Actirhodobacter atriluteus gen. nov., sp. nov., isolated from the surface water of the Yellow Sea

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Abstract A Gram-stain-negative, aerobic, orange-pigmented bacterial strain, designated HHU K3-1 T, was isolated from the surface water of the Yellow Sea. The strain was observed to grow on 2216E agar medium, and growth occurred at pH 6.0–8.0 (optimum 7.0), 28–37 °C (optimum 28 °C), and in the presence of 0.5–5% (w/v) NaCl (optimum 1–3%). The major fatty acids (> 10%) were summed feature 3 (C16:1ω6c/C16:1ω7c), C17:1ω6c and summed feature 8 (C18:1ω6c/C18:1ω7c). Strain HHU K3-1 T was found to contain ubiquinone-10 as the predominant quinone and the major polar lipids were diphosphatidylglycerol (DPG), phosphatidylethanolamine (PE), phosphatidylglycerol (PG) and sphingoglycolipid (SGL). The 16S rRNA gene sequence analysis indicated that strain HHU K3-1 T shared highest similarities with Pelagerythrobacter marenensis KCTC 22370 T (97.7%) and Qipengyuania oceanensis MCCC 1A09965 T (96.9%). However, a phylogenetic tree based on 288 orthologous clusters (OCs) indicated that HHU K3-1 T was close related to Parapontixanthobacter aurantiacus MCCC 1A09962 T. The pairwise AAI and evolutionary distance between HHU K3-1 T and Parapontixanthobacter aurantiacus MCCC 1A09962 T are 67.1% and 0.43, respectively, which meet the recently proposed standard to differentiate genera in the family Erythrobacteraceae. On the basis of the result obtained by the polyphasic taxonomic study, strain HHU K3-1 T can be considered to represent a novel genus in the family Erythrobacteraceae, for which the name Actirhodobacter atriluteus gen. nov., sp. nov. is proposed. The type strain is HHU K3-1 T (= MCCC 1K04225 T = KCTC 72834 T = CGMCC 1.17395 T).

Keywords Actirhodobacter atriluteus · Erythrobacteraceae · Yellow sea

Introduction

The family Erythrobacteraceae belongs to the order Sphingomonadales of the class Alphaproteobacteria...
in the phylum Proteobacteria (Kosako et al. 2000). At the time of writing, the number of validly published genera of this family has reached 17 including the original 6 ones and the recently proposed 11 ones, Alteraurantiacibacter, Altererythrobacter, Altericroceibacterium, Alteripontixanthobacter (Apb.), Alteriqipengyuania Aurantiacibacter, Croceibacterium, Croceicoccus Erythrobacter, Parapontixanthobacter (Ppb.), Paraaurantiacibacter, Parerythrobacter, Pelagerythrobacter (Pel), Pontixanthobacter, Pseudopontixanthobacter, Qipengyuania and Tsuneonella, according to the genus boundaries of average amino acid identity (AAI, 70%) and evolutionary distance (0.40) recently proposed for the family Erythrobacteraceae (Xu et al. 2020; Sun et al. 2020). Bacteria of the family Erythrobacteraceae were isolated from various habitats, including air (Xue et al. 2016), soil (Li et al. 2020), sediment (Park et al. 2019b), tidal flat (Park et al. 2019a), seawater (Li et al. 2017a; Meng et al. 2019), estuary (Park et al. 2019c) and freshwater (Kang et al. 2016). In addition, they also exist in some plant (Shiba and Simidu 1982), animal (Zhuang et al. 2017) and some extreme environment, such as mudstone core (Zhang et al. 2016), hot spring (Yuan et al. 2017) and desert (Yan et al. 2017). Members of the family Erythrobacteraceae present pink, red, yellow or orange colonies on the media, and the cells are Gram-stain-negative, coccoid, ovoid or rod-shaped, and taking ubiquinone-10 as the dominating quinone (Tonon et al. 2014). Most members contain carotenoids (Huang et al. 2015), and several members could biosynthesize bacteriochlorophyll a (BChl a) (Shiba and Simidu 1982; Yurkov et al. 1994), which are also known as aerobic anoxygenic phototrophic bacteria (AAPB), can harvest light energy, and play a significant role in the carbon cycling of the oceans globally (Li et al. 2017b).

