Distribution, origin and evolution of siderophore systems in *Vibrionaceae*

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Keywords

Siderophore biosynthesis, iron metabolism, bisucaberin, vibrioferrin, piscibactin, catechols, hydroxamates, carboxylates, *Vibrionaceae*.

Abstract

Introduction: Siderophores are low molecular weight compounds synthesized and secreted by e.g., bacteria and fungi to bind and scavenge iron. Extracellular ferri-siderophore complexes are recognized by cognate receptors on the cell surface for transport over membranes. Several siderophore systems found in model bacteria from *Vibrionaceae* are known and well understood, e.g., the molecular structure of the siderophore, the biosynthesis gene cluster and pathway, and the gene expression pattern. Less is however known about how these systems are distributed in the approximately 140 *Vibrionaceae* species, and which evolutionary processes contributed to the present-day distribution. In this work, we compiled existing knowledge on siderophore biosynthesis systems and siderophore receptors from *Vibrionaceae* and used phylogenetic analyses to investigate their distribution, origin and evolution.

Results: A comprehensive literature study identified eight different siderophore biosynthesis systems and twelve siderophore receptors in *Vibrionaceae.* Homologous systems were identified by blast searches, and the result was then mapped onto a *Vibrionaceae* phylogeny. We identified 60 biosynthetic clusters distributed in 42 *Vibrionaceae* species and 14 unclassified *Vibrionaceae*

strains, and 330 siderophore receptors in 78 *Vibrionaceae* species and 40 unclassified *Vibrionaceae* strains. The majority of taxa are associated with at least one type of siderophore biosynthesis system, some (e.g., aerobactin and vibrioferrin) of which are widely distributed, whereas others (i.e., bisucaberin and vibriobactin) are found in only one single lineage. Cognate receptors are even more widespread into many taxa. A phylogenetic analysis of two siderophore systems (piscibactin and vibrioferrin) show that the present-day distribution can be explained by an old insertion into *Vibrionaceae*, followed mainly by stable vertical evolution and extensive loss.

Conclusions: The present work provides the most comprehensive overview of the distribution of siderophore-based iron acquisition systems in *Vibrionaceae*, and presents the first phylogenetic analyses of these systems. The results suggests that the present-day distribution is a result of several evolutionary processes, such as old and new gene acquisitions, gene loss, and both vertical and horizontal gene transfers.

Introduction

Siderophores represent a group of relatively small and low molecular weight secondary metabolites with high-affinity binding potential to ferric iron [1]. They are produced and secreted by a broad range of microorganisms, e.g., bacteria and fungi, and some plants. Under low iron conditions, such as in aquatic environments or inside a vertebrate host, bacteria must use highly specific strategies to acquire iron and other essential micronutrients [2, 3]. To overcome the iron starvation, siderophores are synthesized and secreted to their surroundings where they chelate ferric iron. Once bound, the ferric iron-siderohphore complexes are recognized by cognate siderophore receptors, and transported over the membrane by ABC transporters using TonB complexes as energy transducers.

Interestingly, bacteria produce siderophores of several major classes, each of which can have a diverse set of molecular structures, presumably because production of unique siderophores can provide individual bacterial species with an advantage in the competition with others [4]. For example, polymicrobial studies have shown that siderophores from one species can inhibit growth or functions of other species, e.g. low concentrations of avaroferrin from *Shewanella algae* inhibit swarming of *Vibrio alginolyticus* and a siderophore from *Pseudomonas fluorescens* inhibit growth of *Vibrio anguillarum* [5, 6]. Such kin discrimination strategy can however be bypassed by

"cheaters", i.e., bacteria expressing receptors on their surface with affinity to siderophores produced by others [7]. This mechanism is also known as exogenous or xeno-siderophore utilization. Evidently, there must be a constant battle between microorganisms for available iron; they can produce (i) own siderophores and the respective receptors, and/or (ii) "cheating" receptors for utilization of siderophores produced by others.

In this work, we have studied siderophore biosynthesis systems and their respective receptors from the *Vibrionaceae* family. *Vibrionaceae* represents a large and diverse group of Gram-negative Gamma Proteobacteria, and the evolutionary relationships between many of the approximately 140 different species were recently updated by Sawabe and coworkers [8]. Representatives of this family have been heavily studied, in most cases due to their ability to cause serious disease in humans or animals. The majority of species are however harmless and represent no threat, but instead play important roles in the environment e.g., in recycling of nutrients.

The causative agent of the human disease cholera, *Vibrio cholerae*, is the most famous *Vibrionaceae* representative. *V. cholerae* produces the catechol siderophore vibriobactin using proteins encoded by *vibABCDEFH* [9, 10]. Here, ferric iron-vibriobactin complexes are recognized by the receptor ViuA [11]. Moreover, *V. cholerae* can cheat on derivatives of enterobactin (produced by e.g., *Escherichia coli*) using the receptors IrgA and VctA [12], fluvibactin (synthesized by *Vibrio fluvialis*) using the ViuA, VctA and IrgA receptors, and finally ferrichrome by using the FhuA receptor [12-14]. *Vibrio vulnificus* represents another significant human pathogen [15]. This bacterium produces the catechol siderophores vulnibactin by using proteins encoded by the gene cluster VV2_0830 - VV2_0844 [16], and recognizes ferri-vulnibactin via the VuuA receptor [17]. It has also been proposed that *V. vulnificus* produces an uncharacterized hydroxamate siderophore, and an uncharacterized catechol siderophore using, in part, same genes as for vulnibactin [16, 18]. Finally, *V. vulnificus* can transport and utilize aerobactin (IutA receptor) [19], deferoxamine B (DesA receptor) [20, 21] and vibriobactin [22]. The human pathogen *Vibrio parahaemolyticus* [23] produces the carboxylate siderophore named vibrioferrin (encoded by *pvsABDE*) [24]. Vibrioferrin is sensitive to photolysis and has a lower affinity for iron compared to other catechol-type siderophores in vibrios. Ferri-vibrioferrin is recognized and transported over the membranes using the receptor PvuA [25]. *V. parahaemolyticus* can "cheat" using the exogenous siderophores enterobactin, aerobactin, ferrichrome and possibly vibriobactin and fluvibactin [22, 26-29].

Several *Vibrionaceae* fish pathogens have been studied with respect to siderophore production and utilization, e.g., *V. anguillarum*, a pathogen causing haemorrhagic septicaemia in fish, bivalves and crustaceans [30], *Aliivibrio salmonicida,* causing cold-water vibriosis in Atlantic salmon at low seawater temperatures [31, 32], *Photobacterium damselae subsp. piscicida* [33, 34], and *V. alginolyticus* [35]. Dependent on the strains, *V. anguillarum* can synthesize and utilize the mixed catechol/hydroxamate siderophore anguibactin (serotype O1 strain; biosynthesis encoded by *angABCE*^{B}/$_{G}$*MTHRNUD* and recognized by FatA receptor) [36, 37]. Intriguingly, anguibactin biosynthesis genes are located both on a virulence plasmid named pJM1, and on chromosomes (*angABC* and *angE*) [37]. In contrast, serotype O2 strains produce and utilize the catechol siderophore vanchrobactin (biosynthesis encoded by *dapH* and *vabABCEFH* [38], and recognized by the receptor encoded by *fvtA* [39]). *V. anguillarum* utilize exogenous siderophores like enterobactin, ferrichrome and citrate [40, 41]. *A. salmonicida* synthesizes and utilizes the di-hydroxamate siderophore bisucaberin (biosynthesis encoded by *bibABC* and recognized by the BitA receptor) [42, 43]. It has been postulated that the siderophore production is vital for the virulence of *A. salmonicida*. This assumption is based on that production of significant amounts of bisucaberin is restricted to low temperature conditions (bacterium only causes disease at low temperatures) [42]. Also, we recently showed that the genes responsible for bisucaberin are highly up-regulated under low iron conditions [44]. A system for aerobactin synthesis is in contrast not expressed, probably because the cluster is non-functional due to frameshift mutations and loss of the promotor [45]. The genome of *A. salmonicida* also encode the deferoxamine B receptor DesA and the aerobactin receptor IutA [45]. The fish pathogen *P. damselae subsp. piscicida* produces the mixed carboxylate and hydroxamate siderophore piscibactin (encoded by *dapH* and *irp123459*) and is probably transported by FrpA [33, 34]. *V. alginolyticus* is an emerging foodborne pathogen that causes gastroenteritis and peritonitis in humans [35]. The *V. alginolyticus* B522 strain contains the vibrioferrin biosynthesis cluster [5, 46], and can also utilize siderophores synthesized by *V. cholerae, V. fluvialis* and *V. parahaemolyticus* and ferrichrome [47, 48].

Payne and co-workers recently reviewed siderophore biosynthesis and utilization in *Vibrionaceae* [7]. This inspired us to use the existing knowledge to investigate the distribution and evolution of the different siderophore systems further. In this work, we first performed a comprehensive literature study on *Vibrionaceae* siderophore systems, and compared the gene synteny of the corresponding siderophore gene clusters. Furthermore, we searched the databases

for siderophore systems in all available *Vibrionaceae* genomes, and mapped the result onto a *Vibrionaceae* phylogenetic network. The evolution of individual siderophore biosynthesis systems and receptors was subsequently studied by constructing phylogenetic trees based on amino acids datasets, and by comparing the resulting tree topologies to host trees. Through the presented work we wish to broaden the perspective and existing knowledge on siderophore synthesis and utilization within the *Vibrionaceae* family.

Material and Methods

Data retrieval

Siderophore biosynthesis gene clusters and associated siderophore receptor genes in *Vibrionaceae* were identified by a literature search, and the corresponding protein sequences were retrieved from ENA/GenBank. Updated RefSeq accession numbers for identified proteins with the 'WP' prefix (replaced the 'YP', 'NP' and 'ZP' prefixes) are presented in Table 1 and 2. These sequences were next used as queries in BLASTP searches to find homologous sequences. BLASTP was run using the non-redundant protein database while restricted to the *Vibrionaceae* family (NCBI taxid:641). Only hits with ≥80% coverage and ≥50% identity were considered, and one representative sequence per species was kept (i.e., presence/absence variations within species were not considered). Hits labelled "low quality protein" in the databases were excluded.

Mapping of siderophore systems onto a Vibrionaceae *phylogenetic network*

A *Vibrionaceae* host phylogeny was inferred based on sequence alignments of the genes *ftsZ, gap, gyrB, mreB, pyrH, recA, rpoA* and *topA,* provided by Dr.Sawabe [8]. Splitstree4 [49] was used to concatenate the sequences to construct a multi locus sequence alignment (MLSA), and to generate an unrooten phylogenetic network. Settings were set to 'NeighbourNet' method with 'uncorrected P' distance. Presence/absence of siderophore biosynthesis and receptor genes were mapped onto the phylogenetic network (only complete siderophore biosynthesis clusters are shown). The siderophore receptors were considered separately, and mapped onto the same network. Species with positive hits, but not included in the MLSA dataset, were placed onto the network based on the literature.

149

150 *Phylogeny analysis of siderophore biosynthesis systems and receptors*

151 Amino acid sequences of proteins involved in siderophore biosynthesis were aligned individually
152 using ClustalW [50]. Proteins belonging to same clusters were concatenated using SplitsTree4 [49]
153 and exported to Fasta format, thus generating the final datasets. Next, Mega6 [51] was used to
154 generate Maximum Likelihood (ML) trees based on the individual siderophore biosynthesis
155 datasets. The robustness of nodes in the resulting phylogenies was tested by running Bootstrap
156 analyses, using the ML method (2000 replicates, JTT substitution model, uniform rates, and
157 'Complete deletion' in gap handling).

158 To address inheritance of the siderophore biosynthesis systems, we next constructed host
159 phylogenies of same taxa as those containing the siderophore systems. Host trees were based on
160 concatenated datasets of the same eight genes as described above. ML-trees were constructed using
161 the Tamura-Nei model [52], and all gaps and missing data were removed. Phylogenies of the
162 vibrioferrin (PvsABCDE) and piscibactin (Irp123459) systems, and their corresponding MLSA
163 host trees, were rooted on *Aliivibrio wodanis* and *Photobacterium profundum*, respectively. The
164 phylogeny of siderophore receptors was constructed essentially as described above. Briefly, amino
165 acid sequences of homologous receptor sequences were aligned using ClustalW, and Mega6 [51]
166 was then used to make ML-trees. Bootstrap analysis was done using the ML method, 2000
167 pseudoreplicates, the JTT model, uniform rates, and complete deletion of gaps. Corresponding
168 MLSA trees were constructed as described for the cluster. The receptor phylogenies were compared
169 to host trees, which were constructed as described above.

170

171 **Results and discussion**

172 *Compilation of siderophore biosynthesis gene cluster sequences from* Vibrionaceae

173 In this work we set out to do a comprehensive search, both in the literature and the global sequence
174 databases, to identify gene clusters for biosynthesis of siderophores in *Vibrionaceae*, and compile
175 and visualize the result in a simple and comprehensible manner. Figure 1 and Table 1 summarizes
176 our findings. Based on the literature we identified eight siderophore biosynthesis clusters
177 responsible for producing aerobactin, bisucaberin, vibrioferrin, vibriobactin, vanchrobactin,

178 piscibactin, anguibactin and vulnibactin. Figure 1 shows that genes belonging to the individual
179 siderophore biosynthetic pathways are typically found clustered "bumper-to-bumper" on the
180 chromosome (or as in *V. anguillarum*, on a plasmid). Pathways for hydroxamate or carboxylate
181 type siderophores are encoded by 3−5 genes, all encoded on the same DNA strand, whereas
182 catechol or mixed siderophores pathways are typically encoded by 6−11 genes, including one or
183 more NRPS gene(s), located on both strands and not necessarily in immediate proximity to each
184 other. The synteny and general organization of the latter siderophore biosynthetic gene cluster types
185 therefore appear more complex. *V. fluvialis* and *Vibrio nigripulchritudo* produce the catechol
186 siderophores fluvibactin and nigribactin (Figure 1C), respectively [53, 54]. However, the genes
187 encoding the biosynthesis systems are unknown.
188 Next, we used the known *Vibrionaceae* amino acids sequences (see Figure 1A and 1B) as
189 queries in blastP searches to identify homologous siderophore gene clusters in all available
190 *Vibrionaceae* genomes/ sequences in European Nucleotide Archive (ENA). Threshold values were
191 set to ≥80% coverage and ≥50% identity. Only complete siderophore biosynthesis clusters were
192 kept (i.e., all genes needed for biosynthesis must be present). Our search identified 60 biosynthetic
193 clusters in total, distributed among 42 species and 4 genera, and 14 unclassified *Vibrionaceae*
194 strains (i.e., *Vibrio* sp.), (see Supplementary file S1 for details). The majority of species can
195 potentially produce 1−3 of the known *Vibrionaceae* siderophores, with zero being the minimum
196 and four the maximum.
197 Bacteria must encode and express siderophore receptors on their surface in order to take up
198 and utilize siderophore-Fe^{3+} complexes. It is therefore of equal importance to identify and map the
199 existence of siderophore-associated receptors. In a similar approach as described above, we
200 identified and used siderophore receptor amino acid sequences in blastP searches. Accession
201 numbers of siderophore receptors that were used as queries are presented in Table 2. The receptor
202 searches identified 330 siderophore receptors in 78 classified *Vibrionaceae* species (and 40
203 unclassified *Vibrionaceae* strains), representing 5 genera (when using the same cut-off values as
204 described above). The complete list of identified siderophore receptors are presented in
205 Supplementary file S2. We found homologs of known *Vibrionaceae* siderophore receptors in
206 almost all *Vibrionaceae* species (Twenty-nine of the representatives in the split network do not
207 encode homologs of known *Vibrionaceae* siderophore biosynthesis clusters or receptor. Of the 29,

only 14 are fully sequenced), and the maximum number of different siderophore receptors found in a single genome was eight (i.e., in *V. alginolyticus*).

