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GENOME REPORTS

Complete genome sequence of *Caulobacter flavus* RHGG3^T, a type species of the genus *Caulobacter* with plant growth-promoting traits and heavy metal resistance

Endong Yang[1] · Leni Sun[1] · Xiaoyuan Ding[1] · Dongdong Sun[1] · Jing Liu[1] · Weiyun Wang[1]

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Abstract

Caulobacter flavus RHGG3^T, a novel type species in the genus *Caulobacter*, originally isolated from rhizosphere soil of watermelon (*Citrullus lanatus*), has the ability to improve the growth of watermelon seedling and tolerate heavy metals. In vitro, *C. flavus* RHGG3^T was able to solubilize phosphate (80.56 mg L^{-1}), produce indole-3-acetic acid (IAA) (11.58 mg L^{-1}) and was resistant to multiple heavy metals (copper, zinc, cadmium, cobalt and lead). Inoculating watermelon with this strain increased shoot and root length by 22.1% and 43.7%, respectively, and the total number of lateral roots by 55.9% compared to non-inoculated watermelon. In this study, we present the complete genome sequence of *C. flavus* RHGG3^T, which was comprised of a single circular chromosome of 5,659,202 bp with a G + C content of 69.25%. An annotation analysis revealed that the *C. flavus* RHGG3^T genome contained 5172 coding DNA sequences, 9 rRNA and 55 tRNA genes. Genes related to plant growth promotion (PGP), such as those associated with phosphate solubilization, nitrogen fixation, IAA, phenazine, volatile compounds, spermidine and cobalamin synthesis, were found in the *C. flavus* RHGG3^T genome. Some genes responsible for heavy metal tolerance were also identified. The genome sequence of strain RHGG3^T reported here provides new insight into the molecular mechanisms underlying the promotion of plant growth and the resistance to heavy metals in *C. flavus*. This study will be valuable for further exploration of the biotechnological applications of strain RHGG3^T in agriculture.

Keywords *Caulobacter flavus* RHGG3^T · Complete genome sequence · Plant growth-promoting rhizobacteria · Heavy metal resistance

Introduction

Plant growth-promoting rhizobacteria (PGPR) are well known for their abilities to promote plant growth and enhance the tolerance of plants to stressors, such as heavy metals, drought, salt, and pathogens (Bhattacharyya and Jha 2012; Xie et al. 2018; Zhang et al. 2017). PGPR are able to promote plant growth directly or indirectly through a combination of mechanisms, including nitrogen fixation, phosphate solubilization, biosynthesis of siderophores, plant growth hormones [indole-3-acetic acid (IAA)], hydrolytic enzymes, various antibiotics, as well as the induction of plant resistance (Qin et al. 2009, 2017; Wang et al. 2015). These functional properties are critical when considering the formulation of biofertilizers, which may be an advantage due to less environmental pollution than chemical applications.

In our previous study, a Gram-stain-negative, yellow-pigmented bacterium strain RHGG3^T was isolated from rhizosphere soil of cultivated watermelon (*Citrullus lanatus*) collected from Hefei, China, and identified as a novel species *Caulobacter flavus* RHGG3^T using a polyphasic approach (Sun et al. 2015). The genus *Caulobacter*, which belongs phylogenetically to the family *Caulobacteraceae*, contains 11 species with validly published names (Moya et al. 2017; Sun et al. 2017). Members of the genus *Caulobacter* have the ability to tolerate uranium, copper and chlorophenols (Ash et al. 2014; Hu et al. 2005; Yung et al.

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✉ Weiyun Wang
weiywswzy@163.com

[1] School of Life Science, Anhui Agricultural University, Hefei 230036, People's Republic of China

Table 1 Plant beneficial traits of strain *Caulobacter flavus* RHGG3^T and its promoting effects on watermelon seedlings

	IAA concentration (mg L^{-1})	Solubilized phosphate (mg L^{-1})	Shoot length (cm)	Root length (cm)	Number of lateral roots
RHGG3	11.58 ± 0.19	80.56 ± 1.53	8.00 ± 0.66	11.35 ± 0.65	46.0 ± 7.63
CK	–	–	6.55 ± 0.47	7.90 ± 1.56	29.5 ± 4.84

Table 2 Resistances of strain *Caulobacter flavus* RHGG3^T to heavy metal ions (mg mL^{-1})

