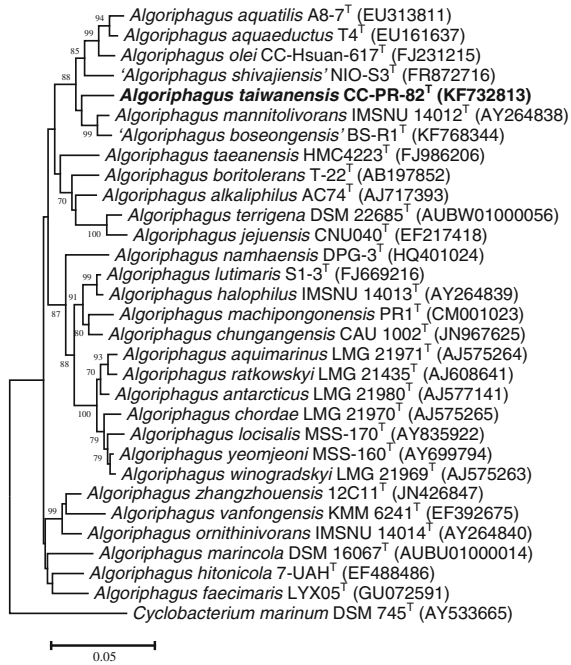

Fig. 1 Neighbor-joining phylogenetic tree based on 16S rRNA gene sequences showing the taxonomic position of strain CC-PR-82^T within the family *Cyclobacteriaceae*. Bootstrap values (>70 %) based on 1,000 replications are shown at the nodes. *Cyclobacterium marinum* DSM 745^T was used as an outgroup. *Bar* 0.05 substitutions per nucleotide position

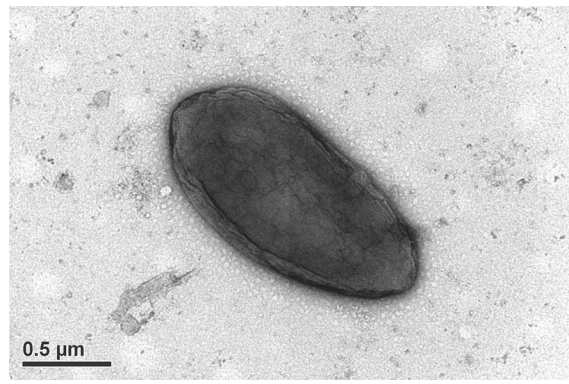

Fig. 2 Transmission electron micrograph of a cell of strain CC-PR-82^T. Cells were cultivated on MA for 24–48 h at 30 °C. *Bar* 0.5 µm

Table 1 Differential phenotypic characteristics of *Algoriphagus* species

Characteristic	1	2	3	4	5
Hydrolysis of					
Casein	+	–	+	+	+
Tween 20	w	+	+	–	+
Tween 80	–	+	+	–	–
Starch	+	+	+	+	–
Xylan	+	–	+	+	–
Growth on					
TSA	–	+	+	+	–
Reduction of nitrate to nitrite	–	+	–	w	–
Assimilation of					
D-Glucose	–	–	+	–	–
D-Mannose	–	+	–	+	–
N-Acetyl-glucosamine, D-maltose	–	+	+	+	–
Activity of					
Trypsin	+	+	+	+	–
α-Mannosidase	+	–	+	+	+
Antibiotic susceptibility					
Ticarcillin, cefepime	R	S	S	S	S
Imipenem	S	S	R	S	S
Ceftazidime, tobramycin	R	R	R	R	S
Amikacin, gentamicin	R	S	R	R	S
Ciprofloxacin	S	I	S	S	I
Colistine	S	I	S	S	R
DNA G+C content (mol%)	42.3	42[a]	43[b]	43[c]	35–36[d]