In summary, we searched the literature for known siderophore biosynthetic gene cluster from the *Vibrionaceae* family and identified eight different. The amino acids sequences corresponding to the known *Vibrionaceae* siderophore biosynthetic clusters and siderophore receptor were used as queries in blastP to identify homologs within the same family. A total of 60 biosynthetic clusters distributed among 42 species and 14 unclassified *Vibrionaceae* strains were identified. Using a similar approach we identified 330 siderophore receptor genes in 78 *Vibrionaceae* species and 40 unclassified *Vibrionaceae* strains.

Distribution of siderophore biosynthesis clusters and siderophore receptors in the Vibrionaceae family

Figure 2 shows the distribution of siderophore biosynthetic systems and receptor genes on a phylogenetic network containing 86 representative species and unclassified strains from *Vibrionaceae*. Overall, the figure shows that the vast majority of species are associated with at least one type of siderophore system. We have however not examined to what extent each of the siderophore system are present in each species. In other words, individual isolates may or may not contain siderophore systems associated with that species, as indicated on the splits network. Moreover, some siderophore systems are restricted to a very narrow phylogenetic lineage, whereas others have a wide but sporadic presence. For example, the aerobactin, vanchrobactin and piscibactin biosynthesis clusters appears to be scattered across multiple phylogenetic lineages, and the anguibactin clusters are found in *V. anguillarum* as well as in the *Splendius* and *Harveyi* clades. Similarly, vibrioferrin biosynthesis clusters are found in *A. wodanis*, *Vibrio navarrensis*, and inside the *Harveyi* and *Splendidus* clades.

In contrast to the widespread, but sporadic distribution of the siderophore biosynthetic genes described above, bisucaberin biosynthesis clusters are narrowly distributed into one lineage, i.e., in three species from the *Fischeri* clade. This finding suggest that bisucaberin was introduced into *Vibrionaceae* through horizontal gene transfer into the most recent common ancestor of *A. wodanis*, *A. logei*, and *A. salmonicida* (indicated by a red arrow in Figure 2). Similarly, vulnibactin is restricted to *V. vulnificus*, and vibriobactin is only found in the closely related species *Vibrio*

albensis and *V. cholerae*. Interestingly, no siderophore biosynthesis clusters were identified in the *Halioticoli* clade.

In addition to showing presence/absence of siderophore biosynthetic gene clusters, Figure 2 also displays how the respective siderophore receptors are distributed in *Vibrionaceae*. Some main findings are that (i) the presence of biosynthetic genes for individual siderophores is accompanied by the presence of the corresponding receptor, (ii) the number of different types of receptors typically exceeds (and in some cases by far) the number of biosynthetic cluster types, and (iii) similar to the biosynthetic clusters the receptors are widely distributed in *Vibrionaceae*. E.g., *iutA* (aerobactin receptor gene) and *desA* (deferroxamine B receptor gene) are found in nearly all clades. Also, the receptor genes *viuA* (for vibriobactin), *vuuA* (for vulnibactin), *pvuA* (for vibrioferrin), *vctA* and *irgA* (both for enterobactin), and finally *fhuA* (for ferrichrome) are widely distributed. In contrast, other receptors are more narrowly distributed, e.g., the bisucaberin receptor gene *bitA*, which is restricted to the *Fischeri* clade, more specifically to the same three *Aliivibrio* species that contain corresponding bisucaberin biosynthesis clusters.

Interestingly, (iv) known pathogens are conspicuously rich in siderophore receptors. E.g., *V. cholerae, V. alginolyticus* and *V. parahaemolyticus* encode seven, eight and five different receptor types, respectively. It is tempting to speculate that this richness likely reflects the lifestyle of these bacteria, where iron acquisition would be critical, especially during the initial phases of infections. Also, having multiple siderophore receptors would make them efficient "cheaters", i.e., they can use siderophores produced by other species rather from themselves. The receptors IrgA, VctA, FhuA and DesA are found in many "cheaters" throughout *Vibrionaceae*. Another explanation for the apparent richness in receptor types is that these species have been characterized in more detail than environmental isolates, but at least pathogens still encode a higher number of known siderophore receptor types.

Evolution siderophore systems

To evaluate the evolutionary history of siderophore systems (biosynthesis and receptors) in *Vibrionaceae*, and to better understand their present-day distribution, we concatenated the protein sequences from the most abundant types of biosynthetic clusters separately, and aligned the resulting sequences using ClustalW. Only species included in Figure 2 were investigated.

Maximum likelihood (ML) trees were generated from PvsABCDE (vibrioferrin cluster) and Irp123459 (piscibactin cluster) datasets. Similarly, datasets and ML-tree were made for siderophore receptors. The rationale for treating receptor sequences separate from biosynthesis genes was that receptor genes are often located elsewhere in the genome, and are much more widely distributed than the biosynthesis genes. ML-trees of the concatenated biosynthesis proteins and receptors were juxtaposed a host phylogeny based on same dataset as that used in Figure 2. Similar tree topologies (congruence) were interpreted as same evolutionary trajectories (i.e., vertical evolution), whereas conflicting topologies would suggest horizontal gene transfer events.

Figure 3 shows the genetic organization and phylogeny of the piscibactin system. Nodes in the trees are highly supported by 95−100% bootstrap values. Although there are some discrepancies in the phylogenies, the overall tree topologies are very similar. Based on the criteria described above the data thus suggest that the piscibactin biosynthesis pathway was introduced early into *Vibrionaceae* and then stably inherited in a few lineages, and lost in the majority of lineages. Similarly, the overall topology for the proposed piscibactin receptor FrpA and the corresponding host tree are in good overall agreement, except for one clear case of misplacement, i.e., *Vibrio harveyi* and *Vibrio rotiferianus* (*Harveyi* clade). Interestingly, these two species only contain the receptor, and not the biosynthesis system. This strongly suggests one horizontal gene transfer event of the FrpA receptor into the common ancestor of these two close related species.

Figure 4 shows the genic organization and phylogeny of the vibrioferrin system. Intriguingly, the result is strikingly similar to that of the piscibactin system. The overall tree topologies for the biosynthesis system and the host phylogenies are very similar, except that *V. harveyi* and *V. rotiferianus* are clearly misplaced (strongly supported by high bootstrap values). The evolution of the associated receptor (PvuA) appears to be more influenced by horizontal gene transfer events. The PvuA and host trees are mostly congruent within the *Splendidus* clade, whereas the remaining branches have multiple clear, highly supported, misplacements in the PvuA protein (compared to the host tree). Therefore, the evolution of the biosynthesis and receptor genes are, in part, different with partly vertical and horizontal gene transfers.

The very narrow distribution of the bisucaberin cluster (in the *Fischeri* clade) suggest a different evolutionary history, i.e., a recent insertion event into a common ancestor of *A. salmonicida*, *A. wodanis* and *Aliivibrio logei* (indicated by an arrow in Fig. 3). Until recently, the

bisucaberin biosynthesis genes (*bibABC*) were found exclusively in *A. salmonicida* (within *Vibrionaceae*) [44]. Here, the system is located on a genomic location (island) flanked by transposable elements. Our current blastP searches show that similar clusters are also found in *A.logei* and *A. wodanis*, together with the corresponding receptor gene *bitA*. Origin of the system is still unclear. We have in vain tried to identify the donor organism by running blastP and PSI-blast searches. The best database hits point to *Shewanella* as a possible source (BibA and BibB has 57% and 60 identity over 98 % and 97% coverage, respectively, to *S. algae*. BibC 60% identity over 74% coverage to *Shewanella baltica* and *Shewanella putrefaciens*), but this needs to be addressed again as more genomic data from environmental marine bacterial strains are added to the databases.

In summary, the present-day distribution of siderophore systems in *Vibrionaceae* appears to be, perhaps as can be expected, a result of a combination of events: both old and new gene acquisitions, extensive gene loss, and both vertical and horizontal gene transfers. We realize that we have only started to scratch the surface of understanding the origin and evolution of siderophore systems in *Vibrionaceae* (and other families). It is our intention to expand our analyses to more siderophore systems and to go even deeper into their gene organization, distribution and evolution. Our preliminary results indicate that the story is far from complete and will likely reveal more surprises and fascinating examples of rampant gene transfers.

Concluding remarks

We have used existing knowledge on siderophore systems to search for homologs in the databases, and mapped the result on a *Vibrionaceae* phylogenetic network. Overall, the result shows that the vast majority of species are associated with at least one type of siderophore biosynthesis system. Some systems (e.g., aerobactin and vibrioferrin) are seemingly scattered throughout the family, with a wide, but sporadic distribution, whereas others are presence in one lineage only (e.g., bisucaberin and vibriobactin). Cognate receptors are generally associated with its biosynthesis system, but are in addition spread into many other taxa (that does not encode the siderophore biosynthesis). A limited analysis of the origin and evolution of a few of the siderophore systems show that the present-day distribution can be explained by a combination of events, i.e., old and new gene acquisitions, extensive gene loss, and vertical and horizontal gene transfers. We realize

that we have only started to scratch the surface of understanding the origin and evolution of siderophore systems in *Vibrionaceae* (and other families), and it is our intention to expand our analyses to more siderophore systems and go deeper into their gene organization, distribution and evolution. Our preliminary results on more system indicate that the story is far from complete, and the future will likely reveal more surprises and fascinating examples of stable, as well as rampant, gene transfers.

Availability of supporting data

Supplementary file S1: Complete lists of homology hits from the blastP query of eight *Vibrionaceae* siderophore biosynthesis clusters.

Supplementary file S2: Complete lists of homology hits from the blastP query of twelve *Vibrionaceae* siderophore receptors.

Abbreviations

aa: Amino acid; MLSA: Multilocus sequence alignment; NRPS: Non-Ribosomal Peptide Synthase; ML: Maximum Liklihood; nt: nucleotide; ABC transporter: ATP-binding cassette transporter; *V.sp*: *Vibrio* species; *A. sp*: *Aliivibrio* species; *G. sp*: *Grimontia* species; *P. sp*: *Photobacterium* species; blastP: Protein Blast; ENA; European Nucleotide Archive.

Competing interests

The authors declare that they have no competing interests.

Ethics statement

The research presented in this paper do not involve human subjects, and we see no ethical issues.

Authors` contributions

PH and SKT conceived the study and drafted the manuscript. PH constructed the *Vibrionaceae* MLSA tree, and supervised the study. SKT performed literature studies, data collections, mapped the data to the MLSA tree, studied and visualized the clusters, developed the method for finding catechol siderophore clusters, constructed the MLSA and cladograms of siderophore biosynthesis clusters and receptors. MK, ER and RA performed data collections and initial trial studies.

Figure and table legends

Table 1. Accession number of known *Vibrionaceae* siderophore biosynthetic proteins used as query for homolog searches using blastP. The table gives an overview of the accession numbers for each protein sequence corresponding to a gene in the siderophore biosynthesis cluster. Provided are also the origin species, references and what siderophore the cluster produce.

Table 2. Accession number of known *Vibrionaceae* siderophore receptor proteins used as query for homolog searches using blastP. The table gives an overview of the accession numbers for protein sequence of the receptors. Provided are also the origin species, references and what siderophore the receptors can transport.

Figure 1. Organization of *Vibrionaceae* siderophore biosynthesis clusters and schematic structure of the known *Vibrionaceae* siderophores. A) *Vibrionaceae* hydroxamate, carboxylate and mixed hydroxamate/carboxylate siderophore biosynthesis clusters. B) *Vibrionaceae* catechol and mixed catechol/hydroxamate siderophore biosynthesis cluster. C) Schematic structure representation of known *Vibrionaceae* siderophores (chirality and lengths of binding are not exact).

Figure 2. Distribution of homologs of known *Vibrionaceae* siderophore biosynthesis clusters and receptors mapped to a phylogenetic split network based on a dataset from Sawabe and co-workers [8], consisting of the genes *ftsZ*, *gap*, *gyrB*, *mreB*, *pyrH*, *recA*, *rpoA* and *topA* for each species. The

tree was constructed using Splitstree4 to concatenate alignments and settings for network was were uncorrected_P and NeighborNet [49]. Branch lengths are to scale and species located outside grey arches were not included in the MLSA files and have been approximately placed according to literature [55-70].

Figure 3. Inheritance of the piscibactin biosynthesis cluster and receptor within the *Vibrionaceae* family. A) The cluster organization of the biosynthesis cluster and the cognate receptor. B) Host phylogeny on the left and piscibactin biosynthesis system (Irp123459) phylogeny on the right. C) Host phylogeny on the left and piscibactin receptor (FrpA) phylogeny on the right. *species that do not encode the piscibactin biosynthesis system, i.e., the FrpA homolog is an exogenous siderophore receptor. Evolutionary analyses were conducted in MEGA6 [51]. The host trees were generated using the ML method and the TM model [52]. The siderophore biosynthesis cluster and receptor trees were generated using the ML method and the JTT model [71]. Bootstrap values are shown at the nodes (JTT model, 2000 replicates) [72]. Branch lengths are measured substitutions per site. Bootstrap values are shown at the nodes (JTT model, 2000 replicates) [72].

