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# Plant Carbohydrate Scavenging through TonB-Dependent Receptors: A Feature Shared by Phytopathogenic and Aquatic Bacteria

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**TonB-dependent receptors (TBDRs) are outer membrane proteins mainly known for the active transport of iron siderophore complexes in Gram-negative bacteria. Analysis of the genome of the phytopathogenic bacterium *Xanthomonas campestris* pv. *campestris* (*Xcc*), predicts 72 TBDRs. Such an overrepresentation is common in *Xanthomonas* species but is limited to only a small number of bacteria. Here, we show that one *Xcc* TBDR transports sucrose with a very high affinity, suggesting that it might be a sucrose scavenger. This TBDR acts with an inner membrane transporter, an amylosucrase and a regulator to utilize sucrose, thus defining a new type of carbohydrate utilization locus, named CUT locus, involving a TBDR for the transport of substrate across the outer membrane. This sucrose CUT locus is required for full pathogenicity on *Arabidopsis*, showing its importance for the adaptation to host plants. A systematic analysis of *Xcc* TBDR genes and a genome context survey suggested that several *Xcc* TBDRs belong to other CUT loci involved in the utilization of various plant carbohydrates. Interestingly, several *Xcc* TBDRs and CUT loci are conserved in aquatic bacteria such as *Caulobacter crescentus, Colwellia psychrerythraea, Saccharophagus degradans, Shewanella* spp., *Sphingomonas* spp. or *Pseudoalteromonas* spp., which share the ability to degrade a wide variety of complex carbohydrates and display TBDR overrepresentation. We therefore propose that TBDR overrepresentation and the presence of CUT loci designate the ability to scavenge carbohydrates. Thus CUT loci, which seem to participate to the adaptation of phytopathogenic bacteria to their host plants, might also play a very important role in the biogeochemical cycling of plant-derived nutrients in marine environments. Moreover, the TBDRs and CUT loci identified in this study are clearly different from those characterized in the human gut symbiont *Bacteroides thetaiotaomicron*, which allow glycan foraging, suggesting a convergent evolution of TBDRs in Proteobacteria and Bacteroidetes.**

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## INTRODUCTION

Bacteria are able to colonize a wide variety of habitats, including the most extreme environments and even living organisms. This remarkable feature likely reflects a high degree of adaptability and the presence of specific genetic programs devoted to the exploitation of nutrients present in these diverse habitats. The bacterial ability to use defined carbohydrates to support cell survival or growth implies the availability of these substrates in their habitat. Moreover, it requires the recognition of these molecules and the coordinated induction of particular uptake systems and of metabolic enzymes [1,2]. Characterization of the repertoire of genes involved in signal perception or transduction and in carbohydrate utilization, in conjunction with analysis of the regulation of their expression, is likely to provide key information about the interaction and adaptation of bacteria with their environment [3].

The analysis and comparison of complete genomic sequences of numerous bacteria from diverse phylogenies and habitats have shown a relationship between the ecological niches that a bacterium occupies and the proportion of genes involved in signal perception and transduction. Bacteria that inhabit stable environments (extremophiles, obligate parasites or symbionts), which generally have small genomes, possess fewer sensory and regulatory genes than free-living bacteria found in complex and changing environments such as those living in soil or in association with plants [2]. Therefore, it was proposed that sensors and regulators can be used as "descriptors of bacterial lifestyle" [2].

With the aim to study the molecular mechanisms controlling adaptation of phytopathogenic bacteria to their host-plants, we undertook a global analysis of receptors and regulators of *Xanthomonas campestris* pv. *campestris* (*Xcc*), the causal agent of black rot of crucifers. This pathogen infects a wide range of *Brassicaceae* plants of economic interest, including cabbage, cauliflower and radish as well as the model plant *Arabidopsis thaliana*. This epiphytic

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bacterium naturally infects host plants *via* wounds in the leaves or hydathodes which are specialized pores on the leaf margins of higher plants that connect to the vascular system. Then bacteria multiply and progress in vascular tissues [4,5]. During the past two decades, classical molecular and genetic studies led to the characterization of several determinants controlling pathogenicity of *Xcc*, such as secretion of extracellular plant cell wall degrading enzymes [6–8], cell-cell signaling [9,10], biofilm formation [11] and *hrp* genes coding for a type III secretion system [12,13]. The characterization of new virulence factors should now be greatly facilitated by the availability of complete genome sequences of two *Xcc* strains (strain ATCC33913 [14] and strain 8004 [15]). Moreover, comparative genomics would improve the analysis of virulence and host adaptation in *Xanthomonas*, since the genomic sequences of four other *Xanthomonas* strains displaying different host specificities and representing three other species are also available, i.e. *Xanthomonas axonopodis* pv. *citri* (*Xac*), the causal agent of citrus canker [14], *Xanthomonas campestris* pv. *vesicatoria* (*Xcv*), the causative agent of bacterial spot disease on pepper and tomato plants [16], and *Xanthomonas oryzae* pv. *oryzae* (*Xoo*) (strain Kacc10331 [17] and strain MAFF311018 [18]), the causal agent of bacterial blight of rice. Thus, the *Xanthomonas* genus, which affects two major model plants (*Arabidopsis* and rice), constitutes a very attractive model to study plant-pathogen interactions.

Our analysis of the *Xcc* (ATCC33913) genome revealed an overrepresentation of a particular family of receptors, named TonB-dependent receptors (TBDRs). These proteins are located in the outer membrane of Gram-negative bacteria and are mainly known to transport iron-siderophore complexes and vitamin B12 into the periplasm [19]. In most cases, the expression of the genes encoding these receptors is under the control of the Fur (Ferric uptake regulator) repressor and activated under conditions of iron starvation [20]. In contrast to diffusion through porins, transport *via* TBDRs requires energy which is provided by the inner membrane energy-coupling TonB-ExbB-ExbD protein complex [21].

The exploration of complete genome sequences of 226 Gram negative bacteria showed that the overrepresentation of TBDRs is restricted to a small proportion of these bacteria, but is a common trait of all sequenced *Xanthomonas* species. Interestingly, most of the bacteria displaying this particularity have diverse lifestyles and belong to different taxonomical lineages, but they all share the ability to exploit complex carbohydrates. Therefore, we postulated that some *Xcc* TBDRs might be involved in the transport of plant-derived molecules. This hypothesis was recently reinforced with the characterization of a TBDR, named MalA, in the oligotrophic aquatic bacterium *Caulobacter crescentus*, which transports maltodextrins [22].

A systematic study of *Xcc* TBDRs, based on mutagenesis, expression analyses and transport assays identified one *Xcc* TBDR involved in the transport of sucrose, a major plant sugar. This TBDR gene is required for full virulence on *Arabidopsis* and is associated with genes required for sucrose metabolism, thus forming a "sucrose utilization locus". Our study also suggests the existence of other TBDR-containing loci involved in the utilization of plant cell wall compounds which are conserved in a wide range of bacteria displaying TBDR overrepresentation.

# RESULTS

## Identification of *Xcc* TBDRs

TBDR proteins consist of two domains, with a C-terminal membrane embedded β-barrel domain that is sealed by the N-terminal plug domain [23–27]. Hidden Markov models (HMMs), PF00593 and PF07715, corresponding to these two domains, are available in the Pfam database [28]. Seventy-six proteins carrying one or both domains were detected in the proteome of the *Xcc* ATCC33913 strain (Table S1). Among these proteins, 64 possess both domains. The remaining 12 proteins, which possess only one of the two domains, can be divided into three groups: 3 proteins (*XCC2208, XCC4131* and *XCC4132*) which do not seem to have a canonical plug domain, one protein (*XCC2497*) which has no domain detected by the PF00593 HMM, and finally 8 proteins (*XCC0304-0305, XCC1750-1751, XCC3215-3216* and *XCC3270-3271*) which are truncated and correspond to 4 pseudogenes having a frame-shift in their coding region (Table S1). Each of these 4 pseudogenes was thereafter studied as a unique entity.

Other conserved features of TBDRs were then used to further characterize these identified proteins. In the N-terminal part of the plug domain, TBDRs display a conserved sequence, the TonB-box, that interacts with the TonB protein [26,27,29]. A TonB-box, with the *Xcc* consensus sequence tLDXVXV (lower case indicates less highly conserved amino acid, X indicates any amino acid) was detected in all studied proteins (Table S1). The localization of TBDRs in the outer membrane implies their transport across the inner membrane and thus the presence of a signal peptide at their N-terminal end. The proteins were therefore analyzed for the presence of such a motif. TBDRs which were not predicted to possess a signal peptide in the annotation proposed by da Silva and colleagues [14] were manually re-annotated, thus revealing putative signal peptides (Table S1). Out of 72 proteins, 1 TBDR (XCC2385) does not have a signal peptide. Finally, the 12 C-terminal amino acids of outer membrane proteins (OMPs) form a membrane anchoring β-sheet with the last residue being aromatic (F in the vast majority of OMPs) [30,31]. The 12 C-terminal amino acid of 55 of the proteins studied here are predicted to form a potential β-sheet, ending with an aromatic residue (Table S1). Among the TBDRs which did not display a typical C-terminal sequence, 8 have a β-sheet ending with an aromatic amino acid followed by a short extension of 1 to 4 amino acids (Table S1).

Taking all this information together, 48 proteins possess all typical features of TBDRs in *Xcc* ATCC33913 and were thus considered as putative functional TBDRs. The other proteins lacking or having degenerated TBDR domains were also included in our study and then named Ps-TBDRs (for Pseudo-TBDRs) (Table S1).

Finally, some TBDRs contain a N-terminal extension, located between the signal peptide and the plug domain [32]. Two types of N-terminal extension have been identified: the transducer and the Oar-like extensions [33]. In *Xcc*, among the 9 TBDRs having an N-terminal extension, one is a member of the TBDR-transducer subclass, seven are in the Oar-like subclass and one displays a N-terminal extension that does not correspond to the two types already identified (Table S1). Among these TBDRs, only two have all canonical features of TBDRs.

## TBDRs are overrepresented in *Xanthomonas* spp. and in bacteria scavenging complex carbohydrates

A survey of TBDRs was performed in 226 eubacterial completely sequenced genomes, by identifying proteins detected by both PF07715 and PF00593 HMMs. This analysis showed that most bacteria (71%) hold less than 14 TBDRs per proteome, whereas the remaining bacteria have a very broad variation in TBDR number, ranging from 14 to 120 (Figure 1 and Table S2). In fact, 27% of the bacteria studied here have no TBDR proteins and

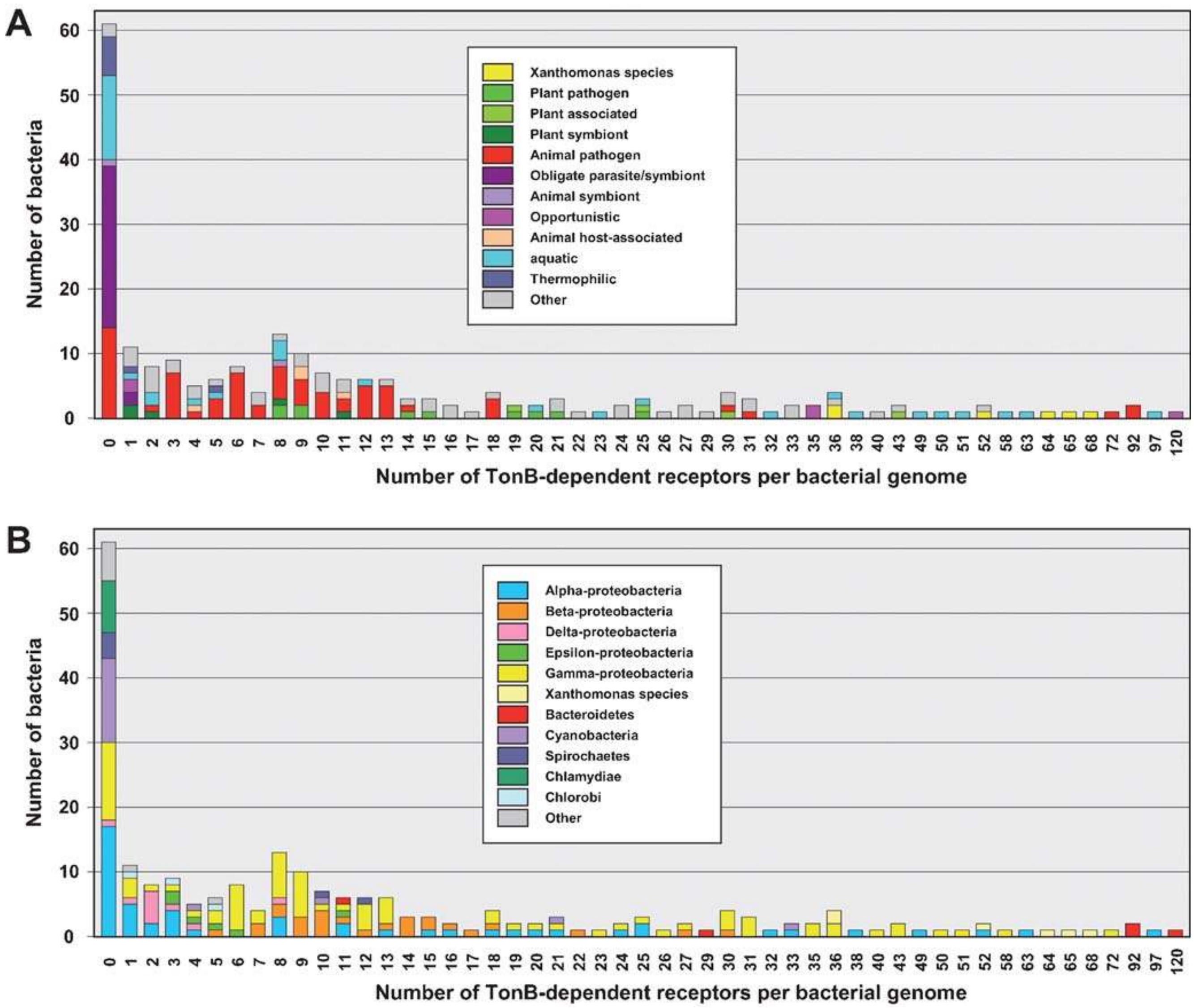


**Figure 1.** Occurrence of TonB-dependent receptor (TBDR) genes in 226 completely sequenced Gram negative bacterial genomes, in ecological (A) or phylogenetic (B) contexts. TBDRs were detected by screening the Pfam database and the UniprotKB protein knowledge database using the two Pfam HMMs (PF07715, Plug; PF00593, TonB_dep_Rec). Only proteins displaying the two Pfam domains were considered. The habitat of bacteria (A) and their phylogeny (B) are represented by colour codes (see the legend boxes).
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43% possess between 1 and 13 TBDRs. Only a very small proportion of bacteria (15.5%) possesses more than 30 TBDRs, thus forming a particular class in which TBDRs seem to be over represented. It is worth noting that most bacteria in this class either belong to the α or γ-Proteobacteria classes or to the *Bacteroides* genus (Figure 1 and Table S2). The ratios between the number of TBDRs found in each proteome and the genome size or the number of annotated coding sequences (CDS) displayed a very similar distribution pattern (Table S2), thus showing that there was no major bias due to annotation. Therefore, the TBDR/Mbp ratio was used to define several bacterial classes: bacteria displaying a ratio higher than 5 were considered as members of a class showing TBDR overrepresentation, while those having a ratio ranging from 3 to 5 belong to an intermediary class. The 4 *Xanthomonas* species whose genomes have been sequenced belong to the class displaying TBDR overrepresentation (Table S2). It is worth noting that phytopathogenic bacteria, such as *Pseudomonas syringae* pathovars or *Erwinia carotovora* subsp. *Atroseptica* belong to the intermediary class.

## Seven *Xcc* TBDR and two Ps-TBDR genes are Fur-regulated

As TBDRs are mainly known to be involved in iron uptake, it was important to determine how many of these receptors are assigned to this function in *Xcc*. In most cases, the expression of genes encoding TBDRs involved in iron transport is regulated by the iron status in the medium. These genes are activated under iron depletion conditions and repressed under iron repletion conditions *via* the Fur repressor (Ferric-uptake regulator), that binds to a specific DNA sequence element called the "Fur-box", which is found in the target promoters of iron-regulated genes [20,34,35]. These features led us to analyze the regulation by the iron status for all identified *Xcc* TBDR and Ps-TBDR genes.

The 76 *Xcc* TBDR and Ps-TBDR genes were mutated by insertion of the suicide plasmid pVO155 [36], leading to transcriptional fusion with the promoterless *uidA* reporter gene. Two insertions (in *XCC1990* and *XCC3209*) were found unstable. Thus, we constructed deletion-mutations in these genes using the *cre-lox* system [37,38]. In order to analyze the expression of these 2 deleted TBDR genes, their promoter regions were cloned upstream of a promoterless *lacZ* gene in a reporter plasmid (see Materials and Methods), and these constructions were introduced into the wild-type strain. Using $\beta$-glucuronidase or $\beta$-galactosidase expression assays, we monitored the expression of all *Xcc* TBDRs and Ps-TBDRs in iron-repleted and -depleted media. Seven genes (*XCC0158, XCC0768, XCC1391, XCC2772, XCC3050, XCC3518*, and *XCC4162*) and 2 Ps-TBDR genes (*XCC3216-3215 and XCC3595*) are induced by iron starvation, compared to iron-replete conditions (Figure 2A). With the exception of Ps-TBDR *XCC3216-3215*, this regulation pattern was confirmed by quantitative real-time reverse transcriptase polymerase chain reaction (qRT-PCR) in a wild-type background (data not shown). We then checked whether these genes are under the control of the Fur regulator. XCC1470, the orthologue of the Fur regulator identified in *Xoo* [39] and in *Xanthomonas campestris* pv. *phaseoli* (*Xap*) [40], was mutated using the manganese method (see Materials and Methods). A point mutant in this latter gene was obtained (*fur*1). As expected for a *fur* mutation, this mutant produced more siderophores than the wild-type strain and this production remained unaffected in response to increased iron levels (from 1 to 50 μM), as determined by using the chrome azurol S assay (data not shown). It is worth noting that the *fur* mutant is unable to induce any disease symptoms (data not shown), as already reported in *Xoo* [39].

We then compared by qRT-PCR analysis the relative expression of the TBDR and Ps-TBDR genes induced by iron starvation, in the wild-type strain *versus* a *fur* mutant, in an iron-containing medium. As presented in Figure 2B, the expression of all these genes was repressed by the Fur protein. However, the repression level of the 2 Ps-TBDR genes was low (less than twofold). We confirmed that the deregulation phenotype of the *fur* mutant was the result of mutation in the *fur* gene by complementation experiments: the repression by iron of the 7 TBDR and the 2 Ps-TBDR genes was restored by providing the wild-type Fur protein on the pL-*XCC1470* plasmid (see Materials and Methods) in the *fur* mutant (Figure 2B).

## The 9 Fur-regulated TBDR/Ps-TBDR genes, but not the other *Xcc* TBDR genes, possess a putative Fur-box

The DNA regions located upstream of the 9 Fur-repressed TBDR and Ps-TBDR genes were analyzed using the MotifSampler program [41,42] to identify putative Fur-boxes. For genes arranged in putative operons (*XCC3050* and *XCC0768*), the DNA region located upstream of the first gene of the putative operon was also studied. *XCC3595*, which belongs to the TBDR transducer subclass, is preceded by two genes displaying significant similarities with the *fecI* (*XCC3593*) and *fecR* (*XCC3594*) genes,

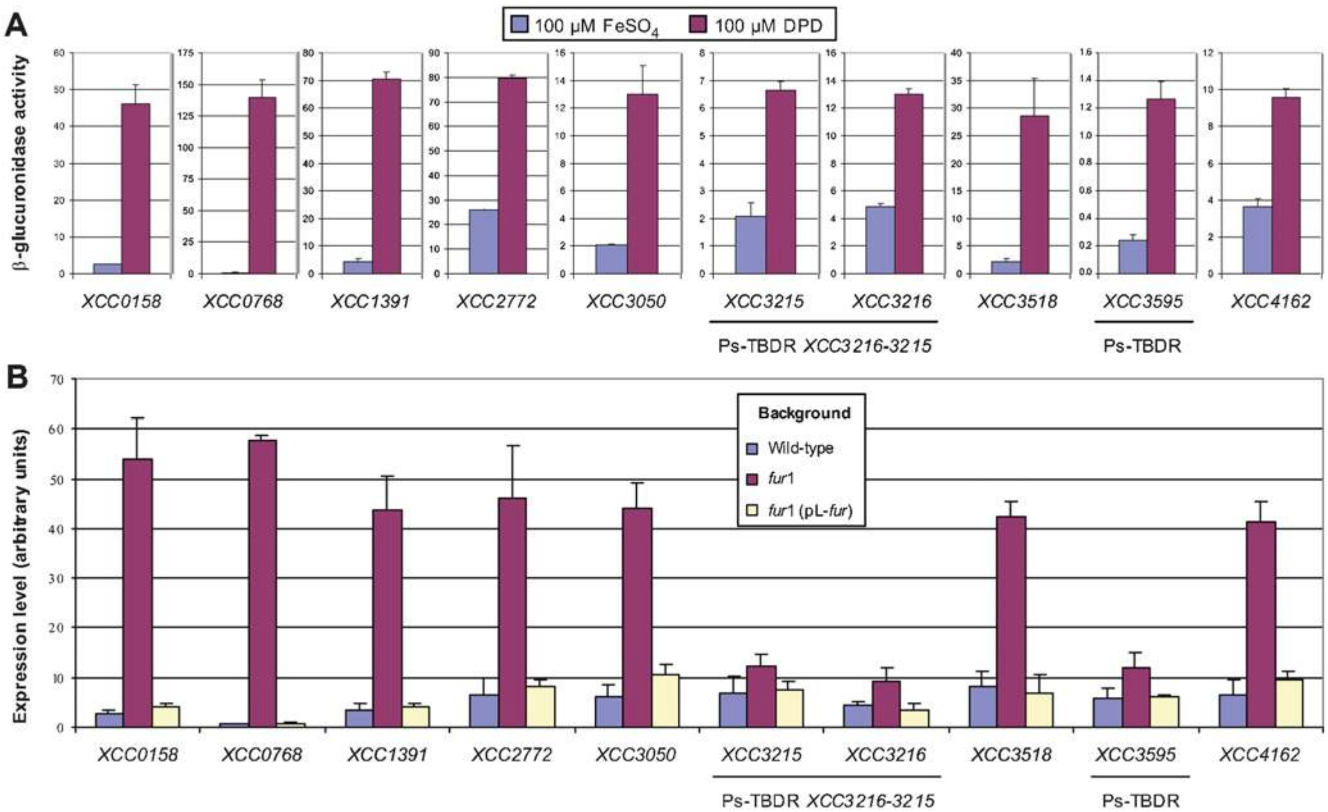


**Figure 2.** Expression levels of 9 *Xanthomonas campestris* pv. *campestris* TonB-dependent receptor genes. (A) $\beta$-glucuronidase assays, performed in at least two independent experiments with pVO155 insertion mutant strains, cultivated in minimal medium supplemented with iron (100 μM $FeSO_4$) or containing an iron chelator (100 μM 2,2′-dipyridyl; DPD). (B) Real-time quantitative RT-PCR (qRT-PCR), performed in at least three independent experiments, on RNA extracted from the wild-type strain, a *fur* mutant strain (*fur*1) or from a complemented strain [*fur*1 (pL-*fur*)], cultivated in minimal medium containing 100 μM $FeSO_4$. Calculation of relative expression includes normalization against the endogenous control gene 16S RNA.
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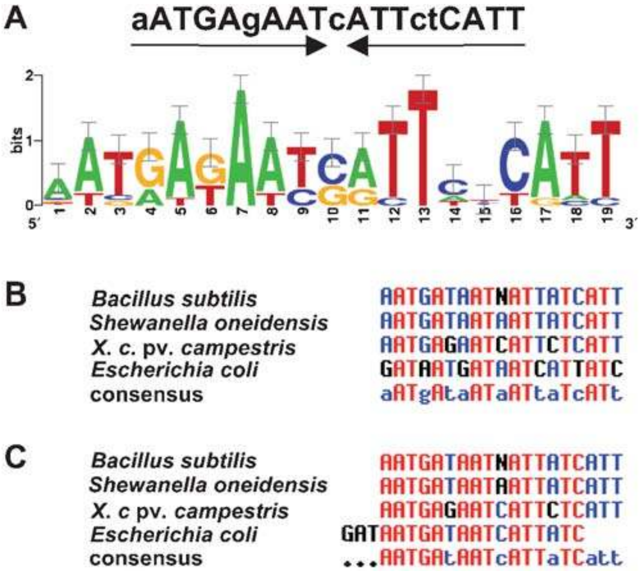


**Figure 3.** Palindromic consensus Fur-box sequence identified upstream of 9 *Xanthomonas campestris* pv. *campestris* Fur regulated TonB-dependent receptor genes. (A) Sequence logos generated by WebLogo (http://weblogo.berkeley.edu/, [123]) of the *Xcc* Fur-box motif as predicted by the MotifSampler program [41,42]. (B and C) Multiple alignement generated with Multalin program [116] with previously proposed Fur-box consensus sequences of *Bacillus subtilis* [46], *Shewanella oneidensis* [45], *X. campestris* pv. *campestris* and *Escherichia coli* [44] (B) and after a 3 bp shift of the *E. coli* sequence (C).
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coding for a sigma factor of the ECF subfamily and its anti-sigma factor, respectively. In most cases, the FecI/FecR system is associated with a TBDR of the transducer subclass and is involved in iron signaling and transport by regulating the expression of the TBDR gene and other ''iron-associated'' genes (for review see [33,43]). We thus also analyzed the DNA regions upstream of these two genes. This analysis allowed the identification of a single significant 19-bp palindromic motif (9-1-9 inverted repeat) in the upstream region of most genes or operons studied here (Figure 3A, Table 1). For *XCC3595*, the palindromic motif was detected in the upstream region of *XCC3593* (*fecI*). For *XCC0768*, two motifs were identified: one in the upstream region of *XCC0767* and one in the coding region of this gene (Table 1). This motif (AATGAgAAT-cATTctCATT; lower case indicates less highly conserved) only showed a weak similarity with the *E. coli* 19 bp Fur-box consensus sequence (GATAATGATAATCATTATC) [44]: it matched this sequence in 10 bp positions out of 19 (52% identity). However, the conservation was significantly higher with Fur-box consensus sequences identified in *Shewanella oneidensis* (AATGATAATAAT-TATCATT; 84% identity) [45] and *Bacillus subtilis* (aaTGAtAAT-nATTaTCAtt; 84% identity) [46]. Interestingly, a multiple alignment of these 4 Fur-box consensus sequences showed that although the *E. coli* consensus sequence seems more divergent, it perfectly matches the 3 other sequences after a 3 bp shift (Figure 3B and C). These results suggest that the palindromic motif identified in this study might correspond to a possible *Xcc* Fur-box. We then explored DNA sequences located upstream of the other *Xcc* TBDR or Ps-TBDR genes as well as the entire *Xcc* genome sequence to detect putative Fur-boxes, using the MotifScanner program [42] or the PatScan pattern matcher software [47]. No putative Fur-box was detected in the promoter region of any other TBDR gene. These analyses identified more than 20 genes having candidate Fur-boxes in the region from −300 to +20 relative to the start of translation (data not shown). Several of these genes are orthologs or homologs of genes regulated by Fur in other bacteria, such as *feoA* (*XCC1834*) [48] and *bfd* (*XCC0481*) [49], or involved in iron storage such as *piuB* (*XCC3955*) [50], thus reinforcing the validity of our Fur-box consensus sequence. Altogether, this analysis suggests that only 7 TBDR and 2 Ps-TBDR are directly associated with iron uptake in *Xcc*. The role of the other TBDRs remained to be deciphered.

## Two TBDR genes belong to the *hrp* regulon of *Xcc*

During the study of TBDR gene promoters, we identified a pip/hrp$_{II}$ box in the promoter of 2 TBDR genes: *XCC1041* and *XCC1719*. In *Xanthomonas*, *hrp* genes coding for a TTSS, as well as other functions related to pathogenicity are positively regulated by *hrpG*/*hrpX* regulatory genes [51]. HrpG regulates the expression of *hrpX*, which controls the expression of genes possessing a pip-box (TTCGCN$_{15}$TTCGC) or a hrp$_{II}$-box (TTCGN$_{16}$TTCG) [52,53]. By qRT-PCR experiments, we showed that *XCC1041* and

**Table 1.** Candidate Fur-boxes identified in the promoter regions of *Xanthomonas campestris* pv. *campestris* Fur regulated TonB-dependent receptor (TBDR) genes, TBDR containing operons and the XCC3593 FecI sigma factor gene.

| Gene ID [a] | Name [a] | Putative function [a] | Putative Fur box sequences [b] | No. of matches/total | Distance from the start codon (bp) [c] |
|---|---|---|---|---|---|
| *XCC0158* | fpvA | ferripyoverdine receptor | AACGATAACGATTTACATT | 14/19 | 136 |
| *XCC0767* | | conserved hypothetical protein | AATGAGAATGGCTCTTGAT | 13/19 | 7 |
| *XCC0768* | phuR | outer membrane hemin receptor | AATGAGAATGGTTATTATT | 15/19 | 374 |
| *XCC1391* | fhuA | iron receptor | TTTGATAACCATTCCCATT | 14/19 | 9 |
| *XCC2772* | fhuA | TonB-dependent receptor | AAGAAGAATGATTTGCATT | 14/19 | 244 |
| *XCC3049* | mphE | 4-hydroxy-2-oxovalerate aldolase | CTTGATAATCATTCCCATC | 14/19 | 41 |
| *XCC3216* | | outer membrane receptor | AATGTGAATCATTCCCATT | 17/19 | 102 |
| *XCC3518* | fpvA | ferripyoverdine receptor | AATAATATTCATTCTCACT | 15/19 | 53 |
| *XCC3593* | fecI | RNA polymerase sigma factor | AATGAGATCCATTCTCATT | 17/19 | 48 |
| *XCC4162* | | ferrichrome-iron receptor 3 | GATAAGAATCGTTATCATT | 15/19 | 12 |

[a]Gene identification (ID), name and putative function from *Xanthomonas campestris* pv. *campestris* strain ATCC33913 as previously reported [14].
[b]Matches to the Fur consensus sequence AATGAgAATcATTctCATT, determined in this study, appear in boldface.
[c]Distance after start codon reannotation (see Table S1).
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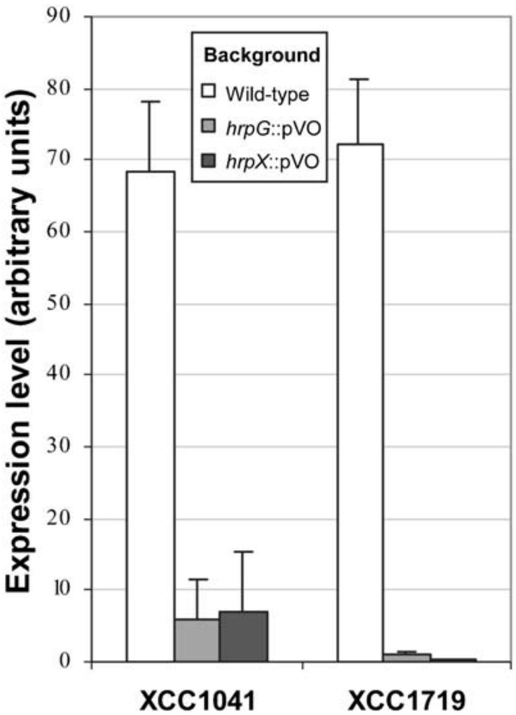


**Figure 4.** Regulation of *Xanthomonas campestris* pv. *campestris* TonB-dependent receptor genes *XCC1041* and *XCC1719* by *hrp* regulators. The relative expression was analyzed by real-time quantitaive RT-PCR (qRT-PCR), perfomed on RNA extracted from the wild-type strain and *hrpG* or *hrpX* insertion mutants (strains XP082 and XP083, respectively). Experiments were repeated at least three times. Calculation of relative expression includes normalization against the endogenous control gene 16S RNA.
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*XCC1719* TBDR genes are activated by HrpG and HrpX (Figure 4). Interestingly, a mutant in the *XCC1719* TBDR gene is weakly affected in pathogenicity (data not shown, see below). This gene seems to be specific to *Xcc* as it is absent in the genomes of *Xcv, Xac, Xoo* and *Xf*, although its surrounding genes are conserved in syntenic regions in all these strains (Table S3). On the other hand, *XCC1041* is present in all *Xanthomonas* species (but absent in *Xf*) and encodes a TBDR with an atypical N-terminal extension.

## *Xcc* TBDRs and plant interactions: *XCC3358* plays a major role in pathogenicity

In order to assess whether *Xcc* TBDRs control the interaction with plants, we tested the 76 TBDR mutants constructed in this study for pathogenicity on the *Arabidopsis thaliana Sf-2* ecotype. Among these mutants, 17 were altered in symptom development (data not shown). However, the alteration was weak and was not reproducible in all the tests we performed, suggesting either that their involvement is not crucial or that functional redundancy mask their individual contribution. However, the *XCC3358* insertion mutant was clearly and reproducibly altered in pathogenicity, showing a clear delay in symptom development in comparison to the wild-type strain (Figure 5A). The *XCC3358* gene is likely to form an operon with the downstream gene, *XCC3359* (Figure 6). The ortholog of the *XCC3359* gene, named *suh*, has been characterized in *Xanthomonas axonopodis* pv. *glycines* (*Xag*), the causal agent of bacterial pustule disease on soybean. This gene codes for a sucrose hydrolase, SUH, which plays a major role in sucrose metabolism in *Xag*. A mutant in this gene is moderately affected in pathogenicity on soybean [54]. This prompted us to construct a non polar deletion-mutation in *XCC3358* (*XCC3358Δ1*, see Materials and Methods and Figure 6). A deletion-mutant was also generated into *XCC3359* (*XCC3359Δ1*, see Materials and Methods and Figure 6). These two mutants showed an altered phenotype, i.e. delayed symptom development, similar to that observed with the pVO155 insertion mutant in *XCC3358* (Figure 5B). The non polar mutation in *XCC3358* was complemented by introducing the plasmid pL-*XCC3358*, which carries a functional *XCC3358* gene, into *XCC3358Δ1* mutant (Figure 5B). This result confirms that the *XCC3358* TBDR plays a role in virulence. Similarly, the deleted mutant in *XCC3359* was complemented by a plasmid carrying this gene (Figure 5B).

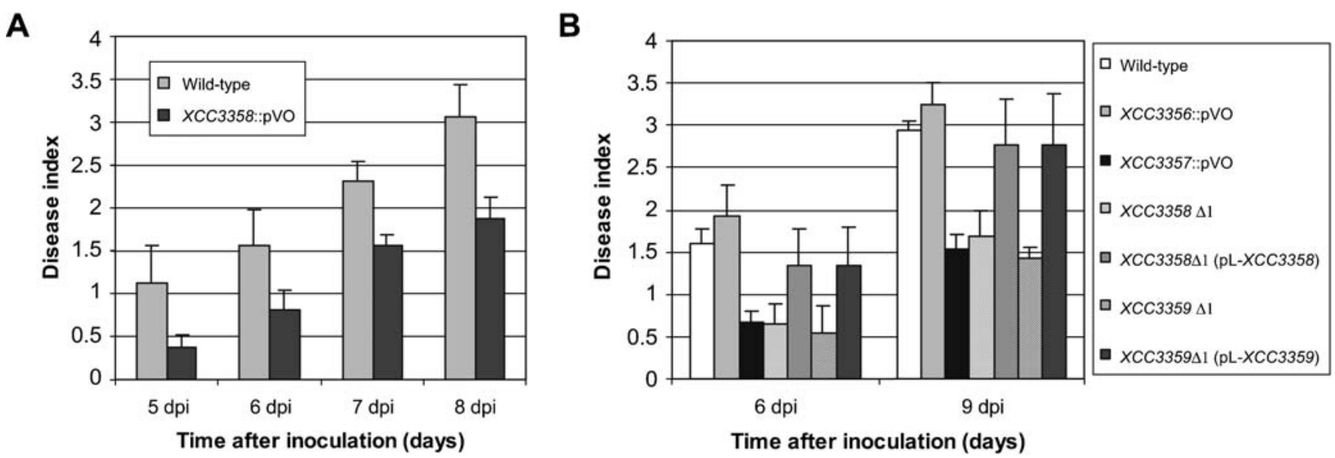


**Figure 5.** Quantitative analysis of the interaction between *Xanthomonas campestris* pv. *campestris* (*Xcc*) and *Arabidopsis thaliana Sf*-2 plants. (A) Pathogenicity tests with the *Xcc* wild-type strain and the *XCC3358* insertion mutant (*XCC3358*::pVO). (B) Pathogenicity and complementation tests with the *Xcc* wild-type strain, the *XCC3356* and *XCC3357* insertion mutants (*XCC3356*::pVO and *XCC3357*::pVO, respectively), the *XCC3358* and *XCC3359* deleted mutants (*XCC3358*D1 and *XCC3359*D1, respectively) and their corresponding complemented strains [*XCC3358*D1 (pL-*XCC3358*) and *XCC3359*D1 (pL-*XCC3359*), respectively]. Disease symptoms were scored 5 to 8 days after inoculation. Each inoculated leaf was individually scored as: no symptom = 0; weak chlorosis surrounding the wound sites = 1; strong V-shaped chlorosis = 2; developing necrosis = 3; leaf death = 4. The represented average disease scores and the standard deviations were calculated from the values of four plants with four inoculated leaves per plant.
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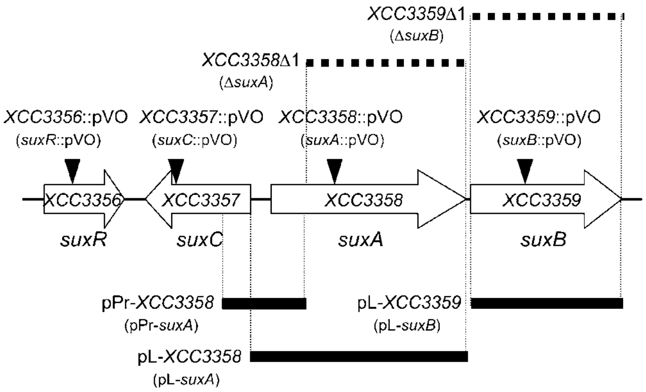


**Figure 6.** Genetic organization of the *Xanthomonas campestris* pv. *campestris sux* locus. Location of mutations are indicated above the map: arrowheads indicate pVO155 insertions and deleted sequences are represented by horizontal dotted bars. Regions cloned in plasmids are indicated below the map: horizontal thick black bars indicate sequences used for plasmid constructions.
doi:10.1371/journal.pone.0000224.g006

## *XCC3358* TBDR belongs to a locus required for full pathogenicity

In *Xcc* genome, *XCC3358* and *XCC3359* are preceded by two other genes that might be related to sugar metabolism: *XCC3356* codes for a putative transcriptional repressor of the LacI/GalR-family and *XCC3357* encodes a putative sugar transporter of the major facilitator family, allowing the transport of substrate molecules through the inner membrane. We constructed insertion mutants in these two genes, presuming that they are monocistronic (Figure 6). These insertions lead to transcriptional fusions with the promoterless *uidA* reporter gene. The insertion mutant in *XCC3357* showed an altered phenotype on the *A. thaliana* Sf-2 ecotype, resembling that using *XCC3358* or *XCC3359* mutants, whereas the insertion mutant in *XCC3356* was not affected in pathogenicity (Figure 5B). These results suggest that *XCC3357*, *XCC3358* and *XCC3359* are required in the same process related to sucrose metabolism and/or transport. The phenotype of a mutant in *XCC3356* was not surprising since this gene encodes a putative repressor, which might negatively control the expression of the other genes of the locus. A mutation in this gene should induce the constitutive expression of the other genes without affecting their function (see below).

## The *XCC3356-3359* locus is required for sucrose utilization

Insertion mutants in *XCC3357, XCC3358* and *XCC3359* and the deletion mutant *XCC3359Δ1* grew like the wild-type strain on minimal medium containing glucose or fructose (data not shown), but were all affected in growth on sucrose (20 mM) (Figure 7A). The growth of the insertion mutant in *XCC3356* and the *XCC3358Δ1* mutant was not impaired in minimal medium containing sucrose. The fact that the insertion mutant in *XCC3358* was impaired in growth on sucrose whereas the deletion mutant in the same gene was not, suggested that the phenotype of the insertion mutant was due to a polar effect of the insertion on *XCC3359* gene expression. This hypothesis was confirmed by complementation experiments. The growth of insertion mutants in *XCC3358* and *XCC3359* on sucrose media was restored when

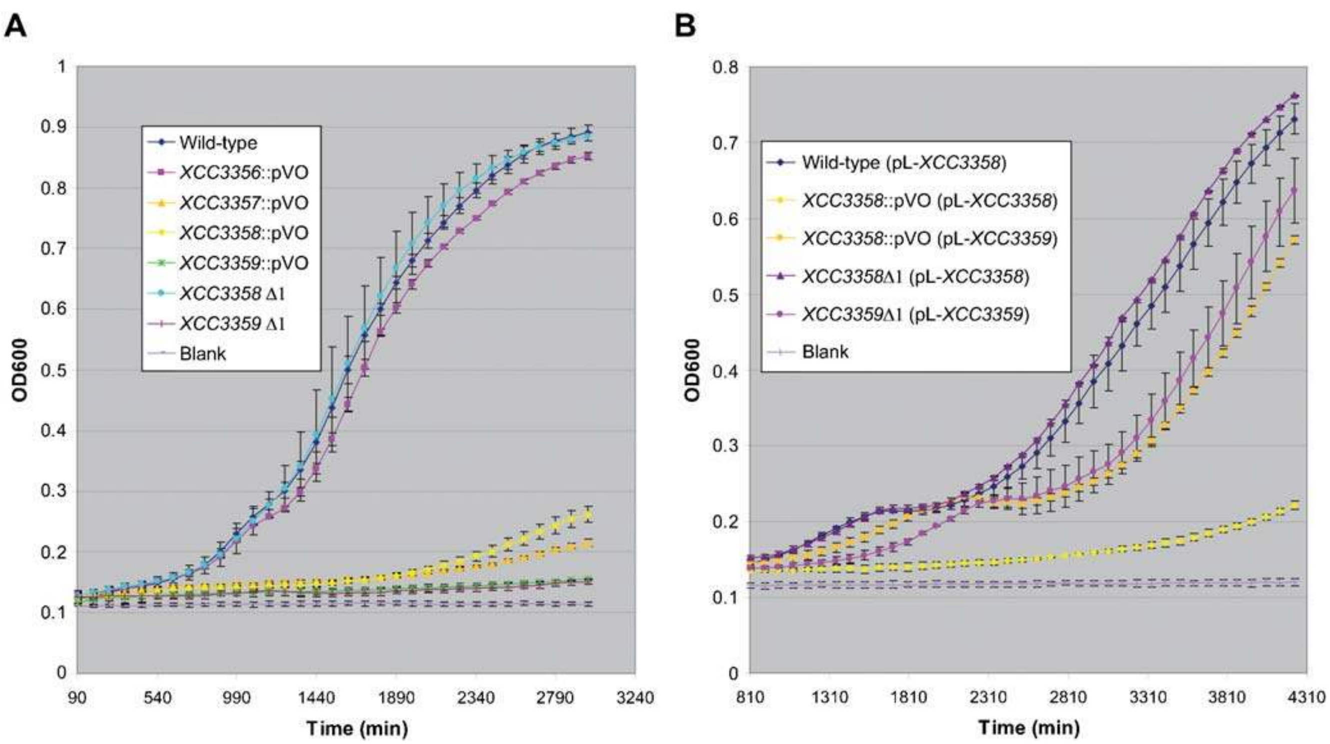


**Figure 7.** Growth of *Xanthomonas campestris* pv. *campestris* wild-type strain and mutants in minimal medium containing 20 mM sucrose. (A) Bacterial growth of insertion mutants *XCC3356*::pVO to *XCC3359*::pVO or deletion mutants *XCC3358Δ1* and *XCC3359Δ1*, compared to the wild-type strain. (B) Growth of strains carrying plamids pL-*XCC3358* or pL-*XCC3359* allowing the constitutive expression of *XCC3358* and *XCC3359* genes, respectively. Bars represent standard deviations from 3 independent experiments.
doi:10.1371/journal.pone.0000224.g007

XCC3359 was supplied *in trans* on the expression plasmid pL-*XCC3359*, which allows constitutive expression of the *XCC3359* gene. No complementation was observed when the *XCC3358* gene was supplied *in trans* in the *XCC3358* insertion mutant (Figure 7B). These results confirmed that *XCC3358* and *XCC3359* form an operon. They also pointed out that this putative operon and the entire locus is important for sucrose utilization in *Xcc*. Thus, we renamed this locus *sux*, for sucrose utilization in *Xanthomonas*. For the purpose of this study, the TBDR-amylosucrase operon was renamed *suxAB*, the putative sugar transporter gene, *suxC*, and the putative regulatory gene, *suxR* (see Figure 6). However, the role of the TBDR SuxA in sucrose utilization remained elusive: this transporter gene was not required for growth on sucrose, but a non polar mutant in this gene was altered in pathogenicity, like *suxB* and *suxC* insertion mutants. This observation suggested that this *suxA* gene might have a particular function.

## SuxA and SuxC allow sucrose uptake

To clarify the role of the SuxA TBDR, we investigated its involvement in sucrose transport, by performing sucrose uptake experiments using [$^{14}$C]sucrose.

First, the uptake rates into the *Xcc* wild-type strain were compared after an overnight preculture in the presence (induced) or absence (uninduced) of sucrose. As shown in figure 8A, induced cells took-up [$^{14}$C]sucrose quicker than uninduced cells, but the values obtained after 2 hours of incubation were lower for induced cells. For further experiments, we worked with uninduced cells, in order to study the effect of different mutations on the transport induction.

Competition experiments were performed to test transport specificity. A 10-fold excess of unlabelled sucrose reduced the transport rate to 52% of the level obtained without unlabelled sucrose, and with a 100-fold or 200-fold excess, the transport rates were reduced to 10.5 and 7% respectively (Table 2). Moreover, the addition of unlabelled fructose or glucose (sucrose degradation sub-products) slightly affected sucrose transport; a 200-fold excess of these carbon sources reduced the sucrose transport to about 80% of the control level (Table 2).

The involvement of the SuxA TBDR in sucrose transport was then checked by comparing the uptake rate of [$^{14}$C]sucrose into the wild-type strain and into a *suxA* non polar mutant (*ΔsuxA*). Sucrose transport was much lower in the *ΔsuxA* strain, compared to the wild-type strain (Figure 8B and Table 2): after 8 minutes, it reached only 3.5% of the transport rate into the wild-type strain. When *suxA* was supplied *in trans* on a constitutive expression plasmid, sucrose transport was more efficient and rapid, with a transport rate value at 8 minutes corresponding to 484% of that of the wild-type strain. This result confirms that SuxA is required for sucrose entry into *Xcc*.

We then studied sucrose transport in *suxR* and *suxC* insertion mutants (*suxR*::pVO and *suxC*::pVO, respectively), and in a *suxB* deletion mutant (*ΔsuxB*). When the inner membrane transporter encoded by *suxC* was absent, the sucrose transport rate reached only 2.1% of the value obtained for the wild-type strain. Thus, this protein is necessary for sucrose entry into *Xcc*. On the contrary, sucrose transport was greatly enhanced in the *suxR* repressor mutant and in the *ΔsuxB* amylosucrase mutant (488% and 241% respectively of the value obtained for the wild-type strain after 8 minutes) (Figure 8C and Table 2). These results confirm the repressor function of SuxR (see below) and suggest that SuxB also has a repressor activity on *suxA* expression. When *suxB* was supplied *in trans* in the *ΔsuxB* mutant, the sucrose transport was reduced to about the same level as the wild-type strain (76.4% of the transport rate level of the wild-type strain).

