



**D-JRP7-4.1 Bibliographic study  
on catalogues of genes**

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# Bibliographic study on catalogues of genes

## Introduction

Antimicrobials, quaternary ammonium compounds (QAC), heavy metals and bacteriocins along with environmental stresses including cold, high salt concentration, low pH, desiccation, and blue-light were considered in the bibliographic study. These stresses are particularly relevant in food processing plants where disinfection as well as food preservation strategies such as low pH, high salt concentration and cold storage are applied as control measures against the survival and growth of foodborne pathogens. An extensive literature search was conducted on the genes associated to these specific phenotypes of physiological adaptation in *L. monocytogenes*. Additionally, since the survival of *L. monocytogenes* in the processing environment is also due to its ability to form biofilm, papers describing genes associated to biofilm formation were also included.

## Methods

An extensive literature review was conducted on PubMed (<https://www.ncbi.nlm.nih.gov/pubmed/>) using following keywords: “antimicrobials”, “quaternary ammonium compounds”, “heavy metals”, “bacteriocins”, “cold”, “high salt concentration”, “low pH”, “desiccation”, “blue-light”, “biofilm”, “*Listeria monocytogenes*” and “genes”. The system retrieved overall 664 published papers. The abstract of each of these papers was read with the purpose to identify genes associated to the response of *L. monocytogenes* to each stress. Around 100 papers were selected based on the abstract. These papers were thoroughly read in order to identify and specifically select genes with a strong association to the related phenotype. For this purpose, only genes confirmed by insertional mutagenesis or mutant selection experiments were included. All GenBank accession numbers and related sequences reported in published papers were checked by nucleotide BLAST (<https://blast.ncbi.nlm.nih.gov/Blast.cgi>) and CLUSTAL Omega (<https://www.ebi.ac.uk/Tools/msa/clustalo/>) for alignment. Overall 41 papers describing 94 genes were included.

## Selected Features

An excel sheet was built including 94 genes with a strong association to the related phenotype of antimicrobial, quaternary ammonium compounds, heavy metal and bacteriocin resistance, environmental stress adaptation and biofilm formation in *Listeria monocytogenes*. For each gene, the following information was reported: name of the gene, locus tag, annotation, main function, localization, reference paper, GenBank accession number and direct link to the web page of the sequence in NCBI (<https://www.ncbi.nlm.nih.gov/nuccore/>). The corresponding table of genes is presented in Annex of this deliverable.





Regarding antimicrobial resistance, 14 genes were included related to resistance to different antimicrobial classes such as tetracycline, ampicillin, vancomycin, streptomycin, chloramphenicol/florfenicol, sulphonamides, erythromycin and fluroquinolones (Poyart-Salmeron et al., 1992; Charpentier et al., 1993; Lungu et al., 2011; Jamali et al., 2015; Srinivasan et al., 2005; Roberts et al., 1996; Godreuil et al., 2003).

Regarding resistance to quaternary ammonium compounds, 7 genes associated to resistance to benzalkonium chloride were included (qacH, qacA, qacC, bcrA, bcrB, bcrC and emrE). These genes are associated to the active efflux pump of the QAC (Muller et al., 2013; Xu et al., 2014; Moller-Nielsen, 2017; Elhanafi et al., 2010; Kovacevic et al., 2015).

Regarding heavy metal resistance, 16 genes associated to resistance to cadmium and arsenic were included. In particular, three gene cassettes, cadA1C, cadA2C and cadA3C were associated to resistance to 70 mg/l of cadmium chloride, whereas cadA4C was associated to resistance to 35 mg/L (Mullapudi et al., 2010; Parsons et al., 2017). Regarding resistance to arsenic, ars genes were associated to resistance to 500 mg/L of sodium (meta)arsenite (Lee et al., 2013). As for quaternary ammonium compounds resistance, heavy metals resistance determinant genes are associated to the active efflux of cadmium or arsenic.

Regarding bacteriocin resistance, 5 genes associated to the response of *L. monocytogenes* to cell-envelope stress were included: virR, virS, mprF, liaR, anrB (Kang et al., 2015; Thedieck et al., 2006; Bergholz et al., 2013; Collins et al., 2010). Bacteriocin are linked to the formation of pores in the cell envelope and its final disruption. Resistance to bacteriocin such as nisin is associated to modification of the cell envelope composition.

