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Revised Genetic Linkage Map of *Bacillus subtilis*†

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INTRODUCTION

Bacillus subtilis is the most widely studied and thoroughly mapped gram-positive microorganism. Two of the driving forces behind the study of the genetics of *B. subtilis* are the quest to understand the simple differentiation cycle of sporulation and germination that this organism undergoes and the basis for copious enzyme excretion in sporulating organisms. The study of these processes has resulted in the accumulation of vast amounts of knowledge of the physiology and genetics of postexponential bacteria. This is reflected in the abundance of loci that have to do with either this phase of the bacterial life cycle or sporulation and germination.

In the several years that have passed since the last compilation of a genetic map for this organism (110, 111) there have been substantial additions to the genetic map. Some 140 loci have been added, making a total of about 500 loci. In addition, there has been refinement of the map in several areas. This has resulted not only from the continuation of classical genetic studies that use deoxyribonucleic acid (DNA)-mediated transformation and tranduction, but also from studies of the molecular cloning of genes of interest in this organism. Several libraries of *B. subtilis* DNA have been constructed in bacteriophage λ (68) and cosmid (14) and other vectors (131, 243), and these libraries have been a rich source of fragments of the chromosome carrying genes of interest. There have been two important advances in the ways of identifying mutations. The first is the use of integrational vectors carrying cloned *B. subtilis* DNA (69). These can integrate into the chromosome at the region of homology by Campbell-like mechanism and in so doing place a drug-resistant determinant on the chromosome next to the cloned region. The second is the use of the transposon Tn*917*, which places a drug resistance marker within mutations it causes. There is now a substantial collection of Tn*917* insertions generated primarily by Youngman, Losick, and colleagues (331). None of these insertions have been included in the present map, primarily because we did not want to deal with problems of nomenclature for such insertions at this time. Any future revision of the map will have to take them into account. It seems likely that the density of genetic markers on the map as we presently know it will double or triple because of the increase in transposon mutants as well as the identification of new open reading frames from cloned DNA fragments.

The size of the *B. subtilis* chromosome was estimated in a previous publication as approximately 2.0×10^9 to 2.5×10^9 daltons, or approximately 4,000 kilobase pairs of DNA (110). Wake (Spore Newsl. 7:21–26, 1980) has suggested that the size of the *B. subtilis* chromosome is more like 3.3×10^9 daltons, or approximately 5,000 kilobase pairs of DNA. The origin of chromosome replication is most likely quite close to the *rrnO* operon, although its exact location has not been determined unequivocally (H. Yoshikawa, personal communication). The terminus of the map is located very close to the *gltA* and *gltB* loci (200).

DETAILED MAP

Figure 1 presents the detailed linkage map of the *B. subtilis* chromosome constructed according to our best estimates of the data from the literature. It is important to emphasize that some areas are known very accurately. The location of genes has been determined at the level of the restriction map or even at the sequence level. In most other places, and for some markers in otherwise well-mapped regions, the map is quite tentative. In many areas we have taken "poetic license" with the data and constructed an order of markers within a region that may be substantially wrong. This uncertainty results from the fact that it is virtually impossible to order markers based upon recombination distances in two-factor crosses, and in this particular region the only available data were those from two-factor crosses. For example, in the region between 120° and 135° we show an order of 20 different loci that is based entirely on two-factor transduction cross results and could be completely scrambled from what the actual order is in this area. The value of the information presented in this map is that it allows one to determine what loci have been mapped in the general area of a region of interest. Such loci can be used for further studies with any locus that happens to be found or to be cloned in that region. Other regions of the chromosome containing a large number of markers, such as that between 240° and 255°, have been extremely well mapped by fine-structure analyses as well as restriction endonuclease and sequence data. Thus, the order of the markers shown on the map is very close to the precise order of genes in this region with one exception noted below. It is difficult to know how accurate the map will be for any given region, and the only solution for the curious is to contact the investigators that have done substantial mapping in the region of the chromosome of interest or, if all else fails, to read the original literature.

One area of particular complexity in this map is the identification, mapping, and ordering of the ribosomal pro-

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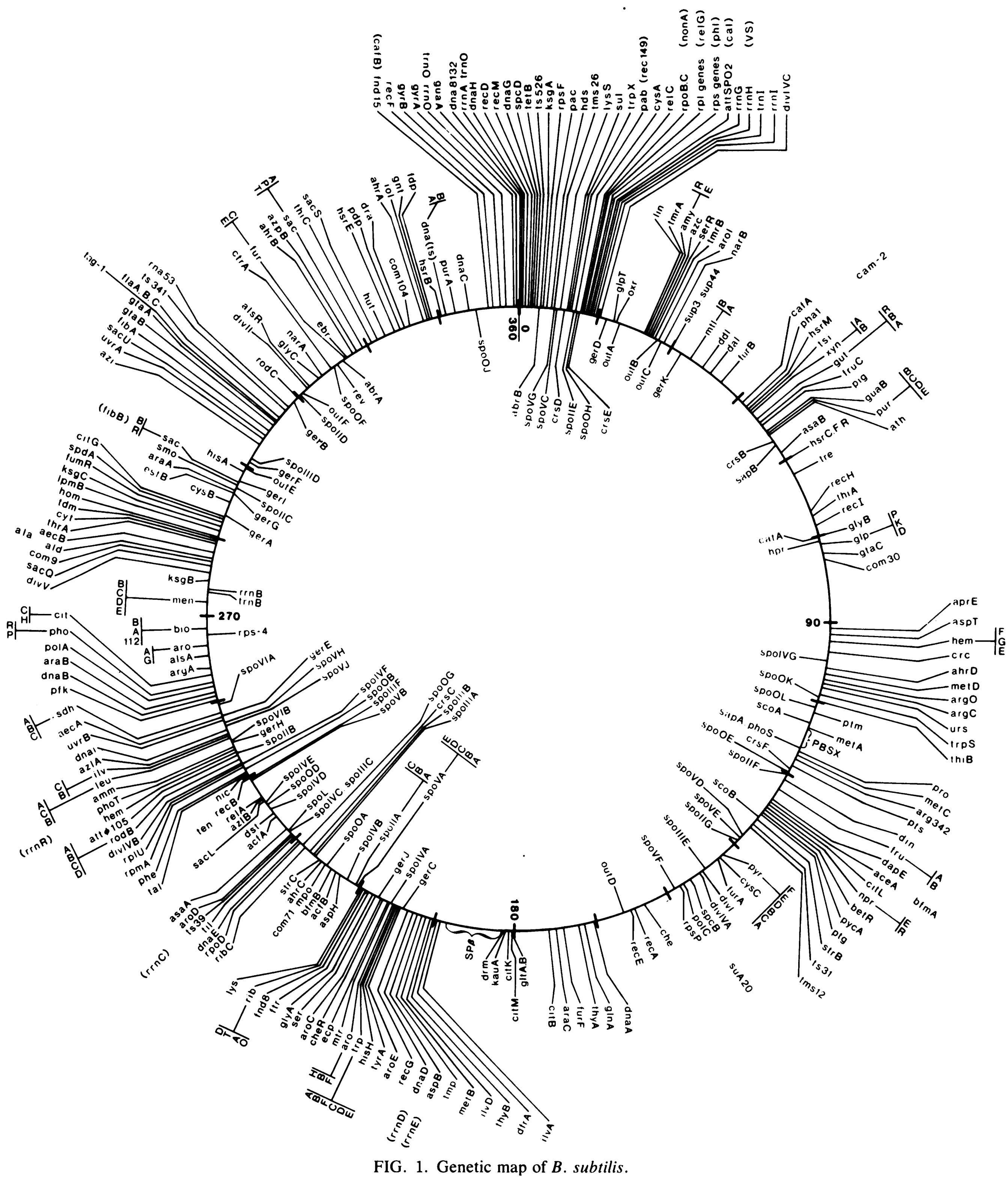

FIG. 1. Genetic map of *B. subtilis.*

rplK-rplA-rplJ-rplL-rpoB-rpsG rpsL-rplC (rpsH, rplE, rplF, rplX)-rpsE-rpmD rpsK-rpsI

cysA-spoOH-rplK——————————rpoB————rpsL-efg-tuf-nea-kan-rpsJ-rplV————rpsE-att SPO2

cysA————————————————rpoB-rpoC rpsL——————————————rplV————rpsE-rpsT

FIG. 2. Partial maps of the principal cluster of ribosomal protein genes. The maps, from top to bottom, were derived from references 50–54, 273, and 218, respectively. Other ribosomal protein genes located in this region include *rpsD* (108); *rplB* and *rplQ* (273); and *rpsC*, *rpsQ*, and *rpsS* along with genes coding for BL4, BL14, BL22, and BL25 (216, 218). Genes for particular proteins are given the name of the *E. coli* homolog if known (50, 115).

