# Comparative genomic analysis of the genus Marinomonas and taxonomic study of Marinomonas algarum sp. nov., isolated from red algae Gelidium amansii

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# Abstract

Members of the genus *Marinomonas* are known for their environmental adaptation and metabolically versatility, with abundant proteins associated with antifreeze, osmotic pressure resistance, carbohydrase and multiple secondary metabolites. Comparative genomic analysis focusing on secondary metabolites and orthologue proteins were conducted with 30 reference genome sequences in genus *Marinomonas*. In this study, a Gram-stain-negative, rod-shaped, non-flagellated and strictly aerobic bacterium, designated as strain E8$^T$, was isolated from the red algae (*Gelidium amansii*) in the coastal of Weihai, China. Optimal growth of the strain E8$^T$ was observed at temperatures 25–30 ℃, pH 6.5-8.0 and 1–3% (w/v) NaCl. The DNA G + C content was 42.8 mol%. The predominant quinone was Q-8 and the major fatty acids were $C_{16:0}$, summed feature 3 and summed feature 8. The main polar lipids were phosphatidylglycerol (PG) and phosphatidylethanolamine (PE). Based on data obtained from this polyphasic taxonomic study, strain E8$^T$ belongs to a novel species of the genus *Marinomonas*, for which the name *Marinomonas algarum* is proposed. The type strain is E8$^T$ (= KCTC 92201$^T$ = MCCC 1K07070$^T$).


# Introduction

The genus *Marinomonas* belongs to the family *Oceanospirillaceae* in the *Gammaproteobacteria,* was created by Van Landschoot and De Ley (1984) to accommodate two reclassified species, namely *Marinomonas vaga* and *Marinomonas communis*. At the time of April of 2022, 39 validly published species (https://lpsn.dsmz.de/genus/marinomonas) had been isolated from marine environment, including 11 species from marine plants, 10 from seawater and 5 from marine sediment. Many of them had been observed special properties like agar degradation (*M.agarivorans* KCTC 52475$^T$) (Yu et al. 2020), algicidal activity (*M.algicida* KEMB 9005-327$^T$) (Kristyanto et al. 2017), plant-beneficial properties (*M.spartinae* KCTC 42958$^T$) (Lucena et al. 2016) and thermophilic characteristic (*M.primoryensis* JCM 11775$^T$) (Romanenko et al. 2003). Members of the genus *Marinomonas* are Gram-stain-negative, rod-shaped, strictly aerobic, some of them could hydrolyze agar, gelatin and have the ability to metabolize quinate, acetate, glycerol, and lactate (Ivanova et al. 2005; Lucas-Elío et al. 2011; Yu et al. 2020). Previous studies have verified that members of genus *Marinomonas* shown genomic, proteomic, physiological adaptations for challenging marine environments (Vance et al. 2014; Liao et al. 2021). Varied kinds of secondary metabolites have been tracked in some strains in genus *Marinomonas*, including ω-ester-containing peptides (OEPs) (as a kind of RiPPs) from *Marinomonas fungiae* JCM 18476$^T$ (Kaweewan et al. 2021), marinocine from *Marinomonas mediterranea* MMB-1 (Lucas-Elio et al. 2005) and antimicrobial potentials (Wang et al. 2016).

In this study, a novel species within the genus *Marinomonas* was isolated from the surface of marine red algae and polyphasic taxonomy method was used to identify the taxonomic position of the novel strain E8$^T$. We have preliminarily analysed the pan-genomes, orthologue proteins in genus and predicted the biosynthetic gene clusters related to secondary metabolism.

# Materials And Methods

## Isolation, cultivation and maintenance

The strain E8$^T$ was isolated from marine red algae (*Gelidium amansii*) collected from the coast of XiaoShi Island Weihai, China (37.5°N, 122.1°E) during a low tide and brought to the laboratory in a cold sterilized chamber. Samples were smashed into small pieces and homogenized. Then 1 g homogenate was weighed out and blended in 9 ml sterilized sea water and mixed homogeneously as $10^{-1}$. After gradient dilution to $10^{-2}$ and $10^{-3}$, 100μl of three dilutions were spread on marine agar 2216 (MA, Becton Dickinson) and incubated at 25 ℃ for 5 days. A single colony of strain E8$^T$ was obtained in pure culture after transferring to fresh MA by previously described method (Xu et al. 2020) and the strain was stored at – 80 °C in sterile 20% (v/v) glycerol supplemented with 1% (v/v) NaCl. The phylogenetically related reference strains *Marinomonas communis* JCM 20766$^T$and *Marinomonas pontica* DSM 17793$^T$, were obtained from Pro. Du.

## 16S rRNA gene sequence and phylogenetic analysis

To identify the taxonomic position of strain E8$^T$, the 16S rRNA gene sequence was amplified by PCR using two universal primers 27f and 1492r (Liu et al. 2014). The purified PCR products were ligated to the pGM-T vector and transferred into E. coli DH5α cells. The positive clones were selected and performed sequencing by BGI Co. Ltd (Qingdao, PR China) using the ABI 3730XL system. The amplifed 16S rRNA gene sequence of strain E8$^T$ was submitted to the GenBank database and the 16S rRNA gene sequence similarities were calculated using the BLAST algorithm at NCBI (https://www.ncbi.nlm.nih.gov) and EzTaxon server (http://www. ezbiocloud.net/) (Yoon et al. 2017). The MEGA version 7.0 (Kumar et al. 2016) was used to constructed phylogenetic trees with the neighbor-joining, maximum-likelihood and the maximum-parsimony algorithms. The stability of the topology was confirmed by performing bootstrap analyses based on 1000 replications (Felsenstein 1985).

## Genome sequencing and function analysis

The genomic DNA of strain E8$^T$ was extracted from a culture grown in MB (Becton Dickinson) for 48h using a Bacteria DNA Kit (Omega) according to the manufacturer's recommendations and then the purified DNA was sent to Beijing Novogene Bioinformatics Technology Co., Ltd. The sequencing library was prepared by using NEBNext® Ultra™ DNA Library Prep Kit for Illumina (NEB, USA) following manufacturer's recommendations and sequenced using the pair-end 350 bp sequencing protocol on the Illumina PE150 platform. To obtain clean data, raw sequencing data were generated by using readfq (Version 10) at first and Illumina base-calling software CASAVA v1.8.2 (http://www.support.illumina.com/) according to its corresponding manuscript. All good quality paried reads were assembled using SOAPdenovo software (Li et al. 2008). To make sure the authenticity of 16S rRNA, the complete 16S rRNA gene sequence which was accessed from the draft genome using the RNAmmer 1.2 server (http://www.cbs.dtu.dk/services/RNAmmer/) had been compared with PCR

