Pseudohongiella nitratireducens sp. nov., isolated from seawater, and emended description of the genus *Pseudohongiella*

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Two Gram-stain-negative, aerobic, motile by a single polar flagellum and rod-shaped strains, designated SCS-49^T and SCS-111, were isolated from seawater of the South China Sea. The two strains grew at 4–35 °C, with 0.5–7.5 % (w/v) NaCl and at pH 6.5–9.0 and were able to reduce nitrate. Q-8 was the sole ubiquinone. The major fatty acids of the two strains were $C_{16:0}$, $C_{18:1}\omega7c$ and summed feature 3 ($C_{16:1}\omega7c$ and/or $C_{16:1}\omega6c$). The polar lipids included diphosphatidylglycerol, phosphatidylethanolamine, phosphatidylglycerol, phospoglycolipid, three unidentified glycolipids, five unidentified phospholipids and two to three unidentified lipids. The isolates formed a stable clade with *Pseudohongiella acticola* and *Pseudohongiella spirulinae* based on phylogenetic analysis of 16S rRNA gene sequences. Strains SCS-49^T and SCS-111 exhibited 16S rRNA gene sequence similarity values of 97.2 and 96.0 % with respect to the type strains of *P. acticola* and *P. spirulinae*, respectively. The average nucleotide diversity and *in silico* DNA–DNA hybridization values between strain SCS-49^T and *P. acticola* KCTC 42131^T were 71.4 and 25.1 %, respectively and the values between strain SCS-49^T and SCS-111 were 99.9 and 99.2 %, respectively. Based upon the phenotypic, chemotaxonomic and genetic data, strains SCS-49^T and SCS-111 represent a novel species in the genus *Pseudohongiella*, for which the name *Pseudohongiella nitratireducens* sp. nov. is proposed. The type strain is SCS-49^T (=CGMCC 1.15425^T=KCTC 52155^T=MCCC 1K03186^T).

The genus *Pseudohongiella*, belonging to the class *Gammaproteobacteria*, was proposed by Wang *et al.* (2013, 2014) and now consists of two species with validly published names, *Pseudohongiella acticola* and *Pseudohongiella spirulinae* (Park *et al.*, 2014). Members of the genus *Pseudohongiella* are Gram-stain-negative, aerobic and motile, and have been isolated from aquatic environments, such as a cultivation pond of *Spirulina platensis* and seawater (Wang *et al.*, 2013; Park *et al.*, 2014). In the present study, two strains isolated from seawater samples were indicated to be affiliated to the genus *Pseudohongiella* based on a polyphasic taxonomic investigation.

Two seawater samples, LEDS1_L16CTD2 (430 m water depth, 115° 54′ E 19° 43′ N) and LEDS1_TSCTD7 (450 m water depth, 115° 14′ E 19° 54′ N), were collected by a rosette sampler connected to the CTD system (SBE911 plus; Sea-Bird Electronics) from the northern South China Sea in October 2014. Samples of approximately 100 µl were inoculated aseptically on to marine agar 2216 (MA; BD Difco) supplemented with Tween 40 (1.5 %, w/v) at 30 °C. After 2 months of cultivation, two pale orange colonies, designated SCS-49^T and SCS-111, were picked. The two isolates were purified by repeated restreaking and the purity was confirmed by the uniformity of cell morphology. Strains SCS-49^T and SCS-111 were maintained in glycerol suspensions (30 %, v/v) at −80 °C for long-term preservation.

Abbreviations: ANI, average nucleotide identity; DDH, DNA–DNA hybridization.

The GenBank/EMBL/DDBJ accession numbers for the 16S rRNA gene sequence of strains SCS-49T and SCS-111 are KT851540 and KT851541, respectively. The GenBank accession numbers for the whole genome sequences of strains SCS-49T and SCS-111 as well as *Pseudohongiella acticola* KCTC 42131T are LWHM00000000, LWHN00000000 and MASR00000000, respectively.

Four supplementary figures and two supplementary tables are available with the online Supplementary Material.