Figure 4. Inheritance of the vibrioferrin biosynthesis cluster and receptor within the *Vibrionaceae* family. A) The cluster organization of the biosynthesis cluster and the cognate receptor. B) Host phylogeny on the left and vibrioferrin biosynthesis system (PvsABCDE) phylogeny on the right. C) Host phylogeny on the left and vibrioferrin receptor (PuvA) phylogeny on the right. *species that do not encode the vibrioferrin biosynthesis system, i.e., the PuvA homolog is an exogenous siderophore receptor. Evolutionary analyses were conducted in MEGA6 [51]. The host trees were generated using the ML method and the TM model [52]. The siderophore biosynthesis cluster and receptor trees were generated using the ML method and the JTT model [71]. Bootstrap values are shown at the nodes (JTT model, 2000 replicates) [72]. Branch lengths are measured substitutions per site. Bootstrap values are shown at the nodes (JTT model, 2000 replicates) [72].

Supplementary file S1. Complete lists of homology hits from the blastP query of eight *Vibrionaceae* siderophore biosynthesis clusters with accession numbers and coverage/ identity/ e-value scores.

Supplementary file S2. Complete lists of homology hits from the blastP query of twelve *Vibrionaceae* siderophore receptor with accession numbers and coverage/ identity/ e-value scores.

References

1. Neilands JB: **Siderophores: structure and function of microbial iron transport compounds.** *J Biol Chem* 1995, **270:**26723-26726.
2. Fillat MF: **The FUR (ferric uptake regulator) superfamily: Diversity and versatility of key transcriptional regulators.** *Arch Biochem Biophys* 2014, **546:**41-52.
3. Miethke M: **Molecular strategies of microbial iron assimilation: from high-affinity complexes to cofactor assembly systems.** *Metallomics* 2013, **5:**15-28.
4. Hibbing ME, Fuqua C, Parsek MR, Peterson SB: **Bacterial competition: surviving and thriving in the microbial jungle.** *Nat rev Microbiol* 2010, **8:**15-25.
5. Böttcher T, Clardy J: **A chimeric siderophore halts swarming Vibrio.** *Angew Chem* 2014, **53:**3510-3513.
6. Holmstrøm K, Gram L: **Elucidation of the *Vibrio anguillarum* genetic response to the potential fish probiont *Pseudomonas fluorescens* AH2, using RNA-arbitrarily primed PCR.** *J Bacteriol* 2003, **185:**831-842.
7. Payne SM, Mey AR, Wyckoff EE: **Vibrio Iron Transport: Evolutionary Adaptation to Life in Multiple Environments.** *Microbiol Mol Biol Rev* 2016, **80:**69-90.
8. Sawabe T, Ogura Y, Matsumura Y, Feng G, Amin AR, Mino S, Nakagawa S, Sawabe T, Kumar R, Fukui Y, et al: **Updating the Vibrio clades defined by multilocus sequence phylogeny: proposal of eight new clades, and the description of *Vibrio tritonius* sp. nov.** *Front Microbiol* 2013, **4:**414.
9. Wyckoff EE, Smith SL, Payne SM: **VibD and VibH are required for late steps in vibriobactin biosynthesis in *Vibrio cholerae*.** *J Bacteriol* 2001, **183:**1830-1834.
10. Butterton JR, Choi MH, Watnick PI, Carroll PA, Calderwood SB: ***Vibrio cholerae* VibF is required for vibriobactin synthesis and is a member of the family of nonribosomal peptide synthetases.** *J Bacteriol* 2000, **182:**1731-1738.
11. Stoebner JA, Butterton JR, Calderwood SB, Payne SM: **Identification of the vibriobactin receptor of *Vibrio cholerae*.** *J Bacteriol* 1992, **174:**3270-3274.
12. Wyckoff EE, Allred BE, Raymond KN, Payne SM: **Catechol Siderophore Transport by *Vibrio cholerae*.** *J Bacteriol* 2015, **197:**2840-2849.
13. Mey AR, Wyckoff EE, Oglesby AG, Rab E, Taylor RK, Payne SM: **Identification of the *Vibrio cholerae* enterobactin receptors VctA and IrgA: IrgA is not required for virulence.** *Infect Immun* 2002, **70:**3419-3426.
14. Rogers MB, Sexton JA, DeCastro GJ, Calderwood SB: **Identification of an operon required for ferrichrome iron utilization in *Vibrio cholerae*.** *J Bacteriol* 2000, **182:**2350-2353.
15. Linkous DA, Oliver JD: **Pathogenesis of *Vibrio vulnificus*.** *FEMS Microbiol Lett* 1999, **174:**207-214.
16. Tan W, Verma V, Jeong K, Kim SY, Jung CH, Lee SE, Rhee JH: **Molecular characterization of vulnibactin biosynthesis in *Vibrio vulnificus* indicates the existence of an alternative siderophore.** *Front Microbiol* 2014, **5:**1.
17. Webster AC, Litwin CM: **Cloning and characterization of *vuuA*, a gene encoding the *Vibrio vulnificus* ferric vulnibactin receptor.** *Infect Immun* 2000, **68:**526-534.
18. Simpson LM, Oliver JD: **Siderophore production by *Vibrio vulnificus*.** *Infect Immun* 1983, **41:**644-649.
19. Tanabe T, Naka A, Aso H, Nakao H, Narimatsu S, Inoue Y, Ono T, Yamamoto S: **A novel aerobactin utilization cluster in *Vibrio vulnificus* with a gene involved in the transcription regulation of the *iutA* homologue.** *Microbiol Immunol* 2005, **49:**823-834.
20. Aso H, Miyoshi S, Nakao H, Okamoto K, Yamamoto S: **Induction of an outer membrane protein of 78 kDa in *Vibrio vulnificus* cultured in the presence of desferrioxamine B under iron-limiting conditions.** *FEMS Microbiol Lett* 2002, **212:**65-70.

21. Tanabe T, Takata N, Naka A, Moon YH, Nakao H, Inoue Y, Narimatsu S, Yamamoto S: **Identification of an AraC-like regulator gene required for induction of the 78-kDa ferrioxamine B receptor in *Vibrio vulnificus*.** *FEMS Microbiol Lett* 2005, **249:**309-314.
22. Andrus CR, Walter M, Crosa JH, Payne SM: **Synthesis of siderophores by pathogenic Vibrio species.** *Curr Microbiol* 1983, **9:**209-214.
23. Daniels NA, MacKinnon L, Bishop R, Altekruse S, Ray B, Hammond RM, Thompson S, Wilson S, Bean NH, Griffin PM, Slutsker L: ***Vibrio parahaemolyticus* infections in the United States, 1973-1998.** *J Infect Dis* 2000, **181:**1661-1666.
24. Tanabe T, Funahashi T, Nakao H, Miyoshi S, Shinoda S, Yamamoto S: **Identification and characterization of genes required for biosynthesis and transport of the siderophore vibrioferrin in *Vibrio parahaemolyticus*.** *J Bacteriol* 2003, **185:**6938-6949.
25. Funahashi T, Moriya K, Uemura S, Miyoshi S, Shinoda S, Narimatsu S, Yamamoto S: **Identification and characterization of *pvuA*, a gene encoding the ferric vibrioferrin receptor protein in *Vibrio parahaemolyticus*.** *J Bacteriol* 2002, **184:**936-946.
26. Tanabe T, Funahashi T, Shiuchi K, Okajima N, Nakao H, Miyamoto K, Tsujibo H, Yamamoto S: **Characterization of *Vibrio parahaemolyticus* genes encoding the systems for utilization of enterobactin as a xenosiderophore.** *Microbiology* 2012, **158:**2039-2049.
27. Tanabe T, Kato A, Shiuchi K, Miyamoto K, Tsujibo H, Maki J, Yamamoto S, Funahashi T: **Regulation of the expression of the *Vibrio parahaemolyticus peuA* gene encoding an alternative ferric enterobactin receptor.** *PLoS One* 2014, **9:**e105749.
28. Funahashi T, Tanabe T, Aso H, Nakao H, Fujii Y, Okamoto K, Narimatsu S, Yamamoto S: **An iron-regulated gene required for utilization of aerobactin as an exogenous siderophore in *Vibrio parahaemolyticus*.** *Microbiology* 2003, **149:**1217-1225.
29. Funahashi T, Tanabe T, Shiuchi K, Nakao H, Yamamoto S: **Identification and characterization of genes required for utilization of desferri-ferrichrome and aerobactin in *Vibrio parahaemolyticus*.** *Bio Pharm Bull* 2009, **32:**359-365.
30. Frans I, Michiels CW, Bossier P, Willems KA, Lievens B, Rediers H: ***Vibrio anguillarum* as a fish pathogen: virulence factors, diagnosis and prevention.** *J Fish Dis* 2011, **34:**643-661.
31. Enger O, Husevåg B, Goksøyr J: **Seasonal variations in precense of *Vibrio salmonicida* and total bacterial counts in Norwegian fish-farm water.** *Can J Microbiol* 1991, **37:**618 - 623.
32. Colquhoun D, Sørum H: **Temperature dependent siderophore production in *Vibrio salmonicida*.** *Microb Pathog* 2001, **31:**213 - 219.
33. Osorio CR, Juiz-Rio S, Lemos ML: **A siderophore biosynthesis gene cluster from the fish pathogen *Photobacterium damselae subsp. piscicida* is structurally and functionally related to the Yersinia high-pathogenicity island.** *Microbiology* 2006, **152:**3327-3341.
34. Souto A, Montaos MA, Rivas AJ, Balado M, Osorio CR, Rodríguez J, Lemos ML, Jiménez C: **Structure and Biosynthetic Assembly of Piscibactin, a Siderophore from *Photobacterium damselae subsp. piscicida*, Predicted from Genome Analysis.** *Eur J Org Chem* 2012, **2012:**5693-5700.
35. Mustapha S, Mustapha EM, Nozha C: ***Vibrio alginolyticus*: an emerging pathogen of food borne diseases.** *Int J Sci Tech* 2013, **2:**302-309.
36. Actis LA, Fish W, Crosa JH, Kellerman K, Ellenberger SR, Hauser FM, Sanders-Loehr J: **Characterization of anguibactin, a novel siderophore from *Vibrio anguillarum 775*(pJM1).** *J Bacteriol* 1986, **167:**57-65.
37. Alice AF, Lopez CS, Crosa JH: **Plasmid- and chromosome-encoded redundant and specific functions are involved in biosynthesis of the siderophore anguibactin in *Vibrio anguillarum* 775: a case of chance and necessity?** *J Bacteriol* 2005, **187:**2209-2214.

38. Balado M, Osorio CR, Lemos ML: **A gene cluster involved in the biosynthesis of vanchrobactin, a chromosome-encoded siderophore produced by *Vibrio anguillarum*.** *Microbiology* 2006, **152:**3517-3528.
39. Balado M, Osorio CR, Lemos ML: **FvtA is the receptor for the siderophore vanchrobactin in *Vibrio anguillarum*: utility as a route of entry for vanchrobactin analogues.** *Appl Environ Microbiol* 2009, **75:**2775-2783.
40. Naka H, Crosa JH: **Identification and characterization of a novel outer membrane protein receptor FetA for ferric enterobactin transport in *Vibrio anguillarum* 775 (pJM1).** *Biometals* 2012, **25:**125-133.
41. Lemos M, Osorio C: **Iron Uptake in *Vibrio* and *Aeromonas*.** In *Iron Uptake and Homeostasis in Microorganisms.* Edited by Cornelis P, Andrews SC. Norfolk, UK: Caister Academic Press; 2010: 117 - 141
42. Winkelmann G, Schmid D, Nicholson G, Jung G, Colquhoun D: **Bisucaberin-a dihydroxamate siderophore isolated from *Vibrio salmonicida*, an important pathogen of farmed Atlantic salmon (*Salmo salar*).** *BioMetals* 2002, **15:**153 - 160.
43. Kadi N, Song L, Challis G: **Bisucaberin biosynthesis: an adenylating domain of the BibC multi-enzyme catalyzes cyclodimerization of N-hydroxy-N-succinylcadaverine.** *Chem Commun (Camb)* 2008, **41:**5119 - 5121.
44. Thode SK, Kahlke T, Robertsen EM, Hansen H, Haugen P: **The immediate global responses of *Aliivibrio salmonicida* to iron limitations.** *BMC Microbiol* 2015, **15:**1-9.
45. Hjerde E, Lorentzen M, Holden M, Seeger K, Paulsen S, Bason N: **The genome sequence of the fish pathogen *Aliivibrio salmonicida* strain LFI1238 shows extensive evidence of gene decay.** *BMC Genomics* 2008, **9:**616.
46. Wang Q, Liu Q, Ma Y, Zhou L, Zhang Y: **Isolation, sequencing and characterization of cluster genes involved in the biosynthesis and utilization of the siderophore of marine fish pathogen *Vibrio alginolyticus*.** *Arch Microbiol* 2007, **188:**433-439.
47. Andrus C, Walter M, Crosa J, Payne S: **Synthesis of siderophores by pathogenic Vibrio species.** *Curr Microbiol* 1983, **9:**209-214.
48. Wang Q, Liu Q, Cao X, Yang M, Zhang Y: **Characterization of two TonB systems in marine fish pathogen *Vibrio alginolyticus*: their roles in iron utilization and virulence.** *Arch Microbiol* 2008, **190:**595-603.
49. Huson DH, Bryant D: **Application of phylogenetic networks in evolutionary studies.** *Mol Biol Evol* 2006, **23:**254-267.
50. Larkin MA, Blackshields G, Brown NP, Chenna R, McGettigan PA, McWilliam H, Valentin F, Wallace IM, Wilm A, Lopez R, et al: **Clustal W and Clustal X version 2.0.** *Bioinformatics* 2007, **23:**2947-2948.
51. Tamura K, Stecher G, Peterson D, Filipski A, Kumar S: **MEGA6: Molecular Evolutionary Genetics Analysis version 6.0.** *Mol Biol Evol* 2013, **30:**2725-2729.
52. Tamura K, Nei M: **Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees.** *Mol Biol Evol* 1993, **10:**512-526.
53. Yamamoto S, Okujo N, Fujita Y, Saito M, Yoshida T, Shinoda S: **Structures of two polyamine-containing catecholate siderophores from *Vibrio fluvialis*.** *J Biochem* 1993, **113:**538-544.
54. Nielsen A, Mansson M, Wietz M, Varming AN, Phipps RK, Larsen TO, Gram L, Ingmer H: **Nigribactin, a novel siderophore from *Vibrio nigripulchritudo*, modulates *Staphylococcus aureus* virulence gene expression.** *Marine drugs* 2012, **10:**2584-2595.
55. Giubergia S, Machado H, Valentina Mateiu R, Gram L: ***Vibrio galatheae sp. nov*., a member of the family *Vibrionaceae* isolated from a mussel.** *Int J Syst Evol Microbiol* 2016, **66:**347-352.