Hereby, we report a bacterium of the family Erythrobacteraceae, designated HHU K3-1 T, which was isolated from the surface water of the Yellow Sea of China. On the basis of data from the average nucleotide identity (ANI) values, digital DNA–DNA hybridization (dDDH), AAI and evolutionary distance between strain HHU K3-1 T and closely related members of the family Erythrobacteraceae, strain HHU K3-1 T should be considered to represent a novel genus within the family Erythrobacteraceae.

Material and methods

Bacteria isolate and culture conditions

Strain HHU K3-1 T was isolated from a surface water sample collected from the Yellow Sea of China (32°30.11’N, 122°18.89’E). Generally, 0.1 mL sea water was spread on 2216E medium (Solarbio, China) immediately after the water sample was collected. The plate was incubated at 28 °C for 7 days, and single colonies were selected and cultivated on 2216E plates. The strain HHU K3-1 T was maintained on 2216E medium and stored as aqueous glycerol suspensions (20%, v/v) at −80 °C. Ppb. aurantiacus MCCC 1A09962 T and Pel. marensis KCTC 22370 T were used as reference strains for morphological, physiological, biochemical and chemotaxonomic analyses under the same experimental conditions as strain HHU K3-1 T. Strains Ppb. aurantiacus MCCC 1A09962 T and Pel. marensis KCTC 22370 T were provided by the Marine Culture Collection of China (MCCC) and Korean Collection for Type Cultures (KCTC), respectively.

Phylogenetic and genome sequence analysis

Genomic DNA of HHU K3-1 T was extracted by using the Ezup Column Bacteria Genomic DNA Purification Kit (Sangon Biotech, China) according to the manufacturer’s instructions. The 16S rRNA gene was amplified with universal bacterial primers 27F and 1492R as described previously (Weisburg et al. 1991). The analysis of the 16S rRNA gene sequences of the strains was performed on the EzBioCloud server (https://www.ezbiocloud.net/) (Yoon et al. 2017). As for phylogenetic analysis, the neighbor-joining (NJ) (Saitou and Nei 1987), maximum-likelihood (ML) (Felsenstein 1981) and maximum-parsimony (MP) (Fitch 1971) methods were used to construct phylogenetic tree in the MEGA X software package (Kumar et al. 2018) after multiple alignments of sequences. Kimura’s two parameter model (Kimura 1980) was used to calculate evolutionary distance matrices of the phylogenetic trees. A bootstrap analysis with 1,000 replicates was also performed (Felsenstein 1985).

Genome sequencing of strain HHU K3-1 T was carried out at Magigene company, Guangzhou, China. Genome assembly and gap filling were done using SPAdes version 3.13.0 (Nurk et al. 2013) in UGENE.
software package (Okonechnikov et al. 2012). The ANI based on BLAST (OrthoANIb) was calculated on the EzBioCloud server (https://www.ezbiocloud.net/) (Richter and Rossello-Mora 2009; Yoon et al. 2017). The digital DNA–DNA hybridization (dDDH) values were calculated using the Genome-to-Genome Distance Calculator (GGDC) available at https://ggdc.dsmz.de (Meier-Kolthoff et al. 2013). Formula 2 was used for the dDDH analysis. AAI value was calculated on web server (http://enve-omics.ce.gatech.edu/aai/) (Qin et al. 2014). The whole genome sequences of the strains were annotated using the NCBI Prokaryotic Genome Annotation Pipeline (Tatusova et al. 2016) and eggNOG online server (https://eggnog-mapper.embl.de/) (Huerta-Cepas et al. 2017). DNA G + C content was determined according to the genome sequences.