TABLE 1. Genetic markers of *B. subtilis*

Gene symbol	Mnemonic	Map position (degrees)[a]	Phenotype, enzyme deficiency, or other characteristic	Reference(s)[b]
abrA	Antibiotic resistance	325	Partial suppressor of stage 0 phenotypes, may be same as *rev-4*	299
abrB	Antibiotic resistance	3	Partial suppressor of stage 0 phenotypes, ribosome alterations have been observed in these mutants; same locus as *cpsX* and probably *absA*, *absB*, and *tolA*	95, 301
abrC	Antibiotic resistance		Weak intragenic suppressors of *spo0A*	299
absA	Antibiotic resistance		Partial suppressor of stage 0 phenotypes; see *abrB*	140
absB	Antibiotic resistance		Partial suppressor of stage 0 phenotypes; see *abrB*	140
aceA	Acetate	126	Pyruvate dehydrogenase defect, defective in E1 (pyruvate decarboxylase) component of pyruvate dehydrogenase	27, 127
acfA	Acriflavin	230	Resistant to acriflavin, also to ethidium bromide and distamycin; sensitive to streptomycin	16, 137, 271
acfB	Acriflavin	215	Same as *acfA*	271
adeC	Adenine	NM	Adenine deaminase	64
adeF	Adenine	NM	Adenine phosphoribosyl transferase	64
aecA	Aminoethylcysteine	250	Aminoethylcysteine resistance, regulation of aspartokinase II	180
aecB	Aminoethylcysteine	290	Aminoethylcysteine resistance, structural gene for aspartokinase II	180
ahrA	Arginine hydroxamate	342	Arginine hydroxamate resistance, linked to *cysA*	104, 202
ahrB	Arginine hydroxamate	328	Arginine hydroxamate resistance	168, 202
ahrC	Arginine hydroxamate	215	Arginine hydroxamate resistance	202
ahrD	Arginine hydroxamate	99	Arginine hydroxamate resistance	18
ala	Alanine	281	Alanine auxotrophy	180
ald	Alanine	280	L-Alanine dehydrogenase	75, 168, 302
alsA	Acetoin	265	Acetolactate synthase	335
alsR	Acetoin	320	Constitutive acetolactate synthase	335
amm	Ammonia	250	Glutamate requirement	60
amt	Aminotyrosine		3-Aminotyrosine resistance; part of or very close to *tyrA* locus	232
amyB	Amylase		Control of amylase synthesis; probably identical to *sacQ* and *pap*; see *sacQ*	264, 286
amyE	Amylase	25	Amylase structural gene, also called *amyA*	333
amyR	Amylase	25	Control of amylase synthesis, also called *amyH*	327, 333
aprE	Alkaline protease	91	Structural gene for subtilisin E, map order (*hpr glyB*)-*aprE*-*metD* (formerly *sprE*)	284, 325
araA	Arabinose	294	Arabinose utilization	222
araB	Arabinose	256	Arabinose utilization	222
araC	Arabinose	172	Arabinose utilization	222
argA	Arginine	100	Arginine requirement, identified by complementation of corresponding locus in *E. coli*	203
argB	Arginine	100	Same as *argA*	203
argC	Arginine	100	Same as *argA*	203
argD	Arginine	100	Same as *argA*	203
argE	Arginine	100	Same as *argA*	203
argF	Arginine	100	Same as *argA*	203
argG	Arginine	260	Same as *argA*, formerly *argA*	203
argH	Arginine	260	Same as *argG*	203
arg-342	Arginine	115	Arginine-ornithine or citrulline requirement	119
aroA	Aromatic	265	3-Deoxy-D-arabinoheptalosonic-7-phosphate synthase	121, 206
aroB	Aromatic	210	Dehydroquinate synthase	206
aroC	Aromatic	210	Dehydroquinate dehydratase	121, 206
aroD	Aromatic	230	Shikimate dehydrogenase	4, 119, 121
aroE	Aromatic	210	3-Enolpyruvylshikimate-5-phosphate synthase	206, 209
aroF	Aromatic	210	Chorismate synthase	121, 206
aroG	Aromatic	270	Chorismate mutase, isozyme 3	121, 206
aroH	Aromatic	210	Chorismate mutase, isozymes 1 and 2	174, 206
aroI	Aromatic	25	Shikimate kinase	168
aroJ	Aromatic		Tyrosine and phenylalanine; see *hisH*	208
asaA	Arsenate	230	Arsenate resistance	1, 2
asaB	Arsenate	57	Arsenate resistance (derived from *B. subtilis* W23)	3
aspA	Aspartate		Pyruvate carboxylase; see *pycA*	33, 119
aspB	Aspartate	200	Aspartate aminotransferase	119
aspH	Aspartate	215	Constitutive aspartase	132, 317
aspT	Aspartate	92	Aspartate transport	316, 317
ath	Adenine-thiamine	55	Adenine-thiamine requirement	334
attSPβ	Attachment	190	Integration site for phage SPβ	336
attSPO2	Attachment	10	Integration site for phage SPO2	136, 278
attφ3T	Attachment		Integration site for phage φ3T, probably maps between *kauA* and SPβ	322

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TABLE 1—*Continued*

Gene symbol	Mnemonic	Map position (degrees)[a]	Phenotype, enzyme deficiency, or other characteristic	Reference(s)[b]
attφ105	Attachment	245	Integration site for phage φ105	224, 258
azi	Azide	310	Resistance to sodium azide	A
azc	Azetidine carboxylate	25	Resistant to azetidine-2-carboxylic acid; *azc* 90% cotransformed with *aroI*	81
azlA	Azaleucine	250	4-Azaleucine resistance, derepressed leucine biosynthetic enzymes	315
azlB	Azaleucine	240	4-Azaleucine resistance	314, 315
azpA	Azopyrimidine		Resistance to azopyrimidines; alteration of DNA polymerase III; see *polC*	49
azpB	Azopyrimidine	330	Resistance to azopyrimidines	40
betR	Betacin	127	Resistant to betacin produced by SPβ lysogens	106
bfmA	Branched fatty acid	126	Lacks branched-chain keto acid dehydrogenase; isolated in *aceA* strain and not separated genetically from *aceA*	27, 320
bfmB	Branched fatty acid	216	Requires branched-chain fatty acid, valine, or isoleucine; maps between *strC* and *lys*	27, 320
bioA	Biotin	270	7-Oxo-8-aminopelargonate:7,8-diaminopelargonate aminotransferase	221
bioB	Biotin	270	Biotin synthetase	221
bio-112	Biotin	270	Early defect in biotin synthesis	221
bry	Bryamycin		Bryamycin (thiostrepton) resistance, maps in ribosomal protein	103, 278
bsr	Restriction, modification		Restriction, modification by *B. subtilis* strain R; see *hsrR*	297
but		NM	5-Bromouracil tolerant	23
cafA	Caffeine	46	Caffeine resistant	39
cafB	Caffeine	359	Caffeine sensitive; also sensitive to nalidixic acid	39
cal	Chalcomycin	12	Chalcomycin resistant	267
cam-2	Chloramphenicol	45	Resistant to chloramphenicol	12
car	Carbamoyl phosphate	100	Carbamoyl phosphate	B
catA	Catabolite resistance	75	Hyperproduction of extracellular proteases, can sporulate in presence of glucose, probably same as *scoC* and possibly *hpr*	114, 141, 168, 191
cdd		NM	Deoxycytidine-cytidine deaminase	248
che	Chemotaxis	155	Chemotaxis	215
cheR	Chemotaxis	205	Chemotactic methyl transferase	215
citB	Citric acid cycle	177	Aconitate hydrotase	256, 335
citC	Citric acid cycle	260	Isocitrate dehydrogenase	122, 256
citF	Citric acid cycle		Succinate dehydrogenase, now split into three loci, *sdhA*, *sdhB*, and *sdhC*	105, 122, 256
citG	Citric acid cycle	295	Fumarate hydratase	256
citH	Citric acid cycle	260	Malate dehydrogenase	86
citK	Citric acid cycle	185	α-Ketoglutarate dehydrogenase complex, enzyme E1	118, 256
citL	Citric acid cycle	125	Lipoamide dehydrogenase (nicotinamide adenine dehydrogenase, reduced form) E3 component of both pyruvate dehydrogenase and α-ketoglutarate dehydrogenase complexes	118
citM	Citric acid cycle	181	Dehydrolipoyltransuccinylase E_3 component of 2-ketoglutarate dehydrogenase complex; closely linked to *citK*	71
cml	Chloramphenicol		Chloramphenicol resistance, caused by mutations in one of at least five 50S ribosomal proteins, all mapping in the ribosomal protein cluster; see ribosomal protein cluster	217
com-9	Competence	280	Poorly competent; defective in DNA binding	66
com-30	Competence	79	Poorly competent; defective in DNA binding	66
com-71	Competence	UC	Poorly competent; defective in DNA binding; may be *spo0A*	66
com-104	Competence	340	Poorly competent; binds DNA, but little enters the cells	66
cpsX			See *abrB*	
crk		NM	Cytidine kinase	248
crsA	Catabolite-resistant sporulation	226	Carbon source-resistant sporulation; resistant to novobiocin and acridine orange during sporulation; mutation in *rpoD*; has similar phenotype to *rvt* mutations	268, 290
crsB	Catabolite-resistant sporulation	55	Requires high glucose for sporulation	290
crsC	Catabolite-resistant sporulation	217	Carbon source-resistant sporulation; maps close to or in *spo0A*	290
crsD	Catabolite-resistant sporulation	8	Carbon source-resistant sporulation	290
crsE	Catabolite-resistant sporulation	10	Carbon source-resistant sporulation; maps in *rpoBC* operon; *rfm-11* suppresses *crsE*	290, 291
crsF	Catabolite-resistant sporulation	119	Carbon source-resistant sporulation	290
css	Cysteine		Cysteine sensitivity; see *cysA*	148
ctrA	Cytidine requirement	325	Requirement for cytidine in the absence of ammonium ion	168, 335
cyc		95	D-Cycloserine resistant	82
cym	Cysteine-methionine		Requirement for cysteine or methionine; see *cysA*	148, 226
cysA	Cysteine	11	Cysteine requirement, serine transacetylase; a complex locus	148