56. Goudenege D, Boursicot V, Versigny T, Bonnetot S, Ratiskol J, Sinquin C, LaPointe G, Le Rous F, Delbarre-Ladrat C: **Genome sequence of *Vibrio diabolicus* and identification of the exopolysaccharide HE800 biosynthesis locus.** *Appl Microbiol Biotechnol* 2014, **98:**10165-10176.
57. Cano-Gomez A, Goulden EF, Owens L, Hoj L: ***Vibrio owensii sp. nov.*, isolated from cultured crustaceans in Australia.** *FEMS Microbiol Lett* 2010, **302:**175-181.
58. Yoshizawa S, Tsuruya Y, Fukui Y, Sawabe T, Yokota A, Kogure K, Higgins M, Carson J, Thompson FL: ***Vibrio jasicida sp. nov.*, a member of the Harveyi clade, isolated from marine animals (packhorse lobster, abalone and Atlantic salmon).** *Int J Syst Evol Microbiol* 2012, **62:**1864-1870.
59. Balcazar JL, Planas M, Pintado J: ***Vibrio inhibens sp. nov*., a novel bacterium with inhibitory activity against Vibrio species.** *J Antibiot* 2012, **65:**301-305.
60. Urbanczyk Y, Ogura Y, Hayashi T, Urbanczyk H: **Description of a novel marine bacterium, *Vibrio hyugaensis sp. nov.*, based on genomic and phenotypic characterization.** *Syst App Microbiol* 2015, **38:**300-304.
61. Yoshizawa S, Wada M, Yokota A, Kogure K: ***Vibrio sagamiensis sp. nov.*, luminous marine bacteria isolated from sea water.** *J Gen App Microbioly* 2010, **56:**499-507.
62. Chimetto LA, Cleenwerck I, Moreira AP, Brocchi M, Willems A, De Vos P, Thompson FL: ***Vibrio variabilis sp. nov.* and *Vibrio maritimus sp. nov*., isolated from *Palythoa caribaeorum*.** *Int J Syst Evol Microbiol* 2011, **61:**3009-3015.
63. Kushmaro A, Banin E, Loya Y, Stackebrandt E, Rosenberg E: ***Vibrio shiloi sp. nov.*, the causative agent of bleaching of the coral *Oculina patagonica*.** *Int J Systc Evol Micr* 2001, **51:**1383-1388.
64. Lasa A, Dieguez AL, Romalde JL: ***Vibrio toranzoniae sp. nov.*, a new member of the *Splendidus* clade in the genus *Vibrio*.** *Syst App Microbiol* 2013, **36:**96-100.
65. Nam YD, Chang HW, Park JR, Kwon HY, Quan ZX, Park YH, Kim BC, Bae JW: ***Vibrio litoralis sp. nov.*, isolated from a Yellow Sea tidal flat in Korea.** *Int J Syst Evol Microbiol* 2007, **57:**562-565.
66. Gomez-Gil B, Thompson FL, Thompson CC, Swings J: ***Vibrio pacinii sp. nov.*, from cultured aquatic organisms.** *Int J Syst Evol Microbiol* 2003, **53:**1569-1573.
67. Kirchberger PC, Turnsek M, Hunt DE, Haley BJ, Colwell RR, Polz MF, Tarr CL, Boucher Y: ***Vibrio metoecus sp. nov*., a close relative of *Vibrio cholerae* isolated from coastal brackish ponds and clinical specimens.** *Int J Syst Evol Microbiol* 2014, **64:**3208-3214.
68. Kumar NR, Nair S*: **Vibrio rhizosphaerae sp. nov*., a red-pigmented bacterium that antagonizes phytopathogenic bacteria.** *Int J Syst Evol Microbiol* 2007, **57:**2241-2246.
69. Rivas R, García-Fraile P, Mateos PF, Martínez-Molina E, Velázquez E: ***Photobacterium halotolerans sp. nov.*, isolated from Lake Martel in Spain.** *Int Jo Syst Evol Micr* 2006, **56:**1067-1071.
70. Gomez-Gil B, Roque A, Rotllant G, Romalde JL, Doce A, Eggermont M, Defoirdt T: ***Photobacterium sanguinicancri sp. nov.* isolated from marine animals.** *Anton Leeuw* 2016, **109:**817-825.
71. Jones DT, Taylor WR, Thornton JM: **The rapid generation of mutation data matrices from protein sequences.** *Comput Appl Biosci: CABIOS* 1992, **8:**275-282.
72. Felsenstein J: **Confidence Limits on Phylogenies: An Approach Using the Bootstrap.** *Evolution* 1985, **39:**783-791.
73. Moon YH, Tanabe T, Funahashi T, Shiuchi K, Nakao H, Yamamoto S: **Identification and characterization of two contiguous operons required for aerobactin transport and biosynthesis in *Vibrio mimicus*.** *Microbiol Immunol* 2004, **48:**389-398.
74. Di Lorenzo M, Stork M, Tolmasky ME, Actis LA, Farrell D, Welch TJ, Crosa LM, Wertheimer AM, Chen Q, Salinas P, et al: **Complete sequence of virulence plasmid pJM1 from the marine fish pathogen *Vibrio anguillarum* strain 775.** *J Bacteriol* 2003, **185:**5822-5830.

75. Tanabe T, Funahashi T, Miyamoto K, Tsujibo H, Yamamoto S: **Identification of genes, *desR* and *desA*, required for utilization of desferrioxamine B as a xenosiderophore in *Vibrio furnissii*.** *Biol Pharm Bull* 2011, **34:**570-574.

Table 1

Siderophore	Organism	Siderophore biosynthesis protein accession numbers	Ref
Aerobactin	*V. mimicus*	IucA(WP_000554936.1) IucB(WP_000033134.1) IucC(WP_000372426.1) IucD(WP_000401386.1)	[73]
Bisucaberin	*A. salmonicida*	BibA(WP_012549025.1) BibB(WP_012549026.1) BibC(WP_012549027.1)	[43]
Vibrioferrin	*V. parahaemolyticus*	PvsA(WP_015313675.1) PvsB(WP_015313676.1) PvsC(WP_015313677.1) PvsD(WP_015313678.1) PvsE(WP_015313679.1)	[24]
Vibriobactin	*V. cholerae*	VibA (WP_000654285.1) VibB (WP_000997093.1) VibC(WP_000245175.1) VibD(WP_000874996.1) VibE (WP_000205544.1) VibF (WP_000523394.1) VibH(WP_001880577.1)	[9, 10]
Vanchrobactin	*V. anguillarum*	DapH(WP_011154675.1) VabA(WP_064624836.1) VabB(WP_064624831.1) VabC(WP_043004165.1) VabE(WP_019281788.1) VabF (WP_019281791.1) VabH (WP_019281793.1)	[38]
Piscibactin	*P. damselae subsp. Piscicida*	DapH (AKQ52526.1)Irp1(AKQ52532.1) Irp2(AKQ52531.1) Irp3(AKQ52533.1) Irp4(AKQ52534.1) Irp5(AKQ52536.1)	[33]
Anguibactin	*V. anguillarum*	AngA(WP_013857267.1) AngB(WP_013857270.1) AngC(WP_043004165.1) AngE(WP_013857269.1) AngB/G(WP_011154672.1) AngM(WP_011154633.1) AngT(WP_011154640.1) AngH(WP_011154645.1) AngR(WP_011154639.1) AngN(WP_011154642.1) AngU(WP_011154641.1) AngD(WP_011154670.1)	[37]
Vulnibactin	*V. vulnificus*	VV2_0830(WP_011081748.1) VV2_0831(AAO07755.1) VV2_0834(WP_011081751.1) VV2_0835(WP_011081752.1) VV2_0836(WP_011081753.1) VV2_0838/VenB(WP_011081755.1) VV2_0839(WP_011081756.1) VV2_0840(WP_011081757.1) VV2_0844(AAO07767.2)	[16]

Table 2

Organism	Receptor	Transport	Ref
V. mimicus	IutA (WP_000843157.1)	Aerobactin	[73]
A. salmonicida	BitA (WP_012549028.1)	Bisucaberin	[43]
V. parahaemolyticus	PvuA (WP_057620147.1)	Vibrioferrin	[25]
V. cholerae	ViuA (WP_000279435.1)	Vibriobactin Fluvibactin	[11]
V. anguillarum	FvtA (WP_019281795.1)	Vanchrobactin	[39]
V. anguillarum	FatA (WP_011154638.1)	Anguibactin	[74]
V.cholerae	VctA (WP_000350325.1)	Enterobactin Fluvibactin	[13]
V. cholerae	IrgA (WP_000086048.1)	Enterobactin Fluvibactin	[13]
V.vulnificus	VvuA (WP_015728225.1)	Vulnibactin	[17]
V. cholerae	FhuA (WP_053043596.1)	Ferrichrome	[14]
V. furnissii	DesA (WP_004725209.1)	Deferoxamine B	[75]
P. damselae subsp. Piscicida	FrpA (AKQ52529.1)	Piscibactin	[33]

Figure 1

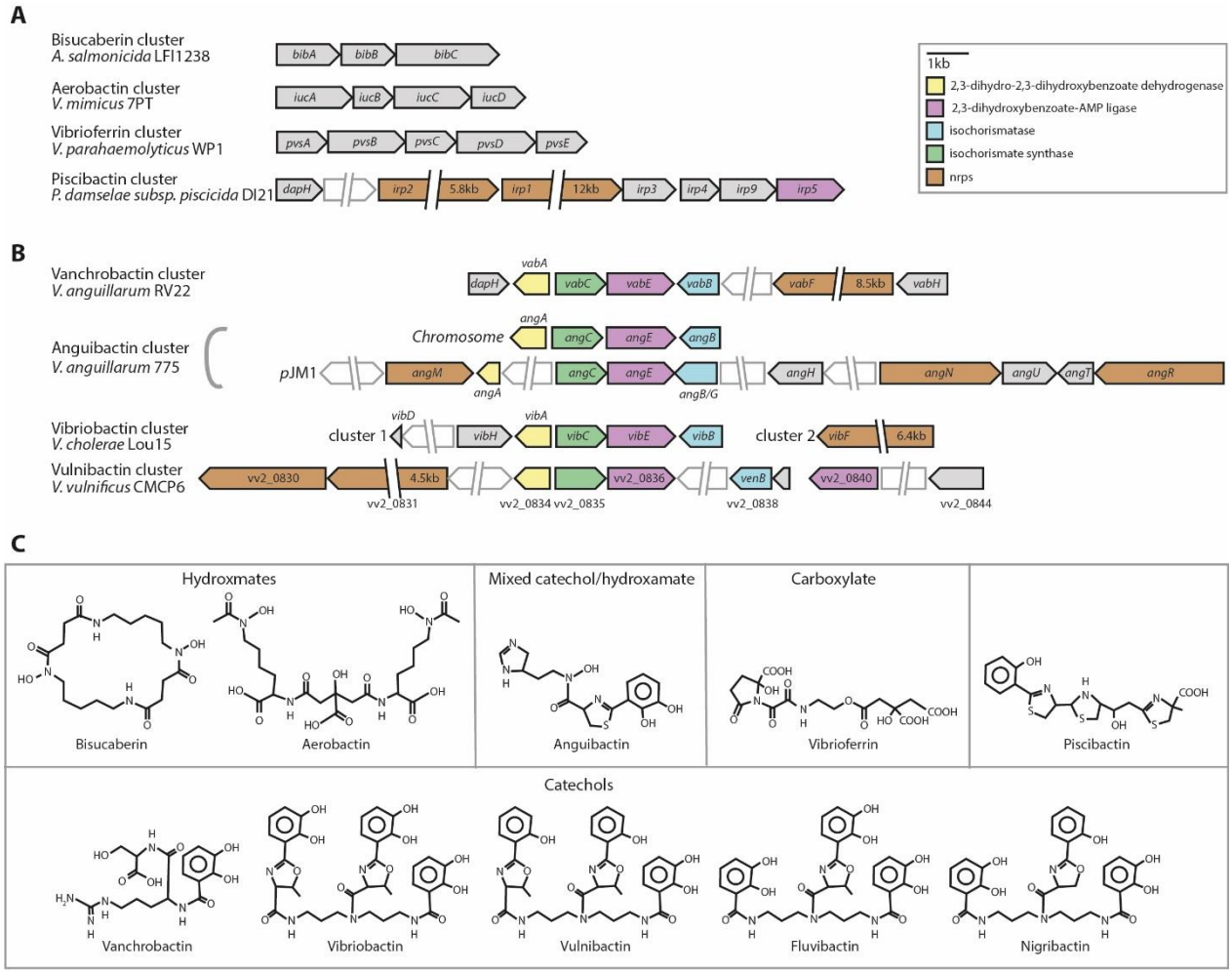

A
Bisucaberin cluster
A. salmonicida LFI1238
bibA
bibB
bibC
Aerobactin cluster
V. mimicus 7PT
iucA
iucB
iucC
iucD
Vibrioferrin cluster
V. parahaemolyticus WP1
pvsA
pvsB
pvsC
pvsD
pvsE
Piscibactin cluster
P. damselae subsp. piscicida DI21
dapH
irp2
5.8kb
irp1
12kb
irp3
irp4
irp9
irp5
1kb
2,3-dihydro-2,3-dihydroxybenzoate dehydrogenase
2,3-dihydroxybenzoate-AMP ligase
isochorismatase
isochorismate synthase
nrps
B
Vanchrobactin cluster
V. anguillarum RV22
vabA
dapH
vabC
vabE
vabB
vabF
8.5kb
vabH
Anguibactin cluster
V. anguillarum 775
Chromosome
angA
angC
angE
angB
pJM1
angM
angA
angC
angE
angB/G
angH
angN
angU
angT
angR
Vibriobactin cluster
V. cholerae Lou15
cluster 1
vibD
vibH
vibA
vibC
vibE
vibB
cluster 2
vibF
6.4kb
Vulnibactin cluster
V. vulnificus CMCP6
vv2_0830
4.5kb
vv2_0831
vv2_0834
vv2_0835
vv2_0836
venB
vv2_0838
vv2_0840
vv2_0844
C
Hydroxmates
Bisucaberin
Aerobactin
Mixed catechol/hydroxamate
Anguibactin
Carboxylate
Vibrioferrin
Piscibactin
Catechols
Vanchrobactin
Vibriobactin
Vulnibactin
Fluvibactin
Nigribactin

