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EXPERIMENTAL ARTICLES

Pseudooceanicola albus sp. nov., Isolated from Mangrove Sediment within the Beibu Gulf

M. Li[a, b], F. T. Li[a, b, c], C. H. Gao[a, b], Y. H. Liu[a, b, *], and X. X. Yi[a, b, c, **]

[a] *Institute of Marine Drugs, Guangxi University of Chinese Medicine, Nanning, 530200 China*

[b] *Guangxi Key Laboratory of Marine Drugs, Guangxi University of Chinese Medicine, Nanning, 530200 China*

[c] *School of Pharmaceutical Sciences, Guangxi University of Chinese Medicine, Nanning, 530200 China*

**e-mail: yonghongliu@scsio.ac.cn*

***e-mail: yixiangxi2017@163.com*

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Abstract—A nonmotile gram-negative, short, rod-shaped strain, BGMRC 2024^T, was isolated from the sediment of *Rhizophora stylosa* collected in the Beibu Gulf, China. The strain BGMRC 2024^T exhibited optimal growth at 25 to 28°C, pH 7.0, and in the presence of 1–4% (wt/v) NaCl. Analysis of the 16S rRNA gene sequences indicated that BGMRC 2024^T was closely related to *Pseudooceanicola antarcticus* CGMCC 1.12662^T (96.23% sequence similarity), *P. algae* Lw-13e^T (96.17%), *P. lipolyticus* 157^T (96.16%), and *P. pacificus* 216_PA32_1^T (96.09%). The digital DNA-DNA hybridization (dDDH) values and the average nucleotide identity (ANI) of the strain *Pseudooceanicola antarcticus* CGMCC 1.12662^T were 24.7 and 77.52%, respectively. The DNA G+C content was 67.4 mol %. The main respiratory quinone was ubiquinone-10. The polar lipids of strain BGMRC 2024^T included four unidentified phospholipids, two unidentified ninhydrin-positive lipids, one unidentified ninhydrin-positive phospholipid, and three unidentified lipids. The major fatty acids were $C_{19:0}$ cyclo ω8*c*, summed feature 8 ($C_{18:1}$ω7*c* and/or $C_{18:1}$ω6*c*), and $C_{16:0}$. Based on these results, BGMRC 2024^T represents a novel species of the genus *Pseudooceanicola*, for which the name *Pseudooceanicola albus* sp. nov. is proposed. The type strain is BGMRC 2024^T (=KCTC52117^T = DSM102086^T).

Keywords: mangrove plant, polyphasic taxonomy, *Rhodobacteraceae*, *Pseudooceanicola albus* sp. nov.

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The genus *Pseudooceanicola*, with *Pseudooceanicola atlanticus* 22II-s11g^T as the type strain belongs to the family *Rhodobacteraceae*. It was proposed by Lai et al. (2015). Based on their genotypic and phenotypic characteristics, six misclassified species were subsequently transferred from the *Oceanicola* genus to the *Pseudooceanicola* genus (Lai et al., 2015). Currently, there are 13 *Pseudooceanicola* species with validly published names: *Pseudooceanicola aestuarii* (Li et al., 2020), *P. algae* (Wolter et al., 2021), *P. antarcticus* (Huo et al., 2014; Lai et al., 2015), *P. atlanticus* (Lai et al., 2015), *P. batsensis* (Cho et al., 2004; Lai et al., 2015), *P. endophyticus* (Zheng et al., 2021), *P. flagellates* (Huo et al., 2014; Lai et al., 2015), *P. lipolyticus* (Huang et al., 2018), *P. marinus* (Lin et al., 2007; Lai et al., 2015), *P. nanhaiensis* (Gu et al., 2007; Lai et al., 2015), *P. nitratireducens* (Zheng et al., 2010; Lai et al., 2015), *P. onchidiid* (Yin et al., 2020), and *P. pacificus* (Lina et al., 2020), (https://lpsn.dsmz.de/genus/pseudooceanicola). All of them were isolated from ocean environmental resources such as seawater, sediments, or invertebrates.

