Description of Prasinibacter coralicola gen. nov., sp. nov., a zeaxanthin-producing bacterium isolated from stony coral Porites lutea

Guanghua Wang · Jianfeng Liu · Yuanjin Li · Jin Li · Jixin Luo · Biao Chen · Zhiheng Liao · Hongfei Su · Jiayuan Liang · Kefu Yu

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Abstract  Thermal stress is considered one of the main causes of mass scleractinian coral degradation; however, it is still unknown how corals can adapt to future global warming. In this study, 11 strains of coral-associated Flavobacteria were shown to produce zeaxanthin, a carotenoid antioxidant, which may help coral holobionts to alleviate thermal stress. In addition, a novel zeaxanthin-producing Flavobacterium, designated R38T, was identified using polyphasic taxonomy. Although strain R38T shared a maximum 16S rRNA gene sequence similarity of 93% with Mesoflavibacter aestuarii KYW614T, phylogenetic analyses based on whole genome and 16S rRNA gene sequences revealed that strain R38T forms a distinct branch in a robust cluster composed of strain R38T and Leptobacterium flavescentis KCTC 22160T under the family Flavobacteriaceae. Strain R38T exhibited average nucleotide identities of 70.2% and 72.5% for M. aestuarii KYW614T and L. flavescentis KCTC 22160T, respectively. The only detected respiratory quinone was menaquinone 6 (MK-6). The major polar lipids were phosphatidylmethyl-ethanolamine, phosphatidylethanolamine, one unidentified ninhydrin phospholipid, three unidentified ninhydrin-positive lipids, and three unidentified lipids. The major cellular fatty acids were iso-C15:0, iso-C15:0 3ω6c, C16:2 DMA, and C13:1 3ω3c. The distinct biochemical, chemotaxonomic, phylogenetic, and phylogenomic differences from validly published taxa suggest that strain R38T represents a new species of a new genus, for which Prasinibacter coralicola gen. nov., sp. nov. is proposed. The type strain R38T (= MCCC 1K03889T = KCTC 72444T).

Keywords  Prasinibacter coralicola · Polyphasic taxonomy · 16S rRNA gene · Zeaxanthin

Abbreviations
KCTC  The Korean Collection for Type Cultures
MCCC  The Marine Culture Collection of China
ANI  Average nucleotide identity
Q  Ubiquinone
DPG  Diphosphatidylglycerol
PG  Phosphatidylglycerol
Introduction

Global coral reefs have degraded dramatically in recent decades (Hughes et al. 2003; Bellwood et al. 2004) and massive corals have replaced branched corals as the dominant assemblages (Perry et al. 2015; Yu et al. 2019). Thermal stress is one of the main causes of scleractinian coral degradation (Gardner et al. 2003; Hughes et al. 2017, 2018, 2019). Recently, it was reported that the phycosphere bacteria Muricauda sp. GF1 protects coral endosymbionts from thermal stress by producing zeaxanthin (Motone et al. 2020). Zeaxanthin is usually synthesized in flavobacteria from terpenoids by the combinations of phytoene synthase (CrtB), phytoene dehydrogenase (CrtI), lycopene cyclase (CrtY), and β-carotene hydroxylase (CrtZ) (Zhang et al. 2018). According to the List of Prokaryotic names with Standing in Nomenclature (https://lpsn.dsmz.de/), to date, up to 152 genera and more than 980 species have been validly published in the family Flavobacteriaceae. Members of the family are ubiquitous in terrestrial, freshwater, and marine environments, and some ones are marine animal associated (McBride, 2014). Genomic and physiological analyses have indicated that flavobacteria can degrade a diverse range of carbohydrates and proteins (Bauer et al. 2006; Qin et al. 2010; Gavriilidou et al. 2020), and a few are animal pathogens (Duchaud et al. 2007; Loch and Faisal 2015; Adamek et al. 2018). To determine the roles of flavobacteria in coral health, pure cultures were isolated from thermal tolerant corals: Porites lutea, Galaxea fascicularis, and Favia sp. The taxonomic position of a new coral-associated Flavobacterium, strain R38T, was identified using polyphasic identification, and the results indicated that strain R38T and other coral-associated Flavobacteria can also produce zeaxanthin. Therefore, coral-associated Flavobacteria may help alleviate host thermal stress caused by global warming.

