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Linkage Map of *Escherichia coli* K-12, Edition 6†

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INTRODUCTION

The rate at which genetic loci are being placed on the linkage map of *Escherichia coli* strain K-12 continues unabated. Over 300 new loci have been added since the 1976 edition of the map (24), bringing the total number of loci listed in Table 1 of this review to almost 1,000. The continued progress in understanding the structure of the genome of this bacterium is even more impressive in view of the technical difficulties involved in mapping many of the newly added loci. A large proportion of the loci added to this and the previous edition of the map are those of essential genes coding for components of the complex machinery required for translation, transcription, and chromosome replication. Another major category among recently identified genetic elements has come from studies at the molecular level of the sequences controlling transcription. Many of these accomplishments were achieved through the use of radically new techniques of mapping, which have permitted the precise determination of many map distances in kilobases. Knowledge of the *E. coli* genome has thus moved to new levels of complexity and precision. A list of the mapping techniques now available is presented in Table 3.

The naming of the genetic elements involved in the control of transcription has presented problems which we feel call for a modification of the accepted system of nomenclature. The modifications adopted in this revision of the map are discussed below. These transcriptional control elements no longer appear on the drawing of the linkage map (see Fig. 1) but are included in the list of genetic markers (see Table 1).

This review is based on a survey of the literature published from July 1975 through June 1979 and on personal communications of mapping data. Some of the latter data have been published since we received them; references to these publications have been included when possible. In some cases in which several papers from the same laboratory described work on the mapping of the same loci, we have referred to only the latest paper. We have not included review articles unless they presented original data. The number of papers cited in this review is close to the total number cited in previous editions of the map. It was therefore impractical to include the earlier references in this edition. The letter A in Table 1 refers the reader to the 1976 edition of the map (24), in which the earlier papers are cited.

The major coordinates of the map are still determined by time-of-entry data, as at least two gaps remain in the cotransduction data for the entire linkage group. So far, only about 15% of the map has been covered by physical mapping data. The precision with which map distances are known thus varies from ± a few kilobases (or base pairs) for some physical mapping to ± a few tenths of a minute for some markers mapped by cotransduction to cases in which a marker has been localized only to a 5- to 10-min segment of the map by conjugation or other less-precise methods. In Fig. 1, markers that have not been ordered with respect to surrounding markers are indicated by an asterisk. Loci mapped only approximately by imprecise methods are shown in parentheses, usually near the center of the region to which they have been localized. We were not able to represent map distances of a few kilobases accurately in Fig. 1, as the scale of the map drawing was not suitable for this.

We wish to emphasize strongly here that this review is intended to provide easy access to the original research papers, not to eliminate the necessity of consulting them. The positions shown for many loci on Fig. 1 are estimates

† Reprints of this paper may be obtained from the authors. Those wishing to have a wall chart consisting of a linear drawing of the *E. coli* linkage map (together with a reprint) suitable for teaching and laboratory use may obtain one for $5 (prepaid) from the ASM Publications Office.

based on analyses of widely varying or even contradictory data. It seems worth pointing out that a marker mapped on the basis of a low frequency of cotransduction with a second marker, and not oriented by three-factor crosses or other means, could be shown in Fig. 1 as much as 4 min away from its proper position, to take the worst possible case as an example.

NOMENCLATURE

The system of nomenclature proposed by Demerec et al. (127a) has served well for the naming of genetic loci and the unambiguous designation of mutant alleles over the past 13 years. It seems worthwhile preserving this valuable system. The genes coding for ribosomal proteins were successfully accommodated in this system in an orderly manner that made their symbols easy to determine and to remember. In this revision, the ribosomal ribonucleic acid (rRNA) genes are named as recommended by Nomura et al. (448b). We have retained on the map drawing the symbols *rrnA*, *rrnB*, etc., for the rRNA operons, as these informal names appear to be very useful. The rRNA genes within these operons are given the symbols *rrs* (16S rRNA), *rrl* (23S rRNA), and *rrf* (5S rRNA). Contrary to the suggestion of the authors mentioned above, we have designated the transfer RNA (tRNA) genes within the rRNA operons in the customary manner: three letters symbolizing the amino acid, followed by T, U, V, etc. The symbols designating genes coding for flagellar components now number more than 26; following the precedent set in naming the genes coding for the proteins of the large ribosomal subunit, the flagellar genes have been given the symbols *flaA* through *flaZ*, followed by *flbA*, *flbB*, etc.

Around 8% of the loci listed in Table 1 are sequences controlling transcription: operators, promoters, leaders, attenuators, etc. Only 3% of the loci on the 1976 map were of this class. The number of such elements identified can be expected to increase greatly in the near future. If these sequences were to be designated according to the system of Demerec et al., new gene symbols would have to be invented for a number of them. This would make the nomenclature very cumbersome and lessen the value of the mnemonics, especially in those cases in which there are many loci with the same gene symbol, e.g., the ribosomal protein genes, the rRNA genes, the flagellar genes, the pyrimidine genes, etc. It seems likely that before long a system will be devised for designating the control sequences precisely in molecular terms. In the meantime, it is necessary to have a method for designating mutations in these sequences. For this reason, we have devised a system for designating these elements by a modification of the Demerec et al. system. This solution was reached in consultation with the members of the Advisory Committee to the *Escherichia coli* Genetic Stock Center: A. J. Clark (University of California, Berkeley), P. E. Hartman (Johns Hopkins University, Baltimore), K. E. Sanderson (University of Calgary, Calgary), and A. L. Taylor (University of Colorado Medical Center, Denver).

In Table 1 the transcriptional control elements for an operon are designated by appending lower case (italicized) letters to the (italicized) gene symbols of the nearest loci controlled. In the case of operators, promoters, leaders, attenuators, and initiators, the designation of the nearest gene downstream is used. Thus, for operon *abcDEF*, in which *abcD* is the first gene transcribed, these symbols would be: *abcDo* (operator), *abcDp* (promoter), *abcDe* (leader), *abcDa* (attenuator), and *abcDi* (initiator). The terminator of transcription of this operon would be designated *abcFt*, using the designation of the nearest gene upstream from the terminator. The naming of mutations in spacer sequences can be accommodated in the same manner by appending an "*s*" to the designation of the first gene downstream from the spacer sequence.

In the case of tandem dual operators and promoters affecting transcription of the same genes, numbers can be inserted into these designations in such a manner that they will not be confused with mutant allele numbers, e.g., *deoC1p* and *deoC2p*, as shown in Table 1 for the *deo* operon. In the case of operons transcribed divergently from overlapping control regions, separate designations have been given to the elements controlling transcription in the two directions on a functional basis, even though this involved naming the same sequence of deoxyribonucleic acid (DNA) twice, e.g., *argEo* and *argEp* and *argCo* and *argCp* in the *argECBH* operon as shown in Table 1. The transcriptional control elements are not shown on the drawing of the genetic map (Fig. 1) but are listed in Table 1.

As in the 1976 edition of the map, we have attempted to reconcile differences in the genetic nomenclature used for *E. coli* with that used for the closely related organism *Salmonella typhimurium*. The degree of homology reflected in the linkage maps of these two organisms is discussed in the most recent edition of the linkage map of *S. typhimurium* (535), and the genetic relatedness of the members of the family *Enterobacteriaceae* as a whole is the subject of a recent review (534).

To bring the nomenclature for *E. coli* in line

TABLE 1. *Genetic markers of E. coli K-12*[a]

Gene symbol	Mnemonic	Map position (min)[b]	Alternate gene symbols; phenotypic trait affected	References[c]
aat		(54)	Aminoacyl-tRNA-protein transferase (EC 2.3.2.6)	113, 580
aceA	Acetate	90	*icl*; utilization of acetate; isocitrate lyase (EC 4.1.3.1)	A
aceB	Acetate	90	*mas*; utilization of acetate; malate synthase A (EC 4.1.3.2)	A
aceE	Acetate	3	*aceE1*; acetate requirement; pyruvate dehydrogenase (decarboxylase component)	A, 345
aceF	Acetate	3	*aceE2*; acetate requirement; pyruvate dehydrogenase (dihydrolipoyltransacetylase component)	A, 345
ack		49	Acetate kinase (ATP:acetate phosphotransferase) activity (EC 2.7.2.1)	65
acrA	Acridine	10	*Mb, mbl, mtc*; sensitivity to acriflavine, phenethyl alcohol, sodium dodecyl sulfate	A
add		36	Adenosine deaminase (EC 3.5.4.4)	291
adh		27	Levels of alcohol dehydrogenase and nitrate reductase activity	92
adk		11	*plsA*; adenylate kinase (EC 2.7.4.3) activity; pleiotropic effects on glycerol-3-phosphate acyltransferase activity	A, 200, 508
alaS	Alanine	58	*ala-act*; alanyl-tRNA synthetase (EC 6.1.1.7)	A, 404, 619
alaT	Alanine	86	*talA*; alanine tRNA1B; in *rrnA* operon	268, 424
alaU	Alanine	70	*talD*; alanine tRNA1B; in *rrnD* operon	268, 424, 688
alk	Alkylation	43	Sensitivity to alkylating agents	678
alnA	Alanine	1	*dad*; D-alanine dehydrogenase	A, 170
alnR	Alanine	99	Regulatory gene	A
alr		92	Alanine racemase (EC 5.1.1.1)	A
ampA	Ampicillin	94	Penicillin resistance; possibly operator or promoter sequence for *ampC*	A, 449, 450
ampC	Ampicillin	94	Resistance to penicillin; penicillinase structural gene (EC 3.5.2.6)	A, 449, 450
ana		27	Reoxidation of reduced pyridine nucleotides	36, 79
apt		10	Adenine phosphoribosyltransferase (EC 2.4.2.7)	316, 317
araA	Arabinose	1	L-Arabinose isomerase (EC 5.3.1.4)	A, 302
araB	Arabinose	1	Ribulokinase (EC 2.7.1.16)	A, 302, 356
araBi	Arabinose	1	*araI*; initiator sequence	A, 98, 574
araBo	Arabinose	1	*araO*; operator sequence for *araBAD*	A, 543, 574
araBp	Arabinose	1	Promoter sequence for *araBAD*	202, 207, 574
araC	Arabinose	1	Regulatory gene; activator and repressor protein	A, 76, 302, 442
araCo	Arabinose	1	Operator sequence for *araC*	76, 574
araCp	Arabinose	1	Promoter sequence for *araC*	253, 574
araD	Arabinose	1	L-Ribulosephosphate 4-epimerase (EC 5.1.3.4)	A, 302
araE	Arabinose	61	L-Arabinose permease	A
araF	Arabinose	45	L-Arabinose periplasmic binding protein	505, M
argA	Arginine	60	*argB, Arg1, Arg$_2$*; amino acid acetyltransferase (EC 2.3.1.1)	A, 145
argAo	Arginine	60	Operator sequence for *argA*	145
argB	Arginine	89	*argC*; acetylglutamate kinase (EC 2.7.2.8)	A, 56, 84, 110, 398
argC	Arginine	89	*argH, Arg2*; *N*-acetyl-γ-glutamyl-phosphate reductase (EC 1.2.1.38)	A, 56, 84, 110, 398
argCo	Arginine	89	Operator sequence for *argCBH*	56, 61, 84, 110, 398
argCp	Arginine	89	Promoter sequence for *argCBH*	56, 61, 84, 110, 398
argD	Arginine	73	*argG, Arg$_1$*; acetylornithine aminotransferase (EC 2.6.1.11)	A
argE	Arginine	89	*argA, Arg4*; acetylornithine deacetylase (EC 5.1.1.16)	A, 56, 84, 110, 398
argEo	Arginine	89	Operator sequence for *argE*	56, 61, 84, 110, 398
argEp	Arginine	89	Promoter sequence for *argE*	56, 61, 84, 110, 398
argF	Arginine	6	*argD, Arg5*; ornithine carbamoyltransferase (EC 2.1.3.3) (duplicate gene)	A, 94, 309, 310, 358, 553
argG	Arginine	68	*argE, Arg6*; argininosuccinate synthetase (EC 6.3.4.5)	A
argH	Arginine	89	*argF, Arg7*; argininosuccinate lyase (EC 4.3.2.1)	A, 56, 84, 110, 398
argHp	Arginine	89	Secondary promoter sequence for *argH*	56, 84, 110, 398
argI	Arginine	96	Ornithine carbamoyltransferase (EC 2.1.3.3) (duplicate gene)	A, 94, 309, 310, 358, 553
argP	Arginine	62	Transport of arginine, ornithine, and lysine	A
argR	Arginine	70	*Rarg*; regulatory gene	A
argS	Arginine	(40)	Arginyl-tRNA synthetase (EC 6.1.1.19)	A
aroA	Aromatic	20	3-Enolpyruvylshikimate-5-phosphate synthetase	A
aroB	Aromatic	74	Dehydroquinate synthetase	A