Concentration-dependent sucrose transport experiments showed a biphasic kinetics (Figure 9), with a fast rate between

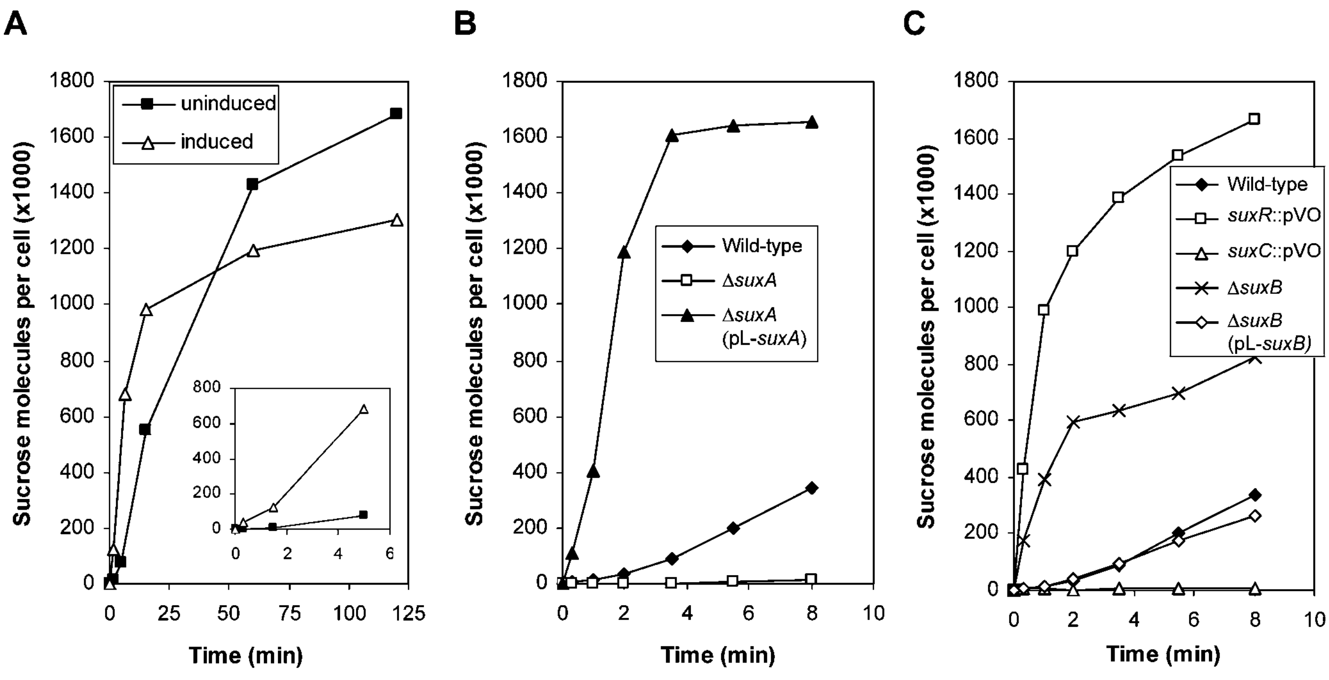


**Figure 8.** [$^{14}$C]sucrose transport into *Xanthomonas campestris* pv. *campestris* (*Xcc*). (A) Transport of [$^{14}$C]sucrose over 120 minutes into the *Xcc* wild-type strain precultured in minimal medium without sugar (uninduced) or supplemented with 20 mM sucrose (induced). (B and C) Transport of [$^{14}$C]sucrose over 8 minutes into the *Xcc* wild-type strain, the insertion mutants in *suxR* and in *suxC* (*suxR*::pVO and *suxC*::pVO, respectively), the deleted mutants in *suxA* and *suxB* (*ΔsuxA* and *ΔsuxB*, respectively) and their corresponding complemented strains [*ΔsuxA* (pL-*suxA*) and *ΔsuxB* (pL-*suxB*), respectively]. Cells were grown in minimal medium without sucrose. Transport was measured using 0.5 μM [$^{14}$C]sucrose.
doi:10.1371/journal.pone.0000224.g008

**Table 2.** [$^{14}$C]sucrose transport rates related to uninduced *Xanthomonas campestris* pv. *campestris* wild-type strain (*Xcc*568).

| *Xcc* strains [a] | Genotype | Transport experiment conditions [b] | Time (min) [c] | % Transport |
|---|---|---|---|---|
| *Xcc*568 | | – | 5 | 100.0 |
| *Xcc*568 [d] | | CCCP 20 μM | 5 | 1.1 |
| *Xcc*568 | | – | 8 | 100.0 |
| XP084 | *suxR*::pVO | – | 8 | 488.0 |
| XP085 | *suxC*::pVO | – | 8 | 2.1 |
| XP087 | *ΔsuxA* | – | 8 | 3.5 |
| XP088 | *ΔsuxB* | – | 8 | 241.3 |
| XP091 | *ΔsuxA* (pL-*suxA*) | – | 8 | 484.3 |
| XP094 | *Δ*suxB (pL-*suxB*) | – | 8 | 76.4 |
| XP100 | *tonB; XCC0008*::pVO155 | – | 8 | 139.1 |
| XP101 | *tonB2; XCC1592*::pVO155 | – | 8 | 99.0 |
| XP102 | *tonB3; XCC1593*::pVO155 | – | 8 | 89.6 |
| XP103 | *tonB4; XCC2081*::pVO155 | – | 8 | 94.4 |
| XP104 | *tonB5; XCC2612*::pVO155 | – | 8 | 90.6 |
| XP105 | *tonB6; XCC2927Δ*1 | – | 8 | 118.4 |
| XP106 | *tonB7; XCC3205*::pVO155 | – | 8 | 82.6 |
| XP107 | *tonB8; XCC3967*::pVO155 | – | 8 | 91.1 |
| *Xcc*568 | | – | 120 | 100.0 |
| XP085 | *suxC*::pVO | – | 120 | 2.5 |
| XP087 | *ΔsuxA* | – | 120 | 9.5 |
| *Xcc*568 | | Sucrose 0,5 μM | 120 | 90.2 |
| *Xcc*568 | | Sucrose 5 μM | 120 | 51.9 |
| *Xcc*568 | | Sucrose 50 μM | 120 | 10.5 |
| *Xcc*568 | | Sucrose 100 μM | 120 | 7.1 |
| *Xcc*568 | | Fructose 0,5 μM | 120 | 87.3 |
| *Xcc*568 | | Fructose 5 μM | 120 | 86.4 |
| *Xcc*568 | | Fructose 50 μM | 120 | 90.6 |
| *Xcc*568 | | Fructose 100 μM | 120 | 86.2 |
| *Xcc*568 | | Glucose 100 μM | 120 | 80.9 |
| *Xcc*568 | | – | 240 | 100.0 |
| XP085 | *suxC*::pVO | – | 240 | 6.9 |
| XP087 | *ΔsuxA* | – | 240 | 23.0 |

[a]*Xcc*568: wild type strain.
[b]Compound added prior to the addition of 0.5 μM [$^{14}$C]sucrose.
[c]Time after [$^{14}$C]sucrose addition.
[d]Cells were incubated for 10 minutes at 30°C with 20 μM carbonyl cyanide 3-chlorophenyl-hydrazone (CCCP) prior to the addition of [$^{14}$C]sucrose.
doi:10.1371/journal.pone.0000224.t002

0.01 and 0.1 μM sucrose ($K_d$ = 0.033 μM), and a slow rate between 0.25 and 5 μM sucrose ($K_d$ = 0.59 μM). This biphasic pattern is very similar to those observed in energy coupled transports of vitamin B12 into *E. coli* through the BtuB TBDR [55,56] and more recently of maltose transport into *C. crescentus* through the MalA TBDR [22]. In both systems, it was concluded that the first phase reflects binding of the transported molecule to the OM TBDR and that the second slower phase reflects binding to a cytoplasmic membrane transporter. Thus, we presume that the low $K_d$ value (0.033 μM) mainly reflects binding to SuxA and that the higher $K_d$ value (0.59 μM) binding to SuxC.

Altogether, these data indicate that both SuxA and SuxC are required for sucrose transport. It is worth noting that if the *ΔsuxA* mutant and the *suxC* insertion mutant have a different phenotype regarding their growth ability in presence of sucrose (see figure 7A), both mutants show a very similar alteration in sucrose transport rate after 8 minutes. However, after 240 minutes, sucrose transport rate in the *suxA*-deleted mutant reached almost 23% of the value obtained for the wild-type strain, whereas in the *suxC* insertion mutant, this rate was less than 7% of that of the wild-type strain. This result suggested the existence of two sucrose uptake pathways, an active and a passive pathway, both requiring transport through SuxC. The active transport pathway depends on SuxA for translocation through the outer membrane, whereas the passive pathway does not. It is assumed that the sucrose uptake rate observed into the *suxA*-deleted mutant is determined by slow and passive diffusion of sucrose across the outer membrane, which is sufficient to support growth in the presence of 20 mM sucrose in the medium.

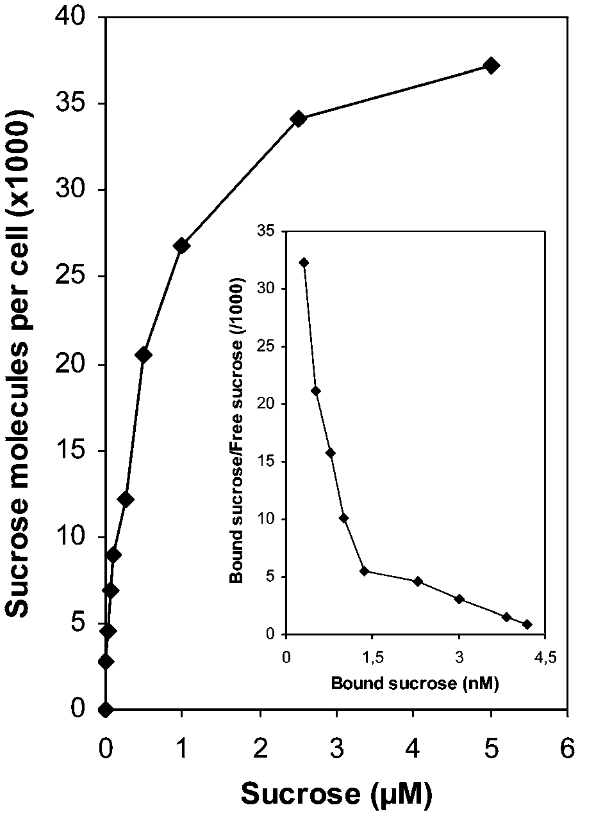


**Figure 9.** Concentration-dependent [14C]sucrose transport into wild-type *Xanthomonas campestris* pv. *campestris*. Cells were grown in minimal medium without sucrose and transport was measured for 15 sec at the indicated [14C]sucrose concentrations. The insert shows the Scatchard transformation of the binding data.
doi:10.1371/journal.pone.0000224.g009

## Sucrose uptake is energy-dependent

Active iron transport through TBDRs depends on the proton motive force (PMF) [56,57]. Thus, we performed sucrose transport experiments in the presence of a PMF inhibitor, carbonyl cyanide 3-chlorophenyl-hydrazone (CCCP). Addition of 20 µM CCCP inhibited [14C]sucrose transport rate to 1.13% of the transport rate in the absence of CCCP (Table 2), demonstrating that sucrose transport through SuxA and/or SuxC is dependent on the proton motive force and does not occur by facilitated diffusion. These experiments did not permit us to conclude whether SuxA-mediated transport depended on the PMF, since SuxC belongs to the $Na^+$-melibiose cotransporter and $H^+$ cotransporters family, which require the transmembrane potential for transport across the cytoplasmic membrane. We then tested whether TonB was required for sucrose uptake. Eight genes coding for proteins displaying significant similarities to TonB are predicted in the genome of *Xcc* (Table 2). These 8 genes were mutated by insertion of the pVO155 plasmid. As the insertion in *XCC2927* was found to be unstable, we constructed a deletion mutant in this gene (Materials and Methods). Sucrose transport was not significantly impaired in the 8 putative *tonB* mutants (Table 2). This result suggests a complete or partial functional redundancy between at least two *Xcc* TonB proteins. Such a redundancy has already been observed in various other bacteria, e.g. *Serratia marcescens* [58], *Vibrio cholerae* [59] and *Pseudomonas aeruginosa* [60,61].

## The expression of *sux* genes is induced by sucrose and repressed by SuxR

Using qRT-PCR analyses, we observed that the expression of *suxR*, *suxC* and *suxAB* is specifically induced by the presence of sucrose in the medium (Table 3).

As *SuxR* has a high degree of similarity with members of the LacI/GalR family of transcriptional repressors [62,63], we tested whether this protein regulates the expression of *sux* genes by comparing their expression by qRT-PCR in the *suxR* insertion mutant and in the wild-type strain, cultivated in minimal medium with or without sucrose. *suxAB*, *suxC* and *suxR* were over-expressed in a *suxR* mutant as compared to the wild-type strain in the absence of sucrose (Table 4), suggesting a negative and effector-dependent control of *sux* genes by SuxR.

We also studied the expression of the *suxAB* operon in the presence of different sucrose concentrations. For this purpose, the promoter region of this operon was cloned upstream of the promoterless *LacZ* gene in a reporter plasmid (see Materials and Methods). This plasmid, named pPr-*suxA*, was introduced into the *Xcc* wild-type strain, the *suxR* and *suxC* insertion mutants (*suxR*::pVO and *suxC*::pVO, respectively), and the *suxA* and *suxB* deletion mutants (*ΔsuxA* and *ΔsuxB*, respectively).

These strains were used to perform β-galactosidase assays after 6 hours growth in minimal medium containing a range of sucrose concentrations (Figure 10A). Induction of the expression of the reporter gene was detected for sucrose concentrations ranging from 20 µM to 20 mM. Maximal induction (3.5 to 4-fold induction) was observed for concentrations higher than 200 µM

**Table 3.** Relative expression ratios of *suxR, suxC, suxA* and *suxB* in the wild-type strain, in minimal medium containing 20 mM sucrose *vs* minimal medium without sucrose.

| Gene name | Ratio (+/− SD) [a] |
|---|---|
| *suxR* | 5.87 (+/−1.98) |
| *suxC* | 11.14 (+/−0.4) |
| *suxA* | 20.92 (+/−8.5) |
| *suxB* | 44.97 (+/−2.64) |

[a]From real-time quantitative reverse-transcriptase polymerase chain reaction perfomed in at least three independent experiments. Cells were cultivated in minimal medium with or without sucrose. Calculation of relative expression includes normalization against the 16S rRNA endogenous control gene. SD: standard deviation.
doi:10.1371/journal.pone.0000224.t003

**Table 4.** Relative expression ratios of *suxR, suxC, suxA* and *suxB* in the *suxR* insertion mutant (*suxR*::pVO) *vs* wild-type strain.

| Gene name | Ratio (+/−SD) [a] | |
|---|---|---|
| | Without sucrose | With sucrose |
| *suxR* | 10.4 (+/−2.3) | 1.01 (+/−0.64) |
| *suxC* | 23.6 (+/−4.8) | 2.56 (+/−0.8) |
| *suxA* | 154 (+/−83.2) | 2.08 (+/−1,8) |
| *suxB* | 176.45 (+/−77.7) | 1.54 (+/−0.8) |

[a]From real-time quantitative reverse-transcriptase polymerase chain reaction perfomed in at least three independent experiments. Cells were cultivated in minimal medium with or without sucrose. Calculation of relative expression includes normalization against the 16S rRNA endogenous control gene. SD: standard deviation.
doi:10.1371/journal.pone.0000224.t004

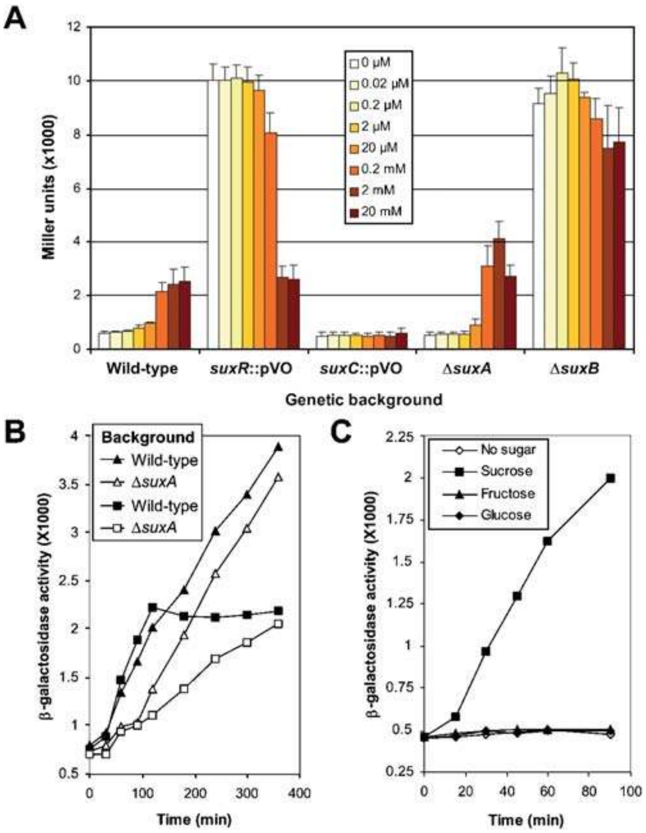


**Figure 10.** Expression of the *Xanthomonas campestris* pv. *campestris suxA* gene in the presence of sucrose, fructose or glucose. The pPr-*suxA* plasmid carrying the promoterless *LacZ* reporter gene under the *suxA* promoter region was used to monitor *suxA* expression in different genetic backgrounds. Expression was measured in minimal medium and cells were harvested at the indicated times. (A) Expression after 6 hours induction in the presence of different sucrose concentrations, in the wild-type background, the *suxR* and *suxC* insertion mutant backgrounds (*suxR*::pVO and *suxC*::pVO, respectively), and the *suxA* and *suxB* deletion mutant backgrounds (*ΔsuxA* and *ΔsuxB*, respectively). (B) Kinetics of *LacZ* expression in the wild-type background or in the *suxA* deletion mutant background (*ΔsuxA*), in presence of 20 mM (triangles) or 100 µM (squares) sucrose. (C) Kinetics of *LacZ* expression in the wild-type background in the presence of 100 µM sucrose, fructose or glucose.
doi:10.1371/journal.pone.0000224.g010

in the wild-type background (Figure 10A). As expected, the expression of *suxA* was highly induced in the *suxR* mutant, confirming the repressor activity of this gene. However, we observed a significant diminution of the induction level at 2 and 20 mM sucrose in this mutant, suggesting the existence of a second level of control. A high and constitutive induction of *suxA* expression was also observed in the *suxB* deletion mutant, suggesting that the amylosucrase gene plays a role in the repression of the *suxAB* operon. At 2 mM sucrose concentration, a reduction in *suxA* expression level was also observed in this mutant, but it was smaller than that detected in the *suxR* mutant. The deregulation of *suxA* expression in the *suxB* mutant is in agreement with transport studies which showed a higher sucrose transport rate in this mutant (Figure 8C). No induction of *suxA* expression was observed in the *suxC* mutant, whatever sucrose concentration was used. This lack of induction certainly reflects the absence of sucrose entry into the cytoplasm of this mutant, thus preventing the alleviation of SuxR repression. This result clearly shows that the induction of *suxA* expression by sucrose requires the entry of this molecule into the cell. The pattern and level of expression of *suxA* observed in the *suxA* mutant were very similar to those observed in the wild-type strain, except that this expression was significantly higher in the mutant in the presence of 2 mM sucrose. This difference was reproducibly observed and further investigations are needed to understand this phenomenon.

Expression assays suggested that sucrose transport through SuxA is not high enough to influence the expression of the *suxAB* operon. Sucrose entry across the outer membrane by slow diffusion seems to be sufficient to promote induction of *sux* genes after 6 hours growth in the presence of sucrose.

## *suxA* is required for its rapid induction as revealed by using low sucrose concentrations

We performed time-course experiments comparing *suxA* expression in the wild-type strain and the *suxA* deletion mutant grown in presence of different sucrose concentrations (0, 20 µM, 50 µM, 100 µM, 200 µM 500 µM, 1 mM, 2 mM, 5 mM and 20 mM). For clarity, only results obtained with 100 µM and 20 mM are shown in Figure 10B. In the presence of 20 mM sucrose (triangles on Figure 10B), *suxA* expression was not significantly different after 6 hours growth in the wild-type and the *suxA* mutant backgrounds. However, a slight difference was observed in the induction level of *suxA*, from 60 to 120 minutes after sucrose addition. The expression level of *suxA* was 1.5 to 1.6 fold higher in the wild type strain than in the *suxA* mutant. Later, this difference tended to decrease and the ratio reached a value of 1.1 after 6 hours. A reproducible and clear difference in curve profiles was noticed in the presence of 100 µM sucrose (squares on Figure 10B). A rapid induction was observed in the wild-type context, from 30 to 120 minutes after sucrose addition, followed by a plateauing, in which expression seems to remain constant. On the other hand, in the *suxA* deletion mutant background, the induction was linear and less rapid. Between 30 and 120 minutes after sucrose addition, the expression level of *suxA* was 2 fold higher in the wild-type strain background than in the *suxA* deletion mutant background, although after 360 minutes, the expression levels were identical in both strains. Similar results were obtained with sucrose concentrations ranging from 20 to 200 µM (data not shown). We propose that these results could reflect the existence of two pathways controlling *suxA* expression, which can be clearly differentiated with low sucrose concentrations. One of these pathways is controlled by SuxA. These results can be related to the transport analyses showing the existence of two types of sucrose transport across the outer membrane, one being SuxA-dependent and the other one, slower, being dependent on passive diffusion. We thus postulate that the induction of *suxA* indirectly reflects these two means of transport. Moreover, this induction is specific to sucrose and is not due to its degradation products glucose and fructose, as no induction was observed following addition of 100 µM of these molecules in the wild-type background (Figure 10C). Therefore, these experiments suggest that SuxA plays a role in sucrose transport which might be crucial at low concentrations of this sugar.

## Identification of other *Xcc* TBDRs in *loci* probably involved in plant carbohydrates utilization

The genome of *Xcc* was then explored to see whether other TBDRs could belong to loci involved in the utilization of other plant compounds. *Xcc* has an extensive repertoire of plant cell-wall degrading enzymes, with cellulolytic, pectinolytic and hemicellulolytic activities [14]. The analysis of carbohydrate active enzymes identified in the predicted proteomes of 209 Gram negative bacteria and referenced in the CAZy database (http://afmb.cnrs-mrs.fr/CAZY/) showed that, after *Bacteroides* sp. and *S. degradans*, which are well known specialists for polysaccharide degradation, *Xcc* has one of the highest number of genes involved in polysaccharide metabolism per megabase (29.9, total 152) (Table S2). These genes encode 82 predicted glycosyl hydrolases, 45 glycosyl transferases, 5 polysaccharide lyases, 18 carbohydrate esterases and 2 carbohydrate binding proteins. Interestingly, 46 of these proteins are encoded in the vicinity of 24 TBDR/Ps-TBDR genes, thus suggesting the existence of 19 new loci putatively involved in carbohydrate utilization (Table S3). Among those loci, 7 also contain an inner membrane transporter coding gene and a regulatory gene. For 3 loci identified in this analysis, the substrate probably utilized and transported could be easily deduced from the nature of the degradative enzymes: the *XCC0120* TBDR gene is localized upstream of genes coding for a pectin methyl esterase and a pectate lyase and might belong to a locus involved in pectin utilization (Figure 11A); the *XCC4120* TBDR gene is found in a cluster of genes probably involved in xylan metabolism (Figure 11B); and the *XCC2469* TBDR gene might be related to maltose/maltodextrin utilization, since it is associated with genes coding for a cyclomaltodextrin glucanotransferase, two α-glucosidases, a sugar transporter and a maltose transport gene repressor (Figure 11C).

To verify whether these TBDRs are really associated with carbohydrate utilization, we studied their regulation by plant compounds. For this purpose, we performed β-glucuronidase expression assays using all *Xcc* TBDR pVO155 insertion mutants. Cells were grown in rich medium or in minimal medium supplemented or not with polygalacturonic acid (PGA), arabinose, glucose, maltose, sucrose, xylose or xylan. Most TBDR (or Ps-TBDR) genes (44 out of 74) were repressed in rich medium, compared to minimal medium (Table S4). We also observed that in minimal medium, 48 *Xcc* TBDR genes are repressed in the presence of sucrose, xylose, arabinose and/or glucose, suggesting that these genes are submitted to catabolic repression (Table S4). However, the repression patterns were variable, suggesting the existence of several repression pathways. It is worth noting that most Fur-regulated TBDR genes were submitted to catabolic repression.

Three TBDR/Ps-TBDR genes were induced by PGA (*XCC0120*, *XCC1749* and *XCC1750-1751*), one by maltose (*XCC2469*), seven by arabinose (*XCC0050*, *XCC1749*, *XCC1750*, *XCC1892*, *XCC2828*, *XCC4120* and *XCC4222*), three by xylan (*XCC2828*, *XCC4120* and *XCC4237*) and finally two by xylose (*XCC2828* and *XCC4120*) (Table S4). Interestingly, the 2 TBDRs induced by xylose were also induced by xylan and arabinose, and *XCC1749* and *XCC1750* were both induced by PGA and arabinose. *suxA* is the only TBDR gene for which expression is specifically induced by sucrose, and *XCC2469*, the orthologue of *C. crescentus malA* TBDR gene [22], is the only one induced by maltose. It is worth noting that the expression of the *XCC0120*, *XCC4120* and *XCC2469* TBDR genes was specifically induced by the postulated substrate of the associated CAZy referenced enzymes (see Figure 11). Altogether, these data suggest that several TBDRs are part of loci which seem to be involved in carbohydrate utilization. We thus propose the existence of 6 putative loci named carbohydrate utilization containing TBDRs (CUT) loci, which were defined by the presence of genes coding for carbohydrate degradative enzymes, inner membrane transporters and sugar related regulators beside TBDR genes. We also identified 15 putative partial CUT loci in the *Xcc* genome (see Table S3).

## Conservation and distribution of TBDRs and CUT *loci* in Xanthomonads

When compared with proteins in the databases using BlastP and the "distance tree of results option" displayed on the BlastP result page, the best homologous genes of *Xcc* TBDRs/Ps-TBDRs were putative TBDRs of other *Xanthomonas* species and in some cases of *Xyllela* strains. These conserved genes might be considered as orthologs. We compared the distribution of *Xcc* TBDRs among Xanthomonads strains for which genome sequences are available, i.e. *Xcc* strain 8004, *Xcv* (strain 85–10), *Xac* (strain 306), *Xoo* (strains KACC10331 and MAFF311018) and *Xf* (strains 9a5c and PD). A

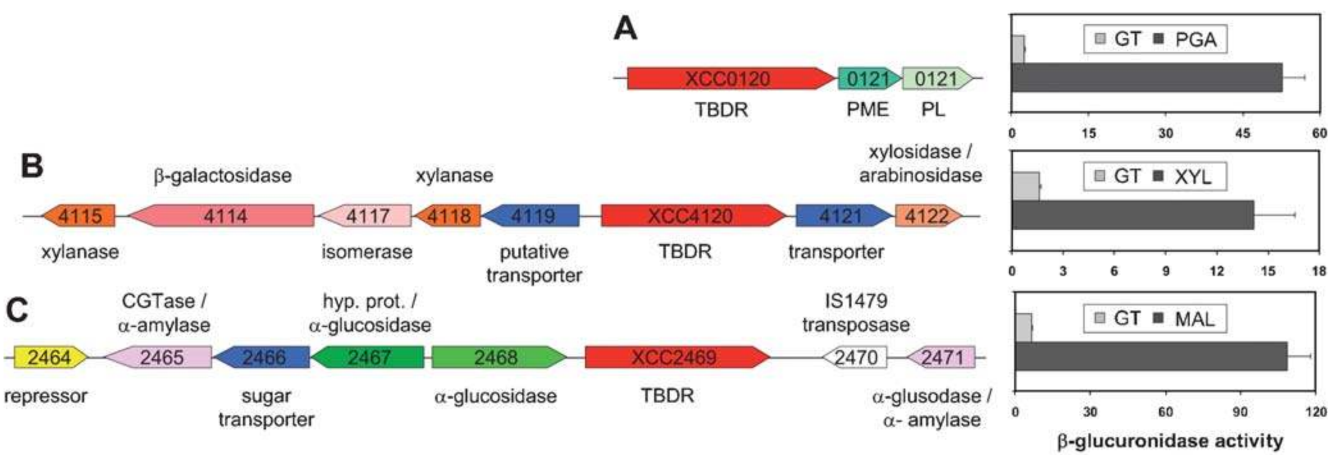


**Figure 11.** Genetic organization of putative *Xanthomonas campestris* pv. *campestris* CUT loci and specific induction of the TonB-dependent receptor gene by plant carbohydrates. Putative pectin (A), xylan (B) and maltodextrin (C) utilization CUT loci and specific induction of the corresponding TBDR gene in the presence of PGA, xylose and maltose, respectively. β-glucuronidase assays were performed in at least two independent experiments with TBDR insertion mutants cultivated in minimal medium supplemented with glutamate 20 mM (GT) or specific carbohydrates (PGA: polygalacturonic acid 0.125%; XYL: xylose 20 mM; MAL: maltose 20 mM). TBDR: TonB-dependent receptor; PME: pectin methyl esterase; PL: pectate lyase; CGTase: cyclomaltodextrin glucanotransferase.
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search similar to that used for *Xcc* allowed us to identify 72 TBDR/Ps-TBDR in the proteome of *Xcc* strain 8004, 74 in that of *Xac*, 61 in *Xcv*, 41 and 42 in *Xoo* strains KACC10331 and MAFF311018 respectively, and finally 10 in each *Xf* strain. To further study the relationship between these TBDRs and *Xcc* TBDRs, we performed a comparative study using alignments generated by ClustalW [64]. To carry out this comparative analysis, we only used TBDRs which seemed to be complete and Ps-TBDRs over 600 amino acids, in order to avoid bias in alignments. Examination of the phylogenetic tree, coupled with Blast results analysis, clearly confirmed that most *Xcc* TBDRs are well conserved in other *Xanthomonas* strains (Figure S1 and Table S3). All TBDR or Ps-TBDR genes detected in *Xcc* strain ATCC33913 are present in strain 8004; 55 seem to have orthologs in *Xac*; 49 are conserved in *Xcv* and 34 only are conserved in *Xoo* strains which possess significantly less TBDRs. In most instances, the grouping and distribution pattern of orthologous TBDRs matched the phylogenetic classification of *Xanthomonas* species [65–67]. This observation suggests that this protein family is ancient in the *Xanthomonas* genus. It is worth noting that branch lengths were variable, suggesting differential evolution rates. Moreover, we noticed that some truncated *Xcc* Ps-TBDRs could be functional in other strains: the Ps-TBDR XCC1750-1751 doublet corresponds to unique and complete TBDR proteins in *Xcv, Xac* and *Xcc* strain 8004. Similarly, the 2 Ps-TBDRs XCC3215-3216 and XCC3270-3271, which are also truncated in *Xcc* strain 8004, correspond to unique proteins in both *Xac* and *Xcv*. Interestingly, *Xac, Xcv* or *Xoo* TBDR orthologs of *Xcc* Ps-TBDR having non-canonical C-terminal regions ($\beta$-sheet ended by an aromatic amino acid followed by a short extension of 1 to 4 amino acids), also displayed this feature (data not shown). In most cases, these non canonical C-terminal domains were identical in all strains. This conservation might reflect a specific functional feature of *Xanthomonas* TBDRs.

The analysis of the phylogenetic tree also showed that Xanthomonads TBDRs can be divided into three main groups, with most TBDRs belonging to group 1. This group can be divided into 8 subgroups (1A to 1H). We noticed that (i) *Xcc* Oar-TBDRs are clustered in subgroup 1D, (ii) most plant carbohydrate induced TBDRs (8 out of 11) are grouped in subgroup 1C, and (iii) most *Xcc* Fur-regulated TBDRs (6 out of 8) are grouped in subgroup 1F. Among these Fur-regulated TBDR genes, *XCC3518*, *XCC3595* and *XCC4162*, which belong to subgroup 1F, seem specific to *Xcc* strains.

The comparison of genes located adjacent to orthologous TBDR genes in the different *Xanthomonas* strains showed that in most cases, these regions are syntenic (Table S3). Thus, all putative CUT loci identified in *Xcc* genome are well conserved in *Xac* and *Xcv* but only 2 out of 6 were found in *Xoo*. Similarly, almost all putative partial CUT loci are present in both *Xcv* and *Xac*, but only 9 out of 15 are conserved in *Xoo* strains. The putative polygalacturonate utilization locus (*XCC0120-XCC0122*) seems unique to *Xcc*. The genes bordering this locus are conserved and contiguous in *Xcv* and *Xac*, thus suggesting insertion or deletion events (Table S3).

Finally, among the 10 TBDRs identified in *Xf* strains, 6 are conserved in *Xcc, Xac, Xcv* and *Xoo*, 1 is conserved in *Xcc, Xac* and *Xcv*, whereas only 1 is present in *Xcc*. The 2 remaining *Xf* TBDRs (XF0339/PD1711; XF0599/PD1552) seem more divergent and thus specific to *Xf* strains. However, XF0599 displays weak similarities with XCC2772, a Fur-regulated TBDR of *Xcc*. None of the other *Xf* TBDRs are related to *Xcc* Fur-regulated TBDRs nor to *Xcc* TBDRs belonging to putative CUT loci identified in this study. Only 2 *Xf* TBDR genes (*XF2713* and *XF1036*) correspond to *Xcc* TBDRs present in partial CUT loci.

## *Xcc* TBDRs are conserved in aquatic bacteria and/or phytopathogenic bacteria.

For each *Xcc* TBDR included in the phylogenetic study, we analyzed the BlastP results obtained on the nr databank, to characterize the next best homologous genes after Xanthomonads orthologs. This analysis allowed us to cluster *Xcc* TBDRs on the basis of the bacterial origin of the homologous TBDR. Thus, *Xcc* TBDRs could be divided into 4 main groups (Table S5). The first group corresponds to TBDRs showing their next best homologies (after Xanthomonads orthologs) with other *Xanthomonas* TBDRs rather than with TBDRs from other genera. This observation mainly concerned TBDRs found in subgroups 1B, 1C and 1D of the phylogenetic tree. Their positions in the tree suggested that they could be generated by successive duplication events that occurred before *Xanthomonas* speciation (Figure S1). The second group corresponds to TBDRs which display high similarities with TBDRs of $\beta$-Proteobacteria and/or *Pseudomonas* species. Interestingly most of these TBDRs are clustered in subgroup 3 of the phylogenetic tree. Moreover, some of these TBDRs showed high similarities with TBDRs of phytopathogenic bacteria such as *Acidovorax avenae* subsp. *citrulli*, *Pseudomonas syringae* pathovars or *Ralstonia solanacearum*. The third group contains two *Xcc* TBDRs proposed to be involved in iron uptake and showing significant similarities with putative TBDRs from *Cyanobacteria*. The fourth group, which is the largest one (with 35 TBDRs out of 70), corresponds to TBDRs which displayed very significant homologies with putative TBDRs of a wide range of aquatic bacteria belonging to the $\alpha$ or $\gamma$ classes of Proteobacteria. It is worth noting that in most cases, *Xcc* TBDRs were not affiliated to TBDRs of a specific bacterial class, but there was rather a variety of origins. Thus, for 16 *Xcc* TBDRs the best similarities (after Xanthomonads similarities) were obtained with putative TBDRs of *C. crescentus* CB15 and *Caulobacter* sp. K31 strains, which are aquatic oligotrophs belonging to the Caulobacterales order of the $\alpha$-Proteobacteria. Homologies were also observed with TBDRs of other $\alpha$-Proteobacteria living in aquatic habitats, such as *Oceanicaulis alexandrii*, *Maricaulis maris* or *Parvilarcula bermudensis* HTCC2503, or found in multiple environments like *Sphingomonas* sp. SKA58, *Sphingopyxis alaskensis* or *Novosphingobium aromacitovorans*. Significant similarities were also obtained with putative TBDRs of aquatic $\gamma$-Proteobacteria classified in the *Alteromonadales*, including *Alteromonas macleodii, Saccharophagus degradans* 2–40, *Pseudoalteromonas* and *Shewanella* species. One common trait of most of these bacteria is that they show TBDRs overrepresentation with values of TBDR number per megabase ranging from 7.4 to 15.7 (Table S2). This raised the question of whether homologies between these TBDRs were fortuitous and a consequence of their large number or whether they reflect common biological functions.

## Conservation of TBDR regions and CUT loci in Gram-negative bacteria

Some regions surrounding TBDR genes were found to be conserved in closely related bacteria such as *Vibrio parahaemolyticus* or *P. aeruginosa*. Thus, the XCC3050 Fur-regulated TBDR belongs to a cluster of 6 genes showing similarities with the *pvuA-pvsABCDE* gene cluster of *V. parahaemolyticus*, involved in the uptake and biosynthesis of the siderophore vibrioferrin [68] (Table S3). Similarly, a group of proteins encompassing XCC3067 TBDR and putatively involved in cobalamin uptake and biosynthesis in *Xcc* was conserved in *Pseudomonas* species (Table S3). Preliminary experiments showed that the expression of this TBDR gene is repressed by the presence of vitamin B12 in *Xcc*, thus suggesting that this cluster is functional (data not shown).

Several CUT loci identified in *Xcc* were not conserved in taxonomically related bacteria but rather in the group of aquatic bacteria showing TBDR conservation and in particular in *C. crescentus*. The *sux* locus, 3 of the putative CUT loci and 4 of the putative partial CUT loci identified in this study were entirely or partially conserved in this group of bacteria (Table S3). Thus, the putative maltose CUT locus was partially conserved with the *mal* locus recently identified in *C. crescentus*, which contains the MalA TBDR proposed to be involved in the uptake of maltodextrins [22] (Figure S2B). Interestingly, MalA shows significant similarities with the *XCC2469* TBDR whose expression is induced by maltose and maps in the maltose CUT locus (Figure 11C).

Similarly, the putative xylose locus, containing the *XCC2828* TBDR gene, is also very well conserved in *C. crescentus* (Figure S2C). The corresponding *CC0999* TBDR gene was shown to be induced by xylose in this bacterium [69]. Moreover, *CC2832*, which was also shown to be xylose-induced in *C. crescentus*, displays significant homologies with the xylose-induced TBDR gene *XCC4120* belonging to a xylose CUT locus. Furthermore, the 20-bp palindromic motif conserved upstream of genes of the *C. crescentus* xylose regulon, was also found upstream of genes putatively involved in xylose metabolism in *Xcc*, as well as in the promoter region of *XCC2828* and *XCC4120* TBDR genes [69].

The *sux* CUT locus seems less well conserved and showed some degree of variation (Figure S2D). The amylosucrase gene (*XCC3359*) is only well conserved in the corresponding *C. crescentus* locus. In the loci conserved in other bacteria, the degradation of sucrose seems to involve more classical pathways (for review see [70]). Moreover, the MFS transporter of the *Xcc* locus is different from that of the *C. crescentus* sucrose locus encoded by *CC1133*, although it is well conserved in both *Sphingomonas* SK58 and *Erythrobacter litoralis*. These differences show the existence of some degree of plasticity in the evolution of the putative CUT loci. Further investigations are needed to see whether all these partially conserved loci are involved in the utilization of the same molecule. However, this wide conservation of CUT loci is in favor of their existence. These results also confirm that the similarities observed between TBDRs are probably not fortuitous.

# DISCUSSION

## Overview

The outer membrane (OM) of Gram negative bacteria serves as a selective permeation barrier, excluding hydrophilic solutes, including most nutrients. However, OMs contain embedded integral proteins, named outer membrane proteins (OMPs), which allow sensing and entry of nutrients into the cell. A major class of OMP with a certain substrate specificity, called porins, allows the translocation of hydrophilic solutes through the OM. Another class of OMPs, the TonB-dependent receptors (TBDRs), is mainly known to be involved in iron or vitamin B12 uptake [71]. Recently, the MalA TBDR of *C. crescentus* was shown to be involved in the ExbBD-dependent uptake of maltodextrins [22]. Here, we show that several Gram negative bacteria, belonging to different lineages and having diverse habitats, display an over-representation of TBDRs, which might be related to the uptake of plant-derived carbohydrates.

## *Xcc* TBDRs belonging to the Fur regulon

Our global study of *Xcc* TBDRs showed that only a small fraction of them seems to be involved in iron uptake. Among the 72 TBDR/Ps-TBDRs identified in the *Xcc* genome, only 9 are up-regulated under iron-limiting conditions. We established that these 9 genes are repressed by the Fur repressor and that they are the only TBDR genes having a Fur-box in their promoter region. Recently, a proteomic approach carried out in *P. aeruginausa* PAO1, which contains 34 putative TBDR genes, identified a very similar number of TBDR genes regulated by iron-stavation. In fact, in this bacterium, 7 TBDRs are produced under iron-starvation conditions and 4 others are specifically induced by the presence of heterologous siderophores, under iron-restricted conditions [72]. Therefore, although it is possible that some *Xcc* TBDR genes need specific heterologous siderophores for their expression, as observed in *P. aeruginosa*, the number of TBDR genes involved in iron uptake seems very comparable in both bacteria. This suggests that the other putative TBDRs/Ps-TBDRs might be required for different biological functions.

## The identification of CUT loci/systems in *Xcc* suggests a relationships between TBDRs and carbohydrate utilization

Our data reveal that several *Xcc* TBDRs are related to plant carbohydrate utilization. A large proportion of *Xcc* TBDR genes are coupled with carbohydrate active enzymes. For 6 of them, an inner membrane transporter gene and a regulatory gene are also present in the same region, thus defining the existence of putative CUT loci involved in the uptake and utilization of plant carbohydrates. Moreover, 15 *Xcc* TBDR genes belong to partial CUT loci, thus suggesting the existence of CUT systems composed of different parts scattered in the genome. The existence of such multipartite CUT systems was supported by the observation that 11 TBDR/Ps-TBDR genes are specifically induced by plant carbohydrates such as sucrose or plant cell wall derived compounds including arabinose, xylan/xylose, pectin/polygalacturonate or maltose. Moreover, in 5 cases, there is a correlation between the inducing carbohydrate and the degradative enzyme(s) present in the CUT locus. This allows us to propose the existence of a sucrose CUT locus as well as loci involved in the utilization of complex carbohydrates such as pectin, xylan or starch.

## The *sux* CUT locus is functional

The existence of functional CUT loci was confirmed by the detailed study of the sucrose CUT locus, which showed its involvement in the entry and utilization of sucrose in *Xcc*. This locus comprises four genes, *suxA, suxB, suxC* and *suxR*, coding for a TBDR, an amylosucrase, a sugar inner membrane transporter and a regulatory protein, respectively. [$^{14}$C]sucrose uptake experiments showed that SuxA and SuxC are both required for sucrose entry into the cell. Concentration-dependent sucrose transport experiments showed a biphasic kinetic, with a similar pattern observed for vitamin B12 uptake into *E. coli* through the BtuB TBDR [55], and more recently for maltose transport into *C. crescentus* through the MalA TBDR [22]. In both of these systems, it has been concluded that the first phase reflects the binding of the transported molecule to the OM TBDR, and that the second slower phase reflects the binding to a cytoplasmic membrane transporter. Thus, we presume in our experiments that the low $K_d$ value (0.033 μM) mainly reflects binding to SuxA and that the higher $K_d$ value (0.59 μM) binding to SuxC. Sucrose transport was significantly lower in the *suxC* mutant than in the *suxA* non polar mutant. This difference might explain the differential phenotype of these two mutants observed for growth on sucrose: the *suxA* non polar mutant was not impaired in growth on media containing sucrose, whereas the *suxC* mutant was unable to grow under these conditions. These observations suggest the existence of an alternative pathway that supports facilitated diffusion of sucrose across the OM, whereas it seems that there is a unique route for crossing the inner membrane, depending on SuxC. The existence of this alternative pathway was also revealed by expression analyses of the *sux* locus. The regulation of *sux* genes seems to follow a classical inducer/repressor control, mediated by the SuxR repressor, sucrose being the inducer. The expression of *sux* genes is induced by sucrose but not by fructose or glucose. This induction was detected with sucrose concentrations ranging from 20 μM to 20 mM. These experiments showed that SuxA transport influenced sucrose induction of *suxA* at low sucrose concentrations (20 to 200 μM), whereas this effect is masked at higher concentrations, probably by interference by passive diffusion.

Our data also indicated that sucrose transport through the *sux* system is active and depends on the proton motive force. However, we could not conclude whether it depends on the TonB-ExbBD energy coupling system. In addition to TonB, the *Xcc* genome harbours 7 TonB-like proteins, which might substitute one for another. Another *Xcc* feature is the presence of a second *exbD* gene, named *exbD2*, mapping downstream of the *tonB-exbBD1* locus. Interestingly, *exbD2* is not required for iron uptake but is essential for HR induction, whereas *tonB*, *exbB* and *exbD1* genes are necessary for both processes [73,74]. This differential behavior might be related to the existence of at least two classes of TBDRs in *Xcc*, one involved in iron uptake and the other one in transport of plant compounds. Further work is needed to address this hypothesis.

## The *sux* locus represents a new sucrose utilization system

The *Xcc sux* locus is clearly different from other sucrose utilization loci already found in bacteria (for review see [70]). In particular, it differs from the *scr* sucrose-utilization system from enteric bacteria, which is also present in the plant pathogenic bacterium *Erwinia amylovora*, where it plays a major role in plant colonization [75]. The differences concern regulation, sucrose utilization and transport. The *scr* genes are regulated by a LacI/GalR family repressor, but fructose is the inducer [76]. In this system, the degradation of sucrose uses a sucrose-6-phosphate hydrolase/fructokinase degradation pathway [70]. On the contrary, the *Xcc sux* locus contains an amylosucrase orthologous to SUH, a unique sucrose hydrolase previously characterized in *Xag* [54]. This enzyme is responsible for intracellular sucrose hydrolysis. It is active on sucrose but not on sucrose-6-phosphate. In the s*cr* system, sucrose metabolism and uptake are coupled by the phosphoeneolpyruvate-dependent carbohydrate:phosphotransferase system (PTS), which controls crossing of the inner membrane and sucrose phosphorylation. The transport across the outer membrane is mediated *via* a porin, named ScrY [77,78]. Thus, the transport of sucrose is very different in *sux* and *scr* systems. Interestingly, the $K_d$ value of sucrose binding to SuxA is 1500- to 3000-fold lower than that of the *E. coli* ScrY sucrose porin, which varies from 13 mM [79] to 50 mM [80]. Similarly, *C. crescentus* MalA TBDR transports maltodextrins with $K_d$ values 1000-fold lower than those of the LamB porin, which facilitates the passive diffusion of maltodextrin [22]. It is worth noting that the $K_d$ values of sucrose binding to SuxA and maltodextrins binding to MalA are comparable. Thus, SuxA and MalA represents a new class of outer membrane carbohydrate transporters showing a much higher affinity for their substrate than porins.

The importance of the *sux* locus in *Xcc* is highlighted by the fact that it is required for full virulence on *Arabidopsis thaliana*. The phenotype of *suxB* and *suxC* mutants on plants can be related to their inability to grow on medium containing sucrose (20 mM). However, the non polar *suxA* mutant, which grows as well as the wild type strain on medium containing sucrose, was also affected in pathogenicity. Thus, it appears that the ability to scavenge sucrose with a very high affinity plays a key role during the interaction with host plants.

In conclusion, data obtained on this sucrose CUT locus strongly support the existence of the other CUT loci identified in *Xcc*, which might have a similar mode of action (see model presented in Figure 12). This suggests the presence of several systems which seem to partially overlap and which are involved in the scavenging of plant molecules. They might form a complex network required for the exploitation of plant resources but which might also participate in signaling.

## TBDRs and CUT loci are ancient in the *Xanthomonas* genus

The importance of TBDRs and CUT loci is not restricted to *Xcc* since they are well conserved in *Xac* and *Xcv*. A phylogenetic study of Xanthomonads TBDRs suggests that these proteins are an ancient class of proteins in the genus. Moreover, the grouping pattern observed in our phylogenetic study seems to correlate with functional features of *Xcc* TBDRs, thus suggesting the existence of structure/function relationships. However, it seems that there is some degree of variation in the repertoire of TBDR genes and CUT loci among *Xanthomonads*, as the number of genes and loci was lower in *Xoo* strains and also in *Xylella*. This latter species is considered as a minimal pathogen in the Xanthomonads with a restricted habitat and a reduced genome [81]. *Xylella* possesses a significantly lower number of TBDRs and only one partially conserved CUT locus.

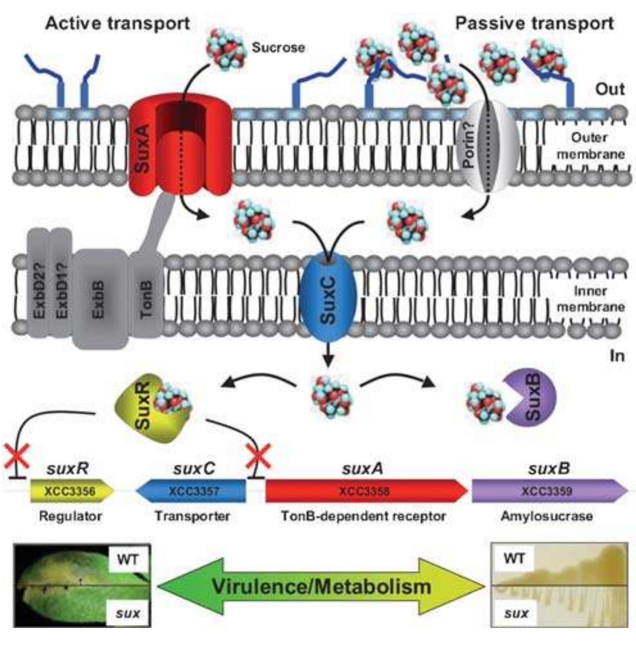


**Figure 12.** Model of CUT loci functioning based on the *Xanthomonas campestris* pv. *campestris sux* locus. This scheme shows sucrose outer membrane transport *via* the SuxA TBDR or by passive diffusion through a putative porin. After crossing the inner membrane through the SuxC transporter, sucrose is proposed to interact with the SuxR repressor (thus allowing *sux* gene induction) and also to serve as a substrate for the SuxB amylosucrase. The large double headed arrow below the *sux* locus represents the balance between metabolic adaptation and virulence control putatively mediated by CUT loci.
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## Conservation of *Xcc* TBDRs and CUT loci reveals carbohydrate scavenging abilities in other bacteria

One of the main surprises of this work was the observation that the large majority of *Xcc* TBDRs (35 out of 72) display significant similarities with TBDRs of bacteria which are mostly found in aquatic habitats and which are not closely related to Xanthomonads (see Table S5). Phylogenetic studies place Xanthomonads as a deep branch in the $\gamma$-Proteobacteria class, close to that of the $\beta$-Proteobacteria [66,82]. The bacteria possessing similar TBDRs belong either to the $\alpha$-Proteobacteria class or to the Alteromonadales order of the $\gamma$-Proteobacteria. Most bacteria in this latter order have been collected from diverse aquatic environments and belong mainly to 6 different genera: *Alteromonas*, *Colwellia*, *Idiomarina*, *Pseudoalteromonas*, *Saccharophagus* and *Shewanella*. The $\alpha$-Proteobacteria mentioned in this study are also found mostly in aquatic habitats and are members of several orders, including Caulobacterales, Sphingomonadales, Rhodospirillales and Rhodobacterales. Similarities were not restricted to TBDRs genes, and genome context analyses showed that at least 8 putative (partial) CUT loci identified in *Xanthomonas* species were conserved among members of these aquatic bacteria. Several of them are found in association with abiotic or biotic surfaces, such as the surface of alga or shellfish. Some are adapted to live in oligotrophic environments, while others are abundant in nutrient-rich habitats or in association with particulate of organic matter. Some others are associated with decaying tissues of plant or algae. Although *Xanthomonas* seems to be very different from these bacteria in terms of habitat, lifestyle and taxonomy, we identified several common traits. All these bacteria belong to the class showing a TBDR overrepresentation (with TBDRs/Mbp ratios>7.4). Most of them are able to degrade a wide variety of plant molecules or other complex carbohydrates such as chitin, alginate, as well as various aromatic compounds. This combination of characters and the similarities with *Xcc* suggest the existence of a shared biology which might be related to the ability to scavenge carbohydrates. If the situation in these bacteria is similar to that observed in *Xcc*, we can speculate that there is a significant proportion of TBDRs involved in the uptake of molecules other than iron-siderophores complexes. Moreover, as previously noticed [33], we observed that bacteria having a restricted habitat, such as obligate parasites or symbionts, have no or only a very small number of TBDRs. Thus, these proteins might be considered as good indicators of bacterial lifestyle.

