



Tropicibacter oceani sp. nov., a novel sulfur-metabolizing bacteria isolated from the intertidal zone sediment of Chinese Yellow Sea

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Abstract In this study, we reported a Gram-stain-negative, rod-shaped, atrichous, and aerobic bacterial strain named YMD87^T, which was isolated from the intertidal zone sediment of Chinese Yellow Sea. Growth of strain YMD87^T occurred at 10.0–40.0 °C (optimum, 25–30 °C), pH 4.0–12.0 (optimum, 8.0) and with 0–6.0% (w/v) NaCl (optimum, 0.0–2.0%). Phylogenetic tree analysis based on 16S rRNA gene sequence indicated that strain YMD87^T belonged to the genus *Tropicibacter* and was closely related to *Tropicibacter alexandrii* LMIT003^T (97.2% sequence similarity). Genomic analysis indicated that strain YMD87^T contains a circular chromosome of 3,932,460 bp with G+C content of 63.8% and three circular plasmids of 116,492 bp, 49,209 bp and 49,673 bp, with G+C content of 64.3%. Genomic functional analysis revealed that strain YMD87^T is potential a novel sulfur-metabolizing bacteria. The predominant respiratory quinone of YMD87^T was

ubiquinone-10 (Q-10). The major polar lipids of YMD87^T contained phosphatidylglycerol, phosphatidylethanolamine, five unidentified lipids, five unidentified phospholipids, phosphatidylcholine, unidentified glycolipid and five unidentified aminolipids. The major fatty acids of strain YMD87^T contained C_{12:1} 3-OH, C_{16:0}, and summed feature 8 (C18:1 ω7c or/ and C18:1 ω6c). Phylogenetic, physiological, biochemical and morphological analyses suggested that strain YMD87^T represents a novel species of the genus *Tropicibacter*, and the name *Tropicibacter oceani* sp. nov. is proposed. The type strain is YMD87^T (=MCCC 1K08473^T =KCTC 92856^T).

Keywords *Tropicibacter* · Intertidal zone · Sediment · Chinese Yellow Sea

Abbreviations

KCTC Korean collection for type cultures
FAME Fatty acid methyl esters
ANIP Average nucleotide identity
GGDC Genome-to-genome distance calculator
DSMZ Deutsche Sammlung von Mikroorganismen und Zellkulturen GmbH
DDH DNA-DNA hybridizations

The GenBank accession number of the 16S rRNA gene sequence of strain YMD87^T is OP942226. The GenBank accession number of complete genome and plasmid sequences of strain YMD87^T are CP124616–CP124619.

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Introduction

The genus *Tropicibacter*, belonging to the family *Rhodobacteraceae*, was first proposed by Harwati

et al. in 2009 (Harwati et al 2009). At the time of writing, there are only two species in this genus, *Tropicibacter naphthalenivorans*, isolated from seawater obtained from Semarang Port in Indonesia (Harwati et al 2009), and *Tropicibacter alexandrii* LMIT003^T, isolated from a liquid culture of the dinoflagellate *Alexandrium minutum* (Wang et al. 2020). Four species previously affiliated with this genus were reclassified into other genera based on genomic analyses. *Tropicibacter multivorans* was reclassified in the genus *Epibacterium*, while *Tropicibacter mediterraneus*, and *Tropicibacter litoreus* were reclassified in the genus *Ruegeria*, and *Tropicibacter phthalicus* was reclassified in the genus *Pelagimonas*. Strains of the genus *Tropicibacter* are Gram-stain-negative, aerobic, oxidase-positive and rod-shaped. Chemotaxonomic characteristics include the predominant lipoprotein ubiquinone-10 (Q-10), and a G+C content of 61.9–64.6 mol% (Harwati et al 2009; Wang et al. 2020). The common major fatty acids identified in this genus include C_{16:0} and summed feature 8 (C_{18:1 ω7c} or/and C_{18:1 ω6c}) (Harwati et al 2009; Wang et al. 2020).