All data from this study except indicated otherwise. All five strains are positive for the following characteristics: activity of catalase and oxidase; hydrolysis of egg yolk, esculin and *p*-nitrophenyl-*β*-D-galactopyranoside; activity of alkaline phosphatase, esterase (C 4), esterase lipase (C 8), leucine arylamidase, valine arylamidase, cystine arylamidase, α-chymotrypsin, acid phosphatase, naphthol-AS-BI-phosphohydrolase, *β*-galactosidase, α-glucosidase, *β*-glucosidase and *N*-acetyl-*β*-glucosaminidase; sensitivity to ampicillin/sulbactam, ticarcillin-pyo, ticarcillin/clavulanic acid, ticarcillin/clavulanic acid-pyo, piperacillin/uretdopen, piperacillin-pyo, piperacillin/tazobactam, piperacillin/tazobactam-pyo, meropenem and cortrimoxazole; growth on MA, NA and R2A. All five strains are negative for the following characteristics: hydrolysis of DNA, colloidal chitin and carboxymethylcellulose; reduction of nitrate to nitrogen; indole production and fermentation of D-glucose; activity of arginine dihydrolase and urease; hydrolysis of gelatin; assimilation of L-arabinose, D-mannitol, potassium gluconate, capric acid, adipic acid, malic acid, trisodium citrate and phenylacetic acid; activity of lipase (C 14), α-galactosidase, *β*-glucuronidase and α-fucosidase

Taxa: *1* strain CC-PR-82^T; *2 A. mannitolivorans* DSM 15301^T; *3 A. olei* BCRC 17886^T; *4 A. aquatilis* NBRC 104237^T; *5 A. ratkowskyi* DSM 22686^T

+ positive; – negative; *w* weakly positive; *S* sensitive; *R* resistant; *I* intermediate

[a] Yi and Chun (2004)

[b] Young et al. (2009)

[c] Liu et al. (2009)

[d] Bowman et al. (2003)

reference strains (Table 2). The qualitative and quantitative differences in terms of several fatty acids that distinguished these five strains of *Algoriphagus* are shown in Table 2.

Strain CC-PR-82^T was found to contain menaquinone-7 (MK-7) as the sole respiratory quinone. Members of the genus *Algoriphagus* may produce MK-7 as predominant (Yi and Chun 2004; Young et al. 2009;

Table 2 Whole cell fatty acid profiles (%) of *Algoriphagus* species

Fatty acid	1	2	3	4	5
Saturated					
$C_{16:0}$	1.4	1	2.5	1	**5**
Branched saturated					
Iso-$C_{14:0}$	1.9	2.2	3.3	2.1	1
Iso-$C_{15:0}$	**25.2**	**31.7**	**27.3**	**36.5**	**31.5**
Iso-$C_{16:0}$	**10.1**	**7.9**	**5.8**	**5.3**	4.7
Anteiso-$C_{11:0}$	3.6	2.1	2.7	–	2.1
Anteiso-$C_{15:0}$	**5.7**	**7.2**	**5.1**	**6.2**	**6.7**
Unsaturated					
$C_{15:1}\omega5c$	2.5	1.7	1.4	1.6	1.7
$C_{15:1}\omega6c$	4.3	3.7	4.7	3.8	1.9
$C_{16:1}\omega5c$	–	–	–	–	**6.1**
$C_{17:1}\omega6c$	**5.7**	3.3	3.8	4.3	1.3
$C_{17:1}\omega8c$	1.7	1.7	1	tr	–
Branched monounsaturated					
Iso-$C_{15:1}$ F	–	–	–	1.5	–
Iso-$C_{15:1}$ G	1	–	–	–	3.5
Iso-$C_{16:1}$ H	4.6	2.2	2.3	2.8	3.1
Anteiso-$C_{17:1}$ $\omega9c$	1.3	–	–	tr	–
Hydroxy					
$C_{15:0}$ 2–OH	1.2	1.3	1.1	–	–
$C_{17:0}$ 2–OH	–	1.4	–	tr	tr
Iso-$C_{17:0}$ 3–OH	tr	**6.2**	3.1	4.8	3.6
Summed feature 3	**14.9**	**11.4**	**23.6**	**13.5**	**17.3**
Summed feature 4	1.4	1.3	1.2	1.7	–
Summed feature 9	**5.8**	**5.3**	3.5	**6.9**	3.8

All data are from this study. Major (>5 %) components are shown in bold type. Fatty acids amounting to <1 % of the total fatty acids in the five strains are not shown. As indicated by Montero-Calasanz et al. (2013) summed features are groups of two or three fatty acids that are treated together for the purpose of evaluation in the MIDI system and include both peaks with discrete equivalent chain lengths (ECL) as well as those where the ECL are not reported separately. Summed feature 3 was listed as $C_{16:1}$ $\omega6c$ and/or $C_{16:1}$ $\omega7c$; Summed feature 4 was listed as anteiso-$C_{17:1}$ B and/or iso-$C_{17:1}$ I; Summed feature 9 was listed as iso-$C_{17:1}$ $\omega9c$ and/or $C_{16:0}$ 10-methyl