TABLE 1—*Continued*

Gene symbol	Mnemonic	Map position (min)[b]	Alternate gene symbols; phenotypic trait affected	References[c]
aroC	Aromatic	50	Chorismate synthetase	A
aroD	Aromatic	37	5-Dehydroquinate dehydratase (EC 4.2.1.10)	A
aroE	Aromatic	72	Dehydroshikimate reductase	A
aroF	Aromatic	56	DAHP synthetase (tyrosine repressible)	A
aroFo	Aromatic	56	*aroK;* operator sequence for *aroF tyrA*	A
aroG	Aromatic	17	DAHP synthetase (phenylalanine repressible)	A
aroH	Aromatic	37	DAHP synthetase (tryptophan repressible)	A
aroHo	Aromatic	37	*aroJ;* operator sequence for *aroH*	A
aroI	Aromatic	83	Function unknown	A
aroL	Aromatic	(10)	Shikimate kinase II (EC 2.7.1.71)	148
aroP	Aromatic	3	General aromatic amino acid transport	A
aroT	Aromatic	27	*aroR, trpP;* transport of aromatic amino acids, alanine, and glycine	A, 265
asd		75	*dap* + *hom*; aspartate semialdehyde dehydrogenase (EC 1.2.1.11)	A
asnA	Asparagine	84	Asparagine synthetase A (EC 6.3.1.1)	A, 159, 264, 414, 641, 642
asnB	Asparagine	15	Asparagine synthetase B (EC 6.3.1.1)	159, 264, 642
asnS	Asparagine	21	*lcs;* asparaginyl-tRNA synthetase	455, 676
asnT	Asparagine	(43)	Asparagine tRNA	269
aspA	Aspartate	94	Aspartate ammonia-lyase (aspartase) (EC 4.3.1.1)	A, 217, 583
aspC	Aspartate	20	Aspartate aminotransferase (EC 2.6.1.1)	190, 191
aspT	Aspartate	84	*tasC;* aspartate tRNA1; in *rrnC* operon	268, 423, 424, 425
atoA	Acetoacetate	47	Acetate CoA-transferase (EC 2.8.3.-)	A
atoB	Acetoacetate	47	Acetyl-CoA acetyltransferase (EC 2.3.1.9)	A
atoC	Acetoacetate	47	Regulatory gene	A
attλ	Attachment	17	Integration site for prophage λ	A, 122, 457
attP2H	Attachment	43	Phage P2 integration site H	A
attP2II	Attachment	86	Phage P2 integration site II	A
attP22	Attachment	6	*ata;* integration site for prophage P22	A
attPA-2	Attachment	50	Integration site for phage PA-2	493
attφ80	Attachment	27	Integration site for prophage φ80	A, 489
att82	Attachment	17	Integration site for prophage 82	A
att186	Attachment	57	Integration site for prophage 186	A
att434	Attachment	17	Integration site for prophage 434	A
azi	Azide	2	*pea;* resistance or sensitivity to sodium azide or phenethyl alcohol; filament formation at 42°C	A
azl	Azaleucine	55	Regulation of *ilv* and *leu* genes; azaleucine resistance	A
bfm		84	Phage BF23 multiplication	A
bglA	β-Glucoside	83	*bglD;* phospho-β-glucosidase A	A, 223
bglB	β-Glucoside	83	*bglA;* phospho-β-glucosidase B	A, 223, 414, 641, 642
bglC	β-Glucoside	83	*bglB;* β-glucoside transport	A, 414
bglR	β-Glucoside	83	*bglB, bglC;* regulatory gene	A, 414
bglS	β-Glucoside	83	*bglC;* regulatory gene	A
bglT	β-Glucoside	84	*bglE;* regulatory gene for phospho-β-glucosidase A synthesis	A
bioA	Biotin	17	Group II; 7KAP→DAPA	A, 117, 608
bioAo	Biotin	17	Operator sequence for *bioA*	116, 117, 308, 462, 490, 608
bioAp	Biotin	17	Promoter sequence for *bioA*	116, 117, 308, 462, 608
bioB	Biotin	17	Conversion of dethiobiotin to biotin	A, 117, 608
bioBo	Biotin	17	*bioO;* operator sequence for *bioBFCD*	116, 117, 308, 462, 490, 608
bioBp	Biotin	17	*bioP;* promoter sequence for *bioBFCD*	116, 117, 308, 462, 608
bioC	Biotin	17	Block before pimeloyl CoA	A, 117, 608
bioD	Biotin	17	Dethiobiotin synthetase	A, 117, 608
bioF	Biotin	17	Pimeloyl CoA→7KAP	A, 117, 608
bioH	Biotin	74	*bioB;* block before pimeloyl CoA	A
bioR	Biotin	89	*dhbB;* regulatory gene	A, 468
bir	Biotin retention	89	Biotin uptake, retention, and regulation	A, 468
bisA	Biotin sulfoxide	17	Reduction of biotin-*d*-sulfoxide; may be *chlA*	95, 144
bisB	Biotin sulfoxide	18	Reduction of biotin-*d*-sulfoxide; may be *chlE*	95, 144
bisC	Biotin sulfoxide	79	Reduction of biotin-*d*-sulfoxide	95, 144
bisD	Biotin sulfoxide	0	Reduction of biotin-*d*-sulfoxide; may be *chlG*	95, 144
brnQ	Branched chain	9	Transport system 1 for isoleucine, leucine, and valine	A, 62, 679

TABLE 1—*Continued*

Gene symbol	Mnemonic	Map position (min)[b]	Alternate gene symbols; phenotypic trait affected	References[c]
brnR	Branched chain	8	Component of transport systems 1 and 2 for isoleucine, leucine, and valine	A
brnS	Branched chain	1	Transport system for isoleucine, leucine, and valine	A
brnT	Branched chain	62	Low-affinity transport system for isoleucine	265
btuB	B_{12} uptake	89	*bfe, btuA, cer;* receptor for vitamin B_{12}, E colicins, and bacteriophage BF23	A, 33, 56, 57, 84, 270, 398
btuC	B_{12} uptake	37	Vitamin B_{12} transport	33
bymA		(93)	Bypass of maltose permease at *malB*	A
can	Canavanine	62	Canavanine resistance	A
capS	Capsule	(24)	Regulation of *galU* and of capsular polysaccharide synthesis	A
carA		1	*arg* + *ura, cap, pyrA*; carbamoylphosphate synthase (EC 2.7.2.9), glutamine (light) subunit	A
carB		1	*arg* + *ura, cap, pyrA*; carbamoylphosphate synthase (EC 2.7.2.9), ammonia (heavy) subunit	A
cbt		16	Uptake of carboxylic acids	A
cca		66	tRNA nucleotidyl transferase	A
cdd		(49)	Deoxycytidine deaminase (EC 3.5.4.5)	A, 179, 547
cet	Colicin E2	100	*ref, refII*; tolerance to colicin E2	A
cheA	Chemotaxis	42	Chemotactic response	A, 397, 476, 477, 569
cheB	Chemotaxis	42	Chemotactic response; protein methylesterase activity	A, 235, 397, 476, 477, 569, 597
cheD	Chemotaxis		See *tsr*	
cheM	Chemotaxis		See *tar*	
cheW	Chemotaxis	42	Chemotactic response	397, 477, 569
cheX	Chemotaxis	42	Chemotactic response; protein methyltransferase activity	206, 397, 477, 569, 597
cheY	Chemotaxis	42	Chemotactic response	397, 477, 569
cheZ	Chemotaxis	42	Chemotactic response	235, 397, 477, 569, 570
chlA	Chlorate	17	*narA;* nitrate reductase and formate dehydrogenase activity; molybdenum-containing factor	A, 381
chlB	Chlorate	86	*narB;* nitrate reductase and formate dehydrogenase activity; molybdenum-containing factor	A, 78, 305, 381
chlC	Chlorate	27	*narC;* nitrate reductase (EC 1.7.99.4) A- (α-) subunit, structural gene	A, 128, 381
chlD	Chlorate	17	*narD;* nitrate reductase and formate dehydrogenase activity; insertion of molybdenum-containing factor	A, 584
chlE	Chlorate	18	*narE;* nitrate reductase (EC 1.7.99.4) C- (γ-) subunit, cytochrome b_1	A, 381
chlF	Chlorate	(27)	Formate dehydrogenase (EC 1.2.2.1) structural gene	A
chlG	Chlorate	0	Nitrate reductase and formate dehydrogenase activity	A
cir	Colicin I resistance	44	*feuA;* production of colicin I receptor affected	A, 120, 494, 582
cls		27	Cardiolipin synthase activity	485
cmlA	Chloramphenicol	18	Resistance or sensitivity to chloramphenicol	A
codA		8	Cytosine deaminase (EC 3.5.4.1)	A
codB		8	Cytosine transport	A
corA	Cobalt resistance	85	Mg^{2+} transport, system I	473
corB	Cobalt resistance	96	Mg^{2+} transport, system I	473
crp		73	*cap;* cyclic AMP receptor protein	A
crr		52	Catabolite repression resistance	297, 523
cxm		6	*cxr;* methylglyoxal synthesis	A, 310
cya		84	Adenylate cyclase (EC 4.6.1.1)	A, 559
cycA	Cycloserine	95	*dagA;* resistance to D-cycloserine and D-serine; transport of D-alanine, D-serine, and glycine	A, 284
cysA	Cysteine	52	Sulfate permease; chromate resistance	A, 204, 303
cysB	Cysteine	28	Regulatory gene for cysteine biosynthesis	A, 162, 628
cysC	Cysteine	59	Adenylylsulfate kinase (EC 2.7.1.25)	A
cysD	Cysteine	59	Sulfate adenylyltransferase (EC 2.7.7.4)	A
cysE	Cysteine	80	Serine acetyltransferase (EC 2.3.1.30)	A, 91
cysG	Cysteine	73	Sulfite reductase activity	A
cysH	Cysteine	59	Adenylylsulfate reductase (EC 1.8.99.2)	A
cysI	Cysteine	59	*cysQ;* sulfite reductase activity	A
cysJ	Cysteine	59	*cysP;* sulfite reductase activity	A
cysK	Cysteine	52	Cysteine synthase (EC 4.2.99.8)	161
cytR		88	Regulatory gene for *deo* operon, *udp*, and *cdd*	A, 630
dacA		14	D-Alanine carboxypeptidase, fraction A; penicillin-binding protein 5	396, 602, W