In the course of the investigation of the bacterial community from offshore areas of the Beibu Gulf, China, a novel bacterium, designated BGMRC 2024^T, was isolated from the soil of *Rhizophora stylosa*. In the present study, we conducted a polyphasic taxonomic study to clarify the taxonomic position of strain BGMRC 2024^T.

MATERIALS AND METHODS

Bacterial Isolation and Cultivation

The sediment sample from the *Rhizophora stylosa* rhizosphere was obtained from the Beibu Gulf, Beihai, PR China (21°44′53″ N, 108°36′14″ E). To obtain bacterial isolates, sediment samples were homogenized in sterile seawater for 1 h. After 1 h, 200-μL aliquots of the suspension were plated on ISP2 medium (2.0 g yeast extract, 2.0 g malt extract, 2.0 g D-(+)-glucose anhydrous, 15.0 g agar powder, and 1 L seawater). The plates were incubated at 28°C for 7 days. An ivory colony was used to isolate the bacterial strain BGMRC 2024. The pure culture of the strain was pre-

served in glycerol suspension (30%, v/v) at −80°C (Li et al., 2021). For comparative analyzes, *P. atlanticus* MCCC1A09160^T and *P. lipolyticus* MCCC 1K03317^T were purchased from the Marine Culture Collection of China (MCCC), and *P. antarcticus* CGMCC1.12662^T was obtained from the China General Microbiological Culture Collection Center (CGMCC).

Phenotypic and Biochemical Characteristics

The cells of strain BGMRC 2024^T were grown in ISP2 at 28°C for 48 h for morphological observation and physiological tests. Scanning electron microscopy (FEI Quanta 250 environmental scanning electron microscope) was used to observe the morphology and size of the cells. The presence of flagella was observed using transmission electron microscopy (HITACHI transmission electron microscope HT7700). Gram staining was tested using a Gram stain kit (Difco) according to the manufacturer's instructions. Hydrolysis tests for casein, gelatin, starch, urea, and Tweens 20 and 40 were carried out by conventional methods (Dong and Cai, 2001). Strain BGMRC 2024^T was incubated in ISP2 medium at different temperatures (4, 10, 15, 20, 25, 28, 37, 40, and 45°C), different concentrations of NaCl (0–5%, w/v, at a 0.5% interval), and different pH values (pH 4.0–12.0 at 1 pH unit intervals) to measure its growth (OD_{600}) using an UV-1800 spectrometer (Lai et al., 2015). Oxidase activity was determined with 1% (w/v) *N*,*N*,*N*',*N*'-tetramethyl-*p*-phenylenediamine, and catalase activity was determined by formation of bubbles upon addition of 3% H_2O_2 (Choi et al., 2014). The GEN III microplate (Biolog, Inc., United States) was used to test the utilization of acid production from different carbon sources. Other enzyme activities and physiological tests were determined using the API ZYM, API 20E, and API 50 CH system strips (bioMérieux), which were used to test the biochemical characteristics of the strain.

Phylogenetic Analysis

Genomic DNA was extracted using a bacterial genomic DNA Mini kit following the manufacturer's recommendations. The 16S rRNA gene was amplified using AccuPower PCR PreMix (Bioneer, Daejeon, Korea) and the bacteria-specific primers 27F and 1492R (Yang et al., 2018). The 16S rRNA gene sequence was used for pairwise sequence alignment performed by the EzBioCloud server (http://www.ezbiocloud.net) (Kim et al., 2012). Multiple sequence alignment was performed with the CLUSTAL W program of the MEGA 7 package (Tamura et al., 2011). Evolutionary distances for the phylogenetic trees were calculated with the Kimura two-parameter model (Kimura et al., 1980). Phylogenetic trees were constructed by using the neighbor-joining (Saitou and Nei, 1987), maximum-likelihood (Felsenstein, 1981), and maximum-parsimony (Fitch et al., 1971), algorithms using the MEGA7.0 version (Tamura et al., 2011). The topologies of the phylogenetic trees were assessed by bootstrap analysis based on 1000 replicates (Felsenstein, 1985).