Genomic DNA was extracted according to the manual of the AxyPrep Bacterial Genomic DNA Miniprep Kit (Axygen; Corning) and examined by 0.6 % (w/v) agarose gel electrophoresis with λ-*Hind*III digest DNA. The whole-genomic sequencing of strains SCS-49^T and SCS-111 was carried out using Solexa paired-end sequencing technology (HiSeq2000 system; Illumina) by a whole-genome shotgun strategy at Anoroad Gene Technology. Clean reads were assembled using ABySS 1.9.0 (Simpson *et al.*, 2009). The ORFs predicted by using Glimmer v.3.0 (Delcher *et al.*, 2007) were analysed through the Rapid Annotation using Subsystem Technology (RAST) server online (Overbeek *et al.*, 2014) for annotation. The DNA G+C content of the strains was calculated by RAST. The ANI value between two genomes was determined through the Orthologous Average Nucleotide Identity Tool (Lee *et al.*, 2016). The *in silico* DDH value was calculated by GGDC 2 (Meier-Kolthoff *et al.*, 2013). The complete 16S rRNA gene sequences of strains SCS-49^T and SCS-111 were annotated via the RNAmmer 1.2 server (Lagesen *et al.*, 2007) and compared through the EzTaxon-e service (Kim *et al.*, 2012). Phylogenetic trees were reconstructed by the neighbour-joining (Saitou & Nei, 1987), maximum-likelihood (Felsenstein, 1981) and maximum-parsimony (Fitch, 1971) algorithms with the MEGA 6 software package (Tamura *et al.*, 2013) based on 16S rRNA gene sequences of related sequences aligned with CLUSTAL W (Thompson *et al.*, 1994). Evolutionary distances were calculated according to the algorithm of the Kimura two-parameter model (Kimura, 1980) for the neighbour-joining method with bootstrap analysis set to 1000 replicates.

The complete 16S rRNA gene sequences (1527 nt) of strains SCS-49^T and SCS-111 were identical. The two strains were closely related to *P. acticola* GBSW-S^T (97.2 % 16S rRNA gene sequence similarity) and *P. spirulinae* Ma-20^T (96.0 %). The 16S rRNA gene sequence similarities between the two novel strains and the type strains of other genera were lower than 92.0 %. Phylogenetic trees based on the neighbour-joining, maximum-likelihood and maximum-parsimony approaches showed that strains SCS-49^T and SCS-111 fell within the clade including *P. acticola* and *P. spirulinae* with high bootstrap values (99.0–100 %; Figs 1, S1 and S2). This robust topology forming an independent clade indicated that strains SCS-49^T and SCS-111 belong to the genus *Pseudohongiella*.

The major genomic characteristics of the novel strains and the two reference strains were similar (Table S1). Strains SCS-49^T and SCS-111 had high ANI (99.9 %) and *in silico* DDH (99.2 %) values between each other, indicating they belong to the same genospecies (Table S2). The ANI and *in silico* DDH values between strain SCS-49^T and *P. acticola* KCTC 42131^T were 71.4 and 25.1 %, respectively, and these values between strain SCS-111 and *P. acticola* KCTC 42131^T were 71.5 % and 25.1 %. The values were strikingly lower than the threshold values (ANI 95.0 % and *in silico* DDH 70.0 %) (Meier-Kolthoff *et al.*, 2013; Kim *et al.*, 2014), revealing that strains SCS-49^T and SCS-111 represent a novel species.

The NaCl concentration range (0, 0.5, 1.0, 2.0, 3.0, 5.0, 7.5, 10.0, 15.0 and 20.0 %, w/v) for growth was investigated in marine broth 2216 (MB; BD Difco). Growth at different pH (4.0–10.0, at 0.5 pH unit intervals) was determined in MB by adding appropriate biological buffers: MES (pH 4.0–6.0), PIPES (pH 6.5–7.5), Tricine (pH 8.0–8.5) and CAPSO (pH 9.0–10.0). The temperature range (4, 10, 15, 20, 25, 30, 35, 40, 45 and 50 °C) for growth was inspected in MB. Cell morphology, size and shape were observed by phase-contrast microscopy (DM 5000B; Leica) and transmission electron microscopy (H-600; Hitachi).