TABLE 1—*Continued*

Gene symbol	Mnemonic	Map position (min)[b]	Alternate gene symbols; phenotypic trait affected	References[c]
dacB		69	D-Alanine carboxypeptidase, fraction B; penicillin-binding protein 4	395, 602
dadR		26	Regulatory gene for D-amino acid deaminases	A, 571
dam		74	DNA adenine methylation	A, 28, 388
dapA	Diaminopimelate	53	Dihydropicolinate synthase (EC 4.2.1.52)	A
dapB	Diaminopimelate	0	Dihydropicolinate reductase	A
dapC	Diaminopimelate	3	Tetrahydropicolinate succinylase	A
dapD	Diaminopimelate	4	Succinyl-diaminopimelate aminotransferase	A
dapE	Diaminopimelate	53	*dapB; N*-succinyl-diaminopimelate deacylase	A
dcd		(45)	2′-Deoxycytidine 5′-triphosphate deaminase (EC 3.5.4.-) activity	179, 444a
dcm		43	*mec;* DNA cytosine methylation	A, 28
dcp		(30)	Dipeptidyl carboxypeptidase	134
dctA		79	Uptake of C_4 dicarboxylic acids	A
dctB		16	Uptake of C_4 dicarboxylic acids	A
ddl		2	D-Alanine:D-alanine ligase	A, 164
del	Deletion	61	Frequency of IS*1*-mediated deletion	445
deoA	Deoxyribose	99	*tpp,* TP; thymidine phosphorylase (EC 2.4.2.4)	A, 6, 300
deoB	Deoxyribose	99	*drm, thyR;* phosphopentomutase (EC 2.7.5.6)	A, 6, 300
deoBo	Deoxyribose	99	OP3; operator sequence for *deoBD*, regulator unknown	6, 69, 70
deoB1p	Deoxyribose	99	P3; promoter sequence for *deoBD*	6, 69, 70
deoB2p	Deoxyribose	99	P4; promoter sequence for *deoBD*	70
deoC	Deoxyribose	99	*dra, thyR;* deoxyribose-phosphate aldolase (EC 4.1.2.4)	A, 6, 300
deoC1o	Deoxyribose	99	*cytO;* operator sequence for *deoCABD* regulated by *cytR*	6, 300
deoC2o	Deoxyribose	99	*deoO;* operator sequence for *deoCABD* regulated by *deoR*	6, 300
deoC1p	Deoxyribose	99	*cytP;* promoter sequence for *deoCABD*	6, 300
deoC2p	Deoxyribose	99	*deoP;* promoter sequence for *deoCABD*	6, 300
deoD	Deoxyribose	99	*pup;* purine-nucleoside phosphorylase (EC 2.4.2.1)	A, 6, 300
deoDp	Deoxyribose	99	P5; promoter sequence for *deoD*	70
deoR	Deoxyribose	18	*nucR;* regulatory gene for *deo* operon	A, 630
dgd		(69)	D-Galactose dehydrogenase production	669
dgk		91	Diglyceride kinase	502
dgoA	D-Galactonate	82	2-Oxo-3-deoxygalactonate 6-phosphate aldolase (EC 4.1.2.21)	102
dgoD	D-Galactonate	82	Galactonate dehydratase (EC 4.2.1.6)	102
dgoK	D-Galactonate	82	2-Oxo-3-deoxygalactonate kinase (EC 2.7.1.58)	102
dgoR	D-Galactonate	82	Regulatory gene	102
dgoT	D-Galactonate	82	Galactonate transport	102
divE	Division	22	Membrane protein biosynthesis	539
dnaA	DNA	82	DNA biosynthesis; initiation	A, 203, 223, 338, 414, 439
dnaB	DNA	91	*exrB, groP, grpA;* DNA biosynthesis; chain elongation	A, 408, 527, 541, 649, 654, 696, R
dnaC	DNA	99	*dnaD;* DNA biosynthesis; initiation and chain elongation	A, 654
dnaE	DNA	4	*polC;* DNA biosynthesis; DNA polymerase III component; mutator activity	A, 261, 325
dnaG	DNA	66	DNA biosynthesis; primase	A, 87, 521
dnaI	DNA	39	DNA biosynthesis	A
dnaJ	DNA	0	*groP*AB, *groP*C; DNA biosynthesis	527, 528, 601, 684
dnaK	DNA	0	*groP*AB, *groP*C, *groP*F, *grpF*; DNA biosynthesis	195, 527, 528, 684
dnaL	DNA	28	*dnaK;* DNA biosynthesis	554
dnaP	DNA	85	DNA biosynthesis; initiation	A
dnaQ	DNA	5	Mutator activity and DNA biosynthesis; may be *mutD*	261
dnaT	DNA	99	DNA biosynthesis; termination	346
dnaW	DNA	10	DNA biosynthesis	50
dnaX	DNA	10	DNA biosynthesis	248
dnaY	DNA	12	DNA biosynthesis	248
dnaZ	DNA	10	DNA biosynthesis; DNA elongation factor II	A, 653, 655
dpp	Dipeptide	(13)	Transport of dipeptides	A, L
dsdA	D-Serine	50	D-Serine deaminase	A, 238
dsdAi	D-Serine	50	Initiator sequence for *dsdA*	238
dsdAo	D-Serine	50	Operator sequence for *dsdA*	238
dsdC	D-Serine	51	Regulatory gene for *dsdA*	A
dut	dUTPase	81	*dnaS, sof;* deoxyuridinetriphosphatase (EC 3.6.1.23)	A, 8, 255, 629
dye		100	Resistance or sensitivity to methylene blue	516

TABLE 1—*Continued*

Gene symbol	Mnemonic	Map position (min)[b]	Alternate gene symbols; phenotypic trait affected	References[c]
ebgA		67	Second β-galactosidase activity appears as result of mutations	A, 20, 220
ebgR		67	Regulatory gene	220
ecfA	Energy coupling factor	65	Pleiotropic effects on active transport coupling to metabolic energy; may be *metC*	364, 365, 626
ecfB	Energy coupling factor	87	Generalized resistance to aminoglycoside antibiotics; coupling of metabolic energy to active transport	624
eda		41	*kdgA, kga;* 2-keto-3-deoxygluconate 6-phosphate aldolase (EC 4.1.2.14)	A
edd		41	Phosphogluconate dehydratase (EC 4.2.1.12)	A
endA		63	DNA-specific endonuclease I	665
eno		59	Enolase (EC 4.2.1.11)	A, 278
entA	Enterochelin	13	2,3-Dihydro-2,3-dihydroxybenzoate dehydrogenase	A, 662, O
entB	Enterochelin	13	2,3-Dihydro-2,3-dihydroxybenzoate synthetase	A, 662, O
entC	Enterochelin	13	Isochorismate synthetase	A, O
entD	Enterochelin	13	Enterochelin synthetase, component D	A, 208
entE	Enterochelin	13	Enterochelin synthetase, component E	A, 208, 663, O
entF	Enterochelin	13	Enterochelin synthetase, component F	A, 208, 663
entG	Enterochelin	13	Enterochelin synthetase, component G	208, 662, O
envA	Envelope	2	Anomalous cell division; chain formation	A, 164, 451, 656
envB	Envelope	70	*mon, rodY;* anomalous formation of spheroidal cells	A, 286, 374
envC	Envelope	80	Anomalous cell division; chain formation	A
envM	Envelope	28	Osmotically remedial envelope defect	A
envN	Envelope	(4)	Osmotically remedial envelope defect	A
envP	Envelope	90	Osmotically remedial envelope defect	A
envQ	Envelope	57	Osmotically remedial envelope defect	A
envT	Envelope	(14)	Osmotically remedial envelope defect	A
eryC	Erythromycin	83	Erythromycin resistance; ribosome assembly	471, 472
esp		17	Site for efficient packaging of phage T1	141
exbB		64	Uptake of enterochelin; resistance or sensitivity to colicins	A, 120, 495
exbC		58	Uptake of enterochelin; resistance or sensitivity to colicins	495
exuR		67	Regulatory gene for *uxaA, uxaB, uxaC,* and *exuT*	393, 443
exuT		67	Transport of hexuronates	393, 443
fabA	Fatty acid biosynthesis	22	β-Hydroxydecanoylthioester dehydrase (EC 4.2.1.60)	A
fabB	Fatty acid biosynthesis	50	*fabC;* β-ketoacyl-acyl carrier protein synthase I (EC 2.3.1.41)	A, 91, 110a
fabD	Fatty acid biosynthesis	25	Malonyl-CoA-acyl carrier protein transacylase (EC 2.3.1.39)	A
fabE	Fatty acid biosynthesis	71	Acetyl-CoA carboxylase (EC 6.4.1.2)	563
fabF	Fatty acid biosynthesis	25	β-Ketoacyl-acyl carrier protein synthase II (EC 2.3.1.41)	J
fadA	Fatty acid degradation	86	*oldA;* thiolase I (EC 2.3.1.16)	A
fadB	Fatty acid degradation	86	*oldB;* 3-hydroxyacyl-CoA dehydrogenase (EC 1.1.1.35)	A
fadD	Fatty acid degradation	40	*oldD;* acyl-CoA synthetase (EC 6.2.1.3)	A, 652
fadE	Fatty acid degradation	5	Electron transport flavoprotein of beta-oxidation	A
fadL	Fatty acid degradation	50	Transport of long-chain fatty acids	454
fadR	Fatty acid degradation	25	*oleR;* regulatory gene	634, 635
fcsA		86	Cell division; septation	334
fda		63	*ald;* fructose-bisphosphate aldolase	A
fdhA		80	Formate dehydrogenase activity	383
fdp		95	Fructosediphosphatase (EC 3.1.3.11)	A
fec	Iron	7	Citrate-dependent iron transport	661
fep	Iron	13	*cbr, cbt, feuB;* receptor for ferrienterochelin and colicins B and D; enterochelin-dependent iron transport	A, 120, 406, 492, 494, 495, 662, 664, O
fes	Iron	13	Enterochelin esterase	A, 209, O
fex		100	Expression of F factor	362
firA		4	RNA polymerase function	350