Genome Analysis

The draft genome sequence of strain BGMRC 2024^T was determined using the Illumina Hiseq 4000 system (Illumina, San Diego, CA, United States) and was sequenced by BGI (Wuhan, China). Genomic information of *Pseudooceanicola antarcticus* Ar-45^T (GCA_002786285.1), *P. atlanticus* 22II-s11g^T (GCA_000768315.1), *P. lipolyticus* 157^T (GCA_002786325.1), *P. nanhaiensis* DSM 18065^T (GCA_000688295.1), *P. batsensis* HTCC2597^T, *P. marinus* CECT7751^T (GCA_900172385.1), and *P. nitratireducens* DSM 29619^T (GCA_900112545.1) was downloaded from GenBank, and the new strain BGMRC 2024^T (WUMU00000000) was sequenced in BGI. The G + C DNA contents of strain BGMRC 2024^T and closely related type strains were calculated from their whole genome sequence. The average nucleotide identity (ANI) and digital DNA-DNA hybridization (dDDH) values between strain BGMRC 2024^T and closely related type strains were calculated using the ANI calculator tool (https://www.ezbiocloud.net/tools/ani) and the genome-to-genome distance calculator tool (https://ggdc.dsmz.de/ggdc.php) (Meier-Kolthoff et al., 2013), respectively. Gene function prediction was performed using the Rapid Annotation using Subsystem Technology (RAST) server (https://rast.nmpdr.org) (Aziz et al., 2008). The codon Tree method selects single-copy PATRIC PGFams and analyzes aligned proteins and coding DNA from single-copy genes using the program RAxML (Stamatakis et al., 2008).

Chemotaxonomic Analysis

The strain BGMRC 2024^T and the reference strains *P. atlanticus* MCCC1A09160^T, *P. lipolyticus* MCCC 1K03317^T, and *P. antarcticus* CGMCC1.12662^T were grown in ISP2 medium supplemented with 3% sea salt at 28°C for three days and then the biomass was collected for chemotaxonomic analysis.

The composition of cellular fatty acids was determined at Yunnan University (Yunnan, China) using the Sherlock Microbial Identification System (Version 6.0). Fatty acids were analyzed using gas chromatography and identified using the microbial identification software package based on the TSBA6 6.0 database (Kämpfer et al., 1996). Polar lipids were extracted with chloroform/methanol (1 : 2, v/v) sol-

vent (Komagata and Suzuki, 1987) and analyzed by the method described previously (Cao et al., 2014). The respiratory quinones were extracted from freeze dried cells of strain BGMRC 2024^T with chloroform/methanol (2 : 1, vol/vol) (Komagata and Suzuki, 1987) and analyzed by ultra-performance liquid chromatography (Nakagawa et al., 1993).

RESULTS AND DISCUSSION

Phenotypic and Physiological Characteristics

Cells of strain BGMRC 2024^T were short nonmotile rods, 0.8 μm wide and 0.5–1.0 μm long (Fig. S1), and stained gram-negative. The colonies were white. The growth of strain BGMRC 2024^T was observed at 1.0–7.0% (w/v) NaCl, (optimum at 3% w/v), the temperature range of 20–37°C (optimum at 28°C), and pH 6.0–9.0 (optimum at pH 7.0) (Table 1). The activities of oxidase and catalase were positive. The comparison of the morphological, physiological, and biochemical characteristics between strain BGMRC 2024^T and the reference strains *P. atlanticus* MCCC1A09160^T, *P. lipolyticus* MCCC 1K03317^T, and *P. antarcticus* CGMCC1.12662^T is presented in Tables 1 and S1.

The strain BGMRC 2024^T shared most of the features with other members of the genus *Pseudooceanicola*. However, there were some differences between the novel isolate and the closely related species. For example, strain BGMRC 2024^T was negative for Tween 20 and Tween 40 hydrolysis (Table 1). In the API ZYM, strain BGMRC 2046^T showed positive activity for α-glucanase and β-glucosidase, unlike *P. atlanticus* MCCC1A09160^T and *P. lipolyticus* MCCC 1K03317^T. In API 50CH, strain BGMRC 2024^T produced acid from L-arabinose, D-fructose, D-sorbitol, D-melibiose, D-turanose, and D-mannose, unike *P. atlanticus* MCCC1A09160^T, *P. antarcticus* CGMCC1.12662^T, and *P. lipolyticus* MCCC 1K03317^T (Table 1 and Table S1).