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TABLE 1—*Continued*

Gene symbol	Mnemonic	Map position (degrees)[a]	Phenotype, enzyme deficiency, or other characteristic	Reference(s)[b]
			consisting of *css* (cysteine sensitivity), *cym* (cysteine or methionine), *hts* (hydrogen sulfide excretion), and *cysA*	
cysB	Cysteine	300	Cysteine requirement	60
cysC	Cysteine	140	Cysteine, methionine, sulfite, or sulfide requirement	119, 330
cyt	Cytidine	284	Requires cytidine	128
dal	D-Alanine	40	D-Alanine requirement; alanine racemase	62, 75
dapE	Diaminopimelic acid	124	*N*-Acetyl-LL-diaminopimelic acid ligase	35
dcd		NM	Deoxycytidine 5′-monophosphate deaminase	199
dck		NM	Deoxycytidine/deoxyadenosine kinase	198, 248
ddd		NM	Deoxycitidine kinase	248
ddl		36	D-Alanyl-D-alanine ligase	35
deoA		NM	Thymidine phosphorylase	181
dfrA	Dihydrofolate	194	Dihydrofolate reductase; co-ordinately regulated with *thyB*	205
din	Deoxyribonuclease inhibitor	120	Deoxyribonuclease inhibitor secretion	235
divI	Division	143	Temperature-sensitive cell division, formerly *divD*	304
divII	Division	320	Temperature-sensitive cell division, formerly *divC*	304
divIVA	Division	144	Minicell production	245
divIVB	Division	245	Minicell production	245
divIVC	Division	15	Minicell production, formerly *divA*	304
divV	Division	285	Temperature-sensitive cell division, formerly *divB*	304
dnaA	DNA	160	DNA synthesis; ribonucleotide reduction, probably ribonucleotide reductase	13, 19, 149, 183, 247
dnaB	DNA	255	DNA synthesis, initiation of chromosome replication, probably more than one gene	135, 149, 183, 186
dnaC	DNA	355	DNA synthesis	11, 149, 183
dnaD	DNA	200	DNA synthesis, initiation of chromosome replication	149, 183
dnaE	DNA	230	DNA synthesis	149, 183
dnaF	DNA		DNA synthesis, DNA polymerase III; see *polC*	149, 183
dnaG	DNA	0	DNA synthesis	149, 183
dnaH	DNA	0	DNA synthesis	149, 183, 300
dnaI	DNA	250	DNA synthesis	149, 183
dnaA(Ts)	DNA	350	DNA synthesis	100, 183
dnaB(Ts)	DNA	350	DNA synthesis	100, 183
dna8132	DNA	0	DNA synthesis, initiation of chromosome replication	100, 102, 300
dpa	Dipicolinic acid	148	Requires dipicolinic acid for heat-resistant spores, linked to *pyrA*	15
dra		339	Deoxyriboaldolase	289
drm		182	Phosphodeoxyribomutase	289
dst	Distamycin	232	Resistant to distamycin and acriflavin	272
D-*try*	D-Tyrosine		Resistance to D-tyrosine; maps within the *tyrA* locus; see *tyrA*	43
ebr	Ethidium bromide	325	Ethidium bromide resistance	23
ecp		204	Resistant to 2-amino-5-ethoxycarbanyl pyrimidine-4(304H)-one	244
efg	Elongation factor G	10	Elongation factor G	5, 61, 157
ery	Erythromycin		Erythromycin resistance, ribosomal protein L22; see *rplV*	294, 295
estB	Esterase	294	Esterase B defect	113
fdpA	Fructose diphosphate	344	Fructose-bisphosphatase	76
fibA		310	Macrofiber formation; weak linkage to *hisA*	262
fibB		295	Macrofiber formation	262
flaA	Flagella	145	Defect in flagellar synthesis, autolysin deficient	94, 234
flaB	Flagella	149	Defect in flagellar synthesis	94, 234
flaC	Flagella	315	Defect in flagellar synthesis	94, 234
flaD	Flagella	219	Defect in flagellar synthesis, autolysin deficient	234
fruA	Fructose	120	Fructose transport	89
fruB	Fructose	120	Fructose-1-phosphate kinase	89
fruC	Fructose	51	Fructokinase	87, 89
ftr		208	Fluorotryptophan resistance	20
fumR	Fumarase	295	Regulation of fumarate hydratase	A
fun		12	Close to, or in, *rpsL*	109
furA	5-Fluorouracil	135	Resistance to 5-fluorouracil	60
furB	5-Fluorouracil	41	Fluorouracil resistance	334
furC	5-Fluorouracil	325	Resistance to 5-fluorouracil in the presence of uracil	C
furE	5-Fluorouracil	325	Resistance to 5-fluorouracil in the presence of uracil	D
furF	5-Fluorouracil	160	Resistance to 5-fluorouracil in the presence of uracil	56
fus	Fusidic acid		Fusidic acid resistance; see *efg*	157
gca	Glucosamine	NM	L-Glutamine-D-fructose-6-phosphate amino-transferase	73
gdh	Glucose dehydrogenase	32	Structural gene for glucose dehydrogenase, cloned on phage vector	45, 308