amplification. The G + C content of the chromosomal DNA was calculated using genome sequence. The genome component prediction was conducted with GeneMarkS program (Besemer et al. 2001), tRNAscan-SE software (Version 1.3.1) (Lowe and Eddy 1997), rRNAmmer software (Version 1.2) (Lagesen et al. 2007), Rfam database (Gardner et al. 2009), IslandPath-DIOMB program (Hsiao et al. 2003), PHAST software (Version 2.3) (Zhou et al. 2011) and CRISPRFinder (Grissa et al. 2007) to predict the related coding genes, tRNA, rRNA, snRNA, Genomics Islands, prophage and Clustered Regularly Interspaced Short Palindromic Repeat Sequences (CRISPR) respectively. Then, a whole genome Blast search (E-value less than 1e-5, minimal alignment length percentage larger than 40%) was performed to predicted gene function by using Gene Ontology (GO) (Ashburner et al. 2000), Kyoto Encyclopedia of Genes and Genomes (KEGG) (Kanehisa et al. 2015), Clusters of Orthologous Groups (COG) (Galperin et al. 2015), Rapid Annotations using Subsystem Technology (Rastekenari et al.) server (Aziz et al. 2008) and Transporter Classification Database (TCDB) (Saier et al. 2014). To further detect the taxonomic relationship between the strain E8$^T$ and within members in the genus *Marinomonas*, phylogenomic analyses based on genomes inferred bac120 marker set via GTDB-Tk (Chaumeil et al. 2020) were reconstructed by using FastTree (Price et al. 2010) with JTT+CAT parameters and performed by using IQ Tree (Trifinopoulos et al. 2016) with the LG+F+I+G4 model and 1000 bootstrap replicates.

## Morphological, physiological, and biochemical analysis

The morphological and physiological features of strain E8$^T$ were examined with cells grown on MA at 28 ℃ for 48 h. Cell morphology, size and the presence of flagella were examined by light microscopy (E600, Nikon) and transmission electron microscopy (JEM-1200; JEOL) at the State Key Laboratory of Bio-Fibers and Eco-Textiles (Qingdao University, China). Gram staining was performed as the method described previously (Smibert and Krieg 1994). Gliding motility was tested in marine broth 2216 (MB; BD) supplemented with 0.3% agar and motility was examined using the hanging-drop method according to the methods of Bernardet *et al*. (2002). Cells of strain E8$^T$ were incubated on MA for 14 days with or without 0.1% (w/v) $KNO_3$ in an anaerobic jar to determine the growth under anaerobic conditions (10% $H_2$, 10% $CO_2$ and 80% $N_2$). Growth ranges and optimum temperature were indicated on MA at 4, 10, 15, 20, 25, 28, 30, 33, 37, 40 and 45 ℃. Growths at range of NaCl were tested in the following medium (per liter: 1 g yeast extract, 5 g peptone, 0.1 g ferric citrate), supplying with artificial seawater (per liter: 3.2 g $MgSO_4$, 2.2 g $MgCl_2$, 1.2 g $CaCl_2$, 0.7 g KCl, 0.2 g $NaHCO_3$) containing 0, 0.5, 1, 2, 3, 4, 5, 6, 7, 8, 9 or 10% (w/v) NaCl at 28 ℃, and recorded the colony growth every 12h. The pH range for growth was tested in marine broth 2216 (MB; BD) with addiction of appropriate buffers, including MES (pH 5.5 and 6.0), PIPES (pH 6.5 and 7.5), HEPES (pH 7.5 and 8.0), Tricine buffer (pH 8.5) and CAPSO (pH 9.0, 9.5 and10.0), at a concentration of 20 mM and monitored the growth of bacterial using a spectrophotometer at 600 nm. The oxidase activity and catalase activity were assessed by using an oxidase reagent kit (bioMérieux) according to the manufacturer's instructions and the production of bubbles after the addition of a drop of 3% (v/v) $H_2O_2$. The nitrate reduction and degradation of agar, starch, cellulose, alginate, casein and lipids (Tween 20, 40, 60 and 80) were examined according to the methods described by Tindall *et al*. (2007). Other physiological or biochemical tests were investigated by using the API 20E, API ZYM and API 50CHB

Kits (all from BioMérieux, France) and Biolog Gen III microPlates according to the manufacturer's instructions except that salinity was adjusted to 3%. All tests were carried out simultaneously with related type strains at least twice. Susceptibility to antibiotics was tested by measuring the size of inhibition zone generated by different drug-sensitive paper on MA at 28 °C for 3 days. A cell suspension (0.5 McFarland standard) was swabbed over MA to create a uniform lawn before aseptic placement of antibiotic discsonto the surface. CLSI standards were strictly followed for cultivation and inhibition zone diameter reading (CLSI 2012).

## Chemotaxonomic characterization analysis

To analyse characterization of cellular fatty acids, respiratory quinone compositions and polar lipids, cells of strain E8$^T$ and two related type strains were harvested from MB medium after growth at 28 ℃ for 3 days and subjected to freeze-drying. The cellular fatty acids were saponified, methylated and extracted according to the standard protocols of MIDI (Sherlock Microbial Identification System, version 6.0B) protocol equipped with an Agilent HP6890 gas chromatograph (Sasser 1990). The designations and percentages of fatty acids were identified with the TSBA40 database using MIS standard software. The respiratory quinones were extracted from 300 mg freeze-dried cell material and separated by TLC after extraction with a chloroform/methanol (2:1, v/v) mixture (Tindall et al. 2007). The content of each quinone type was subsequently analyzed by HPLC according to the method previously described (Kroppenstedt 1982). The polar lipids were extracted with solutions chloroform/methanol/water (65:25:4, by vol) for the first dimension and chloroform/methanol/acetic acid/water (80:12:15:4, by vol) for the second dimension and separated via two-dimensional silica-gel TLC. The lipid material was stained using 10% molybdatophosphoric acid solution (total lipids), molybdenum blue solution (phosphates), α-naphthol sulfuric solution (carbohydrates) and ninhydrin (amines) respectively. The specific experimental process is implemented according to the method described by Minnikin *et al*. (1984) and Tindall *et al*. (2007).

## Comparative genome analysis and pan-genome analysis

Comparative genomics of *M.algarum* E8$^T$ and other species in genus *Marinomonas* was performed using 29 reference genomes available in the GenBank database. The general features of the genomes of strains were obtained from the result of NCBI Prokaryotic Genome Annotation Pipeline (PGAP). To identify the genomic distance between each genomes, the MASH distance was computed by using MASH (Ondov et al. 2016). The pairwise whole genome comparisons of average nucleotide identity (ANI) and average amino acid identity (AAI) were calculated according to Konstantinidis and Tiedje using the scripts (http://enve-omics.gatech.edu/). The digital DNA–DNA hybridization (dDDH) values were determined by using the Genome-to-Genome Distance Calculator (GGDC2.1) (http://ggdc.dsmz.de).

The protein sequences were clustered and compared by Cd-hit (Li and Godzik 2006) and aligned by using MAFFT method (Katoh et al. 2002). The protein sequences were conserved into corresponding codon alignments and automated alignment trimming by using trimAl (Capella-Gutiérrez *et al*., 2009). Then, the

single-copy protein tree was constructed by FastTree (Price et al. 2010). To identify conserved single-copy gene families, the genomes of strain E8$^T$ and 29 reference strains were analysed by using OrthoFinder (Emms and Kelly 2019), following the default parameters and constructed a phylogenetic tree of single-copy Orthologue proteins by FastTree (Price et al. 2010).

