

Demystifying Polyphosphate-Accumulating Organisms Relevant to Wastewater Treatment: A Review of Their Phylogeny, Metabolism, and Detection

Lucia Ruiz-Haddad^{a,b}, Muhammad Ali^c, Mario Pronk^d, Mark C.M. van Loosdrecht^d, Pascal E. Saikaly^{a,b,*}

^aEnvironmental Science and Engineering Program, Biological and Environmental Science and Engineering Division, King Abdullah University of Science and Technology, Thuwal 23955-6900, Saudi Arabia

^bWater Desalination and Reuse Center, Biological and Environmental Science and Engineering Division, King Abdullah University of Science and Technology, Thuwal 23955-6900, Saudi Arabia

^cDepartment of Civil, Structural & Environmental Engineering, Trinity College Dublin, The University of Dublin, Dublin 2, Ireland

^dDepartment of Biotechnology, Delft University of Technology, Delft 2629 HZ, The Netherlands

*Correspondence: PE Saikaly, Environmental Science and Engineering Program, Water Desalination and Reuse Center, Biological and Environmental Science and Engineering Division, King Abdullah University of Science and Technology, Thuwal 23955-6900, Saudi Arabia.

E-mail: pascal.saikaly@kaust.edu.sa

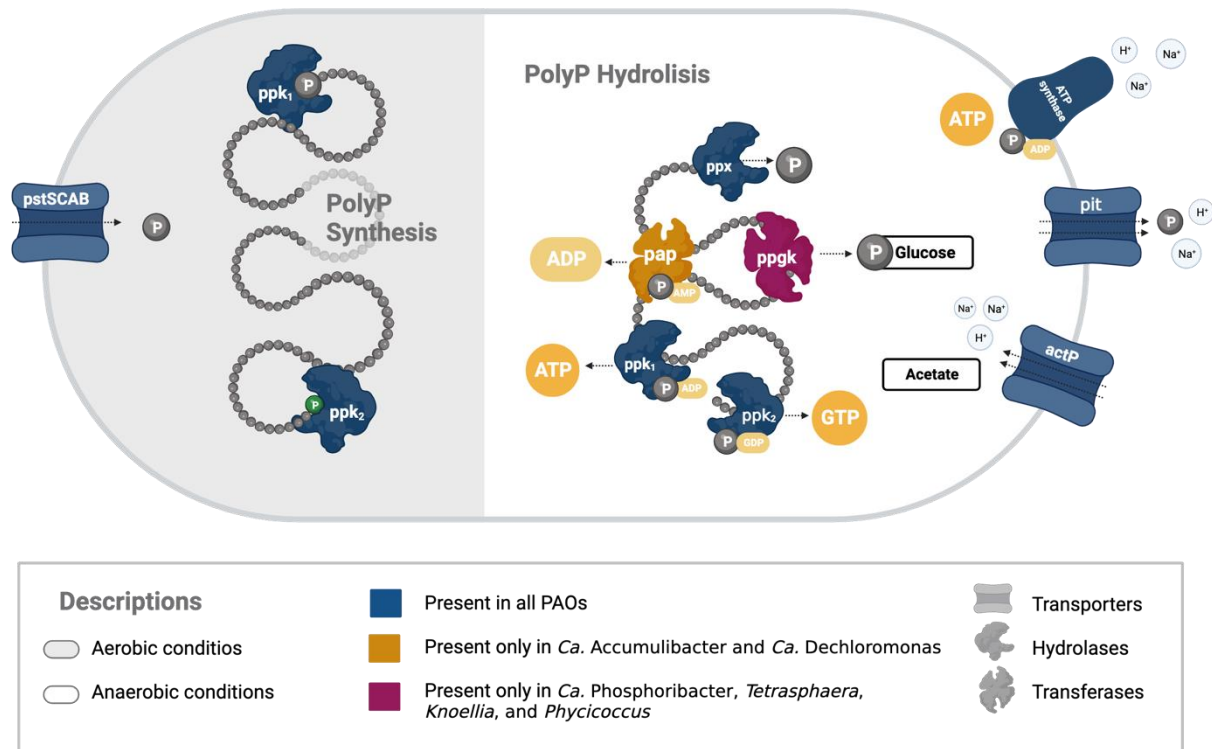


Fig. S1. PolyP synthesis, PolyP hydrolysis, P uptake, and acetate transport. During anaerobic conditions, PolyP hydrolysis in PAOs can be mediated by polyphosphate kinases (encoded by *ppks*) and exopolyphosphatases (encoded by *ppxs*). Among them, PPK1 catalyzes ATP formation, and PPK2 favors GTP formation, both utilizing the phosphate (P) from PolyP. PPX