Materials and methods

Isolation, cultivation, and maintenance

Massive coral P. lutea was collected from Weizhou Island (109° 08’ 35” E, 21° 03’ 42” N), in the Beibu Gulf, China. G. fascicularis and Favia sp. were collected from Daya Bay (114° 38’ 32” E, 22° 34’ 32” N), China. The coral pieces (approximately 1 cm × 1 cm) were washed twice using sterile natural seawater, then the coral tissue was homogenized using silica beads on vortex mixer after scraping with scissors. The homogenate was diluted by ten-fold using sterile seawater, and 100 μl of each dilution was spread on modified R2A plate (R2A agar was obtained from BD, which was dissolved in natural seawater, pH7.6). Bacteria were incubated at 25 °C for two weeks. Colonies were picked and purified on marine R2A plates, and stored at −70 °C in R2A broth (Haibo, China)/glycerol (4:1, v/v).

Preliminary identification using 16S rRNA gene sequence indicated that strain R38T (from P. lutea) may represent a new species in a new genus, therefore, polyphasic identification was performed to identify its exact taxonomic position. Type strains Leptobacterium flavescens KCTC 22160T and Spongiivirga citrea KCTC 32990T, obtained from the Korean Collection for Type Cultures (KCTC), were used as references. Both the new isolate and the reference type strains grew well on marine agar 2216 (BD).

Morphological, cultural, physiological and biochemical characterization

Cellular morphology was observed using an optical microscope (Olympus BX53) and transmission electron microscope (Tecnai G2 F30 S-TWIN/X-MAX 80) after incubation for 2–3 days in marine broth 2216 (BD) at 30 °C. Colony size, shape and margin were checked using magnifier glass on marine agar 2216 after 3 days of incubation. Colony color was recorded reference to standard color cards. Cell mobility was tested using the hanging drop technique (Bernardet et al. 2002). The Gram reaction was determined as described by Gerhardt et al. (1994). Catalase activity was determined by observing bubble production in a 3% (v/v) hydrogen peroxide solution, and oxidase activity was determined using oxidase test strips.
The ability to form endospores was examined as described by Dong & Cai (2001). NaCl requirement and tolerance were tested at 30 °C for 7 days in R2A liquid medium (Haibo, China) with NaCl concentrations ranging from 0 to 16% (w/v), namely 0, 0.5, 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 12, 14, and 16% (w/v). Growth at different pH, adjusted with different buffers (1 interval, pH 4–5, 0.1 M citrate; pH 6–8, 0.1 M phosphate; pH 9–11, 0.1 M carbonate), was tested in R2A liquid medium [including 1% NaCl (w/v)] at 30 °C for 7 days. The optimal growth temperature for bacteria on marine agar 2216 (BD) plates was determined after 7–30 days of growth at temperatures of 4, 10, 15, 20, 25, 30, 33, 37, and 40 °C. Metabolism ability was characterized using API 20NE strips, API ZYM strips, and Biolog Gen III microplates according to the manufacturer’s protocols. Anaerobic fermentation was determined using API 50CH strips according to the manufacturer’s protocol with the inoculum medium being marine broth 2216 (BD).