The pan-genome analysis was conducted by using BPGA (Bacterial Pan Genome Analysis tool) (Chaudhari et al. 2016) to identify the core, accessory and unique genes. The pipeline generated a phylogenetic tree based on pan-matrix data without outgroup used for the pan-genome tree for better evidence the relationship among *Marinomonas* species. Furthermore, the OrthoVenn2 web server (Xu et al. 2019) was performed to analysed the protein sequences for comparison and annotation of the orthologous clusters of the strains E8$^T$ and 11 strains isolated from marine plant including *M.agarivorans* QM202$^T$, *M. alcarazii* CECT 7730$^T$, *M.algicola* SM1966$^T$, *M.aquiplantarum* CECT 7732$^T$, *M.balearica* CECT 7378$^T$, *M.colpomeniae* SM2066$^T$, *M.foliarum* CECT 7731$^T$, *M.pollencensis* CECT 7375$^T$, *M.posidonica* IVIA-Po-181$^T$, *M.rhizomae* IVIA-Po-145$^T$ and *M.spartinae* CECT 8886$^T$.

To further compare the genomic functions and metabolism, Prokka (Seemann 2014) was used to annotated all 30 reference genome sequences. The COG database (Galperin et al. 2015) was used to determine the clusters of orthologous groups of proteins and predict functions and the results of each strains were clustered into a relative abundance heatmap. The COG annotation was selected for E-value below $10^{-5}$. The genomes of the reference strains were analysed using antiSMASH version 6.0 (Blin et al. 2021) with “strict” detection criteria to predict the biosynthetic gene clusters (BGCs) enabled and default parameters. The results of BGCs predictions was generated a stack graph depicting the number of each BGC type using the Rstudio packages “ggplot2” (Villanueva and Chen 2019). The BAGEL4 web server (van Heel et al. 2018) was used to further mine the potential RiPPs and bacteriocins across all reference strains in genus *Marinomonas*.

# Results And Discussion

### Morphological, physiological and biochemical characteristics

Cells of the strain E8$^T$ were Gram-stain-negative, rod-shaped, about 0.2-0.4 μm wide and 1.0-2.5 μm long, without flagella (Fig. S1). A wide range of growth have been observed in temperature, pH and tolerance of salt, including strain E8$^T$ and related species in genus *Marinomonas*. The major differences of biochemical characteristics for strain E8$^T$ and related species are summarized in Table 1. All negative traits of strain E8$^T$ are provided in Table S1. According to the result of API ZYM and API 20E, strain E8$^T$ had the activity of alkaline phosphatase, esterase (C4), esterase lipase (C8), leucine arylamidase, valine arylamidase, acid phosphatase, naphthol-AS-BI-phosphohydrolase. Cellulose, starch, alginate, Tween 40, 60, 80 were not hydrolysed and negative for nitrate reduction in strain E8$^T$.

Strain E8$^T$ was found to be susceptible to (μg per disc) penicillin (10), streptomycin (10), tobramycin (10), gentamicin (10), ampicillin (10), ofloxacin (5), carbenicillin (100), ceftriaxone (30), norfloxacin (10),

cefotaxime (30), clarithromycin (CLR) (15), polymyxin B (300), chloroamphenicol (30), intermediate to neomycin (30), rifampicin (5), kanamycin (30), erythromycin (15), and resistant to vancomycin (VA) (30), tetracycline (30), lincomycin (2).

## Phylogenetic and phylogenomic analyses

A nearly full-length 16S rRNA gene sequence (1425 bp) of strain E8$^T$ obtained from PCR amplification was included in the 16S rRNA gene sequences assembled from genomic sequences which contained only one complete 16s rRNA. The BLAST research in NCBI revealed that strain E8$^T$ exhibited highest similarities with *M.vulgaris* A79$^T$ (98.4%) and *M.pontica* 46-16$^T$ (97.5%). The similarity between strain E8$^T$ and the type strain JCM 20766$^T$ of the type species *Marinomonas communis* was 94.9%. As the topology based on maximum-likelihood phylogenetic tree of 16s rRNA genes, strain E8$^T$ was clustered with *M.vulgaris* A79$^T$ at a bootstrap formed a separated branch (Fig. 1). Both neighbour-joining and maximum-parsimony algorithms were used to confirm the topology of tree (Fig. S2, Fig. S3). In addition, the phylogenomic tree based on the genomic sequences with IQ Tree showed the clade formed by strain E8$^T$ and A79$^T$ could distinguished from other members in the genus and confirming the strain E8$^T$ was a member of genus *Marinomonas* (Fig. 2).

## General genomic features

The sequence of the draft genome of strain E8$^T$ was assembled into 79 contigs with a total length of 3,285,337 bp, a contig N50 value of 126,031 bp, a contig L50 value of 8 and a mean coverage of 150 ×. The longest contig and the shortest contig were 379,893 bp and 618 bp. The DNA G+C content was 45.1mol%, which was in the middle of most of related species. A total of 3,085 genes were predicted with 2,988 protein-coding genes and 97 encode RNAs including 8 5S rRNAs, 4 16S rRNAs, 4 23S rRNAs, 77 rRNAs and 4 ncRNAs. The genome sequence of strain E8$^T$ included 31 Longinterspersed nuclear elements (LINEs), 23 Short interspersed nuclear elements (SINEs), 4 Genomics Islands (GIs), 2 CRISPR-associated genes. Further comparative general features of 30 genome sequence were shown in Table S2.

According to the genomic functions predicted, the strain E8$^T$ has been annotated with complete glycolysis, gluconeogenesis, citrate cycle (TCA cycle) and pentose phosphate pathway for central carbohydrate metabolism and UDP-N-acetyl-D-glucosamine biosynthesis, which was same as *M.vulgaris* A79$^T$ and *M.communis* JCM 20766$^T$. The succinate dehydrogenase, cytochrome bd ubiquinol oxidase, cytochrome o ubiquinol oxidase and F-type ATPase were predicted in strain E8$^T$ and A79$^T$ but lack of cytochrome c oxidase and cytochrome bc1 complex respiratory unit which presented in JCM 20766$^T$ genome. The *ackA* gene was absented in strains E8$^T$ and A79$^T$ genomes which were incapable to convert acetyl-CoA into acetate as a carbon fixation pathway completed in JCM 20766$^T$ genome. The sulfate reduction ability was predicted in strain A79$^T$ with *cysNC*, *cysN*, *cysD*, *cysNC*, *cysC*, *cysH*, *cysJ* and *cysI* genes to convert sulfate into sulfide but the *cysC* gene was absence in strain E8$^T$ genome which

may just convert sulfite into sulfide. The strain E8$^T$ was predicted to metabolism many amino acids including serine, threonine, valine, isoleucine, leucine, lysine, ornithine, arginine, proline and tryptophan. For metabolism of cofactors and vitamins, biosynthesis pathway of Pyridoxal-P (EC 1.4.3.5), NAD (EC 6.3.5.1), pantothenate (EC 6.3.2.1), coenzyme A (EC 6.3.2.5), biotin (EC 2.8.1.6), lipoic acid (EC 2.8.1.8), molybdenum cofactor (EC 2.10.1.1), siroheme (EC 4.99.1.4), heme (EC 1.3.5.3) and cobalamin (EC 6.3.1.10) were completed in strain E8$^T$ genome sequence. The genomes of three strains contain several genes responsible for choline uptake and betaine biosynthesis, including choline dehydrogenase (betA), betaine-aldehyde dehydrogenase (betB) and glycine betaine ABC transport system permease (ProU), as osmoprotectant. All genes for the synthesis of PG and PE have been found in genome of strain E8$^T$, which were similar to other strains in genus *Marinomonas*.

