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Meridianimarinicoccus roseus gen. nov., sp. nov., a novel genus of the family *Rhodobacteraceae* isolated from seawater

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Abstract

A Gram-stain negative, pink-pigmented, strictly aerobic, non-motile and coccoid-shaped bacterial strain, designated TG-679^T, was isolated from a deep-sea water sample collected from the South China Sea. Cells of strain TG-679^T were catalase- and oxidase-positive, lacked bacteriochlorophyll a and carotenoid. Strain TG-679^T was found to grow at 10–40 °C (optimum, 28 °C), pH 5.5–10.0 (optimum, pH 7.5) and with 0.5–2.0 % (w/v) NaCl (optimum, 1.5 %). Chemotaxonomic analysis of strain TG-679^T indicated that the sole respiratory quinone was Q-10, the predominant cellular fatty acid was $C_{18:1}\omega7c$, and the major polar lipids consisted of phosphatidylethanolamine, phosphatidylmonomethylethanolamine, phosphatidylglycerol, phosphatidylcholine, an unidentified phospholipid and two unidentified glycolipids. The genomic DNA G+C content of strain TG-679^T was 65.9 mol%. Phylogenetic analysis based on 16S rRNA gene sequences revealed that strain TG-679^T constituted a separated branch in the family *Rhodobacteraceae*. Differential phenotypic properties, together with phylogenetic distinctiveness, demonstrated that strain TG-679^T is clearly distinct from any validly published genus. Based on polyphasic taxonomic characterization, strain TG-679^T is considered to represent a novel species of a novel genus, for which the name *Meridianimarinicoccus roseus* gen. nov., sp. nov. is proposed. The type strain of the species is TG-679^T (=KCTC 62454^T=MCCC 1K03496^T).

The family *Rhodobacteraceae*, belonging to the class *Alphaproteobacteria*, was proposed in 2006 by Garrity *et al.* [1]. At the time of writing, according to the LPSN (List of Prokaryotic Names with Standing in Nomenclature; www.bacterio.net/index.html) [2], 128 genera have been described. The family *Rhodobacteraceae* is phenotypically, metabolically and ecologically diverse [1]. *Rhodobacteraceae* strains have been isolated from diverse environments, including marine and non-marine habitats [3–7]. In general, cells of the members of the family are Gram-stain-negative and multiply by binary fission or by budding, following monopolar growth. Most species are positive for oxidase. The major or sole respiratory quinone is ubiquinone-10 (Q-10), and their cellular fatty acids are usually dominated by $C_{18:1}\omega7c$, which very often constitutes more than 50 % of the total [5]. The cells usually contain phosphatidylglycerol (PG), diphosphatidylglycerol (DPG), phosphatidylethanolamine (PE), phosphatidylcholine (PC) and/or several amino-, phospho- and glycolipids in different combinations [1, 3–5]. The G+C contents of their DNA is usually above 50 %, with the totals ranging between 47–76 mol% [8]. In this study, a novel Gram-stain-negative, coccoid bacterium was isolated from a seawater sample collected from South China Sea. We describe the polyphasic characterization that included determination of chemotaxonomic and phenotypic properties, and a detailed phylogenetic investigation based on 16S rRNA gene sequences. Based on the present study, strain TG-679^T is considered to represent a novel species of a novel genus within the family *Rhodobacteraceae*.

The seawater sample was collected from the South China Sea (19° 22′ N, 115° 38′ E) in summer 2017, and was stored at 4 °C until used. The sample was serially diluted by sterile water, and then spread onto the modified ZoBell 2216E agar plates [9] which were incubated at 28 °C. The modified ZoBell 2216E medium contained (per litre distilled water):

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Keywords: *Rhodobacteraceae*; *Meridianimarinicoccus roseus*; South China Sea water.
Abbreviations: DPG, diphosphatidylglycerol; MA, marine agar; MB, marine broth; PC, phosphatidylcholine; PE, phosphatidylethanolamine; PG, phosphatidylglycerol.
The GenBank/EMBL/DDBJ accession numbers for the 16S rRNA gene sequence and the whole genome sequence of strain TG-679^T are MG799855 and QGKU00000000, respectively.
Five supplementary figures and one supplementary table are available with the online version of this article.