TABLE 1—*Continued*

Gene symbol	Mnemonic	Map position (min)[b]	Alternate gene symbols; phenotypic trait affected	References[c]
flaA	Flagella	43	*cheC;* flagellar synthesis and chemotaxis	A, 322, 324, 476
flaB	Flagella	43	Flagellar synthesis	A, 322, 324
flaC	Flagella	43	Flagellar synthesis	A, 322, 324
flaD	Flagella	42	Flagellar synthesis	A, 322, 324
flaE	Flagella	43	Flagellar synthesis; length of basal hook	A, 322, 324
flaG	Flagella	41	Flagellar synthesis	A
flaH	Flagella	41	Flagellar synthesis	A
flaI	Flagella	42	Regulation of flagellar synthesis	A
flaK	Flagella	24	Flagellar hook subunit protein	319, 320, 321
flaL	Flagella	24	Flagellar synthesis; basal body	319, 320
flaM	Flagella	24	Flagellar synthesis; basal body	319, 320
flaN	Flagella	43	Flagellar synthesis	A, 322, 324
flaO	Flagella	43	Flagellar synthesis	A, 322, 324
flaP	Flagella	43	Flagellar synthesis	A, 322, 324
flaQ	Flagella	43	Flagellar synthesis	A, 322, 324
flaR	Flagella	43	Flagellar synthesis	A, 322, 324
flaS	Flagella	24	Flagellar synthesis; basal body	319, 320
flaT	Flagella	24	Flagellar synthesis; basal body	319, 320
flaU	Flagella	24	Flagellar synthesis	318
flaV	Flagella	24	Flagellar synthesis; basal body	319, 320
flaW	Flagella	24	Flagellar synthesis	318
flaX	Flagella	24	Flagellar synthesis	318
flaY	Flagella	24	Flagellar synthesis; basal body	318
flaZ	Flagella	24	Flagellar synthesis; basal body	318
flbA	Flagella	24	Flagellar synthesis	318
flbB	Flagella	42	Flagellar synthesis	318
flbC	Flagella	43	Flagellar synthesis	318
flrA	Fluoroleucine	100	Regulation of *ilv* and *leu* genes; fluoroleucine resistance	A
flu	Fluffing	43	Metastable gene affecting surface properties, piliation, and colonial morphology	135a
fnr		29	*frdB*, *nirR*; fumarate, nitrate, and nitrite reductases, hydrogenase, and cytochrome c_{552} activities affected	A, 344
folA	Folate	1	*tmrA*; dihydrofolate reductase (EC 1.5.1.3); trimethoprim resistance	A, 556, 557
folB	Folate	1	*tmrB*; regulatory gene; trimethoprim resistance	A, 556, 557
fpk		46	Fructose-1-phosphate kinase (EC 2.7.1.3)	A, 91
frdA		94	Fumarate reductase	A, 217
ftsA		2	Anomalous filamentous growth	A, 164, 380, 646, 656
ftsE		73	Anomalous filamentous growth	598
ftsH		69	Anomalous filamentous growth	536
fuc	Fucose	60	*prd;* L-fucose utilization	A, 218
fusA	Fusidic acid	73	*far;* protein chain elongation factor G	A, 73, 184, 367
fusB	Fusidic acid	14	Pleiotropic effects on RNA synthesis, ribosomes, and ribosomal protein S6	280, 615
gabC	γ-Aminobutyrate	57	Regulatory gene for *gabP,D,T*	A, 411
gabD	γ-Aminobutyrate	57	Succinyl semialdehyde dehydrogenase (EC 1.2.1.16) activity	411
gabP	γ-Aminobutyrate	57	Transport of γ-aminobutyrate	411
gabT	γ-Aminobutyrate	57	Aminobutyrate aminotransferase (EC 2.6.1.19) activity	A, 411
gadR		81	Regulatory gene for *gadS*	A
gadS		81	Glutamate decarboxylase (EC 4.1.1.15)	A
galE	Galactose	17	*galD;* UDPgalactose 4-epimerase; hexose-1-phosphate uridylyltransferase (EC 2.7.7.12)	A, 137, 436
galEo	Galactose	17	*galC, galO;* operator sequence for *galETK*	A, 137
galEIp	Galactose	17	Promoter sequence for *galETK*, cyclic AMP dependent	137, 436
galE2p	Galactose	17	Promoter sequence for *galETK*, cyclic AMP independent	137, 436
galK	Galactose	17	*galA;* galactokinase (EC 2.7.1.6)	A
galP	Galactose	63	*Pgal;* galactose permease activity	513
galR	Galactose	61	*Rgal;* regulatory gene; repressor of *galETK* operon	A
galT	Galactose	17	*galB;* galactose-1-phosphate uridylyltransferase (EC 2.7.7.10)	A
galU	Galactose	27	Glucose-1-phosphate uridylyltransferase (EC 2.7.7.9)	A, 79
gap		39	*gad;* glyceraldehyde-3-phosphate dehydrogenase (EC 1.2.1.12)	A, 250, 278, 652
gatA	Galactitol	46	Galactitol-specific enzyme II of phosphotransferase system	359, 360, 361

TABLE 1—*Continued*

Gene symbol	Mnemonic	Map position (min)[b]	Alternate gene symbols; phenotypic trait affected	References[c]
gatC	Galactitol	46	Regulatory gene	359, 361
gatD	Galactitol	46	Galactitol-1-phosphate dehydrogenase	359, 361
gdh		27	Glutamate dehydrogenase	467
glc	Glycolate	64	Utilization of glycolate; malate synthase G (EC 4.1.3.2)	A
glgA	Glycogen	75	Glycogen synthase (EC 2.4.1.21)	A, 352
glgB	Glycogen	75	1,4-α-glucan branching enzyme (EC 2.4.1.18)	A, 352
glgC	Glycogen	75	Glucose-1-phosphate adenylyltransferase (EC 2.7.7.27)	A, 352
glk		51	Glucokinase (EC 2.7.1.2)	A
glmS	Glucosamine	83	Glucosaminephosphate isomerase (EC 5.3.1.19)	A, I
glnA	Glutamine	86	Glutamine synthetase (EC 6.3.1.2)	A, 305
glnD	Glutamine	4	Uridylyltransferase	51
glnF	Glutamine	69	Regulation of glutamine synthetase production	467
glnS	Glutamine	15	Glutaminyl-tRNA synthetase (EC 6.1.1.18)	A
glnT	Glutamine	(77)	Affects levels of glutamine tRNA1 and glutamine synthetase	426
glnU	Glutamine	15	*supE, Su2, suII;* glutamine tRNA2	269, S
glnV	Glutamine	15	*supB;* glutamine tRNA1	269, S
glpA	Glycerol phosphate	48	Glycerol-3-phosphate dehydrogenase (anaerobic) (EC 1.1.99.5)	A, 413
glpD	Glycerol phosphate	75	*glyD;* glycerol-3-phosphate dehydrogenase (aerobic) (EC 1.1.99.5)	A
glpF	Glycerol phosphate	88	Facilitated diffusion of glycerol	A
glpK	Glycerol phosphate	88	Glycerol kinase (EC 2.7.1.30)	A
glpT	Glycerol phosphate	48	Glycerol-3-phosphate transport system	A, 413, 566
glpR	Glycerol phosphate	75	Regulatory gene	A
gltA	Glutamate	16	*glut;* citrate synthase	A
gltB	Glutamate	69	*aspB;* glutamate synthase (EC 2.6.1.53)	A, 467
gltE	Glutamate	80	Glutamyl-tRNA synthetase; possible regulatory subunit	A
gltH	Glutamate	(22)	Requirement	A
gltM	Glutamate	(43)	Glutamyl-tRNA synthetase	A
gltR	Glutamate	92	Regulatory gene for glutamate permease	A
gltS	Glutamate	82	Glutamate permease	A
gltSo	Glutamate	82	*gltC;* operator sequence for *gltS;* growth on glutamate as sole source of carbon	A
gltT	Glutamate	89	*tgtB;* glutamate tRNA2; in *rrnB* operon	268, 368, 379, 424, 672, 675
gltU	Glutamate	84	*tgtC;* glutamate tRNA2; in *rrnC* operon	268, 379, 424
gltV	Glutamate	90	*tgtE;* glutamate tRNA2; in *rrnE* operon	268, 424
gltX	Glutamate	52	Catalytic subunit for glutamyl-tRNA synthetase	A
glyA	Glycine	54	Serine hydroxymethyltransferase (EC 2.1.2.1)	A
glyS	Glycine	79	*gly-act;* glycyl-tRNA synthetase (EC 6.1.1.14)	A
glyT	Glycine	89	*supA36, sumA, sup15B;* glycine tRNA2	A, 82, 113, 515, 517, 518, 675
glyU	Glycine	61	*suA36, sufD, sumB, supT;* glycine tRNA1	A
glyV	Glycine	95	*suA58, suA78;* glycine tRNA3 (duplicate gene)	A, 434
glyW	Glycine	(41)	*suA58, suA78;* glycine tRNA3 (duplicate gene)	A
gnd		44	Gluconate-6-phosphate dehydrogenase (EC 1.1.1.43)	A
gntM	Gluconate	75	*usgA;* transport and phosphorylation of gluconate	A, 23
gntR	Gluconate	75	Regulatory gene for *edd;* transport and phosphorylation of gluconate	A, 23
gntS	Gluconate	95	Second system for transport, and possibly phosphorylation, of gluconate	23
gpp		84	Guanosine pentaphosphatase activity	581
gpsA		81	*sn*-Glycerol-3-phosphate dehydrogenase [NAD(P)$^+$] (EC 1.1.1.94)	A, 91
gpt		6	*gpp, gxu;* guanine-hypoxanthine phosphoribosyltransferase (EC 2.4.2.8)	A, 257, 260
grpD		71	Initiation of DNA replication of phage lambda	527
grpE		56	Phage lambda replication; host DNA synthesis	526
gshA		57	γ-Glutamyl-cysteine synthetase (EC 6.3.2.2) activity	16
gsk		13	Guanosine kinase	291
guaA	Guanine	53	gua_b; GMP synthetase (EC 6.3.4.1)	A, 474, 560, 631
guaAp	Guanine	53	Promoter sequence for *guaA*	181
guaB	Guanine	53	gua_a; IMP dehydrogenase (EC 1.2.1.14)	A, 474, 560, 631
guaBo	Guanine	53	Operator sequence for *guaBA*	560

TABLE 1—*Continued*

Gene symbol	Mnemonic	Map position (min)[b]	Alternate gene symbols; phenotypic trait affected	References[c]
guaBp	Guanine	53	Promoter sequence for *guaBA*	560
guaC	Guanine	(99)	GMP reductase (EC 1.6.6.8)	A
gurB		73	Utilization of methyl-β-D-glucuronide; possibly identical to *crp*	A
gurC		(18)	Utilization of methyl-β-D-glucuronide	A
gurD		(67)	Utilization of methyl-β-D-glucuronide	A
gyrA	Gyrase	48	*nalA;* DNA gyrase, subunit A; resistance or sensitivity to nalidixic acid	A, 192, 249, 329, 421, 600
gyrB	Gyrase	82	*acrB, cou;* DNA gyrase, subunit B; resistance or sensitivity to coumermycin	192, 193, 223, 249, 421, 522, 600
hag	H antigen	42	*flaF, H;* flagellin, structural gene; flagellar (H) antigen	A, 324, 568
hemA	Hemin	26	δ-Aminolevulinate synthase (EC 2.3.1.37)	A
hemB	Hemin	8	*ncf;* 5-aminolevulinate dehydratase (EC 4.2.1.24) activity	A, 400
hemC	Hemin	85	*popE;* uroporphyrinogen I synthase (EC 4.3.1.8) activity	401
hemD	Hemin	84	Uroporphyrinogen III cosynthase	85
hemE	Hemin	90	*hemC;* uroporphyrinogen decarboxylase (EC 4.1.1.37)	A
hemF	Hemin	17	*popB, sec;* coproporphyrinogen III oxidase (EC 1.3.3.3)	A
hemH	Hemin	11	*hemG, popA;* ferrochelatase (EC 4.99.1.1)	A
hfl		94	High frequency of lysogenization by phage lambda	A
hisA	Histidine	44	*N*-(5′-Phospho-L-ribosylformimino)-5-amino-1-(5′-phosphoribosyl)-4-imidazolecarboxamide isomerase (EC 5.3.1.16)	A
hisB	Histidine	44	Imidazoleglycerolphosphate dehydratase (EC 4.2.1.19) and histidinolphosphatase (EC 3.1.3.15) (bifunctional enzyme)	A
hisC	Histidine	44	Histidinol-phosphate aminotransferase (EC 2.6.1.9)	A
hisD	Histidine	44	Histidinol dehydrogenase (EC 1.1.1.23)	A
hisE	Histidine	44	Phosphoribosyl-ATP pyrophosphohydrolase	A
hisF	Histidine	44	Cyclase	A
hisG	Histidine	44	ATP phosphoribosyltransferase (EC 2.4.2.17)	A
hisGa	Histidine	44	Attenuator sequence in *hisG* leader region	29, 138
hisGe	Histidine	44	Leader region; regulation of transcription of *his* operon	29, 138
hisGo	Histidine	44	*hisO;* operator sequence for *his* operon	A
hisH	Histidine	44	Amido transferase	A
hisI	Histidine	44	Phosphoribosyl-AMP cyclohydrolase (EC 3.5.4.19)	A
hisR	Histidine	(84)	*hisT;* histidine tRNA	269
hisS	Histidine	54	Histidyl-tRNA synthetase (EC 6.1.1.21)	474
hisT	Histidine	50	Pseudouridylate synthetase	67, 354
hpt		3	Hypoxanthine phosphoribosyltransferase (not EC 2.4.2.8; see *gpt*	291
hsdM	Host specificity	98	*hs, hsm, rm, hsp;* host modification activity; DNA methylase M	A
hsdR	Host specificity	98	*hs, hsr, rm, hsp;* host restriction activity; endonuclease R	A
hsdS	Host specificity	98	*hss;* specificity determinant for *hsdM* and *hsdR* activities	A
hyd		57	Hydrogenase activity	478
iap		59	Altered isozyme pattern of alkaline phosphatase	440
icd		25	Isocitrate dehydrogenase, $NADP^+$ specific (EC 1.1.1.42)	18
iclR		90	Regulation of glyoxylate cycle	A
ileS	Isoleucine	0	Isoleucyl-tRNA synthetase (EC 6.1.1.5)	A, 176
ileT	Isoleucine	86	*tilA;* isoleucine tRNA1; in *rrnA* operon	268, 424
ileU	Isoleucine	70	*tilD;* isoleucine tRNA1; in *rrnD* operon	268, 424, 688
ilvA	Isoleucine-valine	84	*ile;* threonine deaminase (EC 4.2.1.16)	A, 26, 96, 402, 577
ilvB	Isoleucine-valine	82	Acetolactate synthase I (EC 4.1.3.18), valine sensitive	A, 213, 448
ilvC	Isoleucine-valine	84	*ilvA;* ketol-acid reductoisomerase (EC 1.1.1.86)	A, 26, 402, 578, 648
ilvD	Isoleucine-valine	84	*ilvB;* dihydroxyacid dehydrase (EC 4.2.1.9)	A, 26, 96, 402, 577
ilvE	Isoleucine-valine	84	*ilvC, ilvJ;* branched-chain-amino-acid aminotransferase (EC 2.6.1.42)	A, 26, 96, 357, 402, 577
ilvF	Isoleucine-valine	54	Affects production of valine-resistant acetolactate synthase activity	A
ilvG	Isoleucine-valine	84	Acetolactate synthase II (EC 4.1.3.18), valine insensitive	A, 26, 125, 213, 479, 576
ilvH	Isoleucine-valine	2	Acetolactate synthase III (EC 4.1.3.18), valine sensitive	A, 213
ilvI	Isoleucine-valine	2	Acetolactate synthase III (EC 4.1.3.18), valine sensitive	A, 213
ilvO	Isoleucine-valine	84	Locus affecting expression of *ilvG*	A, 26, 96, 479, 576
ilvY	Isoleucine-valine	84	Positive regulatory locus for *ilvC*	648
infC	Initiation factor	38	Protein chain initiation factor 3	243, 588, 589, 590
kat	Catalase	7	Catalase activity	363