Regarding stress adaptation, different mutant selection experiments demonstrated the important role of the gene sigB (sigma factor B) in the regulation of expression of different genes associated to the adaptation to different environmental stresses. In particular the knockout of sigB was directly associated to adaptation to desiccation in *L. monocytogenes* (Huang et al., 2015).

As far as blue-light is considered, the gene lmo0799, coding for a blue-light receptor, was strongly associated to the adaptation of *L. monocytogenes* to this particular stress (Ondrusch and Kreft, 2011). *L. monocytogenes* can adapt to cold following different pathways (Annex I). One pathway includes cold shock proteins cspB and cspD (Schmid et al., 2009). Another pathway includes the glycine/betaine transporter system which mediates the uptake of osmolytes such as glycine, betaine and carnitine, important for adaptation to both cold and high salt concentration (Angelidis and Smith, 2003). Overall 16 genes related to adaptation of *L. monocytogenes* to cold and/or high salt concentration were included in the dataset (Annex II).

The Stress Survival Islet 1 corresponding to a cassette of five genes (lmo0444-lmo0448) was associated to the survival and growth of *L. monocytogenes* under suboptimal conditions. In particular, the knockout of the entire SSI-1 was associated to an impaired ability of this food-borne pathogen to grow at low pH and high salt concentrations (Ryan et al., 2010). Within this gene cassette, lmo0447 (gadD1) and lmo0448 (gadT1) encodes for a glutamate decarboxylase and an amino acid transporter both described as specifically involved in the adaptation to low pH (Feehily et al., 2014). In particular, the Gad System is involved in the uptake of glutamate which is decarboxylated into gamma amino benzoic acid with consumption of protons and consequent increase of pH (Feehily et al., 2014).

Regarding adaptation to low pH, apart from the GAD System another pathway might be activated. The ADI system, including arc genes, is involved in transformation of arginine into ornithine with ammonia as by product, which increases the pH. The ADI system has been described in response to mild acid pH (Feehily et al., 2014). Overall, 13 genes associated to low pH were included in the dataset (Annex II).

The Stress Survival Islet 2 was firstly described in *Listeria innocua* as a cassette of two genes. SSI-2 was more recently associated to alkaline and oxidative stress in *L. monocytogenes*. This islet is often



present in place of SSI-1 in *L. monocytogenes* ST121, a frequently identified ST-Type of food processing environments.

Regarding adaptation to desiccation, seven genes related to the motility of *L. monocytogenes*, were recently associated to this specific phenotype (Hington et al., 2015). In particular, these genes were found to be downregulated in desiccation tolerant *L. monocytogenes*. Authors suggested that since the biosynthesis of flagellum consumes energy, the downregulation of flagellum-associated genes might be an efficient strategy to save energy, which can be redirect into more critical metabolic processes (Hington et al., 2015).

As far as the ability of biofilm is concerned, eight genes associated to biofilm formation were included in the dataset (Annex II). Along the food chain, biofilm formation is essential to the survival of *L. monocytogenes* in the processing environment and further participates to bacterial persistence and resistance to the cleaning and disinfection procedures (Popowska et al., 2017).

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## ANNEX I. List of genes involved in cold adaptation.