0.5 g yeast extract, 0.1 g peptone, 0.1 g ferric citrate, 19.45 g NaCl, 8.8 g $MgCl_2{\cdot}6H_2O$, 1.8 g $CaCl_2{\cdot}2H_2O$, 0.55 g KCl, 0.16 g $NaHCO_3$, 3.24 g Na_2SO_4, 0.08 g KBr, 34 mg $SrCl_2$, 22 mg H_3BO_4, 4 mg $NaSiO_4$, 2.4 mg NaF, 1.6 mg NH_4NO_3, 8 mg Na_2HPO_4; pH 7.4 adjusted with NaOH. After 72 h of incubation, more than 15 colonies were observed on plates, from which a smooth, pink-coloured colony was picked out and named TG-679^T. Strain TG-679^T was purified by streaking on marine agar (MA; BD) and preserved at −80 °C in marine broth (MB; BD) supplemented with 20 % (v/v) glycerol for further study.

Genomic DNA was extracted and purified using a Wizard Genomic DNA purification kit (Promega). The 16S rRNA gene of strain TG-679^T was amplified with universal primers 27F (5′-AGAGTTTGATCMTGGCTCAG-3′) and 1492R (5′-TACGGYTACCTTGTTACGACTT-3′) [10]. PCR products were cloned into pMD 19 T-vector (TaKaRa) for sequencing. The almost-complete 16S rRNA gene sequence (1426 nt) was used for pairwise sequence alignment performed by the BLASTN program (www.ncbi.nlm.nih.gov) and the EzTaxon-e server (http://eztaxon-e.ezbiocloud.net) [11]. Multiple sequence alignments based on the 16S rRNA gene sequences of strain TG-679^T and related taxa were performed as described by Zhang *et al.* [12] using MEGA version 5 [13]. As a result, strain TG-679^T was found to be most related to species within the family *Rhodobacteraceae*, but sharing low sequence similarities among the most closely related genera: *Rhodovulum* (93.0–95.4 %), *Poseidonocella* (94.1–95.3 %), *Roseivivax* (92.0–95.2 %) and *Roseovarius* (93.0–95.1 %). Phylogenetic trees were reconstructed by using strain *Bacillus subtilis* subsp. *subtilis* NCIB 3610^T as the outgroup, by using the neighbour-joining (Fig. 1), maximum-parsimony (Fig. S1, available in the online version of this article) and maximum-likelihood algorithms (Fig. S2), which all illustrated that strain TG-679^T clustered into the clade of family *Rhodobacteraceae* by forming a distinct lineage among the most closely related genera. Based on the phylogenetic analysis, it is suggested that strain TG-679^T could not be assigned to any known genus and should represent a novel species of a novel genus of the family *Rhodobacteraceae.* Hence, *Rhodovulum sulfidophilum* DSM 1374^T (93.0 %), *Poseidonocella pacifica* JCM 17310^T (95.0 %), *Roseivivax halodurans* DSM 15395^T (92.0 %) and *Roseovarius tolerans* DSM 11457^T (93.0 %), which are the type species of the genus *Rhodovulum*, *Poseidonocella*, *Roseivivax* and *Roseovarius*, respectively, were used as reference strains in this study and obtained from the Deutsche Sammlung von Mikroorganismen und Zellkulturen (DSMZ) or the Japan Collection of Microorganisms (JCM). Unless otherwise stated, all strains were incubated in MA or MB at 28 °C.