enzymes hydrolyze PolyP from the polymer ends to release P, which can be expelled from the cell along with cations using the low-affinity P transporter (encoded by *pit*). These cations can then re-enter the cell through the acetate transporter (encoded by *actP*) or ATP synthase. The acetate transporter (encoded by *actP*) acts as a symporter, facilitating the co-transport of acetate and cations, while ATP generation takes place through cation influx, supplying energy for cellular processes. PolyP can also undergo degradation through the transfer of terminal P groups to acceptor molecules. This process involves PolyP-AMP phosphotransferase (encoded by *pap*), transferring P groups from PolyP to AMP, and a PolyP glucokinase (encoded by *ppgk*) phosphorylating glucose using P from PolyP. During aerobic conditions, the cellular uptake of P is facilitated by the high-affinity transporter encoded by *pstSCAB*. Additionally, PolyP synthesis takes place through the enzymatic activity of polyphosphate kinases (encoded by *ppk* genes).

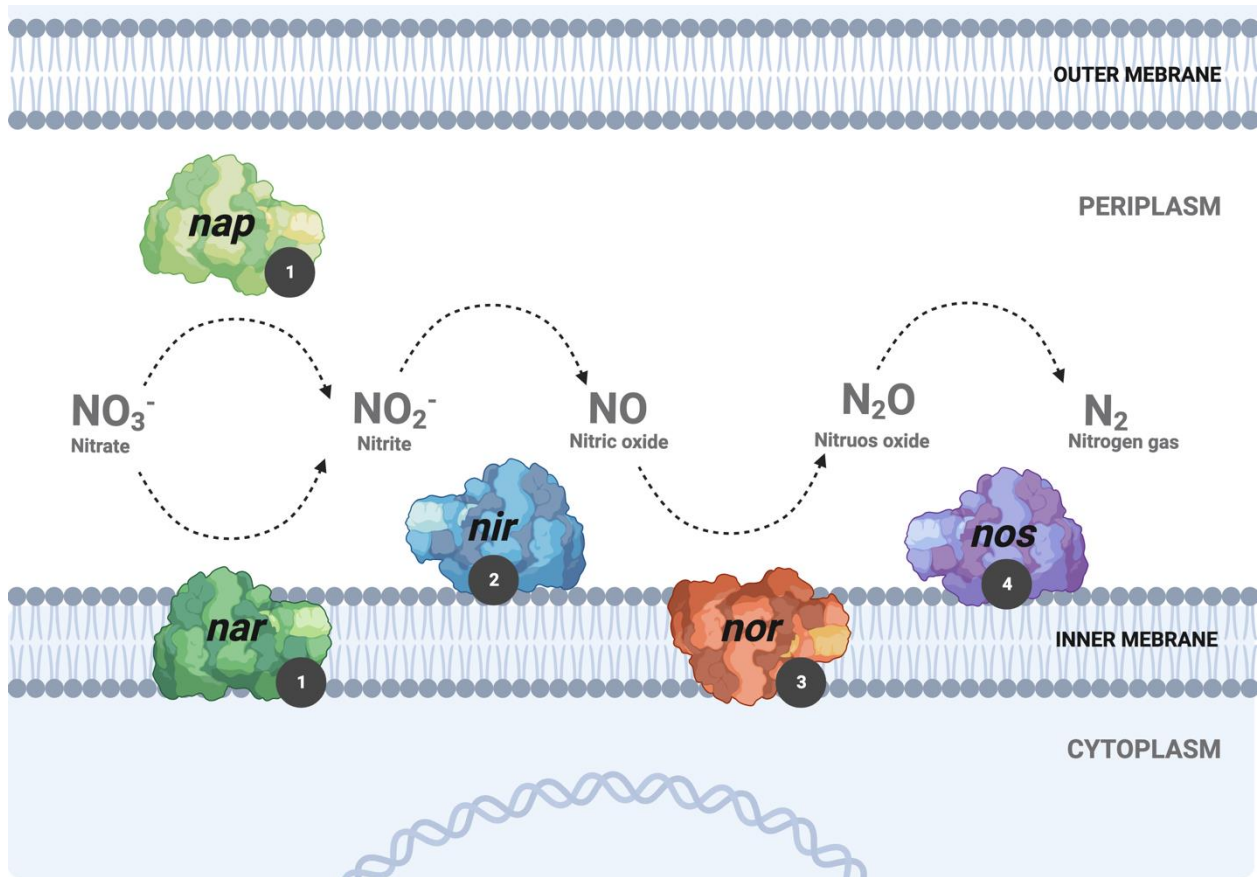


Fig. S2. Denitrification schematic. Nitrate (NO_3^-) reduction to nitrite (NO_2^-) can be done either by the periplasmic nitrate reductase (*nap*) or the transmembrane respiratory nitrate reductase (*nar*). The second step includes *nir* enzyme that catalyzes the conversion of NO_2^- into nitric oxide (NO). In the third step, *nor* catalyzes the reduction of NO to nitrous oxide (N_2O). Finally, *nos* completes the denitrification by reducing N_2O to nitrogen gas (N_2).