Gènes	Locus-tag	Annotations	Conditions	Références
aroA	lmo1600	bifunctional 3-deoxy-7-phosphoheptulonate synthase/chorismate mutase	10°C	Liu et al., 2002, Tasara et al., 2006
betL	lmo2092	glycine betaine transporter BetL		Tasara et al., 2006
bgIG	lmo0501	Similar to transcription antiterminator BgIG family	10°C	Liu et al., 2002, Tasara et al., 2006
celD	lmo1719	Endoglucanase D	10°C	Liu et al., 2002, Tasara et al., 2006
clpB	lmo2206	Clp protease subunit B	10°C	Liu et al., 2002, Tasara et al., 2006
clpP	lmo2468	ATP-dependent Clp protease proteolytic subunit	10°C	Liu et al., 2002, Tasara et al., 2006
cspB	lmo2016	cold-shock protein		Schmid et al., 2009 Chan et al., 2013
cspD	lmo1879	cold-shock protein		Schmid et al., 2009 Chan et al., 2013
ctc	lmo0211	50S ribosomal protein L25	4°C	Hingston et al., 2017
cysS	lmo0239	cysteinyl-tRNA synthetase	10°C	Liu et al., 2002, Tasara et al., 2006
degU	lmo2515	two-component response regulator DegU	10°C	Liu et al., 2002, Tasara et al., 2006
drm	lmo1954	Phosphopentomutase	4°C	Cacace et al., 2010
efeO	lmo0366	hypothetical protein		Chatterjee et al., 2006
eno	lmo2455	enolase glycolyse protein without secretion signal phosphopyruvate hydratase	11°C	Cabrita et al., 2013
fabH	lmo2202	3-oxoacyl-ACP synthase		Chatterjee et al., 2006
flaA	lmo0690	mobility and chemotaxis, flagellin	11 et 20°C	Cabrita et al., 2013
fliD	lmo0707	mobility and chemotaxis, flagellar capping protein FliD	11 et 20°C	Cabrita et al., 2013
flp	lmo0943	ferritin-like protein	10°C	Liu et al., 2002, Tasara et al., 2006
gap	lmo2459	gap protein glycolyse protein without secretion signal	11 et 20°C	Cabrita et al., 2013
gbuA	lmo1014	glycine/betaine ABC transporter ATP-binding protein	4°C	Chan et al., 2013, Tasara et al., 2006
gbuB	lmo1015	glycine/betaine ABC transporter permease	4°C	Tasara et al., 2006
gbuC	lmo1016	glycine/betaine ABC transporter substrate-binding protein	4°C	Tasara et al., 2006
groEL	lmo2068	molecular chaperone GroEL	10°C	Liu et al., 2002, Tasara et al., 2006
hisE	lmo0561	phosphoribosyl-ATP pyrophosphatase	4°C	Hingston et al., 2017
htrA	lmo0292	heat-shock protein htrA serine protease	4°C	Cacace et al., 2010
iap	lmo0582	P60 cell wall process invasion associated secreted endopeptidase	11 et 20°C	Cabrita et al., 2013
ivA	lmo1991	threonine deshydratase	4°C	Hingston et al., 2017
ivB	lmo1984	acetolactate synthase	4°C	Hingston et al., 2017
ivC	lmo1986	keto-acid reductoisomerase	4°C	Hingston et al., 2017
ivD	lmo1983	dihydroxy-acid dehydratase Locus tag	4°C	Hingston et al., 2017
ivH	lmo1985	acetolactate synthase small subunit	4°C	Hingston et al., 2017
inlA	lmo0433	internalinA	4°C	Hingston et al., 2017
inlH	lmo0263	internalinH	4°C	Hingston et al., 2017