## Association between TBDRs and carbohydrate utilization in other Proteobacteria

A specific role for TBDRs has already been attributed to bacteria displaying an overrepresentation of this protein family. Sphingomonads are widely distributed in nature and are mostly found in soils and aquatic environments. Some strains are associated with plants [83]. Strains like *Sphingomonas* sp. A1 are able to take up and metabolize macromolecules such as alginate produced by brown seaweed and certain bacteria. This uptake is mediated by large structures, so called superchannels, which form a pit in the outer membrane, and which function as a funnel or concentrator (for review, see [84]). Four TBDRs seem to be part of this superstructure and are thus proposed to participate in alginate transport [85]. Recently, the manipulation of these superchannels revealed the importance of these structures in bioremediation [86].

In *C. crescentus*, beside the prediction of 67 TBDRs, a genome analysis revealed the presence of several genes for the breakdown of plant polysaccharides as well as transport systems, suggesting that plant polymers are a significant source of nutriment for this organism [87]. Interestingly, several *C. crescentus* TBDR genes have been shown or proposed to be associated with the uptake of plant compounds. As described above, Neugebauer and colleagues showed that *C. crescentus* can grow on maltodextrins and that the transport of these molecules is mediated by the MalA TBDR [22]. Proteomic and transcriptomic studies have shown that TBDR genes are expressed at higher levels in minimal medium than in rich medium [69,88–90], as we observed in *Xcc*. Moreover, several TBDR genes are specifically induced by the presence of xylose [69]. Interestingly, 2 TBDRs induced by xylose are conserved between *C. crescentus* and *Xcc*. Strikingly, putative regulatory *cis*-element motifs are conserved in the promoters of these homologous genes in both species. Moreover, one of these 2 *Xcc* TBDR genes (*XCC2828*) belongs to a putative partial CUT locus which is conserved in *C. crescentus* (Figure S2C). This suggests a possible lineage between these loci. Moreover, 3 other *Xcc* CUT loci are entirely or partially conserved in the *C. crescentus* oligotrophic bacterium, including the maltose and sucrose CUT loci. TBDRs in oligotrophs like *C. crescentus* might play a very important role by allowing the foraging of carbohydrates in nutrient poor environments.

## Common themes between *Xanthomonas* and aquatic bacteria

It is clear that the life cycle of *Xanthomonas* spp. presents common features with the different lifestyles of bacteria described above. The leaf surfaces encountered by *Xanthomonas* during their epiphytic development might correspond to an oligotrophic environment. Plant leaves release secondary metabolites which can be used by epiphytic microorganisms [83]. However, carbon resources have been shown to be the most limiting resource on plants [91]. Simple sugars, like glucose, fructose and sucrose, are the most dominant carbon sources on plants that have been examined [92]. Studies with bacterial biosensors *in situ* on plants revealed a high heterogeneity of sucrose availability, with an average accessibility of only about 20 μM on moist bean leaves [93]. Interestingly, this sucrose concentration allowed the induction of *suxA* gene in our expression assays, thus suggesting that the *sux* uptake system might function on plant surfaces. The involvement of *sux* locus in epiphytic life is now being investigated. Furthermore, TBDRs might facilitate the exploitation of plant debris generated during disease development, thus resembling bacteria living on dead tissues. This phenomenon might have an impact on *Xanthomonas* life cycle by increasing *Xanthomonas* population size and thus facilitating new infections.

## TBDRs and virulence on plants

It appears that in *Xanthomonas*, some TBDRs such as SuxA play an additional and specific role by controlling virulence. Therefore, it is tempting to propose that a strategy shared with non-pathogenic bacteria and based on the active uptake of plant-derived nutrients, could have been diverted by *Xanthomonas* for the control of pathogenicity. It is worth noting that several phytopathogenic bacteria such as *P. syringae* or *E. carotovora* subsp. *Atroseptica*, as well as *Pseudomonas* species associated with plants, have an intermediate overrepresentation of TBDRs, suggesting that this feature could be shared by other bacteria interacting with plants. In *R. solanacearum*, the expression of *hrp* genes coding for a type III secretion system (TTSS) which controls disease and HR development, is specifically induced upon contact with plant cells [94]. This signaling is mediated by PrhA, a TBDR belonging to the transducer subclass. This receptor senses contact with plant cells and transduces this signal into the cytoplasm via PrhI and PrhR, which are FecI/FecR homologs [94–96]. Apparently, this regulatory system does not require the transport of plant molecules [94]. Although *Xac, Xcc, Xoo* or *Xcv* do not carry any TBDR showing a high homology with PrhA, recently a TBDR controlling both HR and pathogenicity was described in *X. oryzae* pv. *oryzicola*, the causal agent of bacterial leaf streak of rice. This TBDR does not belong to the transducer subclass and only shows a weak similarity with PrhA [97]. This TBDR gene is highly conserved in *Xoo* strain MAFF 311018 (*XOO0785*), *Xcv* (*XCV3654*) and *Xcc* (*XCC0674*). Interestingly, in *Xoo* it is located close to *trh* (*XOO0783*), a regulatory gene controlling the expression of *hrp* genes [53]. The orthologue of this regulatory gene is also conserved in *Xcc* (*XCC0672*), in the vicinity of the *XCC0674* TBDR gene. Thus, it is possible to speculate that both genes might be involved in a common circuit controlling the expression of *hrp* genes in *Xanthomonas* spp. In our study, a mutation in *XCC0674* did not affect the pathogenicity of *Xcc*. However, as there are more TBDRs in *Xcc* than in *Xoo* strains, we can speculate that functional redundancy might have masked the effect of the mutation. Further work is needed to see whether these genes regulate *hrp* genes in *Xcc*. Nevertheless, we established a link between *hrp* genes and TBDRs in *Xcc*. Indeed, we observed that 2 *Xcc* TBDR genes are regulated by the *hrpG* and *hrpX* regulatory genes. Therefore, it seems that there is an overlap between *hrp* genes and at least 2 TBDR genes. What is the function of these two TBDRs? Are they specifically required during the infection of plants, through the action of the *hrp* regulon, to exploit specific released plant molecules?

### What other functions for *Xcc* TBDRs?

We have been able to define a putative role for 21 TBDRs out of 72 identified in *Xcc*. The nature of the molecules putatively transported by the other TBDRs remains to be discovered. It is probable that TBDRs are not restricted to the transport of carbohydrates and that they can take up various other molecules produced by plants. *Azospirillum irakensis*, a plant associated bacterium, is able to metabolize salicin, a phenolic glycoside produced by plants. Interestingly, the *sal* operon, which controls the degradation of salicin, contains a TBDR gene which was proposed to be involved in salicin uptake [98]. Thus, secondary metabolites including phenolic compounds might be assimilated through TBDRs. We are now trying to characterize which new molecules may be transported by *Xcc* TBDRs, to better understand the adaptation of this pathogen to host plants.

### TBDRs, CUT loci and evolution in Gram-negative bacteria

This work has identified the existence of an ensemble of bacteria that have an overrepresentation of TBDR genes, and that share specific loci for the scavenging and utilization of carbohydrates. They belong to very different lineages in Proteobacteria and this raises the question of the origin of these TBDRs and CUT loci. Did they arise by convergent evolution or were they transferred from species to species by lateral gene transfer? Our data suggest that this latter hypothesis is most likely. Recently, a genomic comparative study established that *Xcc* and *Xac* have close to 40% of their genes showing highest similarities to genes from non $\gamma$-Proteobacteria, especially from $\alpha$-Proteobacteria (20%). These genes seem to belong to genomic islands, denominated "unusual best-match islands" (UBIs) [82]. Interestingly, among 35 UBIs thus identified in *Xcc* genome, 14 contain TBDRs and/or CUT loci. However, there was no significant difference between the GC content of each of these loci and the overall content of the genome. It is therefore possible that these loci were acquired very early in the evolution of Xanthomonads and thus played a key role in their adaptation to plants. Most bacteria showing a TBDR over-representation possess TBDRs or CUT loci conserved with *Xcc*. However, there is a main exception with members of the Bacteroidetes phylum, as none of the TBDRs characterized in this phylum showed very significant similarities with those identified in *Xcc*. Bacteroidetes can be encountered in two very different niches, the marine environment and the human intestine [99,100]. Marine Bacteroidetes such as *Gramella forsetii* are associated with particulate of organic matter [99], whereas those found in the intestine are assembled on partially digested food particles [101]. In both cases, these bacteria are able to consume biopolymers. *Bacteroides thetaiotaomicron*, which is a prominent mutualist in the distal intestine of adult humans, has the largest ensemble of TBDR genes and glycobiome yet reported (Table S2). Studies have shown that this bacterium has a carbohydrate foraging behavior [100–102]. It is well known to bind starch through a protein complex of the outer membrane, which comprises SusD and the SusC TBDR protein [103]. One hundred and six paralogs of SusC and fifty three paralogs of SusD were predicted in the *B. thetaiotaomicron* genome [104]. In our study, we did not detect in *Xanthomonas* genomes any protein displaying similarities with SusD. Moreover, none of the TBDRs identified in *Xcc* showed strong similarities with SusC. A Blast analysis suggested that the SusC TBDR and the SusD OMP are specifically conserved in Bacteroidetes (data not shown). These results suggest that TBDRs involved in carbohydrate uptake evolved independently in Proteobacteria and Bacteroidetes. The analysis of the function and evolution of TBDRs in these phyla will certainly help us to better understand the adaptation of bacteria to their environment. This knowledge, which concerns the utilization of plant molecules that are widespread in the environment, will have a major impact not only in plant pathology, but also in human health as well as in the cycling of carbon and geobiology in marine environments.

## MATERIALS AND METHODS

### Bacterial strains, plasmids and growth conditions

The *Xanthomonas campestris* pv. *campestris* (*Xcc*) strains and plasmids used in this study are listed in Table S6. *Xcc* cells were grown at 30°C in MOKA rich medium (Yeast Extract 4 g/l, Casamino acids 8 g/l, $K_2HPO_4$ 2 g/l, $MgSO_4.7H_2O$ 0.3 g/l) or in MME minimal medium [12]. *E. coli* cells were grown on LB medium [105]. Antibiotics were used at the following concentrations for *Xcc*: rifampicin, 50 µg/ml; kanamycin: 50 µg/ml; tetracycline: 5 µg/ml. Antibiotics were used at the following concentrations for *E. coli*: ampicillin, 50 µg/ml; kanamycin: 50 µg/ml; tetracycline: 10 µg/ml.

Growth curves were generated using the Bioscreen C instrument (Labsystems, Helsinki, Finland) in three independent experiments. Growth measurements were realized in 200-well microtiter plates on 350 µl volumes of a minimal medium containing 20 mM sucrose, inoculated at an $OD_{600} = 0.15$ from a washed starter culture. Non-inoculated wells were used as asepsis controls. Optical densities at 600 nm values were measured every 30 min over a period of 2 to 3 days at 28°C. The microplates were shaken for 5 sec before each measurement.

### Construction of *Xanthomonas campestris* pv. *campestris* mutants.

Insertion mutants were constructed using the suicide plasmid pVO155 [36]. Oligonucleotide primers used for PCR amplification will be provided upon request. Amplicons were 300 bp in average. Location of insertions are indicated in Table S6. Deletion mutants in *XCC3358, XCC3359, XCC1990, XCC3209* and *XCC2927* were constructed using the *cre-lox* system adapted from Marx and colleagues [37,38]. Deleted regions are indicated in Table S6.

A *fur* mutant strain was obtained using the manganese mutagenesis method [106] in LB medium containing 5 mM $MnCl_2$. After incubation for 48 h at 30°C, surviving colonies were harvested for siderophores over-expression on CAS agar plates [107] adapted for *Xanthomonas* ($K_2HPO_4$ 1 g/l; $MgSO_4$ 1 mM; Casamino acids 0.15 g/l; $(NH_4)_2SO_4$ 1 g/l; sucrose 20 mM; CAS 60.5 mg/l; HDTMA 72.9 mg/l; $FeCl_3$ 10 μM). A resistant strain over-expressing siderophores was selected; the *fur* gene was sequenced and contains a point mutation (T212A leading to L71Q).

## Plasmid constructions

The *XCC3358, XCC3359* and *XCC1470* genes (*suxA, suxB* and *fur* respectively, see Figure 6 and Table S6) were amplified by PCR using appropriately designed primers (Oligonucleotide primers used for PCR amplification will be provided upon request). PCR products corresponding to *suxA* and *suxB* genes were cloned into pCZ525, a derivative of pSC154 [108], without *cyaA*' coding sequence. The obtained plasmids were cloned into pLAFR6 [109] to give pL-*XCC3358* and pL-*XCC3359* respectively. The PCR product corresponding to the *fur* gene with its promoter and terminator sequences was cloned into pFAJ1700 [110] to give pL-*XCC1470*.

The *XCC3358, XCC1990* and *XCC3209* promoter regions (see Table S6) were PCR amplified with appropriately designed primers. These promoter regions were cloned as *Hind*III-*Xba*I fragments, into the pCZ750 plasmid, a pFAJ1700 [110] derivative containing the *Kpn*I-*Asc*I *lacZ* gene from the pCZ367 plasmid [108].

## Expression studies

*β*-galactosidase and *β*-glucuronidase assays: bacterial cultures in the appropriate medium were harvested at different time points and *β*-galactosidase and *β*-glucuronidase assays were performed as previously described [111,112].

Quantitative RT-PCR (qRT-PCR): a 6 hour bacterial culture in the appropriate medium was harvested at an $OD_{600} = 0.4$ to 0.6. RNA were extracted using the Rneasy Mini Kit (QIAGEN). One μg of RNA was treated with RNase-free DNase I (GE-Healthcare) for 15 min at 37°C. After DNase inactivation (10 min at 75°C), RNA were reverse-transcribed by Superscript II (Invitrogen) using random hexamers (Biolabs), for 2 min at 25°C followed by 1 h at 42°C. Quantitative-PCR amplification was performed on Light Cycler (Roche): 10 min 95°C, 1 cycle; 10 sec 95°C, 10 sec 65°C, 20 sec 72°C, 40 to 50 cycles). Experiments were carried out in three independent biological experiments. Oligonucleotide primers used for quantitative-PCR amplification will be provided upon request. As a control for real-time PCR, we used the 16S rRNA as described [113]. The 16S rRNA forward primer (5′-TGACGGTACCCAAAGAATAAGCA-3′) and 16S rRNA reverse primer (5′-ACGCTTGCACCCTTCGTATTA-3′) amplicon was 72 bp in length.

## Pathogenicity tests

Pathogenicity tests were conducted on *Arabidopsis thaliana* Sf-2 ecotype as previously described [114]. Each strain was tested on sets of 4 plants with 4 leaves per plant. Disease development was scored at days 5, 7 and 9 post-inoculation using a disease index ranging from 0 (no symptom), to 4 (leaf death).

## [$^{14}$C]sucrose transport experiments

Overnight cultures in minimal medium (MME) without carbon source (uninduced) or with 20 mM sucrose (induced) were centrifuged. Pellets were resuspended in MME and the $OD_{600}$ was adjusted to 1. [$^{14}$C]sucrose (PerkinElmer, specific activity of 21.8 GBq/mmol) was added to a final concentration of 0.5 μM. For competition experiments, sucrose, fructose or glucose was added to [$^{14}$C]sucrose at a final concentration ranging from 0.5 to 100 μM. After different times, from 20 sec to 2 hours, samples of 0.2 ml were collected on cellulose nitrate filters, washed with 10 ml water, dried, and finally, the radioactivity was determined in a liquid scintillation counter.

The concentration-dependent initial sucrose transport was determined using the rapid dilution method as described [22]. Cells were precultured in minimal medium without sugar. After centrifugation and adjustment to an $OD_{600}$ of 1, cells were incubated for 15 sec in presence of 0.01, 0.025, 0.05, 0.1, 0.25, 0.5, 1, 2.5 and 5 μM [$^{14}$C]sucrose and 0.2 ml samples were diluted into 5 ml MME supplemented with 0.1 mM sucrose. Cells were collected by filtration, washed with 10 ml MME supplemented with 10 mM sucrose, dried and the radioactivity was determined.

For inhibition of the proton motive force (PMF) with carbonyl cyanide 3-chlorophenyl-hydrazone (CCCP), cells were incubated for 10 minutes at 30°C with 20 μM CCCP prior to the addition of [$^{14}$C]sucrose.

## *In silico* analysis

Location of the signal sequence responsible for the outer membrane localization was determined using the SignalP 3.0 server [115] (http://www.cbs.dtu.dk/services/SignalP/) with default parameters for Gram-negative bacteria.

Comparison alignments used to identify the TonB-box were realized using ClustalW [64] (http://www.ebi.ac.uk/clustalw/) or Multalin [116] (http://prodes.toulouse.inra.fr/multalin/multalin.html) softwares.

*β*-sheets in the last 50 amino-acids of *Xcc* TBDRs were located using the secondary structure prediction method [117] on the PSIPRED Protein Structure Prediction Server [118,119] (http://bioinf.cs.ucl.ac.uk/psipred/).

The MotifSampler program [41,42] was used to identify a motif corresponding to the *Xcc* Fux-box upstream of the 9 Fur-repressed TBDR and Ps-TBDR genes. MotifScanner program [42] or the PatScan pattern matcher software [47] were used with the identified motif to locate all the Fur-boxes in the *Xcc* genome.

Pip boxes ($TTCGCN_{15}TTCGC$) [120] and $hrp_{II}$ boxes ($TTCGN_{16}TTCG$) [121] were identified in the *Xcc* genome using the PatScan software [47] http://www-unix.mcs.anl.gov/compbio/PatScan/HTML/patscan.html).

For phylogenetic analysis, amino acid sequences were aligned and phylogenetic trees were reconstructed by the neighbor-joining method as implemented in ClustalX [122].

# SUPPORTING INFORMATION

**Figure S1** Phylogenetic tree of the family of TonB-dependent receptor proteins from Xanthomonas campestris pv. campestris strains ATCC33913 and 8004, Xanthomonas axonopodis pv. citri strain 306, Xanthomonas campestris pv. vesicatoria strain 85–10, Xanthomonas oryzae pv. oryzae strains KACC10331 and MAFF311018 and Xylella fastidiosa strains 9a5c and PD.

Found at: doi:10.1371/journal.pone.0000224.s001 (0.04 MB PDF)

**Figure S2** Genome context of genes associated with TonB-dependent receptors present in putative (partial) CUT loci of Xanthomonas campestris pv. campestris (Xcc) and conservation in non related bacteria. Homologous genes are marked by matching colors. White color indicates non conserved genes. For conserved genes, percentages of identity and similarity to the corresponding Xcc gene are indicated beneath.
Found at: doi:10.1371/journal.pone.0000224.s002 (0.24 MB PDF)

**Table S1** Regions and domains of Xanthomonas campestris pv. campestris putative TonB-dependent receptors (TBDRs).
Found at: doi:10.1371/journal.pone.0000224.s003 (0.04 MB XLS)

**Table S2** Distribution of TonB-dependent receptors in 226 sequenced Gram negative bacterial genomes. The EMBL-EBI, Integr8 web portal (http://www.ebi.ac.uk/integr8/EBI-Integr8-HomePage.do) and the NCBI ENTREZ Genome Project database (http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?db = genomeprj) were used to select sequenced bacterial genomes. TonB-dependent receptors (TBDRs) were detected by screening the Pfam database and the UniprotKB protein knowledge database using the two Pfam domains (PF07715, Plug; PF00593, TonB_dep_Rec). Only proteins displaying the two Pfam domains were considered.
Found at: doi:10.1371/journal.pone.0000224.s004 (0.08 MB XLS)

**Table S3** Genome context of Xanthomonas campestris pv. campestris (Xcc) TonB-dependent receptor (TBDR) genes and definition of putative CUT loci, conservation in Xanthomonads or in other genera, and TBDR conservation in Pseudomonas aeruginosa PAO1.
Found at: doi:10.1371/journal.pone.0000224.s005 (0.18 MB XLS)

**Table S4** Differential expression ratios of Xanthomonas campestris pv. campestris TonB-dependent receptor (TBDR) pVO155 insertion mutants.
Found at: doi:10.1371/journal.pone.0000224.s006 (0.03 MB XLS)

**Table S5** Conservation of Xanthomonas campestris pv. campestris (Xcc) TonB-dependent receptors (TBDRs) beside Xanthomonads orthologies.
Found at: doi:10.1371/journal.pone.0000224.s007 (0.04 MB XLS)

**Table S6** List of plasmids and Xanthomonas campestris pv. campestris strains used or generated in this study.
Found at: doi:10.1371/journal.pone.0000224.s008 (0.03 MB XLS)

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## Author Contributions

Conceived and designed the experiments: EL SB DM MA. Performed the experiments: EL SB DM AB ML CG ND JV. Analyzed the data: EL SB DM MA. Contributed reagents/materials/analysis tools: EL SB DM MA. Wrote the paper: EL MA.

## REFERENCES

1. Galperin MY (2004) Bacterial signal transduction network in a genomic perspective. Environ Microbiol 6: 552–567.
2. Cases I, de Lorenzo V (2005) Genetically modified organisms for the environment: stories of success and failure and what we have learned from them. Int Microbiol 8: 213–222.
3. Papa R, Glagla S, Danchin A, Schweder T, Marino G, et al. (2006) Proteomic identification of a two-component regulatory system in *Pseudoalteromonas haloplanktis* TAC125. Extremophiles 10: 483–91.
4. Williams PH (1980) Black rot: a continuing threat to world crucifers. Plant Disease 64: 736–742.
5. Alvarez AM (2000) Black rot of crucifers. In: al AJSe, ed. Mechanisms of resistance to plant diseases. Dordrecht, Netherlands: Kluwer Academic Publications. pp. 21–52.
6. Gough CL, Dow JM, Keen J, Henrissat B, Daniels MJ (1990) Nucleotide sequence of the engXCA gene encoding the major endoglucanase of *Xanthomonas campestris* pv. *campestris*. Gene 89: 53–59.
7. Tang JL, Gough CL, Daniels MJ (1990) Cloning of genes involved in negative regulation of production of extracellular enzymes and polysaccharide of *Xanthomonas campestris* pathovar *campestris*. Mol Gen Genet 222: 157–160.
8. Dow JM, Clarke BR, Milligan DE, Tang JL, Daniels MJ (1990) Extracellular proteases from *Xanthomonas campestris* pv. *campestris*, the black rot pathogen. Appl Environ Microbiol 56: 2994–2998.
9. Slater H, Alvarez-Morales A, Barber CE, Daniels MJ, Dow JM (2000) A two-component system involving an HD-GYP domain protein links cell-cell signalling to pathogenicity gene expression in *Xanthomonas campestris*. Mol Microbiol 38: 986–1003.
10. Ryan RP, Fouhy Y, Lucey JF, Crossman LC, Spiro S, et al. (2006) Cell-cell signaling in *Xanthomonas campestris* involves an HD-GYP domain protein that functions in cyclic di-GMP turnover. Proc Natl Acad Sci U S A 103: 6712–6717.
11. Dow JM, Crossman L, Findlay K, He YQ, Feng JX, et al. (2003) Biofilm dispersal in *Xanthomonas campestris* is controlled by cell-cell signaling and is required for full virulence to plants. Proc Natl Acad Sci U S A 100: 10995–11000.
12. Arlat M, Gough CL, Barber CE, Boucher C, Daniels MJ (1991) *Xanthomonas campestris* contains a cluster of *hrp* genes related to the larger hrp cluster of *Pseudomonas solanacearum*. Mol Plant Microbe Interact 4: 593–601.
13. Meyer D, Cunnac S, Gueneron M, Declercq C, Van Gijsegem F, et al. (2006) PopF1 and PopF2, two proteins secreted by the type III protein secretion system of *Ralstonia solanacearum*, are translocators belonging to the HrpF/NopX family. J Bacteriol 188: 4903–4917.
14. da Silva ACR, Ferro JA, Reinach FC, Farah CS, Furlan LR, et al. (2002) Comparison of the genomes of two *Xanthomonas* pathogens with differing host specificities. Nature 417: 459–463.
15. Qian W, Jia Y, Ren SX, He YQ, Feng JX, et al. (2005) Comparative and functional genomic analyses of the pathogenicity of phytopathogen *Xanthomonas campestris* pv. *campestris*. Genome Res 15: 757–767.
16. Thieme F, Koebnik R, Bekel T, Berger C, Boch J, et al. (2005) Insights into genome plasticity and pathogenicity of the plant pathogenic bacterium *Xanthomonas campestris* pv. *vesicatoria* revealed by the complete genome sequence. J Bacteriol 187: 7254–7266.
17. Lee BM, Park YJ, Park DS, Kang HW, Kim JG, et al. (2005) The genome sequence of *Xanthomonas oryzae* pathovar *oryzae* KACC10331, the bacterial blight pathogen of rice. Nucleic Acids Res 33: 577–586.
18. Ochiai H, Inoue Y, Takeya M, Sasaki A, Kaku H (2005) Genome sequence of *Xanthomonas oryzae* pv. *oryzae* suggests contribution of large numbers of effector genes and insertion sequences to its race diversity. Japan Agricultural Research Quarterly 39: 275–287.
19. Postle K, Kadner RJ (2003) Touch and go: tying TonB to transport. Mol Microbiol 49: 869–882.
20. Bagg A, Neilands JB (1987) Ferric uptake regulation protein acts as a repressor, employing iron (II) as a cofactor to bind the operator of an iron transport operon in *Escherichia coli*. Biochemistry 26: 5471–5477.
21. Ahmer BM, Thomas MG, Larsen RA, Postle K (1995) Characterization of the *exbBD* operon of *Escherichia coli* and the role of ExbB and ExbD in TonB function and stability. J Bacteriol 177: 4742–4747.
22. Neugebauer H, Herrmann C, Kammer W, Schwarz G, Nordheim A, et al. (2005) ExbBD-dependent transport of maltodextrins through the novel MalA protein across the outer membrane of *Caulobacter crescentus*. J Bacteriol 187: 8300–8311.
23. Chimento DP, Mohanty AK, Kadner RJ, Wiener MC (2003) Substrate-induced transmembrane signaling in the cobalamin transporter BtuB. Nat Struct Biol 10: 394–401.
24. Ferguson AD, Chakraborty R, Smith BS, Esser L, van der Helm D, et al. (2002) Structural basis of gating by the outer membrane transporter FecA. Science 295: 1715–1719.

25. Yue WW, Grizot S, Buchanan SK (2003) Structural evidence for iron-free citrate and ferric citrate binding to the TonB-dependent outer membrane transporter FecA. J Mol Biol 332: 353–368.
26. Pawelek PD, Croteau N, Ng-Thow-Hing C, Khursigara CM, Moiseeva N, et al. (2006) Structure of TonB in complex with FhuA, *E. coli* outer membrane receptor. Science 312: 1399–1402.
27. Shultis DD, Purdy MD, Banchs CN, Wiener MC (2006) Outer membrane active transport: structure of the BtuB:TonB complex. Science 312: 1396–1399.
28. Bateman A, Coin L, Durbin R, Finn RD, Hollich V, et al. (2004) The Pfam protein families database. Nucleic Acids Res 32: D138–141.
29. Lundrigan MD, Kadner RJ (1986) Nucleotide sequence of the gene for the ferrienterochelin receptor FepA in *Escherichia coli*. Homology among outer membrane receptors that interact with TonB. J Biol Chem 261: 10797–10801.
30. Struyve M, Moons M, Tommassen J (1991) Carboxy-terminal phenylalanine is essential for the correct assembly of a bacterial outer membrane protein. J Mol Biol 218: 141–148.
31. Koebnik R (1993) Structural organization of TonB-dependent receptors. Trends Microbiol 1: 201.
32. Braun V (1997) Surface signaling: novel transcription initiation mechanism starting from the cell surface. Arch Microbiol 167: 325–331.
33. Koebnik R (2005) TonB-dependent trans-envelope signalling: the exception or the rule? Trends Microbiol 13: 343–347.
34. de Lorenzo V, Wee S, Herrero M, Neilands JB (1987) Operator sequences of the aerobactin operon of plasmid ColV-K30 binding the ferric uptake regulation (fur) repressor. J Bacteriol 169: 2624–2630.
35. de Lorenzo V, Giovannini F, Herrero M, Neilands JB (1988) Metal ion regulation of gene expression. Fur repressor-operator interaction at the promoter region of the aerobactin system of pColV-K30. J Mol Biol 203: 875–884.
36. Oke V, Long SR (1999) Bacterial genes induced within the nodule during the *Rhizobium*-legume symbiosis. Mol Microbiol 32: 837–849.
37. Marx CJ, Lidstrom ME (2002) Broad-host-range cre-lox system for antibiotic marker recycling in gram-negative bacteria. Biotechniques 33: 1062–1067.
38. Angot A, Peeters N, Lechner E, Vailleau F, Baud C, et al. (2006) *Ralstonia solanacearum* requires F-box-like domain-containing type III effectors to promote disease on several host plants. Proc Natl Acad Sci U S A 103: 14620–14625.
39. Subramoni S, Sonti RV (2005) Growth deficiency of a *Xanthomonas oryzae* pv. *oryzae* fur mutant in rice leaves is rescued by ascorbic acid supplementation. Mol Plant Microbe Interact 18: 644–651.
40. Loprasert S, Sallabhan R, Atichartpongkul S, Mongkolsuk S (1999) Characterization of a ferric uptake regulator (*fur*) gene from *Xanthomonas campestris* pv. *phaseoli* with unusual primary structure, genome organization, and expression patterns. Gene 239: 251–258.
41. Thijs G, Lescot M, Marchal K, Rombauts S, De Moor B, et al. (2001) A higher-order background model improves the detection of promoter regulatory elements by Gibbs sampling. Bioinformatics 17: 1113–1122.
42. Thijs G, Marchal K, Lescot M, Rombauts S, De Moor B, et al. (2002) A Gibbs sampling method to detect overrepresented motifs in the upstream regions of coexpressed genes. J Comput Biol 9: 447–464.
43. Braun V, Mahren S (2005) Transmembrane transcriptional control (surface signalling) of the *Escherichia coli* Fec type. FEMS Microbiol Rev 29: 673–684.
44. Escolar L, Perez-Martin J, de Lorenzo V (1998) Binding of the fur (ferric uptake regulator) repressor of Escherichia coli to arrays of the GATAAT sequence. J Mol Biol 283: 537–547.
45. Wan XF, Verberkmoes NC, McCue LA, Stanek D, Connelly H, et al. (2004) Transcriptomic and proteomic characterization of the Fur modulon in the metal-reducing bacterium *Shewanella oneidensis*. J Bacteriol 186: 8385–8400.
46. Baichoo N, Helmann JD (2002) Recognition of DNA by Fur: a reinterpretation of the Fur box consensus sequence. J Bacteriol 184: 5826–5832.
47. Dsouza M, Larsen N, Overbeek R (1997) Searching for patterns in genomic data. Trends Genet 13: 497–498.
48. Cartron ML, Maddocks S, Gillingham P, Craven CJ, Andrews SC (2006) Feo–transport of ferrous iron into bacteria. Biometals 19: 143–157.
49. Mey AR, Wyckoff EE, Kanukurthy V, Fisher CR, Payne SM (2005) Iron and fur regulation in *Vibrio cholerae* and the role of fur in virulence. Infect Immun 73: 8167–8178.
50. Brown JS, Gilliland SM, Holden DW (2001) A *Streptococcus pneumoniae* pathogenicity island encoding an ABC transporter involved in iron uptake and virulence. Mol Microbiol 40: 572–585.
51. Noel L, Thieme F, Nennstiel D, Bonas U (2001) cDNA-AFLP analysis unravels a genome-wide *hrpG*-regulon in the plant pathogen *Xanthomonas campestris* pv. *vesicatoria*. Mol Microbiol 41: 1271–1281.
52. Koebnik R, Kruger A, Thieme F, Urban A, Bonas U (2006) Specific binding of the *Xanthomonas campestris* pv. *vesicatoria* AraC-type transcriptional activator HrpX to plant-inducible promoter boxes. J Bacteriol 188: 7652–7660.
53. Tsuge S, Nakayama T, Terashima S, Ochiai H, Furutani A, et al. (2006) Gene involved in transcriptional activation of the *hrp* regulatory gene *hrpG* in *Xanthomonas oryzae* pv. *oryzae*. J Bacteriol 188: 4158–4162.
54. Kim HS, Park HJ, Heu S, Jung J (2004) Molecular and functional characterization of a unique sucrose hydrolase from *Xanthomonas axonopodis* pv. *glycines*. J Bacteriol 186: 411–418.
55. Di Girolamo PM, Bradbeer C (1971) Transport of vitamin B 12 in *Escherichia coli*. J Bacteriol 106: 745–750.
56. Kadner RJ (1990) Vitamin B12 transport in *Escherichia coli*: energy coupling between membranes. Mol Microbiol 4: 2027–2033.
57. Bradbeer C, Woodrow ML (1976) Transport of vitamin B12 in *Escherichia coli*: energy dependence. J Bacteriol 128: 99–104.
58. Paquelin A, Ghigo JM, Bertin S, Wandersman C (2001) Characterization of HasB, a *Serratia marcescens* TonB-like protein specifically involved in the haemophore-dependent haem acquisition system. Mol Microbiol 42: 995–1005.
59. Seliger SS, Mey AR, Valle AM, Payne SM (2001) The two TonB systems of *Vibrio cholerae*: redundant and specific functions. Mol Microbiol 39: 801–812.
60. Huang B, Ru K, Yuan Z, Whitchurch CB, Mattick JS (2004) tonB3 is required for normal twitching motility and extracellular assembly of type IV pili. J Bacteriol 186: 4387–4389.
61. Zhao Q, Poole K (2002) Mutational analysis of the TonB1 energy coupler of *Pseudomonas aeruginosa*. J Bacteriol 184: 1503–1513.
62. Weickert MJ, Adhya S (1992) A family of bacterial regulators homologous to Gal and Lac repressors. J Biol Chem 267: 15869–15874.
63. Somers E, Keijers V, Ptacek D, Halvorsen Ottoy M, Srinivasan M, et al. (2000) The salCAB operon of *Azospirillum irakense*, required for growth on salicin, is repressed by SalR, a transcriptional regulator that belongs to the Lacl/GalR family. Mol Gen Genet 263: 1038–1046.
64. Thompson JD, Higgins DG, Gibson TJ (1994) CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. Nucleic Acids Res 22: 4673–4680.
65. Vauterin L, Hoste B, Kersters K, Swings J (1995) Reclassification of *Xanthomonas*. International Journal of Systematic Bacteriology 45: 472–489.
66. Anzai Y, Kim H, Park JY, Wakabayashi H, Oyaizu H (2000) Phylogenetic affiliation of the pseudomonads based on 16S rRNA sequence. Int J Syst Evol Microbiol 50 Pt 4: 1563–1589.
67. Cubero J, Graham JH (2004) The leucine-responsive regulatory protein (*lrp*) gene for characterization of the relationship among *Xanthomonas* species. Int J Syst Evol Microbiol 54: 429–437.
68. Tanabe T, Funahashi T, Nakao H, Miyoshi S, Shinoda S, et al. (2003) Identification and characterization of genes required for biosynthesis and transport of the siderophore vibrioferrin in *Vibrio parahaemolyticus*. J Bacteriol 185: 6938–6949.
69. Hottes AK, Meewan M, Yang D, Arana N, Romero P, et al. (2004) Transcriptional profiling of *Caulobacter crescentus* during growth on complex and minimal media. J Bacteriol 186: 1448–1461.
70. Reid SJ, Abratt VR (2005) Sucrose utilisation in bacteria: genetic organisation and regulation. Appl Microbiol Biotechnol 67: 312–321.
71. Nikaido H (2003) Molecular basis of bacterial outer membrane permeability revisited. Microbiol Mol Biol Rev 67: 593–656.
72. Llamas MA, Sparrius M, Kloet R, Jimenez CR, Vandenbroucke-Grauls C, et al. (2006) The heterologous siderophores ferrioxamine B and ferrichrome activate signaling pathways in *Pseudomonas aeruginosa*. J Bacteriol 188: 1882–1891.
73. Wiggerich HG, Klauke B, Koplin R, Priefer UB, Puhler A (1997) Unusual structure of the *tonB-exb* DNA region of *Xanthomonas campestris* pv. *campestris*: tonB, exbB, and exbD1 are essential for ferric iron uptake, but exbD2 is not. J Bacteriol 179: 7103–7110.
74. Wiggerich HG, Puhler A (2000) The *exbD2* gene as well as the iron-uptake genes *tonB, exbB* and *exbD1* of *Xanthomonas campestris* pv. *campestris* are essential for the induction of a hypersensitive response on pepper (*Capsicum annuum*). Microbiology 146 ( Pt 5): 1053–1060.
75. Bogs J, Geider K (2000) Molecular analysis of sucrose metabolism of *Erwinia amylovora* and influence on bacterial virulence. J Bacteriol 182: 5351–5358.
76. Jahreis K, Lengeler JW (1993) Molecular analysis of two ScrR repressors and of a ScrR-FruR hybrid repressor for sucrose and D-fructose specific regulons from enteric bacteria. Mol Microbiol 9: 195–209.
77. Schmid K, Schupfner M, Schmitt R (1982) Plasmid-mediated uptake and metabolism of sucrose by *Escherichia coli* K-12. J Bacteriol 151: 68–76.
78. Sprenger GA, Lengeler JW (1988) Analysis of sucrose catabolism in *Klebsiella pneumoniae* and in Scr+ derivatives of *Escherichia coli* K12. J Gen Microbiol 134: 1635–1644.
79. Van Gelder P, Dutzler R, Dumas F, Koebnik R, Schirmer T (2001) Sucrose transport through maltoporin mutants of *Escherichia coli*. Protein Eng 14: 943–948.
80. Schulein K, Schmid K, Benzl R (1991) The sugar-specific outer membrane channel ScrY contains functional characteristics of general diffusion pores and substrate-specific porins. Mol Microbiol 5: 2233–2241.
81. Puhler A, Arlat M, Becker A, Gottfert M, Morrissey JP, et al. (2004) What can bacterial genome research teach us about bacteria-plant interactions? Curr Opin Plant Biol 7: 137–147.
82. Lima WC, Van Sluys MA, Menck CF (2005) Non-gamma-proteobacteria gene islands contribute to the *Xanthomonas* genome. Omics 9: 160–172.
83. Hashidoko Y (2005) Ecochemical studies of interrelationships between epiphytic bacteria and host plants via secondary metabolites. Biosci Biotechnol Biochem 69: 1427–1441.
84. Hashimoto W, Momma K, Maruyama Y, Yamasaki M, Mikami B, et al. (2005) Structure and function of bacterial super-biosystem responsible for import and depolymerization of macromolecules. Biosci Biotechnol Biochem 69: 673–692.

85. Hashimoto W, He J, Wada Y, Nankai H, Mikami B, et al. (2005) Proteomics-based identification of outer-membrane proteins responsible for import of macromolecules in *Sphingomonas* sp. A1: alginate-binding flagellin on the cell surface. Biochemistry 44: 13783–13794.
86. Aso Y, Miyamoto Y, Harada KM, Momma K, Kawai S, et al. (2006) Engineered membrane superchannel improves bioremediation potential of dioxin-degrading bacteria. Nat Biotechnol 24: 188–189.
87. Nierman WC, Feldblyum TV, Laub MT, Paulsen IT, Nelson KE, et al. (2001) Complete genome sequence of *Caulobacter crescentus*. Proc Natl Acad Sci U S A 98: 4136–4141.
88. Phadke ND, Molloy MP, Steinhoff SA, Ulintz PJ, Andrews PC, et al. (2001) Analysis of the outer membrane proteome of *Caulobacter crescentus* by two-dimensional electrophoresis and mass spectrometry. Proteomics 1: 705–720.
89. Molloy MP, Phadke ND, Chen H, Tyldesley R, Garfin DE, et al. (2002) Profiling the alkaline membrane proteome of *Caulobacter crescentus* with two-dimensional electrophoresis and mass spectrometry. Proteomics 2: 899–910.
90. Ireland MM, Karty JA, Quardokus EM, Reilly JP, Brun YV (2002) Proteomic analysis of the *Caulobacter crescentus* stalk indicates competence for nutrient uptake. Mol Microbiol 45: 1029–1041.
91. Wilson M, Lindow SE (1994) Coexistence among Epiphytic Bacterial Populations Mediated through Nutritional Resource Partitioning. Appl Environ Microbiol 60: 4468–4477.
92. Mercier J, Lindow SE (2000) Role of leaf surface sugars in colonization of plants by bacterial epiphytes. Appl Environ Microbiol 66: 369–374.
93. Leveau JH, Lindow SE (2001) Appetite of an epiphyte: quantitative monitoring of bacterial sugar consumption in the phyllosphere. Proc Natl Acad Sci U S A 98: 3446–3453.
94. Aldon D, Brito B, Boucher C, Genin S (2000) A bacterial sensor of plant cell contact controls the transcriptional induction of *Ralstonia solanacearum* pathogenicity genes. Embo J 19: 2304–2314.
95. Marenda M, Brito B, Callard D, Genin S, Barberis P, et al. (1998) PrhA controls a novel regulatory pathway required for the specific induction of *Ralstonia solanacearum hrp* genes in the presence of plant cells. Mol Microbiol 27: 437–453.
96. Brito B, Aldon D, Barberis P, Boucher C, Genin S (2002) A signal transfer system through three compartments transduces the plant cell contact-dependent signal controlling *Ralstonia solanacearum hrp* genes. Mol Plant Microbe Interact 15: 109–119.
97. Zou LF, Wang XP, Xiang Y, Zhang B, Li YR, et al. (2006) Elucidation of the *hrp* clusters of *Xanthomonas oryzae* pv. *oryzicola* that control the hypersensitive response in nonhost tobacco and pathogenicity in susceptible host rice. Appl Environ Microbiol 72: 6212–6224.
98. Faure D, Saier MH Jr, Vanderleyden J (2001) An evolutionary alternative system for aryl beta-glucosides assimilation in bacteria. J Mol Microbiol Biotechnol 3: 467–470.
99. Bauer M, Kube M, Teeling H, Richter M, Lombardot T, et al. (2006) Whole genome analysis of the marine Bacteroidetes '*Gramella forsetii*' reveals adaptations to degradation of polymeric organic matter. Environ Microbiol 8: 2201–2213.
100. Backhed F, Ley RE, Sonnenburg JL, Peterson DA, Gordon JI (2005) Host-bacterial mutualism in the human intestine. Science 307: 1915–1920.
101. Sonnenburg JL, Xu J, Leip DD, Chen CH, Westover BP, et al. (2005) Glycan foraging in vivo by an intestine-adapted bacterial symbiont. Science 307: 1955–1959.
102. Xu J, Gordon JI (2003) Inaugural Article: Honor thy symbionts. Proc Natl Acad Sci U S A 100: 10452–10459.
103. Shipman JA, Berleman JE, Salyers AA (2000) Characterization of four outer membrane proteins involved in binding starch to the cell surface of *Bacteroides thetaiotaomicron*. J Bacteriol 182: 5365–5372.
104. Xu J, Bjursell MK, Himrod J, Deng S, Carmichael LK, et al. (2003) A genomic view of the human-*Bacteroides thetaiotaomicron* symbiosis. Science 299: 2074–2076.
105. Miller J (1972) Experiments in Molecular Genetics. Cold Spring Harbor, N.Y.: Cold Spring Harbor Laboratory Press.
106. Hantke K (1987) Selection procedure for deregulated iron transport mutants (fur) in *Escherichia coli* K 12: fur not only affects iron metabolism. Mol Gen Genet 210: 135–139.
107. Schwyn B, Neilands JB (1987) Universal chemical assay for the detection and determination of siderophores. Anal Biochem 160: 47–56.
108. Cunnac S, Occhialini A, Barberis P, Boucher C, Genin S (2004) Inventory and functional analysis of the large Hrp regulon in *Ralstonia solanacearum*: identification of novel effector proteins translocated to plant host cells through the type III secretion system. Mol Microbiol 53: 115–128.
109. Huynh TV, Dahlbeck D, Staskawicz BJ (1989) Bacterial blight of soybean: regulation of a pathogen gene determining host cultivar specificity. Science 245: 1374–1377.
110. Dombrecht B, Vanderleyden J, Michiels J (2001) Stable RK2-derived cloning vectors for the analysis of gene expression and gene function in gram-negative bacteria. Mol Plant Microbe Interact 14: 426–430.
111. Miller J (1992) A Short Course in Bacterial Genetics. A Laboratory Manual and Handbook for Escherichia coliand Related Bacteria. Cold Spring Harbor, N.Y.: Cold Spring Harbor Laboratory Press.
112. Jefferson RA, Kavanagh TA, Bevan MW (1987) GUS fusions: beta-glucuronidase as a sensitive and versatile gene fusion marker in higher plants. Embo J 6: 3901–3907.
113. Morales CQ, Posada J, Macneale E, Franklin D, Rivas I, et al. (2005) Functional analysis of the early chlorosis factor gene. Mol Plant Microbe Interact 18: 477–486.
114. Meyer D, Lauber E, Roby D, Arlat M, Kroj T (2005) Optimization of pathogenicity assays to study the *Arabidopsis thaliana-Xanthomonas campestris* pv. *campestris* pathosystem. Molecular Plant Pathology 6: 327–333.
115. Bendtsen JD, Nielsen H, von Heijne G, Brunak S (2004) Improved prediction of signal peptides: SignalP 3.0. J Mol Biol 340: 783–795.
116. Corpet F (1988) Multiple sequence alignment with hierarchical clustering. Nucleic Acids Res 16: 10881–10890.
117. Jones DT (1999) Protein secondary structure prediction based on position-specific scoring matrices. J Mol Biol 292: 195–202.
118. Bryson K, McGuffin LJ, Marsden RL, Ward JJ, Sodhi JS, et al. (2005) Protein structure prediction servers at University College London. Nucleic Acids Res 33: W36–38.
119. McGuffin LJ, Bryson K, Jones DT (2000) The PSIPRED protein structure prediction server. Bioinformatics 16: 404–405.
120. Fenselau S, Bonas U (1995) Sequence and expression analysis of the *hrpB* pathogenicity operon of *Xanthomonas campestris* pv. *vesicatoria* which encodes eight proteins with similarity to components of the Hrp, Ysc, Spa, and Fli secretion systems. Mol Plant Microbe Interact 8: 845–854.
121. Cunnac S, Boucher C, Genin S (2004) Characterization of the cis-acting regulatory element controlling HrpB-mediated activation of the type III secretion system and effector genes in *Ralstonia solanacearum*. J Bacteriol 186: 2309–2318.
122. Thompson JD, Gibson TJ, Plewniak F, Jeanmougin F, Higgins DG (1997) The CLUSTAL_X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acids Res 25: 4876–4882.
123. Crooks GE, Hon G, Chandonia JM, Brenner SE (2004) WebLogo: a sequence logo generator. Genome Res 14: 1188–1190.

## Supporting Information

**Figure S1.** Phylogenetic tree of the family of TonB-dependent receptor proteins from *Xanthomonas campestris* pv. *campestris* strains ATCC33913 and 8004, *Xanthomonas axonopodis* pv. *citri* strain 306, *Xanthomonas campestris* pv. *vesicatoria* strain 85-10, *Xanthomonas oryzae* pv. *oryzae* strains KACC10331 and MAFF311018 and *Xylella fastidiosa* strains 9a5c and PD.

**Figure S2.** Genome context of genes associated with TonB-dependent receptors present in putative (partial) CUT loci of *Xanthomonas campestris* pv. *campestris* (*Xcc*) and conservation in non related bacteria. Homologous genes are marked by matching colors. White color indicates non conserved genes. For conserved genes, percentages of identity and similarity to the corresponding *Xcc* gene are indicated beneath.