Concentration	Cu^{2+}	Zn^{2+}	Cd^{2+}	Co^{2+}	Pb^{2+}
0.025	+	+	+	+	+
0.05	+	+	+	+	+
0.1	+	+	−	+	+
0.2	+	+	−	+	+
0.3	−	+	−	+	+
0.4	−	+	−	−	+
0.5	−	−	−	−	−

+, growth; −, no growth

Table 3 Genome features of *Caulobacter flavus* RHGG3^T

Features	Value
Genome size (bp)	5,659,202
Number of contigs	1
Average GC content (%)	69.25
Total number of genes	5172
Gene total length (bp)	5,056,212
Protein-coding genes (CDSs)	4989
rRNA genes (5S, 16S, 23S)	9
tRNA genes	55

2015). However, information on the plant growth-promoting traits of *Caulobacter* spp. from rhizosphere, their capacities and mechanisms in plant growth promotion and tolerance to heavy metals is relatively scarce (Pereira et al. 2016).

Notably, *C. flavus* RHGG3^T produces IAA (11.58 mg L^{-1}) and solubilizes phosphorus (80.56 mg L^{-1}), suggesting its potential in plant growth promotion (Table 1). Based on IAA production and phosphate solubilization abilities, the plant root elongation promoting activity of strain RHGG3^T was tested using the modified root elongation assay described by Belimov et al. (2005). Two milliliters of the bacterial suspension (5×10^7 cells mL^{-1}) or sterile water (uninoculated control) was added to glass Petri dishes containing filter paper. The watermelon seeds were surface-sterilized with 10% (v/v) H_2O_2 for 20 min, washed in sterile water, and placed on wetted filter paper. The assay was performed three times with three dishes (four seeds/dish) for each treatment. Root length and the number of lateral roots of the seedlings were measured after a 7-day incubation at 28 °C in the dark. Inoculation with strain RHGG3^T resulted in a significant increase in shoot length, root length and the total number of lateral roots by 22.1%, 43.7% and 55.9%, respectively (Table 1). In addition, strain RHGG3^T showed resistance to multiple heavy metals (copper, zinc, cadmium, cobalt and lead) (Table 2), and tolerated Cu^{2+} concentrations up to 0.2 mg mL^{-1} on GMSB agar (Sun et al. 2015).

We performed whole-genome sequencing of strain RHGG3^T to obtain detailed genetic information of *C. flavus* RHGG3^T with plant growth-promoting and heavy metal resistance abilities. Genomic DNA was extracted using the conventional phenol/chloroform/isoamyl alcohol (25:24:1) extraction method. The efficiency of the DNA extraction was tested using 1.0% agarose gel electrophoresis, and concentration and purity were determined with a TBS-380 spectrophotometer. An 8–10-kb DNA fragment library was constructed according to the manufacturer's instructions and sequenced on the PacBio RSII sequencing platform with a SMART cell (MajorBio Co., Shanghai, China). The filtered subreads (1,202,099,079 bp) with 214-fold genome coverage were assembled de novo using the hierarchical genome-assembly process (HGAP 3.0) (Chin et al. 2013).

Glimmer 3.0 (Delcher et al. 2007) was used to predict the protein-coding genes (open reading frames). The ribosomal RNA (rRNA) genes were predicted using Barrnap 0.4.2. The tRNA genes were predicted using tRNAscan-SEv1.3.1 (Lowe and Eddy 1997). Gene annotation was carried out by BLASTP search against the non-redundant GenBank protein database (http://www.ncbi.nlm.nih.gov/protein), Swiss-Prot database, the Clusters of Orthologous Groups of proteins (COG) database (http://www.ncbi.nlm.nih.gov/COG), and the KEGG database (http://www.genome.ad.jp/kegg). Further annotation was performed using the online RAST server online (Aziz et al. 2008). The circular genome was drawn using Circos v 0.64 (Krzywinski et al. 2009).

