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ORIGINAL PAPER

Genomic potential for inorganic carbon sequestration and xenobiotic degradation in marine bacterium *Youngimonas vesicularis* CC-AMW-E^T affiliated to family *Paracoccaceae*

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Abstract Ecological studies on marine microbial communities largely focus on fundamental biogeochemical processes or the most abundant constituents, while minor biological fractions are frequently neglected. *Youngimonas vesicularis* CC-AMW-E^T, isolated from coastal surface seawater in Taiwan, is an under-represented marine *Paracoccaceae* (earlier *Rhodobacteraceae*) member. The CC-AMW-E^T genome was sequenced to gain deeper insights into its role in marine carbon and sulfur cycles. The draft genome (3.7 Mb) contained 63.6% GC, 3773 coding sequences and 51 RNAs, and displayed maximum relatedness (79.06%) to *Thalassobius litoralis* KU5D5^T, a *Roseobacteraceae* member. While phototrophic genes were absent, genes encoding two distinct subunits of carbon monoxide dehydrogenases (CoxL, BMS/Form II and a novel form III; CoxM and CoxS), and proteins involved in HCO_3^- uptake and interconversion, and anaplerotic HCO_3^- fixation were found. In addition, a gene coding for ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO, form II), which fixes atmospheric CO_2 was found in CC-AMW-E^T. Genes for complete assimilatory sulfate reduction, sulfide oxidation (sulfide:quinone oxidoreductase, SqrA type) and dimethylsulfoniopropionate (DMSP) cleavage (DMSP lyase, DddL) were also identified. Furthermore, genes that degrade aromatic hydrocarbons such as quinate, salicylate, salicylate ester, p-hydroxybenzoate, catechol, gentisate, homogentisate, protocatechuate, 4-hydroxyphenylacetic acid, *N*-heterocyclic aromatic compounds and aromatic amines were present. Thus, *Youngimonas vesicularis* CC-AMW-E^T is a potential chemolithoautotroph equipped with genetic machinery for the metabolism of aromatics, and predicted to play crucial roles in the biogeochemical cycling of marine carbon and sulfur.

Keywords RuBisCO · Carbon monoxide dehydrogenase · Dimethylsulfoniopropionate lyase · Sulfide:quinone oxidoreductase · HCO_3^- transporter

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Introduction

Several members of marine bacterial clades/groups that are numerically important in coastal seawater and sediments have been well characterized for their role in marine carbon and/or sulfur cycle (Swan et al. 2011; Newton et al. 2010; Sorokin 2003; González et al. 1999). *Roseobacter* genomes include genes dedicated to the oxidation of carbon monoxide, demethylation of dimethylsulfoniopropionate (DMSP), and aromatic compound degradation (Moran et al. 2007). Analysis of culturable representatives in vitro validated the metabolic flexibility of the members of one of the dominant clades (Moran et al. 2004). Nonetheless, the ecological role played by minority bacterial communities inhabiting benthic and pelagic oceans has been often neglected.

The marine bacterium *Youngimonas vesicularis* CC-AMW-E^T, originally classified under the family *Rhodobacteraceae,* was recently moved along with several other members to the newly established family *Paracoccaceae* (Liang et al. 2021). While NCBI enlists 96 genera (https://www.ncbi.nlm.nih.gov/datasets/taxonomy/31989/), the List of Prokaryotic names with Standing in Nomenclature (Parte et al. 2020) (LPSN, https://lpsn.dsmz.de/family/paracoccaceae) lists 62 validly published type species under the family *Paracoccaceae* (https://lpsn.dsmz.de/family/paracoccaceae). Bacterial strains currently classified under *Paracoccaceae* are widespread in occurrence, and have been isolated from saline terrestrial habitats (Subhash et al. 2013; Wang et al. 2019; Hu et al. 2018), and marine environments such as deep sea (Wei et al. 2023; Kong et al. 2022), shallow sea sediments (Romanenko et al. 2021), seawater (Lim et al. 2008) and sea creatures (Sun et al. 2022; Kim et al. 2021). Few strains were isolated from clinical specimen (Helsel et al. 2007), non-saline aquatic (Li and Zhou 2015) and estuarine (Hameed et al. 2020a, b) habitats. Some strains are inhabitants of extreme environments like sulfidic hydrothermal area (Sorokin et al. 2005), soda lake (Milford et al. 2000) and hot-springs (Albuquerque et al. 2002; Yin et al. 2013). Strains may produce bacteriochlorophyll a (Labrenz et al. 2009; Sorokin et al. 2000), exhibit denitrification (Xu et al. 2021), and metabolize inorganic sulphur/carbon (Hameed et al. 2020a, b; Sorokin et al. 2005; Robertson and Kuenen 1983) and aromatic hydrocarbon (Wang et al. 2019).

At present, the genus *Youngimonas* accommodates one species (https://lpsn.dsmz.de/species/youngimonas-vesicularis). Similarly, most of the genera that have been classified under *Paracoccaceae* carry few species. This could be due to the difficulty of growing related strains under laboratory conditions owing to our poor understanding of their ecology and niche (Pohlner et al. 2019). Exploring the ecological functions of this minority population may assist in future taxonomic investigation besides opening new channels for biotechnology and bioremediation. Thus, the genetic makeup of *Youngimonas vesicularis* CC-AMW-E^T was investigated.