## Chemotaxonomic characterization

The major fatty acids (>10%) were $C_{16:0}$, summed feature 3 ($C_{16:1}\omega7c$ and/or $C_{16:1}\omega6c$) and summed feature 8 ($C_{18:1}\omega7c$ and/or $C_{18:1}\omega6c$). The summed feature 8 with ratio of 47.8%, which was the most abundant cellular fatty acid of the stain E8$^T$, and was also the most abundant fatty acid of the related type strains *M.pontica* DSM 17793$^T$and *M.communis* JCM 20766$^T$ in ratio of 35.3% and 45.7%. The strain E8$^T$can be distinguished from other type strains in the compounds of $C_{17:0}$ with ratio of 3.1% which composition was less than 0.5% in other type strains. The composition of fatty acid summed features 8 in strain E8$^T$ was significantly higher than that in *M.pontica* DSM 17793$^T$, but similar to that in *M.communis* JCM 20766$^T$. The fatty acids profiles of strain E8$^T$ and reference strains *M.pontica* DSM 17793$^T$and *M.communis* JCM 20766$^T$ were shown in Table S3. The polar lipids were mainly composed of phosphatidylglycerol (PG), phosphatidylethanolamine (PE) and three unidentified lipids (L1-L3), which were similar to other type strains with PG and PE as the major polar lipids (Fig. S4). The isoprenoid quinone detected in the strain E8$^T$ was consistent with the other related type strains, which was Q-8.

## Comparative genome analysis

The result of genomic distance between each genome sequences showed that strain E8$^T$ has the closest distance with *M.vulgaris* A79$^T$ and far distance with *M.agarivorans* QM202$^T$, *M.flavescens* ANRC-JHZ47$^T$ and *M.posidonica* IVIA-Po-181$^T$ (Fig. S5). The ANI and AAI values between strain E8$^T$ and *M.vulgaris* A79$^T$ were 78.7% and 84.3%, which below the recommended cut-off value of 95-96% (Richter and Rossello-Mora) and below the proposed cut-off for a species boundary of 85-90% (Qin et al.), respectively. Strain E8$^T$ also shared low dDDH values with *M.vulgaris* A79$^T$ (22.0%), below the 70% for species boundary (Goris et al. ; Meier-Kolthoff et al.). Moreover, the pairwise comparisons of the digital DDH values were shown in Table S4 and the pairwise genome comparisons in nucleotide level and protein translated genes (ANI and AAI values) were shown in Fig. 3, which suggested that strains E8$^T$ represent a putative novel species of the genus *Marinomonas.*

The single copy core protein tree showed that strain E8$^T$ and *M.vulgaris* A79$^T$ shaped a branch with close distance with bole formed by all 30 reference strains (Fig. S6). The strains *M.agarivorans* QM202$^T$ and *M.algicola* SM1966$^T$ have a long branch length with bole which may portend a rather distant phylogenetic relationships. The phylogenetic tree constructed by single-copy orthologue proteins also conformed the tree (Fig. S6). According to result of single-copy gene families, 6,806 orthogroups with 104,049 genes in orthogroups and 3,629 unassigned genes have been clustered and 1,379 orthogroups which presented in all 30 species.

The pan-genome orthologous groups (POGs) of the 30 *Marinomonas*strains indicated that strain E8$^T$ had 959 core genes, 1,661 accessory genes, 219 unique genes and 10 exclusively absent genes. The plot of core-pan showed that the bifidobacteria pan-genome in *Marinomonas*can be considered as “open” (Fig. S7). The pipeline generated a pan-genome phylogenetic tree without outgroup based on pan-matrix data which highlighted distinct groups and confirmed in the core-genome tree (Fig. S8, S9). According to the KEGG annotation, the strains in genus *Marinomonas*showed active in amino acid metabolism, carbohydrate metabolism, membrane transport, metabolism of cofactors and vitamins and xenobiotics biodegradation and metabolism. Unique genes abundantly distributed among amino acid metabolism, carbohydrate metabolism and xenobiotics biodegradation (Fig. S10). The selected type strains (12 species) related to marine plant formed 5,297 clusters, 3,916 of which are orthologous clusters (at least contains two species) and 1,381 of which are single-copy gene clusters (Table S5). Five genomes shared 1,510 protein coding regions and genome of strain E8$^T$ encodes 2,904 proteins contained 2,604 in clusters and 261 which found as singletons (Fig. 4).

The strain E8$^T$ with *M.aquimarina* CECT 5080$^T$ and *M.vulgaris* A79$^T$ have been observed a low frequency of carbohydrate transport and metabolism (COG function category G) which may associate with their oligotrophic environment. Compare to strain A79$^T$, the strain E8$^T$ showed a relatively high count of proteins in category J, X and D which were related to genetic information transmission and transcription (Fig 5). The proteins relevant to secondary metabolites biosynthesis were observed to present in all strains. According to the antiSMASH annotations, the abundant BGCs have been predicted in the genomic sequences of 30 strains. The genomes of the strain *M.mediterranea* MMB-1$^T$, *M.spartinae* CECT 8886$^T$, *M.posidonica* IVIA-Po-181$^T$ and *M.primoryensis* MPKMM3633$^T$ contained the highest bioclusters, as shown in Fig. 6. In general, the genomes of most of strains were predicted to encode for ectoine, non-ribosomal polyketide synthetases (NRPS), betalactone and some other unspecified ribosomally synthesised and post-translationally modified peptide product (RiPP) cluster (Pipp-like). The Pipp-like in strain E8$^T$ has been annotated with bacteriocin which have been annotated in *Marinomonas primoryensis* MPKMM3633, *Marinomonas pollencensis* CECT 7375 and *Marinomonas spartinae* CECT 8887 showing a high percentage genes similarity. The MiBiG comparison showed that the bacteriocin annotated in strain E8$^T$ had the highest similarity score with compound lanthipeptide (MiBiG accession number BGC0000554) from *Streptomyces filamentosus* NRRL 15998. In addition, *M.spartinae* CECT 8886$^T$ has been annotated with a Type I PKS (Polyketide synthase) genes cluster which may mediate biosynthesis of cylindrospermopsin. According to the BAGEL4 prediction,

lasso peptide was predicted in *M.polaris* DSM 16579$^T$, *M.mediterranea* MMB-1$^T$ and *M.rhizomae* IVIA-Po-145$^T$; Microcin was predicted in both *M.piezotolerans* YLB-05$^T$ and *M.algicola* SM1966$^T$; Butyrivibriocin, garvicin_ML, bottromycin were predicted in *M.rhizomae* IVIA-Po-145$^T$, *M.flavescens* ANRC-JHZ47$^T$ and *M.atlantica* Cmf 18.22$^T$, respectively.

### Description of *Marinomonas algarum* sp. nov.

*Marinomonas algarum* (al.ga'rum. L. gen. pl. n. *algarum* of/from algae).