Table S1. Accession numbers from NCBI for the available PAOs.

Organism	ACC		
<i>Ca. Accumulibacter phosphatis</i> Bin19	GCA_005889575.1	Type and Clades classification for <i>Ca. Accumulibacter</i>	
<i>Ca. Accumulibacter phosphatis</i> HKU2	GCA_000987395.1		
<i>Ca. Accumulibacter cognatus</i> SSA1	GCA_013414765.1		
<i>Ca. Accumulibacter cognatus</i> SK-02	GCA_000584975.2		
<i>Ca. Accumulibacter</i> UW6	GCA_017592725.1		
<i>Ca. Accumulibacter</i> UW11-POB	GCA_017302385.1		
<i>Ca. Accumulibacter vicinus</i>	GCA_000584955.2		
<i>Ca. Accumulibacter vicinus</i> UBA5574	GCA_002425405.1		
<i>Ca. Accumulibacter</i> contiguous SBR-L	GCA_012940005.1		
<i>Ca. Accumulibacter</i> Fred-II3C-720	GCA_016713625.1		
<i>Ca. Accumulibacter</i> necessities UW12-POB	GCA_017302435.1		
<i>Ca. Accumulibacter</i> OdNE-BAT3C-415	GCA_016714935.1		
<i>Ca. Accumulibacter</i> UW10-POB	GCA_017302555.1		
<i>Ca. Accumulibacter</i> Hade BATACT26	GCA_016711725.1		
<i>Ca. Accumulibacter</i> iunctus UBA232A107	GCA_002345025.1		
<i>Ca. Accumulibacter</i> adjunctus SK-12	GCA_000585015.1		
<i>Ca. Accumulibacter</i> conexus UW7	GCA_017592775.1		
<i>Ca. Accumulibacter</i> Conexus UW13-POB	GCA_017302415.1		
<i>Ca. Accumulibacter</i> similis SSB1	GCA_013347225.1		
<i>Ca. Accumulibacter</i> SCELSE-1	GCA_005524045.1		
<i>Ca. Accumulibacter</i> UW8-POB	GCA_020445855.1		
<i>Ca. Accumulibacter</i> UW4	GCA_020445885.1		
<i>Ca. Accumulibacter</i> regalis BA-93	GCA_020445925.1		
<i>Ca. Accumulibacter</i> regalis CANDO-1	GCA_017302345.1		
<i>Ca. Accumulibacter</i> BA-92	GCA_017592785.1		
<i>Ca. Accumulibacter</i> phosphatis HKU1	GCA_000585075.1		
<i>Ca. Accumulibacter</i> phosphatis SBR-S	GCA_009467855.1		
<i>Ca. Accumulibacter</i> meliphilus UW-LDO	GCA_000585055.1		
<i>Ca. Accumulibacter</i> aalborgensis	GCA_000987445.1		
<i>Ca. Accumulibacter</i> UW5	GCA_012939955.1		
<i>Ca. Accumulibacter</i> UW9-POB	GCA_003332265.1		
<i>Ca. Dechloromonas</i> phosphorivorans Skiv	GCA_016721185.1		Type and Clades classification for <i>Ca. Accumulibacter</i>
<i>Ca. Dechloromonas</i> phosphorivorans EsbW	GCA_016709495.1		
<i>Ca. Dechloromonas</i> phosphorivorans OdNE	GCA_016714975.1		
<i>Ca. Dechloromonas</i> phosphoritropha Ribe	GCA_016722705.1		
<i>Ca. Phosphoribacter</i> baldrii Bjer	GCA_016708855.1	Formerly classified as <i>Tetrasphaera</i>	
<i>Ca. Phosphoribacter</i> baldrii EsbW	GCA_016709925.1		
<i>Ca. Phosphoribacter</i> baldrii AalW	GCA_016704565.1		
<i>Ca. Phosphoribacter</i> hodrii AalE	GCA_016705565.1		
<i>Ca. Phosphoribacter</i> hodrii Ribe	GCA_016722305.1		
<i>Tetrasphaera jenkinsii</i> Ben-74	GCA_001046875.1		
<i>Tetrasphaera jenkinsii</i> UW-TS-TETRA1-1	GCA_022641475.1		
<i>Tetrasphaera</i> aved 18-Q3-R54-62 MAXAC378	GCA_016702415.1		
<i>Tetrasphaera australiensis</i> Ben-110	GCA_001050535.1		
<i>Tetrasphaera japonica</i> T1-X7	GCA_001046855.1		
<i>Tetrasphaera</i> hjoer 18-Q3-R7-51-BATACT29	GCA_016710545.1		
<i>Knoellia</i> remsis	GCA_003002895.1	Formerly classified as <i>Tetrasphaera</i>	
<i>Phycococcus</i> duodecadis DSM-12806	GCA_002846495.1		
<i>Phycococcus</i> elongata Lp2	GCA_000367525.2		
<i>Thiothrix</i> caldifontis	GCA_900107695.1		

Table S3. Enzymes involved in PolyP metabolism. KEGG nomenclature of the genes is available in **Table S1**.