Materials and methods

Strain CC-AMW-E^T (=JCM 18819 ^{T}=BCRC 80549 ^{T}) was revived from −80 °C and cultured on marine agar (BD Difco 2216) or marine broth (BD Difco 2216) for 48–72 h at 30 °C. Gram staining was performed according to Murray et al. (1994). Fluorescence, transmission electron and scanning electron microscopic analyses were performed as described earlier (Hameed et al. 2020a, b).

Purified genomic DNA was prepared using the Wizard DNA purification kit (Promega), and sonicated (10 µg) using a Misonix 3000 sonicator to obtain DNA fragments of the size 400−500 bp. The size of the fragments was checked by the Bioanalyzer DNA 1000 chip (Agilent Technologies). Sonicated DNA (1 µg) was end-repaired, A-tailed and adaptor-ligated according to the Illumina TruSeq DNA preparation protocol. Samples were prepared with the MiSeq Reagent Kit v3 (600-cycle) after library construction and loaded onto a MiSeq cartridge. A 2×300 bp paired-end sequencing run was performed using the MiSeq platform (Illumina, San Diego, CA, USA). The raw paired-end reads were trimmed and filtered using Trimmomatic (Bolger et al. 2014) to obtain high-quality reads. The SPAdes genome assembler (Bankevich et al. 2012) was used for de novo genome assembly.

Genes of interest were identified using RAST (Aziz et al. 2008). Genomic relatedness was estimated using the Orthologous Average Nucleotide Identity (OrthoANI) application of EzBioCloud (Lee et al. 2016). Amino acid identity (AAI) was calculated using the enveomics collection, available

at http://enve-omics.ce.gatech.edu/aai/ (Rodriguez-R and Konstantinidis 2016). An up-to-date bacterial core gene set (UBCG) analysis, which utilizes a set of 92 single-copy core genes (Na et al. 2018), was conducted for CC-AMW-E^T. The core genes were extracted from genomes of interest using Prodigal (Hyatt et al. 2010) and hmmsearch (Eddy 2011), aligned using MAFFT (Katoh and Standley 2013) and concatenated into a single alignment. The core gene tree was constructed using FastTree (Price et al. 2010) and RAxML (Stamatakis 2014) through the built-in pipeline, and visualized through MEGA X software. For this analysis and for genome visualization using Proksee (Grant et al. 2023), nine currently available whole genomes of type strains of *Rhodobacterales* that shared the highest pair-wise 16S rRNA gene sequence similarity were used in addition to CC-AMW-E^T genome. The protein identity was verified through UniProt (UniProt 2023). The carbohydrate active enzymes (CAZymes) were identified through the dbCAN2 Meta server (http://cys.bios.niu.edu/dbCAN2/index.php; Zhang et al. 2018). Sulfatases were screened through SulfAtlas (http://sulfatlas.sb-roscoff.fr/; Barbeyron et al. 2016).

Results and discussion

Morphological characteristics and genomic relatedness

Cells of *Youngimonas vesicularis* CC-AMW-E^T were found to be pleomorphic (Fig. 1a–d). This is in line with the phenotype reported in a closely related strain (Iwaki et al. 2013) and some other *Rhodobacterales*. A circular map showing genomic features of CC-AMW-E^T is depicted in Fig. 2a. The draft genome consists of 47 contigs containing 37,95,539 bp, 63.6% GC content, 3773 coding sequences and 51 RNA genes. Genomic relatedness between CC-AMW-E^T and other closely related type strains (based on pairwise 16S rRNA gene sequence similarity) of the order *Rhodobacterales* was investigated through UBCG and orthologous average nucleotide identity (OrthoANI). Phylogenetic tree based on UBCG data (Fig. S1) showed strong phyletic association of CC-AMW-E^T with *Thalassobius litoralis* (formerly *Lutimaribacter litoralis*), a marine cyclohexylacetate-degrading pleomorphic bacterium affiliated to the family *Roseobacteriaceae* isolated from coastal seawater of Japan (Iwaki et al. 2013; Hördt et al.