Unless stated otherwise, physiological and biochemical tests were performed in MB at 30 °C. Gram-staining was determined by the method described by Dong & Cai (2001). Oxidase activity was tested by oxidation of *p*-aminodimethylaniline oxalate solution (1.0 %, w/v). Catalase activity was determined by bubble production in hydrogen peroxide solution (3.0 %, v/v). Hydrolysis of DNA (0.2 %, w/v), gelatin (1.0 %, w/v), starch (0.2 %, w/v) and Tweens 20, 40 and 80 (1.0 %, w/v) was examined according to Xu *et al.* (2015). Nitrate and nitrite reduction was determined using Griess A solution [0.5 g *p*-aminobenzenesulfonic acid with 150 ml (10.0 %, v/v) acetic acid], Griess B solution [0.1 g α-naphthylamine with 150 ml (10.0 %, v/v) acetic acid and 20 ml distilled water] and diphenylamine solution (0.5 g diphenylamine with 100 ml concentrated sulfuric acid and 20 ml distilled water) following cultivation in liquid medium supplemented with 0.5 % (w/v) nitrate or 0.1 % (w/v) nitrite for 5 days. Single carbon, nitrogen and energy source assimilation tests were carried out in basal medium (Baumann *et al.*, 1971) supplemented with Hunter's mineral base and vitamin solution according to Park *et al.* (2014), and usage amounts of filter-sterilized sugars, alcohols, organic acids and amino acids were 0.2, 0.2, 0.2 and 0.1 % (w/v), respectively. Acid production tests were performed in modified marine oxidation-fermentation medium supplemented with 2.0 % (w/v) NaCl and 1.0 % (w/v) filter-sterilized sugars or alcohols (Leifson, 1963; Xu *et al.*, 2008). Anaerobic growth was investigated by using nitrate (20 mM) or nitrite (10 mM) as potential electron acceptors in an AnaroPack system (Mitsubishi Gas Chemical Co.). API 20NE and API ZYM miniaturized systems were used to test enzyme activity and additional phenotypic characteristics according to the manufacturer (bioMérieux). Susceptibility to antibiotics was determined by a two-layer plate method, placing antibiotic discs (Hangzhou Microbial Reagent; Hangwei) on the upper medium, and was considered positive when the radius of the inhibition zone was over 2.0 mm. The antibiotics (μg per disc except where stated) used were: amoxicillin (20), ampicillin (10), bacitracin (0.04 IU), carbenicillin (100), chloramphenicol (30), erythromycin (15), gentamicin (10), kanamycin (30), nalidixic acid (30), neomycin (30), nitrofurantoin (300), nystatin (100), penicillin G (10), polymyxin B (300 IU), rifampin (5), streptomycin (10), tetracycline (30), tobramycin (10) and vancomycin (30).