Cells are Gram-stain-negative, rod-shaped, non-flagellated, catalase- and oxidase-negative and strictly aerobic bacterium, approximately 0.2–0.4 μm wide and 1.0–2.5 μm long. The colonies are white, round and smooth after incubation at 28℃ on marine agar 2216 for 48h. Growth occurs in presence of 0.5-8% NaCl (w/v; optimum 1-3%), at temperature of 15-35 ℃ (optimum 25-30 ℃), and at pH 6.0-9.0 (optimum 6.5-8.0). The strain E8$^T$ is positive to oxidize d-mannose, d-mannitol and utilize citrate, d-ribose, d-xylose, l-xylose, d-fructose, l-sorbose, esculin ferric citrate, d-lyxose, d-tagatose, potassium 5-ketogluconate, and weakly assimilated arabinose, d-turanose. The DNA G+C content is 42.8 mol%. The predominant quinone is Q-8 and the major fatty acids are $C_{16:0}$, summed feature 3 ($C_{16:1}\omega7c$ and/or $C_{16:1}\omega6c$) and summed feature 8 ($C_{18:1}\omega7c$ and/or $C_{18:1}\omega6c$). The main polar lipids are phosphatidylglycerol and phosphatidylethanolamine. The type strain is E8$^T$(=KCTC 92201$^T$ =MCCC 1K07070$^T$), isolated from *red algae Gelidium amansii*.

The GenBank accession number for the 16S rRNA sequence is OK444097, and the draft genome sequence of strain E8$^T$ has been deposited at GenBank under accession number JAJATW000000000.

# Declarations


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**Author's contribution** JHX and BNZ isolated the strain E8$^T$, carried out the phylogenomic analysis, analysed most of the data. JHX, BNZ, WJW, ZMW, ZF, YYL, YS and PXY performed the experiments. JHX carried out comparative genomic analysis. The initial draft of the paper was written by JHX. LHZ and XX conceived of the study, designed the study, critically revised the manuscript and co-corresponding the study. All authors read, discussed the results and revised the manuscript.

**Conflict of interest** Authors declare that there is no conflict of interest.

**Ethical statement** This article does not contain any studies with human participants or animal experiments by any of the authors.

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# Table

**Table 1.** Differential characteristics of strain E8$^T$ compared to its closely related species.

| Characteristic | 1 | 2 | 3 |
|---|---|---|---|
| Motile | – | + | + |
| Growth at 35°C | + | – | + |
| Growth in 10 % NaCl | – | + | + |
| Hydrolysis of: | | | |
| Tween 20 | + | + | w |
| Gelatin | + | – | – |
| Starch | – | – | w |
| Sucrose | – | + | – |
| Enzyme activities: | | | |
| Oxidase | – | + | – |
| Catalase | – | + | + |
| Valine arylamidase | + | w | w |
| α-glucosidase | – | + | + |
| Arginine dihydrolase | – | + | + |
| Oxidation of: | | | |
| d-mannose | + | – | + |
| d-mannitol | + | w | + |
| d-maltose | – | + | + |
| l-rhamnose | – | + | + |
| Utilization of: | | | |
| Citrate | + | + | + |
| Arabinose | w | – | – |
| d-sorbitol | – | + | – |
| l-sorbose | + | + | + |
| l-rhamnose | – | w | + |
| Inositol | – | + | + |
| d-turanose | w | – | + |
| d-lyxose | + | + | w |

| | | | |
|---|---|---|---|
| d-tagatose | + | + | w |
| DNA G+C content (mol%) | 45.1 | 46.5 | 45.8 |

Strains: 1, E8$^T$; 2, *M.pontica* DSM 17793$^T$; 3, *M.communis* JCM 20766$^T$. All data are from this study unless otherwise indicated. + Positive, – negative, w weakly positive.

# Figures

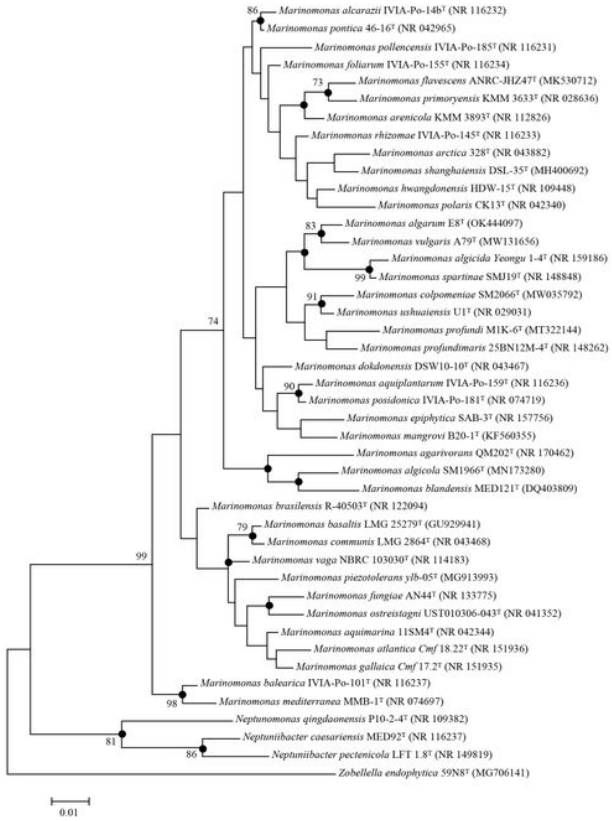
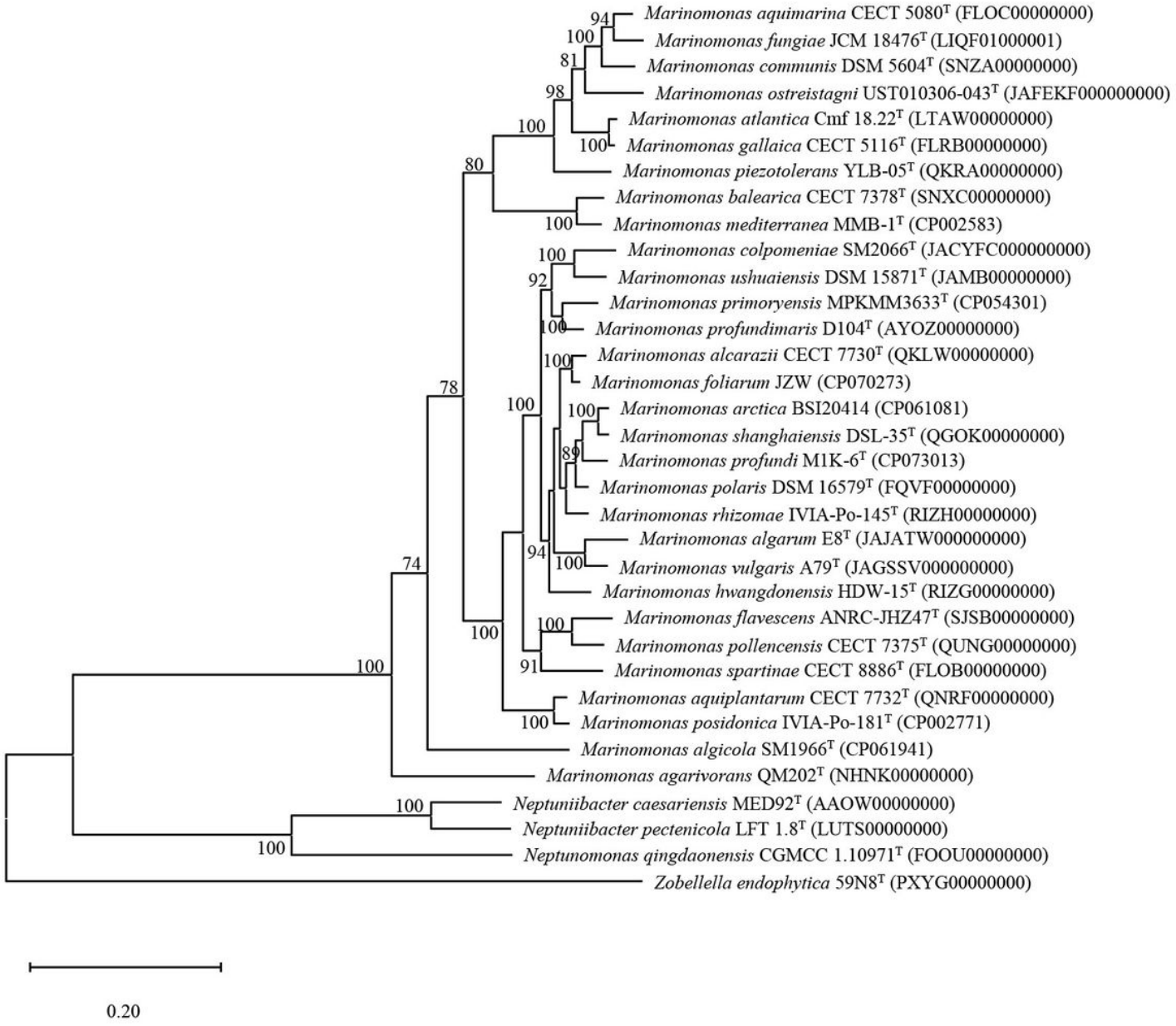