The intertidal zone is a buffer area between sea and land that is rich in sulfur compounds, nitrogen-containing compounds, and toxins, and has been influenced by complex environmental factors and human activities (Cao and Wong 2007; Pan and Wang 2012). The intertidal zone is also featured by high abundant and diverse microbial communities, and the fluctuation of intertidal environmental factors significantly influence the abundance and contribution of the microbial communities (Wilms et al. 2006). Sulfur metabolism bacteria, ubiquitous in intertidal zones, play important roles in the global cycling of sulfur and carbon (Pester et al. 2012; Rabus et al. 2015). The diversity of sulfate-reducing bacteria community in intertidal zones have been revealed in the surface sediments of Yangtze Estuary and Shenzhen Bay (Wu et al. 2019). In this study, a bacterial strain named YMD87^T was isolated from the intertidal zone sediment of Chinese Yellow Sea. Based on the polyphasic taxonomic features, we proposed that strain YMD87^T represents a novel species of the genus *Tropicibacter*, for which the name *Tropicibacter oceani* sp. nov., is proposed.

Materials and methods

Isolation and culture conditions

Strain YMD87^T was isolated from the sediment collected from the intertidal zone of Chinese Yellow Sea (37°23'0"N, 121°36'0"E). For bacterial isolation, the sediment sample was tenfold serially diluted with sterilized seawater, and spread onto the marine 2216EA (Haibo, Qingdao, China) plates. After incubation at 28 °C for 7 days, the pure culture of YMD87^T was obtained after three successive transfers to new 2216EA plates. The strain was stored at –80 °C in marine 2216 EB (Haibo) medium supplemented with 20% (v/v) glycerol.

16S rRNA gene sequence analysis

For 16S rRNA gene and genomic sequencing, genomic DNA of YMD87^T was extracted using a bacterial genomic DNA extraction kit (Tiangen, Beijing, China). The partial 16S rRNA gene sequence of YMD87^T was amplified by universal primers 27F (5'-AGAGTTTGGATCCTGGCTCA-3') and 1492R (5'-GGTTACCTTGTACGACTT-3') (Buchan et al. 2005). The PCR product was further cloned into the pEASY-T1 simple vector (TransGen, Beijing, China), and an almost complete 16S rRNA gene sequence of strain YMD87^T was obtained and submitted to GenBank (accession number OP942226). The 16S rRNA gene sequence was analyzed using EzBioCloud (<http://eztaxon-e.ezbiocloud.net/>) (Kim et al. 2012). The phylogenetic tree was generated using MEGA 7.0 software by neighbour-joining (Saitou et al. 1987), minimum-evolution (Rzhetsky et al. 1992) and maximum-likelihood (Guindon et al. 2003) and algorithms with bootstrap values (1000 replications) (Kumar et al. 2016).

Genome analysis

The whole genome of strain YMD87^T was sequenced using PacBio Sequel and Illumina NovaSeq PE150 platforms in Novogene Bioinformatics Technology Co., Ltd. (Beijing, China). A total of 367,182 reads were obtained, which were further assembled, corrected and authenticity ensured as described previously (Xu et al. 2021). The phylogenomic tree of strain YMD87^T and related species was

constructed using the up-to-date bacterial core gene (UBCG) set (Na et al. 2018). The genome sequence of *T. alexandrii* LMIT003^T (accession number GCA_003667315.2) was obtained from NCBI database to analyze the genomic difference with strain YMD87^T. EzBioCloud ANI calculator (www.ezbiocloud.net/tools/ani) (Lee et al. 2016) was used to determine the average nucleotide identity (ANI). DNA-DNA relatedness was estimated using the Genome-to-Genome Distance Calculator (GGDC) 3.0 provided by the DSMZ (<http://ggdc.dsmz.de/distalc2.php>) (Meier-Kolthoff et al. 2013). The genome component and gene function were further predicted by NCBI Prokaryotic Genome Annotation Pipeline (PGAP) (Tatusova et al. 2016). The COG and KEGG databases were also used to predict the functional genes and pathways. The secretory proteins were predicted with SignalP (Version 4.1) and TMHMM (Version 2.0c) (Petersen et al. 2011). The secondary metabolic gene clusters were analyzed with antiSMASH (version 2.0.2) (Medema et al. 2011). The integrins were predicted with INTEGRALL database (<http://integrall.bio.ua.pt/>). The virulence factors were predicted with pathogen host interactions database and virulence factors of pathogenic bacteria database (Chen et al. 2012; Martin et al. 2015). Antibiotic resistance genes were analyzed with antibiotic resistance genes database and comprehensive antibiotic research database (Jia et al. 2017; Liu and Pop 2009).