TABLE 1—*Continued*

Gene symbol	Mnemonic	Map position (min)[b]	Alternate gene symbols; phenotypic trait affected	References[c]
kba		69	Ketose-bis-phosphate aldolase; temperature-sensitive enzyme; active on D-tagatose-1,6-diphosphate	361
kdgK	Ketodeoxygluconate	78	Ketodeoxygluconokinase (EC 2.7.1.45)	A
kdgR	Ketodeoxygluconate	40	Regulatory gene for *kdgK*, *kdgT*, and *eda*	A
kdgT	Ketodeoxygluconate	88	Ketodeoxygluconate transport system; structural gene	A, 342
kdgTo	Ketodeoxygluconate	88	*kdgP*; operator sequence for *kdgT*	A
kdpA	Potassium dependence	15	*kac*; high-affinity potassium transport system; probably K^+-stimulated ATPase	A, 151, 343, 457, 510
kdpB	Potassium dependence	15	*kac*; high-affinity potassium transport system	A, 343, 457, 510
kdpC	Potassium dependence	15	*kac*; high-affinity potassium transport system	A, 343, 457, 510
kdpD	Potassium dependence	15	*kac*; high-affinity potassium transport system; regulatory gene	A, 343, 457, 510
kpsA	K-polysaccharide	61	Acidic polysaccharide capsular (K) antigen	A
ksgA	Kasugamycin	1	RNA methylase for rRNA	A
ksgB	Kasugamycin	34	Second-step (high-level) resistance to kasugamycin	A, B, N
ksgC	Kasugamycin	12	Kasugamycin resistance; affects ribosomal protein S2	685
lacA	Lactose	8	*a*, *lacAc*; galactoside acetyltransferase (EC 2.3.1.18)	A, 12
lacI	Lactose	8	*i*; regulatory gene; repressor protein of *lac* operon	A, 104, 155, 416, 417, 544
lacIp	Lactose	8	Promoter sequence for *lacI*	74
lacY	Lactose	8	*y*; galactoside permease (M protein)	A, 171, 254
lacZ	Lactose	8	*z*; β-D-galactosidase (EC 3.2.1.23)	A, 169
lacZo	Lactose	8	*lacO*; operator sequence for *lac* operon	A, 27, 135, 382
lacZp	Lactose	8	*lacP*; promoter sequence for *lac* operon	A, 135, 382
lamB	Lambda	91	*malB*; phage lambda receptor protein; maltose high-affinity uptake system	A, 58, 150, 237, 259, 387, 503, 504, 505, 567, 606, 607
lamBp	Lambda	91	Weak promoter for *lamB*	59
lct	Lactate	80	Lactate dehydrogenase (EC 1.1.1.27)	A
leuA	Leucine	2	2-Isopropylmalate synthase (EC 4.1.3.12)	A
leuB	Leucine	2	2-Isopropylmalate dehydrogenase (EC 1.1.1.85)	A
leuC	Leucine	2	α-Isopropylmalate isomerase subunit	A
leuD	Leucine	2	α-Isopropylmalate isomerase subunit	A
leuK	Leucine	18	Regulation of biosynthetic enzymes for leucine, isoleucine-valine, histidine, and tryptophan	64
leuR	Leucine	78	Level of leucyl-tRNA synthetase affected	620
leuS	Leucine	15	Leucyl-tRNA synthetase (EC 6.1.1.4)	A, C
leuSo	Leucine	15	*leuX*; operator sequence for *leuS*	347
leuSp	Leucine	15	*leuX*; promoter sequence for *leuS*	347
leuT	Leucine	(84)	Leucine tRNA1	269
leuU	Leucine	(68)	Leucine tRNA2	269
leuV	Leucine	(93)	Leucine tRNA1	269
leuW	Leucine	15	A leucine tRNA	S
leuY	Leucine	10	Level of leucyl-tRNA synthetase affected	347
lev	Levallorphan	(9)	Resistance to levallorphan	111
lexA		91	*exrA*, *spr*, *tsl*, *umuA*; resistance or sensitivity to X rays and UV	A, 304, 465
ligA	Ligase	52	*dnaL*, *pdeC*; DNA ligase	A, 204, 262, 538
ligAo	Ligase	52	*lop*; possibly operator sequence for *ligA*	A
ligAp	Ligase	52	*lop*; possibly promoter sequence for *ligA*	A
linB	Lincomycin	(29)	High-level resistance to lincomycin	A
lip	Lipoate	14	Requirement	A
lir		(12)	Increased sensitivity to lincomycin, to erythromycin, or to both	A
lit		25	Phage T4 late gene expression	101
livH	Leucine, isoleucine, and valine	75	High-affinity branched-chain amino acid transport system	9
livJ	Leucine, isoleucine, and valine	75	Binding protein, high-affinity branched-chain amino acid transport system	9
livK	Leucine, isoleucine, and valine	75	Binding protein, high-affinity branched-chain amino acid transport system	9
livR	Leucine, isoleucine, and valine	20	*lss*; regulatory gene, high-affinity branched-chain amino acid transport system	10, 498

TABLE 1—*Continued*

Gene symbol	Mnemonic	Map position (min)[b]	Alternate gene symbols; phenotypic trait affected	References[c]
lon	Long form	10	*capR, deg, dir, muc;* filamentous growth; radiation, sensitivity; regulation of *gal* operon; capsular polysaccharide synthesis	A, 42, 188, 205
lpcA	Lipopolysaccharide core	6	*tfrA;* lipopolysaccharide core synthesis; resistance to phages T4, T7, and P1; deficiency in conjugation	A, 232
lpcB	Lipopolysaccharide core	(65)	*pon;* lipopolysaccharide core synthesis	A
lpd		3	*dhl;* lipoamide dehydrogenase (NADH) (EC 1.6.4.3)	A, 345
lpp	Lipoprotein	36	*mlpA;* murein lipoprotein structural gene	252, 277, 366, 519, 603, 667, 682, 683
lstR		20	Leucine-specific transport	10
lysA	Lysine	61	Diaminopimelate decarboxylase (EC 4.1.1.20)	A
lysC	Lysine	91	*apk;* aspartokinase III	A
lysCo	Lysine	91	Operator sequence for *lysC*	77
lysT	Lysine	16	*suβ, supL;* lysine tRNA	269, S
lysX	Lysine	60	Lysine excretion	A
mac	Macrolide	(26)	Erythromycin growth dependence	A
mafA		1	Maintenance of F-like plasmids	A, 643, 644
mafB		2	Maintenance of F-like plasmids	644
malE	Maltose	91	*malB;* periplasmic maltose-binding protein; substrate recognition for transport and chemotaxis	A, 30, 387, 503, 505, 564
malF	Maltose	91	*malB;* maltose transport; cytoplasmic membrane protein	A, 387, 503, 564, 565
malG	Maltose	91	*malB;* active transport of maltose and maltodextrins	503, 564
malK	Maltose	91	*malB;* maltose permeation	A, 387, 503, 504
malP	Maltose	75	*malA;* maltodextrin phosphorylase (EC 2.4.1.1)	A
malPi	Maltose	75	*malI, malA;* initiator sequence for *malPQ*	A, 123
malQ	Maltose	75	*malA;* amylomaltase (EC 2.4.1.25)	A
malT	Maltose	75	*malA;* positive regulatory gene for *malPQ, malEFG,* and *malKlamB*	A, 123
manA	Mannose	36	Mannosephosphate isomerase (EC 5.3.1.8)	A
manC	Mannose	(87)	*mni;* D-mannose isomerase regulation; utilization of D-lyxose	596
mdh		70	Malate dehydrogenase (EC 1.1.1.37)	A
melA	Melibiose	93	*mel-7;* α-galactosidase (EC 3.2.1.22)	A
melB	Melibiose	93	*mel-4;* thiomethylgalactoside permease II	A
menA	Menaquinone	88	Conversion of 1,4-dihydroxy-2-naphthoate to demethylmenaquinone	A, 687
menB	Menaquinone	48	Conversion of 2-succinylbenzoate to 1,4-dihydroxy-2-naphthoate	687, K
menC	Menaquinone	48	Conversion of chorismate to 2-succinylbenzoate	216
metA	Methionine	90	met_3; homoserine acetyltransferase (EC 2.3.1.31)	A
metB	Methionine	88	*met-1,* met_1; cystathionine γ-synthase (EC 4.2.99.9)	A
metC	Methionine	65	Cystathionine γ-lyase (EC 4.4.1.1)	A
metD	Methionine	5	High-affinity uptake of D- and L-methionine	A, 261
metE	Methionine	85	*met-*B_{12}; tetrahydropteroyltriglutamate methyltransferase (EC 2.1.1.14)	A
metF	Methionine	88	*met-2,* met_2; 5,10-methylenetetrahydrofolate reductase (EC 1.1.1.68)	A
metG	Methionine	(46)	Methionyl-tRNA synthetase	A, 79a, 509
metH	Methionine	90	B_{12}-dependent homocysteine-N^5-methyltetrahydrofolate transmethylase	A, 541
metJ	Methionine	88	Regulatory gene	A, 5, 328
metK	Methionine	63	Methionine adenosyltransferase (EC 2.5.1.6)	A, 5, 219
metL	Methionine	88	Aspartokinase II	A
metM	Methionine	88	Homoserine dehydrogenase II	A
metT	Methionine	15	Methionine $tRNA_m$	269, S
metY	Methionine	(68)	Methionine $tRNA_f2$	269
metZ	Methionine	(61)	Methionine $tRNA_f1$	269
mglA	Methyl-galactoside	45	*mglP;* methyl-galactoside transport and galactose taxis	A, 514
mglB	Methyl-galactoside	45	*mglP;* galactose-binding protein; receptor for galactose taxis	A, 514
mglC	Methyl-galactoside	45	*mglP;* methyl-galactoside transport and galactose taxis	A, 514
mglD	Methyl-galactoside	45	Regulatory locus for methyl-galactoside transport	514
mglR	Methyl-galactoside	(17)	R-MG; regulatory gene	A
mgt	Magnesium transport	92	Mg^{2+} transport, system II	473
minA	Minicell	10	Formation of minute cells containing no DNA	A