The genome of *C. flavus* RHGG3^T contained a 5,659,202 bp circular chromosome (69.25% G + C content), including 5172 predicted protein-coding genes, 9 rRNA genes, and 55 tRNA genes (details can be seen in Table 3; Fig. 1). It is notable that *C. flavus* is the first completely sequenced *Caulobacter* genome to have three rRNA operons. A total of 2957 identified genes were classified into functional categories according to the COG designations (Tatusov et al. 2000), and the results were as follows: two genes for

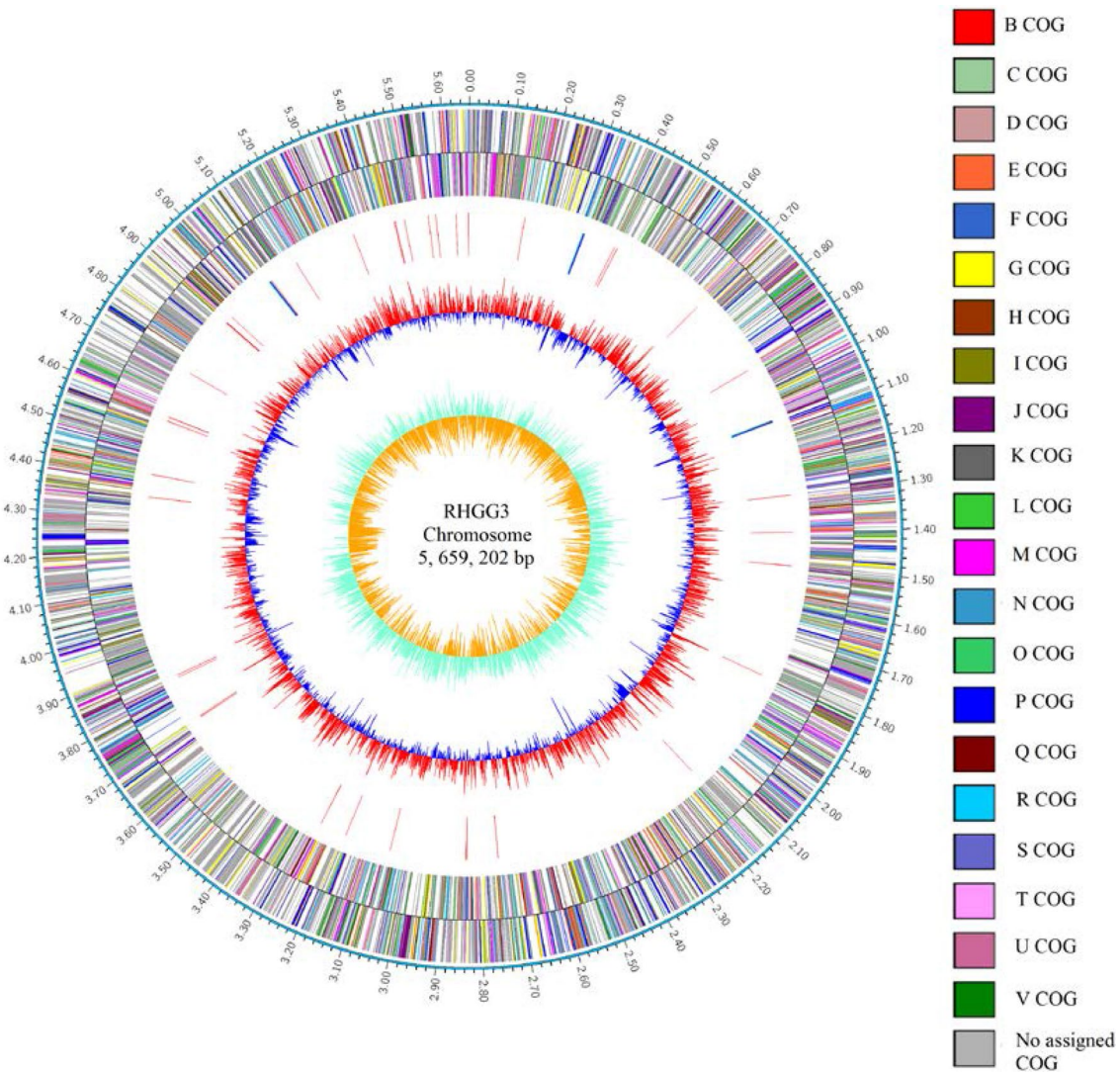

Fig. 1 Circular genome maps of *Caulobacter flavus* RHGG3. Rings from the outermost to the center: (1) scale marks of the genome, (2) protein-coding genes on the forward strand, (3) protein-coding genes on the reverse strand, (4) rRNA operon and tRNA genes, (5) GC content, and (6) GC skew. Circles 2 and 3 are open reading frames encoded by leading and lagging strands, respectively, with color codes for the COG functional categories: A, RNA processing and modification; B, chromatin structure and dynamics; J, translation, ribosomal structure and biogenesis; K, transcription; L, replication, recombination and repair; D, cell cycle control, cell division, chromosome partitioning; M, cell wall/membrane/envelope biogenesis; N, cell motility; O, posttranslational modification, protein turnover, chaperones; T, signal transduction mechanisms; U, intracellular trafficking, secretion, and vesicular transport; V, defense mechanisms; Z, cytoskeleton; C, energy production and conversion; E, amino acid transport and metabolism; F, nucleotide transport and metabolism; G, carbohydrate transport and metabolism; H, coenzyme transport and metabolism, I, lipid transport and metabolism; P, inorganic ion transport and metabolism; Q, secondary metabolite biosynthesis, transport and catabolism; R, general function prediction only; and S, function unknown

'chromatin structure and dynamics', 164 genes for 'translation, ribosomal structure and biogenesis', 200 genes for 'transcription', 138 genes for 'replication, recombination and repair', 22 genes for "cell cycle control, cell division, chromosome partitioning", 192 genes for 'cell wall/membrane/envelope biogenesis', 59 genes for 'cell motility', 136 genes for 'posttranslational modification, protein turnover and chaperones', 168 genes for 'signal transduction mechanisms', 92 genes for 'intracellular trafficking, secretion, and vesicular transport', 35 genes for 'defense mechanisms, 179 genes for 'energy production and conversion', 226 genes for 'amino acid transport and metabolism', 70 genes for 'nucleotide transport and metabolism', 168 genes for 'carbohydrate transport and metabolism', 92 genes for 'coenzyme transport and metabolism', 168 genes for 'lipid transport and metabolism', 190 genes for 'inorganic ion transport and metabolism', 110 genes for 'secondary metabolites biosynthesis, transport and catabolism', 215 genes for 'general function