In order to construct a robust phylogeny, a tree based on the concatenation of the 288 orthologous clusters (OCs) defined among the family Erythrobacteraceae in our previous study (Xu et al. 2020), was inferred by using EasyCGTree software package (https://github.com/zdf1987/EasyCGTree) under Windows operation system (OS), of which the algorithm was originally introduced by Zhang et al. (2020). EasyCGTree under Windows OS integrates blast (Altschul et al. 1997) for gene calling, muscle (Edgar 2004) for sequence alignment and FastTree (Price et al. 2009) for phylogeny construction, while it employs Clustal Omega (Sievers et al. 2011) instead for sequence alignment under Linux OS. The protein sequences of the 288 OCs from *Ppb. aurantiacus* MCCC 1A09962 T (Assembly No. GCA_009827635.1) were retrieve from our previous study (Xu et al. 2020) and used as reference for homolog searching of strain HHU K3-1 T. The evolutionary distance was calculated by using IQ-Tree 1.6.1 software (Nguyen et al. 2015) and LG + F + R9 substitution models, based on the concatenated protein sequences of the 288 OCs defined among the family Erythrobacteraceae in our previous study (Xu et al. 2020).

Morphology, physiology, and biochemical analysis

Gram staining was performed using the Gram Stain kit (G1060, Solarbio, China) according to the manufacturer’s instructions. The temperature range for growth were tested at 4, 10, 20, 28, 37 42 °C on 2216E plates. The salt tolerance range were tested at different NaCl concentrations (0%, 0.5%, 1%, 2%, 3%, 5%, 7%, 10% and 12%, w/v) and pH tolerance range were determined at different pH (pH 4.0–10.0, at intervals of 1.0 unit) in 2216E medium. Motility was determined by observing growth of cells in test tubes containing semisolid 2216E medium with 0.5% agar after 3 days of incubation at 28 °C (Cowan and Steel 1996). Other physiological and biochemical characterization were performed using the Biolog GEN III microtest system (Biolog, USA), API 20NE and API ZYM systems (bioMérieux, France) according to the manufacturer’s instructions.

Chromatographic characterization

Cells of strain HHU K3-1 T and the reference type strains were harvested from cultures grown on 2216E liquid medium for 2 days at 28 °C. Cellular fatty acids were extracted and analyzed according to the method described by the Sherlock Microbial Identification (Sasser 1990). Respiratory quinone was purified (Hiraishi et al. 1996) and analyzed by HPLC (Tamaoka 1986). Polar lipids were examined by using two dimensional thin-layer chromatography according to the previously described method (Collins and Jones 1981; Minnikin et al. 1984).

Results and discussion

Genomic features and phylogenetic analysis

Based on the analysis of the 16S rRNA gene sequences on EzBioCloud server, strain HHU K3-1 T should belonged to the family Erythrobacteraceae and showed highest similarity with *Pel. marenis* KCTC 22370 T (97.6%), which was the only taxon with a similarity > 97%. Phylogenetic trees based on 16S rRNA gene using NJ, ML and MP algorithms, all indicated that strain HHU K3-1 T clustered with *Ppb. aurantiacus* MCCC 1A09962 T (16S rRNA gene similarity 96.7%) and *Apb. maritimus* HME 9302 T (95.4%) (Fig. 1, S1 and S2). However, this phylogeny was not well supported (bootstrap value < 70%) in all three trees.