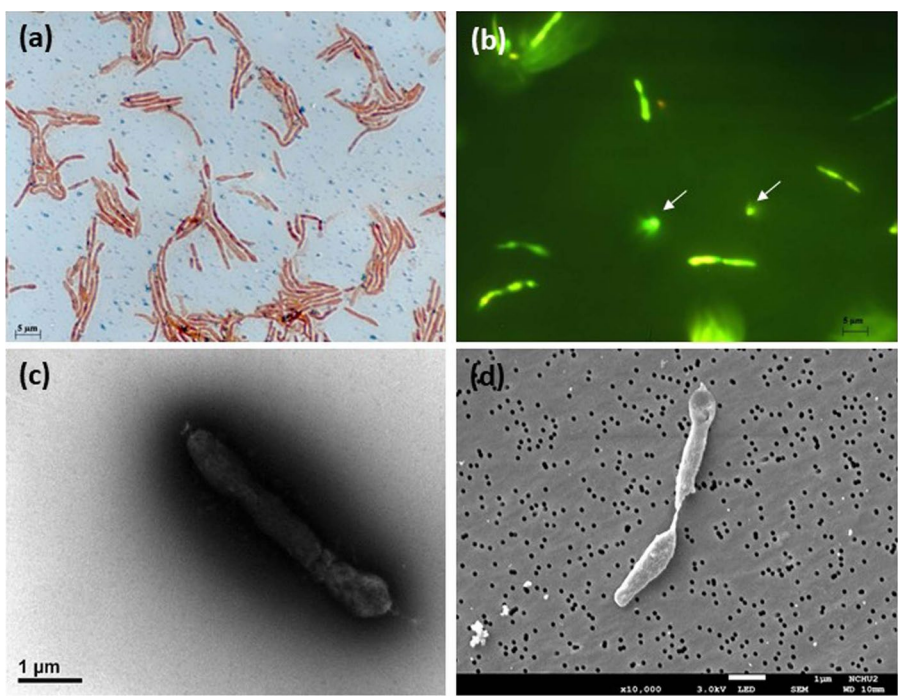

Fig. 1 Micrographs of cells of *Youngimonas vesicularis* CC-AMW-E^T. Light microscopic image of Gram-stained cells (**a**); epifluorescence microscopic image (**b**). transmission electron microscopic image of negatively stained cells (**c**); scanning microscopic image (**d**); Cells were grown in marine broth (BD Difco 2216) at 30 °C for 24 h under darkness. Scale bar: 5 µm (a and b); 1 µm (c and d); Arrow, vesicle

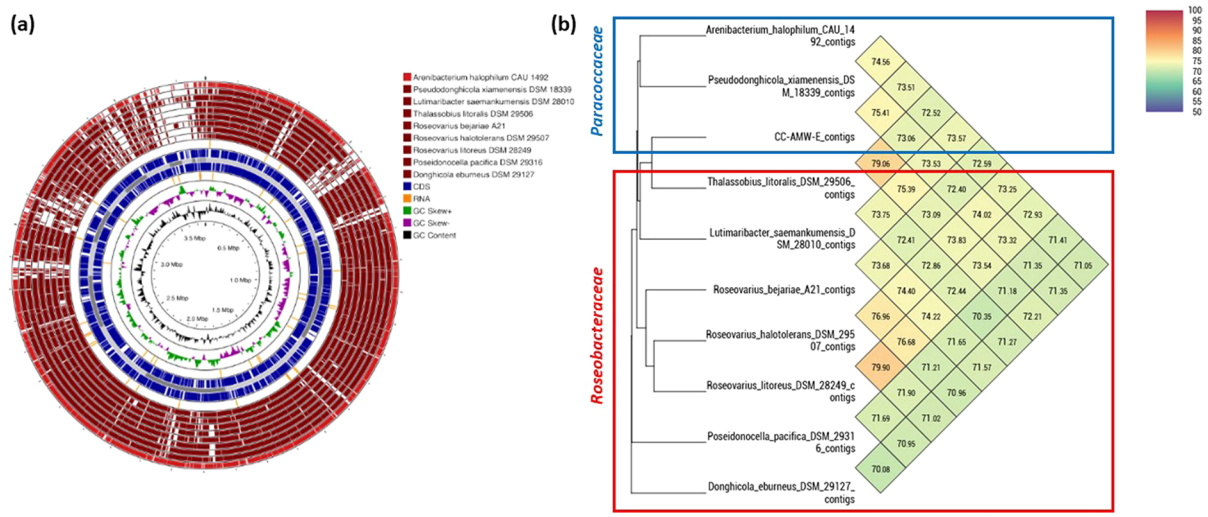

Fig. 2 Genomic features of *Youngimonas vesicularis* CC-AMW-E^T. Circular genome map of *Youngimonas vesicularis* CC-AMW-E^T showing genome features, base composition, and similarity to closely related type strains (**a**). From center to the outside: GC content, GC skew, RNA genes on the reverse strand, coding sequences on the reverse strand, contigs (alternating colors), coding sequences on the forward strand, RNA genes on the forward strand, BLAST comparisons with closely related type strains of the order *Rhodobacterales*. The map was generated using the Proksee (Grant et al. 2023). OrthoANI heatmap showing genomic relatedness between CC-AMW-E^T and the same type strains (**b**)

2020). Furthermore, CC-AMW-E^T shared highest OrthoANI value (79.06%, Fig. 2b) and AAI value (81%, Fig. S2) with *Thalassobius litoralis* (Fig. 2b). These data indicated close genetic relatedness of CC-AMW-E^T and *Thalassobius litoralis.*

Carbohydrate-active enzymes and sulfatases

Analysis of the CC-AMW-E^T genome in dbCAN2 for genes encoding carbohydrate-active enzymes (CAZymes) revealed maximum genes dedicated to glycosyl transferases (GT, $n=42$), followed by glycosyl hydrolases (GH, $n=12$), auxiliary activities (AA, $n=10$) and carbohydrate esterases (CE, $n=4$). Genes coding for polysaccharide lyases and carbohydrate-binding modules were missing. Similarly, no significant hits were found for sulfatases. The CAZymes found in CC-AMW-E^T ($n=68$) were numerically lower as compared to that of *Alteromonas fortis* 1 ^{T} ($n=130$), isolated from marine alga (Rekha et al. 2023). While GH predominated in *A. fortis* 1 ^{T}, GT dominated in CC-AMW-E^T. Analysis of the genome at SulfAtlas revealed no significant hits for sulfatases. These data indicated poor biopolymer hydrolytic ability of CC-AMW-E^T.