Physiological and chemotaxonomic characterization

The type strain *T. alexandrii* LMIT003^T (KCTC 62895^T) was obtained from Korean Collection for Type Cultures (KCTC, Korean), and used as a reference strain for biochemistry and fatty acid analysis. For cell morphology analysis, strain YMD87^T was grown on marine 2216 EB for 24 h at 28 °C, after harvesting and washing with distilled water, cells were negatively stained with 1% phosphotungstic acid and observed by transmission electron microscopy HT-7700 (Hitachi, Tokyo, Japan). Gram staining was performed using a Gram-staining kit (Haibo). Growth temperature of 4, 10, 15, 20, 25, 30, 35, 37, 40 and 45 °C were evaluated on 2216 EB to measure the growth range of YMD87^T. The NaCl range for growth was tested by using NaCl-free 2216 EB with different NaCl concentrations

(0–15.0%, at intervals of 1.0%) at 28 °C. The optimal pH was determined by growing at pH 4.0–12.0 (at intervals of 1.0 pH unit) using the buffer system described by Xu et al. (2005). In order to investigate anaerobic growth, strain YMD87^T was cultured at 28 °C on 2216 EB and supplemented with resazurin (0.02%, w/v) as an indicator of anaerobic condition. The plates were incubated in an anaerobic incubator YQX (Yuejin, Shanghai, China) filled with nitrogen. Oxidase activity was evaluated with the oxidase reagent (Haibo), and catalase activity was tested by the production of oxygen bubbles in 3% (v/v) H₂O₂ solution. Hydrolysis of starch, casein, tween 20, and 80 was examined on 2216EA plates with the corresponding substrate. Nitrate reductase, gelatinase, urease activities and other enzyme productions were examined using the API 20NE and API ZYM system (bioMérieux, Marcy-l'Étoile, France) in 28 °C, according to the instructions. Acid production from different carbohydrates was performed using the API 50CH system (bioMérieux). For fatty acid methyl esters (FAME) analysis, bacteria were grown on 2216EA until the late of the exponential growth phase (2 days) at 28 °C, and the cells were harvested and analyzed as reported by Sasser (Sasser et al. 1990). Polar lipids were extracted according to the protocol of Minnikin et al. and examined using two-dimensional TLC (Minnikin et al. 1984). Respiratory quinones of strain YMD87^T was analyzed using freeze-dried cells as reported previously (Sasser et al. 1990). Antibiotic susceptibility was determined on 2216 EA plates using antibiotic discs containing the following (µg per disc unless otherwise stated): polymyxin B (300 IU), furazolidone (300), piperacillin (100), cefoperazone (75), midecamycin (30), minocycline (30), doxycycline (30), tetracycline (30), neomycin (30), amikacin (30), ceftriaxone (30), ceftazidime (30), cefuroxime (30), cefradine (30), cefamezin (30), cephalixin (30), penicillin (10 U), gentamicin (10), norfloxacin (10), ciprofloxacin (5), ofloxacin (5), clindamycin (2), sulfamethoxazole (1.25).

Results and discussion

Phylogeny analysis of 16S rRNA gene sequence

The 16S rRNA gene sequence analysis showed that strain YMD87^T belonged to the genus *Tropicibacter* and was most closely related to *T. alexandrii* LMIT003^T with 97.18% sequence similarities, and the identities between strain YMD87^T and other close members were all below 97.0%. The NJ phylogenetic tree showed that strain YMD87^T formed a group with *T. alexandrii* LMIT003^T (Fig. S1). The corresponding ML and ME trees showed similar topologies (Fig. S1), which supported the proposal that strain YMD87^T belonged to the genus *Tropicibacter*.