Whole Genome Shotgun project of strain HHU K3-1 T has been performed and the genome sequence was
deposited at GenBank/EMBL/DDBJ under the accession number JABWGVO000000000. The draft genome sequence of strain HHU K3-1 \( ^\text{T} \) was 2,939,611 bp in length with 23 contigs, and the genome G + C content was 0.02.
was 62.1%. And there was no photosynthesis gene cluster (PGC) present in the genome based on eggNOD online annotation result. As for the phylogenetic tree based on the 288 OCs, all the clades were well supported (bootstrap value > 70%) (Fig. 2). Different from the phylogenetic relationships based on 16S rRNA gene, strain HHU K3-1T formed a clade with 
P. aurantiacus MCCC 1A09962T, while A.p. maritimus HME 9302T and P. marensis KCTC 22370T were distant. Such a disagreement between phylogenetic trees based on 16S rRNA gene and core/house-keeping gene sets in the family Erythrobacteraceae have been well characterized previously (Xu et al. 2020), and the trees based on core/house-keeping gene sets are considered more reliable. In this study, the tree of the family Erythrobacteraceae based on the 288 OCs showed a very similar topology with the tree based on 288 single-copy orthologous clusters (Xu et al. 2020), and the trees based on core/house-keeping gene sets are considered more reliable. In this study, the tree of the family Erythrobacteraceae based on the 288 OCs showed a very similar topology with the tree based on 288 single-copy orthologous clusters (Xu et al. 2020). The ANI value between strain HHU K3-1T and P. marensis KCTC 22370T was 73.6% (Table 1), which was significantly lower than the threshold value of the species boundary (95–96%) (Richter and Rossello-Mora 2009). While, dDDH value (results from the recommended formula 2) between strain HHU K3-1T and P. marensis KCTC 22370T was 18.5% (Table 1), which is also lower than the proposed and generally accepted species boundaries of 70% (Goris et al. 2007). For the family Erythrobacteraceae, it was proposed that the AAI value of < 70% and evolutionary distance of > 0.4 based on the 288 OCs be used to define different genera (Xu et al. 2020). Therefore, we further analyzed the pairwise AAI and evolutionary distance between strain HHU K3-1T and close related taxa as previously described method (Xu et al. 2020). The AAI values between HHU K3-1T and P. aurantiacus MCCC 1A09962T, A.p. maritimus HME 9302T and P. marensis KCTC 22370T were 67.1%, 67.2% and 68.5%, respectively, while the evolutionary distances were 0.43, 0.68 and 0.61, respectively. According to the analysis of phylogeny, ANI, dDDH, AAI and evolutionary distance, strain HHU K3-1T should represent a novel genus in the family Erythrobacteraceae.

Physiology, and biochemical analysis

Cells of strain HHU K3-1T were Gram-staining negative, aerobic, nonmotile, catalase- and oxidase-positive. Optimal growth was observed at pH 7.0, at 28 °C and with 2% (w/v) NaCl. In the API ZYM tests, HHU K3-1T was positive for acid phosphatase, alkaline phosphatase, esterase (C4), esterase lipase (C8), leucine arylamidase, naphthol-AS-BI-phosphohydrolase and a-chymotrypsin, but negative for cystine arylamidase, lipase (C14), N-acetyl-beta-glucosaminidase, trypsin, valine arylamidase, a-fucosidase, a-galactosidase, a-glucosidase, a-mannosidase, beta-galactosidase, beta-glucosidase and beta-glucuronidase. In the API 20NE tests, HHU K3-1T was only positive for hydrolysis of esculin, but negative for arginine dihydrolase, D-glucose fermentation, indole production, hydrolysis of urea and gelatin, nitrate reduction and 4-nitrophenyl beta-D-galactopyranoside. As for assimilation, HHU K3-1T could not assimilate adipic acid, capric acid, D-glucose, D-maltose, D-mannitol, D-mannose, L-arabinose, malic acid, N-acetylglucosamine, phenylacetic acid, potassium gluconate, and trisodium citrate. In the BIOLOG GEN III tests, HHU K3-1T was positive for utilization of acetic acid, acetoacetic acid, L-glutamic acid, tween 40, was
resistant to nalidixic acid, and could utilize L-pyroglutamic acid (Table 2).

Chemotaxonomic characterization

The total cellular fatty acids of strain HHU K3-1 $^T$ and its most related species were shown in Table S1. The predominant fatty acids (> 10% of the total fatty acids) of strain HHU K3-1 $^T$ were summed feature 8 ($C_{18:1\omega 7c}/C_{18:1\omega 6c}$) (33.5%), $C_{17:1\omega 6c}$ (24.0%) and summed feature 3 ($C_{16:1\omega 7c}/C_{16:1\omega 6c}$) (12.3%). The major polar lipid of strain HHU K3-1 $^T$ were diphosphatidylglycerol (DPG), phosphatidylethanolamine (PE), phosphatidylglycerol (PG) and sphingoglycolipid (SGL), which is similar to those of the closely related type strains *Parapontixanthobacter aurantiacus* MCCC 1A09962 $^T$ and *Pelagerythrobacter marensis* KCTC 22370 $^T$. In addition, two unknown phospholipid and one unidentified lipid were also detected. The major respiratory quinone of strain HHU K3-1 $^T$ was ubiquinone-10, which is common in the species of the genus *Altererythrobacter* and other genera (Feng et al. 2015).