PolyP Metabolism		
Synthesis		
PolyP kinase 1	<i>ppk1</i>	P transfer between ATP/ADP to PolyP (anabolic reaction is favored)
PolyP kinase 2	<i>ppk2</i>	P transfer between GTP/GDP to PolyP (catabolic reaction is favored)
Hydrolysis		
Endo-polyphosphatase	<i>ppn</i>	Cleaves PolyP internally
Exo-polyphosphatase	<i>ppx</i>	Hydrolysis of the terminal P of PolyP
Transferases		
Polyphosphate glucokinase	<i>ppgK</i>	Phosphorylation of glucose using polyphosphate as the P donor
AMP-polyphosphate phosphotransferase	<i>pap</i>	Phosphorylation of AMP using polyphosphate as the P donor
Transport		
Low-affinity P transporters	<i>pit</i>	Single membrane protein energized by proton motive force
Phosphate-specific transport	<i>pstABCS</i>	Multi-subunit transporter usually encoded by a four-gene operon

Table S4. Polyhydroxyalkanoates (PHAs) made from volatile fatty acids.

Volatile Fatty Acid	Resulting PHAs
Acetate	Polyhydroxy butyrate (PHB)
Propionate	Polyhydroxy-2-methyl valerate (PH2MV)
Acetate and Propionate	Polyhydroxy valerate (PHV) Polyhydroxy-2-methyl butyrate (PH2MB)

Table S5. Various bacterial strains exhibiting PolyP accumulation and complete denitrification capabilities have been reported, having been isolated from diverse environmental sources. DPAOs include microorganisms that have proven to have full PAO phenotype (i.e., capable of P uptake under aerobic conditions for synthesizing PolyP, and in the anaerobic phase, PolyP is hydrolyzed, and P is released for energy generation and organic carbon uptake). While potential DPAOs can store PolyP aerobically, but more evidence is needed to confirm their full PAO phenotype.

Organism	Source environment	Ref.
DPAOs		
<i>Paracoccus denitrificans</i> YCP	Sludge from a full-scale anaerobic/ anoxic/aerobic process	[1]
<i>Paracoccus</i> sp. YKP-9	Activated sludge from sewage treatment plant	[2]
<i>Thauera</i> sp. SND5	Activated sludge from an anoxic tank at the Ulu Pandan Water Plant, Singapore	[3]
Potential DPAOs		
<i>Pseudomonas stutzeri</i> YG-24	Sediment of the eutrophic Taihu Lake	[4]
<i>Pseudomonas stutzeri</i> ADP-19	Landfill leachate, biogas residue, contaminated sediments, and pickle wastewater	[5]
<i>Pseudomonas chloritidismutans</i> K14	Sediment samples from a freshwater aquaculture pond in Tianjin	[6]
<i>Paracoccus denitrificans</i> ISTOD1	Okhla Sewage Treatment Plant	[7]
<i>Agrobacterium</i> sp. LAD9	Landfill leachate treatment system	[8]
<i>Enterobacter cloacae</i> HW-15	Water samples from a phosphorus-rich river in Hubei Province of China	[9]
<i>Acinetobacter</i> sp. C-13	Activated sludge from a lab-scale sequencing batch reactor	[10]
<i>Delftia tsuruhatensis</i> ZK-1	Activated sludge from Datansha WWTP Guangzhou, China	[11]
<i>Pseudoxanthomonas</i> sp. YP1	Aerobic granular sludge sequencing batch reactor	[12]
<i>Bacillus cereus</i> GS-5	Pure culture	[13]
<i>Bacillus cereus</i> ZQN2	Lab-scale sequencing batch reactor from a lab-scale reactor	[14]
<i>Arthrobacter</i> sp. HHEP5	Effluents of mariculture ponds	[15]

Table S6. FISH probes targeting 16S rRNA of PAOs belonging to *Ca. Accumulibacter*, *Tetrasphaera*, *Dechloromonas*, *Ca. Phosphoribacter*. Additionally, 23S rRNA probes for *Ca. Phosphoribacter* and *Tetrasphaera* are displayed, along with *ppk1* primers designed to target diverse *Ca. Accumulibacter* types and clades. The aim for including the FISH probes in this review is to highlight the evolution of new probes with the discovery of new PAOs. It is recommended that FISH probes be tested in-silico before being used by researchers.