**Chemotaxonomic characterization**

The biomass of strain R38T and the reference strain for cellular fatty acid analysis were acquired from the third quadrant of the streaked marine agar 2216 plate incubated at 28 °C. Cellular fatty acid composition was analyzed by gas chromatography (Agilent G6890N) and identified using the Sherlock Microbial Identification System (Version 6.0) according to the manufacturer’s instructions. Biomass for the analyses of quinones and polar lipids was obtained from marine broth 2216 after 3 days of incubation at 30 °C. Respiratory quinones were extracted as described by Collins (1994) and analyzed using reversed-phase high-performance liquid chromatography (HPLC) (Komagata & Suzuki, 1987). The isoprenoid quinones were eluted using a mixture of methanol/2-propanol (2:1, v/v) and flow rate of 1 ml/min at room temperature and detected by UV absorbance at 270 nm. Polar lipids were extracted as described by Kamekura (1993) and identified by spraying with ethanolic molybdenum blue, ninhydrin, α-naphthol/sulfuric acid, and Draggendorff’s reagent after two-dimensional thin layer chromatography (TLC) (Tindall 1990).

**Phylogenetic and phylogenomic analysis**

The 16S rRNA gene of strain R38T was obtained using PCR amplification with the universal primers 27F and 1492R (Lane 1991) and sequenced using the Sanger method. The 16S rRNA gene sequence similarities were determined using the EzBioCloud (Yoon et al. 2017a, b) and NCBI database. Alignment of 16S rRNA gene sequences was performed using the SINA software package (Pruesse et al. 2012) and the SILVA rRNA database. Phylogenetic trees were constructed using the maximum likelihood (Felsenstein 1981), neighbor-joining (Saitou & Nei 1987), and maximum-parsimony (Swofford 1993) algorithms in the software package MEGA version 7.0 (Kumar et al. 2016). The phylogenetic distance matrices were estimated using the Kimura two-parameter model (Kimura, 1980). The topology of the phylogenetic tree was analyzed using the bootstrap resampling method of Felsenstein (1985) with 1000 replicates. Whole-genome sequencing was performed using an Illumina HiSeq PE150 platform. Library construction was performed by PCR amplification of a 350 bp insert with A-tail ligated to paired-end adapters, at the Beijing Novogene Bioinformatics Technology Co., Ltd. Good-quality paired reads were assembled into a number of scaffolds using the SOAPdenovo (Li et al. 2008, 2010). Genomic information was extracted as described by Chun et al. (Chun et al. 2018). The phylogenetic tree was reconstructed using the up-to-date bacterial core gene set (UBCG v.3) according to the manual (Na et al. 2018). The average nucleotide identity (ANI) was calculated using the online ANI calculator (Yoon et al. 2017a, b). The average amino acid identity (AAI) was calculated using the EzAAI (Kim et al. 2021). Carbohydrate-active enzyme annotation was performed using the dbCAN meta server (Zhang et al. 2018). Peptidases were annotated using the Hotpep-protease method (Bush, 2020) based on the Merops database.

**Zeaxanthin detection**

The production of zeaxanthin by bacteria from the family *Flavobacteriaceae* was assessed using both genome annotation and HPLC assay. The existence of coding genes for zeaxanthin biosynthesis enzymes, namely phytoene desaturase, lycopene beta-cyclase,
and beta-carotene 3-hydroxylase were checked using the Joint Genome Institute online server (https://genome.jgi.doe.gov/portal/) and the NCBI genome server (https://www.ncbi.nlm.nih.govgenome/). Zeaxanthin was extracted from approximately 10 mg wet weight bacteria grown on an R2A plate using methanol and glass beads on a vortex for 30 s, and then analyzed using HPLC (Thermal Ultimate 3000). Samples were separated using an Agilent ZORBAX Eclipse XDB-C18 (250 mm, 5 µm particle size) at a column temperature of 35 °C, and the mobile phase comprised 90% (vol/vol) methanol containing 0.1% (v/v) formic acid at a flow rate of 1 ml/min (Motone et al. 2020). Zeaxanthin was checked using a photodiode array detector. Standard zeaxanthin was purchased from the Resource Platform of Standard Material (China).