**Table 2** Differential characteristics between strain HHU K3-1 $^T$ and closely related species

| Characteristic          | 1                     | 2                     | 3                     |
|-------------------------|-----------------------|-----------------------|-----------------------|
| Colony colour           | Orange                | Orange                | Yellow                |
| Optimum temperature     | 28 °C                 | 28 °C                 | 28 °C                 |
| Optimum NaCl (%)        | 1–3                   | 3                     | 0.5–5                 |
| Optimum pH              | 7.0                   | 8.0                   | 6.0–8.0               |
| Assimilation of         |                       |                       |                       |
| L-arabinose             | –                     | +                     | –                     |
| Malic acid              | –                     | –                     | +                     |
| Enzyme activities       |                       |                       |                       |
| Valine arylamidase      | –                     | +                     | –                     |
| Cystine arylamidase     | –                     | +                     | –                     |
| Trypsin                 | –                     | +                     | –                     |
| Predominant fatty acids (> 10%) | Summed feature 8 | Summed feature 8 | Summed feature 8 |
|                         | Summed feature 3     | Summed feature 3     | 11-methyl-$C_{18:1\omega 7c}$ |
| Diagnostic phospholipids| DPG, PE, PG, SGL, GL, PL, L | DPG, PE, PG, SGL, GL, L | DPG, PE, PG, SGL, PL, L |
| DNA G + C content (%)   | 62.1                  | 56.9                  | 63.1                  |

**Taxa:** 1, HHU K3-1 $^T$; 2, *Parapontixanthobacter aurantiacus* MCCC 1A09962 $^T$; 3, *Pelagerythrobacter marensis* KCTC 22370 $^T$  

**Summed Feature 3 consists of $C_{16:1\omega 7c}/C_{16:1\omega 6c}$; summed feature 8 consists of $C_{18:1\omega 7c}$ and/or $C_{18:1\omega 6c}$;**

$DPG$ diphosphatidylglycerol, $PE$ phosphatidylethanolamine, $PG$ phosphatidylglycerol, $SGL$ sphingoglycolipid, $GL$ unidentified glycolipid, $PL$ unidentified phospholipid, $L$ unidentified lipid

**Conclusion**

The ANIb and dDDH analysis between HHU K3-1 $^T$ and close related species were all below the generally accepted species boundaries 95%–96% and 70%, respectively (Table 1). The AAI analysis between HHU K3-1 $^T$ and close related genera also showed pairwise AAI values of < 70% and evolutionary distances of > 0.40, which was proposed to define different genera in the family *Erythrobacteraceae* (Xu et al. 2020). The major fatty acids (> 10%) of strain HHU K3-1 $^T$ were summed feature 8 ($C_{18:1\omega 7c}/C_{18:1\omega 6c}$), summed feature 3 ($C_{16:1\omega 7c}/C_{16:1\omega 6c}$) and $C_{17:1\omega 6c}$ (Table S1). Nevertheless, those of *Parapontixanthobacter aurantiacus* MCCC 1A09962 $^T$ were summed feature 3 ($C_{16:1\omega 7c}/C_{16:1\omega 6c}$), $C_{16:0}$ and summed feature 8 ($C_{18:1\omega 7c}/C_{18:1\omega 6c}$), and those of *Pelagerythrobacter marensis* KCTC 22370 $^T$ were summed feature 8 ($C_{18:1\omega 7c}/C_{18:1\omega 6c}$).
Fig. 2 Maximum-likelihood phylogenetic tree based on the 288 orthologous clusters (OCs) showing the position of strain HHU K3-1T. Bootstrap values are shown at the branch points nodes. GenBank accession number or whole genome shotgun (WGS) project number is indicated in the bracket. *Rhodospirillum rubrum* ATCC 1170T is used as out group. Bar, 0.1 substitutions per nucleotide position.
C₁₈:₁₆c) and 11-methyl-C₁₈:₁₀₇c. Strain HHU K₃₋₁ T contained respiratory ubiquinone-10 as the main respiratory quinone, which was consistent with the other members of the family Erythrobacteraceae. As for polar lipids, strain HHU K₃₋₁ T and the close related genera all contained diphosphatidylglycerol (DPG), phosphatidylethanolamine (PE), phosphatidylglycerol (PG) and sphingoglycolipid (SGL). On the basis of phylogenetic, phenotypic and chemotaxonomic data, strain HHU K₃₋₁ T should be proposed as a novel genus within the family Erythrobacteraceae, for which the name Actirhodobacter atriluteus gen. nov., sp. nov. is proposed.