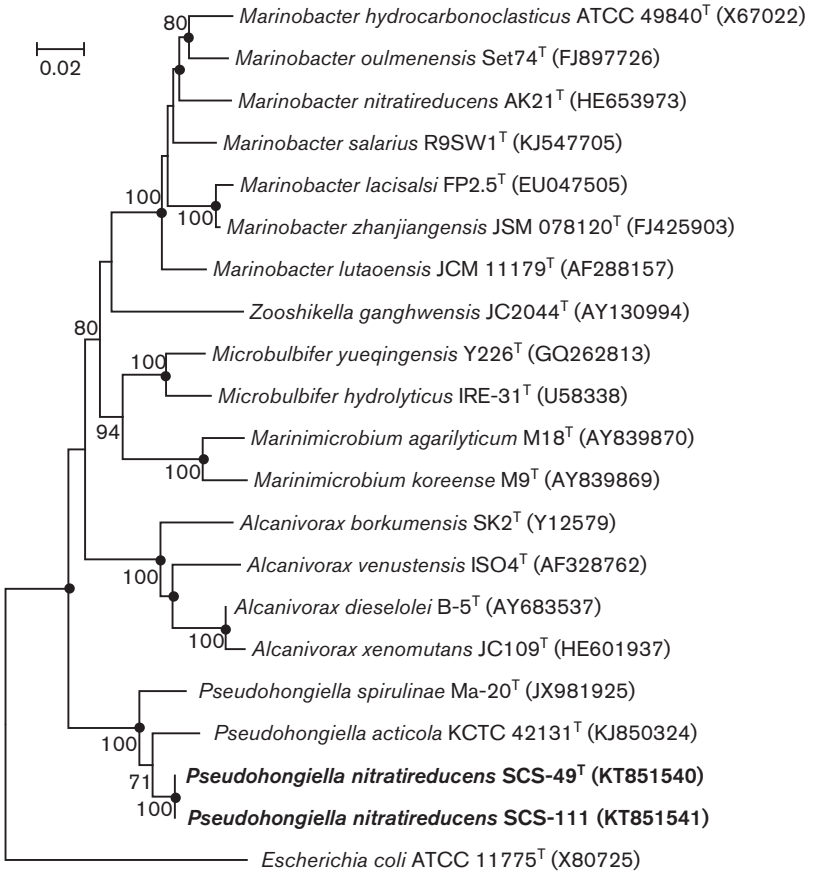

Fig. 1. Neighbour-joining tree based on 16S rRNA gene sequences showing the phylogenetic relationship of strains SCS-49^T and SCS-111 and their closely related taxa. Bootstrap values are based on 1000 replicates; only bootstrap values >70 % are shown. Bar, 0.02 substitutions per nucleotide position. Filled circles indicate nodes that were also recovered in maximum-likelihood and maximum-parsimony phylogenetic trees.

P. acticola KCTC 42131^T and *P. spirulinae* Ma-20^T were used as reference strains in the above tests.

Cells of strains SCS-49^T and SCS-111 were Gram-stain-negative, rod-shaped (approximately 0.5–0.7 μm in width and 1.3–1.7 μm in length) and motile by means of a single polar flagellum (Fig. S3). Colonies were pale orange, circular, convex, opaque and 2 mm in diameter following cultivation on MA for 5 days. Strains SCS-49^T and SCS-111 were oxidase- and catalase-positive and hydrolysed Tweens 20, 40 and 80. Genomic data showed that both strains harboured the ABC-type nitrate transport system and assimilatory nitrate reductase, indicating their potential nitrate-reduction activity. Nitrate reduction of strains SCS-49^T and SCS-111 was confirmed by a nitrate reduction test as well as by the API 20NE miniaturized system. Neither *P. acticola* KCTC 42131^T nor *P. spirulinae* Ma-20^T could reduce nitrate. Detailed differential characteristics are presented in Table 1.

Lyophilized cells of strains SCS-49^T and SCS-111 were used to extract the isoprenoid quinone with chloroform/methanol (2 : 1, v/v). Extracts were evaporated to dryness at 35 °C following filtering and resuspended in chloroform/methanol (2 : 1, v/v). The isoprenoid quinone, separated on GF254 silica gel plates (Branch of Qingdao Haiyang Chemical) with n-hexane/ether (17 : 3, v/v), was analysed by HPLC-MS (Xu *et al.*, 2011). For fatty acid methyl ester analyses, cells collected from quadrant three when it exhibited confluent growth were lyophilized and sent to Shanghai Public Health Clinical Center to detect profiles of fatty acids by using the Microbial Identification System (MIDI). Polar lipids were extracted from cells in accordance with the modified method proposed by Kamekura & Kates (1988) and separated by two-dimensional TLC. Total lipids were identified by using molybdophosphoric acid and sulfuric acid, glycolipids by α-naphthol reagent, phospholipids by ammonium molybdate reagent and lipids containing free amino lipids by ninhydrin reagent (Tindall *et al.*, 2007).

Strains SCS-49^T and SCS-111 as well as the type strains of *Pseudohongiella* species had an identical pattern of ubiquinone (Q-8), which is a typical characteristic used to distinguish the genus *Pseudohongiella* from closely related genera (Wang *et al.*, 2013).

