Research Article

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Plant Growth Promoting Rhizobacteria (PGPR) Regulated Phyto and Microbial Beneficial Protein Interactions

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Abstract: Plant Growth Promoting Rhizobacteria (PGPR) influence plants' physiological characteristics, metabolites, pathways and proteins via alteration of corresponding gene expression. In the current study, a total of 42 upregulated uncharacterized sorghum bicolor root proteins influenced by PGPR were subjected to different analyses: phylogenetic tree, protein functional network, sequences similarity network (SSN), Genome Neighborhood Network (GNN) and motif analysis. The screen for homologous bacterial proteins to uncover associated protein families and similar proteins in non-PGPRs was identified. The sorghum roots' uncharacterized protein sequences analysis indicated the existence of two protein categories, the first being related to phytobeneficial protein family associated with DNA regulation such as Sulfatase, FGGY_C, Phosphodiesterase or stress tolerance such as HSP70. The second is associated with bacterial transcriptional regulators such as FtsZ, MreB_Mbl and DNA-binding transcriptional regulators, as well as the AcrR family, which existed in PGPR and non PGPR. Therefore, Plant Growth-Promoting Rhizobacteria (PGPR) regulated phytobeneficial traits through reciprocal protein stimulation via microbe plant interactions, both during and post colonization.

Keywords: Plant Growth promoting rhizobacteria, Sorghum, phylogenetic analysis, protein family, microbe interactions

1 Introduction

The successful use of Plant-Growth-Promoting Rhizobacteria (PGPR) in agriculture is correlated with reciprocal gene regulation between bacteria and plants during plant colonization. This gene regulation exerts phytobeneficial results on biomass, nutrient uptake and metabolite upregulation [1-5] on proteins and biological pathways [6], as well as on gene expression [7]. In the current study, the PGPR—*Pseudomonas* sp. TLC 6-6.5-4—as previously used [1] was applied to two-day-old sorghum seedlings to check the function of upregulated, uncharacterized root proteins three months after PGPR colonization. The study's main objective was to reveal the function of uncharacterized sorghum bicolor proteins in roots treated with PGPR. In order to identify the functions of these proteins, several steps were conducted. Sorghum root uncharacterized protein sequences were used in a Blast search for homologous protein sequences in bacteria, since they were unidentified in plant protein sequences. In total, 564 proteins were subjected to several analyses to determine their possible role in phytobeneficial traits. The analyses included the following: sequence similarity network (SSN), Genome Neighborhood Network (GNN), functional network and motif identification. The sorghum roots' uncharacterized protein analysis revealed the existence of protein families belonging to plant, Plant-Growth-Promoting Rhizobacteria (PGPR) and Non-Plant-Growth-Promoting Rhizobacteria (non-PGPR), thus emphasizing the role of microbe plant interactions during and post colonization.

2 Material and methods

2.1 Plant growth conditions and treatments

Two-day-old germinated seedlings of sorghum bicolor were inoculated with PGPR *Pseudomonas* sp. TLC 6-6.5-4

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[1] for two hours, after which they were planted in 600 g of pasteurized mixed soil consisting of coarse sand and loam (1:1). *Pseudomonas* sp. TLC 6-6.5-4 was grown on Luria-Bertani (LB) agar for 48 h, harvested, suspended and dissolved in 120 ml of 0.85% NaCl solution to reach 10-8 cfu/mL, which was used for the sorghum seedling inoculation and was sprayed on the soil surface. The growth conditions for sorghum in a greenhouse were 14 hours of light, at 30°C and 65% humidity. The experiment consisted of seven sorghum bicolor treated with PGPR *Pseudomonas* sp. TLC 6-6.5-4 and seven untreated sorghum bicolor as a control. Sorghum bicolor plants were harvested after 90 days for root protein analyses. Roots were washed with distilled water to remove soil then frozen in liquid nitrogen. Protein was extracted from frozen roots; three samples for each group followed the procedure described in Dhawi et al. [6] and modified from Fukao et al. [8].

Three protein samples for each group (treated and control) were digested with trypsin and then analyzed using LC-MS/MS on a Waters/Micromass AB QSTAR Elite (Waters nano ACQUITY ultra high-pressure liquid chromatograph UPLC) for peptide separation. The detected peptides were quantified and normalized to obtain the abundance of each sample according to Progenesis QI (<http://www.nonlinear.com/progenesis/qi/v2.0/faq/hownormalisation-works.aspx>). Protein levels of two folds and above in comparison to the control were considered significant change to be consider in further analysis.