TABLE 1—*Continued*

Gene symbol	Mnemonic	Map position (min)[b]	Alternate gene symbols; phenotypic trait affected	References[c]
minB	Minicell	(29)	Formation of minute cells containing no DNA	A
mng	Manganese	(39)	Resistance or sensitivity to manganese	A
mop	Morphogenesis of phages	94	*groE, tabB;* defect of head assembly of phages T4 and λ	A, 196, 217, 240
motA	Motility	42	*flaJ;* flagellar paralysis	A, 397, 569
motB	Motility	42	*flaJ;* flagellar paralysis	A, 397, 569
mraA	Murein	2	D-Alanine carboxypeptidase	A
mraB	Murein	2	D-Alanine requirement; cell wall peptidoglycan biosynthesis	A
mrbA	Murein	90	UDP-*N*-acetylglucosaminyl-3-enolpyruvate reductase activity	A
mrbB	Murein	90	D-Alanine requirement; cell wall peptidylglycan biosynthesis	A
mrbC	Murein	90	Cell wall peptidylglycan biosynthesis	A
mrcA	Murein	74	*ponA;* penicillin-binding protein 1A	602
mrcB	Murein	3	*ponB;* penicillin-binding protein 1Bs formation and peptidoglycan cross-linking activity	602, 617
msp	Male-specific phage	100	Sensitivity or resistance of male strains to male-specific phages R17 and μ2	70
mtlA	Mannitol	80	Mannitol-specific enzyme II of phosphotransferase system	A, 359, 360
mtlC	Mannitol	80	Regulatory locus	A, 359
mtlD	Mannitol	80	Mannitol-1-phosphate dehydrogenase (EC 1.1.1.17)	A, 359
mtr	Methyltryptophan	68	Resistance to 5-methyltryptophan	A, 311
mul		82	Mutability of UV-irradiated phage λ	A
murC	Murein	2	L-Alanine-adding enzyme	A, 164
murE	Murein	2	*meso*-Diaminopimelate-adding enzyme	A, 164
murF	Murein	2	*mra;* D-alanyl:D-alanine-adding enzyme	A, 164
mutD	Mutator	5	Generalized high mutability; thymidine-stimulated	A
mutH	Mutator	61	*mutR; prv;* increased rates of frameshift and base substitution mutations	A, 258, 444
mutL	Mutator	94	*mut-25;* high rates of AT ⇌ GC transitions	A
mutS	Mutator	58	High rates of AT ⇌ GC transitions	A
mutT	Mutator	3	High rate of AT ⇌ GC transversion	A, 575, E
nadA	NAD	16	*nicA;* quinolinate synthetase, A protein	A
nadB	NAD	55	*nicB;* quinolinate synthetase, B protein	A
nadC	NAD	3	Quinolinate phosphoribosyl transferase	A
nagA	*N*-Acetylglucosamine	15	*N*-Acetylglucosamine-6-phosphate deacetylase (EC 3.5.1.25)	A
nagB	*N*-Acetylglucosamine	15	*glmD;* glucosamine-6-phosphate deaminase	A
nalA	Nalidixic acid	48	See *gyrA*	
nalB	Nalidixic acid	57	Resistance or sensitivity to nalidixic acid	A
nalC	Nalidixic acid	82	*nalD;* resistance or sensitivity to nalidixic and piromidic acids	275
ndh		22	NAD dehydrogenase complex	686
neaB	Neamine	73	Resistance to neamine	A, 127
nek		73	*amk;* resistance to neomycin, kanamycin, and other aminoglycoside antibiotics	A, 263
nfsA	Nitrofurazone sensitivity	(22)	Nitrofuran reductase I activity	399
nfsB	Nitrofurazone sensitivity	(11)	Nitrofuran reductase I activity	399
nirA	Nitrite reductase	29	NADH-nitrite reductase (EC 1.6.6.4) activity and cytochrome c_{552}	A, 88, 447
nirC	Nitrite reductase	26	NADH-nitrite reductase (EC 1.6.6.4) activity	1
nirD	Nitrite reductase	73	NADH-nitrite reductase (EC 1.6.6.4) activity	1
nirE	Nitrite reductase	49	NADH-nitrite reductase (EC 1.6.6.4) activity	1
nirF	Nitrite reductase	(52)	NADH-nitrite reductase (EC 1.6.6.4) activity	1
nmpA	New membrane protein	83	*ompE;* production of outer membrane protein 1c (E,e)	167, 168, 246, 497
nmpB	New membrane protein	9	Production of an outer membrane protein	497
nmpC	New membrane protein	12	Production of an outer membrane protein	497
non	Nonmucoid	45	Capsule formation	A

TABLE 1—*Continued*

Gene symbol	Mnemonic	Map position (min)[b]	Alternate gene symbols; phenotypic trait affected	References[c]
nrdA		48	*dnaF;* ribonucleoside diphosphate reductase (EC 1.17.4.1), subunit B1	A, 179
nrdB		48	Ribonucleoside diphosphate reductase (EC 1.17.4.1), subunit B2	A, 179
nupC		52	Transport of nucleosides, except guanosine	432
nupG		65	Transport of nucleosides	432
nusA		68	Expression of phage λ *N* gene function	172
nusB		10	Expression of phage λ *N* gene function	173
nuvA		9	Uridine thiolation factor A activity	372, 621
nuvC		(44)	Uridine thiolation factor C activity	372
ompA	Outer membrane protein	21	*con, tolG, tut;* outer membrane protein 3a (II*; G; d), structural gene	A, 2, 118, 231, 244, 245, 247, 384, 385
ompB	Outer membrane protein	74	*cry, kmt;* production of outer membrane proteins 1a and 1b (Ia and Ib; b and c)	34, 80, 221, 246, 496, 537, 639
ompC	Outer membrane protein	47	*meoA, par;* outer membrane protein 1b (Ib; c), structural gene	32, 167, 246, 266, 496, 546, 632, 638
ompF	Outer membrane protein	21	*cmlB, coa, cry, tolF;* outer membrane protein 1a (Ia; b; F), structural gene	32, 80, 165, 166, 167, 266, 353, 540, 546, 639, I′
opp		27	Oligopeptide transport	A, P
oriC	Origin of replication	83	*het, poh;* origin of replication of chromosome	157, 251, 391, 392, 409, 410, 414, 599, 641, 642, 645, 680
pabA	*p*-Aminobenzoate	74	Requirement	A
pabB	*p*-Aminobenzoate	40	Requirement	A, 652
panB	Pantothenate	3	Ketopantoate hydroxymethyl transferase (EC 4.1.2.12)	A, 108
panC	Pantothenate	3	Pantothenate synthetase (EC 6.3.2.1)	A, 108
panD	Pantothenate	3	Aspartate 1-decarboxylase	A, 108
pbpA	Penicillin-binding protein	14	Penicillin-binding protein 2	285, 586, W
pbpB	Penicillin-binding protein	2	*ftsI, sep;* penicillin-binding protein 3; septum formation	164, 586, 602, Y
pcsA		81	Cell division; chromosome segregation	333, 335
pdxA	Pyridoxine	1	Requirement	A, 256
pdxB	Pyridoxine	50	Requirement	A, 91
pdxC	Pyridoxine	20	Requirement	A
pdxH	Pyridoxine	36	Pyridoxine phosphate oxidase	A, 561
pdxJ	Pyridoxine	55	Requirement	A, 17
pepD	Peptides	6	*pepH* (carnosinase); peptidase D, a dipeptidase	A, L
pepN	Peptides	(21)	Peptidase N, an aminopeptidase	351
pfkA		88	6-Phosphofructokinase I (EC 2.7.1.11)	A, 22, 466, 623
pfkB		38	Level of 6-phosphofructokinase II production; suppressor of *pfkA*	A, 22
pfkC		(58)	Modifier of 6-phosphofructokinase activity	A
pfl		20	Pyruvate formate lyase	637
pgi		91	Glucosephosphate isomerase (EC 5.3.1.9)	A
pgk		63	Phosphoglycerate kinase (EC 2.7.2.3)	A, 278, 623
pgl		17	*blu;* 6-phosphogluconolactonase (EC 3.1.1.31)	A
pgm		(15)	Phosphoglucomutase (EC 2.7.5.1)	A
pgsA		42	Phosphatidylglycerophosphate synthetase	448 a, Q
pheA	Phenylalanine	56	Chorismate mutase-P-prephenate dehydrogenase	A, 693, 694
pheAe	Phenylalanine	56	*pheL;* regulation of transcription of *pheA*; leader region	692
pheAo	Phenylalanine	56	*pheO;* operator sequence for *pheA*	A, 693, 694
pheS	Phenylalanine	37	*phe-act;* phenylalanyl-tRNA synthetase (EC 6.1.1.20), α subunit	A, 100, 241, 243, 588, 589, 590
pheT	Phenylalanine	37	*pheS;* phenylalanyl-tRNA synthetase (EC 6.1.1.20), β subunit	A, 100, 243, 588, 589, 590
phoA	Phosphate	9	Alkaline phosphatase (EC 3.1.3.1)	A, 62, 276
phoB	Phosphate	9	*phoRc, phoT;* positive regulatory gene for *phoA* and *phoS*	A, 62, 330, 491, 657
phoR	Phosphate	9	*phoR1, R1pho;* negative regulatory gene for *phoA* and *phoS*	A, 62, 330, 491, 657
phoS	Phosphate	83	*phoR2a, R2pho;* periplasmic phosphate-binding protein	A, 338, 657, 670, I
phoT	Phosphate	83	*phoS;* inorganic phosphate transport	A, I
phr	Photoreactivation	16	Deoxyribodipyrimidine photolyase (EC 4.1.99.3)	A, 531, 690