Photosynthesis and phototrophy

The CC-AMW-E^T genome was screened for signature genes involved in photosynthesis. CC-AMW-E^T lacked genes for the photosynthetic reaction centre, bacteriochlorophyll synthesis, light-harvesting complexes, opsin aproprotein and 15,15'-β-carotene dioxygenase (codes for retinal), confirming the absence of both photosynthesis and rhodopsin-based phototrophy that could complement the heterotrophic lifestyle of CC-AMW-E^T (Table 1). The absence of genes coding for bacteriochlorophyll synthesis was in line with the UV−visible spectroscopy (Hameed et al. 2014).

Inorganic carbon concentration, interconversion and metabolism

The CC-AMW-E^T genome was screened for genes involved in inorganic carbon sequestration. First, genes involved in the metabolism of carbon monoxide (CO), a molecule that participates in a broader range of processes ranging from subcellular to planetary scales (King and Weber 2007), were considered. We found potential genes encoding for a smaller (CoxS, WP_136340385.1), a medium (CoxM, WP_136340383.1) and two larger

Table 1 Identification of genes involved in inorganic carbon and sulfur metabolism in *Youngimonas vesicularis* CC-AMW-E^T

Enzyme/protein	Code	Result	Locus tag
Photosynthesis			
Photosynthetic RC Large subunit	PufL	−	
Photosynthetic RC Medium subunit	PufM	−	
LHC 1 α	LH1	−	
LHC 1 α	LH2		
Opsin apoprotein	OA	−	
15,15'-β-carotene dioxygenase	Blh	−	
CO metabolism			
CODH small subunit	CoxS	+	WP_136340385.1
CODH medium subunit	CoxM	+	WP_136340383.1
CODH large subunit (BMS/Form II)	CoxL1	+	WP_136340384.1
CODH large subunit (Form III)	CoxL2	+	WP_136338228.1
CO2/ HCO3- metabolism			
Ribulose-bisphosphate carboxylase	RuBisCO	+	WP_136339082.1
SulP type transporter	BicA	+	WP_136339400.1
			WP_136339214.1
			WP_136339286.1
SbtA type transporter	SbtA	−	
Carbonic anhydrase	CA	+	WP_136339102.1
NADP-dep. malic enzyme	ME	+	WP_136337805.1
			WP_136339705.1
PEP carboxykinase	PEPCK	+	WP_136337394.1
PEP carboxylase	PEPC	−	
Pyruvate carboxylase	PC	+	WP_136339427.1
Assimilatory sulfate reduction			
Sulfate adenylyltransferase	SAT/AST	+	WP_136337378.1
Adenylyl-sulfate kinase	SAT/AST	+	WP_136337378.1
Phosphoadenylyl-sulfate reductase	PASR	+	WP_136339573.1
Ferredoxin:sulfite reductase (β subunit)	SRα	+	WP_136339574.1
Nitrite/sulfite reductase (α subunit)	SRβ	+	WP_136340332.1
Thioredoxin:NADPH reductase	TNR	+	WP_136337377.1
Ferredoxin:NADPH reductase	FNR	+	WP_136338995.1
Sulfide oxidation			
SQR (SqrA)	SqrA	+	WP_136338299.1

RC, reaction center; LHC, light-harvesting complex; CODH, carbon monoxide dehydrogenase; PEP, phosphoenolpyruvate; SQR, sulfide:quinone oxidoreductase; +, positive; −, negative

subunits of CO dehydrogenases (CoxL1 and CoxL2; WP_136340384.1 and WP_136338228.1, respectively) (Table 1). In the UniProt survey, CoxL1 shared the highest amino acid sequence similarity with *Actibacterium lipilyticus* (90.1%), and formed a tight phylogenetic cluster with BMS/Form II of the CoxL clade in the phylogenetic analysis (Fig. 3). In contrast, CoxL2 formed a separate cluster, distantly associated with BMS/Form II and OMP/Form I. Earlier studies on a subset of nine marine *Roseobacter* clade (MRC) strains revealed that only MRC strains with both CoxL forms can oxidize CO (Cunliffe 2011). BMS sequences represent functional CODH proteins that are related to but distinct from previously characterized aerobic CODH as evident through a study on *Mesorhizobium loti* (King 2003). In line with this, the abundance of genes encoding type 1 CODH was used as a marker to quantify soil CO sequestration (Quiza et al. 2014). Thus, CC-AMW-E^T is possibly a marine carboxydovore.

The CC-AMW-E^T genome was examined for genes involved in HCO_3^- transport and sequestration.