**Table S1.** Regions and domains of *Xanthomonas campestris* pv. *campestris* putative TonB-dependent receptors (TBDRs).

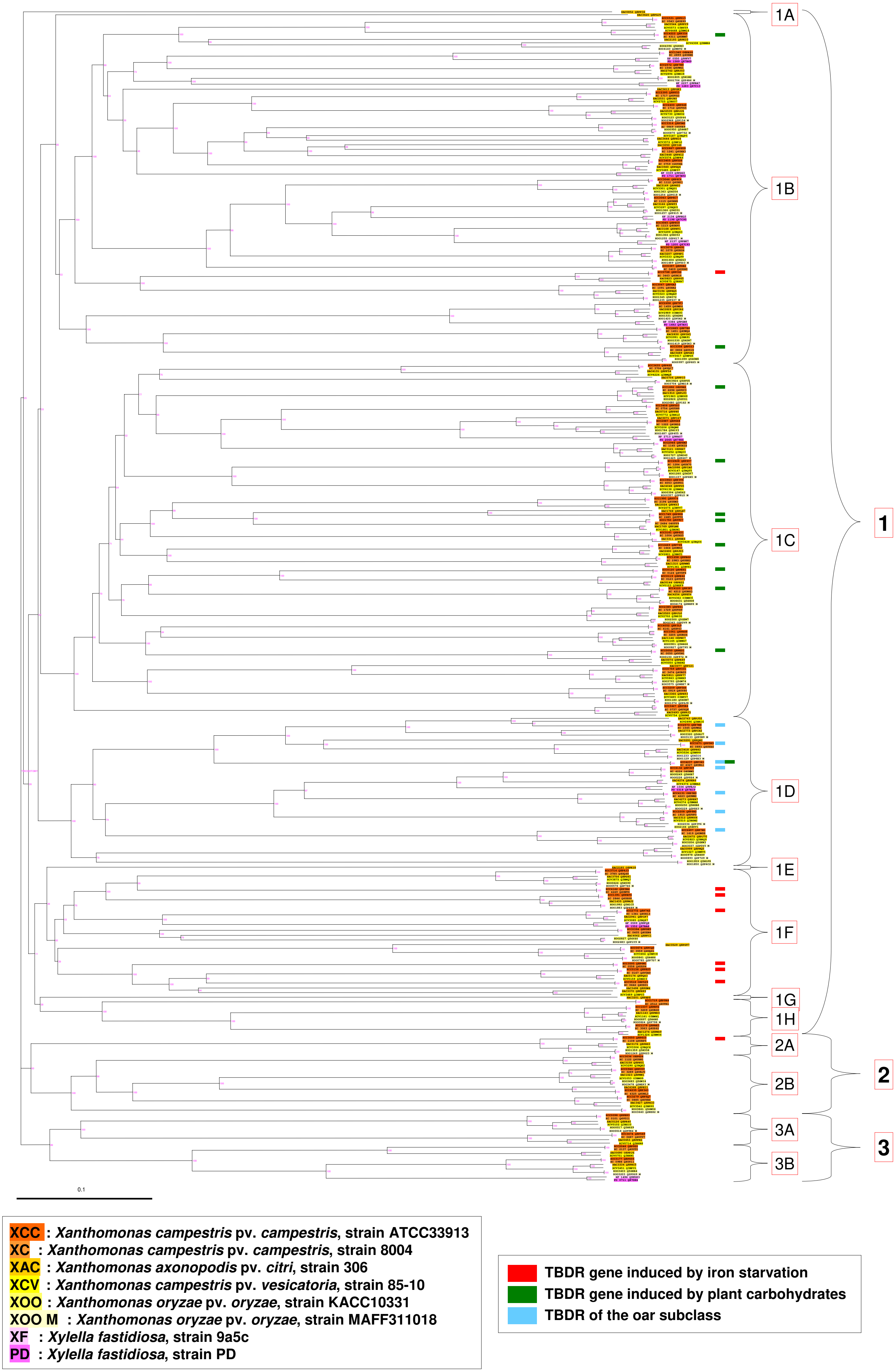
**Table S2.** Distribution of TonB-dependent receptors in 226 sequenced Gram negative bacterial genomes. The EMBL-EBI, Integr8 web portal (http://www.ebi.ac.uk/integr8/EBI-Integr8-HomePage.do) and the NCBI ENTREZ Genome Project database (http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?db=genomeprj) were used to select sequenced bacterial genomes. TonB-dependent receptors (TBDRs) were detected by screening the Pfam database and the UniprotKB protein knowledge database using the two Pfam domains (PF07715, Plug; PF00593, TonB_dep_Rec). Only proteins displaying the two Pfam domains were considered.

**Table S3.** Genome context of *Xanthomonas campestris* pv. *campestris* (*Xcc*) TonB-dependent receptor (TBDR) genes and definition of putative CUT loci, conservation in Xanthomonads or in other genera, and TBDR conservation in *Pseudomonas aeruginosa* PAO1.

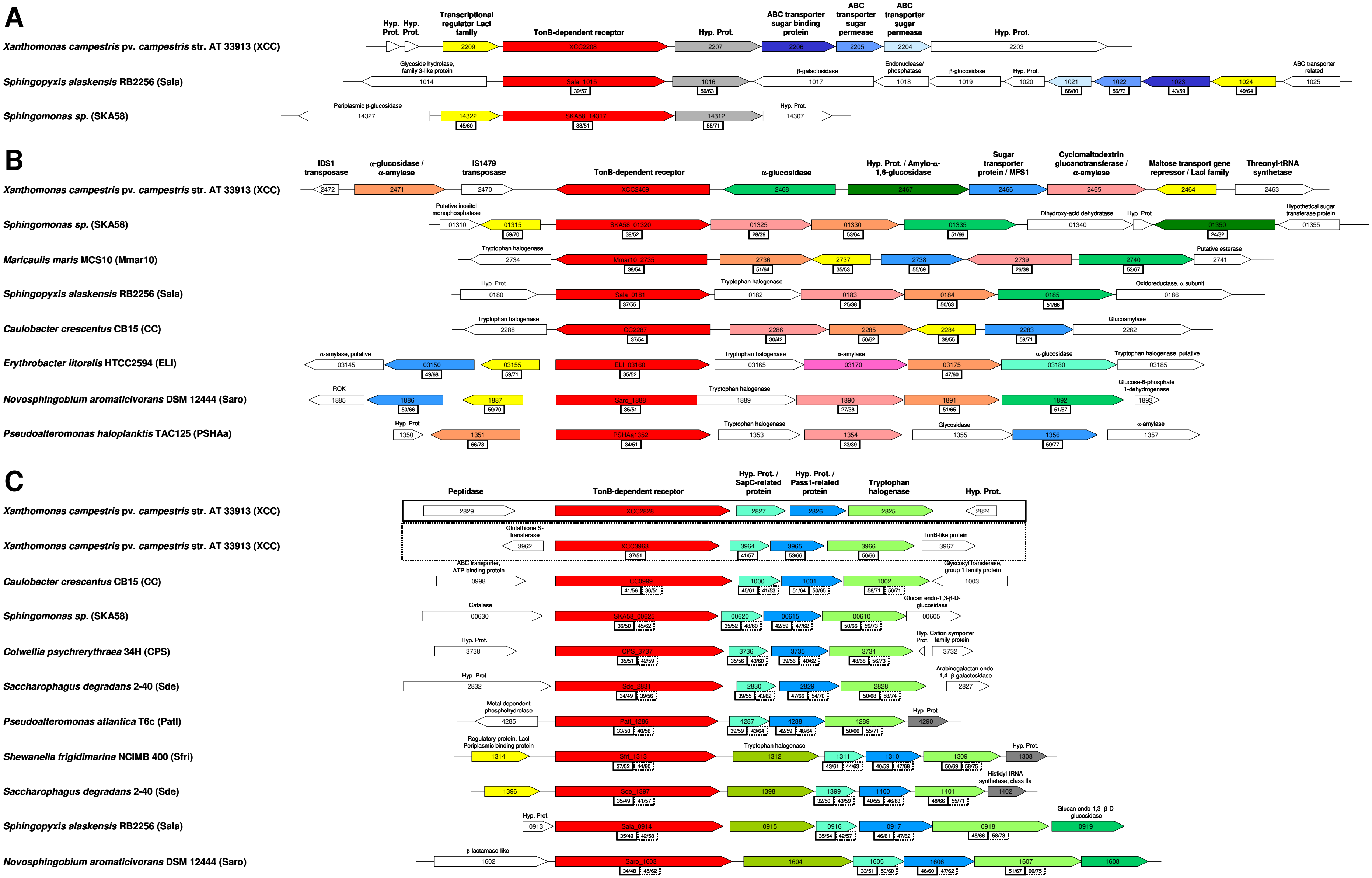
**Table S4.** Differential expression ratios of *Xanthomonas campestris* pv. *campestris* TonB-dependent receptor (TBDR) pVO155 insertion mutants.

**Table S5.** Conservation of *Xanthomonas campestris* pv. *campestris* (*Xcc*) TonB-dependent receptors (TBDRs) beside Xanthomonads orthologies.

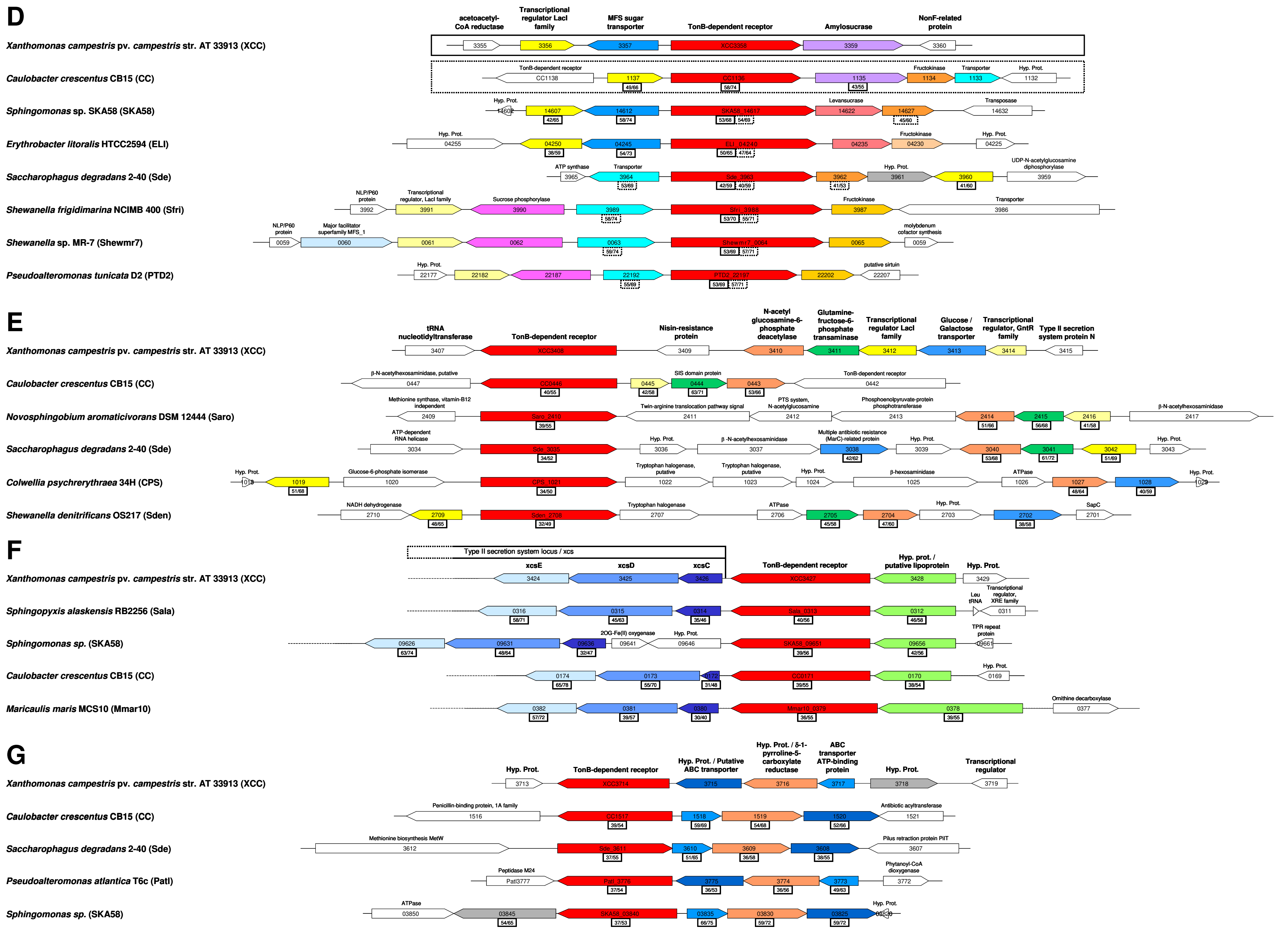
**Table S6.** List of plasmids and *Xanthomonas campestris* pv. *campestris* strains used or generated in this study.



1A
1B
1C
1D
1E
1F
1G
1H
2A
2B
3A
3B
1
2
3
0.1
XCC : *Xanthomonas campestris* pv. *campestris*, strain ATCC33913
XC : *Xanthomonas campestris* pv. *campestris*, strain 8004
XAC : *Xanthomonas axonopodis* pv. *citri*, strain 306
XCV : *Xanthomonas campestris* pv. *vesicatoria*, strain 85-10
XOO : *Xanthomonas oryzae* pv. *oryzae*, strain KACC10331
XOO M : *Xanthomonas oryzae* pv. *oryzae*, strain MAFF311018
XF : *Xylella fastidiosa*, strain 9a5c
PD : *Xylella fastidiosa*, strain PD
TBDR gene induced by iron starvation
TBDR gene induced by plant carbohydrates
TBDR of the oar subclass



A
Hyp. Prot.
Hyp. Prot.
Transcriptional regulator LacI family
TonB-dependent receptor
Hyp. Prot.
ABC transporter sugar binding protein
ABC transporter sugar permease
ABC transporter sugar permease
Hyp. Prot.
Xanthomonas campestris pv. campestris str. AT 33913 (XCC)
2209
XCC2208
2207
2206
2205
2204
2203
Sphingopyxis alaskensis RB2256 (Sala)
Glycoside hydrolase, family 3-like protein
1014
Sala_1015
1016
β-galactosidase
1017
Endonuclease/ phosphatase
1018
β-glucosidase
1019
Hyp. Prot.
1020
1021
1022
1023
1024
ABC transporter related
1025
Sphingomonas sp. (SKA58)
Periplasmic β-glucosidase
14327
14322
SKA58_14317
14312
Hyp. Prot.
14307
B
IDS1 transposase
α-glucosidase / α-amylase
IS1479 transposase
TonB-dependent receptor
α-glucosidase
Hyp. Prot. / Amylo-α-1,6-glucosidase
Sugar transporter protein / MFS1
Cyclomaltodextrin glucanotransferase / α-amylase
Maltose transport gene repressor / LacI family
Threonyl-tRNA synthetase
Xanthomonas campestris pv. campestris str. AT 33913 (XCC)
Sphingomonas sp. (SKA58)
Maricaulis maris MCS10 (Mmar10)
Sphingopyxis alaskensis RB2256 (Sala)
Caulobacter crescentus CB15 (CC)
Erythrobacter litoralis HTCC2594 (ELI)
Novosphingobium aromaticivorans DSM 12444 (Saro)
Pseudoalteromonas haloplanktis TAC125 (PSHAa)
C
Peptidase
TonB-dependent receptor
Hyp. Prot. / SapC-related protein
Hyp. Prot. / Pass1-related protein
Tryptophan halogenase
Hyp. Prot.
Xanthomonas campestris pv. campestris str. AT 33913 (XCC)
Xanthomonas campestris pv. campestris str. AT 33913 (XCC)
Caulobacter crescentus CB15 (CC)
Sphingomonas sp. (SKA58)
Colwellia psychrerythraea 34H (CPS)
Saccharophagus degradans 2-40 (Sde)
Pseudoalteromonas atlantica T6c (Patl)
Shewanella frigidimarina NCIMB 400 (Sfri)
Saccharophagus degradans 2-40 (Sde)
Sphingopyxis alaskensis RB2256 (Sala)
Novosphingobium aromaticivorans DSM 12444 (Saro)


D
Xanthomonas campestris pv. campestris str. AT 33913 (XCC)
Caulobacter crescentus CB15 (CC)
Sphingomonas sp. SKA58 (SKA58)
Erythrobacter litoralis HTCC2594 (ELI)
Saccharophagus degradans 2-40 (Sde)
Shewanella frigidimarina NCIMB 400 (Sfri)
Shewanella sp. MR-7 (Shewmr7)
Pseudoalteromonas tunicata D2 (PTD2)
acetoacetyl-CoA reductase
Transcriptional regulator LacI family
MFS sugar transporter
TonB-dependent receptor
Amylosucrase
NonF-related protein
3355
3356
3357
XCC3358
3359
3360
TonB-dependent receptor
CC1138
1137
CC1136
1135
Fructokinase
1134
Transporter
1133
Hyp. Prot.
1132
49/66
58/74
43/55
Hyp. Prot.
14602
14607
14612
SKA58_14617
Levansucrase
14622
14627
Transposase
14632
42/65
58/74
53/68
54/69
45/60
Hyp. Prot.
04255
04250
04245
ELI_04240
04235
Fructokinase
04230
Hyp. Prot.
04225
38/59
54/73
50/65
47/64
ATP synthase
3965
Transporter
3964
Sde_3963
3962
Hyp. Prot.
3961
3960
UDP-N-acetylglucosamine diphosphorylase
3959
53/69
42/59
40/59
41/53
41/60
NLP/P60 protein
3992
Transcriptional regulator, LacI family
3991
Sucrose phosphorylase
3990
3989
Sfri_3988
Fructokinase
3987
Transporter
3986
58/74
53/70
55/71
NLP/P60 protein
0059
Major facilitator superfamily MFS_1
0060
0061
0062
0063
Shewmr7_0064
0065
molybdenum cofactor synthesis
0059
59/74
53/69
57/71
Hyp. Prot.
22177
22182
22187
22192
PTD2_22197
22202
putative sirtuin
22207
55/69
53/69
57/71
E
Xanthomonas campestris pv. campestris str. AT 33913 (XCC)
Caulobacter crescentus CB15 (CC)
Novosphingobium aromaticivorans DSM 12444 (Saro)
Saccharophagus degradans 2-40 (Sde)
Colwellia psychrerythraea 34H (CPS)
Shewanella denitrificans OS217 (Sden)
tRNA nucleotidyltransferase
TonB-dependent receptor
Nisin-resistance protein
N-acetyl glucosamine-6-phosphate deacetylase
Glutamine-fructose-6-phosphate transaminase
Transcriptional regulator LacI family
Glucose / Galactose transporter
Transcriptional regulator, GntR family
Type II secretion system protein N
3407
XCC3408
3409
3410
3411
3412
3413
3414
3415
β-N-acetylhexosaminidase, putative
0447
CC0446
0445
SIS domain protein
0444
0443
TonB-dependent receptor
0442
40/55
42/58
63/71
53/66
Methionine synthase, vitamin-B12 independent
2409
Saro_2410
Twin-arginine translocation pathway signal
2411
PTS system, N-acetylglucosamine
2412
Phosphoenolpyruvate-protein phosphotransferase
2413
2414
2415
2416
β-N-acetylhexosaminidase
2417
39/55
51/66
56/68
41/58
ATP-dependent RNA helicase
3034
Sde_3035
Hyp. Prot.
3036
β -N-acetylhexosaminidase
3037
Multiple antibiotic resistance (MarC)-related protein
3038
Hyp. Prot.
3039
3040
3041
3042
Hyp. Prot.
3043
34/52
42/62
53/68
61/72
51/69
Hyp. Prot.
1018
1019
Glucose-6-phosphate isomerase
1020
CPS_1021
Tryptophan halogenase, putative
1022
Tryptophan halogenase, putative
1023
Hyp. Prot.
1024
β-hexosaminidase
1025
ATPase
1026
1027
1028
Hyp. Prot.
1029
51/68
34/50
48/64
40/59
NADH dehydrogenase
2710
2709
Sden_2708
Tryptophan halogenase
2707
ATPase
2706
2705
2704
Hyp. Prot.
2703
2702
SapC
2701
48/65
32/49
45/58
47/60
38/58
F
Xanthomonas campestris pv. campestris str. AT 33913 (XCC)
Sphingopyxis alaskensis RB2256 (Sala)
Sphingomonas sp. (SKA58)
Caulobacter crescentus CB15 (CC)
Maricaulis maris MCS10 (Mmar10)
Type II secretion system locus / xcs
xcsE
xcsD
xcsC
TonB-dependent receptor
Hyp. prot. / putative lipoprotein
Hyp. Prot.
3424
3425
3426
XCC3427
3428
3429
0316
0315
0314
Sala_0313
0312
Leu tRNA
Transcriptional regulator, XRE family
0311
58/71
45/63
35/46
40/56
46/58
2OG-Fe(II) oxygenase
Hyp. Prot.
09626
09631
09636
09641
09646
SKA58_09651
09656
TPR repeat protein
09661
63/74
48/64
32/47
39/56
42/56
0174
0173
0172
CC0171
0170
Hyp. Prot.
0169
65/78
55/70
31/48
39/55
38/54
0382
0381
0380
Mmar10_0379
0378
Ornithine decarboxylase
0377
57/72
39/57
30/40
36/55
39/55
G
Xanthomonas campestris pv. campestris str. AT 33913 (XCC)
Caulobacter crescentus CB15 (CC)
Saccharophagus degradans 2-40 (Sde)
Pseudoalteromonas atlantica T6c (Patl)
Sphingomonas sp. (SKA58)
Hyp. Prot.
TonB-dependent receptor
Hyp. Prot. / Putative ABC transporter
Hyp. Prot. / δ-1-pyrroline-5-carboxylate reductase
ABC transporter ATP-binding protein
Hyp. Prot.
Transcriptional regulator
3713
XCC3714
3715
3716
3717
3718
3719
Penicillin-binding protein, 1A family
1516
CC1517
1518
1519
1520
Antibiotic acyltransferase
1521
39/54
59/69
54/68
52/66
Methionine biosynthesis MetW
3612
Sde_3611
3610
3609
3608
Pilus retraction protein PilT
3607
37/55
51/65
36/58
38/55
Peptidase M24
Patl3777
Patl_3776
3775
3774
3773
Phytanoyl-CoA dioxygenase
3772
37/54
36/53
36/56
49/63
ATPase
03850
03845
SKA58_03840
03835
03830
03825
Hyp. Prot.
03820
54/65
37/53
66/75
59/72
59/72

| Gene ID [a] | Signal sequence cleavage position [b] | Signal sequence reannotation [c] | Protein size (aa) | Cleaved protein size (aa) | Plug domain (PF07715) | β-barrel domain (PF00593) | TonB-box sequence [d] | 12 Ct aa [e] | TBDR class/subclass [f] |
|---|---|---|---|---|---|---|---|---|---|
| XCC0050 | 44-45 | No | 887 | 843 | Yes | Yes | 11-TLDAVQV | APTVMVGVNVKL | Ps-TBDR |
| XCC0098 | 43-44 | No | 727 | 684 | Yes | Yes | 9-ALPAVQV | TYTVGLQWDFGS | Ps-TBDR |
| **XCC0119** | 29-30 | No | 922 | 893 | Yes | Yes | 13-DLDTVTV | GRQYLLGLRYKF | TBDR |
| **XCC0120** | 36-37 | No | 1066 | 1030 | Yes | Yes | 14-DLDRVQV | GRQYYVGARYKF | TBDR |
| **XCC0158** | 32-33 | No | 746 | 714 | Yes | Yes | 16-TLDAVSV | PRFVSVSLRWRY | TBDR |
| XCC0304 (Ct) | No | No | 294 | nd | **No** | Yes | | ERNTRLVVTYHF | Ps-TBDR |
| XCC0305 (Nt) | 38-39 | No | 548 | 510 | Yes | **No** | 18-SLDRMIV | | Ps-TBDR |
| **XCC0394** | 29-30 | No | 711 | 682 | Yes | Yes | 8-TLDTVRV | DRRVEFTVDHRF | TBDR |
| **XCC0397** | 27-28 | No | 873 | 846 | Yes | Yes | 14-EFEVITV | GRALFMRAGLTF | Ps-TBDR |
| **XCC0531** | 27-28 | 23 aa removal | 961 | 934 | Yes | Yes | 13-TLDAVSV | GREVAAEYVFTF | Ps-TBDR |
| **XCC0674** | 28-29 | No | 722 | 694 | Yes | Yes | 10-QLDAVNV | PRTARLTVQVDF | TBDR |
| **XCC0759** | 38-39/40-41 | No | 933 | 895/893 | Yes | Yes | 15/17-TLDKVTV | GMTSLVTAKYVF | TBDR |
| **XCC0768** | 24-25 | No | 743 | 719 | Yes | Yes | 15-DFDRLQV | GRTASVSLAVSW | TBDR |
| **XCC0946** | 26-27 | 30 aa removal | 774 | 748 | Yes | Yes | 24-QLDAINV | PRQTFLSLDVKF | TBDR |
| **XCC1037** | 26-27 | No | 738 | 712 | Yes | Yes | 11-RLDAVKV | PRIVGAQFRANF | TBDR |
| *XCC1041* | 27-28 | 131 aa extension | 1034 | 1007 | Yes | Yes | 107-TLDAMQV | TYWVGLRFTPSL | Ps-TBDR/ non conventional N terminal extension |
| XCC1179 | 28-29/31-32 | 18 aa removal | 771 | 743/740 | Yes | Yes | 14/17-ALDTVTV | RIVGVSVNVNWQ | Ps-TBDR |
| **XCC1258** | 39-40 | No | 894 | 855 | Yes | Yes | 22-TLDNITV | GRRYALEATYKF | TBDR |
| **XCC1340** | 25-26 | No | 1038 | 1013 | Yes | Yes | 30-RLDSVMV | GRRYMFTLNHRF | TBDR |
| **XCC1391** | 23-24 | No | 713 | 690 | Yes | Yes | 11-ELDGVNV | PRRIYAQLAYSF | TBDR |
| **XCC1719** | 28-29 | 41 aa removal | 846 | 818 | Yes | Yes | 13/15-TLAALTV | PRTFGMTLRLRY | TBDR |
| **XCC1749** | 41-42 | No | 970 | 929 | Yes | Yes | 14-DLDTVEV | DRRYSLVLRMNW | TBDR |
| XCC1750 (Nt) | 28-29 | 68 aa removal | 662 | 634 | Yes | **No** | 17-QLDTVQV | | Ps-TBDR |
| XCC1751 (Ct) | No | No | 200 | nd | **No** | Yes | | DRRYGLTLRASL | Ps-TBDR |
| **XCC1892** | 29-30 | 17 aa extension | 1030 | 1001 | Yes | Yes | 19-DLDAVTV | GRLAYLGLTYKF | TBDR |
| XCC1990 | 15-16 | No | 872 | 857 | Yes | Yes | 21-TLDAVQV | ERTYSLGLRFRL | Ps-TBDR |
| XCC2046 | 21-22 | No | 682 | 661 | Yes | Yes | 8-TMGSVDV | GRTAFLSFNVKL | Ps-TBDR |
| *XCC2208* | 33-34 | No | 992 | 959 | **No** | Yes | 96-TLDAVQV | MRTFRLAFGLNW | Ps-TBDR/ Oar-like |
| XCC2385 | No | No | 839 | nd | Yes | Yes | 17-DLERLEV | GRTYALGLKVAL | Ps-TBDR |
| **XCC2395** | 30-31/42-43 | No | 966 | 936/924 | Yes | Yes | 12/24-TLDSVVV | GRFYWARATVKF | TBDR |
| **XCC2400** | 43-44 | No | 945 | 902 | Yes | Yes | 16-TLEQVNV | GRYFWSRLRVEF | TBDR |
| **XCC2469** | 24-25 | 22 aa removal | 920 | 896 | Yes | Yes | 21-ELDKVQV | GRTFVLGVNYKF | TBDR |
| *XCC2497* | 27-28 | No | 1085 | 1058 | Yes | **No** | 93-TLGAVQA | RWALQLGFRYQF | Ps-TBDR/ Oar-like |
| **XCC2572** | 31-32 | No | 996 | 965 | Yes | Yes | 12-DLDKVTV | GRFFYLGTTVKF | TBDR |
| ***XCC2573*** | 30-31 | No | 1015 | 985 | Yes | Yes | 91-TLGAITV | PRFVRLSASYDF | TBDR/ Oar-like |
| **XCC2658** | 29-30 | No | 688 | 659 | Yes | Yes | 31-DLDKVVV | GRNASFGVRLFF | TBDR |
| **XCC2665** | 24-25 | No | 792 | 768 | Yes | Yes | 14-TLDAVIV | GRQYQMSVAYRW | TBDR |
| **XCC2772** | 22-23 | No | 772 | 750 | Yes | Yes | 13-DLDAIRV | GRSAVLNATFSF | TBDR |
| **XCC2828** | 24-25 | No | 1047 | 1023 | Yes | Yes | 19-TLDTVNV | QPRYTLGVRYAF | TBDR |
| **XCC2867** | 33-34 | No | 928 | 895 | Yes | Yes | 7-NLDKIEV | GRYMYMQYRQRF | TBDR |
| **XCC2887** | 24-25 | No | 913 | 889 | Yes | Yes | 21-ELDTITV | GRGYQAQLNFKF | TBDR |
| **XCC2944** | 22-23 | No | 878 | 856 | Yes | Yes | 10-ELDAVQV | GRRYMATLHLKF | TBDR |
| XCC3036 | 28-29 | No | 802 | 774 | Yes | Yes | 24-TLDQVQV | PRTLGLTLTLDL | Ps-TBDR |
| **XCC3043** | 23-24 | No | 793 | 770 | Yes | Yes | 10-TLDTVIV | GAYVYGRINYRW | TBDR |
| **XCC3045** | 36-37 | No | 806 | 770 | Yes | Yes | 9-TLDTLIV | GALVYANVNYKW | TBDR |
| **XCC3046** | 26-27 | 49 aa extension | 799 | 773 | Yes | Yes | 8-TLDTLIV | GRYWYGRVTYRF | TBDR |
| **XCC3050** | 26-27 | No | 709 | 683 | Yes | Yes | 16-ALDAVQV | GRTVTAGLEYTF | TBDR |
| XCC3067 | 26-27 | No | 626 | 600 | Yes | Yes | 7-DLDQVVV | AYLLTLRYHPAQ | Ps-TBDR |
| **XCC3079** | 23-24 | No | 811 | 788 | Yes | Yes | 9-TLDTVIV | GAYWYGRVRYSF | TBDR |
| **XCC3161** | 30-31 | No | 978 | 948 | Yes | Yes | 11-ELDKVMV | ERRYYAGLRLRF | TBDR |
| **XCC3177** | 41-42 | No | 689 | 648 | Yes | Yes | 6-TLGKVQV | GRALSLSWDWSF | TBDR |
| **XCC3209** | 24-25 | 74 aa removal | 904 | 880 | Yes | Yes | 9-TMDAVTV | GRAYMLTVGYTY | TBDR |
| XCC3215 (Ct) | No | No | 506 | nd | **No** | Yes | | SRNGMLTFNYTF | Ps-TBDR |
| XCC3216 (Nt) | 37-38 | No | 227 | 190 | Yes | **No** | 15-TLDGVNV | | Ps-TBDR |
| *XCC3270* (Ct) | No | No | 495 | nd | **No** | Yes | | PRSGRVTLSYDF | Ps-TBDR/ Oar-like |
| *XCC3271* (Nt) | 23-24 | No | 605 | 582 | Yes | **No** | 87-TLDSVTV | | Ps-TBDR/ Oar-like |
| **XCC3279** | 43-44 | No | 763 | 720 | Yes | Yes | 5-TLDAVSV | PRQVFASLSYKF | Ps-TBDR |
| **XCC3316** | 30-31 | No | 963 | 933 | Yes | Yes | 10-TLDRIEI | DRFLFVQYNQRF | TBDR |
| **XCC3358** | 33-34 | No | 824 | 791 | Yes | Yes | 20-NLDSVFV | GRTTSLSLRYDF | TBDR |
| **XCC3405** | 27-28 | No | 959 | 932 | Yes | Yes | 11-TLDSVQV | GRSWYVRADLKF | TBDR |
| XCC3408 | 27-28 | 16 aa extension | 873 | 846 | Yes | Yes | 29-TLDEVKV | GRAFMLSLNFKL | Ps-TBDR |
| **XCC3427** | 29-30 | No | 884 | 855 | Yes | Yes | 23-QLDQVVV | GITYDISVTARF | TBDR |
| XCC3474 | 33-34 | No | 794 | 761 | Yes | Yes | 8-WLDRIEV | PRQYLIGVRWAL | Ps-TBDR |
| **XCC3518** | 44-45 | No | 754 | 710 | Yes | Yes | 11-TLDQVLV | PRRLLFNLRANF | TBDR |
| *XCC3595* | 31-32/32-33 | No | 824 | 793/792 | Yes | Yes | 98/99-LLPTVKV | PRNVMVTLRGAL | Ps-TBDR/ transducer |
| **XCC3635** | 32-33 | 39 aa removal | 884 | 852 | Yes | Yes | 12-ELDRVQV | GRTYSLGLRANF | TBDR |
| **XCC3714** | 29-30 | No | 712 | 683 | Yes | Yes | 7-SLDAVQV | PRTWTVGARLRF | TBDR |
| **XCC3963** | 27-28 | No | 999 | 972 | Yes | Yes | 22-TLDTVQV | PRYMLGVRYKFW | TBDR |
| **XCC4052** | 37-38 | No | 900 | 863 | Yes | Yes | 16-QLDAVQV | GRAYYLGVDYAF | TBDR |
| **XCC4120** | 28-29 | 20 aa extension | 980 | 952 | Yes | Yes | 27-QLDTVTV | GRTVMLGIRGTF | TBDR |
| *XCC4131* | 32-33 | No | 1011 | 979 | **No** | Yes | 91-TLDAVQV | PRTLFMSARIIW | Ps-TBDR/ Oar-like |
| *XCC4132* | 32-33 | No | 1010 | 978 | **No** | Yes | 88-TLDTVTV | PRSVVLEVGAKF | Ps-TBDR/ Oar-like |
| **XCC4162** | 36-37 | No | 699 | 663 | Yes | Yes | 5-LLDAIVV | PRTLSATLSMEF | TBDR |
| **XCC4222** | 28-29 | No | 976 | 948 | Yes | Yes | 7-QLDAVTV | GREIAAEYVFDF | Ps-TBDR |
| **XCC4235** | 35-36 | No | 783 | 748 | Yes | Yes | 20-QLDAVSV | PRQVFLTLDAKF | TBDR |
| ***XCC4237*** | 33-34 | No | 1014 | 981 | Yes | Yes | 77-TLDRVEV | PRSFRLTARYDF | TBDR/ Oar-like |

[a] Gene identification (ID) from *Xanthomonas campestris* pv. *campestris* (*Xcc*) strain ATCC33913 [14]. Putative TonB-dependent receptors were identified by automatic search in the EBI databank (http://www.ebi.ac.uk/) of *Xcc* proteins harboring PF07715 or PF00593 HMMs corresponding to plug and β-barrel domains respectively. TBDRs having all canonical domains are boldfaced; TBDRs with a N-terminal extension are in italics; truncated TBDRs are underlined. Nt and Ct indicate that the protein corresponds to the N-terminal or C-terminal part of TonB-dependent receptors, respectively.

[b] As previously determined [14] or by using the signalP software (http://www.cbs.dtu.dk/services/SignalP/).

[c] Manual reannotation of the start codon downstream (removal) or upstream (extension) from the start codon previously determined [14].

[d] Matches to the *Xcc* TonB-box consensus sequence tLDxVxV determined in this study appear in boldface. Numbers on the left indicated the location of the TonB-box from the cleavage site.

[e] Amino acids predicted to form a β-sheet by the PSIPRED secondary structure prediction method (see Materials and Methods for details) are boldfaced.

[f] Proteins having a signal sequence, a plug and a β-barrel domain, a TonB-box and a β-sheet in the last 12 C terminal amino-acids ending with an aromatic residue, are named TBDRs. If one domain or sequence is missing, the protein was named Pseudo-TBDR (Ps-TBDR). For proteins having a N-terminal extension, the subclass is specified.