leuA	lmo1987	2-isopropylmalate synthase	4°C	Hingston et al., 2017
leuB	lmo1988	3-isopropylmalate deshydrogenase	4°C	Hingston et al., 2017
leuC	lmo1989	3-isopropylmalate deshydratase large subunit	4°C	Hingston et al., 2017
leuD	lmo1990	3-isopropylmalate deshydratase small subunit	4°C	Hingston et al., 2017
lisK	lmo1378	histidine kinase	10 et 20°C	Pöntinen et al., 2015
lmo0640	lmo0640	Hypothetical protein lmo0640 similar to oxidoreductase aldo/keto reductase family	4°C	Cacace et al., 2010
lmo0866	lmo0866	ATP-dependent RNA helicase	3°C	Markkula et al., 2012
lmo0927	lmo0927	detoxification and adaptation to atypical conditions hypothetical protein	11 et 20°C	Cabrita et al., 2013
lmo1246		ATP-dependent RNA helicase	3°C	Markkula et al., 2012
lmo1450		DEAD/DEAH box helicase	3°C	Markkula et al., 2012
lmo1722	lmo1722	ATP-dependent RNA helicase	3°C	Markkula et al., 2012
lmo2411	lmo2411	Hypothetical protein lmo2411 cluster assembly protein SuffB	4°C	Cacace et al., 2010
ltrA	lmo0389	low temperature requirement protein A	4°C	Chan et al., 2013
ltrC	lmo2398	hypothetical protein	4°C	Chan et al., 2013
opuCA	lmo1428	glycine/betaine ABC transporter ATP-binding protein	4°C	Hingston et al., 2017, Chan et al., 2013
opuCB	lmo1427	glycine/betaine ABC transporter permease	4°C	Hingston et al., 2017
opuCC	lmo1426	glycine/betaine ABC transporter substrate-binding protein	4°C	Hingston et al., 2017
opuCD	lmo1425	glycine/betaine ABC transporter permease	4°C	Hingston et al., 2017
pflA	lmo1917	Hypothetical protein lmo 1917 similar to formate-acetyltransferase	4°C	Cacace et al., 2010
pgm	lmo2456	Phosphoglycerate mutase 2, 3-bisphosphoglycerate-independent	4°C	Cacace et al., 2010
rpmF	lmo0486	50S ribosomal protein L32	4°C	Hingston et al., 2017
rpoD	lmo1454	RNA polymerase sigma factor RpoD	4°C	Chan et al., 2013
sigB	lmo0895	RNA polymerase sigma factor SigB	4 et 8°C	Huang et al., 2015 Chan et al., 2013
sigL (rpoN)	lmo2461	RNA polymerase sigma factor $\sigma$ 54	4°C	Chan et al., 2013
spI		P45 cell wall process	11 et 20°C	Cabrita et al., 2013
tatA	lmo0362	hypothetical protein		Chatterjee et al., 2006
tatC	lmo0361	membrane protein		Chatterjee et al., 2006
trpG	lmo1632	anthranilate synthase subunit beta	10°C	Liu et al., 2002, Tasara et al., 2006
trxB	lmo2478	thioredoxin reductase	10°C	Liu et al., 2002, Tasara et al., 2006
yycG	lmo0288	two-component sensor histidine kinase	10 et 20°C	Pöntinen et al., 2015
group_912		hypothetical protein	2°C	Fritsch et al., 2019
group_1762		hypothetical protein	2°C	Fritsch et al., 2019
group_362		hypothetical protein	2°C	Fritsch et al., 2019
group_2282		hypothetical protein	2°C	Fritsch et al., 2019
clpP1		ATP-dependent Clp protease proteolytic subunit 1	2°C	Fritsch et al., 2019