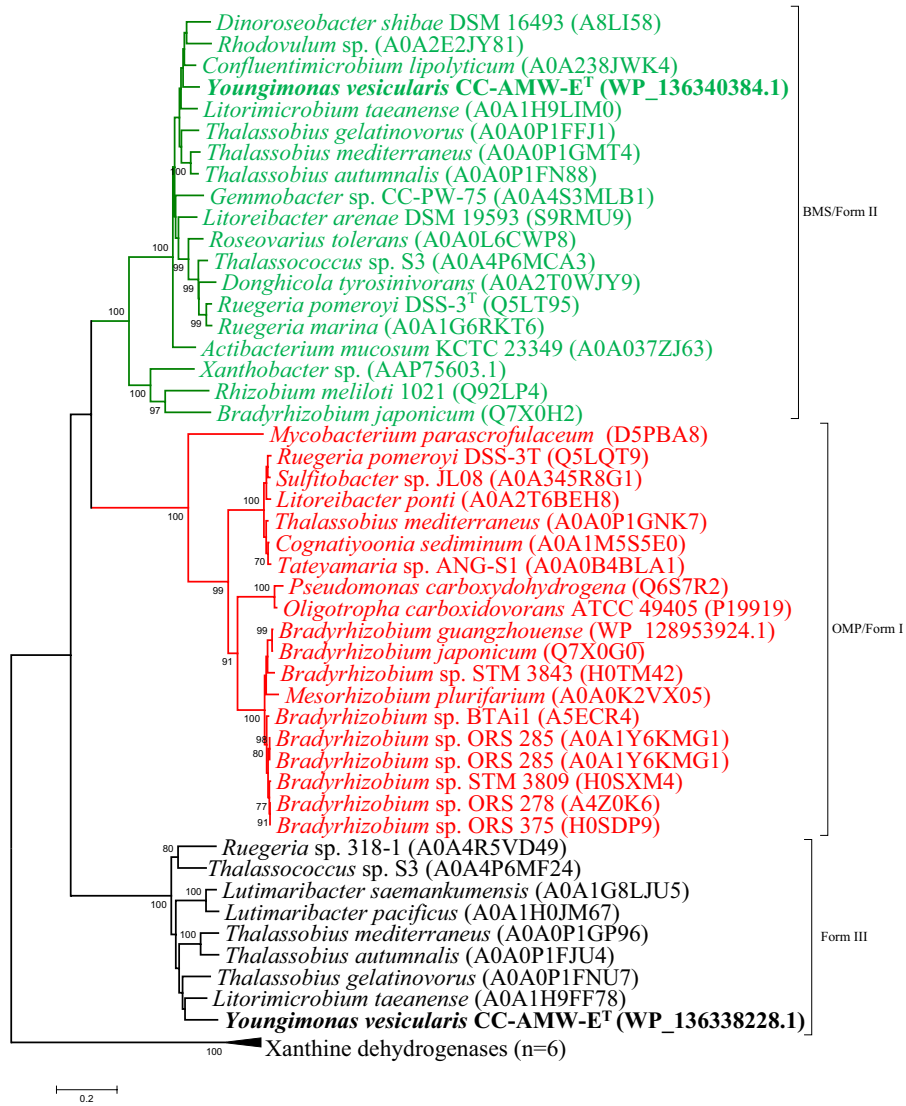

Fig. 3 Neighbor-joining tree of larger subunits of carbon monoxide dehydrogenase (CoxL) detected in *Youngimonas vesicularis* CC-AMW-E^T (highlighted in bold-phase letters) and other related CoxL homologs. The classification BMS/Form II (green fonts) and OMP/Form I (red fonts) are according to King (2003). Bootstrap values (> 70%) based on 1000 replications are shown at the nodes. The accession number of each sequence is shown in parentheses. The strain name followed by a superscript 'T' indicates type strain. Bar, 0.2 substitutions per position. Sequences of xanthine dehydrogenase of CC-AMW-E^T (WP_136339391.1) and four additional bacterial strains (A0A1H9GGY6, A0A0P1G2A4, A0A1M4Y7A1, A0A0X3TKM6) were used as an outgroup

CC-AMW-E^T has three copies of the gene encoding BicA (SulP-type Na^+-dependent HCO_3^- transporter) (Table 1). BicA reportedly has a low affinity for the substrate but has a high flux rate (Price et al. 2004). In contrast, the genome lacked a Na^+-dependent SbtA type HCO_3^- transporter that displays a high affinity towards HCO_3^- (Shibata et al. 2002). Phylogenetic analysis revealed three distinct clusters of CC-AMW-E^T BicA (Fig. 4). These HCO_3^- importer proteins are complemented by a gene coding for monomeric carbonic anhydrase that catalyzes reversible interconversion of CO_2 and HCO_3^- (Guilloton et al. 1992; González et al. 2008). Phylogenetic analysis of carbonic anhydrases showed clustering of CC-AMW-E^T within the clade that heterogeneously accommodated carbonic anhydrases from *Paracoccaceae* and *Roseobacteraceae* (Fig. S3).

A critical part of CO_2 fixation in autotrophs is concentrating carbonate, which could also be an essential step for anaplerotic CO_2 fixation in heterotrophs (González et al. 2008). The CC-AMW-E^T genome harbored a gene encoding pyruvate carboxylase involved in the ATP-dependent oxaloacetate formation from HCO_3^- and pyruvate. In addition, CC-AMW-E^T also possessed a gene encoding ribulose bisphosphate carboxylase (RuBisCO), involved in atmospheric CO_2 fixation directly into organic biomass through the Calvin-Benson-Basham pentose