Phylogenetic Analysis

The sequenced length of the 16S rRNA gene of the strain BGMRC 2024^T was 4588940 bp. Phylogenetic analysis of strain BGMRC 2024^T based on 16S rRNA gene sequences indicated that the novel strain belonged to the genus *Pseudooceanicola* and exhibited 16S rRNA gene sequence similarities with the type strains *Pseudooceanicola antarcticus* CGMCC 1.12662^T (96.23% sequence identity), *P. algae* Lw-13e^T (96.17%), *P. lipolyticus* 157^T (96.16%), and *P. pacificus* 216_PA32_1^T (96.09%), respectively. In the analysis of the neighbor-joining tree, strain BGMRC 2024^T formed a distinct clade with *P. antarcticus* CGMCC 1.12662^T, *P. marinus* CECT 7751^T (96.17%), and *P. lipolyticus* 157^T (Fig. 1). The maximum-parsimony and maximum-likelihood trees also showed the closely phylogenetic relationship of the strain BGMRC 2024^T and the reference strains (Figs. S3 and S4).

The ANI and dDDH values of strain BGMRC 2024^T to its closely related species (*P. antarcticus* Ar-45^T, *P. atlanticus* 22II-s11g^T, *P. lipolyticus* 157^T, *P. nanhaiensis* DSM 18065^T, *P. batsensis* HTCC2597^T, *P. marinus* CECT7751^T, and *P. nitratireducens* DSM 29619^T) ranged from 74.3 to 77.5% and 23.3 to 24.7%, the recommended cutoff for genus delineation at genome level (Goris et al., 2007; Richter et al., 2009) (Table 2). However, the protein-based core genome phylogeny indicated that the strain BGMRC 2024^T formed a subgroup with *P. endophyticus* CBS1P-1^T, *P. marinus* CECT 7751^T, and *P. antarcticus* CGMCC 1.12662^T and a robust clade with genus *Pseudooceanicola* (Fig. S5). Thus, strain BGMRC 2024^T represents a novel species of the genus *Pseudooceanicola*.

Genomic Characteristics

The draft genome size of strain BGMRC 2024^T (4.6 Mb) was much smaller than that of *P. atlanticus* 22II-s11g^T (4.9 Mb). The draft genome of strain BGMRC 2024^T was deposited in DDBJ/ENA/GenBank under the accession number WUMU00000000.

The G + C content of genomic DNA is 67.4 mol %, which is close to the values for *P. nanhaiensis* (67.9%) and *P. marinus* (66.8%). Gene prediction allowed the annotation of 5068 protein-coding genes. The genome of BGMRC 2024^T is much larger than those of *P. antarcticus* Ar-45^T (4.3 Mb), *P. batsensis* HTCC2597^T (4.4 Mb), *P. marinus* CECT7751^T (4.5 Mb), and *P. nitratireducens* DSM 29619^T (4.1 Mb). The numbers of genes putatively involved in various aspects of the stress response, iron acquisition and metabolism, regulation and cell signaling, protein metabolism, respiration, amino acids, and derivatives in the genome of BGMRC 2024^T was higher than those of *P. antarcticus* Ar-45^T and *P. atlanticus* 22II-s11g^T, while the numbers of genes putatively involved in nitrogen metabolism, lipids, fatty acids, motility and chemotaxis, isoprenoids, membrane transport, and virulence, disease, and defense in the genome of BGMRC 2024^T was lower than those of *P. antarcticus* Ar-45^T and *P. atlanticus* 22II-s11g^T (Supplementary Table S2). Furthermore, denitrification genes were present in *P. antarcticus* Ar-45^T and *P. atlanticus* 22II-s11g^T, but not in strain BGMRC 2024^T. Based on the strain annotation, the genome sequences of BGMRC 2024^T unraveled the presence of genes involved in ectoine biosynthesis (Supplementary Table S3). Moreover, the new strain and the other three types strains *P. atlanticus* MCCC1A09160^T, *P. antarcticus* CGMCC1.12662^T, and *P. lipolyticus* MCCC 1K03317^T