The whole genome of strain TG-679^T was sequenced by Solexa PE150 sequencing technology with the HiSeq platform (Beijing Genomics Institute). The *de novo* assembly of the reads was performed using ABySS 1.5.2 [14]. The assembly *k*-value was tested from 32 to 64 to find the optimal *k*-value using abyss-pe script. The quality of microbial genomes was assessed using the bioinformatic tool CheckM [15]. The genome sequences of *R. sulfidophilum* DSM 1374^T (NZ_CP015418), *P. pacifica* JCM 17310^T (NZ_FOJU01000001), *R. halodurans* DSM 15395^T (NZ_JALZ01000001) and *R. tolerans* DSM 11457^T (NZ_FOBO00000000) were retrieved from the GenBank database. The average nucleotide identity (ANI) was calculated using the OrthoANIu algorithm of Chun lab's online Average Nucleotide Identity calculator (www.ezbiocloud.net/tools/orthoani) [16]. *In silico* DNA–DNA hybridization (DDH) values were calculated by using the Genome-to-Genome Distance Calculator (http://ggdc.dsmz.de/ggdc.php) [17].

The temperature range for growth was tested at 4, 10, 15, 20, 25, 28, 30, 35, 40, 45 and 50 °C in MB. The pH range for growth was determined at 0.5 pH intervals by supplementing 30 mM buffering agents in MB, including MES (pH 5.5–6.4), MOPS (pH 6.5–7.9), Tricine (pH 8.0–8.9) and Bis-Tris propane (pH 9.0–9.5). The NaCl tolerance was measured in MB (pH 7.0) with 0–150 g l^{-1} NaCl, which increased at steps of 5 g l^{-1} [18]. Cultures incubated for 3 days were used to determine the optimal growth while those incubated for 14 days were used to determine the growth limits [12]. After incubation at 28 °C for 3 days, the cell morphology of strain TG-679^T was examined and observed by transmission electron microscopy (JEM-1230, Jeol) after uranyl acetate (0.5 %, w/v) staining under 80 kV and by optical microscopy (BX40, Olympus) after Gram staining. The bacteriochlorophyll a and carotenoid content, based on the *in vivo* absorption spectrum as measured in sucrose solution, was detected by using a scanning UV/visible spectrophotometer (U-2900, Hitachi) [19]. Cell motility was examined in semi-solid medium using the stab cultivation method [6]. The gliding motility was checked by the hanging drop method as described by Sun *et al.* [9]. Catalase activity was evaluated by the production of oxygen bubbles in 3 % aqueous hydrogen peroxide solution, and oxidase activity was tested by oxidation of 1 % (w/v) tetramethyl-p-phenylenediamine[20].

Degradation of starch, L-tyrosine and hydrolysis of Tweens (20, 40, 60, 80), hypoxanthine and xanthine were tested as described by Sun *et al.* [21]. Nitrate reduction, urease activity and the ability to hydrolyse casein, chitin, carboxymethyl cellulose (CMC), filter paper and gelatin, and Gram reaction were determined according to Zhang *et al.* [22]. H_2S production, methyl red and Voges–Proskauer reactions were determined as described by Wu *et al.* [23]. Degradation of tyrosine was measured on MA with 5 g l^{-1} tyrosine. Utilization of carbon substrates was tested at concentration of 0.5 % (w/v) according to the protocol of Zhang *et al.* [22] using whole components of soluble material of MB; yeast extract (0.01 % w/v) was added as a growth factor. Anaerobic growth was determined with anaerobic system (Anaero-Pack-MicroAero, 2.5 l, MGC) using MA, to which 20 mM sodium thiosulfate, 5 mM sodium sulfite, 20 mM sodium sulfate, 5 mM sodium nitrite and 20 mM sodium nitrate