Results and discussion

Morphological, cultural, physiological and biochemical characterization

Colonies of strain R38T on marine agar 2216 were yellow and circular. Cells of bacterial strain R38T were gram-negative, non-spore-forming, non-motile, aerobic rods. Cells were usually 0.3–0.5 µm wide and 0.9–2.0 µm long (Supplementary Fig.S1), being narrower than that of L. flavescens KCTC 22160T, S. citrea KCTC 32990T and Fulvibacter tottoriensis MTT-39T, while being wider than that of Mesoflavibacter aestuarii KYW614T (Lee et al. 2014). Cells of strain R38T could reduce nitrate to nitrogen, L. flavescens KCTC 22160T and S. citrea KCTC 32990T could only reduce nitrate to nitrite, whereas M. aestuarii KYW614T (Lee et al. 2014) and F. tottoriensis MTT-39T (Khan et al. 2008) could not reduce nitrate. Enzyme characterization of strain R38T using API ZYM strips showed a spectrum similar to that of M. aestuarii KYW614T and F. tottoriensis MTT-39T with the absence of β-galactosidase, β-glucuronidase, α-glucosidase, β-glucosidase, N-acetyl-β-glucosaminidase, and α-mannosidase (Table 1) (Lee et al. 2014; Yoon et al. 2013). These enzyme results differed from those of L. flavescens KCTC 22160T and S. citrea KCTC 32990T (Table 1). Other characteristics of strain R38T are listed in Table 1 and the species description.

Chemotaxonomic characteristics

The only respiratory quinone detected in strain R38T was menaquinone 6 (MK-6), similar to L. flavescens KCTC 22160T (Mitra et al. 2009), S. citrea KCTC 32990T (Yoon et al. 2015), F. tottoriensis MTT-39T (Khan et al. 2008), and M. aestuarii KYW614T (Lee et al. 2014). Strain R38T contained iso-C15:0 (42.4%), iso-C15:0 ω6c (15.6%), C16:2 DMA (7.8%), and C13:1 ω3c (5.2%) as the major cellular fatty acids, this profile was highly similar to that of L. flavescens KCTC 22160T, although the proportion of individual components varied (Supplementary Table S1). However, the individual fatty acid content of S. citrea KCTC 32990T differed from that of strains R38T and L. flavescens KCTC 22160T (Supplementary Table S1). The major fatty acids of strain R38T, L. flavescens KCTC 22160T, and S. citrea KCTC 32990T were highly different from those of M. aestuarii KYW614T and F. tottoriensis MTT-39T (Lee et al. 2014; Yoon et al. 2013). The major polar lipids of strain R38T were phosphatidylmethylethanolamine (PME), phosphatidylethanolamine (PE), one unidentified ninhydrin-staining-positive phospholipid (NPL), three unidentified ninhydrin-staining-positive lipids (NLs), and three unidentified lipids (Ls) (Supplementary Fig. S2). This polar lipid profile was similar to that of L. flavescens KCTC 22160T, but highly different from that of S. citrea KCTC 32990T, which contains few types of polar lipids (Supplementary Fig. S2). However, strain R38T could still be distinguished from L. flavescens KCTC 22160T by its NPL (Supplementary Fig.S2). Furthermore, no PME has been reported for M. aestuarii KYW614T and F. tottoriensis MTT-39T (Lee et al. 2014; Yoon et al. 2013). Therefore, the polar lipid profile distinguishes strain R38T from other closely related type strains.

Molecular characterization and phylogenetic analysis

A nearly complete 16S rRNA gene sequence (1383 nt) of strain R38T was obtained by Sanger sequencing and deposited in GenBank under accession number MN908337. Global alignment using the EzBioCloud database indicated that the most closely related neighbor of strain R38T is M. aestuarii KYW614T, with a 16S rRNA gene similarity of 93%. The next most
similar members were of Bizionia, Sabulilitribacter, Gaetbulibacter, and Algibacter genera which showed 92.7–92.9% sequence similarity. However, 16S rRNA gene phylogenetic analysis based on the maximum-likelihood algorithm indicated that strain R38T forms a distinct branch in a stable cluster composed of strain R38T and L. flavescens KCTC 22160T (Fig. 1), neighbor-joining and maximum-parsimony algorithms also support this stable cluster.