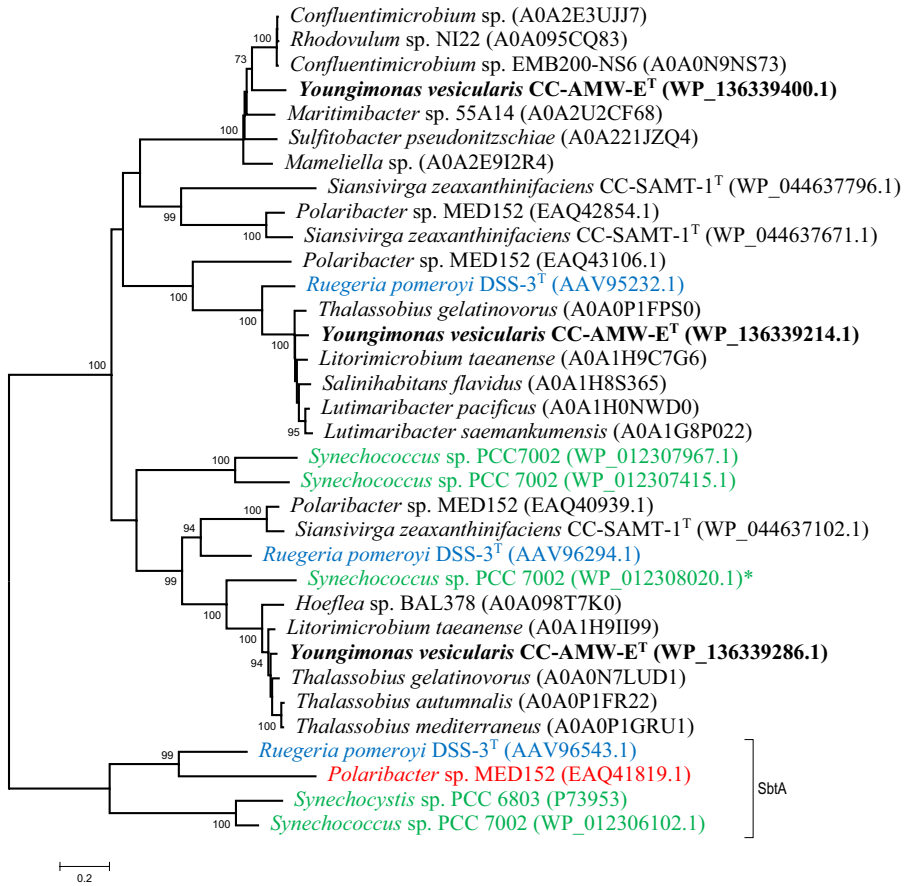

Fig. 4 Neighbor-joining tree showing phylogenetic relatedness of SulP-type HCO_3^- transporters detected in *Youngimonas vesicularis* CC-AMW-E^T (highlighted in bold-phase letters) and other selected bacterial strains. Low-affinity but high flux rate HCO_3^- transport activity (BicA) has been experimentally demonstrated in a Na^+-dependent SulP-type transporter of *Synechococcus* sp. PCC7002 (*Price et al. 2004). Bootstrap values (> 70%) based on 1000 replications are shown at the nodes. The accession number of each sequence is shown in parentheses. Bar, 0.2 substitutions per position. Photosynthetic cyanobacteria are highlighted in green; *Ruegeria pomeroyi*, a well-studied *Roseobacteraceae* member for carbon and sulfur metabolism is shown in blue. Amino acid sequences of Na^+-dependent SbtA-type high-affinity HCO_3^- transporter of *Polaribacter* sp. MED152 (highlighted in red), *Ruegeria pomeroyi* and photosynthetic cyanobacteria were used as outgroup

phosphate pathway. Phylogenetic analysis of the protein sequences indicated that CC-AMW-E^T RuBisCO belongs to form II reported in the photosynthetic purple non-sulfur bacteria *Rhodopseudomonas palustris* and *R. pentothenatexigens* (Fig. 5).

Sulfur metabolism

The CC-AMW-E^T genome was mined for the genes involved in the metabolism of sulfur-containing osmolyte dimethylsulfoniopropionate (DMSP). CC-AMW-E^T harbored a gene encoding DMSP lyase that shared 84.7% sequence similarity with the DddL form of DMSP lyase of *Thalassobius litoralis.* DddL catalyzes the transformation of DMSP to dimethylsulfide (DMS) (Curson et al. 2008), a climate-changing gas in the ocean. We further evaluated the inorganic sulfur oxidation ability of CC-AMW-E^T. A complete set of genes involved in the assimilatory sulfate reduction to sulfide were found in CC-AMW-E^T (Table 1). We also found a gene encoding sulfide:quinone oxidoreductase (SQR) that shared 83.4% amino acid similarity with the SQR of *Thalassobius teanensis*. SQR is essential for photoautotrophic growth on sulfide