	Probe	Specificity	Sequence (5'- 3')	Ref.
FISH Probes for <i>Ca. Accumulibacter</i>				
16S rRNA	RHC439	<i>Rhodocyclus/ Ca. Accumulibacter</i>	CNATTTCTTCCCGCCGA	[16]
	RHC175	Most <i>Rhodocyclaceae</i>	TGCTCACAGAAATATGCGG	[16]
	PAO462	Most <i>Ca. Accumulibacter</i>	CCGTCATCTACWCAGGGTATTAAC	[17]
	PAO651	Most <i>Ca. Accumulibacter</i>	CCCTCTGCCAAACTCCAG	[17]
	PAO846	Most <i>Ca. Accumulibacter</i>	GTTAGCTACGGCACTAAAAGG	[17]
	Acc470	<i>Ca. Accumulibacter aalborgensis</i> and <i>delftensis</i>	TTCGGGTACCGTCATCTACTCAGG	[18]
	Acc635	<i>Ca. Accumulibacter regalis</i>	AACTCCAGCCTGGCAGTCTCAAAT	[18]
	Acc471	<i>Ca. Accumulibacter affinis</i> and <i>proximus</i>	CTCCAGGTACCGTCATCTACACAG	[18]
	Acc469	<i>Ca. Accumulibacter proximus</i>	CCAGGTACCGTCATCTACACAGGC	[18]
	Acc1011	<i>Ca. Accumulibacter propinquus</i>	GCGAGCACTCCAGATCTCTC	[18]
PCR primers for <i>Ca. Accumulibacter</i>				
ppk1	IPCRppk-0289R	Type I <i>ppk</i>	ACGATATCTTGAATCTCGGCTAATAT	[19]
	IPCRppk-1375F	Type I <i>ppk</i>	TTCCACCATTTCGTTTCGGCATGT	[19]
	Nppk1-F	Type I <i>ppk</i>	GGTGGTCATATGAACACCGCCGCCACA	[19]
	Nppk1-R	Type I <i>ppk</i>	GGTGGTTGCTCTTCCGCATCTGCAGATCCTTCAGCAGTTCGATCAGGT	[19]
	ACCppk1-254-F	<i>Ca. Accumulibacter</i> -ppk1 cluster	TCACCACCGACGGCAAGAC	[20]
	ACCppk1-1376-R	<i>Ca. Accumulibacter</i> -ppk1 cluster	ACGATCATCAGCATCTTGCC	[20]
	Acc-I-444	Clade IA and other Type I clades	CCCAAGCAATTTCTTCCCC	[21]
	Acc-II-444	Clade IIA, IIC, and IID	CCCGTGCAATTTCTTCCCC	[21]
	Acc-ppk1-763-F	Acc-I <i>ppk1</i>	GACGAAGAAGCGGTCAAG	[22]
	Acc-ppk1-1170-R	Acc-I <i>ppk1</i>	AACGGTCATCTTGATGGC	[22]
	Acc-ppk1-893-F	Acc-IIA <i>ppk1</i>	AGTTCAATCTCACCGAGAGC	[22]
	Acc-ppk1-997-R	Acc-IIA <i>ppk1</i>	GGAATTCAGGTCGTTGC	[22]
	Acc-ppk1-870-F	Acc-IIB <i>ppk1</i>	GATGACCAGTTCCTGCTCG	[22]
	Acc-ppk1-1002-R	Acc-IIB <i>ppk1</i>	CGGCACGAACTTCAGATCG	[22]
	<u>Acc-ppk1-254-F</u>	Acc-IIC <i>ppk1</i>	TCACCACCGACGGCAAGAC	[22]
	Acc-ppk1-460-R	Acc-IIC <i>ppk1</i>	CCGGCATGACTTCGCGGAAG	[22]
	Acc-ppk1-1123-F	Acc-IIC <i>ppk1</i> excluding OTU NS D3	GAACAGTCCGCCAACGACC	[22]
	<u>Acc-ppk1-1376-R</u>	Acc-IIC <i>ppk1</i> excluding OTU NS D3	ACGATCATCAGCATCTTGCC	[22]
	Acc-ppk1-375-F	Acc-IID <i>ppk1</i>	GGGTATCCGTTCTCAAGCG	[22]
	Acc-ppk1-522-R	Acc-IID <i>ppk1</i>	GAGGCTCTTGTTGAGTACACGC	[22]
FISH Probes for <i>Tetrasphaera</i>				
23S rRNA	HGC69a	Phylum <i>Actinobacteria</i>	TATAGTTACCACCGCCGT	[8]
16S rRNA	HGC236	<i>Actinobacteria</i>	AACAAGCTGATAGGCCGC	[23]
	Actino-1011	<i>T. japonica</i>	TTGCGGGGCACCCATCTCT	[23]
	Actino-221	<i>Actinobacterial PAO</i>	CGCAGGTCCATCCCAGAC	[23]
	Actino-658	<i>Actinobacterial PAO</i>	TCCGGTCTCCCCTACCAT	[23]
	NLIMII175	<i>T. jenkinsii</i> , <i>T. veronensis</i> , and <i>T. vanveeni</i>	GGCTCCGTCTCGTATCCG	[24]
	Tet1-266	<i>Tetrasphaera</i> clade 1	CCCCTCGTCGCTGTAGC	[25]
	Tet2-892	<i>Tetrasphaera</i> clade 2	TAGTTAGCCTTGCGGCCG	[25]
	Tet2-174	<i>Tetrasphaera</i> clade 2	GCTCCGTCTCGTATCCGG	[25]
	Tet3-654	<i>Tetrasphaera</i> clade 3	GGTCTCCCCTACCACT	[25]
	Tetra183	Most off <i>Tetrasphaera</i> -related genera	TAGAGATGCCTCTCCGTCTC	[26]
Tetra67	<i>P. elongata</i> and <i>T. japonica</i>	AGCAAGCTCCGTCACCG	[26]	
FISH Probes for <i>Ca. Phosphoribacter</i>				
23S rRNA	Phos1260-23S-Pbr1	<i>Ca. Phosphoribacter baldrii</i>	AGAGTTCACGGCCGGGCAAAG	[26]
	Phos1260-23S- Pbr2	<i>Ca. Phosphoribacter hodrii</i>	AGACATCACGGCCGGGCAATG	[26]
16S rRNA	Phos741	<i>Ca. Phosphoribacter</i> (Pbr4, Pbr5, Pbro)	TTCTCAGCGTCAGTTGTGGCC	[26]
	Phos601	<i>midas_s_5</i> (<i>Ca. P. hodrii</i>)	GGTTGAGCCTCGGATTTCACTG	[26]
	Actino-658	<i>Ca. Phosphoribacter</i> (<i>Ca. P. hodrii</i> , <i>Ca. P. baldrii</i> , Pbr3)	TCCGGTCTCCCCTACCAT	[26]
FISH Probes for <i>Dechloromonas</i>				
16S rRNA	Dech443	<i>Ca. Dechloromonas phosphorivorans</i>	ACC CAT GCA TTT TCT TCC CGG	[27]
	BET135	<i>Ca. Dechloromonas phosphoritropha</i>	ACGTTATCCCCCACTCAATGG	[27]