prediction only' and 331 genes for 'function unknown' (Table S1).

We identified genes involved in nutrient availability as well as IAA, phenazine, volatile compounds, spermidine, and cobalamin production in the *C. flavus* RHGG3^T genomic sequence (Table 4). Few studies have investigated the function and mechanism of plant growth promotion in *Caulobacter* species. However, *C. flavus* RHGG3^T enhanced

Table 4 Candidate genes related to plant growth promotion in *Caulobacter flavus* RHGG3^T genome

Gene name	Gene ID	Gene annotation
Phosphate solubilization or transport genes		
ppk	ORF1527 (ORF3572)	Polyphosphate kinase
ppnk	ORF2945	Inorganic polyphosphate kinase
pit	ORF3753	Phosphate inorganic transporter
pstB	ORF0866	Phosphate ABC transporter ATP-binding protein
phy	ORF3225	3-Phytase
gcd	ORF3117(ORF5251, ORF1567)	Glucose dehydrogenase
Nitrogen fixation genes		
fixK	ORF0025	Nitrogen fixation-regulating protein FixK
nifU	ORF0965(ORF1242)	Nitrogen fixation protein NifU
nifS1	ORF2037	Nitrogenase metallocluster biosynthesis protein
nifS2	ORF3632	Nitrogenase metallocluster biosynthesis protein
glnA	ORF2439(ORF2447, ORF4112)	Glutamine synthetase genes
Volatile signal-related genes		
acoR	ORF1750	Acetoin catabolism regulatory protein
aco	ORF4739	Acetoin utilization protein
ilvH	ORF2866	Acetolactate synthase small subunit
ilvB	ORF2867	Acetolactate synthase isozyme 3 large subunit
ilvX	ORF0594	Putative acetolactate synthase large subunit
IAA-related genes		
trpA	ORF1509	Tryptophan synthase subunit alpha
trpB	ORF1510	Tryptophan synthase subunit beta
trpF	ORF1511	*N*-(5′-Phosphoribosyl)anthranilate isomerase
trpS	ORF1241	Tryptophan–tRNA ligase
trpR	ORF3001	TrpR-binding protein WrbA
trpE	ORF3811	Anthranilate synthase subunit I
trpG	ORF3814	Anthranilate synthase
trpD	ORF3815	Anthranilate phosphoribosyltransferase
trpC	ORF3816	Indole-3-glycerol phosphate synthase
Antibiotic-related genes		
phzF	ORF0105	Phenazine biosynthesis protein PhzF family
Others		
lysR	ORF4869	LysR transcriptional regulator
potD	ORF2440	Spermidine/putrescine ABC transporter substrate-binding protein
potB	ORF2441	Spermidine/putrescine ABC transporter permease
potC	ORF2442	Spermidine/putrescine ABC transporter permease
potA	ORF2443	Putrescine/spermidine ABC transporter ATP-binding protein
cobT	ORF0043	Cobaltochelatase CobT subunit
cobD	ORF4262	Cobalamin biosynthesis protein CobD
cobP	ORF4254	Cobalamin biosynthesis protein
cobW	ORF0743	Cobalamin biosynthesis protein CobW
cobS	ORF0496	Cobalamin biosynthesis protein CobS
cbiG	ORF4875	Cobalamin biosynthesis protein CbiG