Table 1. Phenotypic characteristics of BGMRC 2024^T and closely related species

Characteristics	1	2	3	4
Isolation source	Rhizosphere soil of *Rhizophora stylosa*	Seawater of the Atlantic Ocean	Seawater of the Southern Ocean	Seawater collected from the Philippine Sea
Catalase/oxidase	+/+	+/+	+/+	+/+
Temperature range for growth (°C)	4–37 (25–28)	25–37 (28)	4–40 (35–37)	25–37 (28)
pH range for growth	5.0–11.0 (7)	6.0–9.0 (7)	5.5–8.5 (7)	6.0–8.5 (7)
NaCl range for growth (%, w/v)	0–10 (1–4)	0–10 (1–3)	1–14 (1–3)	1–8 (3)
Tween 20	–	+	+	+
Tween 40	–	+	+	+
Polar lipids†	NPL, AL_{1-4}, $PL_{1,6}$, $L_{3,4,11}$	PME, $AL_{1-3,5}$, PL_{1-2}, L_{1-4}	PME $AL_{1-2,6}$, PL_{1-2}, L_{3-7}	PME, $AL_{1-2,4}$, $PL_{1-5,7}$, $L_{1,8-10}$
Respiratory quinone	Ubiquinone-10	Ubiquinone-10	Ubiquinone-10	Ubiquinone-10
DNA G+C content (mol%)	67.3	64.1	62.0	64.6
Utilization of (API 20E):				
O-nitrophenyl-β-D-galactopyranoside	+	–	+	–
citrate utilization test	–	–	+	–
VP test	+	+	–	–
sorbitol fermentation	–	–	W	–
sucrose fermentation	–	–	W	–
amygdalin	–	–	W	–
arabinose	–	–	W	–
NO_2	–	+	+	–
N_2	–	–	–	+
Enzyme activities (API ZYM):				
esterase (C4)	+	+	+	–
lipase (C14)	–	W	–	–
yaline arylamidase	W	+	+	+
acid phosphatase	+	W	–	+
α-glucanase	+	–	+	–
β-glucosidase	+	–	W	–
N-acetyl-β-glucosaminidase	–	–	+	–
The acid produced from (API 50CH):				
D-mannose	+	–	–	–
L-arabinose	+	–	–	–
D-fructose	+	–	–	–
D-sorbitol	+	–	–	–
ferric citrate of aesculin	+	–	+	–
D-melibiose	+	–	–	–
D-sucrose	+	+	–	–
D-trehalose	–	–	+	–
D-turanose	+	–	–	–

Strains: 1, GXIMD2024^T; 2, *P. atlanticus* MCCC1A09160^T; 3, *P. antarcticus* CGMCC1.12662^T; 4, *P. lipolyticus* MCCC 1K03317^T. +, positive; –, negative, nd, unknown.
* Data from genome sequencing: WUMU00000000.
† PME, phosphatidylmethylethanolamine; AL, unidentified ninhydrin positive lipid; PL, unidentified phospholipid; NPL, unidentified ninhydrin positive phospholipid; L, unidentified lipid.