2.2 Sorghum root uncharacterized protein processing

The sequences of the 42 uncharacterized sorghum root proteins (Table 1) were used to search for homologous bacterial proteins using PSI Blast (<https://blast.ncbi.nlm.nih.gov/Blast.cgi?PAGE=Proteins>), which resulted in 830 protein sequences. These sequences were filtered using Cluster Database at High Identity with Tolerance (CD-HIT) Suite: Biological Sequence Clustering and Comparison (http://weizhongli-lab.org/cdhit_suite/cgi-bin/index.cgi) with a 90% identity cut-off. The 90% cut-off step resulted in 564 protein sequences for inclusion in the multiple sequence alignment (MSA). MSA was created by using the MEGA7 (Molecular Evolutionary Genetics Analysis) software version 6 [9]. The phylogenetic tree was established in MEGA 6 and aligned via the Muscle program for 564 proteins, 42 of which were sorghum root uncharacterized upregulated proteins. Protein sequences

Table 1. Uncharacterized sorghum proteins fold changes influenced by *Pseudomonas* sp. in comparison with control

Protein ID	Fold change
C5YZ77	5.5
C5XHS5	4.8
C5X5F0	4.7
C5XV25	4.1
C5XFI2	3.9
C5YUN2	3.7
C5XGS9	3.5
C5YPP6	3.2
C5XLV5	2.9
C5Y9B5	2.5
C5WXA4	2.3
C5YPX8	2.3
C5XC95	2.3
C5X4M5	2.3
C5WXN2	2.1
C5YBP8	1.9
C5Y921	1.9
C5XYX0	1.9
C5YC51	1.8
C5YU58	1.8
C5YR14	1.7
C5Y6L4	1.7
C5XG11	1.7
C5YAG2	1.7
C5YYY8	1.7
C5YDJ2	1.7
C5XCI9	1.7
C5YIX7	1.7
C5YYX1	1.7
C5WT78	1.6
C5WXD7	1.6
C5XG44	1.6
C5YXQ9	1.6
C5YEW3	1.6
C5Z7E8	1.6
C5Z1X3	1.6
C5YI64	1.6
C5WRP7	1.5
C5XHR8	1.5
C5Y651	1.5
C5XWM5	1.5
C5Z8A9	1.5

were aligned using neighbor-joining [10] and UPGMA (Unweighted Pair Group Method), with a bootstrap method of 500 replications for a phylogeny test. The interactive tree of life (iTol) online web tool (<http://itol.embl.de>) was then used to display and modify the tree colors [11].

3 Protein functional network and family assignment

A combination of different approaches was used to assign homologous proteins to protein families (Pfam) with a putative function. In total, 564 protein sequences consisting of sorghum root uncharacterized protein and similar bacterial protein sequences were used to determine functions via the genomic, protein and gene interactions through the sequence similarity network (SSN) and Genome Neighborhood Network (GNN) approach, respectively. The GNN approach was performed using the Enzyme Similarity Tool–Enzyme Function Initiative (EFI-EST) <https://efi.igb.illinois.edu/efi-est/> [12]. In order to use EFI-EST, the 564 proteins were converted to UniProt Id, resulting in 554 identified proteins in the UniProt database and 10 unidentified bacterial proteins. The EFI-EST website was used to generate a sequence similarity network (SSN), and the resulting files were visualized in Cytoscape software [13]. Sorghum protein

sequences were screened for motifs using the MEME (Multiple EM for Motif Elicitation) tool (<http://meme-suite.org/tools/meme>) [14], with a maximum number of eight motifs for the detection level and an E-value equal to or less than 0.05. Further analyses were performed for protein families using STRING Consortium 2019 (<https://string-db.org/>) [15].

4 Results

4.1 Phylogenetic tree analysis

The results showed 42 sorghum proteins according to UniProt (<http://www.uniprot.org/>), which were upregulated from 2–5-fold when compared to the control group. The 42 upregulated sorghum proteins have an unknown function; therefore, several analyses and different approaches were used to identify the function and check for similarity of these uncharacterized proteins with bacterial proteins via an NCBI search (<https://blast.ncbi.nlm.nih.gov/Blast.cgi>).