Figure 2

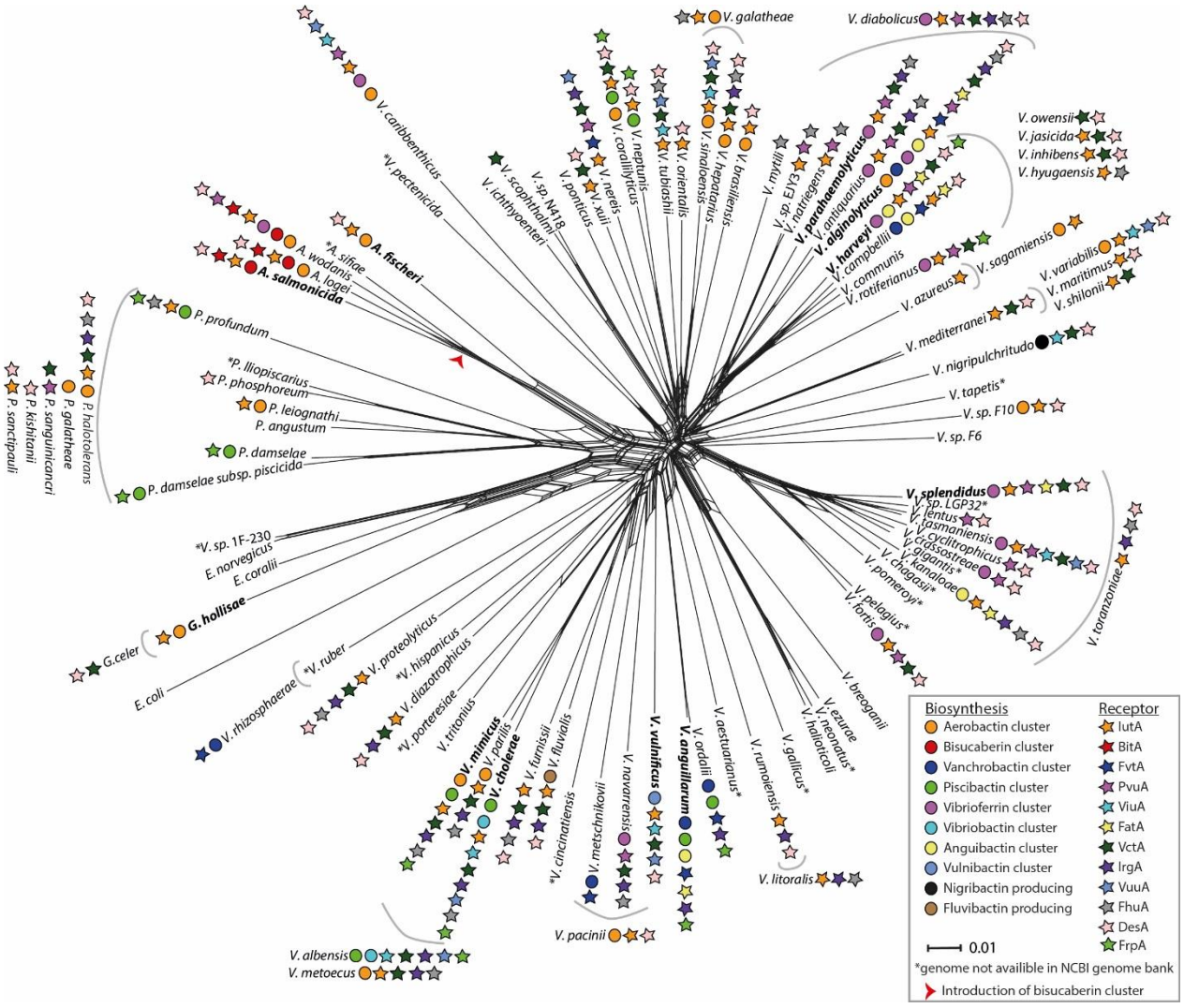

V. galatheae
V. diabolicus
V. caribbenthicus
*V. pectenicida
V. scophthalmi
V. ichthyoenteri
V. sp. N418
V. ponticus
V. xuii
V. nereis
V. coralliilyticus
V. neptunius
V. orientalis
V. tubiashii
V. sinaloensis
V. hepatarius
V. brasiliensis
V. myxini
V. sp. EJY3
V. natriegens
V. parahaemolyticus
V. antiquarius
V. alginolyticus
V. harveyi
V. campbellii
V. communis
V. rotiferianus
V. azureus
V. owensii
V. jasicida
V. inhibens
V. hyugaensis
V. sagamiensis
V. variabilis
V. maritimus
V. shilonii
V. mediterranei
V. nigripulchritudo
V. tapetis*
V. sp. F10
V. sp. F6
*A. sifiae
A. wodanis
A. logei
A. salmonicida
A. fischeri
P. profundum
*P. liliopiscarius
P. phosphoreum
P. leiognathi
P. angustum
P. damselae
P. damselae subsp. piscicida
P. halotolerans
P. galatheae
P. sanguinicancri
P. kishitanii
P. sanctipauli
*V. sp. 1F-230
E. norvegicus
E. coralii
G. hollisae
G. celer
E. coli
V. rhizosphaerae
*V. ruber
V. proteolyticus
*V. hispanicus
V. diazotrophicus
*V. porteresiae
V. tritonius
V. minicus
V. parilis
V. cholerae
V. furnissii
V. fluvialis
*V. cincinatiensis
V. metschnikovii
V. navarrensis
V. vulnificus
V. anguillarum
V. ordalii
V. aestuarianus*
V. rumoiensis
V. gallicus*
V. neonatus*
V. halioticoli
V. ezurae
V. breoganii
V. litoralis
V. pacinii
V. albensis
V. metoecus
V. splendidus
V. sp. LGP32*
V. tasmaniensis
V. cyclitrophicus
V. crassostreae
V. gigantis*
V. kanaloae
V. chagasi*
V. pomeroyi*
V. pelagius*
V. fortis
V. toranzoniae
Biosynthesis
Aerobactin cluster
Bisucaberin cluster
Vanchrobactin cluster
Piscibactin cluster
Vibrioferrin cluster
Vibriobactin cluster
Anguibactin cluster
Vulnibactin cluster
Nigribactin producing
Fluvibactin producing
Receptor
IutA
BitA
FvtA
PvuA
ViuA
FatA
VctA
IrgA
VuuA
FhuA
DesA
FrpA
0.01
*genome not availible in NCBI genome bank
Introduction of bisucaberin cluster

Figure 3

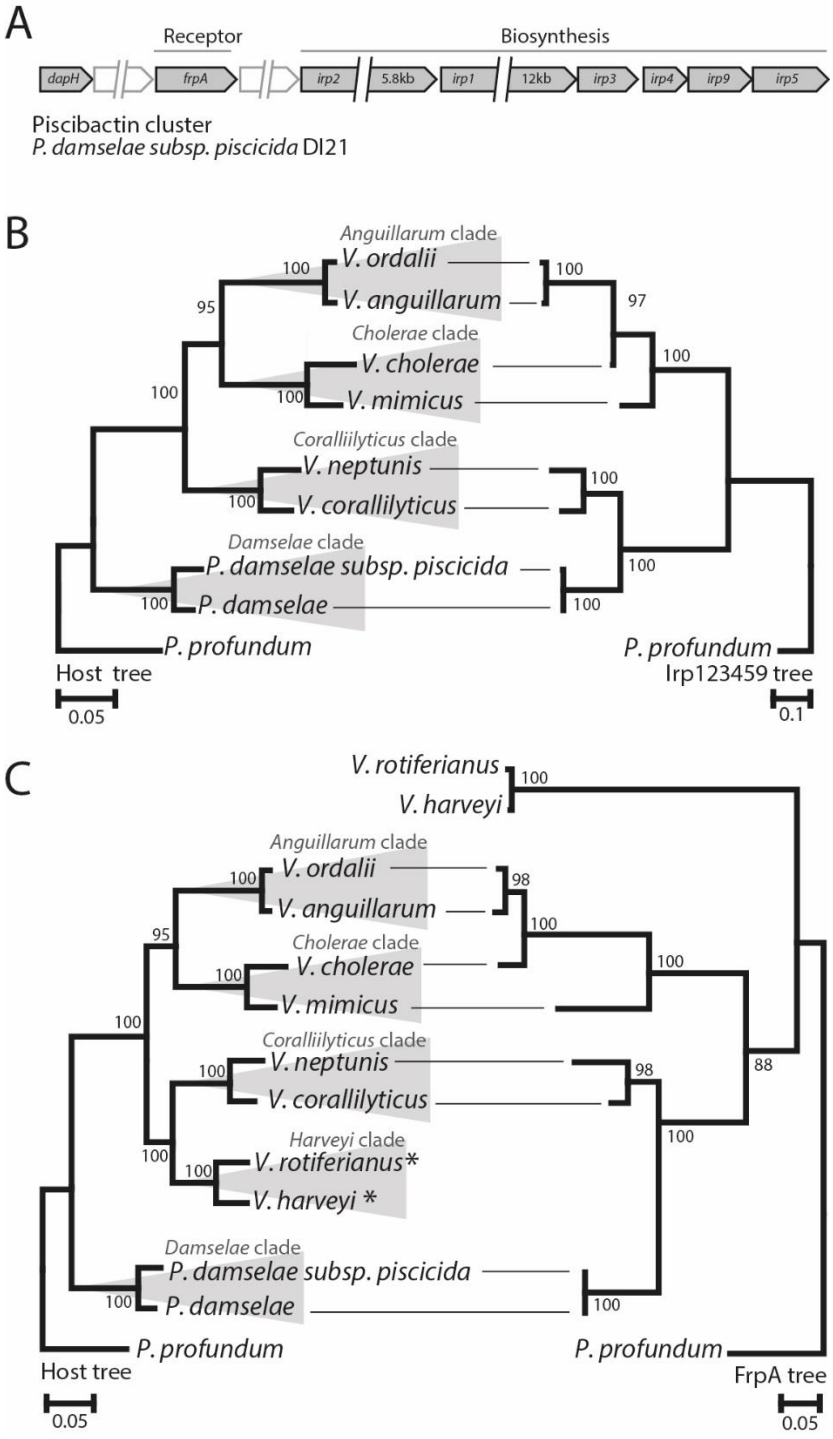
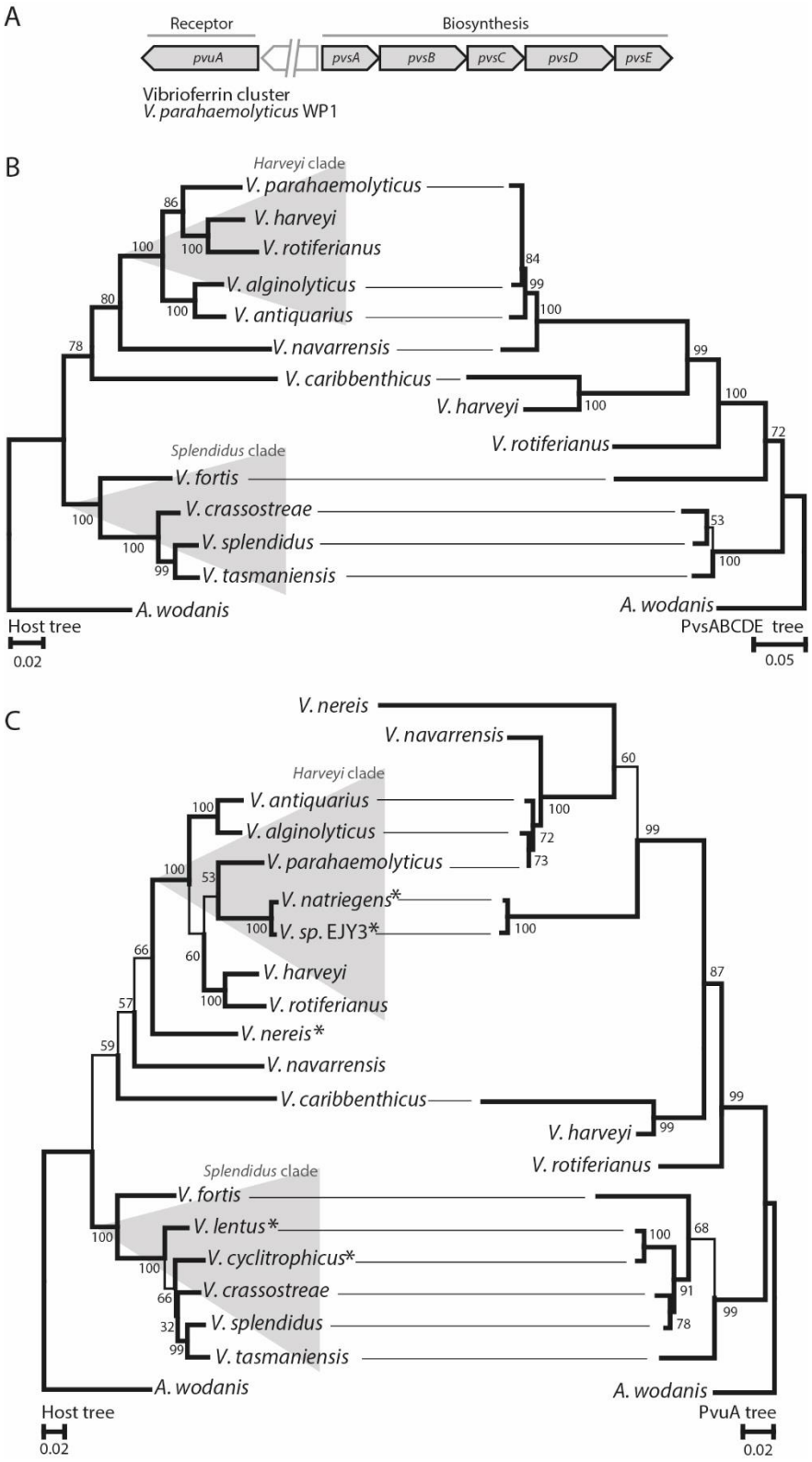

A
Receptor
Biosynthesis
dapH
frpA
irp2
5.8kb
irp1
12kb
irp3
irp4
irp9
irp5
Piscibactin cluster
P. damselae subsp. piscicida DI21
B
Anguillarum clade
V. ordalii
V. anguillarum
Cholerae clade
V. cholerae
V. mimicus
Coralliilyticus clade
V. neptunis
V. corallilyticus
Damselae clade
P. damselae subsp. piscicida
P. damselae
P. profundum
Host tree
0.05
P. profundum
Irp123459 tree
0.1
C
V. rotiferianus
V. harveyi
Anguillarum clade
V. ordalii
V. anguillarum
Cholerae clade
V. cholerae
V. mimicus
Coralliilyticus clade
V. neptunis
V. corallilyticus
Harveyi clade
V. rotiferianus*
V. harveyi *
Damselae clade
P. damselae subsp. piscicida
P. damselae
P. profundum
Host tree
0.05
P. profundum
FrpA tree
0.05