Physiological and chemotaxonomic analysis

The morphological, cultural, physiological and biochemical characteristics of strain YMD87^T are given in the species descriptions (Table 1, S1, and Fig. 1). FAME analysis showed that the major fatty



Fig. 1 Transmission electron micrograph of the cell of strain YMD87^T. Bar, 2.0 μm

acid ($\geq 5\%$ of the total fatty acids) detected in strain YMD87^T was C_{16:0} (9.5%), C_{12:1} 3-OH (5.8%), and summed feature 8 (72.4%) (Table S2). The reference strain, *T. alexandrii* LMIT003^T showed

Table 1 Differential characteristics of strain YMD87^T from the reference strain

Characteristic	1	2
Cell size (μm)	3.4–5.8 × 1.2–2.4	0.8–3.4 × 0.8–1.3*
Temperature (°C) range	10–40	15–45
pH range	4–12	4–12
NaCl (% w/v) range	0–6	0–10
Hydrolysis of:		
Gelatin	–	+
Urea	+	–
Enzyme activity:		
Esterase (C4)	+	–
Esterase lipase (C8)	+	–
Valine arylamidase	+	–
Cystine aramidase	+	–
Acid phosphatase	+	–
Naphthol-AS-BI-phosphohydrolase	+	–
β-glucosidase	–	+
β-fucosidase	nd	–
DNA G + C content (mol%)	63.8	61.9*

*Data from Wang et al. 2020

Strains: 1, YMD87^T; 2, *Tropicibacter alexandrii* LMIT003^T (KCTC 62895^T). Data for strains 1, 2 are from this study, unless otherwise indicated. +, positive; w, weakly positive; –, negative. All strains are positive for the following: activity of oxidase, catalase, alkaline phosphatase, leucine arylamidase, and α-glucosidase. All strains are negative for the following: motility; hydrolysis of tween 20, 40, 60, 80, starch; activity of lipase C14, trypsin, chymotrypsin, α-galactosidase, β-galactosidase, N-acetyl-β-glucosaminidase, and α-mannosidase

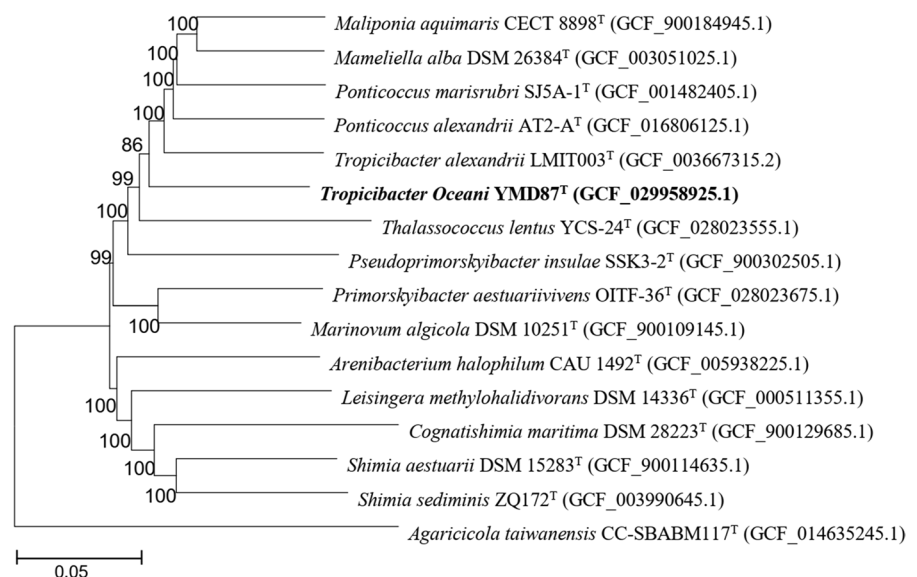
different profile of FAME with strain YMD87^T in some aspects, and contained C_{18:0} (9.5%) as the major fatty acids, but C_{16:0} and C_{12:1} 3-OH were not the major fatty acids (Table S2). The polar lipids of YMD87^T contained phosphatidylglycerol (PG), phosphatidylethanolamine (PE), five unidentified lipids (L), five unidentified phospholipids (PL), phosphatidylcholine (PC), unidentified glycolipid (GL), and five unidentified aminolipids (AL) (Fig. S2). The PC, PE, PG, AL, and PL were also detected in *T. alexandrii* LMIT003^T, but L and GL were not detected. The antibiotic resistance test show that, strain YMD87^T was susceptible to penicillin, piperacillin, cephalixin, cefamezin, cefradine, cefuroxime, ceftazidime, ceftriaxone, cefoperazone, amikacin, neomycin, doxycycline, minocycline, midecamycin, norfloxacin, ofloxacin, ciprofloxacin, polymyxin B, sulfamethoxazole, furazolidone, weekly susceptible to clindamycin, resistant to tetracycline and gentamicin.