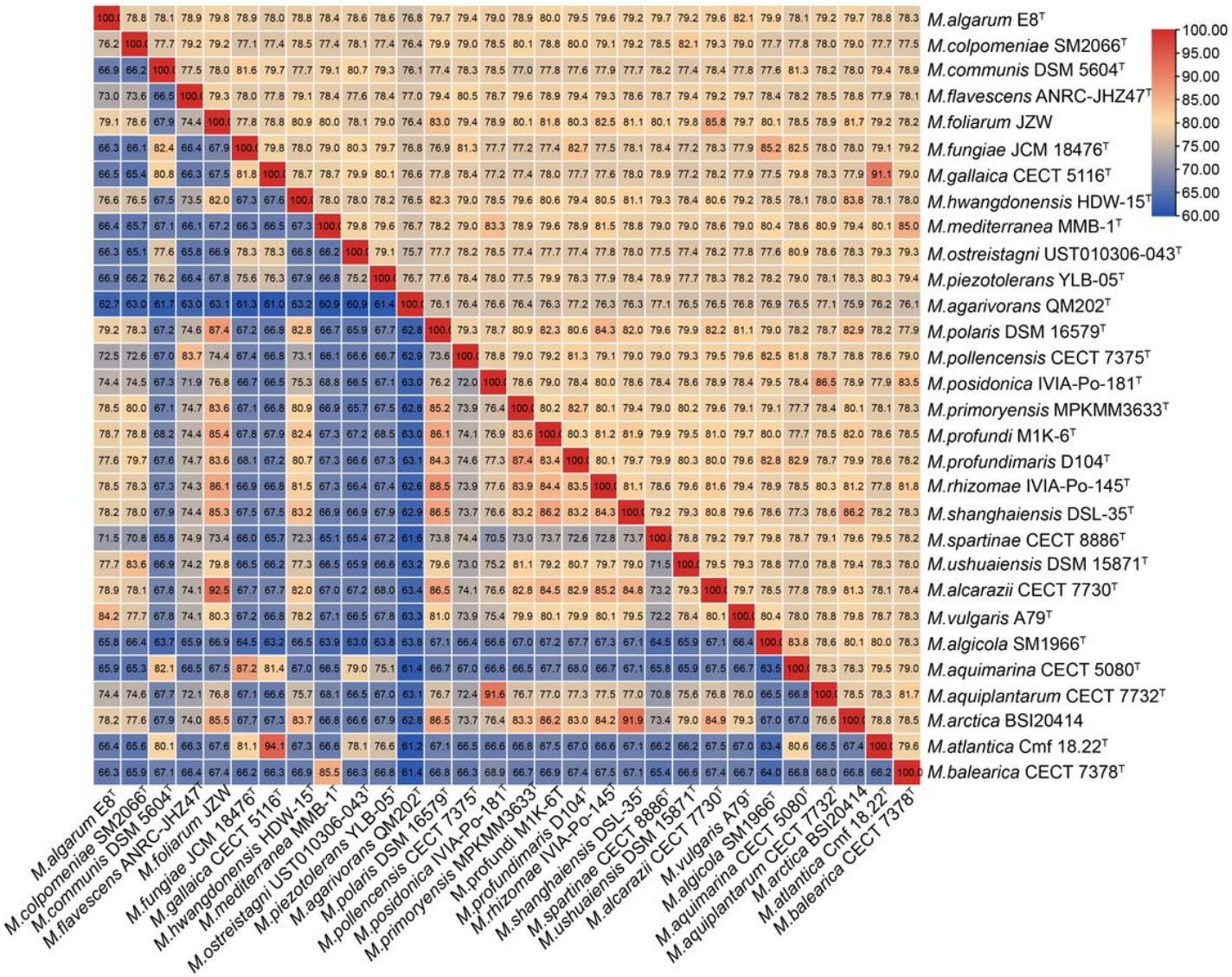

**Figure 1**

Maximum-likelihood phylogenetic tree based on 16S rRNA gene sequences of strain E8$^T$ and representative of the other members of the family *Oceanospirillaceae*. All type strains in genus *Marinomonas* have been concluded. Bootstrap values (>70%) based on 1000 replicates were shown at branch nodes (ML/NJ/MP). *Zobellella endophytica* 59N8$^T$ (GenBank accession number MG706141) was used as an outgroup. Bar, 0.01 substitutions per nucleotide position.