Taxa: *1* strain CC-PR-82^T; *2 A. mannitolivorans* DSM 15301^T; *3 A. olei* BCRC 17886^T; *4 A. aquatilis* NBRC 104237^T; *5 A. ratkowskyi* DSM 22686^T

tr trace (<1 %); – not detected

Nedashkovskaya et al. 2004, 2007; Kang et al. 2013; Park et al. 2014) or sole respiratory quinone (Liu et al. 2009).

Polar lipids of strain CC-PR-82^T included major amounts of an unidentified aminolipid (AL1) and an unidentified lipid (L2) and moderate amounts of phosphatidylethanolamine (PE), phosphatidylserine (PS) and an unidentified aminolipid (AL2) (Fig. 3). In addition, trace amounts of an unidentified phospholipid (PL), an unidentified lipid (L1) and an unidentified glycolipid (GL) were also found. The polar lipid profile of strain CC-PR-82^T was almost in line with that of reference strains as they also consistently showed polar lipids such as PE, AL1, AL2, L1 and L2. A TLC spot designated AL1 (labeled as APL1 in Young et al. 2009, L1 in Oh et al. 2012 and L2 in Park et al. 2014) was poorly stained with ninhydrin reagent indicating the presence of amino-moiety. However, in our study, AL1

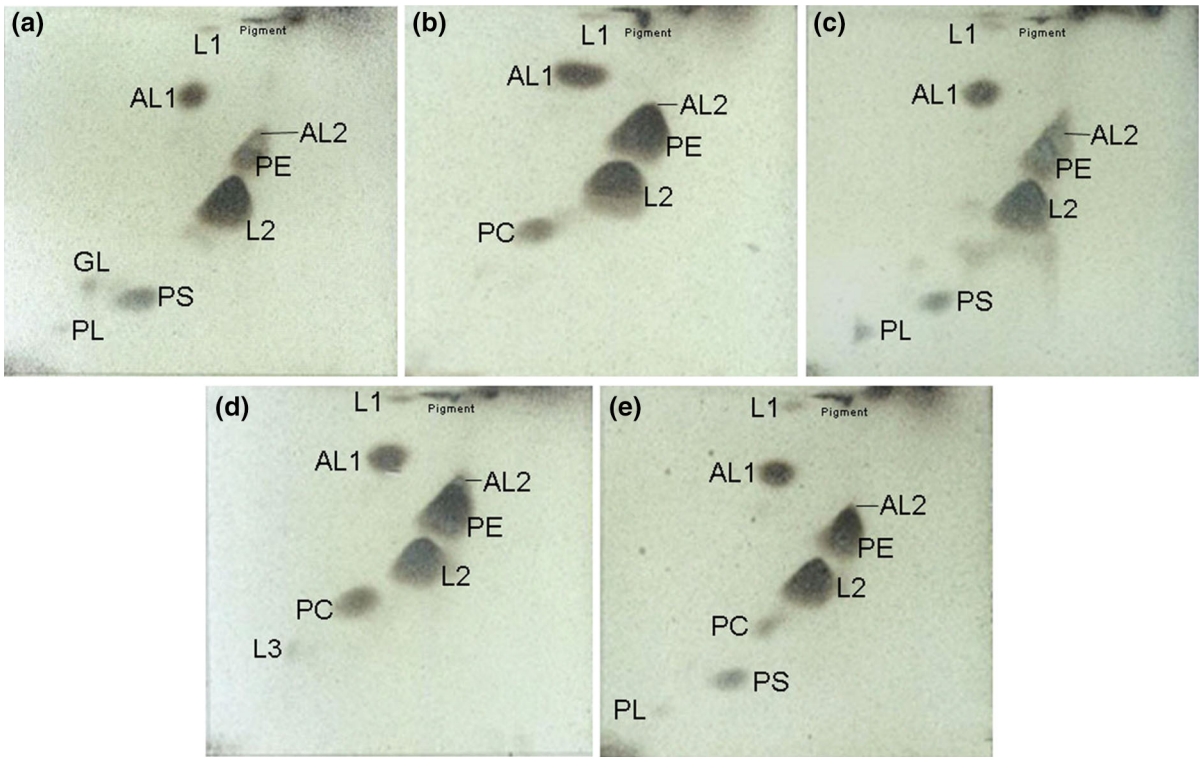

Fig. 3 Polar lipid profiles of *Algoriphagus* species as determined by two-dimensional thin-layer chromatography: strain CC-PR-82^T (**a**), *A. mannitolivorans* DSM 15301^T (**b**), *A. olei* BCRC 17886^T (**c**), *A. aquatilis* NBRC 104237^T (**d**) and *A. ratkowskyi* DSM 22686^T (**e**). Total polar lipids were visualized by spraying the TLC plate with 10 % ethanolic molybdatophosphoric acid. *PE* phosphatidylethanolamine; *PS* phosphatidylserine, *PC* phosphatidylcholine, *L1–3* unidentified lipids; *AL1–2* unidentified aminolipids; *GL* unidentified glycolipid; *PL* unidentified phospholipid

did not get stained with zinzadze's reagent indicating absence of phospho-moiety. A TLC spot designated APL by Park et al. (2014) in *A. ratkowskyi* DSM 22686^T must be PS as it can be stained by both amino- and phospho-specific stains. Strain CC-PR-82^T was clearly distinguished particularly from *A. mannitolivorans* DSM 15301^T by exclusively having PS, PL and GL and lacking phosphatidylcholine (PC) that was found in the latter. Identification of PC and PE in *A. mannitolivorans* DSM 15301^T as well as in *A. ratkowskyi* DSM 22686^T was in line with the data reported earlier (Park et al. 2014; Oh et al. 2012). Furthermore, we report the presence of PS for the first time and confirm heterogeneous distribution of PS, PC, PL and GL in *Algoriphagus* species.