Figure 4


A
Receptor
Biosynthesis
pvuA
pvsA
pvsB
pvsC
pvsD
pvsE
Vibrioferrin cluster
V. parahaemolyticus WP1
B
Harveyi clade
V. parahaemolyticus
V. harveyi
V. rotiferianus
V. alginolyticus
V. antiquarius
V. navarrensis
V. caribbenthicus
V. harveyi
V. rotiferianus
Splendidus clade
V. fortis
V. crassostreae
V. splendidus
V. tasmaniensis
A. wodanis
Host tree
0.02
A. wodanis
PvsABCDE tree
0.05
C
V. nereis
V. navarrensis
Harveyi clade
V. antiquarius
V. alginolyticus
V. parahaemolyticus
V. natriegens*
V. sp. EJY3*
V. harveyi
V. rotiferianus
V. nereis*
V. navarrensis
V. caribbenthicus
V. harveyi
V. rotiferianus
Splendidus clade
V. fortis
V. lentus*
V. cyclitrophicus*
V. crassostreae
V. splendidus
V. tasmaniensis
A. wodanis
Host tree
0.02
A. wodanis
PvuA tree
0.02

Supplementary file S1

Aerobactin biosynthesis cluster

Organism	IucA	Cov/Ident/E	IucB	Cov/Ident/E	IucC	Cov/Ident/E	IucD	Cov/Ident/E
Aliivibrio fischeri	WP_063668674.1	96/61/0	WP_063649197.1	100/63/8e-140	WP_063646176.1	99/68/0	WP_063656611.1	97/71/0
Aliivibrio logei	WP_017023525.1	96/61/0	WP_017023526.1	100/60/3e-137	WP_017023527.1	99/69/0	WP_017023528.1	98/72/0
Aliivibrio salmonicida	pseudo		WP_012551639.1	100/60/3e-135	pseudo		WP_012551640.1	98/72/0
Aliivibrio wodanis	WP_061029794.1	96/61/0	WP_061029792.1	99/61/5e-137	WP_061003472.1	99/71/0	WP_061003473.1	98/72/0
Grimontia hollisae	WP_005505275.1	94/53/0	WP_005505267.1	93/51/2e-101	WP_005505265.1	98/60/0	WP_040529008.1	97/61/0
Photobacterium halotolerans	WP_046220649.1	98/62/0	WP_046220648.1	94/65/2e-136	WP_036752138.1	99/71/0	WP_036752136.1	98/71/0
Photobacterium leiognathi	WP_053988888.1	100/75/0	WP_053988887.1	100/68/4e-161	WP_053988886.1	99/79/0	WP_053988885.1	99/81/0
Photobacterium sp. SKA34	WP_006645231.1	95/52/0	WP_050764797.1	89/55/3e-107	EAR55206.1	83/60/0	WP_006645235.1	97/61/0
Vibrio alginolyticus	WP_053311479.1	96/58/0	WP_053311480.1	100/62/3e-137	WP_053311481.1	99/67/0	WP_053311482.1	99/71/0
Vibrio brasiliensis	WP_006880411.1	100/75/0	WP_006880410.1	100/69/5e-164	WP_006880409.1	99/80/0	WP_006880408.1	99/81/0
Vibrio caribbeanicus	WP_052131268.1	97/67/0	WP_038134820.1	100/67/3e-155	WP_038134818.1	98/75/0	WP_038134815.1	100/76/0
Vibrio coralliilyticus	WP_019276335.1	100/64/0	WP_045986472.1	100/63/2e-144	WP_019276337.1	98/71/0	WP_040122006.1	100/74/0
Vibrio galatheae	WP_045956523.1	99/73/0	WP_045956524.1	100/67/3e-154	WP_045956525.1	99/77/0	WP_045956526.1	99/81/0
Vibrio genomosp. F10	WP_017041124.1	96/61/0	WP_017041125.1	100/60/8e-137	WP_017033971.1	99/67/0	WP_017033970.1	95/71/0
Vibrio hepatarius	WP_053407993.1	100/81/0	WP_053407868.1	100/82/0	WP_053407869.1	99/84/0	WP_053407870.1	100/83/0
Vibrio metoecus	WP_055051039.1	100/99/0	WP_055051038.1	100/99/0	WP_055032970.1	100/98/0	WP_055051036.1	100/99/0
Vibrio mimicus	WP_000554936.1		WP_000033134.1		WP_000372426.1		WP_000401386.1	
Vibrio pacinii	WP_038173493.1	100/81/0	WP_038173492.1	100/83/0	WP_038173490.1	99/82/0	WP_038173488.1	100/84/0
Vibrio parilis	WP_000554940.1	100/96/0	WP_000033136.1	100/95/0	WP_000436133.1	100/97/0	WP_000401383.1	100/97/0
Vibrio sagamiensis	WP_039980470.1	99/70/0	WP_039980472.1	100/62/2e-137	WP_039980473.1	99/74/0	WP_039980474.1	98/82/0
Vibrio sinaloensis	WP_052319139.1	97/67/0	WP_039623864.1	100/67/3e-157	WP_039477140.1	98/74/0	WP_039477142.1	100/76/0
Vibrio sp. 16	WP_043886533.1	97/67/0	WP_043886505.1	100/67/4e-155	WP_005469810.1	98/74/0	WP_043886506.1	100/76/0
Vibrio sp. AND4	WP_009841203.1	99/74/0	WP_009841202.1	100/66/4e-155	WP_009841201.1	99/78/0	WP_009841200.1	99/78/0
Vibrio sp. B183	WP_051912559.1	99/64/0	WP_038160278.1	100/63/1e-143	WP_038160275.1	98/70/0	WP_038160274.1	99/74/0
Vibrio variabilis	WP_052132383.1	97/67/0	WP_038212532.1	100/67/3e-158	WP_038212530.1	98/74/0	WP_043886506.1	100/75/0

Vanchrobactin biosynthesis cluster

Organism	DahP	Cov/Ident/E	VabA	Cov/Ident/E	VabB	Cov/Ident/E	VabC	Cov/Ident/E
Vibrio alginolyticus	WP_047101776.1	97/80/6e-161	WP_047101854.1	100/54/2e-97	WP_053306972.1	83/65/4e-144	WP_047101778.1	99/69/0
Vibrio anguillarum	WP_011154675.1		WP_064624836.1		WP_064624831.1		WP_043004165.1	
Vibrio campbellii	WP_005425950.1	93/53/5e-93	WP_045397519.1	96/48/7e-73	WP_045378486.1	82/64/2e-136	WP_051117323.1	98/49/6e-130
Vibrio metschnikovii	WP_004396943.1	94/70/3e-136	WP_004396942.1	100/66/4e-124	WP_004396939.1	83/67/1e-139	WP_004396941.1	100/76/0
Vibrio ordalii	WP_017044377.1	93/69/4e-135	WP_017050150.1	100/99/0	WP_017050153.1	100/99/0	WP_010318455.1	100/99/0
Vibrio rhizosphaerae	WP_038184547.1	93/52/7e-93	WP_038181208.1	98/68/2e-121	WP_038181214.1	85/63/2e-134	WP_038181209.1	100/77/0
Vibrio sp. MEBiC08052	WP_059122076.1	93/52/7e-93	WP_059122676.1	98/66/2e-118	WP_059120568.1	84/64/9e-139	WP_059120570.1	100/78/0

Organism	VabE	Cov/Ident/E	VabF	Cov/Ident/E	VabH	Cov/Ident/E
Vibrio alginolyticus	WP_017821446.1	99/69/0	WP_054579172.1	99/63/0	WP_054579171.1	99/59/2e-180
Vibrio anguillarum	WP_019281788.1		WP_019281791.1		WP_019281793.1	
Vibrio campbellii	WP_045370524.1	98/56/0	WP_010648829.1	99/62/0	WP_050545982.1	99/59/0
Vibrio metschnikovii	WP_004396940.1	99/68/0	WP_004396933.1	99/60/0	WP_040905265.1	99/61/0
Vibrio ordalii	WP_017045629.1	100/99/0	WP_017044383.1	99/97/0	WP_017044384.1	100/98/0
Vibrio rhizosphaerae	WP_038181212.1	99/68/0	WP_038181227.1	99/61/0	WP_038181233.1	98/56(1e-173
Vibrio sp. MEBiC08052	WP_059120569.1	99/69/0	WP_059120563.1	99/61/0	WP_059120561.1	98/60/0

Anguibactin biosynthesis cluster

Organism	AngC	Cov/Ident/E	AngB	Cov/Ident/E	AngA	Cov/Ident/E	AngE	Cov/Ident/E
Vibrio alginolyticus	WP_047101778.1	99/69/0	WP_053306972.1	83/65/4e-144	WP_047101854.1	100/54/2e-97	WP_017821446.1	99/69/0
Vibrio anguillarum	WP_043004165.1		WP_013857270.1		WP_013857267.1		WP_013857269.1	
Vibrio campbellii	WP_051117323.1	98/49/6e-130	WP_045378486.1	82/64/2e-136	WP_045397519.1	96/48/7e-73	WP_045370524.1	98/56/0
Vibrio harveyi	WP_017188367.1	98/49/2e-132	WP_050913426.1	82/64/8e-127	WP_050902411.1	96/48/2e-73	WP_061065702.1	98/58/0
Vibrio kanaloae	WP_017055790.1	99/70/0	WP_017055788.1	82/64/3e-118	WP_032547875.1	99/56/2e-101	WP_032547877.1	98/63/0

Organism	AngB/G	Cov/Ident/E	AngM	Cov/Ident/E	AngT	Cov/Ident/E	AngH	Cov/Ident/E
Vibrio alginolyticus	WP_047101780.1	100/80/3e-173	WP_047101757.1	100/64/0	WP_047101764.1	99/70/2e-130	WP_047101770.1	96/86/0
Vibrio anguillarum	WP_011154672.1		WP_011154633.1		WP_011154640.1		WP_011154645.1	
Vibrio campbellii	WP_045378486.1	100/79/1e-168	WP_045418437.1	100/63/0	WP_050918968.1	98/63/2e-119	WP_047479187.1	96/81/0
Vibrio harveyi	WP_050913426.1	100/80/9e-160	WP_050913415.1	99/63/0	WP_050913420.1	98/63/5e-118	WP_050913423.1	96/81/0
Vibrio kanaloae	WP_017055788.1	100/95/0	WP_017055763.1	100/90/0	WP_017055797.1	99/91/1e-172	WP_017055794.1	96/96/0

Organism	AngR	Cov/Ident/E	AngN	Cov/Ident/E	AngU	Cov/Ident/E
Vibrio alginolyticus	WP_047101763.1	99/67/0	WP_047101768.1	99/71/0	WP_047101766.1	99/84/0
Vibrio anguillarum	WP_011154639.1		WP_011154642.1		WP_011154641.1	
Vibrio campbellii	WP_050910520.1	99/64/0	WP_005533427.1	99/69/0	WP_005533426.1	99/79/0
Vibrio harveyi	WP_050913419.1	99/63/0	WP_050913422.1	99/69/0	WP_050913421.1	99/79/0
Vibrio kanaloae	AKN37366.1	99/90/0	WP_017055795.1	100/91/0	WP_017055796.1	99/95/0

Vibriobactin biosynthesis cluster

Organism	VibA	Cov/Ident/E	VibB	Cov/Ident/E	VibC	Cov/Ident/E	VibD	Cov/Ident/E
Vibrio albensis	EEO04018.1	100/99/0	WP_000997090.1	100/99/0	WP_032468518.1	99/98/0	WP_001907346.1	100/96/1e-169
Vibrio cholerae	WP_000654285.1		WP_000997093.1		WP_000245175.1		WP_000874996.1	

Organism	VibE	Cov/Ident/E	VibF	Cov/Ident/E	VibH	Cov/Ident/E
Vibrio albensis	WP_000205529.1	100/98/0	WP_000523401.1	100/98/0	EEO04019.1	88/98/0
Vibrio cholerae	WP_000205544.1		WP_000523394.1		WP_001880577.1	

Bisucaberin biosynthesis cluster

Organism	BibA	Cov/Ident/E	BibB	Cov/Ident/E	BibC	Cov/Ident/E
Aliivibrio logei	WP_017021624.1	100/99/0	WP_017021623.1	99/99/0	WP_017021622.1	100/99/0
Aliivibrio salmonicida LFI1238	WP_012549025.1		WP_012549026.1		WP_012549027.1	
Aliivibrio wodanis	WP_060991935.1	100/87/0	WP_060991934.1	99/90/0	WP_060991933.1	100/89/0