The phylogenetic tree of 564 protein sequences included 42 uncharacterized sorghum proteins and similar bacterial proteins aligned using Multiple Sequence alignments (MUSCLE) with a bootstrap of 500. The resulting unrooted phylogenetic tree consisted of

Figure 1. The phylogenetic tree of uncharacterized sorghum proteins and similar bacterial proteins. The unrooted neighbor-joining phylogenetic tree constructed based on 564 multiple proteins sequence alignment using MUSCLE with 500 bootstrap replicates.

20 nodes, in which sorghum uncharacterized protein sequences were clustered in five of them (Figure 1). The motif analysis of these sorghum and bacterial protein sequences clustered in the same nodes identified eight similar protein family domains represented by motif logos in Figure 2, namely, Sulfatase, CARBOHYDRATE KINASES (FGGY_C), Phosphodiester, Cell division protein FtsA, GSDH, MreB_Mbl, StbA and HSP70.

4.2 Sequence similarity network (SSN)

The SSN used to analyze 554 sequences consisted of 42 uncharacterized sorghum protein sequences and 507 bacterial protein sequences. These sequences were obtained by PSI-BLAST at E values of 10⁻¹⁵; the sequences were clustered based on their similarities in seven clusters. The SSN clusters containing sorghum proteins were cluster 1 (61 protein sequences), cluster 3 (23 sequences), cluster 5 (17 protein sequences), cluster 14 (seven protein sequences), cluster 16 (five protein sequences), cluster 19 (four protein sequences) and cluster 24 (three protein families) (Figure 3). Some proteins were separated with no clusters due to a different E value score. These SSN results were used to establish a Genome Neighborhood Network (GNN).

4.3 Genome Neighborhood Networks (GNN), motif screening and functional partners

The SSN results were used to build GNNs. The output of the GNN in the Hub–Nodes format showed the number of Pfam gene neighbors that were found in each cluster of sequences. The SSN revealed that uncharacterized protein sequences of sorghum were clustered in seven nodes. The nodes included 1, 3, 5, 14, 16, 19 and 24 protein families, arranged based on their genomic context (Fig.4). Nodes shared 86 protein families (See appendix Table1). On the other hand, the motif scan analysis of sorghum root proteins identified four main protein families: HSP70, MreB_Mbl, StbA and FtsA (Figure 4). The functional protein association network analysis using STRING 2019 predicted nine functional partners. These functional partners were N-acetyltransferase, the GNAT superfamily (includes histone acetyltransferase HPA2), DNA-binding transcriptional regulator, AcrR family; MFS family permease, SAM-dependent methyltransferase, DNA-binding transcriptional regulator, ArsR family, cAMP-binding domain of CRP or a regulatory subunit of cAMP-dependent protein kinases, glycosyltransferase involved in cell wall biosynthesis, signal transduction histidine kinase, and sugar kinase of the NBD/HSP70 family containing an N-terminal HTH domain (Figure 5).

Figure 2. The phylogenetic tree of uncharacterized sorghum proteins and similar bacterial proteins. The unrooted neighbor-joining phylogenetic tree constructed based on the sequence alignment of 564 multiple proteins using Multiple Sequence alignments (MUSCLE) with 500 bootstrap replicates.

Figure 3. a) Sequence similarity network of uncharacterized sorghum and similar bacterial proteins consisting of 564 sequences at an E value of 10^{-15} . b) Sorghum uncharacterized proteins clustered in seven groups, with different protein nodes. Each node (circle) represents proteins with similar sequences; the lines indicate the pairwise relationship between sequences. Proteins that have no sorghum sequences appeared as separated and are not labelled.

Figure 4. a) Genome Neighborhood Networks (GNNs) in the Hub–Nodes format for 564 protein sequences. b) The hexagon shapes (hubs) represent sequence similarity network (SSN) clusters, and the other shapes (nodes) represent the Pfam genome neighbors. Seven node clusters are indicated with 94 genes. The names of nodes are the short name of the protein family (Pfam).

Figure 5. The functional protein association networks for 86 protein families resulting from GNN using the STRING Consortium 2019 functional protein association networks (<https://string-db.org/>) Szklarczyk et al., [15].