The genomic DNA G+C content of strain CC-PR-82^T was determined to be 42.3 mol%, which is within the range reported from other reference strains (Table 1, Yi and Chun 2004; Young et al. 2009; Liu et al. 2009; Bowman et al. 2003).

Taken together, the present polyphasic data unambiguously indicate that strain CC-PR-82^T is a novel species of the genus *Algoriphagus*, for which the name *Algoriphagus taiwanensis* sp. nov. is proposed. In addition, on the basis of new data obtained in this study, emended descriptions of *A. mannitolivorans, A. aquatilis, A. olei* and *A. ratkowskyi* are also proposed.

Emended description of *Algoriphagus mannitolivorans* Yi and Chun (2004) emend. Nedashkovskaya et al. (2007)

The species description is given by Yi and Chun (2004) and Nedashkovskaya et al. (2007). In addition, polar lipids included major amounts of PE, two unidentified aminolipids (AL1–2) and an unidentified lipid (L2) and moderate amounts of PC and trace amounts of an unidentified lipid (L1).

Emended description of *Algoriphagus olei* Young et al. (2009)

The species description is according to Young et al. (2009) with following modifications/amendments. Polar lipids included major amounts of PE, an unidentified aminolipid (AL1) and an unidentified lipid (L2) and moderate amounts of an unidentified aminolipid (AL2) and trace amounts of PS, an unidentified phospholipid (PL) and an unidentified lipid (L1).

Emended description of *Algoriphagus aquatilis* Liu et al. (2009)

The species description is according to Liu et al. 2009 with following amendments. Polar lipids included major amounts of PE, an unidentified aminolipid (AL1) and an unidentified lipid (L2) and moderate amounts of PC and an unidentified aminolipid (AL2) and trace amounts of two unidentified lipids (L1 and L3).

Emended description of *Algoriphagus ratkowskyi* Bowman et al. (2003) emend. Nedashkovskaya et al. (2004, 2007)

The description is according to Bowman et al. (2003) and Nedashkovskaya et al. (2004, 2007) with following amendments. Polar lipids included major amounts of PE, two unidentified aminolipids (AL1–2) and an unidentified lipid (L2) and trace amounts of PS, PC, an unidentified phospholipid (PL) and an unidentified lipid (L1).

Description of *Algoriphagus taiwanensis* sp. nov.

Algoriphagus taiwanensis (tai.wa.nen′sis. N. L. fem. adj. *taiwanensis* of or pertaining to Taiwan, where the type strain was isolated).