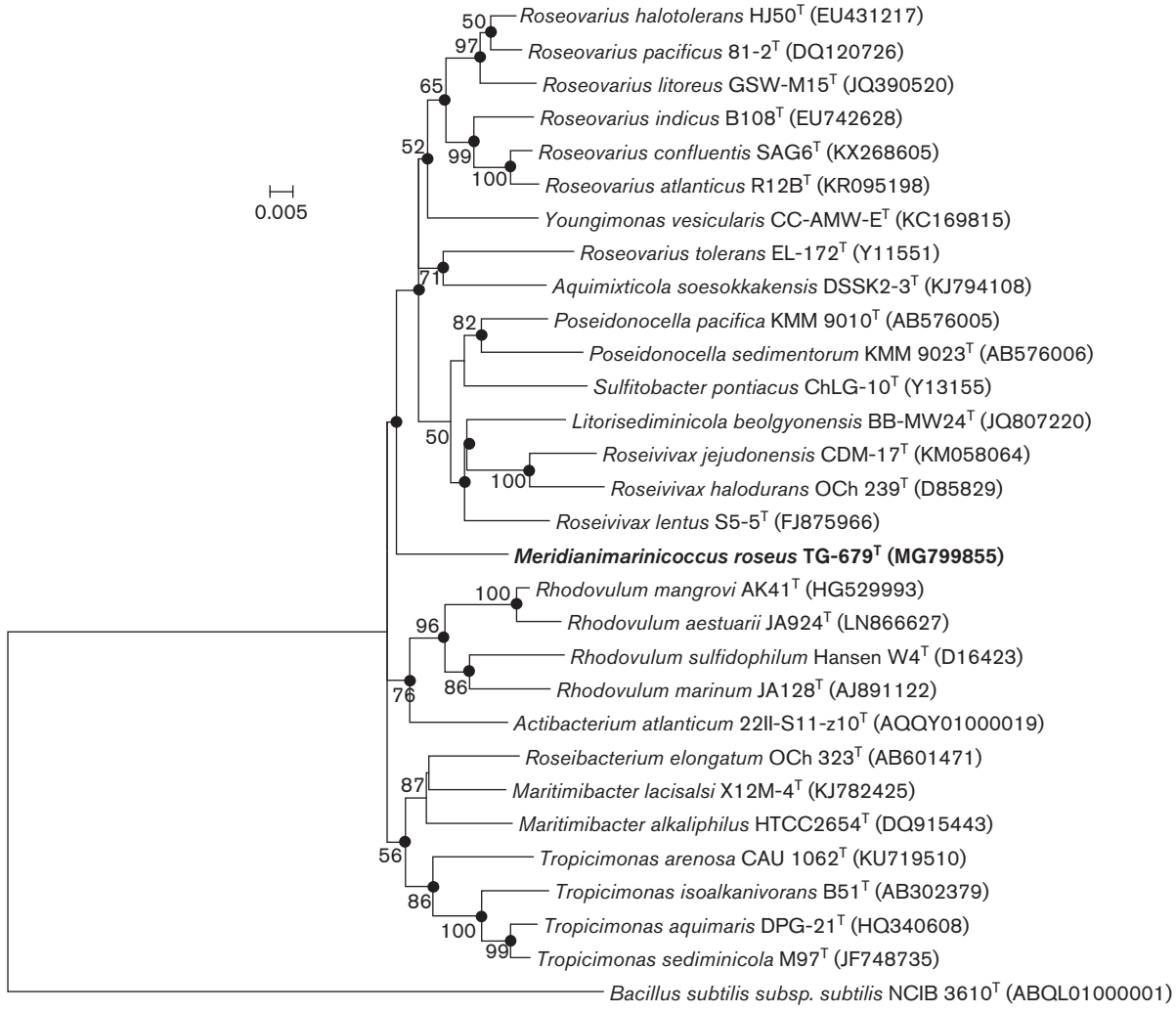

Fig. 1. Neighbour-joining phylogenetic tree based on the 16S rRNA gene sequences of strain TG-679^T and representatives of related taxa. Bootstrap values are expressed as a percentage of 1000 replicates and only those higher than 50 % are given at the branch points. Filled circles indicate nodes also obtained in both maximum-likelihood and maximum-parsimony trees. Bar, 0.005 substitutions per nucleotide position.

were respectively added as electron acceptors [24]. Enzyme activities, acid production and other physiological and biochemical traits were tested using API ZYM, API 20NE and API 50CH systems (bioMérieux) according to the manufacturer's instructions. The four reference strains, *R. sulfidophilum* DSM 1374^T, *P. pacifica* JCM 17310^T, *R. halodurans* DSM 15395^T and *R. tolerans* DSM 11457^T, were tested under identical conditions to the above.