**Table 1** Phenotypic characteristics of strain R38T and related type strains

| Characteristics | 1 | 2 | 3 | 4† | 5‡ |
|-----------------|---|---|---|----|----|
| **Habitat**     | Coral | Marine sponge‡ | Marine sponge† | Seawater | marine sediment |
| **Cell size (μm)** | 0.3–0.5×0.9–2.0 | 0.5–0.6×8.5–9.0‡ | 0.4–0.5×2.0–3.0† | 0.2×1.2–1.5 | 0.5–0.7×5–14 |
| **Colonial color** | Yellow-green | Pale-yellow | Lemon-yellow | Orange | yellowish brown |
| **Temperature range (°C)** | 15–33 | 15–35 | 15–35 | 4–35 | 10–37 |
| **NaCl tolerance (%,** w/v) | 3–6 | 0.5–6 | 1–5 | 1–9 | 1–5 |
| **pH range** | 5–10 | 6–10 | 8–9 | 6–8 | 6–10 |
| **Nitrate reduction** | + | + | + | – | – |
| **API ZYM test** | – | + | + | – | – |
| **N-Acetyl-β-glucosaminidase** | – | + | + | – | – |
| **β-Galactosidase** | – | + | + | – | – |
| **α-Glucosidase** | – | + | + | – | – |
| **β-Glucosidase** | – | + | + | – | – |
| **β-Glucuronidase** | – | + | + | – | – |
| **α-Mannosidase** | – | + | + | – | – |
| **Genome size (Mb)** | 3.94 | 4.21 | 4.15 | 2.92 | ND |
| **ANI of strain R38T to** | 100% | 72.5% | 69.6% | 70.2% | ND |
| **G+C mol%** | 33.2 | 40.9 | 36.3 | 32.1 | 35 |
| **Major polar lipid** | PME,PE,NLs,NPLs,Lsiso-C15:0,iso-C15:0ω6c,C16:2DMA,C13:1ω3c | PME,PE,NLs,Lsiso-C15:0,iso-C15:0ω6c,C16:2DMA,C16:1ω6c | PME,NL,Liso-C15:0,iso-C15:0ω6c,C16:2DMA,C15:0 | PE,2ALs,3LsC15:0,iso-C15:0ω6c,C16:03-OH,C15:0ω6c | iso-C15:1,C16:03-OH,iso-C17:03-OH,iso-C15:3G,C16:1ω7c/ω6c |
| **Major cellular fatty acids** | iso-C15:0,iso-C15:0ω6c,ω7c/ω6c | iso-C15:0,iso-C15:0ω6c,ω7c/ω6c | iso-C15:0,iso-C15:0ω6c,ω7c/ω6c | iso-C15:0,iso-C15:0ω6c,ω7c/ω6c | iso-C15:0,iso-C15:0ω6c,ω7c/ω6c |

**Strains:** 1, R38T; 2, Leptobacterium flavescens KCTC 22160T; 3, Spongiivirga citrea KCTC 32990T; 4, Mesoflavibacter aestuarii KYW614T (data from Lee et al. 2014); 5, Fulvibacter tottoriensis MTT-39 (data from Khan et al. 2008; Yoon et al. 2013). †, positive; ‡, negative; ND, unknown