Cells are Gram-stain negative, strictly aerobic, nonspore-forming, mesophilic, 0.7–1.6 μm in length and 0.6–0.7 μm in diameter. Cells lack appendages and usually present singly or paired. On marine agar, after 1–2 days of incubation at 30 °C, colonies are 1–3 mm in diameter, circular with regular margins, convex and produce reddish non-diffusible pigments. Growth occurs at 20–40 °C (optimum, 30–37 °C), at pH 6.0–11.0 (optimum, pH 7.0–8.0) and on R2A agar supplemented with 0–2 % NaCl (optimum, 1 %). Cells grow well on marine agar, nutrient agar and R2A agar; however, no growth is observed on TSA. Catalase- and oxidase-positive. Positive for the hydrolysis of casein, starch, egg yolk and xylan; weakly positive for hydrolysis of Tween 20 and negative for the hydrolysis of DNA, colloidal chitin, carboxymethylcellulose and Tween 80. In the API 20 NE strip, positive for hydrolysis of esculin and *p*-nitrophenyl-*β*-D-galactopyranoside; negative for nitrate reduction, indole production and fermentation of D-glucose; activity of arginine dihydrolase and urease; hydrolysis of gelatin; assimilation of D-glucose, L-arabinose, D-mannose, D-mannitol, *N*-acetyl-glucosamine, D-maltose, potassium gluconate, capric acid, adipic acid, malic acid, trisodium citrate and phenylacetic acid. In the API ZYM strip, positive for the activity of alkaline phosphatase, esterase (C 4), esterase lipase (C 8), leucine arylamidase, valine arylamidase, cystine arylamidase, trypsin, α-chymotrypsin, acid phosphatase, naphthol-AS-BI-phosphohydrolase, *β*-galactosidase, α-glucosidase, *β*-glucosidase, *N*-acetyl-*β*-glucosaminidase and α-mannosidase; negative for the activity of lipase (C 14), α-galactosidase, *β*-glucuronidase, and α-fucosidase. In the Biolog GN2 MicroPlate, positive for the oxidation of α-cyclodextrin, glycogen, Tween 40, D-arabitol, D-fructose, L-fucose, D-galactose, gentiobiose, α-D-glucose, m-inositol, α-D-lactose, lactulose, maltose, D-mannitol, *β*-methyl-D-glucoside, D-psicose, D-raffinose, L-rhamnose, D-sorbitol, sucrose, D-trehalose, turanose, acetic acid, citric acid, D-galacturonic acid, D-gluconic acid, D-glucosaminic acid, α-keto butyric acid, α-keto glutaric acid, D,L-lactic acid, quinic acid, succinic acid, glucuronamide, L-alaninamide, D-alanine, L-alanine, L-alanyl glycine, L-asparagine, L-aspartic acid, L-glutamic acid, hydroxy-L-proline, L-ornithine, L-proline, D-serine, L-serine, L-threonine, glycerol; negative for the oxidation of the remaining Biolog GN2 substrates. In the API 50 CH strip, positive for acid production only from esculin ferric citrate; negative for acid production from remaining 48 substrates. In ATB PSE 5 antibiotic strip, sensitive to ampicillin/sulbactam, ticarcillin-pyo, ticarcillin/clavulanic acid, ticarcillin/clavulanic acid-pyo, piperacillin/uretdopen, piperacillin-pyo, piperacillin/tazobactam, piperacillin/tazobactam-pyo,

imipenem, meropenem, ciprofloxacin, colistine,and cortrimoxazole; resistant to ticarcillin, cefepime, ceftazidime, amikacin, gentamicin and tobramycin. The major fatty acids are iso-$C_{15:0}$, $C_{16:1}$ $\omega6c$ and/or $C_{16:1}$ $\omega7c$, iso-$C_{16:0}$, iso-$C_{17:1}$ $\omega9c$ and/or $C_{16:0}$ 10-methyl, anteiso-$C_{15:0}$ and $C_{17:1}$ $\omega6c$. Polar lipids included major amounts of an unidentified aminolipid (AL1) and an unidentified lipid (L2) and moderate amounts of PE, PS and an unidentified aminolipid (AL2). In addition, trace amounts of an unidentified phospholipid (PL), an unidentified lipid (L1) and an unidentified glycolipid (GL) are also found. The sole respiratory quinone is MK-7. The DNA G+C content of the type strain is 42.3 mol%.