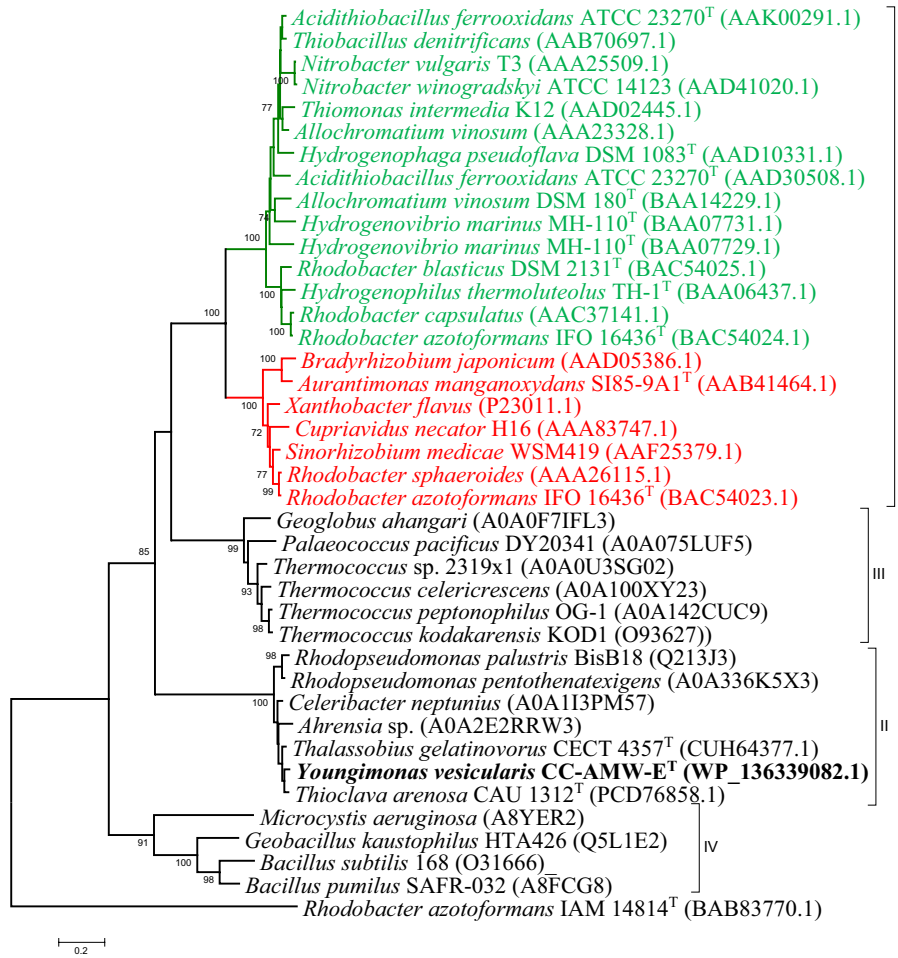

Fig. 5 Neighbor-joining tree of RuBisCO detected in *Youngimonas vesicularis* CC-AMW-E^T (highlighted in bold-phase letters) as compared to other RuBisCO homologs. The classification I, II, III and IV are according to Tabita et al. (2008). Phylogenetic positions of 'Green-like' and 'red-like' RuBisCO (Uchino and Yokota, 2003) affiliated to Form I are highlighted in green and red fonts, respectively. Bootstrap values (> 70%) based on 1000 replications are shown at the nodes. The accession number of each sequence is shown in parentheses. The strain name followed by a superscript 'T' indicates the type strain. Bar, 0.2 substitutions per position. The GyrB sequence of *Rhodobacter azotoformans* IAM 14814 ^{T} (BAB83770.1) was used as an outgroup

as determined by the analysis of deletion and interruption strains (Schütz et al. 1999). Bacterial SQR oxidize sulfide during sulfide-dependent chemo- and phototrophic growth (Chan et al. 2009). The detection of genes involved in assimilatory sulfate reduction and sulfide oxidation is in line with *Siansivirga zeaxanthinifaciens* CC-SAMT-1 ^{T}, a marine flavobacterium isolated from coastal seawater (Hameed et al. 2018). Our phylogenetic analysis revealed that the SQR of CC-AMW-E^T occupied the SqrA cluster (Fig. 6). Purple non-sulfur bacteria and *Cyanobacteria* usually harbor SqrA in addition to some *Proteobacteria* and *Aquificaceae* (Gregerson et al. 2011). SqrA includes the functionally well-characterized SQRs from *Oscillatoria limnetica* (Bronstein et al. 2000), *Rhodobacter capsulatus* (Schütz et al. 1999) and *Aquifex aeolicus* (Nübel et al. 2000; Marcia et al. 2009).

Aromatic hydrocarbon metabolism

The genes involved in the aromatic hydrocarbon degradation found in CC-AMW-E^T are summarized in Table S1. Key genes dedicated to the degradation of aromatic hydrocarbons such as quinate (3-dehydroquinate dehydratase), salicylate/salicylate ester (salicylate esterase), p-hydroxybenzoate (P-hydroxybenzoate hydroxylase), gentisate (gentisate 1,2-dioxygenase), homogentisate (homogentisate 1,2-dioxygenase), protocatechuate (protocatechuate 3,4-dioxygenase), *N*-heterocyclic aromatic compounds (isoquinoline 1-oxidoreductase) and aromatic amines (3,4-dihydroxyphenylacetate 2,3-dioxygenase) were found in CC-AMW-E^T. These data suggested that *Youngimonas vesicularis* CC-AMW-E^T is capable of metabolizing aromatic hydrocarbons in marine environments.