plant growth through the production of IAA (Table 1). A sequence analysis of the *C. flavus* RHGG3^T genome also indicated the existence of genes responsible for IAA production, such as the tryptophan biosynthesis gene cluster (*trp*ABCDEFGRS). The *C. flavus RHGG3*^{T} genome also encoded glucose dehydrogenase (*gcd*), polyphosphate kinase [EC 2.7.4.1] (*ppk*), phosphate inorganic transporter (*pit*), phytase (*phy*) and nitrogenase (*fikK*), which increase plant phosphorus and nitrogen uptake abilities (Table 4). Glucose dehydrogenase is critical in the production of gluconic acid which is the major mechanism for phosphate solubilization in bacteria (Achal et al. 2007). Besides IAA, volatiles (acetoin and 2,3-butanediol) produced by bacteria can promote plant growth (Ping and Boland 2004). Acetolactate synthase (*alsS*) and acetolactate decarboxylase (*alsD*) catalyze the reaction from pyruvate to acetoin, and then acetoin is converted to 2,3-butanediol, either by the bacteria or by the host plant (Ryu et al. 2003). Moreover, the *C. flavus* RHGG3^T genome contained genes encoding acetolactate synthase (*alsS*), transcriptional regulator (*alsR*), and the acetoin utilization protein (Table 4). Antibacterial compounds, such as phenazine produced by PGP bacteria, inhibit pathogenic microbes and promote plant growth (Chen et al. 2015; He et al. 2012). The plant growth regulator spermidine has newly found roles in plant growth and the response to various abiotic stressors such as salt, drought, cold and oxidative stress (Alcazar et al. 2011). Additionally, *C. flavus* RHGG3^T contained gene clusters responsible for spermidine/putrescine ABC transporter permease (*potABCD*), phenazine and cobalamin.

Based on the annotation, many genes involved in heavy metal resistance were identified in the *C. flavus* RHGG3^T genome, including those encoding copper resistance proteins, multicopper oxidase, a cation transporter, and multiple heavy metal efflux pumps for cadmium, zinc and cobalt (Table 5). The *C. flavus* RHGG3^T genome also contained *czcCBA* operons, including outer membrane protein genes (*czcC*), inner membrane protein genes (*czcA*), and membrane fusion protein genes (*czcB*) and *czcD* genes (Table 5). The efflux transporter protein czcCBA exports cobalt/zinc/cadmium cations from both the cytoplasm and the periplasm to outside of the cell to protect the cell from heavy metal stress (Vaccaro et al. 2016).

The general features of *C. flavus* RHGG3^T and some other *Caulobacter* genomes are summarized in Table 6. Genomes in the genus *Caulobacter* showed a high G + C content ranging from 65.8 to 69.3% (Table 6). The genome sizes of the 9 strains of *Caulobacter* ranged from 3.96 to 5.89 Mb, with 3630–5378 predicted genes (Table 6). Strain *Caulobacter* sp. K31 had the largest genome size and the maximum number of predicted genes, whereas strain *C. henricii* CB4^T had the smallest genome size and the minimum number of predicted genes. Strains *C. henricii* CB4^T contained one plasmid, while strain *Caulobacter* sp. K31 contained two plasmids. These differences in genome size suggest that the evolution of *Caulobacter* is coupled with different levels of horizontal gene transfer, including gene insertion and deletion.