contigs were obtained, the obtained genome size was 3.94 Mb, and the genomic DNA G+C content was 33.2 mol%. The genome sequencing depth of L. flavescens KCTC 22160T was 154×, the N50 was 1,032,064 bp, a total of 9 contigs were obtained, the obtained genome size was 4.21 Mb, and the genomic DNA G+C content was 40.9 mol%. The genome sequencing depth of S. citrea KCTC 32990T was 155×, the N50 was 637,254 bp, a total of 17 contigs were obtained, the obtained genome size was 4.15 Mb, and the genomic DNA G+C content was 36.3 mol%. The genomes of closely related type strains were 2.92–5.03 MB, with G+C content of 31.8–55.3 mol% (Supplementary Table S2). Thus, strain R38T has a low genomic G+C content.
(33.2 mol%). The complete 16S rRNA gene of strain R38T obtained by genome sequencing was 1508 nt, and showed two nucleotide differences compared to the sequence obtained by Sanger sequencing. Meanwhile, the result obtained by Sanger sequencing indicated there were at least two copies of the 16S rRNA gene in cells of strain R38T. The ANI of strain R38T to L. flavescens KCTC 22160T, S. citrea KCTC 32990T, and M. aestuarii KYW614T were 72.5%, 69.6%, and 70.2%, respectively. The AAI of strain R38T to L. flavescens KCTC 22160T was 74.6%, and for other type strains, namely Poritiphilus flavus R33T, Robiginitalea biformata HTCC2501T, Muritcola jejuensis KCTC 22299T, Aureitalea marina NBRC 107741T, Aureicoccus marinus SG-18T, Robertkochia marina CC-AMO-30DT, Sinomicrobium oceani CGMCC 1.12145T, Zhouia amylytica CGMCC 1.6114T, Galbibacter marinus ck-12-15T, Joostella marina DSM 19592T, Pustulibacterium marinum CGMCC 1.12333T, Intechella halotolerans K1T, S. citrea KCTC 32990T, Aurantibacter aestuarii KCTC 32269T, Aligibacter alginicilyticus HZ22T, Bizonia paragorgiae DSM 23842T, and Gaetbulibacter saemankumensis DSM 17032T, the indices were lower than 70% (Supplementary Table S2). Similar to the 16S rRNA gene-based phylogenetic results, phylogenomic analysis based on 92 genes also indicated that strain R38T forms a distinct branch in a stable cluster composed of strain R38T and L. flavescens KCTC 22160T, other type strains close to the strain R38T and L. flavescens KCTC 22160T cluster are A. marina NBRC 107741T, A. marinus SG-18T, P. flavus R33T, R. biformata HTCC2501T, M. jejuensis KCTC 22299T, R. marina CC-AMO-30DT, Z. amylytica CGMCC 1.6114T, J. marina DSM 19592T, G. marinus ck-12-15T, and so on (Fig. 2 & Supplementary Fig.S4).

Approximately 37 families of carbohydrate-active enzymes were detected in strain R38T, while in closely related type strains this number was between...
A limited quantity of enzymes for carbon hydrate utilization (glycoside hydrolases, polysaccharide lyases, and carbohydrate esterases) (28 vs. 20–91) indicates that strain R38\(^{T}\) is weak in carbohydrate utilization (Supplementary Table S2). Approximately 71 families of peptidases were detected in strain R38\(^{T}\). This quantity is higher than in most of the closely related type strains (Supplementary Table S2), indicating that strain R38\(^{T}\) is versatile in protein utilization.

**Taxonomic conclusion**

Based on phylogenetic analyses, strain R38\(^{T}\) was found to be associated with the family Flavobacteriaceae. The ANI of strain R38\(^{T}\) to closely related type strains (≤72.5%) indicates that strain R38\(^{T}\) belongs to a novel species (Chun et al. 2018), and both biochemical and chemotaxonomic characteristics (Table 1) support this species-level assignment. Furthermore, the low 16S rRNA gene similarities (≤93%) of strain R38\(^{T}\) to closely related type strains indicate that strain R38\(^{T}\) represents a new genus (Yarza et al. 2014), which is also supported by the differences in polar lipid profile (Table 1 & Supplementary Fig.S2). Therefore, strain R38\(^{T}\) represents a new species in a new genus under the family Flavobacteriaceae.