TABLE 1—*Continued*

Gene symbol	Mnemonic	Map position (min)[b]	Alternate gene symbols; phenotypic trait affected	References[c]
phxB	Phi-X	17	Adsorption of φX174	433
pilA	Pili	98	*fim;* formation of type 1 somatic pili	A, 604, 605
pilB	Pili	98	*fim;* formation of type 1 somatic pili	A, 604, 605
pilC	Pili	98	*fim;* formation of type 1 somatic pili	A, 604, 605
pit	Inorganic phosphate transport	76	Inorganic phosphate transport system	A
pldA		85	Detergent-resistant phospholipase A activity	A
plsA	Phospholipid synthesis		See *adk*	
plsB	Phospholipid synthesis	91	Glycerolphosphate acyltransferase activity	A, 579, U
pncA	Pyridine nucleotide cycle	39	*nam;* nicotinamide deamidase (EC 3.5.1.19)	A, 652
pncH	Pyridine nucleotide cycle	39	Hyperproduction of nicotinamide deamidase	A
pnp		68	Polynucleotide phosphorylase (EC 2.7.7.8)	A
pnt		35	Pyridine nucleotide transhydrogenase (EC 1.6.1.1)	224
poaR		62	Regulation of proline oxidase production	A
polA	Polymerase	86	*resA;* DNA polymerase I (EC 2.7.7.7)	A, 305, 306
polB	Polymerase	2	DNA polymerase II (EC 2.7.7.7)	A
polC	Polymerase	4	See *dnaE*	
popC	Porphyrin	3	Synthesis of δ-aminolevulinate	A
popD	Porphyrin	(1)	Deficiency of 5-aminolevulinate dehydratase (EC 4.2.1.24) activity	A, 400
ppc	Phosphoenolpyruvate	89	*glu, asp;* phosphoenolpyruvate carboxylase (EC 4.1.1.31)	A, 56, 84, 110, 398
pps	Phosphoenolpyruvate	37	Phosphoenolpyruvate synthase	A
prmA		71	*prm-1;* methylation of 50S ribosomal subunit protein L11	99
prmB		50	*prm-2;* methylation of 50S ribosomal subunit protein L3	99
proA	Proline	6	pro_1; block before L-glutamate semialdehyde	A
proB	Proline	6	pro_2; block before L-glutamate semialdehyde	A
proC	Proline	9	pro_3, Pro_2; probably Δ-pyrroline-5-carboxylate reductase	A
proT	Proline	83	Proline transport	430
psd		94	Phosphatidylserine decarboxylase	A, 234
pss		56	Phosphatidylserine synthetase (EC 2.7.8.8)	456, 500, 501
pst		83	Inorganic phosphate transport system	A, 642
pta		49	Phosphotransacetylase (EC 2.3.1.8) activity	65
pth		26	Peptidyl-tRNA hydrolase	A
ptsF	Phosphotransferase system	46	Fructosephosphotransferase enzyme II	A, 7, 514
ptsG	Phosphotransferase system	24	*cat, CR, gpt, gptA, tgl, umg;* glucosephosphotransferase enzyme II	A, 152
ptsH	Phosphotransferase system	52	*ctr, Hpr;* phosphohistidinoprotein-hexose phosphotransferase (EC 2.7.1.69)	A, 204
ptsI	Phosphotransferase system	52	*ctr;* phosphotransferase system enzyme I	A, 204
ptsM	Phosphotransferase system	40	*gptB, mpt, pel, ptsX;* mannosephosphotransferase enzyme II; penetration of phage λ	A, 147, 296
purA	Purine	94	ade_k, Ad_4; adenylosuccinate synthetase (EC 6.3.4.4)	A
purB	Purine	25	ade_h; adenylosuccinate lyase (EC 4.3.2.2)	A
purC	Purine	53	ade_g; phosphoribosylaminoimidazole-succinocarboxamide synthetase (EC 6.3.2.6)	A
purD	Purine	89	$adth_a$; phosphoribosylglycineamide synthetase (EC 6.3.4.13)	A
purE	Purine	12	ade_3, ade_f, Pur_2; phosphoribosylaminoimidazole carboxylase (EC 4.1.1.21)	A
purF	Purine	49	$ade_{u,b}$, *purC;* amidophosphoribosyl transferase (EC 2.4.2.14)	A
purG	Purine	53	$adth_b$; phosphoribosylformylglycineamide synthetase (EC 6.3.5.3)	A, 474, 631
purH	Purine	89	ade_i; phosphoribosylaminoimidazolecarboxamide formyltransferase (EC 2.1.2.3)	A
purI	Purine	55	Phosphoribosylaminoimidazole synthetase (EC 6.3.3.1)	A
putA		22	*poaA;* proline oxidase	A
pyrA	Pyrimidine	1	See *car*	A
pyrB	Pyrimidine	96	Aspartate carbamoyltransferase (EC 2.1.3.2), catalytic subunit	A, 284, 309, 310, 482

TABLE 1—*Continued*

Gene symbol	Mnemonic	Map position (min)[b]	Alternate gene symbols; phenotypic trait affected	References[c]
pyrC	Pyrimidine	23	Dihydro-orotase (EC 3.5.2.3)	A
pyrD	Pyrimidine	21	Dihydro-orotate oxidase (EC 1.3.3.1)	A
pyrE	Pyrimidine	81	Orotate phosphoribosyltransferase (EC 2.4.2.10)	A
pyrF	Pyrimidine	28	Orotidine-5′-phosphate decarboxylase (EC 4.1.1.23)	A
pyrG	Pyrimidine	59	CTP synthetase (EC 6.3.4.2)	174, 177
pyrH	Pyrimidine	(4)	UMP kinase	A
qmeA		28	*gts;* unspecified membrane defect	A
qmeC		74	Unspecified membrane defect; tolerance to glycine; penicillin sensitivity	A
qmeD		61	Unspecified membrane defect; tolerance to glycine; penicillin sensitivity	A
qmeE		37	Unspecified membrane defect	A
rac			See *recE* and *sbcA*	
ranA		55	Defect in RNA metabolism	A
ras	Radiation sensitivity	(9)	Sensitivity to UV and X rays	A
rbsK	Ribose	84	Ribokinase (EC 2.7.1.15)	A, 641, 642
rbsP	Ribose	84	D-Ribose permease	A, 641, 642
recA	Recombination	58	*lexB, recH, tif, umuB, zab;* general recombination; repair of radiation damage; induction of phage lambda	A, 149, 215, 304, 373, 403, 405, 422, 533, 558
recB	Recombination	60	*rorA;* recombination and repair of radiation damage; exonuclease V subunit	A, 201, 636
recC	Recombination	60	Recombination and repair of radiation damage; exonuclease V subunit	A
recE	Recombination	30	Locus of Rac prophage; exonuclease VIII	A, 153, N
recF	Recombination	82	*uvrF;* recombination and repair of radiation damage	A, D
recG	Recombination	(82)	Recombination	A
relA	Relaxed	59	RC; regulation of RNA synthesis; stringent factor; ATP: GTP 3′-pyrophosphotransferase	A, 174, 177
relB	Relaxed	34	Regulation of RNA synthesis	136, 429
relX	Relaxed	59	Control of synthesis of guanosine-5′-diphosphate-3′-diphosphate	470
rep		84	DNA-melting activity involved in replication of certain phages	A, 549
rer		89	Resistance to UV and gamma radiation	592
rfa	Rough	81	*con, lpsA, phx;* cluster of genes coding for enzymes involved in lipopolysaccharide core biosynthesis	A, 222, 233
rfbA	Rough	45	TDP-glucose pyrophosphorylase	A
rfbB	Rough	45	TDP-glucose oxidoreductase	A
rfbD	Rough	45	TDP-rhamnose synthetase	A
rfe	Rough	(85)	Synthesis of enterobacterial common antigen and O antigen	545
rff	Rough	(85)	Synthesis of enterobacterial common antigen	545
rhaA	Rhamnose	87	L-Rhamnose isomerase (EC 5.3.1.14)	A
rhaB	Rhamnose	87	Rhamnulokinase (EC 2.7.1.5)	A
rhaC	Rhamnose	87	Regulatory gene	A
rhaD	Rhamnose	87	Rhamnulosephosphate aldolase (EC 4.1.2.19)	A
rho		84	*nitA, psu, rnsC, SuA, sun, tsu;* transcription termination factor rho; polarity suppressor	A, 66, 115, 214, 272, 273, 274, 326, 506, 507
rimA	Ribosomal modification	83	Maturation of 50S ribosomal subunit	A, 223
rimB	Ribosomal modification	37	Maturation of 50S ribosomal subunit	A
rimC	Ribosomal modification	(26)	Maturation of 50S ribosomal subunit	A
rimD	Ribosomal modification	(87)	Maturation of 50S ribosomal subunit	A
rimE	Ribosomal modification	72	Modification of ribosomal proteins	340
rimF	Ribosomal modification	1	*res;* ribosomal modification	A
rimG	Ribosomal modification	(1)	*ramB;* modification of 30S ribosomal subunit protein S4	A
rimH	Ribosomal modification	13	*stsB;* ribosomal modification	A, 294

TABLE 1—*Continued*

Gene symbol	Mnemonic	Map position (min)[b]	Alternate gene symbols; phenotypic trait affected	References[c]
rimI	Ribosomal modification	99	Modification of 30S ribosomal subunit protein S18; acetylation of N-terminal alanine	283
rimJ	Ribosomal modification	(31)	Modification of 30S ribosomal subunit protein S5; acetylation of N-terminal alanine	109
rit		89	Affects thermolability of 50S ribosomal subunit	459
rna	Ribonuclease	14	*rns, rnsA;* ribonuclease I	A
rnb	Ribonuclease	28	Ribonuclease II	460
rnc	Ribonuclease	55	Ribonuclease III	A, 15
rne	Ribonuclease	24	Ribonuclease E activity	13
rnpA	Ribonuclease	82	Ribonuclease P activity; processing of tRNA precursors	14, 332, 464, 530
rnpB	Ribonuclease	70	Ribonuclease P activity	332, 464, 530
rodA	Rod shape	14	Rounded morphology; radiation resistance; drug sensitivities	A, 286, 602, W
rpiA		62	Ribose phosphate isomerase (EC 5.3.1.6) (constitutive)	A
rplA	Ribosomal protein, large	89	50S ribosomal subunit protein L1	A, 160, 368, 370, 488, 675
rplB	Ribosomal protein, large	72	50S ribosomal subunit protein L2	A, 288, 289, 367
rplC	Ribosomal protein, large	72	50S ribosomal subunit protein L3	A, 288, 289, 367
rplD	Ribosomal protein, large	72	*eryA;* 50S ribosomal subunit protein L4	A, 73, 288, 289, 367
rplE	Ribosomal protein, large	72	50S ribosomal subunit protein L5	A, 288, 290, 367
rplF	Ribosomal protein, large	72	50S ribosomal subunit protein L6	A, 288, 290, 367
rplI	Ribosomal protein, large	95	50S ribosomal subunit protein L9	284
rplJ	Ribosomal protein, large	89	50S ribosomal subunit protein L10	A, 160, 371, 488, 674, 675
rplJp	Ribosomal protein, large	89	P; promoter sequence for *rplJLrpoBC* operon	160, 371, 488, 674
rplK	Ribosomal protein, large	89	*relC;* 50S ribosomal subunit protein L11	A, 39, 160, 368, 370, 475, 488, 674, 675
rplKp	Ribosomal protein, large	89	P_{L11}; promoter sequence for *rplKA*	488
rplL	Ribosomal protein, large	89	50S ribosomal subunit protein L7/L12	A, 39, 160, 368, 371, 446, 488, 674, 675
rplN	Ribosomal protein, large	72	50S ribosomal subunit protein L14	A, 288, 290, 367
rplNp	Ribosomal protein, large	72	P_{spc}; promoter sequence for *rplN* operon	487
rplO	Ribosomal protein, large	72	50S ribosomal subunit protein L15	A, 288, 289, 290, 367
rplP	Ribosomal protein, large	72	50S ribosomal subunit protein L16	A, 288, 367, 487
rplQ	Ribosomal protein, large	72	50S ribosomal subunit protein L17	A, 288, 367
rplR	Ribosomal protein, large	72	50S ribosomal subunit protein L18	A, 73, 288, 290, 367
rplS	Ribosomal protein, large	56	50S ribosomal subunit protein L19	312, 526
rplU	Ribosomal protein, large	69	50S ribosomal subunit protein L21	311, 614, 616
rplV	Ribosomal protein, large	72	50S ribosomal subunit protein L22	A, 288, 367
rplW	Ribosomal protein, large	72	50S ribosomal subunit protein L23	288, 289, 367
rplX	Ribosomal protein, large	72	50S ribosomal subunit protein L24	A, 72, 288, 290, 367
rplY	Ribosomal protein, large	46	50S ribosomal subunit protein L25	547
rpmA	Ribosomal protein, large	69	50S ribosomal subunit protein L27	311, 614
rpmB	Ribosomal protein, large	81	50S ribosomal subunit protein L28	282