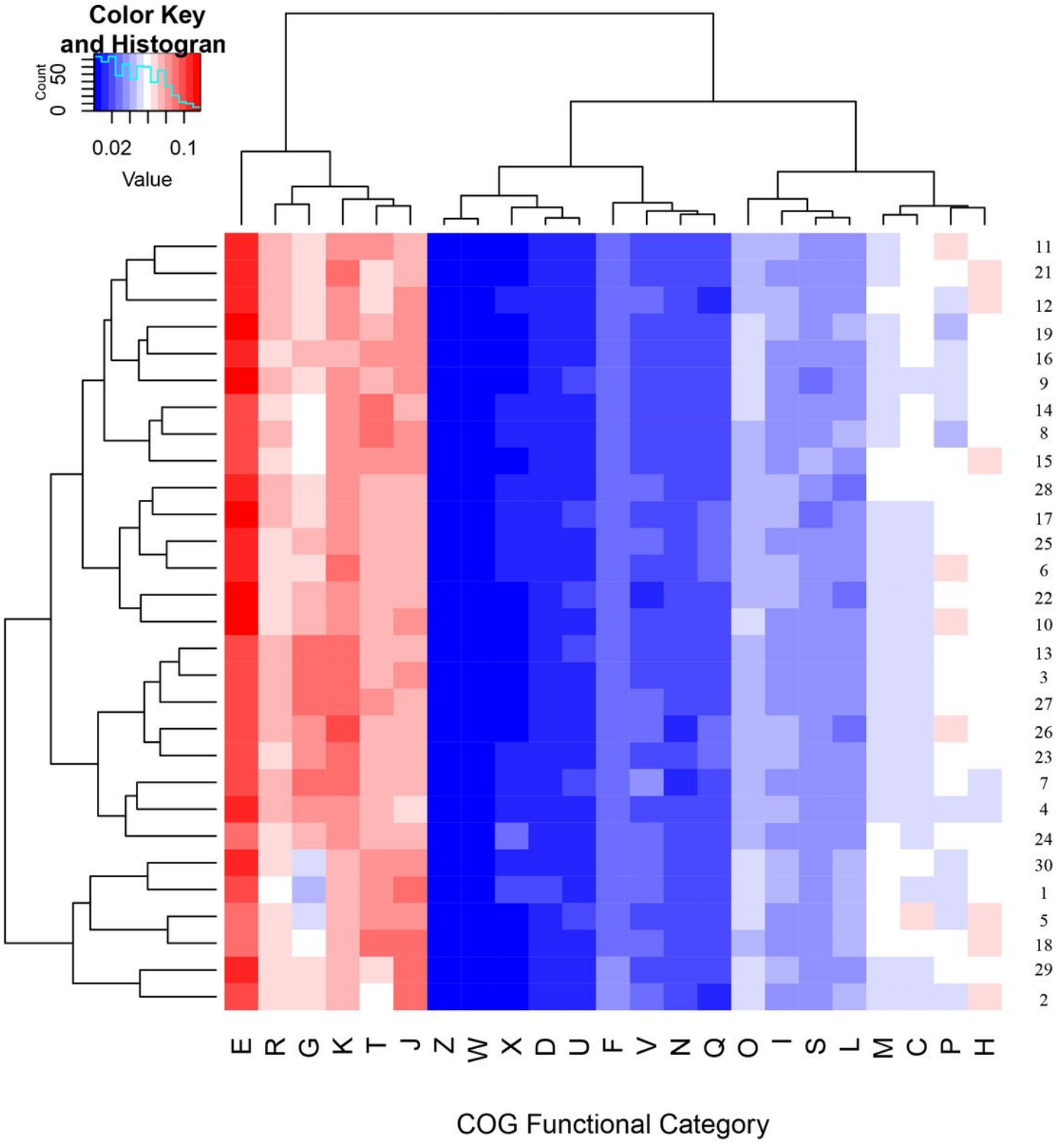

## Figure 2

Phylogenomic tree reconstructed by IQtree showing the position of strains E8$^T$ and related strains of the family *Oceanospirillaceae* with reference genome sequences. GenBank accession numbers were given in parentheses. Bootstrap values (expressed as percentages of 1000 replications) above 70% were shown at branch points. *Zobellella endophytica* 59N8$^T$ (GenBank accession number PXYG00000000) was used as an outgroup. Bar, 0.2 substitutions per nucleotide position.



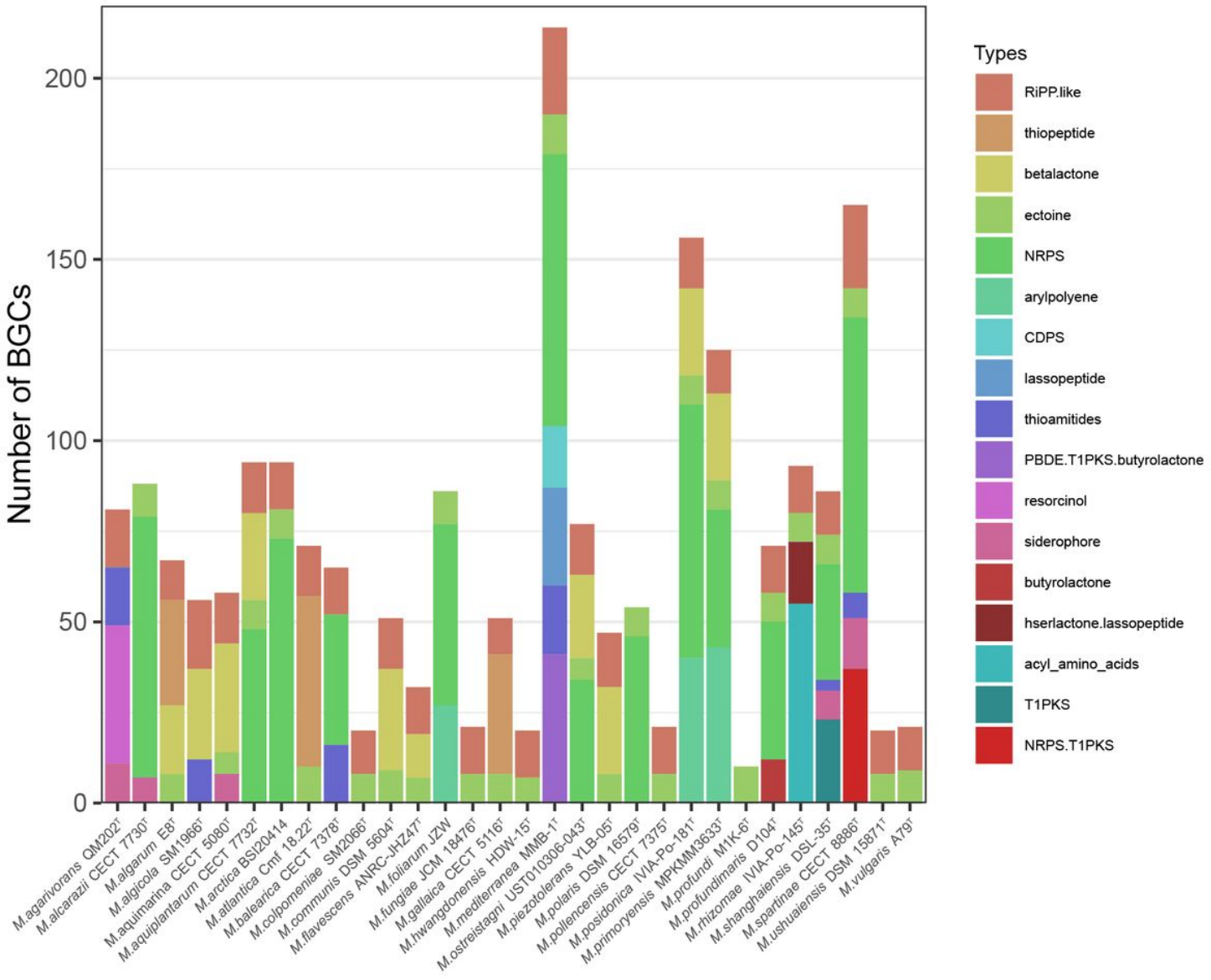

## Figure 3

Pairwise comparisons of the average nucleotide identity (ANI) and average amino acid identity (AAI) between genome sequencing of strain E8$^T$ and reference genome sequences in genus *Marinomonas.* Upper triangle: ANI values; Lower triangle: AAI values.