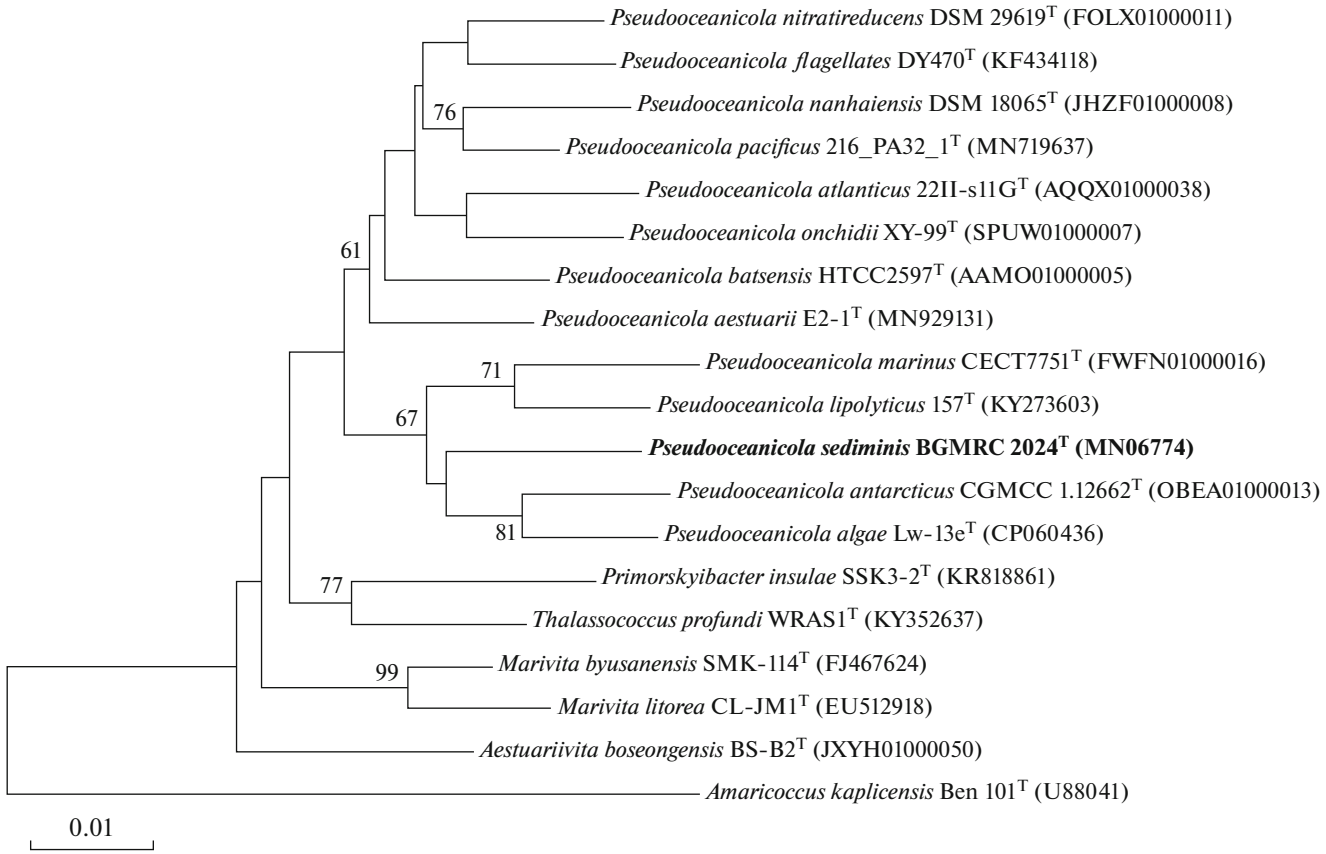

Fig. 1. Neighbor-joining phylogenetic tree based on the 16S rRNA gene sequences showing the relationships between strain BGMRC 2024^T and related taxa. *Amaricoccus kaplicensis* Ben101^T was used as the outgroup. The numerals at the nodes represent the percentage bootstrap values (>50%) of 1000 bootstrap replicates from NJ algorithms. Bar, 0.01 substitutions per nucleotide position.

possessed the genes putatively encoding riboflavin synthesis clusters.

Chemotaxonomic Analysis

The main cellular fatty acids (>5%) of strain BGMRC 2024^T were identified as $C_{19:0}$ cyclo ω8*c* (37.14%), summed feature 8 ($C_{18:1}$ω7*c* and/or $C_{18:1}$ω6*c* (28.32%)), $C_{16:0}$ (17.92%), and $C_{18:1}$ω7*c* 11-methyl (6.18%) (Table 2). Overall, strain BGMRC 2024^T had a fatty acid profile similar to those of reference strains *P. atlanticus* MCCC1A09160^T, *P. lipolyticus* MCCC 1K03317^T, and *P. antarcticus* CGMCC1.12662^T. However, strain BGMRC 2024^T possessed relatively higher amounts of $C_{19:0}$ cyclo ω8*c* and summed feature 8 ($C_{18:1}$ω7*c* and/or $C_{18:1}$ω6*c*), and lower amounts of $C_{14:0}$, $C_{18:0}$, $C_{10:0}$ 3-OH, and $C_{12:0}$ 3-OH (Table 2). The polar lipids profile of strain BGMRC 2024^T consisted of two unidentified phospholipids ($PL_{1,6}$), one unidentified ninhydrin-positive phospholipids (NPL), four unidentified ninhydrin-positive lipids ($AL_{1–4}$), and three unidentified lipids ($L_{3,4,11}$) (Fig. S2). However, the presence of one unidentified ninhydrin-positive phospholipid (NPL), one unidentified phospholipid (PL_6), one unidentified ninhydrin-positive lipid (AL_4), and one unidentified lipid (L_{11}) differentiates the novel strain from those reference strains (Fig. S2). The predominant respiratory quinone was the ubiquinone Q-10, which was identical to that of other type strains of the genus *Pseudooceanicola*.