Genomic features and phylogenomic analysis

The complete genome and three plasmid sequences of strain YMD87^T was obtained and submitted to GenBank (accession number CP124616-CP124619). Genomic analysis indicated that strain YMD87^T contains a circular chromosome of 3,932,460 bp with G+C content of 63.8% and three circular plasmids of 116,492 bp with G+C content of 63.09%, 49,209 bp with G+C content of 66.34%

and 49,673 bp with G+C content of 65.3%, respectively. The G+C content of YMD87^T genomic is higher than the related reference strain *T. alexandrii* LMIT003^T (Table 1). The predicted numbers of 5S rRNA, 16S rRNA, 23S rRNA, and tRNA sequences were 3, 3, 3, and 49, respectively (Table S3). The phylogenomic tree constructed using the 92 core genes of the genome showed the evolutionary position of strain YMD87^T. According to its distribution, strain YMD87^T clustered compactly with the strains *T. alexandrii* LMIT003^T, *Ponticoccus alexandrii* AT2-A^T (GCF_016806125.1), *Ponticoccus marisrubri* SJ5A-1^T (GCF_001482405.1), *Mameliella alba* DSM 26384^T and *Maliponia aquimaris* CECT 8898^T, of which YMD87^T was more closely related to the type strain *T. alexandrii* LMIT003^T (Fig. 2). Combining with the phylogenetic tree analysis of 16S rRNA gene sequence, YMD87^T belongs to the genus of *Tropicibacter*. The ANI value and the digital DDH value between strain YMD87^T and *T. alexandrii* LMIT003^T are 76.5% and 21.3%, respectively. These values are much lower than the threshold values for prokaryotic species delineation, which are 95–96% for ANI and 70% for DDH (Kim et al. 2014; Wayne et al. 1987). In addition, 10 genomic islands, 3 prophages, 2 CRISPR, and 341 secreted proteins were also detected in the genome of strain YMD87^T (Table S3). Moreover, secondary metabolites analysis revealed 8 gene clusters, i.e., hserlactone (2 clusters), NRPS,

Fig. 2 The phylogenomic tree based on 92 bacterial core genes showing the relationship of *Tropicibacter Oceani* YMD87^T with other strains. *Agaricola taiwanensis* CC-SBABM117^T was selected as outgroup. Bootstrap values are shown at the branch points. Bar, 0.05 substitutions per nucleotide position



RiPP-like, terpene, betalactone, ectoine, NRPS-like, and T1PKS, including a total of 186 genes (Table S1).

Functional genomics analysis

The whole genome of strain YMD87^T was further analyzed to reveal its potential functional genes in intertidal environmental adaptation. The distributions of COG categories were showed in Table S4, and the most 3 abundant categories were amino acid transport and metabolism (343 genes), carbohydrate transport and metabolism (236 genes), and energy production and conversion (230 genes). Different from the reference strain *T. alexandrii* LMIT003^T, which inhabit in the phycosphere, and capable of transforming DMSP to methylmercaptpropionate by the DMSP demethylase (*dmdA*) gene, *dmdA* was not detected in strain YMD87^T (Wang et al. 2020). According to KEGG pathway analysis, the functional gene were most abundant in metabolic (53 pathways), of which the top 3 pathways were microbial metabolism in diverse environments (250 genes), carbon metabolism (128 genes), and nucleotide metabolism (96 genes), which conducive to utilize the complex nutrients of the intertidal environment. For sulfur metabolism pathways, 29 genes were identified, both YMD87^T and the reference strain *T. alexandrii* LMIT003^T had a complete assimilatory sulfate reduction (CysN, CysD, CysC, CysH, CysJ, and CysI) and a complete SOX system pathways (SoxB, SoxZ, SoxY, SoxX, SoxC, SoxD, and SoxB) (Fig S3). Concerning on the DNA repair pathways, a total of 37 genes were detected in YMD87^T, which were categorized into three groups: DNA repair genes *RadA*, *RadC*, *RecF*, *RecO*, and *RecN*, the DNA mismatch repair genes *MutS*, *MutT*, and *MutL*, the double-strand DNA break repair genes *AddB*, and *AddA*, and DNA alkylation repair genes. Moreover, pathogenicity analysis based on PHI and VFDB databases revealed 278 and 159 genes related to pathogenicity, respectively. However, ARDB and CARD databases depended analysis only revealed two genes related to antibiotic (tetracycline and aminoglycoside) resistance, which were consistent with the results of drug sensitivity test. On the contrary, 214 genes were found to participate in the pathways of biosynthesis of antibiotics, which indicated a potential environmental adaptation mechanism of YMD87^T by inhibiting the growth of other bacteria.