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TABLE 1—*Continued*

Gene symbol	Mnemonic	Map position (degrees)[a]	Phenotype, enzyme deficiency, or other characteristic	Reference(s)[b]
gerA	Germination	289	Germination defective, defective in germination response to alanine and related amino acids, consists of at least three genes	194–196, 274, 197, 259
gerB	Germination	314	Germination defective, defective in germination response to the combinations of glucose, fructose, asparagine, and KCl	196, 197, 274
gerC	Germination	201	Germination defective, temperature-sensitive germination in alanine; has not been separated from linked mutations in original isolate	196, 197, 274
gerD	Germination	16	Germination defective, defective germination in range of germinants	196, 197, 230, 274
gerE	Germination	253	Germination defective, defective germination in range of germinants, may be a spore coat defect	193, 196, 197, 274
gerF	Germination	301	Germination defective, defective germination in a range of germinants	196, 197, 230, 274
gerG	Germination	294	Germination defective, mutant lacks phosphoglycerate kinase (*pgk*) activity; germinates poorly in alanine; sporulates poorly	74, 196, 237, 274
gerH	Germination	246	Defective germination in a range of germinants	230
gerI	Germination	296	Defective germination in a range of germinants	230
gerJ	Germination	206	Defective germination in a range of germinants; allele *gerJ51* (also called *tzm*) is present in many laboratory strains	313
gerK	Germination	32	Defective germination response to glucose	138
glnA	Glutamine	167	Glutamine synthetase structural gene	26, 56, 72, 83, 246
glpD	Glycerol phosphate	75	Glycerol-3-phosphate dehydrogenase	171
glpK	Glycerol phosphate	75	Glycerol kinase	171
glpP	Glycerol phosphate	75	Pleiotropic glycerol mutant	171
glpT	Glycerol phosphate	15	Fosfomycin resistant, glycerol phosphate transport defect	155
gltA	Glutamate	180	Glutamate or aspartate requirement, glutamate synthase	56, 119, 200
gltB	Glutamate	180	Glutamate synthase	200
glyA	Glycine	210	Glycine requirement	153–155
glyB	Glycine	75	Glycine requirement	102
glyC	Glycine	320	Glycine requirement	40
gnt	Gluconate	344	Gluconate kinase and permease genes, inability to use gluconate as carbon source	76, 77
groEL		NM	Phage growth	41
gtaA		310	Glucosylation of teichoic acid, lacks uridine-diphosphate-glucose-poly(glycerolphosphate)α-glucosyltransferase	168, 329
gtaB		310	Glucosylation of teichoic acid	329
gtaC		75	Glucosylation of teichoic acid, lacks phosphoglucomutase	329
guaA	Guanine	0	Inosine monophosphate dehydrogenase	300
guaB	Guanine	50	Guanine requirement	A, E
guaC	Guanine	NM	Guanosine monophosphate reductase	64
guaF	Guanine	NM	Hypoxanthine-guanine phosphoribosyl transferase	64
guaP	Guanine	NM	Inosine-guanosine phosphorylase	64
gutA	Glucitol	50	D-Glucitol permease	42, 87
gutB	Glucitol	50	D-Glucitol dehydrogenase	42, 87
gutR	Glucitol	50	Constitutive synthesis of D-glucitol permease and D-glucitol dehydrogenase, regulatory gene for glucitol catabolism	42, 87
gyrA	Gyrase	357	DNA gyrase (*nalA*)	40, 88, 163
gyrB	Gyrase	354	DNA gyrase (*novA*)	40, 163
hag	Flagella	315	Flagellar antigen	94, 178
hds		5	Pleiotropic extragenic suppressors of DNA mutations	272
hemA	Heme biosynthesis	245	δ-Aminolevulinate synthase	156
hemB	Heme biosynthesis	245	Porphobilinogen synthase	22
hemC	Heme biosynthesis	245	Porphobilinogen deaminase	22
hemD	Heme biosynthesis	245	Uroporphyrinogen III cosynthase	189
hemE	Heme biosynthesis	90	Uroporphyrinogen decarboxylase	188
hemF	Heme biosynthesis	90	Coproporphyrinogen oxidase	188
hemG	Heme biosynthesis	90	Ferrochelatase	188
hisA	Histidine	299	Histidine requirement, probable location of all histidine enzymes except *hisH*	25, 65, 312
hisH	Histidine	205	Histidinol-phosphate aminotransferase, tyrosine and phenylalanine and aminotransferase	1, 208
hom	Homoserine	290	Threonine and methionine requirement, deletion lacking homoserine dehydrogenase	C
hpr	Protease	76	Overproduction of proteases	114

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TABLE 1—*Continued*

Gene symbol	Mnemonic	Map position (degrees)[a]	Phenotype, enzyme deficiency, or other characteristic	Reference(s)[b]
hsrB	Host-specific restriction	345	Host-specific restriction and modification of *B. subtilis* IAM 1247; endonuclease *Bsu*B, isoschizomer of *Pst*I	134, 269
hsrC	Host-specific restriction	60	Host-specific restriction and modification of *B. subtilis* 1247 II; endonuclease *Bsu*C	134
hsrE	Host-specific restriction	337	Host-specific restriction and modification of *B. subtilis* IMA 1231; endonuclease *Bsu*E; isoschizomer of *Fnu*DII	134, 146
hsrF	Host-specific restriction	60	Endonuclease *Bsu*F; isoschizomer of *Hpa*II	134, 146
hsrM	Host-specific restriction	47	Host-specific restriction and modification of *B. subtilis* Marburg, probably identical to *nonB*; endonuclease *Bsu*M; isoschizomer of *Xho*I	134, 146
hsrR	Host-specific restriction	60	Endonuclease *Bsu*R; isoschizomer of *Hae*III	31, 146, 298
hts	Hydrogen sulfide		Excretion of hydrogen sulfide; see *cysA*	148
hut	Histidine utilization	345	Histidine degradation	44, 289
ifm	Flagella	304	Hypermotility, suppresses *flaA* and *flaD* mutations	94, 234
igf		343	Deletion covering *iol*, *gnt*, *fdpA*, and *hsrB* (formerly *fdpA1*)	76
ilvA	Isoleucine-valine	200	Threonine dehydratase	17, 118
ilvB	Isoleucine-valine	250	Condensing enzyme	17, 315
ilvC	Isoleucine-valine	250	α-Hydroxy-β-keto acid reductoisomerase	17, 315
ilvD	Isoleucine-valine	200	Dihydroxyacid dehydratase	91
inh	Inhibition by histidine		Inhibition by histidine; probably within *tyrA* locus; see *tyrA*	206, 209
iol	Inositol	343	Inability to grow on myo-inositol, possibly myo-inositol dehydrogenase gene	76
kan	Kanamycin	10	Kanamycin resistance, maps in the ribosomal protein cluster	92
kauA	Keto acid uptake	185	Branched-chain α-keto transport	91
kir	Kiromycin		Probable mutation in the structural gene for elongation factor Tu; see *tuf*	275
ksgA	Kasugamycin	4	High-level kasugamycin resistance	38, 296, 300, 323
ksgB	Kasugamycin	280	Low-level kasugamycin resistance	296
ksgC	Kasugamycin	UC	Fumarate hydratase defective, kasugamycin resistance	A
leuA	Leucine	250	α-Isopropylmalate synthase	17, 60, 314, 315
leuB	Leucine	250	Isopropylmalate isomerase	315
leuC	Leucine	250	β-Isopropylmalate dehydrogenase	17, 314, 315
lin	Lincomycin	25	Lincomycin resistance	93, 103
lpm	Lipiarmycin		Lipiarmycin resistance; RNA[c] polymerase; see *rpoC*	281
lpmB	Lipiarmycin	286	Lipiarmycin resistance	280
lys	Lysine	210	Lysine requirement, diaminopimelate decarboxylase	132, 153
lysS	Lysine	5	Lysyl-transfer RNA synthetase	242
lyt	Lytic		Autolytic enzymes; see *flaA*	67, 232
mdh			Malate dehydrogenase; see *citH*	86
menB	Menaquinone	273	Menaquinone deficient, multiple aminoglycoside resistant; dihydroxynaphthoate synthase	185, 293
menC,D	Menaquinone	273	Menaquinone deficient, multiple aminoglycoside resistant; blocked in formation of *o*-succinylbenzoic acid from chorismic acid	293
menE	Menaquinone	273	Menaquinone deficient, multiple aminoglycoside resistant; *o*-succinylbenzoyl coenzyme A synthetase	185, 293
metA	Methionine	115	Responds to methionine, cystathionine, or homocysteine	285
metB	Methionine	200	Responds to methionine or homocysteine	10
metC	Methionine	115	Responds to methionine	60
metD	Methionine	95	Responds to methionine	329
mic	Micrococcin		Resistance to micrococcin; see *rplC*	279
mit	Mitomycin	UC	Resistance to mitomycin C; maps near *rplV*	143
mpo		220	Membrane protein over-production, temperature-sensitive sporulation	179
mtlA	Mannitol	34	Lacks mannitol transport; maps near *mtlB*	F
mtlB	Mannitol	35	Mannitol-1-phosphate dehydrogenase	168
mtr	5-Methyltryptophan	210	Resistance to 5-methyl-tryptophan, derepression of the tryptophan biosythetic pathway	124, 126
nalA	Nalidixic acid	355	Resistance to nalidixic; see *gyrA*	102
narA	Nitrate	320	Inability to use nitrate as a nitrogen source	168, 335
narB	Nitrate	30	Inability to use nitrate as a nitrogen source	60, 335
nea	Neamine		Neamine resistance; see ribosomal protein cluster	93
neo	Neomycin		Neomycin resistance; see ribosomal protein cluster	93, 103
nic	Nicotinic acid	245	Nicotinic acid requirement	117, 153