Table S7. Different phylogenetic taxonomies of species in *Ca. Accumulibacter* and their FISH probes. Metagenome Assembled Genome (MAG) identifier as shown in NCBI and **Figure 2**, MiDAS4-classification, and new names proposed by Petriglieri and colleagues (Petriglieri et al., 2022). “-”: not applicable. FISH probe sequences are available in **Table S6**.

MAG identifier	MiDAS4-classification	Proposed species name	FISH probe
IB			
BA-92	-	appositus BA-92	-
phosphatis HKU1	-	adiacens HKU1	-
IC			
UW-LDO	-	meliphilusUW-LDO	-
delftensis	aalborgensis	delftensis	Acc470
phosphatis SBR S	-	delftensis SBR S	Acc470
IA			
BA-93	-	regalis BA-93	Acc635
phosphatis CANDO 1	-	regalis CANDO 1	Acc635
phosphatis UW3	-	regalis UW3	Acc635
UW4	-	regalis UW4	Acc635
UW8-POB	-	regalis UW8- POB	Acc635
IIA			
aalborgensis	aalborgensis	aalborgensis	Acc470
UW9-POB	-	phosphatis UW9-POB	Acc635
phosphatis UW1	phosphatis	phosphatis UW1	Acc635
IIB			
UW5	-	phosphatis UW5	Acc635
Hade BATAc.726	phosphatis	propinquus	Acc1011
OdNE BAT3C.415	phosphatis	propinquus	Acc1011
Fred MAXAC.027	phosphatis	propinquus	Acc1011
UW10-POB	-	propinquus UW10-POB	Acc1011
phosphatis SBR L	-	contiguous SBR L	-
IIC			
SK01	-	vicinus SK-01	-
phosphatis EUBA5574	-	vicinus UBA5574	-
phosphatis Bin19	-	cognatus Bin19	-
phosphatis HKU2	-	cognatusHKU2	-
SK-02	-	cognatus SK-02	-
phosphatis SSA1	-	cognatusSSA1	-
UW11-POB	-	cognatus UW11-POB	-
UW6	-	cognatus UW6	-
IIG			
Fred II3C.720	phosphatis	affinis	Acc471
IID			
EsbW BATAc.285	phosphatis	proximus	Acc469 and Acc471
UW12-POB	-	necessaries UW12-POB	-
IIF			
BUBA2327	midas s 12920	iunctus UBA2327	Acc471 2
SK-12	-	adjunctus SK-12	-
SCELSE-1	-	similis SCELSE-1	Acc471 2
phosphatis SSB1	midas s 12920	similis SSB1	Acc471 2
UW13-POB	-	Conexus UW13-POB	-
UW7	-	conexus UW7	-

Table S8. Complete gene names and KEGG nomenclature.