Conclusion

Strain YMD87^T phylogenetically formed a distinct group with *T. alexandrii* LMIT003^T, and the chemotaxonomic profiles of strain YMD87^T were generally similar to *T. alexandrii* LMIT003^T. However, some physiological and biochemical properties, such as enzyme activities, acid production substrates and antibiotic resistance, distinguished strain YMD87^T from *T. alexandrii* LMIT003^T. Therefore, strain YMD87^T represents a novel species of the genus *Tropicibacter*, for which the name *Tropicibacter oceani* sp. nov. is proposed.

Description of *Tropicibacter oceani* sp. nov.

Tropicibacter oceani (o.ce.a'ni. L. gen. n. *oceani*, of the ocean).

Cells of strain YMD87^T are Gram-stain-negative, rod-shaped, atrichous, and aerobic, 1.2–2.4 µm in width and 3.4–5.8 µm in length. Colonies of YMD87^T on 2216EA are circular, smooth, white, and approximately 1–2 mm in diameter after incubation for 7 days at 28 °C. Growth of strain YMD87^T occurred at 10.0–40.0 °C (optimum, 25–30 °C), pH 4.0–12.0 (optimum, 8.0) and with 0–6.0% (w/v) NaCl (optimum, 0–2.0%). Activities of oxidase, catalase and urease are positive, but tween-20, 40, 60, 80, starch and gelatin cannot be hydrolyzed. API ZYM reaction tests were positive for alkaline phosphatase, esterase (C4), esterase lipase (C8), leucine arylamidase, valine arylamidase, cystine aramidase, acid phosphatase, Naphthol-AS-BI-phosphohydrolase, α-glucosidase, negative for lipase C14, trypsin, chymotrypsin, α-galactosidase, β-galactosidase, N-acetyl-β-glucosaminidase, β-uronidase, β-glucosidase, α-fucosidase and α-mannosidase. Acid cannot be produced. The G+C content of the genomic DNA of strain YMD87^T is 63.8%. The principal respiratory quinone is Q-10. The polar lipids of YMD87^T contained phosphatidylglycerol, phosphatidylethanolamine, five unidentified lipids, five unidentified phospholipids, phosphatidylcholine, unidentified glycolipid, and five unidentified amino lipids. The major fatty acids of strain YMD87^T contained C_{12:1} 3-OH, C_{16:0}, and summed feature 8 (C18:1 ω7c or/and C18:1 ω6c).

The type strain is YMD87^T (=MCCC 1K08473^T=KCTC 92856^T), which was isolated

from the intertidal sediment obtained from the intertidal zone sediment of Chinese Yellow Sea. The GenBank accession numbers of the 16S rRNA gene sequence and the complete genome sequence of strain YMD87^T are OP942226 and CP124616, respectively.

Author contributions DDZ: investigation, conceptualization, writing original draft. XDX: isolated the bacterium. BZZ and JXF: phylogenetic and genomic characterisation. JZ: supervision and writing-reviewing and editing, funding acquisition. All authors read and approved the manuscript.

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Data availability The 16S rRNA gene and the complete genome sequences of strain YMD87^T have been deposited under the GenBank accession numbers OP942226 and CP124616, respectively.

Declarations

Conflicts of interest The authors declare that they have no competing interests.

Ethical statement This article does not contain any studies with animals performed by any of the authors.

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