Continued on following page

TABLE 1—*Continued*

Gene symbol	Mnemonic	Map position (degrees)[a]	Phenotype, enzyme deficiency, or other characteristic	Reference(s)[b]
nonA	Nonpermissive	UC	Permissive for bacteriophage SP10 and φNR2, closely linked to *rfm*	258
nonB	Nonpermissive	45	Permissive for bacteriophage SP10 and φNR2; see *hsrM*	258
novA	Novobiocin	0	Resistance to novobiocin *gyrB*	103, 300
nprE	Neutral protease	126	Structural gene for neutral (metallo) protease	303, 307
nprR	Neutral protease	125	Regulatory gene for neutral protease	303
ole	Oleandomycin		Oleandomycin resistance; see ribosomal protein cluster	93, 103
ordA		NM	Ornithine:2-oxoacid aminotransferase	317
outA	Outgrowth	21	Blocked in outgrowth after RNA, protein, and DNA syntheses have started; previous designation *gspIV*	8, 80, 230
outB	Outgrowth	28	Blocked in outgrowth before most macromolecular synthesis has started; previous designation *gsp-81*	7, 78, 230
outC	Outgrowth	27	Blocked in outgrowth after RNA and protein syntheses have started, but before DNA synthesis; previous designation *gsp-25*	8, 230
outD	Outgrowth	122	Blocked in outgrowth; protein and DNA syntheses reduced; previous designation *gsp-1*	79, 230
outE	Outgrowth	300	Block in outgrowth; RNA synthesis normal, protein synthesis reduced; DNA synthesis prevented; previous designation *gsp-42*	8, 230
outF	Outgrowth	316	Blocked in outgrowth; RNA and protein syntheses reduced; DNA synthesis prevented; previous designation *gsp-4*	8, 230
oxr		19	Oxolinic acid resistant	309
pab	*p*-Aminobenzoic acid	10	*p*-Aminobenzoic acid requirement, subunit A of *p*-aminobenzoate synthase	147
pac	Pactamycin	5	Resistance to pactamycin	103, 300
pap			Hyperproduction of proteases and amylase; see *sacQ*	286, 327
pdp		342	Pyrimidine nucleoside phosphorylase	255
pfk		250	Phosphofructokinase	87, 89
pgk		NM	3′-Phosphoglycerolkinase	E
phaI		50	Resistance to phage SPO1	168
pheA	Phenylalanine	245	Phenylalanine requirement, prephenate dehydratase	17
phl	Phleomycin	12	Phleomycin resistance; mutator strain linked to *rpsL*	133
phoA	Phosphatase	NM	Two adjacent structural genes for alkaline phosphatase in *B. licheniformis*	130
phoP′	Phosphatase	260	Regulation of alkaline phosphatase and alkaline phosphodiesterase	165, 326
phoR	Phosphatase	260	Regulation of alkaline phosphatase	164, 165, 190
phoS	Phosphatase	110	Constitutive alkaline phosphatase	231
phoT	Phosphatase	245	Constitutive alkaline phosphatase	G
pig	Pigment	50	Sporulation-associated pigment	251
polA	Polymerase	260	DNA polymerase A	86, 160
polC	Polymerase	145	DNA polymerase III, azopyrimidine resistance	13, 49, 175, 249
pro	Proline	115	Proline requirement	34, 81
ptg	Peptidoglycan	128	Peptidoglycan biosynthesis	35
ptm		105	Pyrithymine resistance	H
pts		120	Phosphoenolpyruvate phosphotransferase	88, 212
pupA		NM	Adenosine phosphorylase	99
pupI		NM	Inosine phosphorylase	99
purA	Purine	355	Adenine requirement	220
purB	Purine	55	Adenine, guanine, or hypoxanthine requirement	174, 214
purC	Purine	55	Adenine or hypoxanthine requirement	174
purD	Purine	55	Adenine or hypoxanthine requirement	174
purE	Purine	55	Adenine requirement	174
pycA		127	Pyruvate carboxylase	33, 119
pyrA	Pyrimidine	135	Carbamyl phosphate synthetase	236
pyrB	Pyrimidine	135	Aspartate carbamoyl transferase	236
pyrC	Pyrimidine	135	Dihydroorotase	236
pyrD	Pyrimidine	135	Dihydroorotate dehydrogenase	236
pyrE	Pyrimidine	135	Orotate phosphoribosyl-transferase, also called *pyrX*	236
pyrF	Pyrimidine	135	Orotidine-5′-phosphate decarboxylase	236
pyrG	Pyrimidine	NM	Cytidine-5′-triphosphate synthetase	248
recA	Recombination	145	Genetic recombination and radiation resistance	117, 183
recB	Recombination	245	Genetic recombination and radiation resistance	117, 183
recC	Recombination		Genetic recombination; indirect effect of bacteriophage SPO2 lysogeny; see *attSPO2*	59, 85, 183

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TABLE 1—*Continued*

Gene symbol	Mnemonic	Map position (degrees)^{a}	Phenotype, enzyme deficiency, or other characteristic	Reference(s)^{b}
recE	Recombination	157	Genetic recombination and radiation resistance, adenosine triphosphate-dependent nuclease; complemented by *E. coli recA*	57, 59, 182, 183
recF	Recombination	355	Genetic recombination and radiation resistance	101, 183, 300
recG	Recombination	205	Genetic recombination and radiation resistance	182
recH	Recombination	70	Genetic recombination and radiation resistance, adenosine triphosphate-dependent nuclease	184, 208
recI	Recombination	70	Genetic recombination and radiation resistance	183, 207
recL	Recombination	UC	Genetic recombination and radiation resistance, linked to *cysA*	59, 182, 183
recM	Recombination	5	Genetic recombination and radiation resistance	59, 182, 183
recN	Recombination	150	Genetic recombination and radiation resistance	182, 183
rec-149	Recombination	11	Reduced recombination and high sensitivity to mytomycin C, prevents φ105 restriction in BsuR^{+} hosts	233
relA	Relaxed	235	ATP:GTP^{d} 3′-phosphotransferase	277, 292
relC	Relaxed		See *tsp*, *rplK*	277
relG	Relaxed	13	Defect in glucose uptake	239, 240
rev-4	Reversion	324	Suppressor of some pleiotropic effects (but not asporogeny) of *spo0* mutations; suppresses effect on sporulation of various drug-resistant mutations; may be same as *abrA*	265, 266
rfm	Rifampin		Rifampin resistance; RNA polymerase; see *rpoB*	97, 223
rgn		UC	Improved protoplast regeneration, maps near *cysA*	6
ribA	Riboflavin	209	Riboflavin requirement	154, 241
ribB	Riboflavin	209	Riboflavin requirement	30, 241
ribC	Riboflavin	222	Riboflavin requirement	30
ribD	Riboflavin	209	Riboflavin requirement	30, 241
ribO	Riboflavin	209	Riboflavin requirement	30, 241
rna-53	RNA synthesis	315	Temperature-sensitive RNA synthesis	250
rodB		242	Cell wall defective	150
rodC		320	Cell wall defective	150
rodD		198	Cell wall defective	G
rplA	Ribosomal protein, large	12	Ribosomal protein BL1, chloramphenicol resistance II	54, 217, 219
rplB	Ribosomal protein, large	12	Ribosomal protein L2 (BL2)	276
rplC	Ribosomal protein, large	12	Ribosomal protein L3 (BL3), probable micrococcin resistance	51, 219, 279
rplE	Ribosomal protein, large	12	Ribosomal protein L5 (BL6)	51
rplF	Ribosomal protein, large	12	Ribosomal protein L6 (BL8)	51
rplJ	Ribosomal protein, large	12	Ribosomal protein L10 (BL5)	54
rplK	Ribosomal protein, large	12	Ribosomal protein L11 (BL11), thiostrepton resistance (*relC*)	54, 219, 223, 319
rplL	Ribosomal protein, large	12	Ribosomal protein L12 (BL9), chloramphenicol resistance VI	54, 217, 219
rplO	Ribosomal protein, large	10	Ribosomal protein L15, chloramphenicol resistance III	217, 219
rplQ	Ribosomal protein, large	12	Ribosomal protein L17 (BL15)	276
rplU	Ribosomal protein, large	244	Ribosomal protein L21 (BL20)	53
rplV	Ribosomal protein, large	12	Ribosomal protein L22 (BL17), erythromycin resistance	219, 276, 294
rplX	Ribosomal protein, large	12	Ribosomal protein L24 (BL23)	276
rpmA	Ribosomal protein	244	Ribosomal protein L27 (BL24)	53, 70
rpmD	Ribosomal protein	12	Ribosomal protein L30 (BL27)	52
rpoB	RNA polymerase	10	β subunit of RNA polymerase, rifampin resistance	97, 282
rpoC	RNA polymerase	10	β′ subunit of RNA polymerase, streptolydigin resistance	98, 282
rpoD	RNA polymerase	224	RNA polymerase σ^{43} subunit	238
rpsC	Ribosomal protein, small	12	Ribosomal protein S3 (BS3)	276
rpsD	Ribosomal protein, small	12	Ribosomal protein S4 (BS4)	108, 115
rpsE	Ribosomal protein, small	12	Ribosomal protein S5, spectinomycin resistance	52, 103, 166, 216
rpsF	Ribosomal protein, small	4	Ribosomal protein S6 (BS9)	50
rpsG	Ribosomal protein, small	12	Ribosomal protein S7 (BS7)	54
rpsH	Ribosomal protein, small	12	Ribosomal protein S8 (BS8)	218
rpsI	Ribosomal protein, small	12	Ribosomal protein S9 (BS10)	52
rpsJ	Ribosomal protein, small	12	Ribosomal protein S10 (BS13) (*tetA*)	276
rpsK	Ribosomal protein, small	12	Ribosomal protein S11 (BS11)	52
rpsL	Ribosomal protein, small	12	Ribosomal protein S12 (BS12) (*strA*), streptomycin resistance	51, 52, 93, 219 19
rpsP	Ribosomal protein, small	148	Ribosomal protein S16 (BS17)	50
rpsQ	Ribosomal protein, small	12	Ribosomal protein S17 (BS16)	218
rpsS	Ribosomal protein, small	12	Ribosomal protein S19 (BS19)	218
rpsT	Ribosomal protein, small	12	Ribosomal protein S20 (BS20)	216, 218, 219
Ribosomal			Cluster of ribosomal proteins, including S3, S5, S8, S12, S17,	142, 220