| ORGANISM [a] | TBDR [b] | GENOME SIZE (Mbp) | CDS [c] | TBDR/ genome size (Mbp) | TBDR $x10^3$/CDS | CAZy [d] | CAZy/ genome size (Mbp) | CAZy $x10^3$/CDS | HABITAT | PATHOGENIC IN | SYMBIOTIC IN | LINEAGE |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Bacteroides thetaiotaomicron* | 120 | 6.293669 | 4814 | 19.1 | 24.9 | 370 | 58.78 | 76.85 | Host-associated | Mammals/ opportunistic | | Bacteroidetes; Bacteroidetes; Bacteroidales |
| (*Caulobacter* sp. K31) | 97 | 5.876911 | 5404 | 16.5 | 17.9 | na | - | - | Aquatic | | | Proteobacteria; Alphaproteobacteria; Caulobacterales |
| *Bacteroides fragilis* (strain NCTC 9343) | 92 | 5.2417 | 4235 | 17.6 | 21.7 | 229 | 43.68 | 54.07 | Host-associated | Human | | Bacteroidetes; Bacteroidetes (class); Bacteroidales |
| *Bacteroides fragilis* (strain YCH46) | 92 | 5.31099 | 4612 | 17.3 | 19.9 | 236 | 44.43 | 51.17 | Host-associated | Human | | Bacteroidetes; Bacteroidetes (class); Bacteroidales |
| *Pseudoalteromonas atlantica* T6c | 72 | 5.187007 | 4287 | 13.9 | 16.8 | 123 | 23.71 | 28.69 | Aquatic | Shellfish | | Proteobacteria; Gammaproteobacteria; Alteromonadales |
| *Xanthomonas axonopodis* pv *citri* (strain 306) | 68 | 5.274174 | 4424 | 12.9 | 15.4 | 154 | 29.19 | 34.81 | Host-associated | Plant | | Proteobacteria; Gammaproteobacteria; Xanthomonadales |
| *Xanthomonas campestris* pv *campestris* (strain 8004) | 65 | 5.148708 | 4273 | 12.6 | 15.2 | 148 | 28.74 | 34.63 | Host-associated | Plant | | Proteobacteria; Gammaproteobacteria; Xanthomonadales |
| *Xanthomonas campestris* pv *campestris* (strain ATCC 33913) | 64 | 5.076188 | 4178 | 12.6 | 15.3 | 152 | 29.94 | 36.38 | Host-associated | Plant | | Proteobacteria; Gammaproteobacteria; Xanthomonadales |
| *Caulobacter crescentus* (strain CB15) | 63 | 4.016947 | 3742 | 15.7 | 16.8 | 97 | 24.14 | 25.92 | Aquatic | | | Proteobacteria, Alphaproteobacteria; Caulobacterales |
| (*Pseudoalteromonas tunicata* D2) | 58 | 4.982425 | 4504 | 11.6 | 12.9 | na | - | - | Aquatic | | | Proteobacteria; Gammaproteobacteria; Alteromonadales |
| *Novosphingobium aromaticivorans* (strain DSM 12444) | 52 | 3.561584 | 3324 | 14.6 | 15.6 | 72 | 20.21 | 21.66 | Multiple | | | Proteobacteria; Alphaproteobacteria; Sphingomonadales |
| *Xanthomonas campestris* pv *vesicatoria* (strain 85-10) | 52 | 5.420152 | 4726 | 9.6 | 11 | 149 | 27.49 | 31.52 | Host-associated | Plant | | Proteobacteria; Gammaproteobacteria; Xanthomonadales |
| *Saccharophagus degradans* (strain 2-40) | 51 | 5.057531 | 4008 | 10.1 | 12.7 | 339 | 67.02 | 84.58 | Aquatic | | | Proteobacteria; Gammaproteobacteria; Alteromonadales |
| (*Alteromonas macleodii* ' Deep ecotype') | 50 | 4.413342 | 4163 | 11.3 | 12.0 | na | - | - | Aquatic | | | Proteobacteria; Gammaproteobacteria; Alteromonadales |
| (*Sphingomonas* sp. SKA58) | 49 | 3.948 | 3914 | 12.4 | 12.5 | na | - | - | Aquatic | | | Proteobacteria; Alphaproteobacteria; Sphingomonadales |
| *Colwellia psychrerythraea* (strain 34H) | 43 | 5.37318 | 4900 | 8 | 8.8 | 85 | 15.81 | 17.34 | Specialized: psychrophilic | | | Proteobacteria; Gammaproteobacteria; Alteromonadales |
| *Pseudomonas fluorescens* (strain Pf-5) | 43 | 7.074893 | 6137 | 6.1 | 7 | 99 | 13.99 | 16.13 | Multiple/ Plant-associated | | | Proteobacteria; Gammaproteobacteria; Pseudomonadales |
| *Pseudoalteromonas haloplanktis* (strain TAC 125) | 40 | 3.850272 | 3486 | 10.4 | 11.5 | 41 | 10.64 | 11.76 | Aquatic/ psychrophilic | | | Proteobacteria; Gammaproteobacteria; Alteromonadales |
| *Sphingopyxis alaskensis* RB2256 | 38 | 3.373713 | 3195 | 11.3 | 11.9 | 45 | 13.33 | 14.08 | Aquatic | | | Proteobacteria; Alphaproteobacteria; Sphingomonadales |
| *Shewanella* sp. MR-4 | 36 | 4.706287 | 3924 | 7.6 | 9.2 | 61 | 12.96 | 15.55 | Multiple | | | Proteobacteria; Gammaproteobacteria; Alteromonadales |
| *Shewanella* sp. MR-7 | 36 | 4.799109 | 4014 | 7.5 | 9.0 | 65 | 13.54 | 16.19 | Aquatic | | | Proteobacteria; Gammaproteobacteria; Alteromonadales |
| *Xanthomonas oryzae* pv *oryzae* (strain KACC10331) | 36 | 4.940217 | 4372 | 7.3 | 8.2 | 119 | 24.08 | 27.21 | Host-associated | Plant | | Proteobacteria; Gammaproteobacteria; Xanthomonadales |
| *Xanthomonas oryzae* pv *oryzae* (strain MAFF 311018) | 36 | 4.941439 | 4628 | 7.3 | 7.8 | 123 | 24.89 | 26.57 | Host-associated | Plant | | Proteobacteria; Gammaproteobacteria; Xanthomonadales |
| *Pseudomonas aeruginosa* (strain PAO1) | 35 | 6.264403 | 5569 | 5.6 | 6.3 | 80 | 12.77 | 14.36 | Multiple | Human/ opportunistic | | Proteobacteria; Gammaproteobacteria; Pseudomonadales |
| *Pseudomonas aeruginosa* UCBPP-PA14 | 35 | 6.537648 | 5892 | 5.4 | 5.9 | 80 | 12.24 | 13.58 | Multiple | Human/ opportunistic | | Proteobacteria; Gammaproteobacteria; Pseudomonadales |
| *Gloeobacter violaceus* (strain PCC 7421) | 33 | 4.659019 | 4427 | 7.1 | 7.5 | 104 | 22.32 | 23.49 | Terrestrial | | | Cyanobacteria; Gloeobacteria; Gloeobacterales |
| (*Oceanicaulis alexandrii* HTCC2633) | 33 | 3.168201 | 3029 | 10.4 | 10.9 | na | - | - | Multiple | | | Proteobacteria; Alphaproteobacteria; Rhodobacterales |
| *Hyphomonas neptunium* ATCC 15444 | 32 | 3.705021 | 3505 | 8.6 | 9.1 | 53 | 14.30 | 15.12 | Aquatic | | | Proteobacteria; Alphaproteobacteria; Rhodobacterales |
| *Idiomarina loihiensis* (strain L2-TR) | 31 | 2.839318 | 2627 | 10.9 | 11.8 | 28 | 9.86 | 10.65 | Specialized: hydrothermal vent | | | Proteobacteria; Gammaproteobacteria; Alteromonadales |
| *Pseudomonas entomophila* L48 | 31 | 5.88878 | 5134 | 5.3 | 6.0 | 76 | 12.91 | 14.80 | Multiple | Insects | | Proteobacteria; Gammaproteobacteria; Pseudomonadales |
| *Shewanella frigidimarina* NCIMB 400 | 31 | 4.845257 | 4029 | 6.4 | 7.7 | 63 | 13.00 | 15.64 | Multiple | | | Proteobacteria; Gammaproteobacteria; Alteromonadales |
| *Nitrosomonas europaea* (strain ATCC 19718) | 30 | 2.812094 | 2460 | 10.7 | 12.2 | 49 | 17.42 | 19.91 | Multiple | | | Proteobacteria; Betaproteobacteria; Nitrosomonadales |
| (*Pseudomonas aeruginosa* PA7) | 30 | 6.663529 | 5815 | 4.5 | 5.2 | na | - | - | Multiple | Human/ opportunistic | | Proteobacteria; Gammaproteobacteria; Pseudomonadales |
| (*Pseudomonas putida* F1) | 30 | 5.925059 | 5251 | 5.1 | 5.7 | na | - | - | Multiple | | | Proteobacteria; Gammaproteobacteria; Pseudomonadales |
| *Pseudomonas putida* (strain KT2440) | 30 | 6.181863 | 5349 | 4.9 | 5.6 | 68 | 11.00 | 12.71 | Multiple | | | Proteobacteria; Gammaproteobacteria; Pseudomonadales |
| *Salinibacter ruber* (strain DSM 13855) | 29 | 3.587328 | 2833 | 8.1 | 10.2 | 55 | 15.33 | 19.41 | Specialized: Extreme halophilic | | | Bacteroidetes; Sphingobacteria; Sphingobacteriales |
| *Acinetobacter* sp. (strainADP1) | 27 | 3.598621 | 3323 | 7.5 | 8.1 | 43 | 11.94 | 12.94 | Multiple | Nosocomial infection | | Proteobacteria; Gammaproteobacteria; Pseudomonadales |
| *Burkholderia* sp. (strain 383) | 27 | 8.676277 | 7717 | 3.1 | 3.5 | 123 | 14.17 | 15.93 | Multiple | Human | | Proteobacteria; Betaproteobacteria; Burkholderiales |
| *Pseudomonas fluorescens* (strain PfO-1) | 26 | 6.438405 | 5736 | 4 | 4.5 | 92 | 14.28 | 16.03 | Multiple | | | Proteobacteria; Gammaproteobacteria; Pseudomonadales |
| *Gluconobacter oxydans* (strain 621H) | 25 | 2.922384 | 2660 | 8.6 | 9.4 | 68 | 23.26 | 25.56 | Multiple (including plants) | | | Proteobacteria; Alphaproteobacteria; Rhodospirillales |
| *Maricaulis maris* MCS10 | 25 | 3.36878 | 3063 | 7.4 | 8.2 | 61 | 18.11 | 19.92 | Aquatic | | | Proteobacteria; Alphaproteobacteria; Rhodobacterales |
| *Pseudomonas syringae* pv *tomato* (strain DC3000) | 25 | 6.53826 | 5606 | 3.8 | 4.5 | 104 | 15.90 | 18.55 | Multiple | Plant | | Proteobacteria; Gammaproteobacteria; Pseudomonadales |
| *Rhodopseudomonas palustris* (strain CGA009) | 24 | 5.46764 | 4815 | 4.4 | 5 | 71 | 12.98 | 14.74 | Multiple | | | Proteobacteria; Alphaproteobacteria; Rhizobiales |
| *Shewanella oneidensis* (strain MR-1) | 24 | 5.131416 | 4777 | 4.7 | 5 | 50 | 9.74 | 10.46 | Multiple | | | Proteobacteria; Gammaproteobacteria; Alteromonadales |
| *Shewanella denitrificans OS217* | 23 | 4.54591 | 3754 | 5.1 | 6.1 | 49 | 10.77 | 13.05 | Aquatic | | | Proteobacteria ; Gammaproteobacteria ; Alteromonadales |
| *Methylobacillus flagellatus* (strain KT / ATCC 51484 / DSM 6875) | 22 | 2.971517 | 2753 | 7.4 | 8.0 | 54 | 18.17 | 19.61 | Specialized | | | Proteobacteria; Betaproteobacteria; Methylophilales |
| *Anabaena* sp. (strain PCC 7120) | 21 | 7.211289 | 6130 | 2.9 | 3.4 | 145 | 20.10 | 23.65 | Multiple | | | Cyanobacteria; Nostocales; Nostocaceae |
| *Pseudomonas syringae* pv *phaseolicola* (strain 1448A / Race 6) | 21 | 6.112448 | 5121 | 3.4 | 4.1 | 103 | 16.85 | 20.11 | Multiple | Plant | | Proteobacteria; Gammaproteobacteria; Pseudomonadales |
| *Zymomonas mobilis* subsp. *mobilis* ZM4 | 21 | 2.056416 | 1998 | 10.2 | 10.5 | 31 | 15.07 | 15.52 | Multiple | | | Proteobacteria; Alphaproteobacteria; Sphingomonadales |
| *Erwinia carotovora* subsp. *atroseptica* (strain SCRI 1043) | 20 | 5.064019 | 4471 | 3.9 | 4.5 | 109 | 21.52 | 24.37 | Multiple | Plant | | Proteobacteria; Gammaproteobacteria; Enterobacteriales |
| *Erythrobacter litoralis* HTCC2594 | 20 | 3.052398 | 3011 | 6.6 | 6.6 | 43 | 14.08 | 14.28 | Aquatic | | | Proteobacteria; Alphaproteobacteria; Sphingomonadales |
| *Pseudomonas syringae* pv *syringae* B728A | 19 | 6.093697 | 5089 | 3.1 | 3.7 | 98 | 16.08 | 19.25 | Multiple | Plant | | Proteobacteria; Gammaproteobacteria; Pseudomonadales |
| *Zymomonas mobilis* | 19 | 2.097407 | 2041 | 9 | 9.3 | 31 | 14.78 | 15.18 | Multiple (including plants) | | | Proteobacteria; Alphaproteobacteria; Sphingomonadales |
| *Bordetella bronchiseptica* (strain RB50 ) | 18 | 5.339179 | 4994 | 3.4 | 3.6 | 60 | 11.23 | 12.01 | Host-associated | Animal | | Proteobacteria; Betaproteobacteria; Burkholderiales |
| *Escherichia coli* (strain EDL933 / O157:H7) | 18 | 5.620522 | 5438 | 3.2 | 3.3 | 100 | 17.79 | 18.38 | Host-associated | Human | | Proteobacteria; Gammaproteobacteria; Enterobacteriales |
| *Escherichia coli* O6 (strain CFT073) | 18 | 5.231427 | 5381 | 3.4 | 3.3 | 97 | 18.54 | 18.02 | Host-associated | Human | | Proteobacteria; Gammaproteobacteria; Enterobacteriales |
| *Rhodopseudomonas palustris* (strain HaA2) | 18 | 5.331656 | 4683 | 3.4 | 3.8 | 76 | 14.25 | 16.22 | Multiple | | | Proteobacteria; Alphaproteobacteria; Rhizobiales |
| *Ralstonia metallidurans* (CH34) | 17 | 3.928089 | 3601 | 4.3 | 4.7 | 71 | 18.07 | 19.71 | Specialized | | | Proteobacteria; Betaproteobacteria; Burkholderiales |
| *Dechloromonas aromatica* (strain RCB) | 16 | 4.501104 | 4171 | 3.6 | 3.8 | 67 | 14.88 | 16.06 | Multiple | | | Proteobacteria; Betaproteobacteria; Rhodocyclales |
| *Nitrobacter winogradskyi* (strain Nb-255) | 16 | 3.402093 | 3122 | 4.7 | 5.1 | 54 | 15.87 | 17.29 | Multiple/terrestrial | | | Proteobacteria; Alphaproteobacteria; Rhizobiales |
| *Burkholderia cepacia* AMMD | 15 | 7.528567 | 6617 | 2.0 | 2.3 | 142 | 18.86 | 21.46 | Multiple | | | Proteobacteria; Betaproteobacteria; Burkholderiales |
| *Ralstonia solanacearum* (GMI1000) | 15 | 5.810922 | 5119 | 2.6 | 2.9 | 83 | 14.28 | 16.21 | Multiple | Plant | | Proteobacteria; Betaproteobacteria; Burkholderiales |
| *Rhodospirillum rubrum* (strain ATCC 11170) | 15 | 4.406557 | 3841 | 3.4 | 3.9 | 87 | 19.74 | 22.65 | Multiple | | | Proteobacteria; Alphaproteobacteria; Rhodospirillales |
| (*Acidovorax avenae* subsp. *citrulli* AAC00-1) | 14 | 5.312942 | 4568 | 2.6 | 3.1 | na | - | - | Multiple | Plant | | Proteobacteria; Betaproteobacteria; Burkholderiales |
| *Bordetella pertussis* (strain Tohama I ) | 14 | 4.086189 | 3449 | 3.4 | 4.1 | 49 | 11.99 | 14.20 | Host-associated | Human | | Proteobacteria; Betaproteobacteria; Burkholderiales |
| *Ralstonia eutropha* H16 | 14 | 4.052032 | 3651 | 3.5 | 3.8 | 81 | 19.99 | 22.19 | Specialized | | | Proteobacteria; Betaproteobacteria; Burkholderiales |
| *Bordetella parapertussis* (strain 12822) | 13 | 4.773551 | 4186 | 2.7 | 3.1 | 55 | 11.52 | 13.13 | Host-associated | Human, sheep | | Proteobacteria; Betaproteobacteria; Burkholderiales |
| *Escherichia coli* (strain Sakai / O157:H7 ) | 13 | 5.591171 | 5449 | 2.3 | 2.4 | 95 | 16.99 | 17.43 | Host-associated | Human | | Proteobacteria; Gammaproteobacteria; Enterobacteriales |
| *Nitrobacter hamburgensis* X14 | 13 | 4.406967 | 3804 | 2.9 | 3.4 | 80 | 18.15 | 21.03 | Multiple/terrestrial | | | Proteobacteria; Alphaproteobacteria; Rhizobiales |
| *Yersinia pestis* (biovar *Mediaevalis* , strain 91001) | 13 | 4.803217 | 4150 | 2.7 | 3.1 | 65 | 13.53 | 15.66 | Multiple | Human, rodent | | Proteobacteria; Gammaproteobacteria; Enterobacteriales |
| *Yersinia pestis* (biovar *Mediaevalis* , strain KIM5) | 13 | 4.600754 | 4086 | 2.8 | 3.2 | 71 | 15.43 | 17.37 | Multiple | Human, rodent | | Proteobacteria; Gammaproteobacteria; Enterobacteriales |
| *Yersinia pestis* (biovar *Orientalis* , strain CO-92) | 13 | 4.829855 | 4092 | 2.7 | 3.2 | 72 | 14.90 | 17.59 | Multiple | Human, rodent | | Proteobacteria; Gammaproteobacteria; Enterobacteriales |
| *Chromobacterium violaceum* (strain ATCC 12472) | 12 | 4.75108 | 4407 | 2.5 | 2.7 | 78 | 16.41 | 17.69 | Multiple | Human | | Proteobacteria; Betaproteobacteria; Neisseriales |
| *Hahella chejuensis* (strain KCTC 2396) | 12 | 7.215267 | 6778 | 1.7 | 1.8 | 151 | 20.92 | 22.27 | Aquatic | | | Proteobacteria; Gammaproteobacteria; Oceanospirillales |
| *Leptospira interrogans* (serovar *lai* , strain 56601) | 12 | 4.691184 | 4724 | 2.6 | 2.5 | 56 | 11.93 | 11.85 | Host-associated | Animal | | Spirochaetes; Spirochaetales; Leptospiraceae |
| *Pasteurella multocida* (strain Pm70) | 12 | 2.257487 | 2015 | 5.3 | 6 | 49 | 21.70 | 24.31 | Host-associated | Human, animal | | Proteobacteria; Gammaproteobacteria; Pasteurellales |
| *Photorhabdus luminescens laumondii* (strain TT01) | 12 | 5.688987 | 4680 | 2.1 | 2. 6 | 77 | 13.53 | 16.45 | Host-associated | Insect | | Proteobacteria; Gammaproteobacteria; Enterobacteriales |
| *Yersinia pseudotuberculosis* (serovar I, strain IP32953) | 12 | 4.840899 | 4035 | 2.5 | 3 | 81 | 16.73 | 20.07 | Multiple | Human, animal | | Proteobacteria; Gammaproteobacteria; Enterobacteriales |
| *Bradyrhizobium japonicum* (strain USDA 110) | 11 | 9.105828 | 8314 | 1.2 | 1.3 | 108 | 11.86 | 12.99 | Plant symbiont | | Plant: soybean | Proteobacteria; Alphaproteobacteria; Rhizobiales |
| *Porphyromonas gingivalis* (strain W83) | 11 | 2.343476 | 1908 | 4.7 | 5.8 | 51 | 21.76 | 26.72 | Host-associated | Human | | Bacteroidetes; Bacteroidetes; Bacteroidales |
| *Ralstonia eutropha* (strain JMP134) | 11 | 7.25529 | 6445 | 1.5 | 1.7 | 83 | 11.43 | 12.87 | Multiple | | | Proteobacteria; Betaproteobacteria; Burkholderiales |
| *Rhodopseudomonas palustris* (strain BisB18) | 11 | 5.513843 | 4886 | 2 | 2.3 | 85 | 15.41 | 17.39 | Multiple | | | Proteobacteria; Alphaproteobacteria; Rhizobiales |
| *Vibrio parahaemolyticus* (strain RIMD 2210633) | 11 | 5.16577 | 4832 | 2.1 | 2.3 | 83 | 16.06 | 17.17 | Aquatic | Human | | Proteobacteria; Gammaproteobacteria; Vibrionales |
| *Wolinella succinogenes* (strain DSMZ 1740) | 11 | 2.110355 | 2045 | 5.2 | 5.4 | 28 | 13.26 | 13.69 | Host-associated | | | Proteobacteria; Epsilonproteobacteria; Campylobacterales |
| *Anabaena variabilis* (strain ATCC 29413) | 10 | 7.105752 | 5708 | 1.4 | 1.8 | 145 | 20.40 | 25.40 | Multiple | | | Cyanobacteria; Nostocales; Nostocaceae |
| *Bordetella avium* (strain 197N) | 10 | 3.732255 | 3382 | 2.7 | 3 | 50 | 13.39 | 14.78 | Host-associated | Animal | | Proteobacteria; Betaproteobacteria; Burkholderiales |
| *Burkholderia pseudomallei* (strain 1710b) | 10 | 7.308054 | 6347 | 1.4 | 1.6 | 122 | 16.69 | 19.22 | Terrestrial | Animal | | Proteobacteria; Betaproteobacteria; Burkholderiales |
| *Burkholderia pseudomallei* (strain K96243) | 10 | 7.247547 | 5729 | 1.4 | 1.7 | 124 | 17.10 | 21.64 | Terrestrial | Animal | | Proteobacteria; Betaproteobacteria; Burkholderiales |
| *Burkholderia thailandensis* (strain E264) | 10 | 6.723972 | 5634 | 1.5 | 1.8 | 116 | 17.25 | 20.58 | Terrestrial | | | Proteobacteria; Betaproteobacteria; Burkholderiales |
| *Leptospira interrogans copenhageni* (strain Fiocruz L1-130) | 10 | 4.627366 | 3659 | 2.2 | 2.7 | 57 | 12.31 | 15.57 | Host-associated | Animal | | Spirochaetes; Spirochaetales; Leptospiraceae |
| *Shigella sonnei* (strain Ss046) | 10 | 5.039661 | 4461 | 2 | 2.2 | 76 | 15.08 | 17.03 | Host-associated | Human | | Proteobacteria; Gammaproteobacteria; Enterobacteriales |
| *Chromohalobacter salexigens* DSM 3043 | 9 | 3.696649 | 3298 | 2.4 | 2.7 | 51 | 13.79 | 15.46 | Specialized: Moderate halophilic | | | Proteobacteria; Gammaproteobacteria; Oceanospirillales |
| *Escherichia coli* (strain K12) | 9 | 4.738834 | 4383 | 1.9 | 2.1 | 96 | 20.25 | 21.90 | Host-associated | | | Proteobacteria; Gammaproteobacteria; Enterobacteriales |
| *Escherichia coli* W3110* | 9 | 4.646332 | 4227 | 1.9 | 2.1 | 70 | 15.07 | 16.56 | Host-associated | | | Proteobacteria; Gammaproteobacteria; Enterobacteriales |
| *Haemophilus influenzae* (strain KW20 / Rd) | 9 | 1.830138 | 1718 | 4.9 | 5.2 | 37 | 20.21 | 21.53 | Host-associated | Human | | Proteobacteria; Gammaproteobacteria; Pasteurellales |
| *Neisseria meningitidis* A (strain Z2491) | 9 | 2.184406 | 2064 | 4.1 | 4.4 | 27 | 12.36 | 13.08 | Host-associated | Human | | Proteobacteria; Betaproteobacteria; Neisseriales |
| *Neisseria meningitidis* B (strain MC58) | 9 | 2.27236 | 2061 | 4 | 4.4 | 29 | 12.76 | 14.07 | Host-associated | Human | | Proteobacteria; Betaproteobacteria; Neisseriales |
| *Nitrosospira multiformis* (strain ATCC 25196) | 9 | 3.234309 | 2805 | 2.8 | 3.2 | 68 | 21.02 | 24.24 | Terrestrial | | | Proteobacteria; Betaproteobacteria; Nitrosomonadales |
| *Shigella dysenteriae* (strain Sd197) | 9 | 4.551958 | 4498 | 2 | 2 | 60 | 13.18 | 13.33 | Host-associated | Human | | Proteobacteria; Gammaproteobacteria; Enterobacteriales |
| *Xylella fastidiosa* (strain 9a5c) | 9 | 2.73175 | 2827 | 3.3 | 3.2 | 64 | 23.42 | 22.63 | Host-associated | Plant | | Proteobacteria; Gammaproteobacteria; Xanthomonadales |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Xylella fastidiosa* (strain Temecula1) | 9 | 2.521148 | 2036 | 3.6 | 4.4 | 56 | 22.21 | 27.50 | Host-associated | Plant | | Proteobacteria; Gammaproteobacteria; Xanthomonadales |
| *Agrobacterium tumefaciens* (strain C58 sub strain Cereon) | 8 | 5.673465 | 5302 | 1.4 | 1.5 | 104 | 18.33 | 19.61 | Multiple | Plant | | Proteobacteria; Alphaproteobacteria; Rhizobiales |
| *Agrobacterium tumefaciens* (strain C58 sub strain Dupont) | 8 | 5.674064 | 5405 | 1.4 | 1.5 | na | - | - | Multiple | Plant | | Proteobacteria; Alphaproteobacteria; Rhizobiales. |
| *Burkholderia mallei* (strain ATCC 23344) | 8 | 5.835527 | 5024 | 1.4 | 1.6 | 98 | 16.79 | 19.50 | Host-associated | Human, animal | | Proteobacteria; Betaproteobacteria; Burkholderiales |
| *Nitrosococcus oceani* (strain ATCC 19707) | 8 | 3.481691 | 2974 | 2.3 | 2.7 | 68 | 19.53 | 22.86 | Aquatic | | | Proteobacteria; Gammaproteobacteria; Chromatiales |
| *Pelobacter carbinolicus* (strain DSM 2380) | 8 | 3.665893 | 3119 | 2.2 | 2. 6 | 54 | 14.73 | 17.31 | Aquatic | | | Proteobacteria; Deltaproteobacteria; Desulfuromonadales |
| *Salmonella choleraesuis* (strain SC-B67) | 8 | 4.944 | 4663 | 1.6 | 1.7 | 85 | 17.19 | 18.22 | Host-associated | Human, animal | | Proteobacteria; Gammaproteobacteria; Enterobacteriales |
| *Salmonella typhimurium* (strain LT2) | 8 | 4.951371 | 4540 | 1.6 | 1.8 | 100 | 20.19 | 22.02 | Host-associated | Human | | Proteobacteria; Gammaproteobacteria; Enterobacteriales |
| *Shigella boydii serotype 4* (strain Sb227) | 8 | 4.64652 | 4286 | 1.7 | 1.9 | 63 | 13.55 | 14.69 | Host-associated | Human | | Proteobacteria; Gammaproteobacteria; Enterobacteriales |
| *Sinorhizobium meliloti* (strain 1021) | 8 | 6.691694 | 6201 | 1.2 | 1.3 | 121 | 18.08 | 19.51 | Multiple | | Plant: *Medicago sativa* | Proteobacteria; Alphaproteobacteria; Rhizobiales |
| *Thiobacillus denitrificans* (strain ATCC 25259) | 8 | 2.909809 | 2827 | 2.7 | 2.8 | 62 | 21.30 | 21.93 | Multiple | | | Proteobacteria; Betaproteobacteria; Hydrogenophilales |
| *Thiomicrospira denitrificans* (strain ATCC 33889) | 8 | 2.201561 | 2097 | 3.6 | 3.8 | 32 | 14.53 | 15.25 | Aquatic | | | Proteobacteria; Gammaproteobacteria; Thiotrichales |
| *Vibrio Fischeri* (strain ES114) | 8 | 4.28405 | 3800 | 1.9 | 2.1 | 88 | 20.54 | 23.15 | Multiple | | Squid: *Euprymna scolopes* | Proteobacteria; Gammaproteobacteria; Vibrionales |
| *Vibrio vulnificus* (strain CMCP6) | 8 | 5.126797 | 4526 | 1. 6 | 1.8 | 88 | 17.16 | 19.44 | Aquatic | Human | | Proteobacteria; Gammaproteobacteria; Vibrionales |
| *Azoarcus* sp. (strain EbN1) | 7 | 4.727255 | 4594 | 1.5 | 1.5 | 84 | 17.76 | 18.28 | Terrestrial | | | Proteobacteria; Betaproteobacteria; Rhodocyclales |
| *Neisseria gonorrhoeae* (strain FA 1090) | 7 | 2.153922 | 2002 | 3.2 | 3.5 | 26 | 12.07 | 12.98 | Host-associated | Human | | Proteobacteria; Betaproteobacteria; Neisseriales |
| *Photobacterium profundum* (strain SS9) | 7 | 6.40328 | 5478 | 1.1 | 1.3 | 100 | 15.61 | 18.25 | Multiple | | | Proteobacteria; Gammaproteobacteria; Vibrionales |
| *Vibrio vulnificus* (strain YJ016) | 7 | 5.260086 | 5028 | 1.3 | 1.4 | 104 | 19.77 | 20.68 | Aquatic | Human | | Proteobacteria; Gammaproteobacteria; Vibrionales |
| *Escherichia coli* O6:K15:H31 (strain 536) | 6 | 4.93892 | 4629 | 1.2 | 1.3 | 95 | 19.23 | 20.52 | Host-associated | Human | | Proteobacteria; Gammaproteobacteria; Enterobacteriales |
| *Helicobacter pylori* (strain J99) | 6 | 1.643831 | 1491 | 3.7 | 4 | 27 | 16.42 | 18.10 | Host-associated | Human | | Proteobacteria; Epsilonproteobacteria; Campylobacterales |
| *Methylococcus capsulatus* (strain Bath) | 6 | 3.304561 | 2959 | 1.8 | 2 | 82 | 24.81 | 27.71 | Multiple thermophilic | | | Proteobacteria; Gammaproteobacteria; Methylococcaless |
| *Salmonella paratyphi-a* (ATCC 9150) | 6 | 4.585229 | 4091 | 1.3 | 1.5 | 94 | 20.50 | 22.97 | Host-associated | Human | | Proteobacteria; Gammaproteobacteria; Enterobacteriales |
| *Salmonella typhi* (strain CT18) | 6 | 5.133713 | 4768 | 1.2 | 1.3 | 96 | 18.69 | 20.13 | Host-associated | Human | | Proteobacteria; Gammaproteobacteria; Enterobacteriales |
| *Salmonella typhi* (strain Ty2) | 6 | 4.791961 | 4327 | 1.3 | 1.4 | 91 | 18.99 | 21.03 | Host-associated | Human | | Proteobacteria; Gammaproteobacteria; Enterobacteriales |
| *Shigella flexneri* (serovar 2a, strain 301) | 6 | 4.828821 | 4459 | 1.2 | 1.3 | 70 | 14.49 | 15.69 | Host-associated | Human | | Proteobacteria; Gammaproteobacteria; Enterobacteriales |
| *Vibrio cholerae* (serovar O1, strain ElTor N16961) | 6 | 4.033464 | 3831 | 1.5 | 1.6 | 65 | 16.11 | 16.96 | Multiple | Human, primate | | Proteobacteria; Gammaproteobacteria; Vibrionales |
| *Chlorobium tepidum* (strain TLS ) | 5 | 2.154946 | 2254 | 2.3 | 2.2 | 42 | 19.49 | 18.63 | specialized, thermophilic | | | Chlorobi; Chlorobia; Chlorobiales; Chlorobiaceae |
| *Fusobacterium nucleatum nucleatum* (strain ATCC 25586) | 5 | 2.1745 | 2064 | 2.3 | 2.4 | 31 | 14.25 | 15.01 | Host-associated | Human, animal | | Fusobacteria; Fusobacterales; Fusobacteriaceae |
| *Helicobacter pylori* (strain 26695) | 5 | 1.667867 | 1567 | 3 | 3.2 | 25 | 14.98 | 15.95 | Host-associated | Human | | Proteobacteria; Epsilonproteobacteria; Campylobacterales |
| *Rhodoferax ferrireducens* (strain T118) | 5 | 4.969784 | 4418 | 1 | 1.1 | 66 | 13.28 | 14.93 | Multiple | | | Proteobacteria; Betaproteobacteria; Burkholderiales |
| *Shigella flexneri* (strain 2457T) | 5 | 4.599353 | 4089 | 1.1 | 1.2 | 70 | 15.21 | 17.11 | Host-associated | Human | | Proteobacteria; Gammaproteobacteria; Enterobacteriales |
| *Thiomicrospira crunogena* (strain XCL-2) | 5 | 2.427734 | 2192 | 2.1 | 2.3 | 33 | 13.59 | 15.05 | Aquatic | | | Proteobacteria; Gammaproteobacteria; Thiotrichales |
| *Bdellovibrio bacteriovorus* (strain HD100) | 4 | 3.78295 | 3583 | 1.1 | 1.1 | 40 | 10.57 | 11.16 | Multiple | | | Proteobacteria; Deltaproteobacteria; Bdellovibrionales |
| *Helicobacter hepaticus* (strain ATCC 51449) | 4 | 1.799146 | 1875 | 2.2 | 2.1 | 28 | 15.56 | 14.93 | Host-associated | Animal | | Proteobacteria; Epsilonproteobacteria; Campylobacterales |
| *Mannheimia succiniciproducens* (Strain MBEL55E) | 4 | 2.314078 | 2383 | 1.7 | 1.7 | 51 | 22.03 | 21.40 | Host -associated: bovine rumen | | | Proteobacteria; Gammaproteobacteria; Pasteurellales |
| *Rhodobacter sphaeroides* (strain 2.4.1) | 4 | 4.451915 | 4126 | 0.9 | 1 | 73 | 16.39 | 17.69 | Multiple | | | Proteobacteria; Alphaproteobacteria; Rhodobacterales |
| *Synechocystis* sp. (strain 6803) | 4 | 3.947019 | 3565 | 1 | 1.1 | 84 | 21.28 | 23.56 | Aquatic | | | Cyanobacteria; Chroococcales; Synechocystis |
| *Anaeromyxobacter dehalogenans* (strain 2CP-C) | 3 | 5.013479 | 4346 | 0.6 | 0.7 | 101 | 20.14 | 23.23 | Terrestrial | | | Proteobacteria; Deltaproteobacteria; Myxococcales |
| *Brucella abortus* (biovar 1, strain 9-941) | 3 | 3.286445 | 3085 | 0.9 | 1 | 39 | 11.86 | 12.64 | Host-associated | Human, cattle | | Proteobacteria; Alphaproteobacteria; Rhizobiales |
| *Brucella abortus* (strain 2308) | 3 | 3.278307 | 3034 | 0.9 | 1 | 43 | 13.11 | 14.17 | Host-associated | Human | | Proteobacteria; Alphaproteobacteria; Rhizobiales |
| *Brucella melitensis* (strain 16M) | 3 | 3.294931 | 3193 | 0.9 | 0.9 | 46 | 13.96 | 14.40 | Host-associated | Human, animal | | Proteobacteria; Alphaproteobacteria; Rhizobiales |
| *Brucella suis* (strain 1330) | 3 | 3.315175 | 3273 | 0.9 | 0.9 | 42 | 12.66 | 12.83 | Host-associated | Human, animal | | Proteobacteria; Alphaproteobacteria; Rhizobiales |
| *Campylobacter jejuni* (serovar O:2, strain NCTC 11168) | 3 | 1.6411481 | 1634 | 1.8 | 1.8 | 29 | 17.67 | 17.74 | Multiple | Human | | Proteobacteria; Epsilonproteobacteria; Campylobacterales |
| *Campylobacter jejuni* (strain RM1221) | 3 | 1.777831 | 1838 | 1.7 | 1.6 | 24 | 13.49 | 13.05 | Multiple | Human | | Proteobacteria; Epsilonproteobacteria; Campylobacterales |
| *Haemophilus ducreyi* (strain 35000HP) | 3 | 1.698955 | 1713 | 1.8 | 1.8 | 30 | 17.65 | 17.51 | Host-associated | Human | | Proteobacteria; Gammaproteobacteria; Pasteurellales |
| *Pelodictyon luteolum* (strain DSM 273) | 3 | 2.364842 | 2083 | 1.3 | 1.4 | 64 | 27.06 | 30.72 | Multiple | | | Chlorobi; Chlorobia; Chlorobiales |
| *Desulfovibrio desulfuricans* (strain G20). | 2 | 3.730232 | 3775 | 0.5 | 0.5 | 92 | 24.66 | 24.37 | Multiple | | | Proteobacteria; Deltaproteobacteria; Desulfovibrionales |
| *Desulfovibrio vulgaris* (strain Hildenborough) | 2 | 3.773159 | 3531 | 0.5 | 0.6 | 74 | 19.61 | 20.95 | Multiple | | | Proteobacteria; Deltaproteobacteria; Desulfovibrionales |
| *Geobacter metallireducens* (strain GS-15) | 2 | 4.011182 | 3532 | 0.5 | 0.6 | 84 | 20.94 | 23.78 | Aquatic | | | Proteobacteria; Deltaproteobacteria; Desulfuromonadales |
| *Geobacter sulfurreducens* (strain PCA) | 2 | 3.814139 | 3446 | 0.5 | 0.6 | 74 | 19.40 | 21.47 | Multiple | | | Proteobacteria; Deltaproteobacteria; Desulfuromonadales |
| *Haemophilus influenzae* (strain 86-028NP) | 2 | 1.913428 | 1791 | 1 | 1.1 | 38 | 19.85 | 21.21 | Host-associated | Human | | Proteobacteria; Gammaproteobacteria; Pasteurellales |
| *Magnetospirillum magneticum* (strain AMB-1) | 2 | 4.967148 | 4559 | 0.4 | 0.4 | 82 | 16.50 | 17.98 | Aquatic | | | Proteobacteria; Alphaproteobacteria; Rhodospirillales |
| *Rhizobium etli* (strain CFN 42) | 2 | 6.530228 | 5963 | 0.3 | 0.3 | 136 | 20.82 | 22.80 | Host-associated | | Plant: Common bean | Proteobacteria; Alphaproteobacteria; Rhizobiales |
| *Syntrophus aciditrophicus* (strain SB) | 2 | 3.1793 | 3168 | 0.6 | 0.6 | 77 | 24.21 | 24.30 | Multiple | | | Proteobacteria; Deltaproteobacteria; Syntrophobacterales |
| *Aquifex aeolicus* | 1 | 1.590791 | 1556 | 0.6 | 0.6 | 30 | 18.85 | 19.28 | Specialized, hyperthermophylic | | | Aquificae; Aquificales; Aquificaceae |
| *Bartonella henselae* (strain Houston 1) | 1 | 1.931047 | 1487 | 0.5 | 0.7 | 17 | 8.80 | 11.43 | Host-associated, opportunistic | Human, animal | | Proteobacteria; Alphaproteobacteria; Rhizobiales |
| *Bartonella quintana* (strain Toulouse) | 1 | 1.581384 | 1142 | 0.6 | 0.9 | 11 | 6.95 | 9.63 | Host-associated, opportunistic | Human | | Proteobacteria; Alphaproteobacteria; Rhizobiales |
| *Blochmannia floridanus* | 1 | 0.705557 | 583 | 1.4 | 1.7 | na | - | - | Host associated: Obligate endosymbiont | | Insect: Carpenter ant | Proteobacteria; Gammaproteobacteria; Enterobacteriales. |
| *Blochmannia pennsylvanicus* (strain BPEN) | 1 | 0.791654 | 610 | 1.3 | 1.6 | na | - | - | Host associated: Obligate endosymbiont | | Insect: ants | Proteobacteria; Gammaproteobacteria; Enterobacteriales. |
| *Chlorobium chlorochromatii* (strain CaD3) | 1 | 2.572079 | 2002 | 0.4 | 0.5 | 52 | 20.21 | 25.97 | Phototrophic consortium | | epibiont | Chlorobi; Chlorobia; Chlorobiales |
| *Desulfotalea psychrophila* (strain LSv54 / DSM 12343) | 1 | 3.659634 | 3233 | 0.3 | 0.3 | 41 | 11.20 | 12.68 | Specialized: psychrophilic | | | Proteobacteria; Deltaproteobacteria; Desulfobacterales |
| *Jannaschia* sp. (strain CCS1) | 1 | 4.404049 | 4283 | 0.2 | 0.2 | 71 | 16.12 | 16.57 | Aquatic | | | Proteobacteria; Alphaproteobacteria; Rhodobacterales |
| *Mesorhizobium loti* (strain MAFF30309) | 1 | 7.596297 | 7276 | 0.1 | 0.1 | 104 | 13.69 | 14.29 | Multiple | | Plant: lotus | Proteobacteria; Alphaproteobacteria; Rhizobiales |
| *Psychrobacter arcticum* (strain 273-4) | 1 | 2.650701 | 2120 | 0.4 | 0.5 | 27 | 10.18 | 12.73 | Specialized: psychrophilic | | | Proteobacteria; Gammaproteobacteria; Pseudomonadales |
| *Rhizobium leguminosarum* bv. *viciae* 3841 | 1 | 5.057142 | 4699 | 0.2 | 0.2 | 148 | 29.26 | 31.49 | Host-associated | | Plant: Viciae tribe | Proteobacteria; Alphaproteobacteria; Rhizobiales |
| *Anaplasma marginale* (strain St. Maries) | 0 | 1.197687 | 949 | 0 | 0 | 3 | 2.504 | 3.16 | Host-associated | Cattle | | Proteobacteria; Alphaproteobacteria; Rickettsiales |
| *Anaplasma phagocytophilum* (strain HZ) | 0 | 1.471282 | 1264 | 0 | 0 | 0 | 0.00 | 0.00 | Host-associated | Human, animal | | Proteobacteria; Alphaproteobacteria; Rickettsiales |
| *Baumannia cicadellinicola* (strain HC) | 0 | 0.686194 | 595 | 0 | 0 | 2 | 2.91 | 3.361 | Host associated: obligate endosymbiont | | Insect: leafhopper | Proteobacteria; Gammaproteobacteria; Baumannia |
| *Borrelia burgdorferi* (strain B31) | 0 | 1.519856 | 1637 | 0 | 0 | 10 | 6.57 | 6.10 | Host-associated | Human | | Spirochaetes; Spirochaetales; Spirochaetaceae |
| *Borrelia garinii* (strain PBi) | 0 | 0.986914 | 928 | 0 | 0 | 10 | 10.13 | 10.77 | Host-associated | Human | | Spirochaetes; Spirochaetales; Spirochaetaceae |
| *Buchnera aphidicola* (subsp. APS) | 0 | 0.655725 | 573 | 0 | 0 | 3 | 4.57 | 5.23 | Host associated: obligate endosymbiont | | Insect: Pea aphid | Proteobacteria; Gammaproteobacteria; Enterobacteriales |
| *Buchnera aphidicola graminum* (subsp. Schizaphis) | 0 | 0.654174 | 563 | 0 | 0 | 2 | 3.05 | 3.55 | Host associated: obligate endosymbiont | | Insect: aphid *Schizaphis graminum* | Proteobacteria; Gammaproteobacteria; Enterobacteriales |
| *Buchnera aphidicola pistaciae* (subsp. Baizongia) | 0 | 0.618379 | 507 | 0 | 0 | 3 | 4.85 | 5.91 | Host associated: obligate endosymbiont | | Insect: aphid *Baizongia pistaciae* | Proteobacteria; Gammaproteobacteria; Enterobacteriales |
| *Chlamydia muridarum* (strain Nigg) | 0 | 1.080451 | 916 | 0 | 0 | 12 | 11.11 | 13.10 | Host associated : obligate intracellular parasite | Human, animal | | Chlamydiae; Chlamydiales; Chlamydiaceae |
| *Chlamydia pneumoniae* (strain CWL029) | 0 | 1.230229 | 1053 | 0 | 0 | 9 | 7.31 | 8.54 | Host associated: obligate intracellular parasite | Human | | Chlamydiae; Chlamydiales; Chlamydiaceae |
| *Chlamydia trachomatis* (strain A/HAR-13 ) | 0 | 1.051969 | 919 | 0 | 0 | 10 | 9.50 | 10.88 | Host associated: obligate intracellular parasite | Human | | Chlamydiae; Chlamydiales; Chlamydiaceae |
| *Chlamydia trachomatis* (strain D/UW-3/Cx) | 0 | 1.042519 | 895 | 0 | 0 | 10 | 9.59 | 11.17 | Host associated: obligate intracellular parasites | Human | | Chlamydiae; Chlamydiales; Chlamydiaceae |
| *Chlamydophila abortus* (strain S26/3) | 0 | 1.144377 | 932 | 0 | 0 | 9 | 7.86 | 9.65 | Host associated: obligate intracellular parasites | Human, animal | | Chlamydiae; Chlamydiales; Chlamydiaceae |
| *Chlamydophila caviae* (strain GPIC) | 0 | 1.181356 | 1005 | 0 | 0 | 10 | 8.46 | 9.95 | Host associated: obligate intracellular parasite | Human, animal | | Chlamydiae; Chlamydiales; Chlamydiaceae |
| *Chlamydophila felis* (strain Fe/C-56) | 0 | 1.173991 | 1013 | 0 | 0 | 10 | 8.51 | 9.87 | Host associated: obligate intracellular parasite | Human, animal | | Chlamydiae; Chlamydiales; Chlamydiaceae |
| *Coxiella burnetii* (strain Nine Mile phase I / RSA 493) | 0 | 2.032674 | 2050 | 0 | 0 | 25 | 12.29 | 12.19 | Multiple | Animal | | Proteobacteria; Gammaproteobacteria; Legionellales |
| *Dehalococcoides ethenogenes* (strain 195) | 0 | 1.46972 | 1580 | 0 | 0 | 14 | 9.52 | 8.86 | Multiple | | | Chloroflexi; Dehalococcoidetes; Dehalococcoides |
| *Dehalococcoides* sp. (strain CBDB1) | 0 | 1.395502 | 1458 | 0 | 0 | 8 | 5.73 | 5.48 | Multiple | | | Chloroflexi; Dehalococcoidetes; Dehalococcoides |
| *Ehrlichia canis* (strain Jake) | 0 | 1.31503 | 925 | 0 | 0 | 0 | 0.00 | 0.00 | Host associated | Dog | | Proteobacteria; Alphaproteobacteria; Rickettsiales |
| *Ehrlichia chaffeensis* (strain Arkansas) | 0 | 1.176248 | 1105 | 0 | 0 | 0 | 0.00 | 0.00 | Host associated: obligate intracellular pathogen | Human, animal | | Proteobacteria; Alphaproteobacteria; Rickettsiales |
| *Ehrlichia ruminantium* (strain Gardel) | 0 | 1.49992 | 949 | 0 | 0 | na | - | - | Host associated: obligate intracellular parasite | Ruminant | | Proteobacteria; Alphaproteobacteria; Rickettsiales |
| *Ehrlichia ruminantium* (strain Welgevonden, sub_strain ARC-OVI) | 0 | 1.516355 | 887 | 0 | 0 | 0 | 0.00 | 0.00 | Host associated: obligate intracellular parasite | Ruminant | | Proteobacteria; Alphaproteobacteria; Rickettsiales |
| *Ehrlichia ruminantium* (strain Welgevonden, sub_strain CIRAD) | 0 | 1.512977 | 957 | 0 | 0 | na | - | - | Host associated: obligate intracellular parasite | Ruminant | | Proteobacteria; Alphaproteobacteria; Rickettsiales |
| *Francisella tularensis* (subsp. *holarctica* , strain LVS) | 0 | 1.895994 | 1706 | 0 | 0 | 41 | 21.62 | 24.03 | Host-associated | Human, animal | | Proteobacteria; Gammaproteobacteria; Thiotrichales |
| *Francisella tularensis tularensis* (strain SCHUS4) | 0 | 1.892819 | 1561 | 0 | 0 | 1 | 0.52 | 0.64 | Aquatic | Human, animal | | Proteobacteria; Gammaproteobacteria; Thiotrichales |
| *Lawsonia intracellularis* PHE/MN1-00 | 0 | 1.457619 | 1185 | 0 | 0 | 43 | 29.50 | 36.28 | Host associated: obligate intracellular pathogen | Animal | | Proteobacteria; Deltaproteobacteria; Desulfovibrionales |
| *Legionella pneumophila* (strain Lens) | 0 | 3.345687 | 2877 | 0 | 0 | 36 | 10.76 | 12.51 | Host-associated | Animal | | Proteobacteria; Gammaproteobacteria; Legionellales |
| *Legionella pneumophila* (strain Paris) | 0 | 3.50361 | 3026 | 0 | 0 | 41 | 11.70 | 13.54 | Host-associated | Animal | | Proteobacteria; Gammaproteobacteria; Legionellales |
| *Legionella pneumophila* (subsp. *Pneumophila* strain Philadelphia 1) | 0 | 3.397754 | 2941 | 0 | 0 | 35 | 10.30 | 11.90 | Host-associated | Animal | | Proteobacteria; Gammaproteobacteria; Legionellales |
| *Neorickettsia sennetsu* (strain Miyayama) | 0 | 0.859006 | 932 | 0 | 0 | 0 | 0.00 | 0.00 | Multiple/ intracellular pathogen | Human | | Proteobacteria; Alphaproteobacteria; Rickettsiales |
| *Parachlamydia* sp. (subsp. *Acanthamoeba* sp., strain UWE25) | 0 | 2.414465 | 2030 | 0 | 0 | 29 | 12.01 | 14.28 | Host-associated | Animal | | Chlamydiae; Chlamydiales; Parachlamydiaceae |
| *Pelagibacter ubique* (strain HTCC1062) | 0 | 1.308759 | 1354 | 0 | 0 | na | - | - | Aquatic | | | Proteobacteria; Alphaproteobacteria; Rickettsiales |
| *Prochlorococcus marinus* (strain CCMP 1375) | 0 | 1.75108 | 1882 | 0 | 0 | 33 | 18.84 | 17.53 | Aquatic | | | Cyanobacteria; Prochlorales; Prochlorococcaceae |
| *Prochlorococcus marinus* (strain MIT 9312) | 0 | 1.709204 | 1809 | 0 | 0 | 30 | 17.55 | 16.58 | Aquatic | | | Cyanobacteria; Prochlorales; Prochlorococcaceae |
| *Prochlorococcus marinus* (strain MIT 9313) | 0 | 2.410873 | 2262 | 0 | 0 | 41 | 17.00 | 18.12 | Aquatic | | | Cyanobacteria; Prochlorales; Prochlorococcaceae |
| *Prochlorococcus marinus* (strain NATL2A) | 0 | 1.842899 | 1890 | 0 | 0 | 31 | 16.82 | 16.40 | Aquatic | | | Cyanobacteria; Prochlorales; Prochlorococcaceae |
| *Prochlorococcus marinus* (subsp. *pastoris* , strain CCMP 1378 / MED4) | 0 | 1.65799 | 1712 | 0 | 0 | 33 | 19.90 | 19.27 | Aquatic | | | Cyanobacteria; Prochlorales; Prochlorococcaceae |
| *Rhodopirellula baltica* (strain 1) | 0 | 7.145576 | 7325 | 0 | 0 | 124 | 17.35 | 16.92 | Aquatic | | | Planctomycetes; Planctomycetacia; Planctomycetales |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Rickettsia bellii* (strain RML369-C) | 0 | 1.522076 | 1429 | 0 | 0 | 20 | 13.13 | 13.99 | Host associated: obligate intracellular pathogen | Animal | | Proteobacteria; Alphaproteobacteria; Rickettsiales |
| *Rickettsia conorii* (strain Malish 7) | 0 | 1.268755 | 1372 | 0 | 0 | 16 | 12.61 | 11.66 | Host associated: obligate intracellular pathogen | Human | | Proteobacteria; Alphaproteobacteria; Rickettsiales |
| *Rickettsia felis* (strain URRWXCal2) | 0 | 1.58724 | 1512 | 0 | 0 | 20 | 12.60 | 13.22 | Host associated: obligate intracellular pathogen | Human | | Proteobacteria; Alphaproteobacteria; Rickettsiales |
| *Rickettsia prowazekii* (strain Madrid E) | 0 | 1.111523 | 834 | 0 | 0 | 15 | 13.49 | 17.98 | Host associated: obligate intracellular pathogen | Human | | Proteobacteria; Alphaproteobacteria; Rickettsiales |
| *Rickettsia typhi* (strain Wilmington) | 0 | 1.111496 | 838 | 0 | 0 | 16 | 14.39 | 19.09 | Obligate intracellular pathogens | Human, rodent | | Proteobacteria; Alphaproteobacteria; Rickettsiales |
| *Silicibacter pomeroyi* (DSS-3) | 0 | 4.601053 | 4251 | 0 | 0 | 50 | 10.86 | 11.76 | Aquatic | | | Proteobacteria; Alphaproteobacteria; Rhodobacterales |
| *Sodalis glossinidius* (strain morsitans) | 0 | 4.292502 | 2516 | 0 | 0 | 69 | 16.07 | 27.42 | Host-associated: endosymbiont | | Insect: tsetse fly | Proteobacteria; Gammaproteobacteria; Enterobacteriales |
| *Synechococcus elongatus* (strain BP-1) | 0 | 2.593857 | 2474 | 0 | 0 | na | - | - | Specialized: thermophilic | | | Cyanobacteria; Chroococcales; Synechococcus |
| *Synechococcus* sp. (strain CC 9605) | 0 | 2.510659 | 2638 | 0 | 0 | 54 | 21.50 | 20.47 | Aquatic | | | Cyanobacteria; Chroococcales; Synechococcus |
| *Synechococcus* sp. (strain CC 9902) | 0 | 2.234828 | 2304 | 0 | 0 | 59 | 26.40 | 25.60 | Aquatic | | | Cyanobacteria; Chroococcales; Synechococcus |
| *Synechococcus* sp. (strain JA-2-3B'a(2-13)) | 0 | 3.046682 | 2863 | 0 | 0 | na | - | - | Specialized: thermophilic | | | Cyanobacteria; Chroococcales; Synechococcus |
| *Synechococcus* sp. (strain JA-3-3Ab) | 0 | 2.932766 | 2760 | 0 | 0 | na | - | - | Specialized: thermophilic | | | Cyanobacteria; Chroococcales; Synechococcus |
| *Synechococcus* sp. (strain PCC 6301) | 0 | 2.696255 | 2525 | 0 | 0 | 47 | 17.43 | 18.61 | Aquatic | | | Cyanobacteria; Chroococcales; Synechococcus |
| *Synechococcus* sp. (strain PCC 7942) | 0 | 2.742269 | 2662 | 0 | 0 | 56 | 20.42 | 21.03 | Aquatic | | | Cyanobacteria; Chroococcales; Synechococcus |
| *Synechococcus* sp. (strain WH8102) | 0 | 2.434427 | 2514 | 0 | 0 | 62 | 25.46 | 24.66 | Aquatic | | | Cyanobacteria; Chroococcales; Synechococcus |
| *Thermotoga maritima* (strain MSB8) | 0 | 1.860725 | 1853 | 0 | 0 | 79 | 42.45 | 42.63 | Specialized: hyperthermophilic | | | Thermotogae; Thermotogales; Thermotogacea |
| *Thermus thermophilus* (strain HB27) | 0 | 2.127482 | 2210 | 0 | 0 | 35 | 16.45 | 15.83 | Specialized: thermophilic | | | Deinococcus-Thermus; Deinococci; Thermales |
| *Thermus thermophilus* (strain HB8) | 0 | 2.116056 | 2239 | 0 | 0 | 39 | 18.43 | 17.41 | Specialized: thermophilic | | | Deinococcus-Thermus; Deinococci; Thermales |
| *Treponema denticola* (strain ATCC 35405) | 0 | 2.843201 | 2767 | 0 | 0 | 37 | 13.01 | 13.37 | Host-associated | Human | | Spirochaetes; Spirochaetales; Spirochaetaceae |
| *Treponema pallidum* (strain Nichols) | 0 | 1.138011 | 1029 | 0 | 0 | 6 | 5.27 | 5.83 | Host-associated | Human | | Spirochaetes; Spirochaetales; Spirochaetaceae |
| *Wigglesworthia glossinidia brevipalpis* | 0 | 0.703004 | 612 | 0 | 0 | 9 | 12.80 | 14.70 | Host associated: obligate endosymbiont | | Insect: tsetse fly | Proteobacteria; Gammaproteobacteria; Enterobacteriales |
| *Wolbachia pipientis* wMel | 0 | 1.267782 | 1195 | 0 | 0 | 4 | 3.15 | 3.34 | Host associated: obligate endosymbiont | Invertebrate | Insect: *Drosophila melanogasrer* | Proteobacteria; Alphaproteobacteria; Rickettsiales |
| *Wolbachia* sp. (subsp. Brugia malayi, strain TRS) | 0 | 1.080084 | 805 | 0 | 0 | 2 | 1.85 | 2.48 | Host associated: obligate endosymbiont | | Nematode: *Brugia malayi* | Proteobacteria; Alphaproteobacteria; Rickettsiales |

[a] Bacterial names into brackets correspond to unfinished sequenced genomes available in the NCBI ENTREZ Genome Project database (http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?db=genomeprj).

[b] Number of TonB-dependent receptor (TBDR) proteins having both pfam PF07715 and PF00593 HMMs.

[c] Number of protein coding genes as reported in the EMBL-EBI, Integr8 web portal (http://www.ebi.ac.uk/integr8/EBI-Integr8-HomePage.do) or the NCBI ENTREZ Genome Project database (http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?db=genomeprj).