The type strain is CC-PR-82^T (=JCM 19755^T =BCRC 80746^T), isolated from surface seawater off coastal Pingtung, Taiwan. The GenBank/EMBL/DDBJ accession number for the 16S rRNA gene sequence of strain CC-PR-82^T is KF732813.

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References

Ahmed I, Yokota A, Fujiwara T (2007) *Chimaereicella boritolerans* sp. nov., a boron-tolerant and alkaliphilic bacterium of the family *Flavobacteriaceae* isolated from soil. Int J Syst Evol Microbiol 57:986–992

Alegado RA, Grabenstatter JD, Zuzow R, Morris A, Huang SY, Summons RE, King N (2013) *Algoriphagus machipongonensis* sp. nov., co-isolated with a colonial choanoflagellate. Int J Syst Evol Microbiol 63:163–168

Altschul SF, Gish W, Miller W, Myers EW, Lipman DJ (1990) Basic local alignment search tool. J Mol Biol 215:403–410

Bowman JP, Nichols CM, Gibson JA (2003) *Algoriphagus ratkowskyi* gen. nov., sp. nov., *Brumimicrobium glaciale* gen. nov., sp. nov., *Cryomorpha ignava* gen. nov., sp. nov. and *Crocinitomix catalasitica* gen. nov., sp. nov., novel flavobacteria isolated from various polar habitats. Int J Syst Evol Microbiol 53:1343–1355

Collins MD (1985) Analysis of isoprenoid quinones. Methods Microbiol 18:329–366

Copa-Patiño JL, Arenas M, Soliveri J, Sánchez-Porro C, Ventosa A (2008) *Algoriphagus hitonicola* sp. nov., isolated from an athalassohaline lagoon. Int J Syst Evol Microbiol 58:424–428

Embley TM, Wait R (1994) Structural lipids of eubacteria. In: Goodfellow M, O'Donnell AG (eds) Chemical Methods in Prokaryotic Systematics. John Wiley & Sons, Chichester, pp 121–161

Euzéby JP (1997) List of bacterial names with standing in nomenclature: a folder available on the internet. Int J Syst Bacteriol 47:590–592

Felsenstein J (1981) Evolutionary trees from DNA sequences: a maximum likelihood approach. J Mol Evol 17:368–376

Felsenstein J (1985) Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39:783–791

Fitch WM (1971) Towards defining the course of evolution: minimum change for a specific tree topology. Syst Zool 20:406–416

GCG (1995) Wisconsin Package Version 8.1 Program Manual. Madison, WI: Computer Group

Hameed A, Shahina M, Lin S-Y, Cho J-C, Lai W-A, Young C-C (2013) *Kordia aquimaris* sp. nov., a zeaxanthin-producing member of the family *Flavobacteriaceae* isolated from surface seawater, and emended description of the genus *Kordia*. Int J Syst Evol Microbiol 63:4790–4796

Heiner CR, Hunkapiller KL, Chen SM, Glass JI, Chen EY (1998) Sequencing multimegabase-template DNA with BigDye terminator chemistry. Genome Res 8:557–561

Kämpfer P, Kroppenstedt RM (1996) Numerical analysis of fatty acid patterns of coryneform bacteria and related taxa. Can J Microbiol 42:989–1005

Kang H, Weerawongwiwat V, Jung MY, Myung SC, Kim W (2013) *Algoriphagus chungangensis* sp. nov., isolated from a tidal flat sediment. Int J Syst Evol Microbiol 63:648–653

Kim O-S, Cho Y-J, Lee K, Yoon S-H, Kim M, Na H, Park S-C, Jeon YS, Lee J-H, Yi H, Won S, Chun J (2012) Introducing EzTaxon-e: a prokaryotic 16S rRNA gene sequence database with phylotypes that represent uncultured species. Int J Syst Evol Microbiol 62:716–721

Kim H, Joung Y, Joh K (2014) *Algoriphagus taeanensis* sp. nov., isolated from a tidal flat, and emended description of *Algoriphagus hitonicola*. Int J Syst Evol Microbiol 64:21–26

Kimura M (1980) A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. J Mol Evol 16:111–120