## ANNEX II. List of genes associated to ecophysiology in *Listeria monocytogenes*

Gene	locus-tag	Annotation	Main Function related to stress tolerance	Localization	Reference	GenBank Accession Number	link to reference sequence
tetM	SAG0923	tetracycline resistance protein	tetracycline resistance	Tn1545	Poyart-Salmeron et al., 1992	NC_004116.1	<a href="#">tetM</a>
tetS	pLK0018_p18	tetracycline resistance protein	tetracycline resistance	plasmid	Charpentier et al., 1993	NC_010540.1	<a href="#">tetS</a>
tetA	LMOATCC19117_0857	tetracycline resistance protein	tetracycline resistance	transposon	Lungu et al., 2011	FR733643	<a href="#">tetA</a>
tetL	pAMalpha1_p1	TetL transporter	tetracycline resistance	plasmid	Poyart-Salmeron et al., 1992	NC_005013.1	<a href="#">tetL</a>
ampC	lmo0540	penicillin-binding protein	penicillin resistance	chromosome	Jamali et al., 2015	NC_003210.1	<a href="#">ampC</a>
vanA	pWZ1668_p27	similar to GENE ID: 2598280 vanA	vancomycin resistance	plasmid	Jamali et al., 2015	NC_014475.1	<a href="#">vanA</a>
vanB	VRA0040	D-alanine--D-lactate ligase	vancomycin resistance	plasmid	Jamali et al., 2015	NC_005054.1	<a href="#">vanB</a>
strA	pPSR1_p04	aminoglycoside phosphotransferase	streptomycin resistance	plasmid	Jamali et al., 2015	NC_005205.1	<a href="#">strA</a>
strB	pPSR1_p05	aminoglycoside phosphotransferase	streptomycin resistance	plasmid	Jamali et al., 2015	NC_005205.1	<a href="#">strB</a>
floR	pSCEC2_013	chloramphenicol/lorfenicol efflux MFS transporter FloR	chloramphenicol/lorfenicol resistance	plasmid	Srinivasan et al., 2005	NC_022377.1	<a href="#">floR</a>
sullI	p9123p1	dihydropteroate synthase	sulfonamides resistance	plasmid	Srinivasan et al., 2005	NC_005324.1	<a href="#">sullI</a>
penA	NMB0413	penicillin-binding protein 2	penicillin resistance	chromosome	Srinivasan et al., 2005	NC_003112.2	<a href="#">penA</a>
ermC	pT48_p2	23S RNA methylase	erythromycin resistance	plasmid	Roberts et al., 1996	NC_001395.1	<a href="#">ermC</a>
lde	lmo2741	multidrug transporter	fluoroquinolone resistance	chromosome	Godreuil et al., 2003	NC_003210.1	<a href="#">lde</a>
qacH		Quaternary ammonium compound-resistance protein	benzalkonium chloride resistance	Tn6188	Muller et al., 2013	HF565366.1	<a href="#">qacH</a>
qacA	pSA1379_19	efflux protein QacA	benzalkonium chloride resistance	plasmid	Xu et al., 2014	NC_007931.1	<a href="#">qacA</a>
qacC	VRA0026	quaternary ammonium compound-resistance protein	benzalkonium chloride resistance	plasmid	Weigel et al., 2003; Moller-Nielsen, 2017	NC_005054.1	<a href="#">qacC</a>
bcrA	LMOH7858_RS05735	TetR/AcrR family transcriptional regulator	benzalkonium chloride resistance	IS1216 composite transposon	Elhanafi et al., 2010	NZ_AADR01000010.1	<a href="#">bcrA</a>
bcrB	LMOH7858_RS05740	QacE family quaternary ammonium compound efflux SMR transporter	benzalkonium chloride resistance	IS1216 composite transposon	Elhanafi et al., 2010	NZ_AADR01000010.1	<a href="#">bcrB</a>
bcrC	LMOH7858_RS05745	QacE family quaternary ammonium compound efflux SMR transporter	benzalkonium chloride resistance	IS1216 composite transposon	Elhanafi et al., 2010	NZ_AADR01000010.1	<a href="#">bcrC</a>
emrE	LM5578_1862	small multidrug resistance protein, SMR family	benzalkonium chloride resistance	Listeria genomic island 1 (LGI-1)	Kovacevic et al., 2015	CP001602.1	<a href="#">emrE</a>
cadA1		ATPase	cadmium resistance	Tn5422	Mullapudi et al., 2010	L28104	<a href="#">cadA1</a>
cadC1		accessory protein	cadmium resistance	Tn5422	Mullapudi et al., 2010	L28104	<a href="#">cadC1</a>
cadA2	LMOh7858_pLM80_0083	cation-transporting ATPase	cadmium resistance	plasmid	Mullapudi et al., 2010	AADR01000058	<a href="#">cadA2</a>
cadC2	LMOh7858_pLM80_0082	cadmium efflux system accessory protein	cadmium resistance	plasmid	Mullapudi et al., 2010	AADR01000058	<a href="#">cadC2</a>
cadA3	lmo1100	cadmium resistance protein	cadmium resistance	integrative conjugative element	Mullapudi et al., 2010	NC_003210.1	<a href="#">cadA3</a>
cadC3	lmo1102	cadmium efflux system accessory protein	cadmium resistance	integrative conjugative element	Mullapudi et al., 2010	NC_003210.1	<a href="#">cadC3</a>
cadA4	LMOSA_RS41880	cadmium translocating P-type ATPase	cadmium resistance	Listeria genomic island 2 (LGI-2)	Parsons et al., 2017	NZ_CM001159.1	<a href="#">cadA4</a>