5 Discussion

The phylogenetic tree analysis of the 20 nodes identified that five nodes were sorghum proteins clustered with similar bacterial proteins. The motif analysis of these sorghum and bacterial protein sequences clustered in the same nodes revealed six protein family domains (Sulfatase, CARBOHYDRATE KINASES (FGGY _C), Phosphodiesterase, FtsZ, MreB_Mbl and HSP70). Some members of this protein family have no eukaryotic existence, but this might have remained in root cells following plant treatment and may play an intrinsic role. This resulted in phytobeneficial traits such as tolerance to salinity [16], heavy metal [1, 2], and drought [17], or increased plant biomass under normal environmental conditions [18]. Similarly, the results of SNN, GNN and STRING protein functional networks of sorghum root proteins identified the main protein families: HSP70, MreB_Mbl, StbA and FtsA. Therefore, protein analysis revealed the existence of protein families belonging to plant, Plant-Growth-Promoting Rhizobacteria (PGPR) and Non-Plant-Growth-Promoting Rhizobacteria (non-PGPR), thus emphasizing the reciprocal benefit synchronized *between plant and bacteria during and post colonization*.

5.1 Phytobeneficial proteins induced by PGPR:

Plant-Growth-Promoting Rhizobacteria (PGPR) induced several phytobeneficial and desired traits such as an increase in production or tolerance during biotic or abiotic stress [19]. The beneficial effect is associated with an increase in gene expression and certain protein families such as sulfatase substrates, which are involved in hormone regulation, cellular degradation and the modulation of signaling pathways. The increase of element compositions post plant inoculation with PGPR might be explained by sulfatase’s ability to cycle environmental sulfur via degradation or cellular remodeling [20]. The increase of biomass in plants is associated with the increased sugars and carbohydrates represented in this study due to an increase in the Carbohydrate kinases (FGGY _C) protein family, which is involved in bacterial signaling molecules [21]. In addition, FGGY carbohydrate kinases contributed plant adenosine and thriphosphate (ATP)-dependent phosphorylation of nine distinct sugar enzymes. These enzymes include L-fucolokinase, gluconokinase, glycerol kinase, xylulokinase, D-ribulose kinase and L-xylulose kinase [22]. In the current

study, we identified two distinct protein families, Phosphodiesterase and Heat Shock Protein 70 (Hsp70), that are known to contribute to high plant tolerance. Phosphodiesterase is involved in independent pathways of DNA–protein crosslink repair in plants [23]. However, Heat Shock Protein 70 (Hsp70) is an evolutionarily conserved family of proteins that is typically localized in the cytoplasm and distributed in the intermembrane space of chloroplasts. Hsp70 plays a crucial role in protein biogenesis, protection during stress, assistance in protein translocation [24], protection against several stress types, and the maintenance of cellular homeostasis [25]. The upregulation of several sorghum proteins associated with an increase in N-acetyltransferase, the GNAT superfamily (including histone acetyltransferase HPA2) was observed in the current study, and this is believed to be involved in the regulation of the transcription of many genes [26].

5.2 Rhizobacterial transcriptional regulators

Several protein families related to bacteria were found in sorghum roots post plant inoculation that work as functional gene regulators. Some of these proteins were identified in a previous study and are known to contribute to phytobeneficial traits related to PGPR [7]. Other proteins are known as bacterial proteins induced by plant root exudates and participate in the bacterial gene regulation of PGPR, such as *Bacillus atrophaeus* [27]. Some of the predicted functionally related bacterial protein families are known bacterial transcriptional regulators, such as FtsZ, MreB_Mbl, DNA-binding transcriptional regulator and the AcrR family, as shown by the results of the current study. These functionally related protein families are MFS family permease, SAM-dependent methyltransferase, S-adenosyl methionine (SAM), DNA-binding transcriptional regulator, ArsR family transcriptional regulator, the cAMP-binding domain of CRP or a regulatory subunit of cAMP-dependent protein kinases, DNA-binding and transcription regulation, glycosyltransferase, and histidine kinases (HKs).