Cells used for chemotaxonomic analysis were incubated in MB at 28 °C and 140 r.p.m. for 3 days. Isoprenoid quinones were extracted as described by Collins *et al.* [25] and purified by TLC, and then identified by an HPLC-MS system (Agilent) [26]. Whole-cell fatty acids were analysed according to the instructions of the Microbial Identification System (MIDI; Microbial ID) with the standard MIS Library Generation Software version 4.5. Polar lipids were extracted as described by Kates [27] and separated by two-dimensional TLC on silica gel 60 F254 plates (Merck) as performed by Tindall [28]. Four kinds of spray reagents were used to visualize the corresponding lipids, including molybdophosphoric acid for total lipids, α-naphthol/H_2SO_4 for glycolipids, molybdenum blue (Sigma) for phospholipids and ninhydrin for aminolipids.

The genome sequencing generated 1.246 Gb of clean data (approximately 290-fold genome coverage) [29]. The genome completeness of strain TG-679^T was 99.7 % and with 1.46 % contamination. The genome sequence considered as a good reference genome for deeper analyses ($\geq$95 % completeness, $\leq$5 % contamination) [15]. The DNA G+C content of strain TG-679^T calculated from the draft

Table 1. Characteristics that differentiate the genus *Meridianimarinicoccus* from related genera in family *Rhodobacteraceae*

Genera: 1, *Meridianimarinicoccus* gen. nov. (strain TG-679^T, this study); 2, *Rhodovulum* (this study; Srinivas *et al.* [33]; Divyasree *et al.* [34]; Ramaprasad *et al.* [35]; Nupur *et al.* [36]); 3, *Poseidonocella* (this study; Romanenko *et al.* [37]); 4, *Roseivivax* (this study; Tomonori *et al.* [38]; Sooyeon *et al.* [39]; Dai *et al.* [40]; Wu *et al.* [41]; Zhang *et al.* [42]); 5, *Roseovarius* (this study; Wang *et al.* [43]; Jia *et al.* [44]; David *et al.* [45]; Wang Nan-Nan *et al.* [46]); 6, *Tropicimonas* (Ki-Hoon Oh *et al.* [47]; Mihee Oh *et al.* [48]; Na-Ri Shin *et al.* [49]); 7, *Maritimibacter* (Kiyoung Lee *et al.* [50]; Zhong *et al.* [51]). DPG, diphosphatidylglycerol; PE, phosphatidylethanolamine; PG, phosphatidylglycerol; PC, phosphatidylcholine; SL, 1,2-sulfolipid; PA, phosphatidic acid; +++, positive in all species; –, negative in all species; V, varies; ND, no data available.