Vibrioferrin biosynthesis cluster

Organism	PvsA	Cov/Ident/E	PvsB	Cov/Ident/E	PvsC	Cov/Ident/E	PvsD	Cov/Ident/E
Aliivibrio wodanis	WP_045102246.1	100/74/0	WP_045102247.1	99/73/0	WP_045102248.1	100/74/0	WP_045102249.1	99/77/0
Vibrio alginolyticus	WP_054575389.1	100/97/0	WP_054575388.1	100/98/0	WP_054576553.1	100/99/0	WP_031780477.1	100/99/0
Vibrio antiquarius	WP_006740841.1	100/97/0	WP_006740842.1	100/96/0	WP_006740843.1	100/98/0	WP_006740844.1	100/99/0
Vibrio caribbeanicus	WP_009603302.1	100/72/0	WP_009603303.1	99/74/0	WP_009603304.1	100/70/0	WP_009603305.1	99/73/0
Vibrio crassostreae	WP_057623651.1	100/74/0	WP_057623654.1	99/75/0	WP_017064382.1	100/74/0	WP_048659876.1	100/77/0
Vibrio diabolicus	WP_048625457.1	100/97/0	WP_048625458.1	100/98/0	WP_048625459.1	100/98/0	WP_048625460.1	100/98/0
Vibrio fortis	WP_032550983.1	100/74/0	WP_032550984.1	100/74/0	WP_032550985.1	100/75/0	WP_032550986.1	99/74/0
Vibrio harveyi	WP_029789871.1	100/75/0	WP_049537122.1	99/76/0	WP_050933242.1	100/73/0	WP_050908359.1	100/76/0
Vibrio navarrensis	WP_039433588.1	99/92/0	WP_039439003.1	100/94/0	WP_039433594.1	100/96/0	WP_039439008.1	100/98/0
Vibrio parahaemolyticus	WP_015313675.1		WP_015313676.1		WP_015313677.1		WP_015313678.1	
Vibrio rotiferianus	WP_010453821.1	100/77/0	WP_038887496.1	99/78/0	WP_010453819.1	100/78/0	WP_045390572.1	100/79/0
Vibrio sp. HENC-01	WP_009696138.1	100/74/0	WP_009696137.1	99/76/0	WP_050554537.1	100/73/0	WP_033007960.1	100/76/0
Vibrio sp. J2-12	WP_050644303.1	100/74/0	WP_050644304.1	99/74/0	WP_050644305.1	100/74/0	WP_050644306.1	99/76/0
Vibrio sp. J2-15	WP_050632945.1	100/74/0	WP_050632944.1	99/75/0	WP_050632943.1	100/74/0	WP_050632942.1	99/76/0
Vibrio sp. J2-17	WP_050652641.1	100/74/0	WP_050652640.1	99/75/0	WP_050652639.1	100/74/0	WP_050652638.1	99/76/0
Vibrio sp. J2-29	WP_048614849.1	100/74/0	WP_048614847.1	99/75/0	WP_048614845.1	100/74/0	WP_048614843.1	100/76/0
Vibrio sp. J2-3	WP_050620543.1	100/74/0	WP_050620544.1	99/75/0	WP_050620545.1	100/74/0	WP_050620546.1	99/76/0
Vibrio sp. J2-31	WP_048606054.1	100/74/0	WP_050650869.1	99/74/0	WP_048606050.1	100/74/0	WP_050650871.1	100/76/0
Vibrio sp. OY15	WP_033906632.1	100/96/0	WP_033906631.1	100/94/0	WP_033906630.1	100/98/0	WP_033906629.1	100/98/0
Vibrio splendidus	WP_017089235.1	100/75/0	WP_017092038.1	99/75/0	WP_061038080.1	100/74/0	WP_061022001.1	100/77/0
Vibrio tasmaniensis	WP_012600978.1	100/74/0	WP_012600979.1	99/75/0	WP_012600980.1	100/74/0	WP_012600981.1	100/77/0

Organism	PvsE	Cov/Ident/E
Aliivibrio wodanis	WP_045102250.1	100/83/0
Vibrio alginolyticus	WP_053350159.1	100/98/0
Vibrio antiquarius	WP_006740845.1	100/98/0
Vibrio caribbeanicus	WP_009603306.1	100/83/0
Vibrio crassostreae	WP_059017340.1	100/84/0
Vibrio diabolicus	WP_048625461.1	100/97/0
Vibrio fortis	WP_032550987.1	100/78/0
Vibrio harveyi	WP_050922940.1	100/83/0
Vibrio navarrensis	WP_039439012.1	100/95/0
Vibrio parahaemolyticus	WP_015313679.1	
Vibrio rotiferianus	WP_045390569.1	100/83/0
Vibrio sp. HENC-01	WP_009696133.1	100/84/0
Vibrio sp. J2-12	WP_050644307.1	100/84/0
Vibrio sp. J2-15		
Vibrio sp. J2-17	WP_050652637.1	100/84/0
Vibrio sp. J2-29	WP_048614841.1	100/84/0
Vibrio sp. J2-3	WP_050620547.1	100/82/0
Vibrio sp. J2-31	WP_050650872.1	100/84/0
Vibrio sp. OY15	WP_033906628.1	100/97/0
Vibrio splendidus	WP_060980475.1	100/84/0
Vibrio tasmaniensis	WP_012600982.1	100/83/0

Piscibactin biosynthesis cluster

Organism	Irp1	Cov/Ident/E	Irp2	Cov/Ident/E	Irp3	Cov/Ident/E	Irp4	Cov/Ident/E
Photobacterium damselae	WP_044179415.1	100/99/0	WP_044179418.1	100/99/0	WP_044179412.1	100/100/0	WP_044179406.1	100/100/0
Photobacterium damselae subsp. piscicida	AKQ52532.1		AKQ52531.1		AKQ52533.1		AKQ52534.1	
Photobacterium profundum	CAG20078.1	83/52/0	WP_011218392.1	99/55/0	WP_011218389.1	96/59/2e-140	WP_011218388.1	91/59/5e-114
Vibrio albensis	WP_027694620.1	99/52/0	WP_027694619.1	99/57/0	WP_000842271.1	98/61/2e-144	WP_001077536.1	92/56/2e-98
Vibrio anguillarum	WP_019281879.1	99/52/0	WP_019281878.1	99/57/0	WP_019281880.1	98/61/4e-144	WP_019281881.1	95/54/1e-98
Vibrio cholerae	WP_032479734.1	100/54/0	WP_057558264.1	100/57/0	WP_000842272.1	98/62/9e-145	WP_001077534.1	97/54/2e-99
Vibrio coralliilyticus	WP_006961718.1	100/73/0	WP_006961717.1	100/75/0	WP_019276303.1	100/80/0	WP_045986445.1	100/79/2e-166
Vibrio mimicus	WP_022578908.1	100/54/0	WP_061051252.1	99/58/0	WP_001065237.1	96/61/2e-145	WP_005526076.1	90/60/2e-108
Vibrio neptunius	WP_045975018.1	100/71/0	WP_045975017.1	100/75/0	WP_045975019.1	100/74/0	WP_045975020.1	99/75/2e-156
Vibrio ordalii	WP_017046027.1	99/52/0	WP_017046028.1	99/57/0	WP_010317038.1	98/62/1e-145	WP_017050345.1	97/54/1e-99

Organism	Irp5	Cov/Ident/E	Irp9	Cov/Ident/E
Photobacterium damselae	WP_044179402.1	100/100/0	WP_044179404.1	100/100/0
Photobacterium damselae subsp. piscicida	AKQ52536.1		AKQ52535.1	
Photobacterium profundum	WP_011218386.1	96/60/0	WP_011218387.1	95/64/0
Vibrio albensis	EEO01925.1	94/63/0	WP_001273873.1	96/61/0
Vibrio anguillarum	WP_019281883.1	96/63/0	WP_019281882.1	98/61/0
Vibrio cholerae	WP_042990239.1	96/63/0	WP_001273875.1	98/61/0
Vibrio coralliilyticus	WP_040122045.1	100/77/0	WP_040122044.1	99/79/0
Vibrio mimicus	WP_001000061.1	97/65/0	WP_022578911.1	95/63/0
Vibrio neptunius	WP_045975022.1	98/76/0	WP_045975021.1	100/77/0
Vibrio ordalii	WP_010317045.1	96/64/0	WP_017044479.1	97/61/0

Vulnbactin biosynthesis cluster

Organism	VV2_0830	Cov/Ident/E	VV2_0831	Cov/Ident/E	VV2_0834	Cov/Ident/E	VV2_0835	Cov/Ident/E
Vibrio vulnificus	WP_011081748.1		AAO07755.1		WP_011081751.1		WP_011081752.1	
Organism	**VV2_0836**	**Cov/Ident/E**	**VV2_0838**	**Cov/Ident/E**	**VV2_0839**	**Cov/Ident/E**	**VV2_0840**	**Cov/Ident/E**
Vibrio vulnificus	WP_011081753.1		WP_011081755.1		WP_011081756.1		WP_011081757.1	

Organism	VV2_0844	Cov/Ident/E
Vibrio vulnificus	AAO07767.2	

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Organism	IutA	Cov/Ident/E
Aliivibrio fischeri	WP_063646174.1	98/74/0
Aliivibrio logei	WP_017023529.1	100/73/0
Aliivibrio salmonicida	WP_012551641.1	100/73/0
Aliivibrio wodanis	WP_060992051.1	98/74/0
Grimontia hollisae	WP_005505256.1	99/56/0
Photobacterium halotolerans	WP_027252270.1	95/73/0
Photobacterium leiognathi	WP_053988884.1	98/81/0
Photobacterium profundum	WP_036802510.1	100/56/0
Photobacterium sanctipauli	WP_036821338.1	91/60/0
Photobacterium sp. SKA34	WP_006645229.1	97/54/0
Vibrio alginolyticus	WP_053311483.1	98/69/0
Vibrio antiquarius	WP_012842231.1	98/68/0
Vibrio azureus	WP_021709526.1	94/56/0
Vibrio brasiliensis	WP_006880407.1	98/57/0
Vibrio campbellii	WP_005533358.1	100/61/0
Vibrio caribbeanicus	WP_038134813.1	100/72/0
Vibrio cholerae	KFE32191.1	98/97/0
Vibrio coralliilyticus	WP_040122005.1	100/72/0
Vibrio diabolicus	WP_048625083.1	98/68/0
Vibrio diazotrophicus	WP_042480676.1	100/80/0
Vibrio fluvialis	WP_044365758.1	95/84/0
Vibrio fortis	WP_032550606.1	100/81/0
Vibrio furnissii	WP_047458045.1	95/84/0
Vibrio galatheae	WP_045956527.1	100/80/0
Vibrio genomosp. F10	WP_017036918.1	100/61/0
Vibrio harveyi	WP_038898973.1	95/68/0
Vibrio hepatarius	WP_053407871.1	100/59/0
Vibrio hyugaensis	WP_045401698.1	98/66/0
Vibrio inhibens	WP_063344320.1	95/67/0
Vibrio jasicida	WP_038865785.1	98/66/0
Vibrio kanaloae	WP_017058734.1	98/84/0
Vibrio litoralis	WP_027696548.1	100/57/0
Vibrio maritimus	GAL38192.1	97/79/0
Vibrio mediterranei	WP_062456094.1	98/59/0
Vibrio metoecus	WP_055064999.1	100/99/0
Vibrio mimicus	WP_000843157.1	
Vibrio natriegens	WP_020336334.1	98/80/0
Vibrio neptunius	WP_045977518.1	100/81/0
Vibrio nereis	WP_053394631.1	98/59/0
Vibrio orientalis	WP_004417036.1	95/83/0
Vibrio pacinii	WP_038173486.1	100/85/0
Vibrio parahaemolyticus	WP_031853589.1	94/70/0
Vibrio parilis	WP_000644798.1	100/98/0
Vibrio proteolyticus	WP_021706161.1	98/70/0
Vibrio rotiferianus	WP_045388840.1	94/68/0
Vibrio rumoiensis	WP_026025691.1	100/57/0
Vibrio sagamiensis	WP_039980475.1	94/56/0
Vibrio shilonii	WP_006070381.1	98/59/0
Vibrio sinaloensis	WP_038187421.1	100/72/0
Vibrio sp. 16	WP_005469571.1	100/72/0
Vibrio sp. 3062	WP_063603061.1	98/58/0
Vibrio sp. 712i1	WP_017634648.1	98/67/0
Vibrio sp. AND4	WP_009841199.1	98/57/0
Vibrio sp. B183	WP_038160271.1	100/62/0
Vibrio sp. ECSMB14106	WP_046225040.1	98/84/0
Vibrio sp. EJY3	WP_014231930.1	98/80/0
Vibrio sp. ER1A	WP_038227377.1	98/58/0
Vibrio sp. HENC-01	EKM20725.1	98/66/0
Vibrio sp. HI00D65	WP_063522285.1	100/58/0
Vibrio sp. JCM 18905	GAJ76753.1	98/68/0
Vibrio sp. MED222	WP_009847194.1	100/81/0
Vibrio splendidus	WP_004736323.1	100/82/0
Vibrio tasmaniensis	WP_017104136.1	100/80/0
Vibrio toranzoniae	WP_060469444.1	98/84/0
Vibrio tubiashii	WP_004743922.1	100/83/0
Vibrio variabilis	WP_038212523.1	100/72/0
Vibrio vulnificus	WP_011152720.1	100/82/0
Vibrio xuii	WP_053440998.1	98/82/0

Organism	BitA	Cov/Ident/E
Aliivibrio logei	WP_017021621.1	100/99/0
Aliivibrio salmonicida	WP_012549028.1	
Aliivibrio wodanis	WP_060991932.1	100/85/0

Organism	ViuA	Cov/Ident/E
Vibrio albensis	WP_000279436.1	100/99/0
Vibrio caribbeanicus	WP_038136065.1	93/57/0
Vibrio cholerae	WP_000279435.1	
Vibrio nigripulchritudo	WP_004405074.1	100/60/0
Vibrio sinaloensis	WP_039625029.1	93/57/0
Vibrio sp. 16	WP_043886606.1	93/57/0
Vibrio sp. MED222	WP_009846388.1	100/57/0
Vibrio tasmaniensis	WP_017104270.1	100/57/0
Vibrio tubiashii	WP_038201292.1	100/55/0
Vibrio variabilis	WP_038217008.1	93/57/0
Vibrio vulnificus	WP_045590134.1	100/76/0

Organism	VuuA	Cov/Ident/E
Vibrio albensis	WP_000279436.1	100/75/0
Vibrio caribbeanicus	WP_038136065.1	92/58/0
Vibrio cholerae	WP_046126980.1	100/75/0
Vibrio nigripulchritudo	WP_004405074.1	100/62/0
Vibrio sinaloensis	WP_038188975.1	92/59/0
Vibrio sp. 16	WP_043886606.1	92/58/0
Vibrio sp. MED222	WP_009846388.1	100/57/0
Vibrio tasmaniensis	WP_017104270.1	100/57/0
Vibrio tubiashii	WP_038201292.1	99/59/0
Vibrio variabilis	WP_038217008.1	92/58/0
Vibrio vulnificus	WP_015728225.1	

Organism	PvuA	Cov/Ident/E
Aliivibrio wodanis	WP_045102244.1	100/82/0
Photobacterium sanguinicancri	WP_062689355.1	97/69/0
Vibrio alginolyticus	WP_046875681.1	100/99/0
Vibrio antiquarius	WP_006740839.1	100/99/0
Vibrio caribbeanicus	WP_009603300.1	100/79/0
Vibrio crassostreae	WP_017064386.1	100/83/0
Vibrio cyclitrophicus	WP_016795660.1	100/82/0
Vibrio diabolicus	WP_048625455.1	100/91/0
Vibrio fortis	WP_032550981.1	100/81/0
Vibrio harveyi	WP_050908356.1	100/85/0
Vibrio lentus	WP_050613138.1	100/82/0
Vibrio natriegens	WP_049873777.1	98/85/0
Vibrio navarrensis	WP_039433582.1	100/97/0
Vibrio nereis	WP_053395920.1	100/82/0
Vibrio parahaemolyticus	WP_057620147.1	
Vibrio rotiferianus	WP_045390585.1	100/86/0
Vibrio sp. EJY3	WP_049794697.1	98/85/0
Vibrio sp. HENC-01	WP_009696140.1	100/85/0
Vibrio sp. J2-12	WP_050644301.1	100/83/0
Vibrio sp. J2-15	WP_050632946.1	100/83/0
Vibrio sp. J2-17	WP_050652643.1	100/83/0
Vibrio sp. J2-29	WP_048614853.1	100/83/0
Vibrio sp. J2-3	WP_050620541.1	100/83/0
Vibrio sp. J2-31	WP_050650866.1	100/83/0
Vibrio sp. MED222	WP_009844801.1	100/82/0
Vibrio sp. OY15	KFJ86288.1	100/98/0
Vibrio splendidus	WP_061016597.1	100/82/0
Vibrio tasmaniensis	WP_017103812.1	100/82/0