[d] Number of Carbohydrate active enzymes (CAZy) or functional domains of enzymes that degrade, modify, or create glycosidic bonds. CAZy database (http://afmb.cnrs-mrs.fr/CAZY/). na: not available in CAZy database.

| | *Xanthomonas campestris* pv. *campestris* strain ATCC33913 | | | | | Orthologs [c] in: | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Gene ID [a] | Function [a] | Orientation [a] | Gene name [a] | CAZy family [b] | Characteristics | *Xcc* strain 8004 | *X. campestris* pv. *vesicatoria* strain 85-10 | *X. axonopodis* pv. *citri* strain 306 | *X. oryzae* pv. *oryzae* strain KACC10331 | *Xylella fastidiosa* strain 9a5c | Representative homologs in non Xanthomonads bacteria [d] | Conservation in *Pseudomonas aeruginosa* PAO1 (Identity/Similarity%) [e] |
| | putative partial CUT locus, arabinose induced TBDR | | | | | | | | | | | |
| XCC0043 | transcriptional regulator | + | | | | XC_0043 | abs | abs | abs | abs | | |
| XCC0044 | transcriptional regulator | - | | | | XC_0044 | abs | abs | abs | abs | | |
| XCC0045 | methicillin resistance protein | + | mecI | | | XC_0045 | XCV0045 | XAC0069 | abs | abs | | |
| XCC0046 | ankyrin-like protein | + | | | | XC_0046 | XCV0046 | XAC0070 | abs | abs | | |
| XCC0047 | hypothetical protein | + | | | | XC_0047 | XCV0047 | XAC0071 | abs | abs | | |
| XCC0048 | hypothetical protein | + | | | | XC_0048 | XCV0048 | XAC0072 | XOO0173 | abs | | |
| XCC0049 | hypothetical protein | - | | | | XC_0049 | XCV0049 | XAC0073 | XOO0172 | abs | CC1790 | |
| XCC0050 | Ps-TBDR | - | cirA | | Arabinose induced | XC_0050 | XCV0050 | XAC0074 | XOO0171-70 | abs | CC1791, *Caulobacter crescentus* CB15 | |
| XCC0051 | xylose repressor-like protein | + | xylR | | | XC_0051 | XCV0051 | XAC0075 | XOO0169 | abs | CC1792 | |
| XCC0052 | avirulence protein | + | avrBs2 | | | XC_0052 | XCV0052 | XAC0076 | XOO0168 | abs | | |
| XCC0053 | hypothetical protein | - | | | | XC_0053 | XCV0054 | XAC0077 | XOO0167 | abs | | |
| XCC0095 | TldD protein | - | tldD | | | XC_0097 | XCV0093 | XAC0122 | abs | abs | | |
| XCC0096 | fructose-1,6-bisphosphatase | - | cbbFC | | | XC_0098 | XCV0098 | XAC0124 | XOO0015 | abs | | |
| XCC0097 | aromatic-amino-acid aminotransferase | - | tyrB | | | XC_0100 | XCV0101 | XAC0125 | XOO0016 | XF0036 | | |
| XCC0098 | Ps-TBDR | + | yncD | | | XC_0101 | XCV0102 | XAC0126 | XOO0017 | abs | BB0832, *Bordetella bronchiseptica* RB50 | PA2289 (39/54) |
| XCC0099 | hypothetical protein | + | | | | XC_0102 | XCV0103 | XAC0127 | abs | abs | | |
| XCC0100 | hypothetical protein | + | | | | XC_0103 | XCV0104 | abs | abs | abs | | |
| XCC0101 | chloroacetaldehyde dehydrogenase | + | aldA | | | XC_0104 | XCV0105 | XAC0129 | abs | abs | | |
| | putative partial CUT locus, CAZy associated TBDR, polygalacturonate induced TBDR | | | | | | | | | | | |
| XCC0115 | hypothetical protein | + | | | | XC_0119 | XCV0120 | XAC0141 | XOO0027 | XF1835 | | |
| XCC0116 | hypothetical protein | + | | | | XC_0120 | XCV0121 | XAC0142 | abs | abs | | |
| XCC0117 | hypothetical protein | - | | | | XC_0121 | abs | abs | abs | abs | | |
| XCC0118 | 2-keto-3-deoxygluconate kinase | - | kdgK | | | XC_0122 | XCV0122 | XAC0143 | XOO0028 | abs | | |
| XCC0119 | TBDR | + | iroN | | | XC_0123 | XCV0123 | XAC0144 | abs | abs | Mmar10_0224, *Maricaulis maris* MCS10 | |
| XCC0120 | TBDR | + | iroN | | PGA induced | XC_0124 | abs | abs | abs | abs | CC0442, *Caulobacter crescentus* CB15 | |
| XCC0121 | pectin methyl esterase | + | | CE8 | | XC_0125 | abs | abs | abs | abs | | |
| XCC0122 | pectate lyase | + | | PL10 | | XC_0126 | abs | abs | abs | abs | | |
| XCC0123 | hypothetical protein | + | | | | XC_0127 | XCV0124 | XAC0145 | abs | abs | | |
| XCC0124 | hypothetical protein | + | | | | XC_0128 | abs | abs | abs | abs | | |
| XCC0125 | hypothetical protein | + | | | | XC_0130 | abs | abs | abs | abs | | |
| XCC0126 | deoxycytidylate deaminase | + | | | | XC_0132 | abs | abs | abs | abs | | |
| XCC0127 | IS1479 transposase | - | | | | XC_0133 | XCV0129 | abs | abs | abs | | |
| | Fur regulated TBDR | | | | | | | | | | | |
| XCC0154 | rhamnogalacturonan acetylesterase | + | | CE12 | | XC_0163 | XCV0155 | XAC0171 | XOO0265 | abs | | |
| XCC0155 | hypothetical protein | - | | | | XC_0164 | XCV0156 | XAC0173 | XOO0266 | abs | | |
| XCC0156 | phenylalanine hydroxylase | - | pah | | | XC_0165 | XCV0157 | XAC0174 | XOO0267 | abs | | |
| XCC0157 | transcriptional regulator asnC family | + | | | | XC_0166 | XCV0158 | XAC0175 | XOO0268 | abs | | |
| XCC0158 | TBDR | + | fpvA | | Fur-regulated | XC_0167 | XCV0159 | XAC0176 | XOO0271-70-69 | abs | PSEEN2482, *Pseudomonas entomophila* L48 | PA2398; FpvA (36/52) |
| XCC0159 | hypothetical protein | - | | | | XC_0168 | XCV0160 | XAC0177 | XOO4518 | XF0066 | | |
| XCC0160 | hypothetical protein | - | | | | XC_0169 | XCV0162 | XAC0178 | XOO4517 | abs | | |
| XCC0161 | ABC transporter ATP-binding protein | - | ylma | | | XC_0170 | XCV0163 | XAC0179 | XOO4515 | abs | | |
| XCC0162 | fatty acid desaturase | + | | | | XC_0171 | XCV0164 | XAC0180 | XOO4514 | abs | | |
| | putative partial CUT locus | | | | | | | | | | | |
| XCC0301 | transcriptional regulator lysR family | - | | | | XC_0312 | XCV0325 | XAC0316 | XOO4350 | abs | | |
| XCC0302 | MFS transporter | + | ynfM | | | XC_0313 | XCV0326 | XAC0317 | XOO4349 | abs | | |
| XCC0303 | hypothetical protein | - | | | | XC_0314 | abs | abs | abs | abs | | |
| XCC0304 | Ps-TBDR | - | | | | XC_0315 | abs | abs | abs | abs | Sala_0305, *Sphingopyxis alaskensis* RB2256 | |
| XCC0305 | | - | fhuA | | | XC_0316 | abs | abs | abs | abs | CPS_3961, *Colwellia psychrerythraea* 34H | |
| XCC0306 | SIR2-like regulatory protein | + | | | | XC_0318 | XCV0329 | XAC0320 | XOO4347 | abs | | |
| XCC0307 | FMN oxidoreductase | + | frp | | | XC_0319 | XCV0330 | XAC0321 | XOO4346 | abs | | |
| XCC0308 | dehydrogenase | + | | | | XC_0320 | XCV0331 | XAC0322 | XOO4345 | abs | | |
| XCC0391 | tRNA | + | | | | XC_0001_tRNA | XCV0001_tRNA | XAC0391_tRNA | XOO4657_tRNA | XFt02_tRNA | | |
| XCC0392 | phage-related integrase | + | | | | XC_0403 | abs | abs | abs | abs | | |
| XCC0393 | IS1481 transposase | + | | | | abs | abs | XAC4328 | abs | abs | | |
| XCC0394 | TBDR | - | fhuA | | | XC_0405 | abs | abs | abs | abs | Bcep18194_B2705, *Burkholderia* sp. 383 | PA2911 (41/57) |
| XCC0395 | superoxidase dismutase | - | sodM | | | XC_0407 | abs | abs | XOO2828 | XF1921 | | |
| XCC0396 | hypothetical protein | + | | | | XC_0408 | abs | abs | abs | abs | | |
| XCC0397 | Ps-TBDR | + | bfeA | | | XC_0409 | abs | abs | abs | abs | Patl_3441, *Pseudoalteromonas atlantica* T6c | PA2590 (31/46); PA2089 (31/46) |
| XCC0398 | isopenicillin N epimerase | + | nifS | | | XC_0411 | abs | abs | abs | abs | | |
| XCC0399 | IS1404 transposase | + | | | | XC_0412 | abs | abs | abs | abs | | |
| XCC0400 | IS1404 transposase | + | | | | XC_0413 | XCV0022 D | XAC3936 | abs | abs | | |
| XCC0523 | 60kDa chaperonin | + | groEL | | | XC_0535 | XCV0571 | XAC0542 | XOO4288 | XF0615 | | |
| XCC0524 | helicase | + | | | | XC_0536 | abs | abs | abs | abs | | |
| XCC0525 | ATP-dependent DNA helicase | + | | | | XC_0537 | abs | abs | abs | abs | | |
| XCC0526 | hypothetical protein | + | | | | XC_0538 | abs | abs | abs | abs | | |
| XCC0527 | hypothetical protein | + | | | | XC_0539 | abs | abs | abs | abs | | |
| XCC0528 | hypothetical protein | + | | | | XC_0540 | abs | abs | abs | abs | | |
| XCC0529 | hypothetical protein | - | | | | XC_0541 | XCV0572 | XAC0543 | XOO4287 | abs | | |
| XCC0530 | hypothetical protein | - | | | | XC_0542 | XCV0572 | XAC0543 | XOO4287 | abs | | |
| XCC0531 | Ps-TBDR | + | | | | XC_0543 | XCV0573 | XAC0544 | XOO4285 | abs | PA2057, *Pseudomonas aeruginosa* PAO1 | PA2057 (33/48) |
| XCC0532 | hypothetical protein | - | | | | XC_0544 | abs | abs | abs | abs | | |
| XCC0533 | ISxcd1 transposase | + | | | | XC_0545 | abs | abs | abs | abs | | |
| XCC0534 | ISxcd1 transposase | + | | | | XC_0546 | abs | abs | abs | abs | | |
| XCC0535 | IS1478 transposase | - | | | | abs | XCV2716 | XAC2423 | abs | abs | | |
| XCC0536 | hypothetical protein | + | | | | XC_3697 | abs | abs | abs | abs | | |
| XCC0537 | hypothetical protein | - | | | | XC_3696 | XCV3784 | abs | abs | abs | | |
| | Putative CUT locus (unknown substrate) | | | | | | | | | | | |
| XCC0671 | hypothetical protein | + | | | | XC_3562 | XCV3657 | XAC3533 | XOO0858 | abs | | |
| XCC0672 | transcriptional regulator | - | | | | XC_3561 | XCV3656 | XAC3532 | XOO0859 | abs | | |
| XCC0673 | Nicotinamide mononucleotide transporter | - | pnuC | | | XC_3560 | XCV3655 | XAC3531 | XOO0860 | abs | | |
| XCC0674 | TBDR | - | | | | XC_3559 | XCV3654 | XAC3529 | XOO0861 | abs | Psyr_3769, *Pseudomonas syringae* pv. *syringae* B728a | PA1910 (26/43) |
| XCC0675 | hypothetical protein | - | | | | XC_3558 | XCV3653 | XAC3528 | XOO0862 | abs | | |
| XCC0676 | glycosyl transferase | + | gtrB | GT2 | | XC_3557 | XCV3652 | XAC3526 | XOO0863 | XF1637 | | |
| XCC0677 | hypothetical protein | + | | | | XC_3556 | XCV3651 | XAC3525 | abs | abs | | |
| XCC0678 | hypothetical protein | + | | GT2 | | XC_3555 | XCV3650 | XAC3524 | abs | abs | | |
| XCC0679 | hypothetical protein | + | | | | XC_3554 | XCV3649 | XAC3523 | abs | abs | | |
| XCC0680 | hypothetical protein | + | | | | XC_3553 | XCV3648 | XAC3522 | abs | abs | | |
| XCC0681 | nicotinate phosphoribosyltransferase | + | pncB | | | XC_3552 | XCV3647 | XAC3521 | abs | XF1097 | | |
| XCC0755 | transcriptional regulator tetR/acrR family | + | | | | XC_3478 | XCV0859 | XAC0807 | XOO3795 | abs | | |
| XCC0756 | hypothetical protein | + | | | | XC_3477 | XCV0860 | XAC0808 | abs | abs | | |
| XCC0757 | hypothetical protein | + | | | | XC_3476 | XCV0861 | XAC0809 | abs | abs | | |
| XCC0758 | hypothetical protein | + | | | | XC_3475 | XCV0862 | abs | abs | abs | | |
| XCC0759 | TBDR | + | cirA | | | XC_3474 | XCV0863 | XAC0811 | XOO3793 | abs | GOX1188, *Gluconobacter oxydans* 621H | |
| XCC0760 | phosphoanhydride phosphohydrolase | + | appA | | | XC_3473 | XCV0864 | XAC0812 | XOO3792 | abs | GOX1190 | |
| XCC0761 | methionine adenosyltransferase | - | metK | | | XC_3471 | XCV0865 | XAC0813 | XOO3791 | XF0392 | | |
| XCC0762 | hypothetical protein | + | | | | XC_3470 | XCV0866 | XAC0814 | XOO3789 | abs | | |
| | Fur regulated TBDR | | | | | | | | | | | |
| XCC0765 | nucleoside transporter | - | yeiM | | | XC_3467 | XCV0871 | XAC0819 | XOO3783 | abs | | |
| XCC0766 | voltage-gated potassium channel beta subunit | + | | | | XC_3466 | XCV0873 | XAC0821 | XOO3782 | XF0367 | | |
| XCC0767 | hypothetical protein | + | | | | XC_3464 | XCV0874 | XAC0822 | XOO3781 | abs | | |
| XCC0768 | TBDR | + | phuR | | Fur-regulated | XC_3463 | XCV0875 | XAC0823 | abs | abs | alr2153, *Nostoc* sp. PCC 7120 | PA4710; PhuR (33/49) |
| XCC0769 | hypothetical protein | + | | | | XC_3462 | XCV0876 | XAC0824 | XOO3775 | abs | | |
| XCC0770 | hypothetical protein | + | | | | XC_3461 | XCV0878 | XAC0825 D | abs | abs | | |
| XCC0771 | hypothetical protein | - | | | | abs | XCV0879 | XAC0826 | XOO3774 | XF0449 | | |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| XCC0772 | permease | - | nrtB | | | XC_3459 | XCV0880 | XAC0827 | XOO3772 | abs | | |
| XCC0773 | ABC transporter ATP-binding component | - | nrtCD | | | abs | XCV0881 | XAC0828 | XOO3770 D | XF0412 | | |
| XCC0774 | ABC transporter substrate binding protein | - | | | | XC_3457 | XCV0882 | XAC0829 | XOO3768 | abs | | |
| | | | | | | | | | | | | |
| XCC0942 | ABC transporter sulfate permease | + | cysW | | | XC_3293 | XCV1049 | XAC1019 | XOO3688 | XF1346 | | |
| XCC0943 | sulfate ABC transporter ATP-binding protein | + | cysA | | | XC_3292 | XCV1050 | XAC1020 | XOO3686 | XF1347 | | |
| XCC0944 | hypothetical protein | + | | | | XC_3291 | XCV1051 | XAC1021 | XOO3685 | abs | | |
| XCC0945 | threonine 3-dehydrogenase | - | tdh | | | XC_3290 | XCV1052 | XAC1022 | XOO3684 | abs | | |
| XCC0946 | TBDR | - | fecA | | | XC_3289 | XCV1053 | XAC1023 | XOO3683 | abs | Psyr_4483, *Pseudomonas syringae pv. syringae* B728a | |
| XCC0947 | non-hemolytic phospholipase C | + | | | | XC_3288 | XCV1054 | XAC1024 | XOO3682 | abs | | |
| XCC0948 | phosphoglycerate mutase | + | pgmA | | | XC_3287 | XCV1057 | XAC1028 | XOO3680 | XF1886 | | |
| XCC0949 | hypothetical protein | + | | | | XC_3286 | abs | abs | abs | abs | | |
| XCC0950 | folylpolyglutamate synthase/dihydrofolate synthase | + | folC | | | XC_3285 | XCV1058 | XAC1029 | XOO3679 | XF1946 | | |
| | CAZy associated TBDR | | | | | | | | | | | |
| XCC1033 | aconitate hydratase 1 | + | acnA | | | XC_3213 | XCV1158 | XAC1139 | XOO0894 | abs | | |
| XCC1034 | hypothetical protein | + | | | | XC_3212 | abs | XAC1140 | abs | abs | | |
| XCC1035 | hypothetical protein | + | | | | XC_3211 | abs | XAC1141 | XOO0895 | abs | | |
| XCC1036 | hypothetical protein | + | | | | XC_3210 | XCV1160 | XAC1142 | XOO0896 | XF1243 | | |
| XCC1037 | TBDR | + | fyuA | | | XC_3209 | XCV1161 | XAC1143 | XOO0897 | abs | Sala_0027, *Sphingopyxis alaskensis* RB2256 | PA2335 (27/43) |
| XCC1038 | inosine-uridine preferring nucleoside hydrolase | + | | | | XC_3208 | XCV1162 | XAC1144 | XOO0898 | abs | | |
| XCC1039 | hypothetical protein | + | | | | XC_3207 | XCV1164 | XAC1145 | abs | XF1252 | | |
| XCC1040 | hypothetical protein | - | | | | XC_3206 | XCV1177 | abs | abs | abs | | |
| XCC1041 | Ps-TBDR | + | fecA | | HrpX regulated | XC_3205 | XCV1165 | XAC1146 | XOO0901 | abs | CC1113, *Caulobacter crescentus* CB15 | |
| XCC1042 | glycerophosphodiester phosphodiesterase | + | glpQ | | | XC_3204 | XCV1166 | XAC1147 | XOO0902 | abs | | |
| XCC1043 | hypothetical protein | + | | | | XC_3203 | abs | abs | abs | abs | | |
| XCC1044 | bifunctional penicillin-binding protein 1C | + | pbpC | GT51 | | XC_3202 | XCV1168 | XAC1148 | abs | XF2235 | | |
| XCC1045 | bacterioferritin | - | | | | XC_3201 | XCV1169 | XAC1149 | XOO0907 | abs | | |
| XCC1046 | peroxiredoxin | - | | | | XC_3200 | XCV1170 | XAC1150 | XOO0908 | abs | | |
| XCC1047 | low molecular weight heat shock protein | + | hspA | | | XC_3199 | XCV1172 | XAC1151 | XOO0909 | XF2234 | | |
| | Putative  partial CUT locus, CAZy associated TBDR | | | | | | | | | | | |
| XCC1174 | two-component system regulatory protein | + | | | | XC_3069 | XCV1322 | XAC1272 | abs | abs | | |
| XCC1175 | two-component system sensor protein | + | | | | XC_3068 | XCV1323 | XAC1273 | abs | abs | | |
| XCC1176 | histidine kinase/response regulator hybrid protein | + | cvgSY | | | XC_3067 | XCV1324 | XAC1274 | abs | abs | | |
| XCC1177 | IS1480 transposase | + | | | | abs | abs | abs | XOO4178 | abs | | |
| XCC1178 | xylosidase/arabinosidase | - | xylB | GH43 | | XC_3064 | XCV1325 | XAC1275 | XOO4422 | abs | | |
| XCC1179 | Ps-TBDR | + | fyuA | | | XC_3063 | XCV1326 | XAC1276 | abs | abs | CC1970, *Caulobacter crescentus* CB15 | PA2335 (27/40) |
| XCC1180 | thioredoxin | - | trx | | | XC_3062 | XCV1327 | XAC1277 | abs | abs | | |
| XCC1181 | hypothetical protein | - | | | | XC_3061 | XCV1328 | XAC1278 | abs | abs | | |
| XCC1182 | two-component system regulatory protein | - | | | | XC_3060 | XCV1329 | XAC1279 | abs | abs | | |
| XCC1183 | protein-glutamate methylesterase | - | cheB | | | XC_3059 | XCV1330 | XAC1280 | abs | abs | | |
| XCC1184 | chemotaxis protein | - | cheR | | | XC_3058 | XCV1331 | XAC1281 | abs | abs | | |
| XCC1185 | two-component system sensor protein | - | | | | XC_3057 | XCV1332 | XAC1283 | abs | abs | | |
| XCC1186 | two-component system sensor protein | + | | | | XC_3056 | XCV1333 | XAC1282 | abs | abs | | |
| XCC1187 | two-component system regulatory protein | + | | | | XC_3055 | XCV1334 | XAC1284 | abs | abs | | |
| | Putative partial CUT locus | | | | | | | | | | | |
| XCC1250 | Beta-glucosidase | + | bglX | GH3 | | XC_2991 | XCV3988 | XAC3869 | XOO4123 | abs | | |
| XCC1251 | hypothetical protein | + | | GH29; CBM32 | | XC_2990 | XCV1357 | XAC1306 | XOO1835 | abs | | |
| XCC1252 | hypothetical protein | + | | | | XC_2989 | XCV1358 | XAC1307 | XOO1836 | abs | | |
| XCC1253 | hypothetical protein | - | | | | XC_2988 | abs | abs | abs | abs | | |
| XCC1254 | hypothetical protein | - | | | | XC_2987 | abs | abs | abs | abs | | |
| XCC1255 | IS1478 transposase | + | | | | XC_2986 | XCV2716 | XAC2423 | XOO1863 | abs | | |
| XCC1256 | beta-galactosidase | - | bga | GH2 | | XC_2985 | XCV1359 | XAC1308 | XOO1837-8 D | abs | | |
| XCC1257 | arabinogalactan endo-1,4-beta-galactosidase | - | galA | GH53 | | XC_2984 | XCV1360 | XAC1309 | XOO1838 D | abs | | |
| XCC1258 | TBDR | - | btuB | | | XC_2983 | XCV1361 | XAC1310 | XOO1839 | abs | Sde_3880, *Saccharophagus degradans* 2-40 | |
| XCC1259 | transcriptional regulator | - | | | | XC_2982 | XCV1362 | XAC1311 | XOO1841 | abs | | |
| XCC1260 | methylmalonate-semialdehyde dehydrogenase | + | mmsA | | | XC_2981 | XCV1363 | XAC1312 | XOO1842 | abs | | |
| XCC1261 | acyl-CoA dehydrogenase | + | fadE9 | | | XC_2980 | XCV1364 | XAC1313 | XOO1843 | abs | | |
| | | | | | | | | | | | | |
| XCC1336 | hypothetical protein | - | | | | XC_2903 | XCV1438 | XAC1382 | XOO1921 | abs | | |
| XCC1337 | ferredoxin II | - | ydgM | | | XC_2902 | XCV1439 | XAC1384 | XOO1922 | XF0547 | | |
| XCC1338 | phosphotransferase | - | cicA | | | XC_2901 | XCV1440 | XAC1385 | XOO1923 | abs | | |
| XCC1339 | methionyl-tRNA synthetase | - | metS | | | XC_2900 | XCV1441 | XAC1386 | XOO1924 | XF0549 | | |
| XCC1340 | TBDR | - | btuB | | | XC_2899 | abs | abs | abs | XF0550 | GOX0945, *Gluconobacter oxydans* 621H | PA2070 (24/37) |
| XCC1341 | hypothetical protein | - | | | | XC_2898 | XCV1442 | XAC1387 | XOO1925 | abs | | |
| XCC1342 | glyoxylase I family protein | - | | | | XC_2897 | XCV1445 | XAC1390 | XOO1927 | abs | | |
| XCC1343 | S-methylmethionine permease | + | ykfD | | | XC_2895 | XCV1448 | XAC1391 | XOO1929 | abs | | |
| XCC1344 | homocysteine S-methyltransferase | + | mmuM | | | XC_2894 | XCV1449 | XAC1392 | XOO1930 | abs | | |
| | Fur regulated TBDR | | | | | | | | | | | |
| XCC1389 | hypothetical protein | - | | | | XC_2850 | abs | abs | abs | abs | | |
| XCC1388 | asparagine synthase B | + | asnB | | | XC_2848 | XCV1490 | XAC1433 | XOO1990 | XF0118 | | |
| XCC1390 | hypothetical protein | - | | | | XC_2847 | XCV1491 | XAC1434 | XOO1991 | XF0119 | | |
| XCC1391 | TBDR | - | fhuA | | Fur-regulated | XC_2846 | XCV1493 | XAC1435 | XOO1992 | abs | PSHAb0279, *Pseudoalteromonas haloplanktis* TAC125 | PA2466 (27/43) |
| XCC1392 | penicillin acylase II | - | acylI | | | XC_2845 | XCV1494 | XAC1437 | XOO1993 | abs | | |
| XCC1393 | bacterioferritin | + | brf | | | XC_2844 | XCV1495 | XAC1438 | XOO1994 | abs | PSHAb0284 | |
| XCC1394 | thiopurine methyltransferase | - | tpmT | | | XC_2843 | XCV1496 | XAC1439 | XOO1995 D | abs | | |
| | | | | | | | | | | | | |
| XCC1715 | tRNA delta(2)-isopentenylpyrophosphate transferase | + | miaA | | | XC_2516 | XCV1767 | XAC1734 | XOO2947 | XF0090 | | |
| XCC1716 | host factor-I protein | + | hfq | | | XC_2515 | XCV1768 | XAC1735 | XOO2946 | XF0089 | | |
| XCC1717 | GTP-binding protein | + | hflX | | | XC_2514 | XCV1769 | XAC1736 | XOO2945 | XF0088 | | |
| XCC1718 | hypothetical protein | + | | | | XC_2513 | XCV1770 | XAC1737 | XOO2944 | XF0086 | | |
| XCC1719 | TBDR | + | | | HrpX regulated | XC_2512 | abs | abs | abs | abs | CC3336, *Caulobacter crescentus* CB15 | PA2335 (29/43); PA0192 (28/41) |
| XCC1720 | ubiquinone biosynthesis protein | + | aarF | | | XC_2511 | XCV1771 | XAC1738 | XOO2943 | abs | | |
| XCC1721 | LexA repressor | + | lexA | | | XC_2510 | XCV1772 | XAC1739 | XOO2942 | XF0122 | | |
| XCC1722 | RecA protein | + | recA | | | XC_2509 | XCV1773 | XAC1740 | XOO2941 | XF0123 | | |
| XCC1723 | RecX protein | + | recX | | | XC_2508 | XCV1774 | XAC1741 | XOO2940 | abs | | |
| XCC1724 | alanyl-tRNA synthetase | + | alaS | | | XC_2507 | XCV1775 | XAC1742 | XOO2939 | XF0124 | | |
| XCC1725 | carbon storage regulator | + | csrA | | | XC_2506 | XCV1776 | XAC1743 | XOO2938 | XF0125 | | |
| XCC1726 | tRNA | + | | | | XC_4359_tRNA | XCV0024_tRNA | XAC1744_tRNA | XOO4650_tRNA | XFt05_tRNA | | |
| | Putative CUT locus (pectin/polygalacturonate?) | | | | | | | | | | | |
| XCC1744 | 2-oxo-3-deoxygalactonate kinase | - | dgoK | | | XC_2490 | XCV1794 | XAC1763 | XOO2920 | abs | | |
| XCC1745 | regucalcin | - | | | | XC_2489 | XCV1795 | XAC1764 | XOO2918 | abs | | |
| XCC1746 | 4-hydroxy-2-oxoglutarate aldolase/2-deydro-3-deoxyphosphogluconate aldolase | - | dgoA | | | XC_2488 | XCV1796 | XAC1765 | XOO2919 | abs | | |
| XCC1747 | 4-hydroxy-2-oxoglutarate aldolase/2-deydro-3-deoxyphosphogluconate aldolase | - | dgoA | | | XC_2487 | XCV1797 | XAC1766 | XOO2917 | abs | | |
| XCC1748 | galactose-binding protein regulator | + | gbpR | | | XC_2486 | XCV1798 | XAC1767 | XOO2916 | abs | | |
| XCC1749 | TBDR | + | | | PGA/Arabinose induced | XC_2485 | XCV1799 D | XAC1768 | abs | abs | CC2804, *Caulobacter crescentus* CB15 | |
| XCC1750 | Ps-TBDR | + | | | PGA/Arabinose induced | XC_2484 | XCV1801 | XAC1769 | abs | abs | Sde_2502, *Saccharophagus degradans* 2-40 | |
| XCC1751 | | + | | | PGA induced | XC_2484 | XCV1801 | XAC1769 | abs | abs | | |
| XCC1752 | cellulase | + | | GH74 | | XC_2483 | XCV1802 | XAC1770 | abs | abs | | |
| XCC1753 | sialic acid-specific 9-O-acetylesterase | + | | | | XC_2482 | XCV1803 | XAC1771 | abs | abs | Sde_2492 | |
| XCC1754 | hypothetical protein | + | | GH35 | | XC_2481 | XCV1804 | XAC1772 | abs | abs | Sde_2501 | |
| XCC1755 | alpha-xylosidase | + | xylS | GH31 | | XC_2480 | XCV1805 | XAC1773 | XOO2914 | abs | Sde_2500 | |
| XCC1756 | hypothetical protein | + | | GH95 | | XC_2479 | XCV1806 | XAC1774 | XOO2913 | abs | Sde_2503 | |
| XCC1757 | D-xylulokinase | + | | | | XC_2478 | XCV1807 | XAC1775 | XOO2911 | abs | | |
| XCC1758 | xylose isomerase | + | xylA | | | XC_2477 | XCV1808 | XAC1776 | XOO2910 | abs | Sde_2504 | |
| XCC1759 | MFS transporter | + | xylE | | | XC_2476 | XCV1809 | XAC1777 | XOO2909 | abs | | |
| XCC1760 | sensor kinase | + | | | | XC_2475 | XCV1810 | XAC1778 | abs | abs | | |
| | Arabinose induced TBDR | | | | | | | | | | | |
| XCC1889 | chromosome partioning protein | - | parA | | | XC_2299 | XCV1960 | XAC1907 | XOO2832 | abs | | |
| XCC1890 | MotB protein | - | motB | | | XC_2298 | XCV1961 | XAC1908 | XOO2831 | abs | | |
| XCC1891 | MotA protein | - | motA | | | XC_2297 | XCV1962 | XAC1909 | XOO2830 | abs | | |
| XCC1892 | TBDR | + | cirA | | Arabinose induced | XC_2296 | XCV1963 | XAC1910 | XOO2826 | abs | PSHAb0165, *Pseudoalteromonas haloplanktis* TAC125 | |
| XCC1893 | hypothetical protein | + | | | | abs | abs | abs | abs | abs | | |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| XCC1894 | hypothetical protein | + | | | | abs | abs | abs | abs | abs | | |
| XCC1895 | hypothetical protein | - | | | | abs | abs | abs | abs | abs | | |
| | | | | | | | | | | | | |
| XCC1987 | GTP-binding protein | + | engA | | | XC_2197 | XCV2072 | XAC2021 | XOO2529 | XF0465 | | |
| XCC1988 | molybdopterin biosynthesis | + | moeA | | | XC_2196 | XCV2073 | XAC2022 | XOO2528 | abs | | |
| XCC1989 | molybdopterin biosynthesis protein | - | moeB | | | XC_2195 | XCV2074 | XAC2023 | XOO2514 | XF0466 | | |
| XCC1990 | Ps-TBDR | + | cirA | | | XC_2194 | XCV2075 | XAC2024 | abs | abs | Rfer_3396, *Rhodoferax ferrireducens* T118 | |
| XCC1991 | hypothetical protein | + | | | | XC_2193 | XCV2076 | XAC2025 | abs | abs | | |
| XCC1992 | glucose 1-dehydrogenase homolog | - | yxnA | | | XC_2192 | abs | abs | abs | abs | | |
| XCC1993 | fatty acid alpha hydroxylase | + | cypC | | | XC_2191 | abs | abs | abs | abs | | |
| XCC1994 | hypothetical protein | + | | | | XC_2190 | XCV2077 | XAC2026 | abs | abs | | |
| | | | | | | | | | | | | |
| XCC2043 | hypothetical protein | - | | | | XC_2140 | abs | abs | abs | abs | | |
| XCC2044 | hypothetical protein | - | | | | XC_2139 | abs | abs | abs | abs | | |
| XCC2045 | hypothetical protein | - | | | | XC_2138 | abs | XAC2134 | abs | abs | | |
| XCC2046 | Ps-TBDR | + | fecA | | | XC_2137 | XCV0751 | XAC0690 | abs | abs | PP_3340, *Pseudomonas putida* KT2440 | PA2289 (22/39) |
| XCC2047 | chemotaxis protein | - | tsr | | | XC_2136 | XCV1702 | XAC1666 | abs | abs | | |
| XCC2048 | hypothetical protein | + | | | | XC_2135 | abs | abs | abs | abs | | |
| XCC2049 | hypothetical protein | - | | | | XC_2134 | abs | abs | XOO3309 | abs | | |
| | Putative partial CUT locus, conserved locus | | | | | | | | | | | |
| XCC2203 | hypothetical protein | - | | | | XC_1915 | XCV2505 | XAC2307 | XOO2173 | XF2445 | | |
| XCC2204 | ABC transporter sugar permease | - | lacG | | | XC_1914 | XCV2506 | XAC2308 | XOO2172 | XF2446 | Sala_1021 | |
| XCC2205 | ABC transporter sugar permease | - | lacF | | | XC_1913 | XCV2507 | XAC2309 | XOO2171 | XF2447 | Sala_1022 | |
| XCC2206 | ABC transporter sugar binding protein | - | malE | | | XC_1912 | XCV2508 | XAC2310 | XOO2170 | XF2448 | Sala_1023 | |
| XCC2207 | hypothetical protein | - | | | | XC_1911 | XCV2509 | XAC2311 | XOO2169 | XF2449 | Sala_1016 | |
| XCC2208 | Ps-TBDR/oar | - | | | | XC_1910 | XCV2510 | XAC2312 | XOO2166 | abs | Sala_1015, *Sphingopyxis alaskensis* RB2256 | |
| XCC2209 | transcriptional regulator lacI family | - | | | | XC_1909 | XCV2511 | XAC2313 | XOO2165 | abs | Sala_1024 | |
| XCC2210 | hypothetical protein | - | | | | XC_1908 | XCV2513 | XAC2314 | abs | XF2450 | | |
| XCC2211 | hypothetical protein | - | | | | XC_1907 | XCV2514 | XAC2315 | XOO2164 | abs | | |
| | Putative partial CUT locus, CAZy associated TBDR | | | | | | | | | | | |
| XCC2380 | transcriptional regulator asnC/lrp family | - | | | | XC_1734 | XCV2697 | XAC2515 | XOO2486 | abs | | |
| XCC2381 | L-lysine 6-aminotransferase | + | | | | XC_1733 | XCV2698 | XAC2516 | XOO2487 | abs | | |
| XCC2382 | hypothetical protein | - | | | | XC_1732 | XCV2699 | XAC2517 | XOO2488 | abs | | |
| XCC2383 | hypothetical protein | - | | | | XC_1731 | XCV2700 | XAC2518 | XOO2497 | abs | | |
| XCC2384 | hypothetical protein | - | | | | XC_1730 | XCV2701 | XAC2519 | XOO2499 | abs | | |
| XCC2385 | Ps-TBDR | - | cirA | | | XC_1729 | XCV2702 | XAC2520 | XOO2500 | abs | PSHAa0437, *Pseudoalteromonas haloplanktis* TAC125 | |
| XCC2386 | putative UMP pyrophosphorylase | + | upp | | | XC_1728 | XCV2703 | XAC2521 | XOO2501 | abs | | |
| XCC2387 | cellulase | - | egl2 | GH9 | | XC_1727 | XCV2704 | XAC2522 | abs | abs | | |
| XCC2388 | gamma-glutamyltranspeptidase | - | ggt | | | XC_1726 | XCV2706 | XAC2523 | XOO2505 | XF0984 | | |
| XCC2389 | ferredoxin | - | | | | XC_1725 | XCV2707 | XAC2524 | XOO2506 | XF0983 | | |
| XCC2390 | hypothetical protein | - | | | | XC_1724 | XCV2708 | XAC2525 | XOO2507 | XF0981 | | |
| | CAZy associated TBDR | | | | | | | | | | | |
| XCC2391 | lipopolysaccharide synthesis enzyme | - | kdtB | | | XC_1723 | XCV2709 | XAC2526 | XOO2508 | XF0980 | | |
| XCC2392 | hypothetical protein | - | | | | XC_1722 | XCV2710 | XAC2527 | XOO2509 | XF0979 | | |
| XCC2393 | heat shock protein G | + | htpG | | | XC_1721 | XCV2711 | XAC2528 | XOO2510 | XF0978 | | |
| XCC2394 | hypothetical protein | - | | | | XC_1718 | XCV2724 | XAC2530 | XOO3112 | abs | | |
| XCC2395 | TBDR | - | btuB | | | XC_1717 | XCV2725 | XAC2531 | abs | abs | Sden_2427, *Shewanella denitrificans* OS217 | PA2070 (27/44) |
| XCC2396 | avirulence protein | - | avrXccA2 | | | XC_1716 | abs | abs | abs | abs | | |
| XCC2397 | peptidase | - | | | | XC_1715 | XCV2726 | XAC2532 | XOO3120 | abs | | |
| XCC2398 | xylosidase/arabinosidase | - | xsa | GH43 | | XC_1714 | XCV2728 | XAC2533 | XOO3121 | abs | | |
| XCC2399 | hypothetical protein | - | | | | XC_1713 | XCV2729 | XAC2534 | XOO3122 | abs | | |
| XCC2400 | TBDR | - | btuB | | | XC_1712 | XCV2730 | XAC2535 | XOO3123 | abs | CC1623, *Caulobacter crescentus* CB15 | PA2070 (27/43) |
| XCC2401 | hypothetical protein | - | | | | XC_1711 | XCV2732 | XAC2536 | XOO3124 | abs | | |
| XCC2402 | hypothetical protein | + | | | | XC_1710 | abs | XAC2538 D | abs | abs | | |
| XCC2403 | hypothetical protein | - | | | | XC_1709 | XCV2735 | XAC2539 | XOO3126 | abs | | |
| | Putative CUT locus (starch/maltodextrin?) | | | | | | | | | | | |
| XCC2464 | maltose transport gene repressor | + | | | | XC_1649 | XCV2796 | XAC2595 | abs | abs | CC2284 | |
| XCC2465 | cyclomaltodextrin glucanotransferase (CGTase) | - | | GH13 | | XC_1648 | XCV2797 | XAC2596 | abs | abs | CC2286 | |
| XCC2466 | transport protein | - | suc1 | | | XC_1647 | XCV2798 | XAC2597 | abs | abs | CC2283 | |
| XCC2467 | hypothetical protein | - | | | | XC_1646 | XCV2799 | XAC2598 | abs | abs | | |
| XCC2468 | alpha-glucosidase | + | algA | GH97 | | XC_1645 | XCV2800 | XAC2599 | abs | abs | | |
| XCC2469 | TBDR, MalA | + | btuB | | Maltose induced | XC_1644 | XCV2801 | XAC2600 | abs | abs | CC2287, *Caulobacter crescentus* CB15 | |
| XCC2470 | IS1479 transposase | - | | | | XC_1643 | abs | abs | abs | abs | | |
| XCC2471 | alpha-glucosidase | - | algA | GH13 | | XC_1642 | XCV2803 | XAC2602 | abs | abs | CC2285 | |
| XCC2472 | ISD1 transposase | + | | | | abs | abs | abs | abs | abs | | |
| XCC2473 | ISD1 transposase | + | | | | XC_1640 | abs | abs | abs | abs | | |
| XCC2474 | VirB4 protein | - | virB4 | | | XC_1639 | abs | XAC2614 | abs | abs | | |
| | | | | | | | | | | | | |
| XCC2494 | pre-pilin leader sequence | - | pilV | | | XC_1622 | XCV2820 | abs | XOO3201 | no XF0474 | | |
| XCC2495 | pre-pilin like leader sequence | - | fimT | | | XC_1621 | XCV2821 | abs | XOO3202 | no XF0473 | | |
| XCC2496 | hypothetical protein | - | | | | XC_1620 | XCV2822 | XAC2671 | XOO3203 | XF0472 | | |
| XCC2497 | Ps-TBDR/oar | - | oar | | | XC_1619 | XCV2823 | XAC2672 | XOO3204 | abs | PSHAb0340, *Pseudoalteromonas haloplanktis* TAC125 | |
| XCC2498 | hypothetical protein | - | | | | XC_1618 | XCV2824 | XAC2674 | XOO3205 | XF2666 | | |
| XCC2499 | short chain dehydrogenase | - | | | | XC_1617 | XCV2825 | XAC2675 | XOO3206 | abs | | |
| XCC2500 | hypothetical protein | - | | | | XC_1616 | XCV2826 | XAC2676 | XOO3207 | XF2669 | | |
| | | | | | | | | | | | | |
| XCC2569 | hypothetical protein | + | | | | XC_1549 | XCV2891 | XAC2739 | XOO3277 | abs | | |
| XCC2570 | deoxycytidine triphosphate deaminase | - | dcd | | | XC_1548 | XCV2892 | XAC2740 | XOO3278 | XF0762 | | |
| XCC2571 | hypothetical protein | - | | | | XC_1547 | XCV2893 | XAC2741 | XOO3279 | XF2301 | | |
| XCC2572 | TBDR | + | btuB | | | XC_1546 | XCV2894 | XAC2742 | abs | abs | Shewmr4_0124, *Shewanella* sp. MR-4 | PA2070 (27/42) |
| XCC2573 | Ps-TBDR/oar | + | oar | | | XC_1545 | XCV2896 | XAC2743 | XOO3320 | abs | Patl_1148, *Pseudoalteromonas atlantica* T6c | |
| XCC2574 | metallopeptidase | + | | | | XC_1544 | XCV2898 | XAC2745 | abs | XF0576 | | |
| XCC2575 | metallopeptidase | + | | | | XC_1543 | XCV2899 | XAC2746 | abs | abs | | |
| XCC2576 | metallopeptidase | + | | | | XC_1542 | XCV2900 | XAC2747 | XOO3281 | abs | | |
| XCC2577 | integral membrane protein | - | | | | XC_1541 | XCV2901 | XAC2748 | XOO3282 | XF0649 | | |
| XCC2578 | methylated-DNA-protein-cysteine S-methyltransferase related protein | - | | | | XC_1540 | XCV2902 | XAC2749 | XOO3283 | abs | | |
| XCC2579 | reductase | - | | | | XC_1539 | XCV2903 | XAC2750 | XOO3286-87 | abs | | |
| XCC2580 | D-amino acid dehydrogenase subunit | - | dadA | | | XC_1538 | XCV2904 | XAC2751 | XOO3288 | abs | | |
| XCC2581 | transport protein | - | yxaH | | | XC_1537 | XCV2905 | XAC2752 | XOO3289 | XF0651 | | |
| XCC2582 | peptidyl-prolyl cis-trans isomerase | - | slyD | | | XC_1536 | XCV2906 | XAC2754 | XOO3290 | XF0652 | | |
| XCC2583 | lipoprotein | + | | | | XC_1535 | XCV2907 | XAC2753 | XOO3291 | XF0653 | | |
| | | | | | | | | | | | | |
| XCC2655 | chloride channel | + | yadQ | | | XC_1462 | XCV2986 | XAC2825 | XOO1536 | abs | | |
| XCC2656 | hypothetical protein | - | | | | XC_1461 D | XCV2987 D | XAC2827 | XOO1534 | XF0382 | | |
| XCC2657 | hypothetical protein | - | | | | XC_1460 | XCV2988 | XAC2828 | XOO1533 | XF0383 | | |
| XCC2658 | TBDR | + | phuR | | | XC_1459 | XCV2989 | XAC2829 | XOO1531 | XF0384 | Mfla_0134, *Methylobacillus flagellatus* KT | PA0781 (36/52) |
| XCC2659 | transcriptional regulator | + | | | | XC_1457 | abs | abs | abs | abs | | |
| XCC2660 | transmembrane transport protein | + | | | | XC_1456 | abs | abs | abs | abs | | |
| XCC2661 | cytochrome D oxidase subunit B | - | qxtB | | | XC_1455 | abs | abs | abs | abs | | |
| XCC2662 | cytochrome D oxidase subunit A | - | qxtA | | | XC_1454 | abs | abs | abs | abs | | |
| XCC2663 | hypothetical protein | - | | | | XC_1453 | abs | abs | abs | abs | | |
| XCC2664 | formate dehydrogenase related protein | - | | | | XC_1452 | abs | abs | abs | abs | | |
| XCC2665 | TBDR | + | fhuA | | | XC_1451 | XCV2991 | XAC2830 | XOO1530 | abs | Sala_0305, *Sphingopyxis alaskensis* RB2256 | |
| XCC2666 | extracellular serine protease | + | | | | XC_1450 | XCV2993 | XAC2831 | abs | abs | | |
| XCC2667 | extracellular serine protease | + | | | | XC_1449 | XCV2993 D | XAC2831 | abs | abs | | |
| XCC2668 | hypothetical protein | + | | | | XC_1448 | XCV2994 | XAC2832 | abs | abs | | |
| XCC2669 | extracellular serine protease | + | | | | XC_1447 | XCV2993 D | XAC2831 | abs | abs | | |
| XCC2670 | oxidoreductase | - | mocA | | | XC_1446 | abs | abs | abs | abs | | |
| XCC2671 | oxidoreductase | - | mocA | | | XC_1445 | XCV2995 D | XAC2835 | abs | abs | | |
| XCC2672 | MFS transporter | - | | | | XC_1444 | XCV2996 | XAC2837 | abs | abs | | |
| XCC2673 | transcriptional regulator lysR family | + | | | | XC_1443 | XCV2997 | XAC2838 | abs | abs | | |
| | Fur regulated TBDR | | | | | | | | | | | |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| XCC2766 | ABC transporter permease | + | ynhE | | | XC_1347 | XCV3079 | XAC2935 | XOO1405 | XF1476 | | |