<b>cadC4</b>	LMOSA_R S41875	ArsR family transcriptional regulator	cadmium resistance	Listeria genomic island 2 (LGI-2)	Parsons et al., 2017	NZ_CM001 159.1	<a href="#">cadC4</a>
<b>arsD1</b>	LMOSA_R S41820	arsenical resistance operon transcriptional repressor ArsD	arsenic resistance	Listeria genomic island 2 (LGI-2)	Lee et al., 2013	NZ_CM001 159.1	<a href="#">arsD1</a>
<b>arsA1</b>	LMOSA_R S41825	arsenical pump-driving ATPase	arsenic resistance	Listeria genomic island 2 (LGI-2)	Lee et al., 2013	NZ_CM001 159.1	<a href="#">arsA1</a>
<b>arsR1</b>	LMOSA_R S30085	ArsR family transcriptional regulator	arsenic resistance	Listeria genomic island 2 (LGI-2)	Lee et al., 2013	NZ_CM001 159.1	<a href="#">arsR1</a>
<b>arsD2</b>	LMOSA_R S41830	arsenical resistance operon transcriptional repressor ArsD	arsenic resistance	Listeria genomic island 2 (LGI-2)	Lee et al., 2013	NZ_CM001 159.1	<a href="#">arsD2</a>
<b>arsR2</b>	LMOSA_R S41835	transcriptional regulator	arsenic resistance	Listeria genomic island 2 (LGI-2)	Lee et al., 2013	NZ_CM001 159.1	<a href="#">arsR2</a>
<b>arsA2</b>	LMOSA_R S41840	arsenical pump-driving ATPase	arsenic resistance	Listeria genomic island 2 (LGI-2)	Lee et al., 2013	NZ_CM001 159.1	<a href="#">arsA2</a>
<b>arsB1</b>	LMOSA_R S41845	arsenical-resistance protein	arsenic resistance	Listeria genomic island 2 (LGI-2)	Lee et al., 2013	NZ_CM001 159.1	<a href="#">arsB1</a>
<b>arsB2</b>	LMOSA_R S41850	arsenical-resistance protein	arsenic resistance	Listeria genomic island 2 (LGI-2)	Lee et al., 2013	NZ_CM001 159.1	<a href="#">arsB2</a>
<b>virR</b>	lmo1745	two-component response regulator	cell-envelope stress response (nisin resistance)	chromosome	Kang et al., 2015	NC_003210.1	<a href="#">virR</a>
<b>virS</b>	lmo1741	histidine kinase	cell-envelope stress response (nisin resistance)	chromosome	Kang et al., 2015	NC_003210.1	<a href="#">virS</a>
<b>mprF</b>	lmo1695	hypothetical protein	cell-envelope stress response (nisin resistance)	chromosome	Thedieck et al., 2006	NC_003210.1	<a href="#">mprF</a>
<b>liaR</b>	lmo1022	two-component response regulator	cell-envelope stress response (nisin resistance)	chromosome	Bergholz et al., 2013	NC_003210.1	<a href="#">liaR</a>
<b>anrB</b>	lmo2115	ABC transporter permease	cell-envelope stress response (nisin resistance)	chromosome	Collins et al., 2010	NC_003210.1	<a href="#">anrB</a>
<b>sigB</b>	lmo0895	RNA polymerase sigma factor SigB	stress adaptation	chromosome	Huang et al., 2015	NC_003210.1	<a href="#">sigB</a>
<b>lmo0799</b>	lmo0799	hypothetical protein (blue-light receptor)	adaptation to blue-light	chromosome	Ondrusch and Kreft, 2011	NC_003210.1	<a href="#">lmo0799</a>
<b>cspB</b>	lmo2016	cold-shock protein	cold adaptation	chromosome	Schmid et al., 2009	NC_003210.1	<a href="#">cspB</a>
<b>cspD</b>	lmo1879	cold-shock protein	cold adaptation	chromosome	Schmid et al., 2009	NC_003210.1	<a href="#">cspD</a>
<b>spoV G I</b>	lmo0196	regulatory protein SpoVG	lysozyme resistance, global posttranscriptional gene regulator	chromosome	Burke and Portnoy, 2016	NC_003210.1	<a href="#">spoVG I</a>
<b>spoV G II</b>	lmo0197	regulatory protein SpoVG	lysozyme resistance, global posttranscriptional gene regulator	chromosome	Burke and Portnoy, 2016	NC_003210.1	<a href="#">spoVG II</a>
<b>lmo0866</b>	lmo0866	ATP-dependent RNA helicase	cold adaptation	chromosome	Markkula et al., 2012	NC_003210.1	<a href="#">lmo0866</a>
<b>lmo1722</b>	lmo1722	ATP-dependent RNA helicase	cold adaptation	chromosome	Markkula et al., 2012	NC_003210.1	<a href="#">lmo1722</a>
<b>lisK</b>	lmo1378	histidine kinase	cold adaptation	chromosome	Pöntinen et al., 2015	NC_003210.1	<a href="#">lisK</a>
<b>yycG</b>	lmo0288	two-component sensor histidine kinase	cold adaptation	chromosome	Pöntinen et al., 2015	NC_003210.1	<a href="#">yycG</a>
<b>lmo2748</b>	lmo2748	hypothetical protein	adaptation to high salt concentration	chromosome	Abram et al., 2008	NC_003210.1	<a href="#">lmo2748</a>
<b>betL</b>	lmo2092	glycine betaine transporter BetL	adaptation to high salt concentration	chromosome	Angelidis and Smith, 2003	NC_003210.1	<a href="#">betL</a>
<b>gbuA</b>	lmo1014	glycine/betaine ABC transporter ATP-binding protein	adaptation to high salt concentration and cold	chromosome	Angelidis and Smith, 2003	NC_003210.1	<a href="#">gbuA</a>
<b>gbuB</b>	lmo1015	glycine/betaine ABC transporter permease	adaptation to high salt concentration and cold	chromosome	Angelidis and Smith, 2003	NC_003210.1	<a href="#">gbuB</a>
<b>gbuC</b>	lmo1016	glycine/betaine ABC transporter substrate-binding protein	adaptation to high salt concentration and cold	chromosome	Angelidis and Smith, 2003	NC_003210.1	<a href="#">gbuC</a>