Characteristic	1	2	3	4	5	6	7
Cell shape	Coccoid	Ovoid to rod	Ovoid/rod-shaped	Rod-shaped	Ovoid/rod-shaped	Rod-shaped	Rod-shaped
Motility	Non-motile	V	Non-motile	V	V	V	Non-motile
NaCl concentration for growth (%) (optimal)	0.5–2 (1.5)	0–12 (1–9)	0.5–8 (2–4)	0–20 (4–10)	0.3–20 (1–12)	0–8 (1–2)	0–11 (2.5–6)
Temperature range for growth (°C) (optimum)	10–40 (28)	20–40 (25–30)	5–42 (25–30)	4–40 (27–35)	3–50 (8.5–34)	10–46 (30-37)	15–40 (25-30)
Catalase	+++	V	+++	+++	+++	V	+++
Oxidase	+++	V	+++	+++	+++	+++	+++
Bacteriochlorophyll a production	–	+++	–	V	+++	ND	ND
Major fatty acids (>10 %)	$C_{18:1}\omega7c$, $C_{18:0}$	$C_{18:1}\omega7c$ $C_{16:0}$, $C_{18:0}$	$C_{18:1}\omega7c$, 11-methyl $C_{18:1}\omega7c$	$C_{18:1}\omega7c$, 11-methyl $C_{18:1}\omega7c$, $C_{19:0}$ cyclo$\omega8c$	$C_{18:1}\omega7c$, $C_{16:0}$, $C_{18:0}$	$C_{18:1}\omega7c$, $C_{16:0}$, $C_{19:0}$ cyclo$\omega8c$	$C_{18:1}\omega7c$, $C_{16:0}$
Major quinone(s)	Q-10	Q-10	Q-10	Q-10	Q-10	Q-10/Q-9	Q-10
Major known polar lipids	DPG, PE, PG, PC	PE, PG, SL	DPG, PG, PC, PA	PE, PG, PC	DPG, PE, PG, PC	DPG, PG, PC	DPG, PG, PC
DNA G+C content (mol%)	65.9	61.2–67.7	60.5–65.4	59.7–68.8	59.1–68.1	65.7–69.6	64.1–65.7

genome sequence was 65.9 mol%, which is slightly lower than the genome-based G+C content of *R. sulfidophilum* DSM 1374^T (66.8 mol%) and *R. halodurans* DSM 15395^T (67.3 mol%), but slightly higher than *P. pacifica* JCM 17310^T (61.3 mol%) and *R. tolerans* DSM 11457^T (63.6 mol %). The *in silico* DDH values and ANI values between strain TG-679^T and *R. sulfidophilum* DSM 1374^T, *P. pacifica* JCM 17310^T, *R. halodurans* DSM 15395^T and *R. tolerans* DSM 11457^T were 23.0, 25.0, 25.0 and 23.0 %, and 72.7, 70.5, 71.4 and 71.6 %, respectively, which were below the 70 % threshold value for GGDC and 95 % for ANI proposed for the delineation of bacterial species [30–32].

The testing results of the chemotaxonomic revealed Q-10 was the sole respiratory quinone in strain TG-679^T. The detailed fatty acid profiles of strain TG-679^T and the reference strains is shown in Table S1. The major fatty acids (>5 %) detected in strain TG-679^T were $C_{18:1}\omega7c$ (79.0 %) and $C_{18:0}$ (10. 9 %). As shown in Fig. S5, the polar lipid profile of strain TG-679^T were PE, PG, PC, DPG, an unidentified phospholipid, and two unknown glycolipids.

A comparison of the physiological and biochemical characteristics between genus *Meridianimarinicoccus* (strain TG-679^T) and related genera in family *Rhodobacteraceae* is given in Table 1. They all share many similarities, such as oxidase and catalase being positive in most species, coloured colonies, isolated from diverse saline environments, containing $C_{18:1}\omega7c$ as the most abundant fatty acid, and Q-10 being the predominant respiratory quinone. However, the genus *Meridianimarinicoccus* still has some characteristics which can differentiate it from related genera in family *Rhodobacteraceae*. Such as, the cell shape of genus *Meridianimarinicoccus* is coccoid (Fig. S4), while the cell shape of other genera varies from ovoid to rod-shaped. The NaCl concentration for growth of strain TG-679^T is 0.5–2 % (w/v), which is lower than most members of the related taxa. Bacteriochlorophyll a and carotenoid were not detected in strain TG-679^T (Fig. S3), indicating that strain TG-679^T is not a photosynthetic bacterium [17], while some most related strains are photosynthetic bacteria. The major known polar lipids of strain TG-679^T are DPG, PE, PG and PC. When compared with strain TG-679^T, the major known polar lipids of genus *Rhodovulum* lack DPG and PC; genera *Poseidonocella* and *Roseivivax* lack PE and DPG, respectively. In addition, the genera *Rhodovulum* and *Poseidonocella* contain 1,2-sulfolipid and phosphatidic acid, respectively, which are absent in strain TG-679^T.