The family of FtsZ is a bacterial membrane tubulin-related cell division protein [28]. MreB/Mbl is a gene-coding protein related to the bacterial protein FtsZ cell membrane protein [29]. Additionally, the analysis identified possible roles of the bacteria–DNA-binding transcriptional regulators known as the AcrR family [30] and the association of amino acid transfer proteins known as MFS family permease [31]. Thus, we emphasized the role of plant root exudates in enhancing bacterial growth activity via the activation of functional partner proteins

such as SAM-dependent methyltransferase S-adenosyl methionine (SAM), which is known to transfer the methyl group to DNA [32]. The DNA-binding transcriptional regulator and ArsR family transcriptional regulator are involved in lipid metabolism regulation [33], cAMP-dependent protein kinase DNA-binding and transcription regulation [34], while glycosyltransferase is involved in cell wall biosynthesis [35], and histidine kinases (HKs) are known to function in bacterial signal transduction [36].

6 Conclusion

Plant Growth Promoting Rhizobacteria (PGPR) regulated phytobeneficial traits by reciprocal protein stimulation via microbe–plant interactions during and post colonization. Furthermore, plant root exudates stimulated bacterial gene regulators associated with bacterial signaling, DNA-binding transcriptional regulators, and cell growth.

Data Availability: Data that are supplementary to the manuscript will be available by request.

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Conflict of interest: Authors state no conflict of interest.

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Appendix

Table 2. The protein families (Pfam) and their description resulted from analysis on Genome Neighbourhood Networks GNN in Hub-Nodes format from 564 protein sequences resulted in seven node clusters indicated with 86 genes.

Pfam	Pfam Description
Node 1	
HrcA	HrcA protein C terminal domain
GrpE	Factor GrpE domain
Node 14	
Ribonuc_L-PSP	Endoribonuclease L-PSP
Amidohydro_1	Amidohydrolase family
Abhydrolase_3	alpha/beta hydrolase fold
Ycel	Ycel-like domain
SnoaL_2	Snoal-like domain
DUF1643	Protein of unknown function (DUF1643)
Flavodoxin_2	Flavodoxin-like fold
Pyr_redox_3	Pyridine nucleotide-disulphide oxidoreductase
Glyco_hydro_3-Glyco_hydro_3_C	Glycosyl hydrolase family 3 N terminal domain-Glycosyl hydrolase family 3 C-terminal domain
Pkinase	Protein kinase domain
Cupin_1	Cupin
Response_reg-Trans_reg_C	Response regulator receiver domain-Transcriptional regulatory protein, C terminal
Chlorophyllase2	Chlorophyllase enzyme
STAS_2	STAS domain
DNA_ligase_A_M-DNA_ligase_A_C	ATP dependent DNA ligase domain-ATP dependent DNA ligase C terminal region
DNA_primase_S	DNA primase small subunit
PQQ_2	PQQ-like domain
SpolIE	Stage II sporulation protein E (SpolIE)
HisKA-HATPase_c	His Kinase A (phospho-acceptor) domain-Histidine kinase-, DNA gyrase B-, and HSP90-like ATPase
ABC_tran	ABC transporter
ABC2_membrane_2	ABC-2 family transporter protein
Peptidase_A24-DiS_P-DiS	Type IV leader peptidase family-Bacterial Peptidase A24 N-terminal domain
HisKA-HATPase_c-PAS_4	His Kinase A (phospho-acceptor) domain-Histidine kinase-, DNA gyrase B-, and HSP90-like ATPase-PAS fold
Cupin_2	Cupin domain
Pkinase-PD40	Protein kinase domain-WD40-like Beta Propeller Repeat
PBP-DUF1028	Phosphatidylethanolamine-binding protein-Family of unknown function (DUF1028)
Mce4_CUP1	Cholesterol uptake porter CUP1 of Mce4, putative
MlaD	MlaD protein
MlaD-Mce4_CUP1	MlaD protein-Cholesterol uptake porter CUP1 of Mce4, putative
RelE	RelE toxin of RelE / RelB toxin-antitoxin system
VirC1	VirC1 protein
AAA_31	AAA domain
T4SS-DNA_transf	Type IV secretory system Conjugative DNA transfer
PRiA4_ORF3	Plasmid pRI4b ORF-3-like protein
GntR-FCD	Bacterial regulatory proteins, gntR family-FCD domain