Description of Actirhodobacter gen. nov.

Actirhodobacter (Ac.ti.rho.do.bac’ter. L. fem. n. acta, seaside, shore; Gr. neut. n. rhodon, the rose; N.L. masc. n. bacter, rod; N.L. masc. n. Actirhodobacter, red-colored rod from the seaside).

Cells are Gram-staining-negative, non-motile, aerobic and have no soluble pigments. Colonies are orange, smooth and opaque. The dominant respiratory quinone is ubiquinone-10. The major polar lipids are diphosphatidylglycerol (DPG), phosphatidylethanolamine (PE), phosphatidylglycerol (PG) and sphingoglycolipid (SGL). The genomic G + C content is 62.1%. As determined by 16S rRNA gene sequence analysis, the genus is a member of the family Erythrobacteraceae, class Alphaproteobacteria. The type species is Actirhodobacter atriluteus.

Description of Actirhodobacter atriluteus sp. nov.

Actirhodobacter atriluteus (at.ri.lu’te.us. L. mas. adj. ater dark; L. masc. adj. luteus yellow-orange; N.L. masc. adj. atriluteus dark orange).

Cells are Gram-stain-negative, non-motile and aerobic. After incubation on 2216E agar for 3 days. Colonies are orange, smooth and opaque. Growth occurs at 28–37 °C (optimum 28 °C), at pH 6.0–8.0 (optimum pH 7.0) and in the presence of NaCl concentrations of 0.5–5% (optimum 1–3%). The predominant respiratory quinone is ubiquinone-10. The major polar lipids are diphosphatidylglycerol (DPG), phosphatidylethanolamine (PE), phosphatidylglycerol (PG) and sphingoglycolipid (SGL), two unknown phospholipid and one unidentified lipid. The predominant fatty acids (>10%) were summed feature 8 (C₁₈:₁₀₇c/C₁₈:₁₀₆c), C₁₇:₁₀₆c and summed feature 3 (C₁₆:₁₀₇c/C₁₆:₁₀₆c).

The type strain, HHU K₃₋₁ T (= MCCC 1K04225 T = KCTC 72834 T = CGMCC 1.17395 T), was isolated from the surface water of Yellow Sea, China. The DNA G + C content is 62.1%.

The 16S rRNA gene sequence has been deposited at GenBank/EMBL/DDBJ accession number MW172823, while the genome sequence has been deposited at GenBank/EMBL/DDBJ under accession number JABWGV000000000.

Author’s contributions DFZ designed research and project outline. HPX, DFZ, and LX performed isolation, deposition and polyphasic taxonomy. DFZ, XNW and HPX performed genome analysis. HPX, DFZ, XNW and AHZ drafted the manuscript. JKH and CL revised the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials Most of the data supporting the conclusions of this article are included within the article and its additional files. The genome datasets and the 16S rRNA gene sequence of Actirhodobacter atriluteus HHU K₃₋₁ T generated during the current study are available in the GenBank repository under accession number JABWGV000000000 and MW172823, respectively. Other datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

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