<b>opuC A</b>	lmo1428	glycine/betaine ABC transporter ATP-binding protein	adaptation to high salt concentration and cold	chromosome	Angelidis and Smith, 2003	NC_003210.1	<a href="#">opuCA</a>
<b>opuC B</b>	lmo1427	glycine/betaine ABC transporter permease	adaptation to high salt concentration and cold	chromosome	Angelidis and Smith, 2003	NC_003210.1	<a href="#">opuCB</a>
<b>opuC C</b>	lmo1426	glycine/betaine ABC transporter substrate-binding protein	adaptation to high salt concentration and cold	chromosome	Angelidis and Smith, 2003	NC_003210.1	<a href="#">opuCC</a>
<b>opuC D</b>	lmo1425	glycine/betaine ABC transporter permease	adaptation to high salt concentration and cold	chromosome	Angelidis and Smith, 2003	NC_003210.1	<a href="#">opuCD</a>
<b>lmo0 444</b>	lmo0444	hypothetical protein	adaptation to low pH and high salt concentration	Stress survival islet 1 (SSI-1)	Ryan et al., 2010	NC_003210.1	<a href="#">lmo0444</a>
<b>lmo0 445</b>	lmo0445	transcriptonal regulator	adaptation to low pH and high salt concentration	Stress survival islet 1 (SSI-1)	Ryan et al., 2010	NC_003210.1	<a href="#">lmo0445</a>
<b>pva</b>	lmo0446	penicillin acylase	adaptation to low pH and high salt concentration	Stress survival islet 1 (SSI-1)	Ryan et al., 2010	NC_003210.1	<a href="#">pva</a>
<b>gadD 1</b>	lmo0447	glutamate decarboxylase	adaptation to low pH	Stress survival islet 1 (SSI-1)	Ryan et al., 2010; Feehily et al., 2014	NC_003210.1	<a href="#">gadD1</a>
<b>gadT1</b>	lmo0448	amino acid antiporter	adaptation to low pH	Stress survival islet 1 (SSI-1)	Ryan et al., 2010; Feehily et al., 2014	NC_003210.1	<a href="#">gadT1</a>
<b>arcA</b>	lmo0043	arginine deiminase	adaptation to low pH	chromosome	Ryan et al., 2009	NC_003210.1	<a href="#">arcA</a>
<b>arcB</b>	lmo0036	putrescine carbamoyltransferase	adaptation to low pH	chromosome	Ryan et al., 2009	NC_003210.1	<a href="#">arcB</a>
<b>arcC</b>	lmo0039	carbamate kinase	adaptation to low pH	chromosome	Ryan et al., 2009	NC_003210.1	<a href="#">arcC</a>
<b>arcD</b>	lmo0037	amino acid transporter	adaptation to low pH	chromosome	Ryan et al., 2009	NC_003210.1	<a href="#">arcD</a>
<b>argR</b>	lmo1367	arginine repressor ArgR	adaptation to low pH	chromosome	Ryan et al., 2009	NC_003210.1	<a href="#">argR</a>
<b>gadD 2</b>	lmo2363	glutamate decarboxylase	adaptation to low pH	chromosome	Feehily et al., 2014	NC_003210.1	<a href="#">gadD2</a>
<b>gadD 3</b>	lmo2434	glutamate decarboxylase	adaptation to low pH	chromosome	Feehily et al., 2014	NC_003210.1	<a href="#">gadD3</a>
<b>gadT2</b>	lmo2362	amino acid antiporter	adaptation to low pH	chromosome	Feehily et al., 2014	NC_003210.1	<a href="#">gadT2</a>
<b>lmo0 796</b>	lmo0796	hypothetical protein	adaptation to low pH	chromosome	Abram et al., 2008	NC_003210.1	<a href="#">lmo0796</a>