Table 1. Differential characteristics between strains SCS-49^T and SCS-111 and their closest relatives within the genus *Pseudohongiella*

Strains: 1, SCS-49^T; 2, SCS-111; 3, *P. spirulinae* Ma-20^T; 4, *P. acticola* KCTC 42131^T. All strains were positive for oxidase and catalase activities, esterase (C4), esterase lipase (C8) and leucine arylamidase activities (API ZYM), hydrolysis of Tweens 20, 40 and 80, assimilation of D-mannose, maltose and malic acid (API 20NE), utilization of glycerol, maltose, D-mannose, malate, pyruvate, L-glutamate, L-isoleucine and L-lysine as sole carbon, nitrogen and energy sources, acid production from L-arabinose, maltose, D-ribose and sorbose and susceptibility to amoxicillin, ampicillin, carbenicillin, chloramphenicol, erythromycin, nitrofurantoin, penicillin G, polymyxin B, rifampin and vancomycin. All strains were negative for anaerobic respiration with nitrate or nitrite as a potential electron acceptor, hydrolysis of DNA, gelatin and starch, lipase (C14), α-chymotrypsin, cysteine arylamidase, valine arylamidase, α-fucosidase, α-galactosidase, β-galactosidase, α-glucosidase, β-glucosidase, *N*-acetyl-β-glucosaminidase, β-glucuronidase, α-mannosidase, naphthol-AS-BI-phosphohydrolase and trypsin activities (API ZYM), arginine dihydrolase, fermentation of glucose, β-galactosidase, hydrolysis of gelatin, nitrite reduction, urease and assimilation of L-arabinose, D-glucose, potassium gluconate, adpic acid, capric acid, trisodium citrate and phenylacetic acid (API 20NE), utilization of L-arabinose, D-fructose, D-galactose, *myo*-inositol, α-D-lactose, L-rhamnose, sorbitol, sucrose, citrate, formate, fumarate, malonate, glycine and L-methionine as sole carbon, nitrogen and energy sources, acid production from D-fructose, D-galactose, D-glucose, *myo*-inositiol, α-D-lactose, D-mannose, raffinose, sucrose, trehalose and D-xylose, and susceptibility to bacitracin, gentamicin, kanamycin, nystatin and tobramycin. +, Positive; −, negative; W, weakly positive; PO, pale orange; PY, pale yellow.

Characteristic	1	2	3	4
Colony colour	PO	PO	PY	PY
Range of growth				
Temperature (°C)	4–35	4–35	10–43*	10–35†
NaCl concentration (%, w/v)	0.5–7.5	0.5–7.5	0.5–11.0*	0.5–8.0†
Growth at pH 6.5	+	+	−*	+†
Optimum pH for growth	7.0	7.0	7.5–9.0*	7.0–8.0†
Hydrolysis of aesculin	+	+	−	+
Nitrate reduction	+	+	−	−
Enzyme activities:				
Acid phosphatase	−	−	+	−
Alkaline phosphatase	−	−	+	+
Utilization of:				
Cellobiose	+	+	W	−
Ethanol	W	+	+	−
Mannitol and melezitose	+	+	W	−
Raffinose, trehalose, succinate, L-histidine and L-valine	−	−	+	−
L-Asparate, L-alanine and L-arginine	+	+	+	−
Acid production from:				
Ethanol	+	+	+	−
Glycerol, mannitol and L-rhamnose	W	W	+	−
Antibiotic susceptibility:				
Nalidixic acid	+	+	+	−
Neomycin and tetracycline	+	+	−	−
Streptomycin	+	−	−	−
DNA G+C content (mol%) (by genome)	51.8	51.8	54.0	55.2

*Data from Wang *et al.* (2013).
†Data from Park *et al.* (2014).