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TABLE 1—*Continued*

Gene symbol	Mnemonic	Map position (degrees)[a]	Phenotype, enzyme deficiency, or other characteristic	Reference(s)[b]
protein cluster			S19, S20, BL1, BL2, BL4, BL5, BL6, BL8, BL12, BL14, BL15, BL16, BL17, BL22, BL23, and BL25	
rrnA	Ribosomal RNA	0	Ribosomal RNA operon	214, 323
rrnB	Ribosomal RNA	275	Ribosomal RNA operon	287
rrnC	Ribosomal RNA	225	Ribosomal RNA operon with uncertain location in *lys-aroD* region	I
rrnD	Ribosomal RNA	UC	Ribosomal RNA operon with possible location near 200°	I
rrnE	Ribosomal RNA	UC	Ribosomal RNA operon with possible location near 200°	I
rrnF	Ribosomal RNA	NM	Ribosomal RNA operon known to exist but not cloned or mapped	I
rrnG	Ribosomal RNA	15	Ribosomal RNA operon	I
rrnH	Ribosomal RNA	15	Ribosomal RNA operon	I
rrnI	Ribosomal RNA	15	Ribosomal RNA operon	I
rrnO	Ribosomal RNA	0	Ribosomal RNA operon	214
rrnR	Ribosomal RNA	240	Ribosomal RNA operon located in *leu* region of the chromosome	J
rvt	Revertant		Mutations causing same phenotype as *rvtA* mutations but not mapping in the *rvtA* region	268
rvtA	Revertant	217	Suppressor of sporulation defect in *spo0B*, *spo0E*, *spo0F*, and *spoIIA* mutants; may be same as *sof-1*; intergenic suppression of *spo0* mutations; probably maps in *spo0A*	268
sacA	Sucrose	335	β-Fructofuranosidase	166, 167
sacB	Sucrose	305	Levansucrase	167
sacL	Sucrose	240	Levanase	159
sacP	Sucrose	335	Sucrose transport	166
sacQ	Sucrose	285	Hyperproduction of levansucrase and proteases	158, 167
sacR	Sucrose	305	Constitutive α-fructofuranosidase production	167
sacS	Sucrose	335	Constitutive α-fructofuranosidase production	167
sacT	Sucrose	335	Constitutive α-fructofuranosidase production	167
sacU	Sucrose	310	Regulatory gene for levansucrase	158, 167, 169, 288
sapA	Sporulation-associated phosphatase	114	Mutations overcome sporulation, phosphatase-negative phenotype of early blocked *spo* mutants	227, 231
sapB	Sporulation-associated phosphatase	56	Mutations overcome sporulation, phosphatase-negative phenotype of early blocked *spo* mutations	231
sas		211	Weak intragenic suppressor mutations of *spoIIA*	332
scoA		109	Sporulation control, protease and phosphatase overproduction; delayed spore formation	191
scoB		129	Sporulation control, protease and phosphatase overproduction; delayed spore formation	58, 191
scoC		75	Sporulation control	191
scoD		130	Sporulation control	191
sdhA	Succinate dehydrogenase	252	Cytochrome b_{558}; subunit of succinate dehydrogenase	105
sdhB	Succinate dehydrogenase	252	Flavoprotein subunit of succinate dehydrogenase	105
sdhC	Succinate dehydrogenase	252	Iron protein subunit of succinate dehydrogenase	105
ser	Serine	210	Requirement for serine	124
serR	Serine	25	Serine resistance	D
smo	Smooth	295	Smooth/rough colony morphology	94, 150
sof-1		217	Suppressor of sporulation defects in *spo0B*, *spo0E*, and *spo0F* mutants; mutation is an alteration in codon 12 of the *spo0A* gene; probably same as *rvtA*	123, 151
spcA	Spectinomycin		Spectinomycin resistance; see *rpsE*	37, 103, 142
spcB	Spectinomycin	140	Spectinomycin resistance	103, 175
spcD	Spectinomycin	3	Spectinomycin dependence, maps between *cysA* and *purA*	107
spdA		288	Sporulation derepressed; low pyruvate carboxylase activity	63
spg	Sporangiomycin		Sporangiomycin resistance, 50S ribosomal alteration; see ribosomal protein cluster	21
spoCM	Sporulation	355	Stage 0 sporulation, possibly identical to *spo0J*	29
spoL1	Sporulation	230	"Decadent" sporulation	16
spo0A	Sporulation	215	Sporulation, mutants blocked at stage 0, mutants exhibit wide variety of pleiotropic phenotypes	90, 120, 122, 187, 337
spo0B	Sporulation	245	Sporulation, mutants blocked at stage 0, mutants have most phenotypes of mutants bearing *spo0A* mutations	27a, 70, 120
spo0C	Sporulation	218	Stage 0 sporulation, mutations with less pleiotropic phenotypes known to be missense alterations in the *spo0A* gene product	123