Description of *Pseudooceanicola albus* sp. nov.

Pseudooceanicola albus. (al'bus. L. masc. adj. *albus* white, referring to the color of the colonies).

The cells are short nonmotile rods with a size 0.4–0.8 μm wide and 0.5–1.0 μm long, and stain gram-negative. The colonies are white. The oxidase and catalase activities are positive. Growth occurs at 20 to 37°C (optimum at 28°C), pH 6.0 to 9.0 (optimum at pH 7.0) and 1.0 to 7.0% (w/v) NaCl (optimum, 1–3%). The main fatty acids are $C_{19:0}$ cyclo ω8*c*, summed feature 8 ($C_{18:1}$ω7*c* and/or $C_{18:1}$ω6*c*), and $C_{16:0}$. The main respiratory quinone is ubiquinone-10. The DNA G+C content is 67.4 mol %. In the API 20E tests, the

Table 2. Comparative fatty acid compositions of strains BGMRC 2024^T and related strains‡

Fatty acid, %	1	2	3	4
$C_{12:0}$	–	–	2.34	–
$C_{14:0}$	1.42	–	–	–
$C_{16:0}$	17.92	**18.51**	24.09	6.50
$C_{17:0}$	–	–	1.44	–
$C_{18:0}$	1.89	1.73	2.39	–
$C_{19:0}$ cyclo ω8*c*	**37.14**	**34.17**	–	**15.22**
$C_{10:0}$ 3-OH	3.16	–	1.84	5.94
$C_{12:0}$ 3-OH	2.26	5.94	3.70	–
$C_{16:0}$ 2-OH	–	–	–	7.44
$C_{18:1}$ω7*c* 11-methyl	6.18	5.43	27.00	2.44
Summed feature 3	–	1.04	–	–
Summed feature 8	28.32	**29.33**	**35.06**	**57.11**

Strains: 1, BGMRC 2024^T; 2, *Pseudooceanicola antarcticus* CGMCC 1.12662^T; 3, *Pseudooceanicola atlanticus* MCCC 1A09160^T; 4, *Pseudooceanicola lipolyticus* MCCC 1K03317^T. All data were from this study. Trace amount (<1.0%). Not detected.
‡ Summed feature 2 contains *iso* I-$C_{16:1}$/$C_{14:0}$ 3-OH; Summed feature 3 contains $C_{16:1}$ω7*c*/$C_{16:1}$ω6*c*; Summed feature 8 contains $C_{18:1}$ω7*c*/$C_{18:1}$ω.

strain was positive for O-nitrophenyl-β-D-galactopyranoside, urease test, and the VP test. In the API ZYM system, positive reactions are observed with leucine arylamidase, esterase (C4), esterase lipase (C8), naphthol-ASBI-phosphohydrolase, alkaline phosphatase, acid phosphatase, α-glucanase, and β-glucosidase. The results for D-fructose, D-sorbitol, D-melibiose, D-sucrose, D-turanose, L-arabinose and D-mannose, and ferric citrate of esculin are positive in the API 50CH system.

The type strain, BGMRC 2024^T (=KCTC52117^T = DSM102086^T), was isolated from the rhizosphere soil of *Rhizophora stylosa* collected from the Beibu Gulf of China. The GenBank/EMBL/DDBJ accession numbers for the draft genome and 16S rRNA gene sequences of strain BGMRC 2024^T are WUMU00000000 and MN067774, respectively.

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COMPLIANCE WITH ETHICAL STANDARDS

The authors declare that they have no conflicts of interest. This article does not contain any studies involving animals or human participants performed by any of the authors.

SUPPLEMENTARY INFORMATION

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