Strains SCS-49^T and SCS-111 had similar profiles of polar lipids, including diphosphatidylglycerol, phosphatidylethanolamine, phosphatidylglycerol, phosphoglycolipid, three unidentified glycolipids, five unidentified phospholipids and two unidentified lipids (L1 and L2), except for one unidentified lipid (L3) detected in strain SCS-111 (Fig. S4). One unidentified aminolipid (AL1) was detected in *P. acticola* KCTC 42131^T and *P. spirulinae* Ma-20^T that was absent in both strain SCS-49^T and strain SCS-111. In addition, moderate or minor amounts of an unidentified glycolipid (GL2), unidentified lipids (L1 and L2) and unidentified phospholipids (PL1, PL2 and PL5) were only observed in strains SCS-49^T and SCS-111.

The components of major fatty acids (>10.0 %) were similar in all of the four strains, including $C_{16:0}$, $C_{18:1}\omega7c$ and summed feature 3 ($C_{16:1}\omega7c$ and/or $C_{16:1}\omega6c$) (Table 2). However,

Table 2. Fatty acid profiles of strains SCS-49^T and SCS-111 and the type strains of two *Pseudohongiella* species

Strains: 1, SCS-49^T; 2, SCS-111; 3, *P. spirulinae* Ma-20^T; 4, *P. acticola* KCTC 42131^T. –, Not detected; TR, trace (<0.2 %). Fatty acids for which amounts were lower than 0.2 % among the four strains were omitted. Values are percentages of the total. ECL, equivalent chain length.

Fatty acid	1	2	3	4
Straight-chain				
$C_{10:0}$	2.8	3.1	3.5	0.5
$C_{11:0}$	TR	TR	0.3	–
$C_{12:0}$	2.2	2.5	7.3	2.9
$C_{14:0}$	0.8	0.7	1.5	0.4
$C_{15:0}$	0.3	0.4	–	TR
$C_{16:0}$	27.9	28.5	13.9	22.1
$C_{17:0}$	0.3	0.2	–	TR
$C_{18:0}$	0.8	1.1	–	0.8
Unsaturated				
$C_{17:1}\omega 8c$	0.4	0.4	0.6	0.3
$C_{18:1}\omega 7c$	33.8	31.9	22.6	35.6
Branched-chain				
anteiso-$C_{17:0}$	–	–	–	0.3
iso-$C_{11:0}$	TR	TR	0.8	TR
iso-$C_{12:0}$	–	–	1.6	TR
iso-$C_{15:0}$	0.5	0.5	0.9	TR
iso-$C_{16:0}$	–	–	1.6	1.5
iso-$C_{17:0}$	0.8	0.7	1.3	2.0
$C_{18:1}\omega 7c$ 11-methyl	–	–	–	0.3
Hydroxy				
$C_{10:0}$ 3-OH	2.0	1.8	4.0	1.1
$C_{12:0}$ 3-OH	2.5	2.2	6.4	2.2
$C_{12:1}$ 3-OH	TR	TR	–	0.2
iso-$C_{11:0}$ 3-OH	TR	TR	1.7	0.6
iso-$C_{12:0}$ 3-OH	–	–	0.7	TR
Summed feature 3*	22.9	24.2	24.6	24.5
Summed feature 7*	–	–	–	0.4
Unknown				
ECL 11.799	0.5	0.7	6.6	2.5
ECL 12.484	0.2	0.2	–	TR

*Summed feature 3 contains $C_{16:1}\omega 7c$ and/or $C_{16:1}\omega 6c$, and summed feature 7 contains ECL 18.846, $C_{19:1}\omega 6c$ and/or cyclo $C_{19:0}\omega 10c$.

several kinds of fatty acids present in minor amounts (<2.0 %) could be used to distinguish strains SCS-49^T and SCS-111 and recognized *Pseudohongiella* species. For instance, iso-$C_{12:0}$, iso-$C_{16:0}$ and iso-$C_{12:0}$ 3-OH were detected in both *P. acticola* KCTC 42131^T and *P. spirulinae* Ma-20^T, but were absent from strains SCS-49^T and SCS-111.