In summary, *C. flavus* RHGG3^T contained genes related to the promotion of plant growth and stress tolerance, such as phosphate solubilization, nitrogen fixation, production and utilization of IAA, acetoin, and spermidine, as well as the tolerance to heavy metals. Our findings provide a good explanation for the growth promotion of plants and resistance to heavy metals in plants. This is the first report on the complete genome sequence of the type strain *C. flavus* RHGG3^T. The detailed analysis of the complete *C. flavus* RHGG3^T genome sequence provides a molecular basis for biotechnological exploitation and applications in the field of agriculture and the environment.

Nucleotide sequence accession numbers and culture deposition

The whole-genome sequence of *C. flavus* RHGG3^T is available in the GenBank database under accession number CP026100. The strain has been deposited into the general collection of microorganism of the Korean Collection for Type Cultures (KCTC) under accession number KCTC42581^T, China General Microbiological Culture Collection Center under accession number CGMCC 1.15093^T and Japan Collection of Microorganisms under accession number JCM 30763^T.

Table 5 Metal resistance gene operons in the *Caulobacter flavus* RHGG3^T genome

Gene name	Gene ID	Gene annotation
Cd^{2+}, Zn^{2+}, Co^{2+}		
czcD	ORF0854	Cobalt transporter [*Caulobacter* cation diffusion facilitator family transporter]
	ORF0862	Cobalt transporter
czcC	ORF1649	Outer membrane protein
czcB	ORF1650	RND family efflux transporter, MFP subunit
czcA	ORF1651	Heavy metal efflux pump, cobalt–zinc–cadmium
zntA	ORF1654	Cadmium-exporting ATPase
czcD	ORF1658	PREDICTED: metal tolerance protein 1-like
czcC	ORF3713	Metal transporter [*Caulobacter* metal ion efflux outer membrane factor protein family]
czcB	ORF3714	Cation transporter [*Caulobacter* cation efflux system protein]
czcA	ORF3715	Cation transporter [*Caulobacter* AcrB/AcrD/AcrF family protein]
czcD	ORF3918	Cation diffusion facilitator family transporter
czcA	ORF3920	Heavy metal efflux pump, cobalt–zinc–cadmium
czcB	ORF3921	RND family efflux transporter, MFP subunit
czcC	ORF3922	Outer membrane protein
cusB	ORF3929	RND transporter [*Caulobacter* RND family efflux transporter]
cusA	ORF3930	Cation transporter [*Caulobacter* CzcA family heavy metal efflux pump]
Cu^{2+}		
copB	ORF0330	Copper resistance protein CopB
copA	ORF0332	Copper-binding protein
cueR	ORF1760	Transcriptional regulator
cutA	ORF2296	Cation tolerance protein CutA
copS	ORF2381	Histidine kinase
copR	ORF2382	Transcriptional regulator
cueO	ORF3812	Multicopper oxidase type 3
copA	ORF3931	Heavy metal translocating P-type ATPase
copC	ORF3936	Copper resistance protein CopC
copD	ORF3937	Copper resistance D domain-containing protein
copB	ORF3944	Copper resistance protein CopB
copA	ORF3945	Copper-binding protein
	ORF4873	Copper-binding protein

Table 6 Genomic features of strains in the genus *Caulobacter*

Num.	Strain	Size (Mb)	Number of plasmid	Contigs	GC content (%)	CDS	rRNA	tRNA	ncRNA	Pseudogene	Type strain	GenBank accession number
1	*C. flavus* RHGG3^T	5.66	0	1	69.3	4989	9	55			Yes	CP026100
2	*C. henricii* CB4^T	3.96	1	2	65.8	3630	6	50	3	70	Yes	CP013002; CP013003
3	*C. mirabilis* FWC38	4.58	0	1	69.3	4246	6	46	3	44	No	CP024201
4	*C. segnis* TK0059	4.66	0	1	67.7	4201	6	51	3	100	No	CP027850
5	*C. vibrioides* CB2	4.12	0	1	67.2	3896	6	52	0	102	Yes	P0C23313
6	*C. vibrioides* CB15	4.02	0	1	67.2	3737	6	51	1		No	AE005673
7	*C. vibrioides* CB1	4.14	0	1	67.2	3990	6	51	4	46	No	CP023314
8	*C. vibrioides* CB13b1a	4.14	0	1	67.0	3775	6	51	4	0	No	CP023315
9	*Caulobacter* sp. K31	5.89	2	3	67.4	5378	6	49	3	74	No	CP000927; CP000928; CP000929

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Compliance with ethical standards

Conflict of interest The authors declare no conflicts of interest.

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