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TABLE 1—*Continued*

Gene symbol	Mnemonic	Map position (degrees)[a]	Phenotype, enzyme deficiency, or other characteristic	Reference(s)[b]
spo0D	Sporulation	234	Stage 0 sporulation, single allele resulting in stage 0 block of sporulation, mapped but not further characterized	137
spo0E	Sporulation	120	Stage 0 sporulation, oligosporogenous mutations giving stage 0 block, possibly more than one gene, phenotypes less than *spo0A*, *spo0B* or *spo0F* mutations	47, 228
spo0F	Sporulation	323	Stage 0 sporulation, DNA sequence contains single open reading frame for protein of 19,055 daltons; inhibits sporulation when present in multiple copies	120, 152, 271
spo0G	Sporulation	223	Stage 0 sporulation, single allele resulting in stage 0 block of sporulation, maps in region of *spo0A* locus but genetically distinct from *spo0A*	137
spo0H	Sporulation	11	Stage 0 sporulation, locus codes for protein of 22,000 daltons determined from sequence of *B. licheniformis* cloned gene complementing *spo0H* mutations of *B. subtilis*, least pleiotropic *spo0* mutation	120, 226, 228
spo0J	Sporulation	352	Stage 0 sporulation, locus consisting of two alleles yielding phenotype similar to *spo0H* mutations	129, 300
spo0K	Sporulation	101	Stage 0 sporulation, maps close to tryptophanyl transfer RNA synthetase gene	47, 228
spo0L	Sporulation	106	Stage 0 sporulation, uncharacterized allele giving *spo0* phenotype, maps near *spo0K* but genetically distinct	A
spoIIA	Sporulation	211	Stage II sporulation, blocked at stage II of sporulation, DNA sequence has three adjacent open reading frames coding for proteins of 13, 16, and 22 kilodaltons; 22-kilodalton one has homology to *rpoD*	137, 173, 228, M
spoIIB	Sporulation	244	Stage II sporulation	47, 228
spoIIC	Sporulation	296	Stage II sporulation	228
spoIID	Sporulation	316	Stage II sporulation	228
spoIIE	Sporulation	10	Stage II sporulation	228
spoIIF	Sporulation	120	Stage II sporulation	129, 228
spoIIG	Sporulation	135	Stage II sporulation, DNA sequence has homology with *rpoD* gene	229, 288
spoIIIA	Sporulation	220	Stage III sporulation, blocked at stage III of sporulation	225, 228
spoIIIB	Sporulation	221	Stage III sporulation, blocked at stage III of sporulation, possibly the same as *spoIVC*	225, 228
spoIIIC	Sporulation	227	Stage III sporulation, blocked at stage III of sporulation	137, 228
spoIIID	Sporulation	302	Stage III sporulation, blocked at stage III of sporulation	137, 228
spoIIIE	Sporulation	142	Stage III sporulation, blocked at stage III of sporulation	137, 228
spoIIIF	Sporulation	239	Stage III sporulation, blocked at stage III of sporulation; map order *nic-recB-spoIIIF-spoVB*	162
spoIVA	Sporulation	204	Stage IV sporulation, linked to *trpC* by transformation	228
spoIVB	Sporulation	213	Stage IV sporulation, may be allele of *spo0A*	47, 228
spoIVC	Sporulation	227	Stage IV sporulation, contains at least two cistrons, linked to *aroD* by transformation	55, 228, 230
spoIVD	Sporulation	233	Stage IV sporulation	129, 228
spoIVE	Sporulation	234	Stage IV sporulation	137, 228
spoIVF	Sporulation	242	Stage IV sporulation, linked to *spo0B* by transformation	47, 162, 228
spoIVG	Sporulation	97	Stage IV sporulation	225, 228
spoVA	Sporulation	211	Stage V sporulation, transcribed as polycistronic unit with open reading frames for proteins of 23, 15, 16, 36, and 34 kilodaltons	228; P. Fort and J. Errington, J. Gen. Microbiol., in press
spoVB	Sporulation	239	Stage V sporulation	129, 162
spoVC	Sporulation	7	Stage V sporulation, cloned on plasmid vectors	201
spoVD	Sporulation	133	Stage V sporulation, linked to *spoVE* by transformation	47, 129
spoVE	Sporulation	133	Stage V sporulation	47, 129, 228
spoVF	Sporulation	148	Stage V sporulation, probably the same as *dpa*; mutants form octanol- and chloroform-resistant, heat-sensitive spores; form heat-resistant spores in presence of dipicolinic acid	15, 228, 230
spoVG	Sporulation	6	Stage V sporulation, previously called 0.4-kilobase gene, transcription turned on within 30 min of start of sporulation	96, 254
spoVH	Sporulation	251	Stage V sporulation	116
spoVJ	Sporulation	250	Stage V sporulation	116
spoVIA	Sporulation	255	Blocked at stage VI of sporulation; map order *argA-spoVIA-gerE-leuA*	144

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TABLE 1—*Continued*

Gene symbol	Mnemonic	Map position (degrees)[a]	Phenotype, enzyme deficiency, or other characteristic	Reference(s)[b]
spoVIB	Sporulation	247		145
spoL		227	"Decadent" sporulation	16
sprA		NM	Derepression of homoserine kinase, homoserine dehydrogenase, and the minor threonine dehydratase (*tdm*)	305
sprB		290	Partial suppression of isoleucine requirement allows threonine dehydratase *sprA* mutants to grow in minimal medium, maps near *tdm* locus; see *tdm*	306
sprE			See *aprE*	
srm		12	Modifies resistance of *spcA* strains; maps in ribosomal cluster	38
ssa		217	Alcohol-resistant sporulation; maps close to *spo0A*; *rvt* mutations have same phenotype	24, 268
ssp-1	Ultraviolet repair	NM	Endonuclease exicising spore photoproducts	204
std	Streptolydigin		Streptolydigin resistance; RNA polymerase; see *rpoC*	98, 282
strA	Streptomycin		Streptomycin resistance; see *rpsL*	93
strB	Streptomycin	130	Streptomycin resistance	283
strC	Streptomycin	220	Streptomycin uptake deficient, possible cytochrome oxidase regulator	184, 283
sul	Sulfonilamide	10	Sulfonilamide resistance	136, 147
suA20	Suppressor	145	Suppressor of *recH* mutations with increased ATP-dependent deoxyribonuclease	161
sup-3	Suppressor	30	Suppressor transfer RNA	112
sup-44	Suppressor	29	Suppressor transfer RNA	172
tag		309	Cell wall synthesis *hisA*	28, 150
tal	β-Thienylalanine	239	Resistant to β-thienylalanine	46
tdm		290	Minor threonine dehydratase	306
ten	Transfection enhancement	245	Constitutive transfection enhancement of SP82 DNA, transformation defective	K
tetB	Tetracycline	3	Resistant to tetracycline	321
thiA	Thiamine	70	Thiamine requirement	153
thiB	Thiamine	100	Thiamine requirement	119
thiC	Thiamine	331	Thiamine requirement	D
thrA	Threonine	290	Threonine requirement, homoserine kinase	60, 305
thyA	Thymidine	160	Thymidylate synthetase A	10, 211, 324
thyB	Thymidine	200	Thymidylate synthetase B	10, 211, 324
til	Tilerone	230	Tilerone resistance	A
tkt		NM	Transketolase	260, 261
tmp	Trimethoprim	200	Trimethoprim resistance	311
tmrA	Tunicamycin	25	Tunicamycin resistance, hyperproductivity of extracellular α-amylase	213
tmrB	Tunicamycin	25	Tunicamycin resistance	213
tms-12		130	Temperature-sensitive cell division	48
tms-26		5	Temperature-sensitive cell division	48, 297
tolA	Tolerance		Tolerance to bacteriophage; see *abrB*	139, 140
tolB	Tolerance	NM	Tolerance to bacteriophage	139, 140
tre	Trehalose	60	Trehalose	168
trnA	Transfer RNA	0	Genes for Ile and Ala transfer RNAs located between 16S and 23S RNAs in the *rrnA* operon	310
trnB	Transfer RNA	275	Linked set of transfer RNA genes distal to *rrnB* that contains transfer RNAs for Val, Thr, Lys, Leu, Gly, Leu, Arg, Pro, Ala, Met, Ile, Ser, fMet, Asp, Phe, His, Gly, Ile/Met, Asn, Ser, and Glu	310
trnI	Transfer RNA	15	Linked set of transfer RNA genes including transfer RNAs for Ala, Pro, Arg, Gly, Thr, and Asn located between *rrnH* and *rrnI*, formerly *trnH*	310
trnO		0	Same as *trnA*	310
trpA	Tryptophan	205	Tryptophan synthase α	9, 125, 317
trpB	Tryptophan	205	Tryptophan synthase β	9, 125, 317
trpC	Tryptophan	205	Indol-3-glycerol-phosphate synthase	9, 125, 318
trpD	Tryptophan	205	Anthranilate phospho-ribosyltransferase	9, 125, 318
trpE	Tryptophan	205	Anthranilate synthase	9, 125, 318
trpF	Tryptophan	205	*N*-(142′-Phosphoribosyl)-anthranilate isomerase	125, 318
trpS	Tryptophan	100	Tryptophanyl-transfer RNA synthase	285
trpX	Tryptophan	10	Glutamine-binding protein common to anthranilate synthase and *p*-amino-genzoate synthase	147
tsi		50	Temperature-sensitive induction of all known SOS functions	176, 274
tsp	Thiostrepton		Thiostrepton resistance, 50S subunit, maps in ribosomal protein cluster	223