ANNOTATION	KEGG	GENE
Denitrification		
Nitrate Reductase	K00370	narG- narZ- nxrA
Nitrate Reductase	K00371	narH- narY- nxrB
Nitrate Reductase Gamma Subunit	K00374	narI- narV
Nitrate Reductase (Cytochrome)	K02567	napA
Nitrate Reductase (Cytochrome)-Electron Transfer Subunit	K02568	napB
Nitrite Reductase (NO-Forming)	K00368	nirK
Nitrite Reductase (NO-Forming)/Hydroxylamine Reductase	K15864	nirS
Nitric Oxide Reductase Subunit B	K04561	norB
Nitric Oxide Reductase Subunit C	K02305	norC
Nitrous-Oxide Reductase	K00376	nosZ
Assimilatory Nitrate Reduction		
Ferredoxin-Nitrate Reductase	K00367	narB
Nitrate Reductase (NADPH)	K10534	NR
Assimilatory Nitrate Reductase Catalytic Subunit	K00372	nasA
Assimilatory Nitrate Reductase Electron Transfer Subunit	K00360	nasB
Ferredoxin-Nitrite Reductase	K00366	nirA
Nitrite Reductase (NADPH)	K17877	NIT-6
Dissimilatory Nitrate Reduction		
Nitrite Reductase (NADH) Large Subunit	K00362	nirB
Nitrite Reductase (NADH) Small Subunit	K00363	nirD
Nitrite Reductase (Cytochrome C-552)	K03385	nrfA
Cytochrome C Nitrite Reductase Small Subunit	K15876	nrfH
Nitrogen Fixation		
Nitrogenase Molybdenum-Iron Protein Beta Chain	K02591	nifK
Nitrogenase Molybdenum-Iron Protein Alpha Chain	K02586	nifD
Nitrogenase Iron Protein Nifh	K02588	nifH
P Transport Proteins		
Inorganic Phosphate Transporter, Pit Family	K03306	pit
Phosphate Transport System Substrate-Binding Protein	K02040	pstS
Phosphate Transport System Permease Protein	K02037	pstC
Phosphate Transport System Permease Protein	K02038	pstA
Phosphate Transport System ATP-Binding Protein	K02036	pstB
PolyP Metabolism		
Polyphosphate Kinase	K00937	ppk1
Polyphosphate Kinase	K22468	ppk2
Endopolyphosphatase	K06018	ppn1
Exopolyphosphatase	K01524	ppx
Exopolyphosphatase	K01514	ppx1
Polyphosphate Glucokinase	K00886	ppgK
AMP-Polyphosphate Phosphotransferase	K23753	pap
Polyhydroxyalkanoates		