| XCC2767 | ABC transporter ATP-binding protein | + | ynhD | | | XC_1346 | XCV3080 | XAC2936 | XOO1404 | XF1475 | | |
| XCC2768 | ABC transporter permease | + | ynhC | | | XC_1345 | XCV3081 | XAC2937 | XOO1403 | XF1474 | | |
| XCC2769 | cysteine desulfurase | + | nifS | | | XC_1344 | XCV3082 | XAC2938 | XOO1402 | XF1473 | | |
| XCC2770 | acetyltransferase | + | | | | XC_1343 | XCV3083 | XAC2939 | XOO1401 | abs | | |
| XCC2771 | benzene 1,2-dioxygenase, ferredoxin protein | + | bedB | | | XC_1342 | XCV3084 | XAC2940 | XOO1400 | XF1472 | | |
| XCC2772 | TBDR | + | fhuA | | Fur-regulated | XC_1341 | XCV3085 | XAC2941 | abs | XF0599 | PA1322, *Pseudomonas aeruginosa* PAO1 | PA4514; PiuA (35/50) |
| XCC2773 | hypothetical protein | + | | | | XC_1340 | XCV3086 | XAC2942 | abs | abs | | |
| XCC2774 | hypothetical protein | + | | | | XC_1339 | XCV3087 | XAC2943 | abs | abs | | |
| XCC2775 | hypothetical protein | + | | | | XC_1338 | XCV3088 | XAC2944 | abs | XF0597 | | |
| | Putative partial CUT locus, conserved locus | | | | | | | | | | | |
| XCC2824 | hypothetical protein | + | | | | XC_1288 | XCV3142 | XAC2993 | XOO1265 | abs | | |
| XCC2825 | tryptophan halogenase | - | prnA | | | XC_1287 | XCV3144 | XAC2995 | XOO1263 | abs | Patl_3277 | |
| XCC2826 | hypothetical protein | - | | | | XC_1286 | XCV3145 | XAC2996 | XOO1262 | abs | Patl_4288 | |
| XCC2827 | hypothetical protein | - | | | | XC_1285 | XCV3146 | XAC2997 | XOO1261 | abs | Patl_4287 | |
| XCC2828 | TBDR | - | fecA | | Arabinose/xylan/xylose induced | XC_1284 | XCV3147 | XAC2998 | XOO1260 | abs | Patl_3278 / Patl_4286, *Pseudoalteromonas atlantica* T6c | |
| XCC2829 | peptidase | - | | | | XC_1282 | XCV3148 | XAC2999 | XOO1259-8 | abs | | |
| XCC2830 | hypothetical protein | - | | | | XC_1281 | XCV3148 D | XAC2999 | XOO1258 | abs | Patl_4270 | |
| XCC2831 | transcriptional regulator soxR family | - | soxR | | | XC_1280 | XCV3149 | XAC3000 | XOO1257 | abs | | |
| XCC2832 | MFS transporter | + | | | | XC_1279 | XCV3150 | XAC3001 | XOO1255-4-3 | abs | | |
| | CAZy associated TBDR | | | | | | | | | | | |
| XCC2863 | glucosyl transferase | - | gtrB | GT2 | | XC_1245 | XCV3183 | XAC3046 | abs | XF0176 | | |
| XCC2864 | monofunctional biosynthetic peptidoglycan transglycosylase | - | mtgA | GT51 | | XC_1244 | XCV3184 | XAC3047 | XOO1808 | XF1715 | | |
| XCC2865 | heat shock protein | + | | | | XC_1243 | XCV3185 | XAC3048 | XOO1807 | XF1714-13 | | |
| XCC2866 | hypothetical protein | + | | | | XC_1242 | XCV3186 | XAC3049 | XOO1806 | XF1712 | | |
| XCC2867 | TBDR | + | btuB | | | XC_1241 | XCV3187 | XAC3050 | XOO1805 | abs | SO1822, *Shewanella oneidensis* MR-1 | PA2070 (29/45) |
| XCC2868 | transcriptional regulator | - | | | | XC_1240 | XCV3188 | XAC3052 | XOO1804 | abs | | |
| XCC2869 | hypothetical protein | + | | | | XC_1239 | XCV3189 | XAC3053 | XOO1803 | abs | | |
| XCC2870 | acyl-CoA dehydrogenase | + | | | | XC_1238 | XCV3190 | XAC3054 | XOO1802 | abs | | |
| | Putative partial CUT locus, CAZy associated TBDR, conserved locus | | | | | | | | | | | |
| XCC2883 | ADP compounds hydrolase | - | nudE | | | XC_1226 | XCV3201 | XAC3067 | XOO1789 | XF0188 | | |
| XCC2884 | adenosylmethionine-8-amino-7-oxononanoate aminotransferase | + | bioA | | | XC_1225 | XCV3202 | XAC3068 | XOO1787 | XF0189 | | |
| XCC2885 | hypothetical protein | + | | | | XC_1224 | XCV3203 | XAC3069 | XOO1786 | XF0190 | | |
| XCC2886 | glucose kinase | - | glk | | | XC_1223 | XCV3204 | XAC3070 | XOO1785 | abs | | |
| XCC2887 | TBDR | + | iroN | | | XC_1222 | XCV3206 | XAC3071 | XOO1784 | XF2713 | Saro_2410, *Novosphingobium aromaticivorans* DSM 12444 | |
| XCC2888 | alpha-L-fucosidase | + | fucA1 | GH29 | | XC_1221 | XCV3207 | XAC3072 | XOO1783 | XF2714 | Saro_2423 | |
| XCC2889 | hypothetical protein | + | | | | XC_1220 | XCV3208 | XAC3073 | XOO1782 | XF0848 | | |
| XCC2890 | beta-hexosaminidase | + | nahA | GH20 | | XC_1219 | XCV3209 | XAC3074 | XOO1781 | XF0847 | Saro_2417 | |
| XCC2891 | beta-hexosaminidase | + | | GH2 | | XC_1218 | XCV3210 | XAC3075 | XOO1780 | XF0846 | Saro_2418 | |
| XCC2892 | glucan 1,4-beta-glucosidase | + | | GH3 | | XC_1217 | XCV3211 | XAC3076 | XOO1779 | XF0845 | Saro_2419 | |
| XCC2893 | hypothetical protein | + | | | | XC_1216 | XCV3212 | XAC3082 | XOO1771 | XF0843 | Saro_2420 | |
| XCC2894 | hypothetical protein | + | | GH92 | | XC_1215 | XCV3213 | XAC3083 | XOO1770 | XF0842 | Saro_2421 | |
| XCC2895 | beta-galactosidase | + | bga | GH35 | | XC_1214 | XCV3214 | XAC3084 | XOO1769 | XF0840 | | |
| XCC2896 | virulence protein | - | psvA | | | XC_1213 | XCV0437 | abs | abs | abs | | |
| XCC2897 | ISxac3 transposase | - | | | | XC_1212 | XCV0024 D | abs | XOO2820 | abs | | |
| | | | | | | | | | | | | |
| XCC2941 | hypothetical protein | + | | | | XC_1168 | XCV3249 | XAC3118 | XOO1732 | abs | | |
| XCC2942 | hypothetical protein | + | | | | XC_1167 | XCV3250 | XAC3119 | XOO1731 | XF1384 | | |
| XCC2943 | glucose kinase | + | glk | | | XC_1166 | XCV3251 | XAC3120 | XOO1785 | abs | | |
| XCC2944 | TBDR | + | fepA | | | XC_1165 | XCV3252 | XAC3121 | XOO1727 | abs | CC0446, *Caulobacter crescentus* CB15 | |
| XCC2945 | ATP dependent RNA helicase | + | hrpA | | | XC_1164 | XCV3253 | XAC3122 | XOO1725 | XF1383 | | |
| XCC2946 | DNA-binding related protein | + | | | | XC_1163 | XCV3254 | XAC3123 | XOO1724 | XF1382 | | |
| XCC2947 | DNA helicase | + | recQ | | | XC_1162 | XCV3255 | XAC3124 | XOO1723 | XF1381 | | |
| | Putative CUT locus (unknown substrate) | | | | | | | | | | | |
| XCC3033 | hypothetical protein | - | | | | XC_1125 | XCV3288 | XAC3156 | XOO1654 | abs | | |
| XCC3034 | transmembrane transport protein | + | | | | XC_1124 | XCV3289 | XAC3157 | XOO1653 | abs | | |
| XCC3035 | alpha,alpha-trehalose-phosphate synthase | + | | GT20 | | XC_1123 | abs | abs | abs | abs | | |
| XCC3036 | Ps-TBDR | + | fhuA | | | XC_1122 | XCV3290 | XAC3158 | abs | abs | IL2594, *Idiomarina loihiensis* L2TR | |
| XCC3037 | phospholipase C | + | plcN | | | XC_1121 | XCV3291 | XAC3160 | XOO1651 | abs | | |
| XCC3038 | xylanase | - | xynB | CE10 | | XC_1120 | XCV3292 | abs | XOO1371 | abs | | |
| XCC3039 | beta lactamase | - | bla | | | XC_1119 | XCV3293 | XAC3162 | XOO1370 | abs | | |
| XCC3040 | transcriptional activator ampR family | + | ampR | | | XC_1118 | XCV3294 | XAC3163 | XOO1369 | abs | | |
| | | | | | | | | | | | | |
| XCC3040 | transcriptional activator ampR family | + | ampR | | | XC_1118 | XCV3294 | XAC3163 | XOO1369 | abs | | |
| XCC3041 | hypothetical protein | - | | | | XC_1117 | XCV3295 | XAC3164 | XOO1368 | abs | | |
| XCC3042 | ABC transporter ATP-binding protein | - | yheS | | | XC_1116 | XCV3296 | XAC3165 | XOO1367 | XF2133 | | |
| XCC3043 | TBDR | + | bfeA | | | XC_1115 | XCV3297 | XAC3166 | XOO1366 | XF2134 | Psyr_2290, *Pseudomonas syringae pv. syringae* B728a | PA2590 (39/54); PA2089 (38/54) |
| XCC3044 | hypothetical protein | + | | | | XC_1114 | XCV3298 | XAC3167 | XOO1365 | abs | | |
| XCC3045 | TBDR | + | bfeA | | | XC_1113 | XCV3299 | XAC3168 | XOO1364 | XF2137 | Psyr_2290, *Pseudomonas syringae pv. syringae* B728a | PA2590 (35/51); PA2089 (35/50) |
| XCC3046 | TBDR | + | bfeA | | | XC_1112 | XCV3301 | XAC3169 | XOO1363 | abs | Shewmr7_0415, *Shewanella sp. MR-7* | PA2590 (35/52); PA2089 (35/50) |
| XCC3047 | cytochrome P450 hydroxylase | - | biol | | | XC_1111 | XCV3302 | XAC3170 | abs | abs | | |
| XCC3048 | cation:proton antiporter | + | ybaL | | | XC_1110 | XCV3304 | XAC3171 | XOO1362 | XF2140 | | |
| XCC3049 | 4-hydroxy-2-oxovalerate aldolase | + | mphE | | | XC_1109 | XCV3305 | XAC3175 | XOO1360 | abs | | |
| | Fur regulated TBDR, conserved locus | | | | | | | | | | | |
| XCC3047 | cytochrome P450 hydroxylase | - | biol | | | XC_1111 | XCV3302 | XAC3170 | abs | abs | | |
| XCC3048 | cation:proton antiporter | + | ybaL | | | XC_1110 | XCV3304 | XAC3171 | XOO1362 | XF2140 | | |
| XCC3049 | 4-hydroxy-2-oxovalerate aldolase | + | mphE | | | XC_1109 | XCV3305 | XAC3175 | XOO1360 | abs | | |
| XCC3050 | TBDR | + | fecA | | Fur-regulated | XC_1108 | XCV3306 | XAC3176 | XOO1359 | abs | VPA1656 (PvuA), *Vibrio parahaemolyticus* RIMD 2210633 | PA3901 (31/48) |
| XCC3051 | hypothetical protein | + | | | | XC_1107 | XCV3307 | XAC3177 | XOO1358 | abs | VPA1658 (PvsA) | |
| XCC3052 | hypothetical protein | + | | | | XC_1106 | XCV3308 | XAC3178 | XOO1357 | abs | VPA1659 (PvsB) | |
| XCC3053 | transport protein | + | yceE | | | XC_1105 | XCV3309 | XAC3179 | XOO1356 | abs | VPA1660 (PvsC) | |
| XCC3054 | iron transporter | + | iucA | | | XC_1104 | XCV3310 | XAC3180 | XOO1355 | abs | VPA1661 (PvsD) | |
| XCC3055 | diaminopimelate decarboxylase | + | lysA | | | XC_1103 | XCV3311 | XAC3181 | XOO1354 | abs | VPA1662 (PvsE) | |
| XCC3056 | transcriptional regulator araC family | - | | | | XC_1102 | XCV3312 | abs | abs | abs | | |
| | Putative Cobalamin locus | | | | | | | | | | | |
| XCC3057 | cobalamin synthase | - | cobS | | | XC_1101 | XCV3313 | XAC3184 | XOO1353 | abs | PaerPA_01001759 / PaerP_01003967 | |
| XCC3058 | conserved hypothetical protein | - | | | | XC_1100 | XCV3314 | XAC3185 | XOO1352 | abs | PaerPA_01001758 / PaerP_01003966 | |
| XCC3059 | nicotinate-nucleotide-dimethylbenzimidazole phosphoribosyltransferase | - | cobT | | | XC_1099 | XCV3315 | XAC3186 | XOO1351 | abs | PaerPA_01001757 / PaerP_01003965 | |
| XCC3060 | adenosyl cobinamide kinase/adenosyl cobinamide phosphate guanylyltransferase | - | cobU | | | XC_1098 | XCV3316 | XAC3187 | XOO1350 | abs | PaerPA_01001756 / PaerP_01003964 | |
| XCC3061 | cobyric acid synthase | - | | | | XC_1097 | XCV3317 | XAC3188 | XOO1350 D | abs | PaerPA_01001755 / PaerP_01003963 | |
| XCC3062 | cobalamin biosynthesis protein | - | cobD | | | XC_1096 | XCV3319 | XAC3190 | XOO1350 D | abs | PaerPA_01001753 / PaerP_01003961 | |
| XCC3063 | cobyrinic acid a,c-diamide synthase | - | cobB | | | XC_1095 | abs | abs | abs | abs | PaerPA_01001751 / PaerP_01003959 | |
| XCC3064 | cob(I)alamin adenolsyltransferase | - | btuR | | | XC_1094 | XCV3320 | XAC3191 | XOO1349 | abs | - / PaerP_01003958 | |
| XCC3065 | conserved hypothetical protein | - | | | | XC_1093 | XCV3321 | XAC3192 | XOO1348 | abs | | |
| XCC3066 | hypothetical protein | - | | | | XC_1092 | XCV3322 | XAC3193 | XOO1347 | abs | | |
| XCC3067 | Ps-TBDR | - | btuB | | | XC_1091 | XCV3323 | XAC3194 | XOO1345 | abs | PaerPA_01001749, strain PACS2 / PaerP_01003957, strain PA7 | PA1271 (51/65) |
| XCC3068 | homocysteine synthase PA5025 | - | metB | | | XC_1090 | abs | abs | abs | abs | | |
| XCC3069 | hypothetical protein | - | | | | XC_1089 | abs | abs | XOO1338 | abs | | |
| XCC3070 | ATP-dependent Clp protease subunit | - | clpB | | | XC_1088 | XCV3324 | XAC3195 | XOO1337 | XF0381 | | |
| XCC3071 | ABC transporter ATP-binding subunit | - | | | | XC_1087 | XCV3325 D | XAC3196 | abs | abs | | |
| XCC3072 | hypothetical protein | + | | | | XC_1086 | XCV3326 | XAC3202 | XOO1336 | abs | | |
| XCC3073 | glutathione transferase | + | | | | XC_1085 | XCV3327 | XAC3203 | XOO1335 D | abs | | |
| XCC3074 | hypothetical protein | - | | | | XC_1084 | XCV3328 | XAC3204 | abs | abs | | |
| | CAZy associated TBDR | | | | | | | | | | | |
| XCC3076 | hypothetical protein | - | | | | XC_1082 | XCV3330 | XAC3206 | XOO1607 | abs | | |
| XCC3077 | hypothetical protein | - | | | | XC_1081 | XCV3331 | XAC3208 | abs | abs | | |
| XCC3078 | hypothetical protein | - | | | | XC_1080 | XCV3332 | abs | XOO1605 | abs | Pfl_2344 | |
| XCC3079 | TBDR | + | bfeA | | | XC_1079 | XCV3333 | XAC3207 | XOO1604 | abs | Pfl_2342, *Pseudomonas fluorescens* PfO-1 | PA2590 (35/48); PA2089 (35/47) |
| XCC3080 | trehalose-6-phosphate phosphatase | + | ostB | | | XC_1078 | XCV3334 | XAC3209 | XOO1603 | abs | | |
| XCC3081 | hypothetical protein | + | | GH15 | | XC_1077 | XCV3335 | XAC3210 | XOO1602 | abs | | |
| XCC3082 | trehalose-6-phosphate synthase | + | ostA | GT20 | | XC_1076 | XCV3336 | XAC3211 | XOO1601 | abs | | |
| XCC3083 | glucose dehydrogenase | + | | | | XC_1075 | XCV3337 | XAC3212 | abs | abs | | |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|
| XCC3084 | chemotaxis protein | + | mcp1 | | | XC_1074 | XCV3338 | XAC3213 | abs | abs | | |
| | Putative partial CUT locus, CAZy associated TBDR | | | | | | | | | | | |
| XCC3157 | aminopeptidase | + | | | | XC_1008 | XCV3425 | XAC3309 | abs | abs | | |
| XCC3158 | aminopeptidase | + | | | | XC_1007 | XCV3425 D | XAC3309 | abs | abs | | |
| XCC3159 | transcriptional regulator lacI family | + | salR | | | XC_1006 | XCV3427 | XAC3310 | abs | abs | | |
| XCC3160 | 1,4-beta-cellobiosidase | - | | GH6 | | XC_1005 | abs | abs | XOO4035 | XF1267 | | |
| XCC3161 | TBDR | - | iroN | | | XC_1004 | XCV3428 | XAC3311 | abs | abs | Sde_4006, *Saccharophagus degradans* 2-40 | |
| XCC3162 | glycosyl hydrolase | - | | GH2 | | XC_1003 | XCV3430 | XAC3312 | abs | abs | | |
| XCC3163 | alpha-glucosidase | + | susB | GH97 | | XC_1002 | XCV3431 | XAC3313 | abs | abs | | |
| XCC3164 | carboxylesterase | - | | | | XC_1001 | XCV3433 | XAC3315 | XOO3386 | abs | | |
| XCC3171 | ATP sulfurylase/adenylylsulfate kinase | - | nodQ | | | XC_0994 | XCV3445 | XAC3328 | XOO3396 | XF1501 | | |
| XCC3172 | ATP sulfurylase small subunit | - | cysD | | | XC_0993 | XCV3446 | XAC3329 | XOO3397 | XF1500 | | |
| XCC3173 | NADPH-sulfite reductase flavoprotein subunit | + | cysJ | | | XC_0992 | XCV3447 | XAC3330 | XOO3398 | XF1499 | | |
| XCC3174 | NADPH-sulfite reductase iron-sulfur protein | + | cysI | | | XC_0991 | XCV3448 | XAC3331 | XOO3400 | XF1498 | | |
| XCC3175 | 3'-phosphoadenosine 5'-phosphosulfate reductase | + | cysH | | | XC_0990 | XCV3449 | XAC3332 | XOO3401 | XF1497 | | |
| XCC3176 | hypothetical protein | - | | | | XC_0989 | XCV3450 | XAC3333 D | XOO3402 D | abs | | |
| XCC3177 | TBDR | - | fecA | | | XC_0988 | XCV3451 | XAC3334 | XOO3403 | XF1496 | PP_3340, *Pseudomonas putida* KT2440 | |
| XCC3178 | sensor histidine kinase | + | | | | XC_0987 | XCV3453 | XAC3335 | XOO3405 | abs | | |
| XCC3179 | hypothetical protein | - | | | | XC_0985 | XCV3456 | XAC3338 | XOO3406 | abs | | |
| XCC3180 | transcriptional regulator lysR family | - | cysB | | | XC_0984 | XCV3457 | XAC3339 | XOO3407 | XF0833 | | |
| XCC3181 | siroheme synthase | + | cysG | | | XC_0983 | XCV3458 | XAC3340 | XOO3408 | XF0832 | | |
| XCC3182 | cysteine synthase | + | cysK | | | XC_0982 | XCV3459 | XAC3341 | XOO3409 | XF0831 | | |
| XCC3205 | TonB-like protein | - | | | | XC_0915 | XCV3479 D | XAC3362 | XOO1191 | abs | | |
| XCC3206 | transcriptional regulator blaI family | - | blaI | | | XC_0916 | XCV3481 | XAC3363 | XOO1190 | abs | | |
| XCC3207 | hypothetical protein | + | | | | XC_0917 | XCV3482 | XAC3364 | XOO1182 | abs | | |
| XCC3208 | hypothetical protein | + | | | | XC_0918 | XCV3483 | XAC3365 | XOO1181 | abs | | |
| XCC3209 | TBDR | + | cirA | | | XC_0919 | XCV3485 | XAC3366 | XOO1180 | abs | CC0563, *Caulobacter crescentus* CB15 | |
| XCC3210 | hypothetical protein | + | | | | XC_0920 | XCV3486 | XAC3367 | XOO1179 | abs | | |
| XCC3211 | hypothetical protein | + | | | | XC_0921 | XCV3487 | XAC3368 | XOO1178 | abs | | |
| XCC3212 | reductase | - | | | | XC_0922 | abs | abs | abs | abs | | |
| | Fur regulated TBDRs | | | | | | | | | | | |
| XCC3211 | hypothetical protein | + | | | | XC_0921 | XCV3487 | XAC3368 | XOO1178 | abs | | |
| XCC3212 | reductase | - | | | | XC_0922 | abs | abs | abs | abs | | |
| XCC3213 | transcriptional regulator | + | | | | XC_0923 | XCV3880 | abs | abs | abs | | |
| XCC3214 | IS1478 transposase | - | | | | abs | XCV2716 | XAC2423 | XOO1863 | abs | | |
| XCC3215 | Ps-TBDR | - | fhuE | | Fur-regulated | XC_0924 | XCV3489 | XAC3370 | abs | abs | Csal_3182, *Chromohalobacter salexigens* DSM 3043 | PA2398; FpvA (43/65) |
| XCC3216 | Ps-TBDR | - | | | Fur-regulated | XC_0925 | XCV3489 | XAC3370 | abs | abs | STM1204, Salmonella typhimurium LT2 | PA2398; FpvA (43/65) |
| XCC3217 | IS1404 transposase | + | | | | XC_0926 | abs | abs | abs | abs | | |
| XCC3218 | IS1404 transposase | + | | | | XC_0927 | XCV0022 D | XAC3936 | abs | abs | | |
| XCC3219 | proline imino-peptidase | + | | | | XC_0928 | abs | XAC3371 | abs | abs | | |
| XCC3220 | transketolase 1 | - | tktA | | | XC_0929 | XCV3490 | XAC3372 | XOO1176 | XF1936 | | |
| XCC3267 | conserved hypothetical protein | + | | | | XC_0897 | XCV3530 | XAC3413 | XOO1125 | XF1494 | | |
| XCC3268 | rubredoxin | - | rubA | | | XC_0896 | XCV3531 | XAC3414 | XOO1124 | XF0379 | | |
| XCC3269 | thiamin-phosphate pyrophosphorylase | + | thiE | | | XC_0895 | XCV3532 | XAC3415 | XOO1123 | XF0378 | | |
| XCC3270 | Ps-TBDR/oar | - | | | | XC_0894 | XCV3534 | XAC3418 | XOO1233 | abs | PatI_1148, *Pseudoalteromonas atlantica* T6c | |
| XCC3271 | | - | | | | XC_0893 | XCV3534 | XAC3418 | XOO1233 | abs | PatI_1148, *Pseudoalteromonas atlantica* T6c | |
| XCC3272 | glutamate-1-semialdehyde 2,1-aminomutase | + | hemL | | | XC_0892 | XCV3535 | XAC3420 | XOO1232 | XF2302 | | |
| XCC3273 | transcriptional regulator | + | acoK | | | XC_0891 | XCV3536 | XAC3421 | XOO1230 | abs | | |
| XCC3274 | electron transfer protein azurin I | - | az1 | | | XC_0890 | XCV3537 | XAC3422 | XOO1229 | XF0557 | | |
| XCC3276 | TdcF protein | - | tdcF | | | XC_0888 | XCV3539 | XAC3424 | XOO1226 | abs | | |
| XCC3277 | cytochrome C6 | - | | | | XC_0887 | XCV3540 | XAC3425 | XOO1225 | abs | | |
| XCC3278 | flavin monoamine oxidase-related protein | - | | | | XC_0886 | XCV3541 | XAC3426 | XOO1223 | abs | | |
| XCC3279 | Ps-TBDR | - | fhuA | | | XC_0885 | XCV3542 | XAC3427 | XOO1222-1 | abs | CC3436, *Caulobacter crescentus* CB15 | |
| XCC3280 | hypothetical protein | + | | | | XC_0884 | XCV3543 | XAC3428 | XOO1220 | abs | | |
| XCC3281 | hypothetical protein | + | | | | XC_0883 | XCV3543 | XAC3428 | XOO1220 | abs | | |
| XCC3282 | acetylornithine aminotransferase | - | argD | | | XC_0882 | XCV3544 | XAC3429 | XOO1219 | XF1427 | | |
| XCC3313 | hypothetical protein | - | | | | XC_0852 | XCV3569 | XAC3441 | XOO0953 | abs | | |
| XCC3314 | inorganic pyrophosphatase | + | ppa | | | XC_0851 | XCV3570 | XAC3442 | XOO0952 | XF2171 | | |
| XCC3315 | response regulator | + | | | | XC_0850 | XCV3571 | XAC3443 | XOO0951 | abs | | |
| XCC3316 | TBDR | - | btuB | | | XC_0849 | XCV3572 | XAC3444 | XOO0950 | abs | SO1822, *Shewanella oneidensis* MR-1 | PA2070 (27/43) |
| XCC3317 | transcriptional regulator | - | | | | XC_0848 | XCV3573 | XAC3445 | XOO0949 | abs | | |
| XCC3318 | hypothetical protein | - | | | | XC_0847 | XCV3574 | XAC3446 | XOO0948 | abs | | |
| XCC3319 | thiamine biosynthesis protein | - | thiC | | | XC_0846 | XCV3575 | XAC3447 | XOO0947 | XF1888 | | |
| | Sucrose utilization locus (sux locus) | | | | | | | | | | | |
| XCC3356 | transcriptional regulator, SuxR | + | cebR | | Sucrose induced | XC_0808 | XCV3615 | XAC3487 | XOO1101 | abs | CC1137 | |
| XCC3357 | sugar transporter, SuxC | - | suc1 | | Sucrose induced | XC_0807 | XCV3616 | XAC3488 | XOO1100 | abs | | |
| XCC3358 | TBDR, SuxA | + | fyuA | | Sucrose induced | XC_0806 | XCV3617 | XAC3489 | XOO1099 | abs | CC1136, *Caulobacter crescentus* CB15 | |
| XCC3359 | amylosucrase or alpha amylase, SuxB | + | | GH13 | Sucrose induced | XC_0805 | XCV3618 | XAC3490 | XOO1098 | abs | CC1135 | |
| | CAZy associated TBDR | | | | | | | | | | | |
| XCC3402 | high-affinity choline transport | + | betT | | | XC_0762 | XCV0776 | XAC0720 | XOO3886 D | abs | | |
| XCC3403 | betaine aldehyde dehydrogenase | + | betB | | | XC_0761 | XCV0775 | XAC0719 | abs | abs | | |
| XCC3404 | choline dehydrogenase | + | betA | | | XC_0760 | XCV0774 | XAC0718 | abs | abs | | |
| XCC3405 | TBDR | - | btuB | | | XC_0759 | XCV3685 | XAC3560 | abs | abs | SO1822, *Shewanella oneidensis* MR-1 | PA2070 (27/42) |
| XCC3406 | soluble lytic murein transglycosylase | + | slt | GH23 | | XC_0758 | XCV3686 | XAC3561 | XOO0820 | XF1363 | | |
| XCC3407 | tRNA nucleotidyltransferase | + | cca | | | XC_0757 | XCV0773 | XAC0717 | XOO3900 | XF1362 | | |
| | Putative CUT locus (unknown substrate) | | | | | | | | | | | |
| XCC3407 | tRNA nucleotidyltransferase | + | cca | | | XC_0757 | XCV0773 | XAC0717 | XOO3900 | XF1362 | | |
| XCC3408 | Ps-TBDR | - | fyuA | | | XC_0756 | XCV0772 | XAC0716 | XOO1784 | abs | CC0446, *Caulobacter crescentus* CB15 | |
| XCC3409 | nisin-resistance protein | - | | | | XC_0755 | abs | abs | abs | abs | | |
| XCC3410 | N-acetylglucosamine-6-phosphate deacetylase | - | nagA | CE9 | | XC_0754 | XCV0771 | XAC0715 | XOO3915 | XF1465 | CC0443 | |
| XCC3411 | glucosamine-fructose-6-phosphate aminotransferase | - | glmS | | | XC_0753 | XCV0770 | XAC0714 | XOO3917 | XF1464 | CC0444 | |
| XCC3412 | transcriptional regulator lacI family | - | | | | XC_0752 | XCV0769 | XAC0713 | XOO3918 | XF1463 | | |
| XCC3413 | glucose/galactose transporter | - | gluP | | | XC_0751 | XCV0768 | XAC0712 | XOO3919 | XF1462 | | |
| XCC3414 | transcriptional regulator gntR family | - | | | | XC_0750 | XCV0767 | XAC0711 | XOO3920 | XF1461 D | CC0445 | |
| XCC3415 | type II secretion system protein N | - | xcsN | | | XC_0749 | XCV0766 | XAC0705 | abs | abs | | |
| | Conserved locus | | | | | | | | | | | |
| XCC3415 | type II secretion system protein N | - | xcsN | | | XC_0749 | XCV0766 | XAC0705 | abs | abs | Sala_0325 | |
| XCC3416 | type II secretion system protein M | - | xcsM | | | XC_0748 | XCV0765 | XAC0704 | abs | abs | | |
| XCC3417 | type II secretion system protein L | - | xcsL | | | XC_0747 | XCV0764 | XAC0703 | abs | abs | Sala_0323 | |
| XCC3418 | type II secretion system protein K | - | xcsK | | | XC_0746 | XCV0763 | XAC0702 | abs | abs | Sala_0322 | |
| XCC3419 | type II secretion system protein J | - | xcsJ | | | XC_0745 | XCV0762 | XAC0701 | abs | abs | Sala_0321 | |
| XCC3420 | type II secretion system protein I | - | xcsI | | | XC_0744 | XCV0761 | XAC0700 | abs | abs | Sala_0320 | |
| XCC3421 | type II secretion system protein H | - | xcsH | | | XC_0743 | XCV0760 | XAC0699 | abs | abs | Sala_0319 | |
| XCC3422 | type II secretion system protein G | - | xcsG | | | XC_0742 | XCV0759 | XAC0698 | XOO0849 | XF1519 | Sala_0318 | |
| XCC3423 | type II secretion system protein F | - | xcsF | | | XC_0741 | XCV0758 | XAC0697 | XOO0848 | XF1518 | Sala_0317 | |
| XCC3424 | type II secretion system protein E | - | xcsE | | | XC_0740 | XCV0757 | XAC0696 | XOO0847 | XF1517 | Sala_0316 | |
| XCC3425 | type II secretion system protein D | - | xcsD | | | XC_0739 | XCV0756 | XAC0695 | abs | abs | | |
| XCC3426 | type II secretion system protein C | - | xcsC | | | XC_0738 | XCV0755 | XAC0694 | abs | abs | Sala_0314 | |
| XCC3427 | TBDR | - | fecA | | | XC_0737 | XCV0754 | XAC0693 | abs | abs | Sala_0313, *Sphingopyxis alaskensis* RB2256 | |
| XCC3428 | hypothetical protein | - | | | | XC_0736 | XCV0753 | XAC0692 | abs | abs | Sala_0312 | |
| XCC3429 | hypothetical protein | + | | | | XC_0735 | XCV0752 | XAC0691 | abs | abs | | |
| XCC3430 | hypothetical protein | - | | | | XC_0734 | XCV0750 | XOO0689 | abs | XF1459 | | |
| | Putative partial CUT locus | | | | | | | | | | | |
| XCC3471 | sugar kinase | + | | | | XC_0690 | XCV0716 | XAC0655 | XOO3971 | abs | | |
| XCC3472 | transcriptional regulator | + | acoR | | | XC_0689 | XCV0715 | XAC0654 | abs | abs | | |
| XCC3473 | IS1480 transposase | + | | | | XC_0688 | abs | abs | XOO3975 | abs | | |
| XCC3474 | Ps-TBDR | - | fepA | | | XC_0687 | XCV0714 | XAC0653 | abs | abs | H16_B1039, *Ralstonia eutropha* H16 | PA2289 (22/39) |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| XCC3475 | alcohol dehydrogenase class III | - | adhC | | | XC_0686 | XCV0713 | XAC0652 | XOO3867 | abs | | |
| XCC3476 | surface antigen gene | - | | | | XC_0685 | XCV0712 | XAC0651 | abs | abs | | |
| XCC3477 | hypothetical protein | - | | | | XC_0684 | XCV0711 | XAC0650 | abs | abs | | |
| | Fur regulated TBDR | | | | | | | | | | | |
| XCC3515 | periplasmic glucan biosynthesis protein | - | hrpM | GT2 | | XC_0645 | XCV0675 | XAC0618 | XOO4011 | XF1623 | | |
| XCC3516 | sulfur deprivation response regulator | - | sac1 | | | XC_0644 | abs | abs | abs | abs | | |
| XCC3517 | aminopeptidase | - | | | | XC_0643 | XCV0673 | XAC0615 | XOO4015 | XF0820 | | |
| XCC3518 | TBDR | + | fpvA | | Fur-regulated | XC_0642 | abs | abs | abs | abs | Pfl 2583, *Pseudomonas fluorescens* PfO-1 | PA2398; FpvA (38/55) |
| XCC3519 | GGDEF family protein | - | | | | XC_0641 | XCV0672 | XAC0614 | XOO4016-7 | abs | | |
| XCC3520 | sulfate permease | - | ybaR | | | XC_0640 | XCV0671 | XAC0613 | XOO4018 | abs | | |
| XCC3521 | cellulase | + | engXCA | GH5; CBM2 | | XC_0639 | XCV0670 | XAC0612 | XOO4019 | XF0818 | | |
| | Fur regulated TBDR | | | | | | | | | | | |
| XCC3592 | hypothetical protein | - | | | | XC_0555 | XCV0578 | XAC0549 | XOO4275 | abs | | |
| XCC3593 | RNA polymerase sigma factor | + | fecI | | | XC_0556 | abs | abs | abs | abs | PFL_2291 | |
| XCC3594 | transmembrane sensor | + | fecR | | | XC_0557 | abs | abs | abs | abs | | |
| XCC3595 | Ps-TBDR/transducer | + | pbuA | | Fur-regulated | XC_0558 | abs | abs | abs | abs | PFL_2293, *Pseudomonas fluorescens* Pf-5 | PA4168; FpvB (35/51) |
| XCC3596 | hypothetical protein | + | | | | XC_0559 | abs | abs | abs | abs | | |
| XCC3597 | hypothetical protein | + | | | | XC_0560 | abs | abs | abs | abs | | |
| XCC3598 | hypothetical protein | + | | | | XC_0561 | abs | abs | abs | abs | | |
| | | | | | | | | | | | | |
| XCC3632 | hypothetical protein | + | | | | XC_3703 | XCV3791 | XAC3671 | XOO0711 | abs | | |
| XCC3633 | hypothetical protein | + | | | | XC_3704 | XCV3795 | XAC3675 | XOO0707 | XF1204 | | |
| XCC3634 | hypothetical protein | - | | | | XC_3705 | abs | abs | abs | abs | | |
| XCC3635 | TBDR | - | | | | XC_3706 | XCV4224 | XAC4131 | abs | abs | CC1131, *Caulobacter crescentus* CB15 | |
| XCC3636 | oxidoreductase | + | | | | XC_3707 | XCV3797 | XAC3676 | XOO0705 | abs | | |
| XCC3637 | hydrolase | - | | | | XC_3708 | XCV3798 | XAC3677 | XOO0704 | XF1201 | | |
| XCC3638 | ribosomal small subunit pseudouridylate synthase | - | | | | XC_3709 | XCV3799 | XAC3678 | XOO0703 | XF1200 | | |
| | Conserved locus | | | | | | | | | | | |
| XCC3711 | hypothetical protein | + | | | | XC_3782 | XCV3872 | XAC3753 | XOO0629 | abs | | |
| XCC3712 | chemotaxis protein | + | | | | XC_3783 | XCV3873 | abs | XOO0628 | abs | | |
| XCC3713 | hypothetical protein | + | | | | XC_3784 | XCV3874 | XAC3755 | XOO0627 | abs | | |
| XCC3714 | TBDR | - | | | | XC_3785 | XCV3875 | XAC3756 | XOO0626 | abs | CC1517, *Caulobacter crescentus* CB15 | PA4837 (36/53) |
| XCC3715 | hypothetical protein | - | | | | XC_3786 | XCV3876 | XAC3757 | XOO0625 | abs | CC1520 | |
| XCC3716 | hypothetical protein | - | | | | XC_3787 | XCV3877 | XAC3758 | XOO0624 | abs | CC1519 | |
| XCC3717 | ABC transporter ATP-binding protein | - | drrA | | | XC_3788 | XCV3878 | XAC3759 | XOO0623 | abs | CC1518 | |
| XCC3718 | hypothetical protein | + | | | | XC_3789 | XCV3879 | XAC3760 | abs | abs | | |
| XCC3719 | transcriptional regulator | - | | | | XC_3790 | XCV3880 | XAC3761 | abs | abs | | |
| | Conserved locus | | | | | | | | | | | |
| XCC3958 | hypothetical protein | + | | | | XC_4047 | XCV4133 | XAC4042 | XOO0400 | abs | | |
| XCC3959 | hypothetical protein | - | | | | XC_4049 | XCV4134 | XAC4044 | XOO0399 | abs | | |
| XCC3960 | hypothetical protein | - | | | | XC_4050 | XCV4135 | abs | abs | abs | | |
| XCC3961 | dipeptidyl peptidase IV | - | | | | XC_4051 | XCV4136 | XAC4046 | XOO0398 | abs | | |
| XCC3962 | glutathione S-transferase | - | gst | | | XC_4052 | XCV4137 | XAC4047 | XOO0397 | abs | | |
| XCC3963 | TBDR | + | iroN | | | XC_4053 | XCV4138 | XAC4048 | XOO0394 | abs | Saro_1603, *Novosphingobium aromaticivorans* DSM 12444 | |
| XCC3964 | SapC related protein | + | | | | XC_4054 | XCV4139 | XAC4049 | XOO0393 | abs | Saro_1605 | |
| XCC3965 | Pass1-related protein | + | | | | XC_4055 | XCV4140 | XAC4050 | XOO0392 | abs | Saro_1606 | |
| XCC3966 | tryptophan halogenase | + | prnA | | | XC_4056 | XCV4141 | XAC4051 | XOO0391 | abs | Saro_1607 | |
| XCC3967 | TonB-like protein | + | | | | XC_4057 | XCV4142 | XAC4052 | XOO0390 | abs | | |
| | | | | | | | | | | | | |
| XCC4049 | ankyrin-like protein | - | | | | XC_4138 | abs | abs | abs | abs | | |
| XCC4050 | ankyrin-like protein | - | | | | XC_4139 | abs | abs | abs | abs | | |
| XCC4051 | hypothetical protein | - | | | | XC_4140 | abs | abs | abs | abs | | |
| XCC4052 | TBDR | - | fecA | | | XC_4141 | abs | abs | abs | abs | CC1791, *Caulobacter crescentus* CB15 | |
| XCC4053 | transcriptional regulator | + | | | | XC_4142 | abs | XAC4172 | XOO4549 | abs | CC1792 | |
| XCC4054 | hypothetical protein | - | | | | XC_4143 | abs | XAC4173 | abs | abs | | |
| XCC4055 | peptidyl-prolyl cis-trans isomerase | - | | | | XC_4144 | abs | XAC4174 | abs | abs | | |
| | Putative partial CUT locus (xylan/xylose) | | | | | | | | | | | |
| XCC4113 | gluconolactonase precursor | - | gnl | | | XC_4205 | XCV4353 | XAC4248 | abs | abs | | |
| XCC4114 | hypothetical protein | + | | | | XC_4206 | abs | abs | abs | abs | | |
| XCC4115 | endo-1,4-beta-xylanase A | - | xynA | GH10 | | XC_4207 | XCV4355 | XAC4249 | abs | abs | | |
| XCC4116 | beta-galactosidase | - | | GH2 | | XC_4208 | XCV4356 | XAC4250 | abs | abs | | |
| XCC4117 | hexuronic acid isomerase | - | hrmL | | | XC_4209 | XCV4357 | XAC4251 | XOO4427 | abs | | |
| XCC4118 | xylanase | - | xynB | GH10 | | XC_4210 | XCV4360 | XAC4254 | XOO4429 | abs | | |
| XCC4119 | putative hexuronate transporter | - | exuT | | | XC_4211 | XCV4361 | XAC4255 | XOO4430 | abs | | |
| XCC4120 | TBDR | + | cirA | | Arabinose/xylan/xylose induced | XC_4212 | XCV4362 | XAC4256 | XOO4431 | abs | CC2832, *Caulobacter crescentus* CB15 | |
| XCC4121 | transport protein | + | xylP | | | XC_4213 | XCV4363 | XAC4257 | XOO4432 | abs | | |
| XCC4122 | xylosidase/arabinosidase | + | xsa | GH43 | | XC_4214 | XCV4364 | XAC4258 | XOO4433 | abs | | |
| XCC4123 | outer membrane lipoprotein | + | blc | | | XC_4215 | XCV4365 | XAC4259 | XOO0274 | abs | | |
| XCC4124 | hypothetical protein | - | | | | XC_4216 | XCV4366 | XAC4260 | abs | abs | | |
| XCC4126 | hypothetical protein | - | | | | XC_4217 | XCV4368 | XAC4267 | XOO0259 D | abs | | |
| | Putative partial CUT locus | | | | | | | | | | | |
| XCC4128 | glycerol-3-phosphate acyltransferase | - | plsB | | | XC_4220 | XCV4371 | XAC4270 | XOO0254 | XF1031 | | |
| XCC4130 | hypothetical protein | - | | | | XC_4221 | XCV4372 | XAC4271 | XOO0253 | abs | | |
| XCC4129 | transcriptional regulator lacI family | + | | | | XC_4222 | XCV4373 | XAC4272 | XOO0252 | abs | | |
| XCC4131 | Ps-TBDR/oar | + | | | | XC_4223 | XCV4374 | XAC4273 | XOO0250 | abs | Sala_1015, *Sphingopyxis alaskensis* RB2256 | |
| XCC4132 | Ps-TBDR/oar | + | | | | XC_4224 | XCV4375-6 | XAC4274 | XOO0249 | XF1036 | Sala_1015, *Sphingopyxis alaskensis* RB2256 | |
| XCC4133 | tryptophan halogenase | + | prnA | | | XC_4225 | XCV4377 | XAC4275 | XOO0248 | abs | | |
| XCC4134 | orotidine 5'-phosphate decarboxylase | - | pyrF | | | XC_4226 | XCV4378 | XAC4276 | XOO0247 | XF0034 | | |
| XCC4135 | acid phosphatase | - | lppC | | | XC_4227 | XCV4379 | XAC4277 | XOO0246 | abs | | |
| | Fur regulated TBDR | | | | | | | | | | | |
| XCC4159 | hypothetical protein | - | | | | XC_4246 | XCV4397 | XAC4297 | XOO0286 | abs | | |
| XCC4160 | hypothetical protein | + | | | | XC_4247 | XCV0647 D | abs | abs | abs | | |
| XCC4161 | hypothetical protein | + | | | | XC_4248 | XCV4398 | XAC4298 | abs | abs | | |
| XCC4162 | TBDR | - | | | Fur-regulated | XC_4249 | abs | abs | abs | abs | slr1490, *Synechocystis* sp. PCC 6803 | PA4837 (35/51) |
| XCC4163 | hypothetical protein | - | | | | XC_4250 | XCV4399 | XAC4299 | XOO4595 | abs | | |
| XCC4164 | hypothetical protein | - | | | | XC_4251 | XCV4400 | XAC4300 | XOO4596 | abs | | |
| XCC4165 | hypothetical protein | - | | | | XC_4252 | XCV4401 | XAC4301 | XOO4597 | abs | | |
| | Putative partial CUT locus, CAZy associated TBDR, arabinose induced TBDR | | | | | | | | | | | |
| XCC4219 | hypothetical protein | + | | | | XC_4308 | XCV4465 | XAC4353 | abs | abs | | |
| XCC4220 | amino acid transporter | + | yhdG | | | XC_4309 | XCV4466 | XAC4354 | XOO4572 | XF0408 | | |
| XCC4221 | hypothetical protein | - | | GH92 | | XC_4310 | XCV4467 | XAC4355 | abs | abs | | |
| XCC4222 | Ps-TBDR | - | | | Arabinose induced | XC_4311 | XCV4468 | XAC0544 | abs | abs | Pfl_3124, *Pseudomonas fluorescens* PfO-1 | PA2057 (31/46) |
| XCC4223 | hypothetical protein | - | | | | XC_4312 | XCV4369 | XAC4357 | abs | abs | | |
| XCC4224 | hypothetical protein | - | | | | XC_4313 | XCV4470 | XAC4358 | abs | abs | | |
| XCC4225 | sugar diacide regulator | - | | | | XC_4314 | XCV4471 | XAC4359 | XOO4619 D | abs | | |
| | Putative partial CUT locus, CAZy associated TBDR, xylan induced TBDR | | | | | | | | | | | |
| XCC4232 | export protein | + | ygjT | | | XC_4321 | XCV4477 | XAC4365 | XOO4626 | XF0406 | | |
| XCC4233 | hypothetical protein | + | | | | XC_4322 | XCV4478 | XAC4366 | XOO4627 | abs | | |
| XCC4234 | glycerophosphoryl diester phosphodiesterase | - | glpQ | | | XC_4324 | XCV4479 | XAC4367 | XOO4628 | abs | | |
| XCC4235 | TBDR | - | fecA | | | XC_4325 | XCV4480 | XAC4368 | XOO6430 | abs | Psyr_4483, *Pseudomonas syringae* pv. *syringae* B728a | |
| XCC4236 | phosphatase precursor | + | phoC | | | XC_4326 | XCV4482 | XAC4369 | XOO4633 | abs | | |
| XCC4237 | Ps-TBDR/oar | + | oar | | Xylan induced | XC_4327 | abs | abs | abs | abs | Patl_1148, *Pseudoalteromonas atlantica* T6c | |
| XCC4238 | thiophene and furan oxidation protein | - | thdF | | | XC_4328 | XCV4483 | XAC4370 | XOO4634 | XF2778 | | |
| XCC4239 | polysaccharide deacetylase | - | | CE4 | | XC_4329 | XCV4484 | XAC4371 | XOO4635 | XF2779 | | |
| XCC4240 | 60kDa inner-membrane protein | - | | | | XC_4330 | XCV4485 | XAC4372 | XOO4636 | XF2780 | | |