Additionally, strains SCS-49^T and SCS-111 could be differentiated from *P. acticola* KCTC 42131^T and *P. spirulinae* Ma-20^T by phenotypic characteristics, such as nitrate reduction, colour of colonies, growth range of temperature and NaCl concentration, alkaline phosphatase activity and assimilation of *N*-acetylglucosamine (Table 1).

Based upon genetic, chemotaxonomic and phenotypic analyses, strains SCS-49^T and SCS-111 represent a novel species of the genus *Pseudohongiella*, for which the name *Pseudohongiella nitratireducens* sp. nov. is proposed.

Emended description of the genus *Pseudohongiella* Wang *et al.* (2013), Emend. Park *et al.* (2014)

The common phospholipids are phosphatidylglycerol, phosphatidylethanolamine, diphosphatidylglycerol and one unidentified phospholipid (PL3). Two to five glycolipids are present. The DNA G+C content is 51.8–55.2 mol% (by genome).

Description of *Pseudohongiella nitratireducens* sp. nov.

Pseudohongiella nitratireducens (ni.tra.ti.re.du′cens. N.L. n. *nitras -atis* nitrate; L. pres. part. *reducens* converting to a different state; N.L. part. adj. *nitratireducens* reducing nitrate).

Cells are Gram-stain-negative, rod-shaped and motile by means of a single polar flagellum. Colonies are pale orange, convex, circular, opaque, smooth and 0.2 mm in diameter following incubation on MA at 30 °C for 5 days. Growth occurs between 4 and 35 °C with optimum growth at 30 °C. The NaCl concentration and pH range for growth are 0.5–7.5 % (w/v) and pH 6.5–9.0 with an optimum of 2.0 % (w/v) NaCl and pH 7.0. Anaerobic growth is not observed on MA supplemented with nitrate or nitrite. Oxidase- and catalase-positive. Tweens 20, 40 and 80 are hydrolysed, but DNA, aesculin, gelatin, starch and urea are not. Nitrate is reduced to nitrite, but nitrite is not reduced. Negative for arginine dihydrolase and indole production. The following enzyme activities are positive: esterase (C4), esterase lipase (C8) and leucine arylamidase; but negative for *N*-acetyl-β-glucosaminidase, acid phosphatase, alkaline phosphatase, α-chymotrypsin, cystine arylamidase, valine arylamidase, α-fucosidase, α-galactosidase, β-galactosidase, β-glucuronidase, α-glucosidase, β-glucosidase, lipase (C14), α-mannosidase, naphthol-AS-BI-phosphohydrolase and trypsin. Cellobiose, ethanol, glycerol, maltose, mannitol, D-mannose, melezitose, malate, pyruvate, L-alanine, L-arginine, L-aspartate, L-glutamate, L-isoleucine and L-lysine are utilized as sole carbon, nitrogen and energy sources. L-Arabinose, D-fructose, D-galactose, *myo*-inositol, α-D-lactose, raffinose, L-rhamnose, sorbitol, sucrose, trehalose, citrate, formate, fumarate, malonate, succinate, glycine, L-histidine, L-methionine and L-valine are not utilized. Acid can be produced from L-arabinose, ethanol, ribose and sorbose; acid is weakly produced from glycerol, mannitol and L-rhamnose, but not from D-fructose, D-galactose, D-glucose, *myo*-inositiol, α-D-lactose, D-mannose, raffinose, sucrose, trehalose or D-xylose.

The sole ubiquinone is Q-8. The major fatty acids are $C_{16:0}$, $C_{18:1}\omega7c$ and summed feature 3 ($C_{16:1}\omega7c$ and/or $C_{16:1}\omega6c$). The polar lipids include diphosphatidylglycerol, phosphatidylethanolamine, phosphatidylglycerol, phosphoglycolipid, three unidentified glycolipids, five unidentified phospholipids and two to three unidentified lipids.

The type strain, SCS-49^T (=CGMCC 1.15425^T=KCTC 52155^T=MCCC 1K03186^T), was isolated from seawater of the South China Sea. The DNA G+C content of the type strain is 51.8 mol% (by genome). SCS-111 is a second strain of the species.

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