Acetyl-Coa Acetyltransferase	K00626	phaA
Acetoacetyl-Coa Reductase	K03821	phaB
3-Hydroxybutyryl-Coa Dehydratase	K17865	phaJ
Poly[(R)-3-Hydroxyalkanoate] Polymerase Subunit	K03821	phaC
Poly(3-Hydroxyoctanoate) Depolymerase	K22250	phaZ
Poly(3-Hydroxybutyrate) Depolymerase	K05973	phaZ _a
Poly(3-Hydroxyoctanoate) Depolymerase	K22249	phaZ _b
Glycogen Synthesis		
Glucose-1-Phosphate Adenylyltransferase	K00975	glgC
Starch Synthase	K00703	glgA
1,4-Alpha-Glucan Branching Enzyme	K00700	glgB
Alpha-Maltose-1-Phosphate Synthase	K16148	glgM
Starch Synthase (Maltosyl-Transferring)	K16147	glgE
Glycogen Degradation		
Glycogen Phosphorylase	K00688	glgP
Alpha-Amylase	K01176	amyA
Beta-Amylase	K01177	amyB
Maltogenic Alpha-Amylase	K05992	amyM
Cyclomaltodextrinase / Neopullulanase	K01208	ma
Atp Transporters		
Basic Membrane Protein A And Related Proteins	K07335	bmpA- bmpB- tmpC
Branched-Chain Amino Acid Transport System Atp-Binding Protein	K01996	livF
Branched-Chain Amino Acid Transport System Atp-Binding Protein	K01995	livG
Branched-Chain Amino Acid Transport System Permease Protein	K01997	livH
Branched-Chain Amino Acid Transport System Permease Protein	K01998	livM
Branched-Chain Amino Acid Transport System Substrate-Binding Protein	K01999	livK
Capsular Polysaccharide Transport System Atp-Binding Protein	K09689	kpsT
Capsular Polysaccharide Transport System Permease Protein	K10107	kpsE
Capsular Polysaccharide Transport System Permease Protein	K09688	kpsM
General Nucleoside Transport System Atp-Binding Protein	K23537	nupA
General Nucleoside Transport System Permease Protein	K23535	nupB
General Nucleoside Transport System Permease Protein	K23536	nupC
Glutamate/Aspartate Transport system atp-Binding Protein	K10004	gltL- aatP
Glutamate/Aspartate Transport system permease Protein	K10003	gltJ- aatQ
Glutamate/Aspartate Transport system permease Protein	K10002	gltK- aatM
Glutamate/Aspartate Transport system substrate-Binding Protein	K10001	gltI- aatJ
Glycine Betaine/Proline Transport System Atp-Binding Protein	K02000	proV
Glycine Betaine/Proline Transport System Permease Protein	K02001	proW
Glycine Betaine/Proline Transport System Substrate-Binding Protein	K02002	proX
Lipopolysaccharide Export System Permease Protein	K07091	lptF
Lipopolysaccharide Export System Permease Protein	K11720	lptG
Lipopolysaccharide Transport System Atp-Binding Protein	K09691	wzt
Lipopolysaccharide Transport System Permease Protein	K09690	wzm
Multiple Sugar Transport System Permease	K02026	msSP1

Multiple Sugar Transport System Permease Protein	K02025	msP
Multiple Sugar Transport System Substrate-Binding Protein	K02027	msS
Peptide/Nickel Transport System Atp-Binding Protein	K02031	ddpD
Peptide/Nickel Transport System Atp-Binding Protein	K02032	ddpF
Polar Amino Acid Transport System Atp-Binding Protein	K02028	paA
Polar Amino Acid Transport System Permease Protein	K02029	paP
Polar Amino Acid Transport System Substrate-Binding Protein	K02030	paS
Putative Multiple Sugar Transport System Atp-Binding Protein	K10548	gguA
Putative Multiple Sugar Transport System Permease Protein	K10547	gguB
Putative Multiple Sugar Transport System Substrate-Binding Protein	K10546	chvE
Putrescine Transport System Atp-Binding Protein	K11075	potG
Putrescine Transport System Permease Protein	K11075	potH
Putrescine Transport System Permease Protein	K11074	potI
Putrescine Transport System Substrate-Binding Protein	K11073	potF
Rhamnose Transport System Atp-Binding Protein	K10562	rhaT
Rhamnose Transport System Permease Protein	K10560	rhaP
Rhamnose Transport System Permease Protein	K10561	rhaQ
Rhamnose Transport System Substrate-Binding Protein	K10559	rhaS
Sugar Transport System Atp-Binding Protein	K23547	yphD
Sugar Transport System Permease Protein	K23546	yphD
Sugar Transport System Substrate-Binding Protein	K23545	yphF

Electrochemical Potential-Driven Transporters

Anaerobic C4-Dicarboxylate Transporter	K07791	dcuA
Anaerobic C4-Dicarboxylate Transporter	K07792	dcuB
Anaerobic C4-Dicarboxylate Transporter	K11103	dctA
Benzoate-Proton Symporter	K05548	benK
Branched Chain Amino Acid Efflux Pump	K05846	azIC
Branched Chain Amino Acid Efflux Pump	K05847	azID
C4-Dicarboxylate Transporter	K11689	dctQ
C4-Dicarboxylate Transporter	K11690	dctM
C4-Dicarboxylate-Binding Protein	K11688	dctP
Cation-Acetate Symporter	K14393	actP
Cytosine Permease	K10974	codB
Ethanolamine Permease	K16238	eat
Fucose-Proton Symporter	K02429	fucP
Galactose-Proton Symporter	K08137	galP
Glutamate-Na ⁺ Symporter	K03312	gltS
Glycine Betaine	K05020	opuD
L-Asparagine Permease	K11738	ansP
Lactate-Proton Symport	K08178	jen
Malonate-Proton Symporter	K13936	mdcF
Maltose-Moltooligosaccharide Transporter	K16211	malY
Oxalate-Formate Antiporter	K08177	oxIT
Proline-Betaine-Proton Symporter	K03762	proP
Putrescine Importer	K14052	puuP
Tartrate Transporter	K13021	ttuB

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