Pfam	Pfam Description
Transp_cyt_pur	Permease for cytosine/purines, uracil, thiamine, allantoin
Resolvase	Resolvase, N terminal domain
DUF4158	Domain of unknown function (DUF4158)
HTH_31	Helix-turn-helix domain
DDE_Tnp_Tn3	Tn3 transposase DDE domain
Flavin_Reduct	Flavin reductase like domain
Asp_Glu_race	Asp/Glu/Hydantoin racemase
Node 16	
PTS-HPr	PTS HPr component phosphorylation site
Glyco_hydro_32N-Glyco_hydro_32C	Glycosyl hydrolases family 32 N-terminal domain-Glycosyl hydrolases family 32 C terminal
Hydrolase_3	haloacid dehalogenase-like hydrolase
tRNA-synt_1-Anticodon_1	tRNA synthetases class I (I, L, M and V)-Anticodon-binding domain of tRNA
Peptidase_C26	Peptidase C26
23S_rRNA_IVP	23S rRNA-intervening sequence protein
Trans_reg_C	Transcriptional regulatory protein, C terminal
Phage_integrase-Arm-DNA-bind_4-Phage_int_SAM_3	Phage integrase family-Arm DNA-binding domain-Phage integrase, N-terminal SAM-like domain
PTS_EIIB-PTS_EIIC	phosphotransferase system, EIIB-Phosphotransferase system, EIIC
Vsr-DUF559	DNA mismatch endonuclease Vsr-Protein of unknown function (DUF559)
LacI-Peripla_BP_3	Bacterial regulatory proteins, lacI family-Periplasmic binding protein-like domain
ATP-cone-NRDD	ATP cone domain-Anaerobic ribonucleoside-triphosphate reductase
PDDEXK_9-AAA-ATPase_like	PD-(D/E)XK nuclease superfamily-Predicted AAA-ATPase
BPD_transp_1	Binding-protein-dependent transport system inner membrane component
Sulfate_transp-STAS	Sulfate permease family-STAS domain
DEAD-Helicase_C-HRDC-RecQ_Zn_bind	DEAD/DEAH box helicase-Helicase conserved C-terminal domain-HRDC domain-RecQ zinc-binding
ECF-ribofla_trS	ECF-type riboflavin transporter, S component
Node 19	
Plug-CarboxypepD_reg_2	TonB-dependent Receptor Plug Domain-CarboxypepD_reg-like domain
Hexapep	Bacterial transferase hexapeptide (six repeats)
GSHPx	Glutathione peroxidase
MarR	MarR family
Pyr_redox_2-Reductase_C	Pyridine nucleotide-disulphide oxidoreductase-Reductase C-terminal
OsmC	OsmC-like protein
DEDD_Tnp_IS110-Transposase_20	Transposase-Transposase IS116/IS110/IS902 family
Aldo_ket_red	Aldo/keto reductase family
Node 24	
VCBS	Repeat domain in Vibrio, Colwellia, Bradyrhizobium and Shewanella
Asn_synthase-GATase_7	Asparagine synthase-Glutamine amidotransferase domain
UvrA_DNA-bind-UvrA_inter	UvrA DNA-binding domain-UvrA interaction domain
adh_short_C2	Enoyl-(Acyl carrier protein) reductase
E1_dh-Transket_pyr-Transketolase_C	Dehydrogenase E1 component-Transketolase, pyrimidine binding domain-Transketolase, C-terminal domain
Lysine_decarbox	Possible lysine decarboxylase
HEM4	Uroporphyrinogen-III synthase HemD
ALAD	Delta-aminolevulinic acid dehydratase

Pfam	Pfam Description
ACP_syn_III_C-ACP_syn_III	3-Oxoacyl-[acyl-carrier-protein (ACP)] synthase III C terminal -3-Oxoacyl-[acyl-carrier-protein (ACP)] synthase III
UnbV_ASPIc-VCBS	ASPIc and UnbV-Repeat domain in <i>Vibrio</i> , <i>Colwellia</i> , <i>Bradyrhizobium</i> and <i>Shewanella</i>
PseudoU_synth_2	RNA pseudouridylate synthase
HisKA-HATPase_c-PAS_3-PAS_4	His Kinase A (phospho-acceptor) domain-Histidine kinase-, DNA gyrase B-, and HSP90-like ATPase-PAS fold-PAS fold
Polysacc_deac_1	Polysaccharide deacetylase
Glyco_hydro_11	Glycosyl hydrolases family 11
Response_reg-Sigma54_activat-HTH_8	Response regulator receiver domain-Sigma-54 interaction domain-Bacterial regulatory protein, Fis family
Aminotran_3	Aminotransferase class-III
AMP-binding-PP-binding	AMP-binding enzyme-Phosphopantetheine attachment site