<b>lmo0 913</b>	lmo0913	succinate semialdehyde dehydrogenase	adaptation to low pH	chromosome	Abram et al., 2008	NC_003210.1	<a href="#">lmo0913</a>
<b>lmo2 391</b>	lmo2391	hypothetical protein	adaptation to low pH	chromosome	Abram et al., 2008	NC_003210.1	<a href="#">lmo2391</a>
<b>LM61 79_0 748</b>	LM6179_0 748	putative transcriptor regulator	adaptation to alkaline and oxidative stress	Stress survival islet 2 (SSI-2)	Harter et al., 2017	HG813249.1	<a href="#">LM6179_0 748</a>
<b>yoaZ</b>	LM6179_0 749	Uncharacterized protease yoaZ	adaptation to alkaline and oxidative stress	Stress survival islet 2 (SSI-2)	Harter et al., 2017	HG813249.1	<a href="#">yoaZ</a>
<b>fliP</b>	lmo0676	flagellar biosynthesis protein FliP	adaptation to desiccation	chromosome	Hingston et al., 2015	NC_003210.1	<a href="#">fliP</a>
<b>fliH</b>	lmo0679	flagellar biosynthesis protein FliH	adaptation to desiccation	chromosome	Hingston et al., 2015	NC_003210.1	<a href="#">fliH</a>
<b>figD</b>	lmo0696	flagellar basal body rod modification protein	adaptation to desiccation	chromosome	Hingston et al., 2015	NC_003210.1	<a href="#">figD</a>
<b>figL</b>	lmo0706	flagellar hook-associated protein FigL	adaptation to desiccation	chromosome	Hingston et al., 2015	NC_003210.1	<a href="#">figL</a>
<b>motB</b>	lmo0686	flagellar motor rotation MotB	adaptation to desiccation	chromosome	Hingston et al., 2015	NC_003210.1	<a href="#">motB</a>
<b>fliM</b>	lmo0699	flagellar motor switch protein FliM	adaptation to desiccation	chromosome	Hingston et al., 2015	NC_003210.1	<a href="#">fliM</a>
<b>fliY</b>	lmo0693	flagellar motor switch protein FliY	adaptation to desiccation	chromosome	Hingston et al., 2015	NC_003210.1	<a href="#">fliY</a>
<b>inlL</b>	LMON_RS 10535	class 1 internalin InlL	Biofilm	chromosome	Popowska et al., 2017	NC_022568.1	<a href="#">inlL</a>
<b>prfA</b>	lmo0200	listeriolysin positive regulatory protein	Biofilm	chromosome	Luo et al., 2013	NC_003210.1	<a href="#">prfA</a>
<b>actA</b>	lmo0204	actin-assembly inducing protein precursor	Biofilm	chromosome	Travier et al., 2013	NC_003210.1	<a href="#">actA</a>
<b>lmo0 673</b>	lmo0673	hypothetical protein	Biofilm	chromosome	Renier et al., 2011	NC_003210.1	<a href="#">lmo0673</a>
<b>bapL</b>	lmo0435	peptidoglycan binding protein	Biofilm	chromosome	Renier et al., 2011	NC_003210.1	<a href="#">bapL</a>
<b>recO</b>	lmo1460	DNA repair protein RecO	Biofilm	chromosome	Tremoulet et al., 2002	NC_003210.1	<a href="#">recO</a>





<b>lmo2504</b>	lmo2504	cell wall-binding protein	Biofilm	chromosome	Lourenço et al.,2013	NC_003210.1	<a href="#">lmo2504</a>
<b>luxS</b>	lmo1288	S-ribosylhomocysteinase	Biofilm	chromosome	Bonsaglia et al.,2014	NC_003210.1	<a href="#">luxS</a>