[a] Gene identification (ID), gene name, function and orientation are from *Xanthomonas campestris* pv. *campestris* (*Xcc*) strain ATCC33913 [14].

[b] Family number of proteins having functional domains of enzymes that degrade, modify, or create glycosidic bonds and referenced in the CAZy database (http://afmb.cnrs-mrs.fr/CAZY/). GH: Glycoside Hydrolase; GT: Glycosyl Transferase; PL: Polysaccharide Lyase; CE: Carbohydrate Esterase; CBM: Carbohydrate-Binding Module.

[c] Orthologs (i.e, a minimum of 40% identity and a ratio of 0.8 of the length of the smallest protein) were identified by Blastp searches in the corresponding genomes. Genes belonging to the same syntheny group are bright yellow shadowed and genes present elswere in the genome are dark yellow shadowed. D: deleted protein; Abs: no blast or blast with an identity lower than 40%.

[d] Homologs were obtained by using the BlastP program without filter on the nr database with *Xcc* TBDRs as query sequences. A representative non Xanthomonads strain completely sequenced was considered. Synthenic regions (blue shadowed) were identified by reiterating the blast search using contiguous genes. Only proteins showing bidirectional identity above 30% and a ratio of 0.8 of the length of the smallest protein were considered.

[e] Best homologs obtained in *Pseudomonas aeruginosa* PAO1 proteome by using BlastP program with *Xcc* TBDRs as query sequences. PAO1 TBDRs induced under iron restricted conditions [72] are orange shadowed.

| Gene ID [a] | MM+PGA vs MM (+/- SD) [b] | MM+MAL vs MM (+/- SD) [b] | MM+ARA vs MM (+/- SD) [b] | MM+XYLAN vs MM (+/- SD) [b] | MM+XYL vs MM (+/- SD) [b] | MM+SUC vs MM (+/- SD) [b] | MM+GLC vs MM (+/- SD) [b] | RM vs MM (+/- SD) [b] |
|---|---|---|---|---|---|---|---|---|
| XCC0050 | - | - | 6.57 (+/- 0.64) | - | - | - | - | - |
| XCC0098 | 0.96 (+/- 0.04) | 0.94 (+/- 0.00) | 0.58 (+/- 0.02) | 0.96 (+/- 0.02) | 0.33 (+/- 0.01) | 0.27 (+/- 0.00) | 0.31 (+/- 0.01) | 0.16 (+/- 0.00) |
| **XCC0119** | 0.99 (+/- 0.06) | 0.89 (+/- 0.00) | 0.48 (+/- 0.02) | 1.26 (+/- 0.02) | 0.40 (+/- 0.02) | 0.29 (+/- 0.00) | 0.42 (+/- 0.01) | 0.20 (+/- 0.06) |
| **XCC0120** | 19.13 (+/- 1.45) | 0.86 (+/- 0.12) | 0.45 (+/- 0.29) | 0.75 (+/- 0.04) | 0.55 (+/- 0.05) | 0.35 (+/- 0.11) | 0.48 (+/- 0.11) | 0.53 (+/- 0.05) |
| **XCC0158** | 0.89 (+/- 0.09) | 1.08 (+/- 0.02) | 0.12 (+/- 0.02) | 0.12 (+/- 0.00) | 0.48 (+/- 0.05) | 0.62 (+/- 0.06) | 0.46 (+/- 0.00) | 0.27 (+/- 0.07) |
| XCC0304 | - | - | - | - | - | - | - | - |
| XCC0305 | - | - | - | - | - | - | - | - |
| **XCC0394** | 1.41 (+/- 0.53) | 1.12 (+/- 0.02) | 0.31 (+/- 0.03) | 0.79 (+/- 0.03) | 0.27 (+/- 0.05) | 0.22 (+/- 0.08) | 0.28 (+/- 0.01) | 0.16 (+/- 0.01) |
| **XCC0397** | - | - | 0.05 (+/- 0.07) | 1.17 (+/- 0.22) | - | - | - | - |
| **XCC0531** | 1.10 (+/- 0.02) | 0.94 (+/- 0.02) | 1.24 (+/- 0.00) | 1.83 (+/- 0.57) | 0.72 (+/- 0.05) | 0.43 (+/- 0.00) | 0.34 (+/- 0.05) | 0.63 (+/- 0.02) |
| **XCC0674** | 1.03 (+/- 0.01) | 1.13 (+/- 0.03) | 1.29 (+/- 0.32) | 1.18 (+/- 0.93) | 1.13 (+/- 0.11) | 1.01 (+/- 0.12) | 1.21 (+/- 0.04) | 0.38 (+/- 0.00) |
| **XCC0759** | - | - | - | - | - | - | - | - |
| **XCC0768** | 0.93 (+/- 0.03) | 0.88 (+/- 0.02) | 0.21 (+/- 0.09) | 0.14 (+/- 0.12) | 0.44 (+/- 0.09) | 0.43 (+/- 0.04) | 0.38 (+/- 0.01) | 0.38 (+/- 0.01) |
| **XCC0946** | - | - | - | - | - | - | - | - |
| **XCC1037** | 1.08 (+/- 0.03) | 0.89 (+/- 0.00) | 1.05 (+/- 0.32) | 1.15 (+/- 0.21) | 0.74 (+/- 0.01) | 0.88 (+/- 0.02) | 0.91 (+/- 0.06) | 0.26 (+/- 0.06) |
| *XCC1041* | 0.79 (+/- 0.21) | 0.86 (+/- 0.01) | 1.27 (+/- 0.59) | 1.77 (+/- 0.81) | 0.17 (+/- 0.02) | 0.13 (+/- 0.03) | 0.23 (+/- 0.01) | 0.16 (+/- 0.04) |
| XCC1179 | - | - | - | - | - | - | - | - |
| **XCC1258** | 1.06 (+/- 0.00) | 0.87 (+/- 0.02) | 0.92 (+/- 0.07) | 1.40 (+/- 0.38) | 0.49 (+/- 0.02) | 0.29 (+/- 0.00) | 0.21 (+/- 0.01) | 0.14 (+/- 0.01) |
| **XCC1340** | 1.02 (+/- 0.12) | 0.99 (+/- 0.01) | 0.53 (+/- 0.04) | 1.56 (+/- 0.49) | 0.32 (+/- 0.05) | 0.37 (+/- 0.05) | 0.39 (+/- 0.09) | 0.17 (+/- 0.01) |
| **XCC1391** | 0.64 (+/- 0.16) | 0.98 (+/- 0.08) | 0.68 (+/- 0.03) | 0.67 (+/- 0.02) | 0.49 (+/- 0.01) | 0.49 (+/- 0.07) | 0.40 (+/- 0.01) | 0.34 (+/- 0.04) |
| **XCC1719** | 1.04 (+/- 0.01) | 0.80 (+/- 0.10) | 0.48 (+/- 0.02) | 1.29 (+/- 0.05) | 0.18 (+/- 0.01) | 0.20 (+/- 0.01) | 0.17 (+/- 0.02) | 0.11 (+/- 0.02) |
| **XCC1749** | 2.06 (+/- 0.05) | 0.85 (+/- 0.23) | 2.33 (+/- 0.03) | 1.31 (+/- 0.01) | 0.33 (+/- 0.02) | 0.31 (+/- 0.00) | 0.33 (+/- 0.08) | 0.23 (+/- 0.00) |
| XCC1750 | 13.45 (+/- 0.66) | 0.88 (+/- 0.03) | 9.95 (+/- 1.20) | 1.50 (+/- 0.30) | 0.34 (+/- 0.04) | 0.30 (+/- 0.05) | 0.28 (+/- 0.01) | 1.11 (+/- 0.02) |
| XCC1751 | 1.99 (+/- 0.05) | 0.98 (+/- 0.06) | 1.03 (+/- 0.00) | 1.13 (+/- 0.09) | 0.15 (+/- 0.01) | 0.09 (+/- 0.00) | 0.22 (+/- 0.04) | 0.15 (+/- 0.02) |
| **XCC1892** | 1.01 (+/- 0.00) | 0.90 (+/- 0.06) | 2.58 (+/- 0.07) | 1.35 (+/- 0.04) | 0.22 (+/- 0.00) | 0.22 (+/- 0.00) | 0.18 (+/- 0.03) | 0.15 (+/- 0.00) |
| XCC1990 | nt | nt | nt | nt | nt | nt | nt | nt |
| XCC2046 | 0.97 (+/- 0.05) | 1.16 (+/- 0.06) | 0.85 (+/- 0.28) | 0.92 (+/- 0.74) | 0.56 (+/- 0.03) | 0.40 (+/- 0.06) | 0.44 (+/- 0.00) | 0.33 (+/- 0.06) |
| *XCC2208* | 1.06 (+/- 0.02) | 1.03 (+/- 0.02) | 1.01 (+/- 0.00) | 0.92 (+/- 0.35) | 0.60 (+/- 0.04) | 0.58 (+/- 0.01) | 0.74 (+/- 0.04) | 0.62 (+/- 0.02) |
| XCC2385 | - | - | - | - | - | - | - | - |
| **XCC2395** | - | - | - | - | - | - | - | - |
| **XCC2400** | - | - | - | - | - | - | - | - |
| **XCC2469** | 1.06 (+/- 0.06) | 16.45 (+/- 2.71) | 1.00 (+/- 0.19) | 1.30 (+/- 0.34) | 0.27 (+/- 0.01) | 0.21 (+/- 0.00) | 0.27 (+/- 0.00) | 0.14 (+/- 0.00) |
| *XCC2497* | 1.02 (+/- 0.02) | 0.81 (+/- 0.01) | 1.13 (+/- 0.08) | 1.59 (+/- 0.15) | 0.63 (+/- 0.02) | 0.50 (+/- 0.01) | 0.50 (+/- 0.02) | 0.71 (+/- 0.04) |
| **XCC2572** | - | - | - | - | - | - | - | - |
| ***XCC2573*** | 1.05 (+/- 0.02) | 0.86 (+/- 0.04) | 0.54 (+/- 0.06) | 1.11 (+/- 0.05) | 0.23 (+/- 0.01) | 0.17 (+/- 0.01) | 0.25 (+/- 0.04) | 0.20 (+/- 0.01) |
| **XCC2658** | 0.91 (+/- 0.07) | 1.13 (+/- 0.00) | 0.46 (+/- 0.02) | 0.48 (+/- 0.02) | 0.37 (+/- 0.04) | 0.32 (+/- 0.03) | 0.42 (+/- 0.00) | 0.09 (+/- 0.01) |
| **XCC2665** | 0.98 (+/- 0.02) | 0.95 (+/- 0.01) | 0.71 (+/- 0.01) | 1.06 (+/- 0.01) | 0.26 (+/- 0.01) | 0.18 (+/- 0.01) | 0.20 (+/- 0.02) | 0.10 (+/- 0.01) |
| **XCC2772** | 1.03 (+/- 0.04) | 0.92 (+/- 0.02) | 0.75 (+/- 0.01) | 0.74 (+/- 0.02) | 0.71 (+/- 0.02) | 0.42 (+/- 0.01) | 0.43 (+/- 0.00) | 1.12 (+/- 0.04) |
| **XCC2828** | 0.91 (+/- 0.09) | 0.78 (+/- 0.08) | 16.50 (+/- 1.52) | 63.32 (+/- 0.30) | 5.50 (+/- 0.97) | 0.24 (+/- 0.01) | 0.19 (+/- 0.03) | 0.26 (+/- 0.01) |
| **XCC2867** | 0.94 (+/- 0.11) | 0.82 (+/- 0.03) | 1.03 (+/- 0.04) | 1.72 (+/- 0.07) | 0.38 (+/- 0.02) | 0.32 (+/- 0.02) | 0.31 (+/- 0.01) | 0.36 (+/- 0.00) |
| **XCC2887** | 1.02 (+/- 0.03) | 0.86 (+/- 0.01) | 0.71 (+/- 0.01) | 1.10 (+/- 0.02) | 0.44 (+/- 0.01) | 0.37 (+/- 0.02) | 0.41 (+/- 0.00) | 0.45 (+/- 0.03) |
| **XCC2944** | 1.04 (+/- 0.10) | 0.84 (+/- 0.09) | 0.76 (+/- 0.11) | 1.53 (+/- 0.14) | 0.31 (+/- 0.01) | 0.30 (+/- 0.00) | 0.25 (+/- 0.01) | 0.31 (+/- 0.01) |
| XCC3036 | - | - | - | - | - | - | - | - |
| **XCC3043** | 1.04 (+/- 0.07) | 0.84 (+/- 0.05) | 0.67 (+/- 0.02) | 1.07 (+/- 0.01) | 1.17 (+/- 0.18) | 1.10 (+/- 0.06) | 1.21 (+/- 0.02) | 0.89 (+/- 0.05) |
| **XCC3045** | 1.00 (+/- 0.01) | 0.79 (+/- 0.12) | 0.73 (+/- 0.13) | 1.66 (+/- 0.29) | 0.26 (+/- 0.00) | 0.18 (+/- 0.00) | 0.20 (+/- 0.01) | 0.10 (+/- 0.00) |
| **XCC3046** | 1.02 (+/- 0.05) | 0.91 (+/- 0.06) | 0.92 (+/- 0.06) | 1.83 (+/- 0.11) | 0.23 (+/- 0.02) | 0.18 (+/- 0.02) | 0.22 (+/- 0.00) | 0.11 (+/- 0.00) |
| **XCC3050** | 0.63 (+/- 0.09) | 1.14 (+/- 0.02) | 0.43 (+/- 0.07) | 0.18 (+/- 0.01) | 0.46 (+/- 0.06) | 0.70 (+/- 0.07) | 0.59 (+/- 0.04) | 0.18 (+/- 0.02) |
| XCC3067 | 1.02 (+/- 0.02) | 1.03 (+/- 0.11) | 1.41 (+/- 0.19) | 1.06 (+/- 0.31) | 0.72 (+/- 0.01) | 0.72 (+/- 0.05) | 0.89 (+/- 0.05) | 0.49 (+/- 0.02) |
| **XCC3079** | 1.09 (+/- 0.06) | 1.05 (+/- 0.00) | 1.30 (+/- 0.23) | 1.39 (+/- 0.13) | 1.23 (+/- 0.07) | 1.72 (+/- 0.15) | 1.44 (+/- 0.04) | 0.93 (+/- 0.07) |
| **XCC3161** | 1.04 (+/- 0.03) | 0.80 (+/- 0.12) | 0.76 (+/- 0.03) | 1.45 (+/- 0.01) | 0.30 (+/- 0.01) | 0.23 (+/- 0.03) | 0.24 (+/- 0.01) | 0.23 (+/- 0.02) |
| **XCC3177** | 0.96 (+/- 0.06) | 0.82 (+/- 0.02) | 1.24 (+/- 0.04) | 1.37 (+/- 0.04) | 0.30 (+/- 0.01) | 0.27 (+/- 0.00) | 0.29 (+/- 0.00) | 0.19 (+/- 0.00) |
| **XCC3209** | nt | nt | nt | nt | nt | nt | nt | nt |
| XCC3215 | 1.00 (+/- 0.00) | 0.97 (+/- 0.00) | 1.05 (+/- 0.20) | 0.46 (+/- 0.05) | 0.45 (+/- 0.00) | 0.46 (+/- 0.05) | 0.54 (+/- 0.13) | 0.87 (+/- 0.03) |
| XCC3216 | 1.00 (+/- 0.01) | 1.05 (+/- 0.03) | 1.19 (+/- 0.06) | 0.41 (+/- 0.05) | 0.47 (+/- 0.02) | 0.57 (+/- 0.01) | 0.66 (+/- 0.04) | 0.81 (+/- 0.01) |
| *XCC3270* | - | - | - | - | - | - | - | - |
| *XCC3271* | - | - | - | - | - | - | - | - |
| **XCC3279** | - | - | - | - | - | - | - | - |
| **XCC3316** | 1.08 (+/- 0.07) | 1.08 (+/- 0.26) | 1.08 (+/- 0.10) | 0.92 (+/- 0.03) | 0.37 (+/- 0.08) | 0.34 (+/- 0.05) | 0.77 (+/- 0.30) | 0.62 (+/- 0.02) |
| **XCC3358** | 1.06 (+/- 0.02) | 1.10 (+/- 0.09) | 0.52 (+/- 0.03) | 0.98 (+/- 0.06) | 0.38 (+/- 0.00) | 5.51 (+/- 0.05) | 0.36 (+/- 0.08) | 0.46 (+/- 0.15) |
| **XCC3405** | 1.13 (+/- 0.14) | 0.82 (+/- 0.03) | 0.82 (+/- 0.04) | 1.73 (+/- 0.13) | 0.22 (+/- 0.03) | 0.18 (+/- 0.03) | 0.18 (+/- 0.01) | 0.12 (+/- 0.02) |
| XCC3408 | 0.97 (+/- 0.05) | 0.85 (+/- 0.03) | 1.35 (+/- 1.39) | 1.71 (+/- 1.18) | 0.37 (+/- 0.00) | 0.28 (+/- 0.02) | 0.37 (+/- 0.04) | 0.21 (+/- 0.02) |
| **XCC3427** | - | - | - | - | - | - | - | - |
| XCC3474 | 1.07 (+/- 0.03) | 0.79 (+/- 0.06) | 1.25 (+/- 0.56) | 1.84 (+/- 0.85) | 0.34 (+/- 0.02) | 0.23 (+/- 0.10) | 0.28 (+/- 0.02) | 0.41 (+/- 0.05) |
| **XCC3518** | 1.06 (+/- 0.08) | 1.33 (+/- 0.36) | 1.38 (+/- 0.90) | 0.68 (+/- 0.42) | 0.39 (+/- 0.01) | 0.45 (+/- 0.01) | 1.01 (+/- 0.11) | 0.40 (+/- 0.00) |
| XCC3595 | - | - | - | - | - | - | - | - |
| **XCC3635** | - | - | - | - | - | - | - | - |
| **XCC3714** | 0.96 (+/- 0.02) | 0.95 (+/- 0.01) | 0.77 (+/- 0.30) | 1.16 (+/- 0.09) | 0.30 (+/- 0.01) | 0.18 (+/- 0.03) | 0.40 (+/- 0.15) | 0.20 (+/- 0.02) |
| **XCC3963** | 1.16 (+/- 0.05) | 0.95 (+/- 0.06) | 1.20 (+/- 0.13) | 1.47 (+/- 0.11) | 0.43 (+/- 0.01) | 0.30 (+/- 0.05) | 0.36 (+/- 0.00) | 0.24 (+/- 0.04) |
| **XCC4052** | - | - | - | - | - | - | - | - |
| **XCC4120** | 1.03 (+/- 0.08) | 0.92 (+/- 0.07) | 2.19 (+/- 0.16) | 82.39 (+/- 22.11) | 7.43 (+/- 1.06) | 0.23 (+/- 0.02) | 0.38 (+/- 0.04) | 0.24 (+/- 0.02) |
| *XCC4131* | 1.05 (+/- 0.06) | 0.80 (+/- 0.02) | 0.68 (+/- 0.34) | 1.46 (+/- 0.42) | 0.33 (+/- 0.02) | 0.24 (+/- 0.02) | 0.32 (+/- 0.01) | 0.23 (+/- 0.04) |
| *XCC4132* | 1.01 (+/- 0.01) | 0.90 (+/- 0.13) | 0.97 (+/- 0.05) | 1.73 (+/- 0.29) | 0.37 (+/- 0.01) | 0.31 (+/- 0.01) | 0.24 (+/- 0.03) | 0.27 (+/- 0.00) |
| **XCC4162** | 0.98 (+/- 0.03) | 1.06 (+/- 0.03) | 0.77 (+/- 0.04) | 0.75 (+/- 0.26) | 0.37 (+/- 0.02) | 0.42 (+/- 0.01) | 0.40 (+/- 0.16) | 0.22 (+/- 0.03) |
| **XCC4222** | 1.01 (+/- 0.00) | 0.91 (+/- 0.02) | 3.54 (+/- 0.68) | 1.89 (+/- 0.36) | 0.28 (+/- 0.00) | 0.28 (+/- 0.01) | 0.17 (+/- 0.02) | 0.22 (+/- 0.04) |
| **XCC4235** | - | - | - | - | - | - | - | - |
| ***XCC4237*** | 1.05 (+/- 0.04) | 0.72 (+/- 0.08) | 1.03 (+/- 0.01) | 2.83 (+/- 0.02) | 0.20 (+/- 0.00) | 0.16 (+/- 0.01) | 0.19 (+/- 0.02) | 0.22 (+/- 0.02) |

[a] Gene identification (ID) from *Xanthomonas campestris* pv. *campestris* strain ATCC33913 [14]. Genes coding for proteins possessing all canonical TBDR domains are boldfaced, for TBDRs with an N-terminal extension are in italics and for truncated TBDRs are underlined.

[b] Average ratios of β-galactosidase expression assays on TBDR insertion mutants. Standard deviations (SD) were calculated from at least two independent biological experiments. Genes induced or repressed (by at least a two-fold factor) are dark and bright gray-shadowed respectively. nt: not tested; -: non significant expression (less than 1 Miller unit in both tested media). MM: minimal medium; PGA: polygalacturonic acid 0.125%; MAL: maltose 20 mM; ARA: arabinose 20 mM; Xylan 0.125%; XYL: xylose 20 mM; SUC: sucrose 20 mM; GLC: glucose 20 mM; RM: rich medium.

| Gene ID [a] | Subgroup [b] | Specificity [c] | Ranking of Blast results beside Xanthomonads othologs (Bacterial name; locus_tag; %Identity/%Similarity) [d] 1st | 2nd | 3rd | 4th | 5th |
|---|---|---|---|---|---|---|---|
| XCC0531 | 1B | | X. campestris pv. campestris ATCC33913; XCC4222; 55/69 | | | | |
| XCC3043 | 1B | | X. campestris pv. campestris ATCC33913; XCC3045; 56/70 | | | | |
| XCC3046 | 1B | | X. campestris pv. campestris ATCC33913; XCC3045; 47/61 | | | | |
| XCC3045 | 1B | | X. campestris pv. campestris ATCC33913; XCC3043; 56/70 | | | | |
| XCC3316 | 1B | | X. campestris pv. campestris ATCC33913; XCC2867; 41/57 | | | | |
| XCC3405 | 1B | plant | X. campestris pv. campestris ATCC33913; XCC2867; 37/52 | | | | |
| XCC2395 | 1B | | X. campestris pv. campestris ATCC33913; XCC2400; 40/57 | | | | |
| XCC2400 | 1B | | X. campestris pv. campestris ATCC33913; XCC2395; 39/56 | | | | |
| XCC4222 | 1B | plant | X. campestris pv. campestris ATCC33913; XCC0531; 55/69 | | | | |
| XCC2887 | 1C | | X. campestris pv. campestris ATCC33913; XCC3408; 45/60 | | | | |
| XCC3408 | 1C | | X. campestris pv. campestris ATCC33913; XCC2887; 45/60 | | | | |
| XCC1750 | 1C | plant | X. campestris pv. campestris ATCC33913; XCC1749; 38/54 | | | | |
| XCC1990 | 1C | | X. campestris pv. campestris 8004; XC_2484 (XCC1750); 33/49 (31/46) | | | | |
| XCC2573 | 1D | oar | X. campestris pv. campestris ATCC33913; XCC4237; 34/51 | | | | |
| XCC3271 | 1D | oar | X. campestris pv. campestris ATCC33913; XCC4237; 35/49 | | | | |
| XCC4131 | 1D | oar | X. campestris pv. campestris ATCC33913; XCC4132; 49/64 | | | | |
| XCC2208 | 1D | oar | X. campestris pv. campestris ATCC33913; XCC4132; 42/59 | | | | |
| XCC4132 | 1D | oar | X. campestris pv. campestris ATCC33913; XCC4131; 48/64 | | | | |
| XCC0158 | 1F | iron | X. campestris pv. campestris ATCC33913; XCC3518; 38/52 | | | | |
| XCC0946 | 2B | | X. campestris pv. campestris ATCC33913; XCC4235; 41/57 | | | | |
| XCC3714 | 1F | | Ralstonia solanacearum GMI1000; RSp0100; 41/57 | (Ralstonia solanacearum UW551); RRSL_03417; 41/57 | Ralstonia solanacearum GMI1000; RSc2729; 42/55 | (Ralstonia solanacearum UW551); RRSL_00729; 42/56 | Burkholderia cepacia AMMD; Bamb_4928; 40/57 |
| XCC0394 | 1F | | Burkholderia sp. 383; Bcep18194_B2705; 50/69 | (Burkholderia cenocepacia HI2424); Bcen2424DRAFT_6742; 48/68 | Rhodopseudomonas palustris HaA2; RPB_0102; 42/61 | Pseudomonas fluorescens Pf-5; PFL_0646; 42/59 | Pseudomonas fluorescens PfO-1; Pfl_0594; 42/60 |
| XCC3474 | 3A | | Ralstonia eutropha H16; H16_B1039; 51/68 | Ralstonia eutropha JMP134; Reut_A1787; 49/66 | (Rubrivivax gelatinosus PM1); Rgel02002002; 44/59 | (Polaromonas naphthalenivorans CJ2); PnapDRAFT_2142; 35/50 | Methylobacillus flagellatus KT; Mfla_1253; 35/49 |
| XCC0098 | 3A | | Bordetella bronchiseptica RB50; BB0832; 47/60 | Azoarcus sp. EbN1; ebA6096; 44/58 | (Rubrivivax gelatinosus PM1); Rgel02003219; 43/57 | Nitrosospira multiformis ATCC 25196; Nmul_A1426; 41/57 | Escherichia coli W3110; yncD; 41/59 |
| XCC2046 | 3B | | (Acidovorax avenae subsp. citrulli AAC00-1); AaveDRAFT_1098; 63/76 | Pseudomonas putida KT2440; PP_3340; 44/60 | (Pseudomonas putida F1); PputDRAFT_4622; 43/59 | Pseudomonas syringae pv. tomato str. DC3000; PSPTO_1855; 42/59 | (Acidovorax avenae subsp. citrulli AAC00-1); AaveDRAFT_0325; 42/58 |
| XCC3177 | 3B | | (Acidovorax avenae subsp. citrulli AAC00-1); AaveDRAFT_0325; 58/72 | Pseudomonas putida KT2440; PP_3340; 50/64 | (Pseudomonas putida F1); PputDRAFT_4622; 50/63 | Pseudomonas syringae pv. tomato str. DC3000; PSPTO_1855; 49/63 | Caulobacter crescentus CB15; CC1781; 45/60 |
| XCC3079 | 1B | | Pseudomonas fluorescens PfO-1; Pfl_2342; 54/67 | X. campestris pv. campestris ATCC33913; XCC3043; 41/56 | | | |
| XCC3067 | 1B | | Pseudomonas aeruginosa PAO1; PA1271; 50/64 | Pseudomonas aeruginosa UCBPP-PA14; PA14_47800; 50/64 | (Pseudomonas aeruginosa PA7); PaerP_01003957; 50/64 | (Pseudomonas aeruginosa C3719): PaerC_01000244; 50/64 | Nitrosomonas europaea ATCC 19718; NE0636; 45/63 |
| XCC0674 | 1F | | Pseudomonas syringae pv. syringae B728a; Psyr_3769; 56/71 | Pseudomonas syringae pv. tomato str. DC3000; PSPTO_1610; 56/72 | Pseudomonas syringae pv. phaseolicola 1448A; PSPPH_1484; 55/71 | Pseudomonas fluorescens Pf-5; PFL_3835; 52/71 | Burkholderia sp. 383; Bcep18194_B2436; 46/63 |
| XCC3518 | 1F | iron | Pseudomonas fluorescens PfO-1; Pfl_2583; 40/55 | Pseudomonas entomophila L48; PSEEN2482; 38/56 | Pseudomonas fluorescens Pf-5; PFL_3315; 38/56 | (Pseudomonas aeruginosa 2192); Paer2_01001533; 38/55 | (Shewanella sp. W3-18-1); Sputw3181DRAFT_3279; 36/55 |
| XCC3595 | 1F | iron | Pseudomonas fluorescens Pf-5; PFL_2293; 40/58 | (Pseudomonas putida F1); PputDRAFT_3079; 39/57 | Pseudomonas sp.; pbuA; 40/57 | Pseudomonas fluorescens PfO-1; Pfl_1848; 38/56 | (Pseudomonas putida F1); PputDRAFT_3127; 39/57 |
| XCC3050 | 2A | iron | (Pseudomonas aeruginosa PA7); PaerP_01004786; 56/68 | (Azotobacter vinelandii AvOP); AvinDRAFT_7778; 49/64 | (Vibrio splendidus 12B01); V12B01_16041; 45/59 | (Vibrio alginolyticus); vfgA; 44/60 | (Vibrio alginolyticus 12G01); V12G01_04486; 44/60 |
| XCC4235 | 2B | | Pseudomonas syringae pv. syringae B728a; Psyr_4483; 42/57 | X. campestris pv. campestris ATCC33913; XCC0946; 43/59 | | | |
| XCC0768 | 1B | iron | Anabaena sp. PCC 7120; alr2153; 37/54 | Caulobacter crescentus CB15; CC2194; 36/52 | Chromobacterium violaceum ATCC 12472; CV3896; 36/52 | Synechococcus sp. JA-3-3Ab; CYA_2031; 35/51 | (Caulobacter sp. K31); CaulDRAFT_0034; 35/50 |
| XCC4162 | 1F | iron | Synechocystis sp. PCC 6803; slr1490; 35/53 | Anabaena sp. PCC 7120; alr2588; 35/52 | Anabaena sp. PCC 7120; all2610; 36/54 | Anabaena sp. PCC 7120; alr2626; 34/51 | Gloeobacter violaceus PCC 7421; glr0349; 34/50 |
| XCC2572 | 1B | | Shewanella sp. MR-4; Shewmr4_0124; 39/57 | (Pseudoalteromonas tunicata D2); PTD2_18885; 40/57 | Shewanella frigidimarina NCIMB 400; Sfri_2471; 38/57 | (Alteromonas macleodii 'Deep ecotype'); MADE_02756; 39/55 | (Idiomarina baltica OS145); OS145_10882; 39/56 |
| XCC2658 | 1B | | (Idiomarina baltica OS145); OS145_12066; 37/51 | Methylobacillus flagellatus KT; Mfla_0134; 36/55 | (Pseudomonas putida F1); PputDRAFT_2116; 36/53 | Ralstonia eutropha H16; H16_A0191; 35/50 | Pseudomonas entomophila L48; PSEEN1173; 35/51 |
| XCC2867 | 1B | | (Alteromonas macleodii 'Deep ecotype'); MADE_16410; 41/57 | X. campestris pv. campestris ATCC33913; XCC3405; 37/52 | | | |
| XCC2828 | 1C | plant | Pseudoalteromonas atlantica T6c; Patl_3278; 42/58 | Colwellia psychrerythraea 34H; CPS_3698; 41/56 | Caulobacter crescentus CB15; CC0999; 41/56 | (marine gamma proteobacterium HTCC2207); GB2207_09881; 39/55 | (Caulobacter sp. K31); CaulDRAFT_3041; 40/57 |
| XCC1892 | 1C | plant | Pseudoalteromonas haloplanktis TAC125; PSHAb0165; 37/54 | (Pseudoalteromonas tunicata D2); PTD2_22047; 37/54 | (Shewanella amazonensis SB2B); SamaDRAFT_2978; 37/53 | Pseudoalteromonas atlantica T6c; Patl_0122; 35/51 | (Caulobacter sp. K31); CaulDRAFT_2836; 28/43 |
| XCC3161 | 1C | | Saccharophagus degradans 2-40; Sde_4006; 37/54 | (Caulobacter sp. K31); CaulDRAFT_1586; 36/52 | Saccharophagus degradans 2-40; Sde_2542; 33/47 | (Caulobacter sp. K31); CaulDRAFT_1582; 34/51 | X. campestris pv. campestris ATCC33913; XCC1749; 28/43 |
| XCC4237 | 1D | oar/plant | (Pseudoalteromonas tunicata D2); PTD2_04266; 43/59 | X. campestris pv. campestris ATCC33913; XCC2573; 34/51 | | | |
| XCC1391 | 1F | iron | Pseudoalteromonas haloplanktis TAC125; PSHAb0279; 47/67 | Shewanella sp. MR-4; Shewmr4_2386; 44/59 | Shewanella sp. MR-7; Shewmr7_2458; 43/59 | (Shewanella sp. ANA-3); Shewana3DRAFT_4183; 44/60 | Pseudoalteromonas atlantica T6c; Patl_1142; 41/58 |
| XCC1037 | 1H | | (Pseudoalteromonas tunicata D2); PTD2_15087; 44/62 | Sphingopyxis alaskensis RB2256; Sala_0027; 45/60 | Pseudoalteromonas haloplanktis TAC125; PSHAa2180; 44/62 | Caulobacter crescentus CB15; CC1970; 44/61 | Colwellia psychrerythraea 34H; CPS_1977; 43/60 |
| XCC3036 | 2B | | Idiomarina loihiensis L2TR; IL2594; 44/61 | (gamma proteobacterium KT 71); KT71_02412; 42/58 | Pseudoalteromonas atlantica T6c; Patl_3410; 41/58 | Pseudoalteromonas atlantica T6c; Patl_2585; 39/58 | (Alteromonas macleodii 'Deep ecotype'); MADE_16255; 39/56 |
| XCC2385 | 1C | | (Desulfuromonas acetoxidans DSM 684); Dace_2425; 34/51 | (Alteromonas macleodii 'Deep ecotype'); MADE_18984; 34/51 | (Pseudoalteromonas tunicata D2); PTD2_04446; 33/53 | (Sphingomonas sp. SKA58); SKA58_03800; 33/51 | (Azotobacter vinelandii AvOP); AvinDRAFT_2260; 35/52 |
| XCC2665 | 1B | | Sphingopyxis alaskensis RB2256; Sala_0305; 40/60 | Shewanella frigidimarina NCIMB 400; Sfri_3503; 36/54 | Colwellia psychrerythraea 34H; CPS_0977; 34/53 | (Pseudoalteromonas tunicata D2); PTD2_20302; 34/51 | Pseudoalteromonas atlantica T6c; Patl_1822; 33/52 |
| XCC3358 | 1B | plant | Caulobacter crescentus CB15; CC1136; 58/74 | (Shewanella baltica OS195); Sbal195DRAFT_3485; 43/69 | (Shewanella baltica OS155); SbalDRAFT_3744; 53/69 | Shewanella sp. MR-7; Shewmr7_0064; 53/69 | Shewanella frigidimarina NCIMB 400; Sfri_3988; 53/70 |
| XCC0397 | 1B | | (Oceanicaulis alexandrii HTCC2633); OA2633_12910; 35/50 | Pseudoalteromonas atlantica T6c; Patl_3441; 34/50 | Caulobacter crescentus CB15; CC1666; 34/50 | Pseudoalteromonas haloplanktis TAC125; PSHAa2973; 33/50 | Pseudoalteromonas haloplanktis TAC125; PSHAa1271; 33/50 |
| XCC1340 | 1B | | (Caulobacter sp. K31); CaulDRAFT_0125; 40/55 | Gluconobacter oxydans 621H; GOX0945; 28/45 | (Oceanicaulis alexandrii HTCC2633); OA2633_07829; 29/46 | Zymomonas mobilis subsp. mobilis ZM4; ZMO1040; 28/45 | (Pseudoalteromonas tunicata D2); PTD2_06374; 30/46 |
| XCC3427 | 1C | | Sphingopyxis alaskensis RB2256; Sala_0313; 41/57 | (Sphingomonas sp. SKA58); SKA58_09651; 39/56 | Caulobacter crescentus CB15; CC0171; 40/55 | Novosphingobium aromaticivorans DSM 12444; Saro_2438; 39/56 | (Oceanicaulis alexandrii HTCC2633); OA2633_11970; 36/54 |
| XCC3963 | 1C | | Novosphingobium aromaticivorans DSM 12444; Saro_1603; 45/62 | (Sphingomonas sp. SKA58); SKA58_00625; 45/61 | Shewanella frigidimarina NCIMB 400; Sfri_1313; 44/60 | (Shewanella baltica OS195); Sbal195DRAFT_0485; 43/60 | Colwellia psychrerythraea 34H; CPS_3737; 42/59 |
| XCC0119 | 1C | | Maricaulis maris MCS10; Mmar10_0224; 43/56 | Caulobacter crescentus CB15; CC0442; 40/56 | Saccharophagus degradans 2-40; Sde_0952; 40/56 | X. campestris pv. campestris ATCC33913; XCC0120; 39/52 | |
| XCC0759 | 1C | | Gluconobacter oxydans 621H; GOX1188; 35/50 | Caulobacter crescentus CB15; CC0562; 35/51 | X. campestris pv. campestris ATCC33913; XCC3209; 27/43 | | |
| XCC0050 | 1C | plant | Caulobacter crescentus CB15; CC1791; 35/51 | Caulobacter crescentus CB15; CC1113; 29/45 | X. campestris pv. campestris ATCC33913; XCC4052; 28/44 | | |
| XCC3635 | 1C | | Caulobacter crescentus CB15; CC1131; 48/62 | (Caulobacter sp. K31); CaulDRAFT_3050; 37/55 | (Caulobacter sp. K31); CaulDRAFT_3053; 37/54 | (marine gamma proteobacterium HTCC2207); GB2207_01907; 32/48 | Colwellia psychrerythraea 34H; CPS_2359; 29/49 |
| XCC1041 | 1C | hrp | Caulobacter crescentus CB15; CC1113; 31/45 | X. campestris pv. campestris ATCC33913; XCC4052; 28/45 | | | |
| XCC4052 | 1C | | Caulobacter crescentus CB15; CC1113; 30/47 | X. campestris pv. campestris ATCC33913; XCC1041; 28/45 | | | |
| XCC3209 | 1C | | Caulobacter crescentus CB15; CC0563; 30/49 | X. campestris pv. campestris ATCC33913; XCC0759; 27/43 | | | |
| XCC2944 | 1C | | Caulobacter crescentus CB15; CC0446; 37/54 | X. campestris pv. campestris ATCC33913; XCC3408; 37/52 | | | |
| XCC0120 | 1C | plant | Caulobacter crescentus CB15; CC0442; 38/51 | Maricaulis maris MCS10; Mmar10_0224; 36/50 | (Sphingomonas sp. SKA58); SKA58_03670; 34/51 | (Caulobacter sp. K31); CaulDRAFT_2832; 33/46 | Sphingopyxis alaskensis RB2256; Sala_3041; 33/47 |
| XCC4120 | 1C | plant | (Caulobacter sp. K31); CaulDRAFT_3665; 51/65 | (Sphingomonas sp. SKA58); SKA58_04811; 44/61 | Caulobacter crescentus CB15; CC2832; 44/58 | X. campestris pv. campestris ATCC33913; XCC0119; 28/42 | |
| XCC1749 | 1C | plant | (Caulobacter sp. K31); CaulDRAFT_2405; 43/59 | X. campestris pv. campestris ATCC33913; XCC1750; 38/54 | | | |
| XCC2469 | 1C | plant | (Caulobacter sp. K31); CaulDRAFT_1654; 38/55 | Caulobacter crescentus CB15; CC1754; 36/54 | Maricaulis maris MCS10; Mmar10_2735; 38/54 | Shewanella frigidimarina NCIMB 400; Sfri_1787; 37/55 | Caulobacter crescentus CB15; CC2287; 36/54 |
| XCC1258 | 1C | | (Caulobacter sp. K31); CaulDRAFT_1139; 46/60 | Saccharophagus degradans 2-40; Sde_3880; 36/55 | (Alteromonas macleodii 'Deep ecotype'); MADE_11505; 33/52 | Saccharophagus degradans 2-40; Sde_0682; 30/48 | (Caulobacter sp. K31); CaulDRAFT_1147; 29/46 |
| XCC2497 | 1D | oar | (Parvularcula bermudensis HTCC2503); PB2503_02212; 34/50 | (Oceanicaulis alexandrii HTCC2633); OA2633_12585; 32/48 | Pseudoalteromonas haloplanktis TAC125; PSHAb0340; 32/48 | Maricaulis maris MCS10; Mmar10_0368; 34/48 | (Alteromonas macleodii 'Deep ecotype'); MADE_07746; 32/47 |
| XCC2772 | 1F | iron | (Sphingomonas sp. SKA58); SKA58_12165; 47/61 | (Pseudomonas aeruginosa PA7); PaerP_01004007; 40/56 | (Pseudomonas aeruginosa 2192); Paer2_01000319; 39/55 | Pseudomonas aeruginosa PAO1; PA1322; 39/55 | (Pseudomonas aeruginosa PACS2); PaerPA_01001801; 39/55 |
| XCC1179 | 1H | | (Caulobacter sp. K31); CaulDRAFT_3818; 73/83 | Caulobacter crescentus CB15; CC1970; 50/63 | (Caulobacter sp. K31); CaulDRAFT_0617; 48/63 | (Alteromonas macleodii 'Deep ecotype'); MADE_03081; 45/59 | (Oceanicaulis alexandrii HTCC2633); OA2633_01564; 43/59 |
| XCC1719 | 1H | hrp | (Caulobacter sp. K31); CaulDRAFT_0763; 50/65 | Caulobacter crescentus CB15; CC3336; 49/63 | (Caulobacter sp. K31); CaulDRAFT_5326; 48/62 | Maricaulis maris MCS10; Mmar10_1115; 41/57 | (Oceanicaulis alexandrii HTCC2633); OA2633_00415; 41/56 |
| XCC3279 | 2B | | Caulobacter crescentus CB15; CC3436; 31/47 | (Parvularcula bermudensis HTCC2503); PB2503_08669; 30/49 | Hyphomonas neptunium ATCC 15444; HNE_2355; 30/47 | (Caulobacter sp. K31); CaulDRAFT_4856; 32/46 | Pseudomonas syringae pv. tomato str. DC3000; PSPTO_0671; 29/45 |

[a] Gene identification (ID) from *Xanthomonas campestris* pv. *campestris* strain ATCC33913 [14].

[b] From the phylogenetic tree presented on Figure S1.

[c] Iron: TBDR probably involved in iron uptake; plant: TBDR probably involved in plant carbohydrate uptake; Oar: TBDR of the Oar-like subclass; hrp: TBDR gene regulated by *hrp* regulators.

[d] Blast hit results with similarities lower than those obtained with non orthologous *Xcc* TBDRs were not included. Only the five first results were shown. Colors correspond to bacterial classification: α- (blue), β- (orange), δ-proteobacteria (pink), γ- (green) proteobacteria, *Xanthomonas* (yellow) or cyanobacteria (violet).

| Plasmids | Features | *Xcc* sequence cloned relative to the putative start codon | Reference |
|---|---|---|---|
| pVO155 | pUC119 derivative, containing the promoterless *gus* (*uidA*) reporter gene encoding β-glucuronidase, used for insertion mutagenesis; $Km^R$ $Amp^R$ | | [36] |
| pLAFR6 | pLAFR1 with trp terminators; $Tet^R$ | | [108] |
| pFAJ1700 | pTR102-derived expression vector, containing a multiple cloning site and transcriptional terminators in both orientations; $Tet^R$ $Amp^R$ | | [109] |
| pSC154 | pET-26b(+) derived vector with the cyaA' gene from pMS107 used for translational fusion constructs. The T7 promoter has been replaced by Ptac promoter sequence; $Km^R$ | | [107] |
| pCZ367 | pUC18-derived vector used for insertional mutagenesis; $Amp^R$ $Gm^R$ | | [107] |
| pCZ750 | pFAJ1700 containing the *KpnI*-*AscI* *lacZ* gene from the pCZ367 plasmid; $Tet^R$ $Amp^R$ | | This study |
| pCZ525 | pSC154 Δ*cyaA'*; $Km^R$ | | This study |
| pL-*XCC3358*; pL-*suxA* | pCZ525-*XCC3358*-pLAFR6; $Tet^R$ $Km^R$ | from - 247 to + 2474 | This study |
| pL-*XCC3359*; pL-*suxB* | pCZ525-*XCC3359*-pLAFR6; $Tet^R$ $Km^R$ | from - 15 to + 1913 | This study |
| pL-*XCC1470*; pL-*fur* | pFAJ1700-*XCC1470*; $Tet^R$ $Amp^R$ | from - 95 to + 545 | This study |
| pPr-*XCC3358*; pPr-*suxA* | pFAJ1700-*lacZ*-pr*XCC3358*; $Tet^R$ $Amp^R$ | from - 580 to + 459 | This study |
| pPr-*XCC1990* | pFAJ1700-*lacZ*-pr*XCC1990*; $Tet^R$ $Amp^R$ | from - 500 to + 1 | This study |
| pPr-*XCC3209* | pFAJ1700-*lacZ*-pr*XCC3209*; $Tet^R$ $Amp^R$ | from - 500 to + 1 | This study |

| Strains | Genotype and/or phenotype | Location of insertion or deletion relative to the putative start codon | Reference |
|---|---|---|---|
| *Xcc*568 | Wild-type strain; Rifampycin resistant strain derivative of *Xanthomonas campestris* pv. *campestris* LMG568/ATCC33913 | | [113] |
| XP001 | *XCC0050*::pVO155; $Rif^R$ $Km^R$ | + 2473 | This study |
| XP002 | *XCC0098*::pVO155; $Rif^R$ $Km^R$ | + 784 | This study |
| XP003 | *XCC0119*::pVO155; $Rif^R$ $Km^R$ | + 1084 | This study |
| XP004 | *XCC0120*::pVO155; $Rif^R$ $Km^R$ | + 3119 | This study |
| XP005 | *XCC0158*::pVO155; $Rif^R$ $Km^R$ | + 691 | This study |
| XP006 | *XCC0304*::pVO155; $Rif^R$ $Km^R$ | + 765 | This study |
| XP007 | *XCC0305*::pVO155; $Rif^R$ $Km^R$ | + 1007 | This study |
| XP008 | *XCC0394*::pVO155; $Rif^R$ $Km^R$ | + 2082 | This study |
| XP009 | *XCC0397*::pVO155; $Rif^R$ $Km^R$ | + 406 | This study |
| XP010 | *XCC0531*::pVO155; $Rif^R$ $Km^R$ | + 736 | This study |
| XP011 | *XCC0674*::pVO155; $Rif^R$ $Km^R$ | + 1958 | This study |
| XP012 | *XCC0759*::pVO155; $Rif^R$ $Km^R$ | + 418 | This study |
| XP013 | *XCC0768*::pVO155; $Rif^R$ $Km^R$ | + 387 | This study |
| XP014 | *XCC0946*::pVO155; $Rif^R$ $Km^R$ | + 2091 | This study |
| XP015 | *XCC1037*::pVO155; $Rif^R$ $Km^R$ | + 502 | This study |
| XP016 | *XCC1041*::pVO155; $Rif^R$ $Km^R$ | + 1249 | This study |
| XP017 | *XCC1179*::pVO155; $Rif^R$ $Km^R$ | + 1632 | This study |
| XP018 | *XCC1258*::pVO155; $Rif^R$ $Km^R$ | + 2524 | This study |
| XP019 | *XCC1340*::pVO155; $Rif^R$ $Km^R$ | + 1205 | This study |
| XP020 | *XCC1391*::pVO155; $Rif^R$ $Km^R$ | + 878 | This study |
| XP021 | *XCC1719*::pVO155; $Rif^R$ $Km^R$ | + 244 | This study |
| XP022 | *XCC1749*::pVO155; $Rif^R$ $Km^R$ | + 966 | This study |
| XP023 | *XCC1750*::pVO155; $Rif^R$ $Km^R$ | + 1657 | This study |
| XP024 | *XCC1751*::pVO155; $Rif^R$ $Km^R$ | + 304 | This study |
| XP025 | *XCC1892*::pVO155; $Rif^R$ $Km^R$ | + 1274 | This study |
| XP026 | *XCC2046*::pVO155; $Rif^R$ $Km^R$ | + 200 | This study |
| XP027 | *XCC2208*::pVO155; $Rif^R$ $Km^R$ | + 2036 | This study |
| XP028 | *XCC2385*::pVO155; $Rif^R$ $Km^R$ | + 1285 | This study |
| XP029 | *XCC2395*::pVO155; $Rif^R$ $Km^R$ | + 1258 | This study |
| XP030 | *XCC2400*::pVO155; $Rif^R$ $Km^R$ | + 2355 | This study |
| XP031 | *XCC2469*::pVO155; $Rif^R$ $Km^R$ | + 201 | This study |
| XP032 | *XCC2497*::pVO155; $Rif^R$ $Km^R$ | + 1880 | This study |
| XP033 | *XCC2572*::pVO155; $Rif^R$ $Km^R$ | + 830 | This study |
| XP034 | *XCC2573*::pVO155; $Rif^R$ $Km^R$ | + 866 | This study |
| XP035 | *XCC2658*::pVO155; $Rif^R$ $Km^R$ | + 1556 | This study |
| XP036 | *XCC2665*::pVO155; $Rif^R$ $Km^R$ | + 780 | This study |
| XP037 | *XCC2772*::pVO155; $Rif^R$ $Km^R$ | + 833 | This study |
| XP038 | *XCC2828*::pVO155; $Rif^R$ $Km^R$ | + 2871 | This study |
| XP039 | *XCC2867*::pVO155; $Rif^R$ $Km^R$ | + 293 | This study |
| XP040 | *XCC2887*::pVO155; $Rif^R$ $Km^R$ | + 1558 | This study |
| XP041 | *XCC2944*::pVO155; $Rif^R$ $Km^R$ | + 334 | This study |
| XP042 | *XCC3036*::pVO155; $Rif^R$ $Km^R$ | + 451 | This study |

| | | | |
|---|---|---|---|
| XP043 | *XCC3043*::pVO155; Rif$^R$ Km$^R$ | + 428 | This study |
| XP044 | *XCC3045*::pVO155; Rif$^R$ Km$^R$ | + 1572 | This study |
| XP045 | *XCC3046*::pVO155; Rif$^R$ Km$^R$ | + 702 | This study |
| XP046 | *XCC3050*::pVO155; Rif$^R$ Km$^R$ | + 295 | This study |
| XP047 | *XCC3067*::pVO155; Rif$^R$ Km$^R$ | + 929 | This study |
| XP048 | *XCC3079*::pVO155; Rif$^R$ Km$^R$ | + 1195 | This study |
| XP049 | *XCC3161*::pVO155; Rif$^R$ Km$^R$ | + 835 | This study |
| XP050 | *XCC3177*::pVO155; Rif$^R$ Km$^R$ | + 723 | This study |
| XP051 | *XCC3215*::pVO155; Rif$^R$ Km$^R$ | + 365 | This study |
| XP052 | *XCC3216*::pVO155; Rif$^R$ Km$^R$ | + 397 | This study |
| XP053 | *XCC3270*::pVO155; Rif$^R$ Km$^R$ | + 747 | This study |
| XP054 | *XCC3271*::pVO155; Rif$^R$ Km$^R$ | + 961 | This study |
| XP055 | *XCC3279*::pVO155; Rif$^R$ Km$^R$ | + 1481 | This study |
| XP056 | *XCC3316*::pVO155; Rif$^R$ Km$^R$ | + 2262 | This study |
| XP057 | *suxA*::pVO; *XCC3358*::pVO155; Rif$^R$ Km$^R$ | + 817 | This study |
| XP058 | *XCC3405*::pVO155; Rif$^R$ Km$^R$ | + 1813 | This study |
| XP059 | *XCC3408*::pVO155; Rif$^R$ Km$^R$ | + 1897 | This study |
| XP060 | *XCC3427*::pVO155; Rif$^R$ Km$^R$ | + 2236 | This study |
| XP061 | *XCC3474*::pVO155; Rif$^R$ Km$^R$ | + 1443 | This study |
| XP062 | *XCC3518*::pVO155; Rif$^R$ Km$^R$ | + 452 | This study |
| XP063 | *XCC3595*::pVO155; Rif$^R$ Km$^R$ | + 2148 | This study |
| XP064 | *XCC3635*::pVO155; Rif$^R$ Km$^R$ | + 367 | This study |
| XP065 | *XCC3714*::pVO155; Rif$^R$ Km$^R$ | + 922 | This study |
| XP066 | *XCC3963*::pVO155; Rif$^R$ Km$^R$ | + 1243 | This study |
| XP067 | *XCC4052*::pVO155; Rif$^R$ Km$^R$ | + 1673 | This study |
| XP068 | *XCC4120*::pVO155; Rif$^R$ Km$^R$ | + 1217 | This study |
| XP069 | *XCC4131*::pVO155; Rif$^R$ Km$^R$ | + 952 | This study |
| XP070 | *XCC4132*::pVO155; Rif$^R$ Km$^R$ | + 2804 | This study |
| XP071 | *XCC4162*::pVO155; Rif$^R$ Km$^R$ | + 952 | This study |
| XP072 | *XCC4222*::pVO155; Rif$^R$ Km$^R$ | + 2401 | This study |
| XP073 | *XCC4235*::pVO155; Rif$^R$ Km$^R$ | + 1405 | This study |
| XP074 | *XCC4237*::pVO155; Rif$^R$ Km$^R$ | + 225 | This study |
| XP075 | *XCC1990*Δ1; Rif$^R$ | from + 1 to + 2619 | This study |
| XP076 | *XCC3209*Δ1; Rif$^R$ | from + 1 to + 2715 | This study |
| XP077 | *fur*1; *XCC1470* T212A leading to L71Q; Rif$^R$ | T212A leading to L71Q | This study |
| XP078 | *Xcc*568 (pL-*fur*); *Xcc*568 (pL-*XCC1470*); Rif$^R$ Tet$^R$ Amp$^R$ | | This study |
| XP079 | *fur*1 (pL-*fur*); *XCC1470* T212A (pL-*XCC1470*); Rif$^R$ Tet$^R$ Amp$^R$ | | This study |
| XP080 | *Xcc*568 (pPr-*XCC1990*); Rif$^R$ Tet$^R$ Amp$^R$ | | This study |
| XP081 | *Xcc*568 (pPr-*XCC3209*); Rif$^R$ Tet$^R$ Amp$^R$ | | This study |
| XP082 | *hrpG*::pVO; *XCC1166*::pVO155; Rif$^R$ Km$^R$ | + 487 | [113] |
| XP083 | *hrpX*::pVO; *XCC1167*::pVO155; Rif$^R$ Km$^R$ | + 1013 | This study |
| XP084 | *suxR*::pVO; *XCC3356*::pVO155; Rif$^R$ Km$^R$ | + 350 | This study |
| XP085 | *suxC*::pVO; *XCC3357*::pVO155; Rif$^R$ Km$^R$ | + 896 | This study |
| XP086 | *suxB*::pVO; *XCC3359*::pVO155; Rif$^R$ Km$^R$ | + 757 | This study |
| XP087 | Δ*suxA*; *XCC3358*Δ1; Rif$^R$ | from + 474 to + 2475 | This study |
| XP088 | Δ*suxB*; *XCC3359*Δ1; Rif$^R$ | from + 1 to +1914 | This study |
| XP089 | *Xcc*568 (pL-*suxA*); *Xcc*568 (pL-*XCC3358*); Rif$^R$ Tet$^R$ | | This study |
| XP090 | *suxA*::pVO (pL-*suxA*); *XCC3358*::pVO155 (pL-*XCC3358*); Rif$^R$ Km$^R$ Tet$^R$ | | This study |
| XP091 | Δ*suxA* (pL-*suxA*); *XCC3358*Δ1 (pL-*XCC3358*); Rif$^R$ Tet$^R$ | | This study |
| XP092 | *Xcc*568 (pL-*suxB*); Xcc568 (pL-*XCC3359*); Rif$^R$ Tet$^R$ | | This study |
| XP093 | *suxA*::pVO (pL-*suxB*); *XCC3358*::pVO (pL-*XCC3359*); Rif$^R$ Km$^R$ Tet$^R$ | | This study |
| XP094 | Δ*suxB* (pL-*suxB*); *XCC3359*Δ1 (pL-*XCC3359*); Rif$^R$ Tet$^R$ | | This study |
| XP095 | *Xcc*568 (pPr-*suxA*); Xcc568 (pPr-*XCC3358*); Rif$^R$ Tet$^R$ Amp$^R$ | | This study |
| XP096 | *suxR*::pVO (pPr-*suxA*); *XCC3356*::pVO155 (pPr-*XCC3358*); Rif$^R$ Km$^R$ Tet$^R$ Amp$^R$ | | This study |
| XP097 | *suxC*::pVO (pPr-*suxA*); *XCC3357*::pVO155 (pPr-*XCC3358*); Rif$^R$ Km$^R$ Tet$^R$ Amp$^R$ | | This study |
| XP098 | Δ*suxA* (pPr-*suxA*); *XCC3358*Δ1 (pPr-*XCC3358*); Rif$^R$ Tet$^R$ Amp$^R$ | | This study |
| XP099 | Δ*suxB* (pPr-*suxA*); *XCC3359*Δ1 (pPr-*XCC3358*); Rif$^R$ Tet$^R$ Amp$^R$ | | This study |
| XP100 | *XCC0008*::pVO155; Rif$^R$ Km$^R$ | + 425 | This study |
| XP101 | *XCC1592*::pVO155; Rif$^R$ Km$^R$ | + 293 | This study |
| XP102 | *XCC1593*::pVO155; Rif$^R$ Km$^R$ | + 243 | This study |
| XP103 | *XCC2081*::pVO155; Rif$^R$ Km$^R$ | + 143 | This study |
| XP104 | *XCC2612*::pVO155; Rif$^R$ Km$^R$ | + 124 | This study |
| XP105 | *XCC2927*Δ1; Rif$^R$ | from +3 to + 876 | This study |
| XP106 | *XCC3205*::pVO155; Rif$^R$ Km$^R$ | + 704 | This study |
| XP107 | *XCC3967*::pVO155; Rif$^R$ Km$^R$ | + 274 | This study |