A comparison between strain TG-679^T and the reference strains is shown in Table 2. Several characteristics, including bacteriochlorophyll a production, Voges–Proskauer reaction, degradation of Tweens (20, 40, 60 and 80), tyrosine, production of cysteine arylamidase, production of α-

Table 2. Characteristics, that differentiate strain TG-679^T from the reference strains

Strains: 1, TG-679^T; 2, *Rhodovulum sulfidophilum* DSM 1374^T; 3, *Poseidonocella pacifica* JCM 17310^T; 4, *Roseivivax halodurans* DSM 15395^T; 5, *Roseovarius tolerans* DSM 11457^T. Unless stated otherwise, All data were obtained from this study under identical growth conditions. GS, genome sequence; DPG, diphosphatidylglycerol; PE, phosphatidylethanolamine; PG, phosphatidylglycerol; PC, phosphatidylcholine; SL, 1,2-sulfolipid; PA, phosphatidic acid; +, positive; –, negative.

Characteristic	1	2	3	4	5
Bacteriochlorophyll a production	–	+*	-†	+‡	+§
Voges–Proskauer reaction	–	–	–	+	+
Degradation of:					
Tween 20	+	–	–	–	+
Tweens 40, 60, 80	+	–	–	–	–
Tyrosine	–	–	+	–	–
API ZYM tests:					
Cystine arylamidase	–	–	–	+	–
α-Chymotrypsin	+	–	–	+	–
Trypsin	–	+	+	–	+
α-Galactosidase	–	–	+	–	+
α-Mannosidase	+	–	–	–	–
API 20NE tests:					
Reduction of nitrates to nitrogen	+	–	–	–	–
Glucose fermentation	+	–	+	+	–
Potassium gluconate	+	–	+	–	+
Acid production from (API 50CH):					
D-Mannose	+	–	+	+	–
D-Mannitol	+	–	–	+	–
Methyl α-D-mannopyranoside	+	+	+	–	–
Methyl α-D-glucopyranoside	+	+	–	–	–
Maltose	+	–	+	+	+
Lactose	+	–	+	–	–
Raffinose	+	–	–	–	+
Gentiobiose	–	–	–	+	+
D-Lyxose	–	+	+	–	–
D-Fucose	–	–	–	+	–
Utilization of single carbon sources:					
Sodium malonate	+	–	–	+	–
D-Sorbitol	–	+	+	+	+
Galactose	–	+	+	+	+
Ribose	+	–	+	–	–
Lactose	–	–	–	+	+
Major fatty acids (>5 %)	$C_{18:1}\omega7c$, $C_{18:0}$	$C_{18:1}\omega7c$, $C_{16:0}$*	$C_{18:1}\omega7c$, 11-methyl $C_{18:1}\omega7c$†	$C_{18:1}\omega7c$, $C_{16:0}$‡	$C_{18:1}\omega7c$, $C_{16:0}$§
G+C (mol%)	65.9 (GS)	66.8 (GS)	61.3 (GS)	67.3 (GS)	63.6 (GS)

*Data from Hansen *et al*. [52].

†Data from Romanenko A *et al*. [37].

‡Data from Tomonori *et al*. [38].

§Data from Wang *et al.* [43].

mannosidase, reduction of nitrates to nitrogen, acid production from different substrates, and utilization of different substrates as single carbon source, were found to differentiate strain TG-679^T from the reference strains. The major fatty acids (>5 %) of strain TG-679^T were $C_{18:1}\omega7c$ and $C_{18:0}$, which differentiates it from *R. sulfidophilum* DSM 1374^T ($C_{18:1}\omega7c$ and $C_{16:0}$), *P. pacifica* JCM 17310^T ($C_{18:1}\omega7c$ and 11-methyl $C_{18:1}\omega7c$), *R. halodurans* DSM 15395^T ($C_{18:1}\omega7c$ and $C_{16:0}$), and *R. tolerans* DSM 11457^T ($C_{18:1}\omega7c$ and $C_{16:0}$). Generally, the content and proportion of predominant and major fatty acids for strain TG-679^T were different to all members of the reference strains.