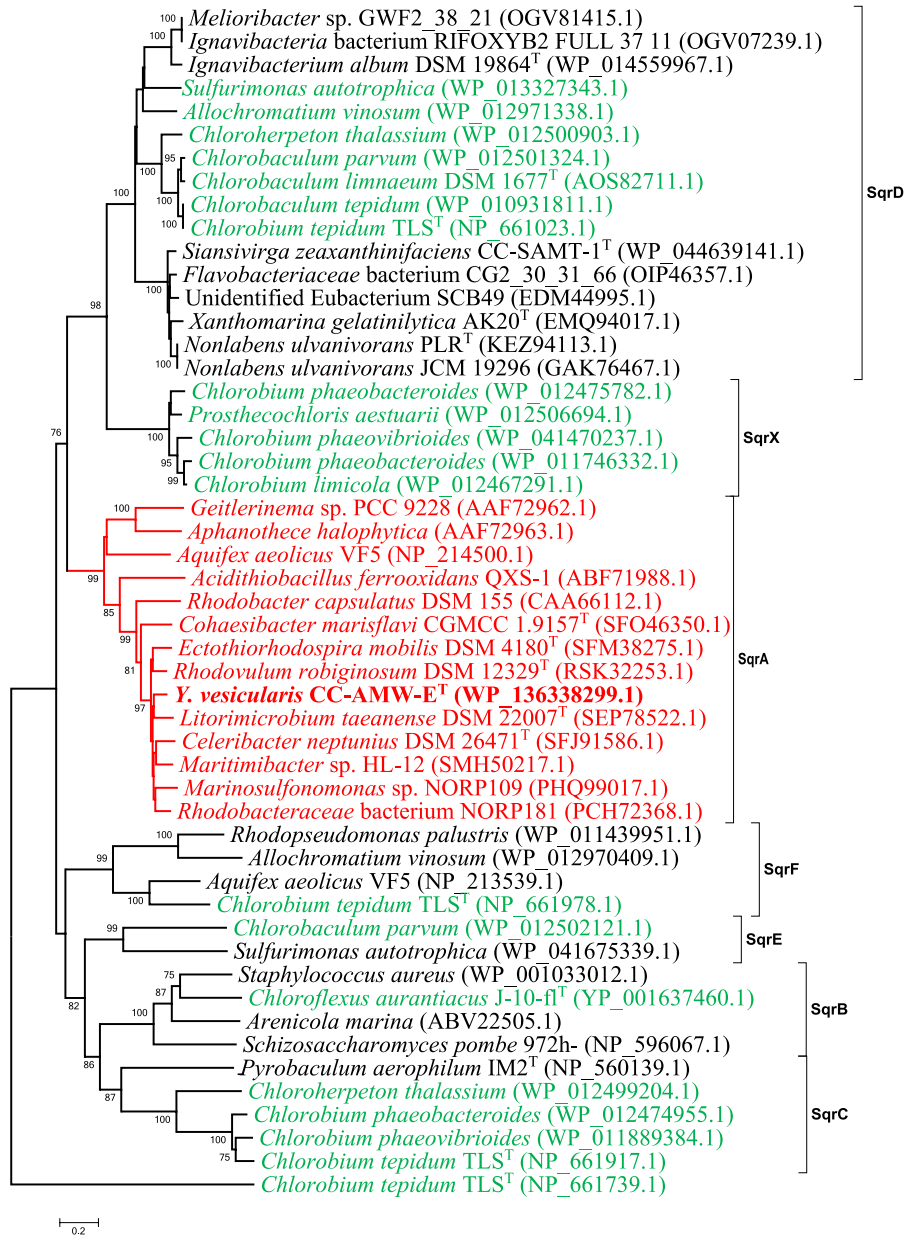

Fig. 6 Neighbor-joining tree of sulfide:quinone oxidoreductase (Sqr) detected in *Youngimonas vesicularis* CC-AMW-E^T (highlighted in bold-phase letters) and other related Sqr homologs. The classification SqrA (red fonts), SqrB, SqrC, SqrD, SqrE, SqrF and SqrX are according to Gregersen et al. (2011). Sequences from phylum *Chlorobi* (green sulfur bacteria) are shown in green. Bootstrap values (> 70%) based on 1000 replications are shown at the nodes. The accession number of each sequence is shown in parentheses. The strain name followed by a superscript 'T' indicates the type strain. Bar, 0.2 substitutions per position. Uncharacterized membrane protein YadS from *Chlorobium tepidum* TLS^T (NP_661739.1) was used as an outgroup

Conclusion

The presence of genes encoding all subunits of carbon monoxide dehydrogenase (CoxS, CoxM and CoxL), RuBisCO (atmospheric CO_2 fixation), HCO_3^- transporter (BicA), carbonic anhydrase (catalyzes the reversible interconversion of CO_2 and HCO_3^-) and anaplerotic inorganic carbon fixation enzymes (malic enzyme and pyruvate carboxylase) indicates a definite role played by CC-AMW-E^T in marine carbon cycling. Similarly, the detection of genes involved in assimilatory sulfate reduction, sulfide oxidation (SqrA) and DMSP metabolism reflects a possible role played by CC-AMW-E^T in marine sulfur cycling. Furthermore, the strain harbored genomic signatures for the degradation of xenobiotic aromatic organic compounds besides having the ability to utilize sole organic carbons in vitro (Hameed et al. 2014). Thus, *Youngimonas vesicularis* CC-AMW-E^T is a potential chemolithoautotroph adapted to metabolize inorganic

compounds (carbon monoxide, carbon dioxide and sulfide) to complement heterotrophy. Heterotrophic and lithoautotrophic dual-life strategies are likely to assist cells of CC-AMW-E^T in copiotrophic coastal waters and oligotrophic open oceans.

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Author contributions CCY and AH conceptualized the work. AH drafted the manuscript. AH, SKV and PS performed genomic data mining, annotation and comparative genomics. AH analyzed the data and restructured the manuscript with scientific input from all the authors. SYL performed AAI, UBCG and microscopic analysis. All the authors discussed the results and revised the manuscript.

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Data availability This whole-genome shotgun project for *Youngimonas vesicularis* CC-AMW-E^T has been deposited at DDBJ/ENA/GenBank under BioProject no. PRJNA531816, and the accession no. is SSMD00000000. The version described in this paper is the first version.

Declarations

Competing interests The authors declare no competing interests.

Conflict of interest The authors declare no competing interests.

Ethical approval None.

Informed consent None.

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