Kumar PA, Bhumika V, Ritika C, Bhaskar YV, Priyashanth P, Aravind R, Bindu E, Srinivas TN (2013) *Algoriphagus shivajiensis* sp. nov., isolated from Cochin back water, India. Syst Appl Microbiol 36:106–111

Lee D-H, Kahng H-Y, Lee SB (2012) *Algoriphagus jejuensis* sp. nov., isolated from seawater. Int J Syst Evol Microbiol 62:409–413

Li Y, Yan S, Yang Q, Qi Z, Zhang X-H, Fu Y-B (2011) *Algoriphagus faecimaris* sp. nov., isolated from coastal sediment. Int J Syst Evol Microbiol 61:2856–2860

Liu Y, Li H, Jiang J-T, Liu Y-H, Song X-F, Xu C-J, Liu Z-P (2009) *Algoriphagus aquatilis* sp. nov., isolated from a freshwater lake. Int J Syst Evol Microbiol 59:1759–1763

Mesbah M, Premachandran U, Whitman WB (1989) Precise measurement of the G+C content of deoxyribonucleic acid by high-performance liquid chromatography. Int J Syst Bacteriol 39:159–167

Minnikin DE, O'Donnell AG, Goodfellow M, Alderson G, Athalye M, Schaal A, Parlett JH (1984) An integrated procedure for the extraction of bacterial isoprenoid quinones and polar lipids. J Microbiol Methods 2:233–241

Montero-Calasanz MD, Göker M, Rohde M, Spröer C, Schumann P, Busse H-J, Schmid M, Tindall BJ, Klenk H-P,

Camacho M (2013) *Chryseobacterium hispalense* sp. nov., a plant growth-promoting bacterium isolated from a rainwater pond in an olive plant nursery and emendation of the species *Chryseobacterium defluvii*, *Chryseobacterium indologenes*, *Chryseobacterium wanjuense* and *Chryseobacterium gregarium*. Int J Syst Evol Microbiol 63: 4386–4395

Murray RGE, Doetsch RN, Robinow CF (1994) Determinative and cytological light microscopy. In: Gerhardt P, Murray RGE, Wood WA, Krieg NR (eds) Methods for general and molecular bacteriology. American Society of Microbiology, Washington, DC, pp 21–41

Nedashkovskaya OI, Vancanneyt M, Van Trappen S, Vandemeulebroecke K, Lysenko AM, Rohde M, Falsen E, Frolova GM, Mikhailov VV, Swings J (2004) Description of *Algoriphagus aquimarinus* sp. nov., *Algoriphagus chordae* sp. nov. and *Algoriphagus winogradskyi* sp. nov., from sea water and algae, transfer of *Hongiella halophila* Yi and Chun 2004 to the genus *Algoriphagus* as *Algoriphagus halophilus* comb. nov. and emended descriptions of the genera *Algoriphagus* Bowman et al. 2003 and Hongiella Yi and Chun 2004. Int J Syst Evol Microbiol 54:1757–1764

Nedashkovskaya OI, Kim SB, Kwon KK, Shin DS, Luo X, Kim S-J, Mikhailov VV (2007) Proposal of *Algoriphagus vanfongensis* sp. nov., transfer of members of the genera *Hongiella* Yi and Chun 2004 emend. Nedashkovskaya et al. 2004 and *Chimaereicella* Tiago et al. 2006 to the genus *Algoriphagus*, and emended description of the genus *Algoriphagus* Bowman et al. 2003 emend. Nedashkovskaya et al. 2004. Int J Syst Evol Microbiol 57:1988–1994

Nedashkovskaya OI, Ludwig W (2011) Family II. *Cyclobacteriaceae* fam. nov. In: Krieg NR, Staley JT, Brown DR, Hedlund BP, Paster BJ, Ward NL, Ludwig W, Whitman WB (eds) Bergey's manual of systematic bacteriology. Springer, New York, p 423

Oh K-H, Kang S-J, Lee S-Y, Park S, Oh T-K, Yoon J-H (2012) *Algoriphagus namhaensis* sp. nov., isolated from seawater. Int J Syst Evol Microbiol 62:575–579

Park S, Kang S-J, Oh K-H, Oh T-K, Yoon J-H (2010) *Algoriphagus lutimaris* sp. nov., isolated from a tidal flat sediment. Int J Syst Evol Microbiol 60:200–204