**Zeaxanthin production**

Coding genes for Zeaxanthin biosynthesis enzymes phytoene desaturase, lycopene beta-cyclase, and beta-carotene 3-hydroxylase were examined in 115 of the 177 total genera in Flavobacteriaceae, and over 50% of these genera (62) had all three enzymes (Supplementary Table S3). Of note, all 11 strains of coral-associated flavobacteria (from approximately ten genera), including strain R38\(^{T}\), were able to produce zeaxanthin according to HPLC analysis (Supplementary Table S4). These results indicate that the Flavobacteriaceae family contains important zeaxanthin producers, and corals may benefit from these symbiotic flavobacteria when confronting thermal stress (Motone et al. 2020).

**Description of Prasinibacter gen. nov.**

Prasinibacter (Pra.si.ni.bac’ter. L. masc. adj. prasi-nus, yellowish-green; N.L. masc. bacter, rod: N.L. masc. n. Parisinibacter, a translucent yellowish green rod.)

Cells are gram-negative, non-spor-forming, non-motile, aerobic rods. Catalase- and oxidase-positive. Nitrate is reduced to nitrogen. The only menaquinone is MK-6. The major polar lipids are phosphatidyl-methyl ethanolamine, phosphatidylethanolamine, one unidentified ninhydrin-staining-positive phospholipid, three unidentified ninhydrin-staining-positive lipids, and three unidentified lipids.

The type species is Prasinibacter corallicola. Member of the family Flavobacteriaceae.

**Description of Prasinibacter corallicola sp. nov.**

Prasinibacter corallicola (co.rar.li.co’la. L. neut. n. corallum, coral; L. masc. suff. -cola, inhabitant dweller; N.L. n. corallicola, coral-dweller).

The description is as for the genus with the following additional properties: Cells are usually 0.3–0.5 μm wide and 0.9–2.0 μm long. Colonies are yellow-green, circular, and smooth on marine agar 2216. Cells can grow at 15–33 °C (optimum 25–30 °C), pH 5–10 (optimum 7–8) in 3–6% (w/v) NaCl (optimum 3–4%) in R2A liquid medium. Zeaxanthin is produced. Production of H\(_2\)S does not occur. Starch is hydrolyzed. In the API 20NE test, nitrate reduction and protease are positive. In the API ZYM test, alkaline phosphatase, esterase (C4), esterase lipase (C8) and (C14), leucine arylamidase, valine arylamidase, cysteine arylamidase, trypsin, α-chymotrypsin, acid phosphatase, naphtol-AS-BI phosphohydrolase, and α-galactosidase are positive. In the Biolog Gen III microplate, dextrin, D-maltose, α-D-glucose, D-mannose, L-alanine, L-glutamic acid, L-histidine, α-keto-glutaric acid, L-malic acid, bromo-succinic acid, Tween 40, acetoacetic acid, and acetic acid are oxidized. The major fatty acids are iso-C\(_{15:0}\), iso-C\(_{15:0}\) \(\omega6c\), C\(_{16:2}\) DMA, and C\(_{13:1}\) \(\omega3c\). The genomic DNA G+C ratio is 33.2 mol%.

The type strain, R38\(^{T}\) (=MCCC 1K03889\(^{T}\) =KCTC 72444\(^{T}\) ) was isolated from stony coral Porites lutea collected from Weizhou Island in the Beibu Gulf, China. The GenBank accession
number of the 16S rRNA gene sequence of the type strain is MN908337.

Author contributions GW, JL and YL isolated strains, performed experiments and wrote the manuscript. BC and ZL collected samples. HS and JL gave advices about bacteria cultivation. KY conceived and designed the experiments and approved the final manuscript.

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Declarations

Conflict of interest We have no conflict of interest to declare.

Ethical approval Not applicable.

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