## Figure 4

The venn diagrams constructed by OrthoVenn2 online service, showing the distribution of the shared gene families (orthologous clusters) in the strain E8$^{T}$ and 4 four marine-plants associated strains.




## Figure 5

The relative abundance of cluster of orthologous groups of proteins function for each strains. The RNA processing and modification has not been annotated.

E, Amino acid transport and metabolism; R, General function prediction only; G, Carbohydrate transport and metabolism; T, Signal transduction mechanisms; K, Transcription; J, Translation, ribosomal structure and biogenesis; Z, Cytoskeleton; W, Extracellular structures; X, Mobilome: prophages, transposons; D, Cell cycle control, cell division, chromosome partitioning; U, Intracellular trafficking, secretion, and vesicular transport; F, Nucleotide transport and metabolism; V, Defense mechanisms; N, Cell motility; Q, Secondary metabolites biosynthesis, transport and catabolism; O, Posttranslational modification, protein turnover, chaperones; I, Lipid transport and metabolism; S, Function unknown; L, Replication, recombination and repair; M, Cell wall/membrane/envelope biogenesis; C, Energy production and conversion; P, Inorganic ion transport and metabolism; H, Coenzyme transport and metabolism;

Strains: 1, *M.algarum* E8$^{T}$; 2, *M.agarivorans* QM202$^{T}$; 3, *M.alcarazii* CECT 7730$^{T}$; 4, *M.algicola* SM1966$^{T}$; 5, *M.aquimarina* CECT 5080$^{T}$; 6, *M.aquiplantarum* CECT 7732$^{T}$; 7, *M.arctica* BSI20414$^{T}$; 8, *M.atlantica* Cmf 18.22$^{T}$; 9, *M.balearica* CECT 7378$^{T}$; 10, *M.colpomeniae* SM2066$^{T}$; 11, *M.communis* DSM 5604$^{T}$; 12, *M.flavescens* ANRC-JHZ47$^{T}$; 13, *M.foliarum* JZW$^{T}$; 14, *M.fungiae* JCM 18476$^{T}$; 15, *M.gallaica* CECT 5116$^{T}$; 16, *M.hwangdonensis* HDW-15$^{T}$; 17, *M.mediterranea* MMB-1$^{T}$; 18, *M.ostreistagni* UST010306-043$^{T}$; 19, *M.piezotolerans* YLB-05$^{T}$; 20, *M.polaris* DSM 16579$^{T}$; 21, *M.pollencensis* CECT 7375$^{T}$; 22, *M.posidonica* IVIA-Po-181$^{T}$; 23, *M.primoryensis* MPKMM3633$^{T}$; 24, *M.profundi* M1K-6$^{T}$; 25, *M.profundimaris* D104$^{T}$; 26, *M.rhizomae* IVIA-Po-145$^{T}$; 27, *M.shanghaiensis* DSL-35$^{T}$; 28, *M.spartinae* CECT 8886$^{T}$; 29, *M.ushuaiensis* DSM 15871$^{T}$; 30, *M.vulgaris* A79$^{T}$.

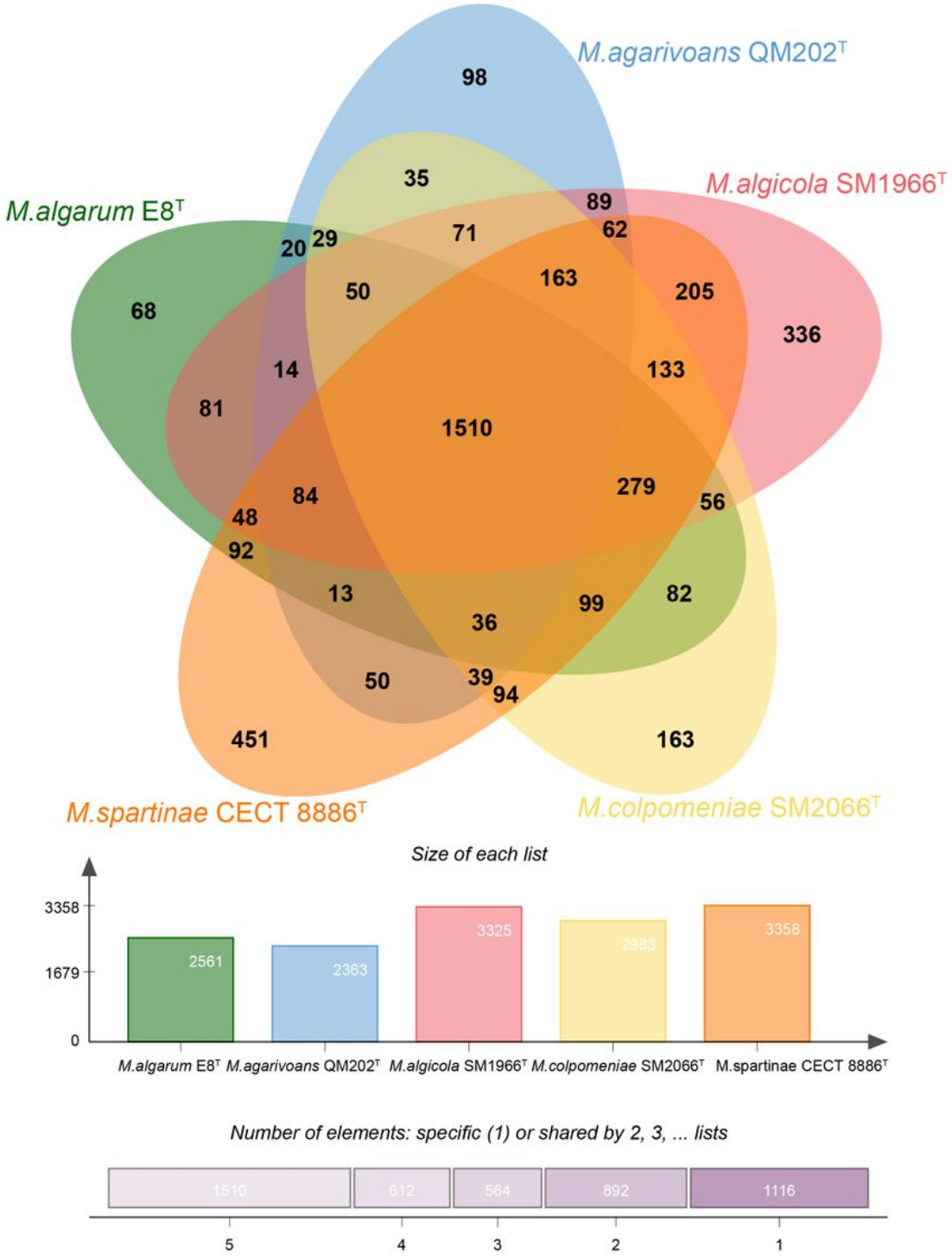



**Figure 6**

Biosynthetic gene clusters found in the genomes of strain E8$^T$ and reference strains in genus *Marinomonas* using antiSMASH 6.0 software.

# Supplementary Files

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