Park S, Park J-M, Lee K-C, Yoon J-H (2014) *Algoriphagus boseongensis* sp. nov., a member of the family *Cyclobacteriaceae* isolated from a tidal flat. Antonie Van Leeuwenhoek 105:523–531

Rau JE, Blotevogel K-H, Fischer U (2012) *Algoriphagus aquaeductus* sp. nov., isolated from a freshwater pipe. Int J Syst Evol Microbiol 62:675–682

Saitou N, Nei M (1987) The neighbor-joining method: a new method for reconstructing phylogenetic trees. Mol Biol Evol 4:406–425

Sasser M (1990) Identification of bacteria by gas chromatography of cellular fatty acids. USFCC Newsl 20:16

Shahina M, Hameed A, Lin S-Y, Hsu Y-H, Liu Y-C, Cheng I-C, Lee M-R, Lai W-A, Lee R-J, Young C-C (2013) *Sphingomicrobium astaxanthinifaciens* sp. nov., an astaxanthin-producing glycolipid-rich bacterium isolated from surface seawater and emended description of the genus *Sphingomicrobium*. Int J Syst Evol Microbiol 63:3415–3422

Smibert RM, Krieg NR (1994) Phenotypic characterization. In: Gerhardt P, Murray RGE, Wood WA, Krieg NR (eds) Methods for general and molecular bacteriology. American Society of Microbiology, Washington, DC, pp 607–654

Tamura K, Peterson D, Peterson N, Stecher G, Nei M, Kumar S (2011) MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. Mol Biol Evol 28: 2731–2739

Thompson JD, Gibson TJ, Plewniak F, Jeanmougin F, Higgins DG (1997) The CLUSTAL_X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acids Res 25:4876–4882

Tiago I, Mendes V, Pires C, Morais PV, Veríssimo A (2006) *Chimaereicella alkaliphila* gen. nov., sp. nov., a Gram-negative alkaliphilic bacterium isolated from a nonsaline alkaline groundwater. Syst Appl Microbiol 29:100–108

Tindall BJ, Rosselló-Móra R, Busse H-J, Ludwig W, Kämpfer P (2010) Notes on the characterization of prokaryote strains for taxonomic purposes. Int J Syst Evol Microbiol 60: 249–266

Van Trappen S, Vandecandelaere I, Mergaert J, Swings J (2004) *Algoriphagus antarcticus* sp. nov., a novel psychrophile from microbial mats in Antarctic lakes. Int J Syst Evol Microbiol 54:1969–1973

Watts D, MacBeath JR (2001) Automated fluorescent DNA sequencing on the ABI PRISM 310 genetic analyzer. Methods Mol Biol 167:153–170

Yang C, Li Y, Guo Q, Lai Q, Zheng T, Tian Y (2013) *Algoriphagus zhangzhouensis* sp. nov., isolated from mangrove sediment. Int J Syst Evol Microbiol 63:1621–1626

Yi H, Chun J (2004) *Hongiella mannitolivorans* gen. nov., sp. nov., *Hongiella halophila* sp. nov. and *Hongiella ornithinivorans* sp. nov., isolated from tidal flat sediment. Int J Syst Evol Microbiol 54:157–162

Yoon J-H, Yeo S-H, Oh T-K (2004) *Hongiella marincola* sp. nov., isolated from sea water of the East Sea in Korea. Int J Syst Evol Microbiol 54:1845–1848

Yoon J-H, Kang S-J, Jung S-Y, Lee C-H, Oh T-K (2005a) *Algoriphagus yeomjeoni* sp. nov., isolated from a marine solar saltern in the Yellow Sea, Korea. Int J Syst Evol Microbiol 55:865–870

Yoon J-H, Kang S-J, Oh T-K (2005b) *Algoriphagus locisalis* sp. nov., isolated from a marine solar saltern. Int J Syst Evol Microbiol 55:1635–1639

Yoon J-H, Lee M-H, Kang S-J, Oh T-K (2006) *Algoriphagus terrigena* sp. nov., isolated from soil. Int J Syst Evol Microbiol 56:777–780

Young C-C, Lin S-Y, Arun AB, Shen F-T, Chen W-M, Rekha PD, Langer S, Busse H-J, Wu Y-H, Kämpfer P (2009) *Algoriphagus olei* sp. nov., isolated from oil-contaminated soil. Int J Syst Evol Microbiol 59:2909–2915