Organism	FvtA	Cov/Ident/E
Vibrio anguillarum	WP_019281795.1	
Vibrio ordalii	WP_017050158.1	100/99/0
Vibrio campbellii	WP_029388829.1	100/75/0
Vibrio alginolyticus	WP_054579170.1	100/76/0
Vibrio sp. MEBiC08052	WP_059120560.1	100/73/0
Vibrio rhizosphaerae	WP_038181236.1	100/73/0
Vibrio metschnikovii	WP_004396931.1	100/72/0
Vibrio nereis	WP_053394472.1	100/72/0

Organism	FatA	Cov/Ident/E
Vibrio alginolyticus	WP_005375288.1	100/80/0
Vibrio anguillarum	WP_011154638.1	
Vibrio campbellii	WP_050910521.1	99/78/0
Vibrio harveyi	WP_050913418.1	99/78/0
Vibrio kanaloae	WP_017055759.1	100/95/0
Vibrio sp. AND4	WP_009841728.1	99/69/0
Vibrio sp. OY15	WP_033906769.1	100/80/0
Vibrio splendidus	WP_017094255.1	100/99/0

Organism	FrpA	Cov/Ident/E
Photobacterium damselae	WP_044179775.1	94/100/0
Photobacterium damselae subsp. piscicida	AKQ52529.1	
Photobacterium profundum	WP_011218394.1	100/66/0
Salinivibrio sp. DV	WP_069588086.1	94/94/0
Vibrio albensis	WP_032468567.1	95/65/0
Vibrio anguillarum	WP_064626367.1	94/66/0
Vibrio atlanticus	WP_065679247.1	100/56/0
Vibrio cholerae	WP_069648789.1	95/65/0
Vibrio coralliilyticus	WP_045986450.1	100/84/0
Vibrio harveyi	WP_050922393.1	100/57/0
Vibrio mimicus	WP_061051254.1	100/65/0
Vibrio neptunius	WP_045975015.1	100/80/0
Vibrio ordalii	WP_017044474.1	94/64/0
Vibrio rotiferianus	WP_045392643.1	100/57/0
Vibrio sp. HENC-01	WP_009695982.1	100/57/0

Organism	IrgA	Cov/Ident/E
Photobacterium ganghwense	WP_047884933.1	100/63/0
Photobacterium halotolerans	WP_036756649.1	98/63/0
Salinivibrio socompensis	WP_025674231.1	97/58/0
Salinivibrio sp. KP-1	WP_046075193.1	97/60/0
Vibrio albensis	WP_000088795.1	100/98/0
Vibrio alginolyticus	WP_053311394.1	100/97/0
Vibrio anguillarum	WP_013857808.1	100/68/0
Vibrio antiquarius	WP_006743085.1	100/68/0
Vibrio cholerae	WP_000086048.1	
Vibrio diabolicus	CDT94561.1	100/68/0
Vibrio diazotrophicus	WP_042483111.1	96/59/0
Vibrio fluvialis	WP_020332665.1	100/60/0
Vibrio furnissii	WP_047459440.1	100/60/0
Vibrio hepatarius	WP_053408789.1	100/68/0
Vibrio kanaloae	WP_050546269.1	96/70/0
Vibrio litoralis	WP_027696627.1	97/62/0
Vibrio metoecus	WP_055065300.1	100/99/0
Vibrio mimicus	WP_000086042.1	100/94/0
Vibrio navarrensis	WP_039439461.1	100/67/0
Vibrio nereis	WP_053394255.1	98/66/0
Vibrio ordalii	WP_017045434.1	100/68/0
Vibrio parahaemolyticus	WP_025502123.1	100/67/0
Vibrio parilis	WP_000086453.1	100/96/0
Vibrio proteolyticus	WP_040903254.1	97/69/0
Vibrio rumoiensis	WP_017025449.1	100/60/0
Vibrio sp. 2538-88	WP_061897465.1	97/68/0
Vibrio sp. 712i1	WP_017633560.1	100/69/0
Vibrio sp. ECSMB14106	WP_046223384.1	96/70/0
Vibrio sp. JCM 18904	GAJ73542.1	100/68/0
Vibrio sp. JCM 18905	GAJ77987.1	100/68/0
Vibrio sp. OY15	WP_033907452.1	100/68/0
Vibrio sp. S512-13	KJQ87368.1	100/68/0
Vibrio sp. ZOR0018	WP_047688185.1	100/68/0
Vibrio toranzoniae	WP_060468643.1	96/70/0

Organism	VctA	Cov/Ident/E
Grimontia celer	WP_062665201.1	99/62/0
Grimontia sp. AD028	WP_046303643.1	99/62/0
Photobacterium halotolerans	WP_036756816.1	100/54/0
Photobacterium jeanii	OAN11739.1	99/55/0
Photobacterium sanguinicancri	WP_062691924.1	99/55/0
Vibrio albensis	EEO01325.1	100/97/0
Vibrio alginolyticus	WP_046875988.1	99/65/0
Vibrio antiquarius	WP_006742779.1	99/65/0
Vibrio cholerae	WP_000350325.1	
Vibrio coralliilyticus	WP_043010499.1	99/67/0
Vibrio diabolicus	WP_048624949.1	99/65/0
Vibrio diazotrophicus	WP_042479836.1	99/74/0
Vibrio fluvialis	WP_044362327.1	100/71/0
Vibrio fortis	WP_032552715.1	99/67/0
Vibrio furnissii	WP_047460619.1	100/70/0
Vibrio harveyi	WP_017190702.1	99/65/0
Vibrio hepatarius	WP_053407879.1	99/64/0
Vibrio inhibens	WP_063345324.1	99/64/0
Vibrio jasicida	WP_038880693.1	99/65/0
Vibrio mediterranei	WP_062457880.1	99/60/0
Vibrio metoecus	WP_055050054.1	100/92/0
Vibrio mimicus	WP_000350338.1	100/91/0
Vibrio navarrensis	WP_039427354.1	99/61/0
Vibrio nereis	WP_053394603.1	99/66/0
Vibrio nigripulchritudo	WP_022561450.1	99/50/0
Vibrio owensii	WP_045412290.1	99/65/0
Vibrio parahaemolyticus	WP_024701351.1	99/66/0
Vibrio parilis	WP_000350334.1	100/90/0
Vibrio proteolyticus	WP_021704796.1	99/67/0
Vibrio rotiferianus	WP_045389041.1	99/65/0
Vibrio scophthalmi	WP_040757791.1	99/58/0
Vibrio shilonii	WP_006070015.1	99/61/0
Vibrio sinaloensis	WP_008072564.1	99/64/0
Vibrio sp. 1048-83	WP_061900259.1	99/61/0
Vibrio sp. 16	WP_043886787.1	99/63/0
Vibrio sp. 2423-01	WP_061894514.1	99/60/0
Vibrio sp. 2538-88	WP_061898659.1	99/61/0
Vibrio sp. 712i1	WP_017635378.1	99/65/0
Vibrio sp. ER1A	WP_038229421.1	99/61/0
Vibrio sp. HENC-01	WP_009695870.1	99/65/0
Vibrio sp. HENC-02	KM28232.1	97/65/0
Vibrio sp. HENC-03	WP_009704150.1	99/65/0
Vibrio sp. JCM 18904	GAJ70526.1	99/65/0
Vibrio sp. JCM 19053	GAK19199.1	98/65/0
Vibrio sp. MED222	WP_009845519.1	99/65/0
Vibrio sp. N418	WP_038218985.1	100/58/0
Vibrio sp. OY15	KFJ87325.1	99/65/0
Vibrio sp. S234-5	WP_045569166.1	99/61/0
Vibrio splendidus	WP_004737311.1	99/66/0
Vibrio tasmaniensis	WP_017101366.1	99/65/0
Vibrio tubiashii	WP_004742845.1	99/67/0
Vibrio vulnificus	WP_060533657.1	99/61/0
Vibrio xuii	WP_053439033.1	99/65/0

Organism	DesA	Cov/Ident/E
Aliivibrio fischeri	WP_011263609.1	99/59/0
Aliivibrio logei	WP_017021400.1	99/60/0
Aliivibrio salmonicida	WP_012552174.1	99/60/0
Aliivibrio wodanis	WP_061029250.1	99/61/0
Photobacterium halotolerans	WP_052729927.1	99/52/0
Photobacterium kishitanii	WP_045044119.1	94/59/0
Photobacterium phosphoreum	WP_045030314.1	100/56/0
Photobacterium sanctipauli	WP_036832716.1	97/53/0
Photobacterium swingsii	WP_048897482.1	98/53/0
Vibrio alginolyticus	WP_047009840.1	98/50/0
Vibrio brasiliensis	EGA65619.1	88/58/0
Vibrio campbellii	WP_005533381.1	99/60/0
Vibrio caribbeanicus	WP_038136114.1	99/60/0
Vibrio coralliilyticus	WP_006960102.1	98/59/0
Vibrio crassostreae	WP_048668812.1	99/61/0
Vibrio cyclitrophicus	WP_010430390.1	99/60/0
Vibrio diabolicus	WP_048626473.1	98/50/0
Vibrio diazotrophicus	WP_042481746.1	98/72/0
Vibrio fluvialis	WP_032081496.1	100/96/0
Vibrio fortis	WP_032552731.1	100/53/0
Vibrio furnissii	WP_004725209.1	
Vibrio genomosp. F10	WP_017033505.1	99/60/0
Vibrio harveyi	WP_061035573.1	99/60/0
Vibrio hepatarius	WP_053409345.1	99/59/0
Vibrio inhibens	WP_063344221.1	99/60/0
Vibrio jasicida	WP_038865297.1	99/61/0
Vibrio kanaloae	WP_017058127.1	99/60/0
Vibrio litoralis	WP_027697455.1	97/60/0
Vibrio maritimus	WP_042496488.1	99/51/0
Vibrio mediterranei	WP_062457030.1	99/50/0
Vibrio neptunius	WP_045974315.1	98/59/0
Vibrio nigripulchritudo	WP_022610261.1	99/53/0
Vibrio orientalis	WP_004412948.1	98/65/0
Vibrio owensii	WP_045483410.1	99/60/0
Vibrio pacinii	WP_038172738.1	99/58/0
Vibrio proteolyticus	WP_021706544.1	100/66/0
Vibrio rumoiensis	WP_039836685.1	98/59/0
Vibrio sinaloensis	WP_039482114.1	99/61/0
Vibrio sp. 16	EED28639.1	99/60/0
Vibrio sp. 3062	WP_063606139.1	99/50/0
Vibrio sp. 712i1	WP_017634564.1	98/50/0
Vibrio sp. AND4	WP_009841883.1	99/59/0
Vibrio sp. B183	WP_038157617.1	98/60/0
Vibrio sp. CAIM 1540	WP_047043906.1	98/63/0
Vibrio sp. ECSMB14106	WP_046224905.1	99/60/0
Vibrio sp. ER1A	WP_038225588.1	99/50/0
Vibrio sp. HI00D65	WP_063525104.1	99/53/0
Vibrio sp. J2-15	WP_050633003.1	99/61/0
Vibrio sp. J2-26	WP_050711850.1	99/61/0
Vibrio sp. J2-3	WP_050620734.1	99/61/0
Vibrio sp. J2-31	WP_048606204.1	99/60/0
Vibrio sp. J2-6	WP_050645620.1	99/52/0
Vibrio sp. JCM 19052	GAK23108.1	99/60/0
Vibrio sp. MED222	WP_009845539.1	99/52/0
Vibrio splendidus	WP_019822843.1	99/61/0
Vibrio tasmaniensis	WP_017109449.1	99/61/0
Vibrio toranzoniae	WP_060469588.1	99/60/0
Vibrio tubiashii	WP_004745724.1	98/60/0
Vibrio variabilis	GAL24804.1	97/52/0
Vibrio vulnificus	WP_061057750.1	98/59/0
Vibrio xuii	WP_053439432.1	98/65/0

Organism	FhuA	Cov/Ident/E
Photobacterium ganghwense	WP_047886182.1	99/60/0
Photobacterium halotolerans	WP_046220079.1	99/51/0
Photobacterium profundum	WP_011218298.1	100/64/0
Vibrio alginolyticus	WP_053350062.1	98/65/0
Vibrio antiquarius	WP_012842430.1	98/65/0
Vibrio cholerae	WP_053043596.1	
Vibrio diabolicus	WP_048625353.1	98/64/0
Vibrio furnissii	WP_055466431.1	100/73/0
Vibrio galatheae	WP_045954466.1	99/57/0
Vibrio hepatarius	WP_053407570.1	99/60/0
Vibrio hyugaensis	WP_045462290.1	95/66/0
Vibrio kanaloae	WP_017058066.1	100/63/0
Vibrio litoralis	WP_038150238.1	95/50/0
Vibrio metoecus	WP_055051882.1	100/98/0
Vibrio mimicus	WP_000763684.1	100/97/0
Vibrio mytili	WP_041154089.1	98/63/0
Vibrio natriegens	WP_020335445.1	98/63/0
Vibrio navarrensis	WP_039435429.1	98/63/0
Vibrio parahaemolyticus	WP_025553671.1	98/65/0
Vibrio parilis	WP_001204838.1	100/98/0
Vibrio proteolyticus	WP_021706425.1	100/64/0
Vibrio sp. 2423-01	WP_061895609.1	98/64/0
Vibrio sp. 2538-88	WP_061897033.1	98/64/0
Vibrio sp. ECSMB14106	WP_046225153.1	100/64/0
Vibrio sp. EJY3	WP_014234892.1	98/63/0
Vibrio sp. JCM 18904	GAJ71497.1	96/66/0
Vibrio sp. OY15	KFJ86518.1	98/65/0
Vibrio toranzoniae	WP_060469744.1	100/64/0
Vibrio tubiashii	WP_038204349.1	100/57/0