Based on its phenotypic, chemotaxonomic and genotypic characterizations, it is proposed that strain TG-679^T represents a novel species of a novel genus within the family *Rhodobacteraceae*, for which the name *Meridianimarinicoccus roseus* gen. nov., sp. nov. is proposed.

DESCRIPTION OF *MERIDIANIMARINICOCCUS* GEN. NOV.

Meridianimarinicoccus [Me.ri.di.a.ni.ma.ri.ni.coc′cus. L. masc. adj. *meridianus* of or belonging to the south, southern, meridional; L. masc. adj. *marinus* of the sea; N.L. masc. n. *coccus* (from Gr. masc. n. *kokkos* a grain or berry) a coccus; N.L. masc. n. *Meridianimarinicoccus*, a coccus bacterium isolated from the South China Sea].

Cells are Gram-stain-negative, strictly aerobic, catalase-positive and oxidase-positive. Bacteriochlorophyll a is not produced. The sole respiratory quinone is Q-10. The major fatty acids (>5 %) are $C_{18:1}\omega7c$ and $C_{18:0}$. The polar lipid profile consists of phosphatidylethanolamine, phosphatidylglycerol, phosphatidylcholine, diphosphatidylglycerol, an unidentified phospholipid and two unknown glycolipids. The DNA G+C contents of members of this genus are near 65.9 mol%. Phylogenetically, the genus is a member of the family *Rhodobacteraceae*. The type species is *Meridianimarinicoccus roseus*.

DESCRIPTION OF *MERIDIANIMARINICOCCUS ROSEUS* SP. NOV.

Meridianimarinicoccus roseus (ro′se.us. L. masc. adj. *roseus* rose coloured, pink).

Cells are coccoid (approximately 1.1–1.6 µm in diameter), non-motile and lacking gliding motility. Colonies on MA are circular, smooth, pink-pigmented. Growth occurs at 10–40 °C (optimum, 28 °C), pH 5.5–10 (optimum, pH 7.5) and 0.5–2.0 % (w/v) NaCl (optimum, 1.5 %). Na^+ ions are required for growth. Tests for production of alkaline phosphatase, esterase (C4), esterase lipase (C8), leucine arylamidase, valine arylamidase, acid phosphatase, napthol-AS-Biphosphopydrase, β-galactosidase, α-glucosidase, β-glucosidase and α-mannosidase are positive. Tests for production of lipase (C14), cysteine arylamidase, trypsin, α-galactosidase, β-glucuronidase, N-acetyl-β-glucosaminidase and α-fucosidase are negative. Nitrate can be reduced to nitrogen. Tween 20, Tween 40, Tween 60, Tween 80 and urea are hydrolysed, but starch, L-tyrosine, filter paper, casein, xanthine and hypoxanthine are not. The Voges–Proskauer reaction is negative. The methyl red reaction is positive. Production of H_2S is weakly positive. Production of indole is negative. Fermentation of glucose is positive. The following compounds are utilized as sole carbon and energy sources: sodium malonate, D-mannose, erythritol, citric acid, sucrose, trehalose, succinic acid, D-mannitol, inositol, ribose, sodium malonate, L-fucose, D-alanine, sodium acetate, glycerin and sodium gluconate. It cannot utilize lactose, D-galactose, maltose, sorbitol, cellobiose, xylitol, xylose and L-arabinose as sole carbon and energy sources.

The type strain is TG-679^T (=KCTC 62454^T=MCCC 1K03496^T), which was isolated from a seawater sample collected from the South China Sea (19° 22′ N, 115° 38′ E). The GenBank/EMBL/DDBJ accession numbers for the 16S rRNA gene sequence and the whole genome sequence of strain TG-679^T are MG799855 and QGKU00000000, respectively.

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

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