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TABLE 1—*Continued*

Gene symbol	Mnemonic	Map position (degrees)[a]	Phenotype, enzyme deficiency, or other characteristic	Reference(s)[b]
tsl		145	Temperature-sensitive division	36
ts31		131	Temperature-sensitive division	192
ts39		230	Temperature-sensitive synthesis of phosphatidylethanolamine	170
ts341		312	Temperature-sensitive division	192
ts526		3	Temperature-sensitive division	192
tuf	Tu factor	10	Elongation factor Tu	61
tyrA	Tyrosine	205	Tyrosine requirement, prephenate dehydrogenase	206, 209
tzm	Tetrazolium	205	Tetrazolium reaction; probably an allele of *gerJ*	302, 313
udk	Uridine kinase	NM	Uridine kinase, also lacks cytidine kinase, mutant resistant to fluorouridine	210
upp		NM	Uracil phosphoriboxyl transferase	210
urg		NM	*N*-Glycosidase	177
urs		100	Uracil sensitivity, arginine-specific carbamyl-phosphate synthase	L
uvrA	Ultraviolet repair	310	Excision of ultraviolet light-induced pyrimidine dimers in DNA	117, 168, 204
uvrB	Ultraviolet repair	250	Excision of ultraviolet light-induced pyrimidine dimers in DNA	204
vas			Valine sensitivity; maps within threonine dehydratase locus; see *ilvA*	204
VS		12	Virginiamycin (VS component) resistance	252
xhi		112	Heat-inducible PBS-X	32, 34
xlt		115	Induced PBS-X bacteriophage lack tails	84
xynA		48	Extracellular β-xylanase	253
xynB		48	Cell-associated β-xyloxidase	253

[a] UC, Map position not fully defined; NM, not mapped.

[b] References include unpublished data from: (A) J. Hoch, (B) S. Baumberg, (C) C. Anagnostopoulos, (D) S. Zahler, (E) E. Freese, (F) P. Gay, (G) P. Piggot, (H) A. Galizzi, (I) K. Bott, (J) R. Rudner, (K) D. Green, (L) R. Switzer, and (M) P. Fort.

[c] RNA, Ribonucleic acid

[d] ATP, Adenosine triphosphate; GTP, guanosine triphosphate.

tein genes, particularly in the major ribosomal protein gene cluster located in the origin region of the chromosome. This stems from the fact that the number codes for ribosomal proteins in *B. subtilis* are different from those of *Escherichia coli* and the assignment of the number to the corresponding locus in *E. coli* is not altogether clear because of it. In any case, in Fig. 2 we show the available data in the literature with regard to the ordering of ribosomal genes in the origin region. The original literature should be consulted and studied if one is interested in gene order in this area.

The map as presented shows almost entirely developmental genes on the interior of the circle and other loci on the outside of the circle. A more detailed description of the developmental loci can be obtained in a recent article by Piggot and Hoch (229).

Several minor changes in the map that became clear after the map had been drawn should be noted. The position of the *aecA* and *sdh* genes at approximately 255° should be reversed. The *hag* locus which should be located at 307° on the map is missing from Fig. 2. The *pfa* locus mapping at approximately 240° is missing from the map. This locus is very close to the *phe* gene. The *ribB* gene is mislabeled as *ribT* at approximately 210°. Several loci are only given tentative locations and are enclosed in parentheses. These include genes such as the *rrn* loci that have only been generally located to certain areas of the genome. Several mistakes in the assignment of *fla* genes have come to light by the recent work of Pooley and Karamata (234). These alterations have not been made to the map shown in Fig. 1. *flaA* and *flaB* are now mapped at approximately 145° in the region of the *che* genes. *flaD* has been mapped between the *lys* and *aroD* markers at approximately 220°. A suggested location would be between the *ribC* and *strC* loci. The *ifm* locus leading to hypermotility mapping at 304° has been deleted from Fig. 1. The arginine genes have been expanded and renamed in Table 1 but the old designations appear on the map.

The map shown is for *B. subtilis* 168. Other strains, notably 166, have substantial rearrangements of the chromosome as compared with 168. This has been beautifully characterized and exploited by Schneider et al. (263). By suitable crosses with 166 as donor and 168 as recipient or vice versa, it is possible to force rearrangements of the recipient chromosome that lead to duplication of substantial portions of the chromosome. There appear to be only a few sites on the chromosome where the crossovers required for these rearrangements can occur.

CODON USAGE IN *B. SUBTILIS*

The cloning and sequencing of a number of *B. subtilis* genes have allowed us to compile a codon usage table for *B. subtilis* and compare it with that of *E. coli* (8a) (Table 2). Such codon usage tables are sometimes useful for determining whether newly sequenced open reading frames are likely to code for proteins or not. Comparison of the codon usage between *E. coli* and *B. subtilis* provides a few surprises. Two of the amino acids with six possible codons, *leu* and *arg*, have a strong bias toward one of the six codons in their genes in *E. coli*. In *B. subtilis* the six codons are more evenly distributed among the genes so far sequenced. In both organisms, however, the leucine codon CUA is the least utilized of the leucine codons. Both *E. coli* and *B. subtilis* tend to use the ochre codon as a translation terminator in the majority of the genes analyzed. Although slight differences

TABLE 2. Codon usage table for *B. subtilis* and *E. coli*[a]

AA	Codon	F_{BS}	F_{EC}	AA	Codon	F_{BS}	F_{EC}	AA	Codon	F_{BS}	F_{EC}	AA	Codon	F_{BS}	F_{EC}
Phe	UUU	0.57	0.37	Ser	UCU	0.23	0.23	Tyr	UAU	0.65	0.40	Cys	UGU	0.68	0.43
Phe	UUC	0.43	0.63	Ser	UCC	0.09	0.27	Tyr	UAC	0.35	0.60	Cys	UGC	0.32	0.57
Leu	UUA	0.24	0.07	Ser	UCA	0.20	0.07	Ter	UAA	0.71	0.75	Ter	UGA	0.21	0.17
Leu	UUG	0.14	0.09	Ser	UCG	0.11	0.11	Ter	UAG	0.08	0.08	Trp	UGG	1.00	1.00
Leu	CUU	0.25	0.07	Pro	CCU	0.30	0.12	His	CAU	0.67	0.54	Arg	CGU	0.22	0.56
Leu	CUC	0.10	0.07	Pro	CCC	0.09	0.07	His	CAC	0.33	0.46	Arg	CGC	0.19	0.36
Leu	CUA	0.06	0.02	Pro	CCA	0.21	0.16	Gln	CAA	0.52	0.24	Arg	CGA	0.12	0.03
Leu	CUG	0.21	0.68	Pro	CCG	0.40	0.65	Gln	CAG	0.48	0.76	Arg	CGG	0.14	0.03
Ile	AUU	0.50	0.36	Thr	ACU	0.15	0.25	Asn	AAU	0.56	0.26	Ser	AGU	0.11	0.06
Ile	AUC	0.37	0.61	Thr	ACC	0.16	0.50	Asn	AAC	0.44	0.74	Ser	AGC	0.26	0.26
Ile	AUA	0.13	0.03	Thr	ACA	0.45	0.07	Lys	AAA	0.73	0.76	Arg	AGA	0.22	0.01
Met	AUG	1.00	1.00	Thr	ACG	0.24	0.18	Lys	AAG	0.27	0.24	Arg	AGG	0.11	0.01
Val	GUU	0.31	0.36	Ala	GCU	0.27	0.26	Asp	GAU	0.61	0.46	Gly	GGU	0.24	0.48
Val	GUC	0.24	0.15	Ala	GCC	0.22	0.21	Asp	GAC	0.39	0.54	Gly	GGC	0.31	0.39
Val	GUA	0.21	0.22	Ala	GCA	0.29	0.22	Glu	GAA	0.70	0.73	Gly	GGA	0.32	0.05
Val	GUG	0.24	0.27	Ala	GCG	0.22	0.31	Glu	GAG	0.30	0.27	Gly	GGG	0.13	0.08

[a] F, Fraction usage for each codon compared with total for indicated amino acid; BS, *B. subtilis*; EC, *E. coli*. Usage calculated for 6,121 and 16,351 codons for *B. subtilis* and *E. coli*, respectively. AA, Amino acid.

can be observed among the various codons, it appears that *B. subtilis* tends to more evenly distribute the codons for its amino acids than *E. coli*.

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