TABLE 1—*Continued*

Gene symbol	Mnemonic	Map position (min)[b]	Alternate gene symbols; phenotypic trait affected	References[c]
rpmC	Ribosomal protein, large	72	50S ribosomal subunit protein L29	A, 288, 367, 487
rpmD	Ribosomal protein, large	72	50S ribosomal subunit protein L30	A, 197, 288, 289, 290, 367
rpmG	Ribosomal protein, large	81	50S ribosomal subunit protein L33	282
rpoA	RNA polymerase	72	RNA polymerase (EC 2.7.7.6), α-subunit	A, 180, 236, 367
rpoB	RNA polymerase	90	*groN, nitB, rif, ron, stl, stv, tabD;* RNA polymerase (EC 2.7.7.6), β-subunit	A, 21, 103, 160, 236, 270, 368, 371, 446, 488, 674, 675
rpoC	RNA polymerase	90	*tabD;* RNA polymerase (EC 2.7.7.6), β′-subunit	A, 21, 103, 160, 211, 236, 368, 371, 446, 674, 675
rpoD	RNA polymerase	67	*alt;* RNA polymerase (EC 2.7.7.6), σ subunit	210, 229, 236, 439, 439a, 627
rpsA	Ribosomal protein, small	20	30S ribosomal subunit protein S1	461
rpsB	Ribosomal protein, small	4	30S ribosomal subunit protein S2	A, 175, 441, 613, 677
rpsC	Ribosomal protein, small	72	30S ribosomal subunit protein S3	A, 288, 367
rpsD	Ribosomal protein, small	72	*ramA, sud2;* 30S ribosomal subunit protein S4	A, 288, 289, 367, 369
rpsE	Ribosomal protein, small	72	*eps, spcA, spc;* 30S ribosomal subunit protein S5	A, 11, 71, 73, 288, 290, 367, 369, 484, 660
rpsF	Ribosomal protein, small	95	30S ribosomal subunit protein S6	A, 284
rpsG	Ribosomal protein, small	72	*K12;* 30S ribosomal subunit protein S7	A, 288, 289, 367, 487
rpsH	Ribosomal protein, small	72	30S ribosomal subunit protein S8	A, 197, 288, 290, 367, 369, 659
rpsJ	Ribosomal protein, small	72	30S ribosomal subunit protein S10	A, 288, 289, 367
rpsK	Ribosomal protein, small	72	30S ribosomal subunit protein S11	A, 288, 289, 367, 369
rpsL	Ribosomal protein, small	72	*strA;* 30S ribosomal subunit protein L12	A, 11, 73, 288, 289, 367, 487, 660
rpsLp	Ribosomal protein, small	72	P_{str}; promoter sequence for *rpsL* operon	486, 487
rpsM	Ribosomal protein, small	72	30S ribosomal subunit protein S13	A, 288, 289, 367, 369
rpsN	Ribosomal protein, small	72	30S ribosomal subunit protein S14	A, 288, 290, 367, 369
rpsO	Ribosomal protein, small	68	30S ribosomal subunit protein S15	311, 614, 616
rpsP	Ribosomal protein, small	56	30S ribosomal subunit protein S16	281, 526
rpsQ	Ribosomal protein, small	72	*neaA;* 30S ribosomal subunit protein S17	A, 53, 288, 367, 487, 671
rpsR	Ribosomal protein, small	95	30S ribosomal subunit protein S18	A, 284
rpsS	Ribosomal protein, small	72	30S ribosomal subunit protein S19	A, 288, 367
rpsT	Ribosomal protein, small	0	*supS20;* 30S ribosomal subunit protein S20	A, 68, 176, 613
rpsU	Ribosomal protein, small	67	30S ribosomal subunit protein S21	282, 614
rrfB	rRNA, 5S	89	5S rRNA gene of *rrnB* operon	368, 672, 675
rrfC	rRNA, 5S	84	5S rRNA gene of *rrnC* operon	668
rrlB	rRNA, 23S	89	23S rRNA gene of *rrnB* operon	368, 672, 675
rrlC	rRNA, 23S	84	23S rRNA gene of *rrnC* operon	299, 668
rrlD	rRNA, 23S	72	23S rRNA gene of *rrnD* operon	688
rrlG	rRNA, 23S	56	23S rRNA gene of *rrnG* operon	694
rrnA	rRNA	86	*cqsA;* rRNA operon; see *rrfA, rrlA, rrsA, ileT,* and *alaT*	A, 55, 124, 268, 307, 640

TABLE 1—*Continued*

Gene symbol	Mnemonic	Map position (min)[b]	Alternate gene symbols; phenotypic trait affected	References[c]
rrnB	rRNA	89	*cqsE, rrnB*$_1$; rRNA operon; see *rrfB, rrlB, rrsB,* and *gltT*	A, 55, 307, 368, 640, 672, 675
rrnC	rRNA	84	*cqsB, rrnB, rrnB*$_2$; rRNA operon; see *rrfC, rrlC, rrsC, gltU, aspT,* and *trpT*	A, 55, 299, 307, 423, 425, 640, 668
rrnD	rRNA	72	*cqsD;* rRNA operon; see *rrfD, rrlD, rrsD, ileU,* and *alaU*	55, 298, 307, 640, 688, 689
rrnE	rRNA	90	*rrnD;* rRNA operon, see *rrfE, rrlE, rrsE,* and *gltV*	55, 124, 673
rrnF	rRNA	74	*cqsC, rrnC;* rRNA operon; see *rrfF, rrlF,* and *rrsF*	55, 640
rrnG	rRNA	56	rRNA operon; see *rrlG* and *rrsG*	55, 694
rrsA	rRNA, 16S	86	16S rRNA gene of *rrnA* operon	124
rrsA1p	rRNA, 16S	86	Promoter sequence for *rrnA* operon	124
rrsA2p	rRNA, 16S	86	Promoter sequence for *rrnA* operon	124
rrsB	rRNA, 16S	89	16S rRNA gene of *rrnB* operon	63, 368, 672, 675
rrsC	rRNA, 16S	84	16S rRNA gene of *rrnC* operon	299, 668
rrsD	rRNA, 16S	72	16S rRNA gene of *rrnD* operon	688, 689
rrsD1p	rRNA, 16S	72	Promoter sequence of *rrnD* operon	689
rrsD2p	rRNA, 16S	72	Promoter sequence of *rrnD* operon	689
rrsE	rRNA, 16S	90	16S rRNA gene of *rrnE* operon	124
rrsE1p	rRNA, 16S	90	Promoter sequence for *rrnE* operon	124
rrsE2p	rRNA, 16S	90	Promoter sequence for *rrnE* operon	124
rrsG	rRNA, 16S	56	16S rRNA gene of *rrnG* operon	694
rts		89	*ts-9;* uncharacterized growth defect	A, 39, 370
ruv		41	Filament formation and sensitivity to UV radiation	A
sbcA		30	Regulatory gene affecting *recE*; locus of Rac prophage	A, D
sbcB		44	*xonA;* exonuclease I; suppressor of *recB, recC*	A
sdh		16	Succinate dehydrogenase (EC 1.3.99.1)	A
sefA		4	Septum formation	451
seg	Segregation	100	Replication of F-factors	A, 287
serA	Serine	62	Phosphoglycerate dehydrogenase (EC 1.1.1.95)	A
serB	Serine	100	Phosphoserine phosphatase (EC 3.1.3.3)	A
serC	Serine	20	*pdxF;* phosphoserine aminotransferase (EC 2.6.1.52)	A, 562
serR	Serine	2	Level of seryl-tRNA synthetase	620
serS	Serine	20	Seryl-tRNA synthetase (EC 6.1.1.11)	A
serSo	Serine	20	*serO;* operator sequence for *serS*	A
serT	Serine	(16)	Serine tRNA1	269
serV	Serine	(61)	Serine tRNA3	269
shiA	Shikimate	43	Shikimate and dehydroshikimate permease	A
sloB	Slow growth	73	Low growth rate; tolerance to amidinopenicillin and nalidixic acid	374, 650
speA	Spermidine	63	Arginine decarboxylase (EC 4.1.1.19)	A
speB	Spermidine	63	Agmatinase (EC 3.5.3.11)	A
speC	Spermidine	64	Ornithine decarboxylase (EC 4.1.1.17)	A, 219
speD	Spermidine	3	*S*-Adenosylmethionine decarboxylase (EC 4.1.1.50)	609
spoT		81	Guanosine 5′-diphosphate, 3′-diphosphate pyrophosphatase	A, 8
srlA	Sorbitol	58	*gutA, sbl;* D-glucitol-specific enzyme II of phosphotransferase system	A, 359, 360, 404
srlC	Sorbitol	58	*gutC, sbl;* regulatory gene	A, 359, 404
srlD	Sorbitol	58	*gutD, sbl;* sorbitol-6-phosphate dehydrogenase (EC 1.1.1.140)	A, 359, 404
srlR	Sorbitol	58	Regulatory gene	D
srnA		9	Degradation of stable RNA	A
ssb	Single-strand binding	92	*exrB, lexC;* single-strand DNA-binding protein	292, 412, 532
strC	Streptomycin	5	*strB;* low-level streptomycin resistance	A
strM	Streptomycin	76	Control of ribosomal ambiguity	A
stsA		83	Altered ribonuclease activity	A
sucA	Succinate	16	*lys + met, suc;* succinate requirement; α-ketoglutarate dehydrogenase (decarboxylase component)	A
sucB	Succinate	16	*lys + met, suc;* succinate requirement; α-ketoglutarate dehydrogenase (dihydrolipoyltranssuccinase component)	A
sulA		22	*sfiA, suf;* suppressor of *lon*	A, 188, 194, 293
sulB		2	*sfiB;* suppressor of *lon*	188, 194, 293
supB	Suppressor	15	*su*$_B$; suppressor of ochre (UAA) and amber (UAG) mutations; see *glnU*	

TABLE 1—*Continued*

Gene symbol	Mnemonic	Map position (min)[b]	Alternate gene symbols; phenotypic trait affected	References[c]
supC	Suppressor	27	su_C, *Su-4;* suppressor of ochre (UAA) and amber (UAG) mutations	A
supD	Suppressor	43	su_I, *Su-1;* suppressor of amber (UAG) mutations	A, 324
supE	Suppressor	15	su_{II}, *Su-2;* suppressor of amber (UAG) mutations; see *glnV*	
supF	Suppressor	27	su_{III}, *Su-3;* suppressor of amber (UAG) mutations; see *tyrT*	
supG	Suppressor	16	*Su-5;* suppressor of ochre (UAA) and amber (UAG) mutations	A, H
supH	Suppressor	43	Suppressor	A
supK	Suppressor	61	Suppressor of opal (UGA) mutations; a tRNA methylase	X
supL	Suppressor	16	Su_β; suppressor of ochre (UAA) and amber (UAG) mutations; see *lysT*	
supM	Suppressor	89	Suppressor of ochre (UAA) and amber (UAG) mutations; see *tyrU*	
supN	Suppressor	51	Suppressor of ochre (UAA) and amber (UAG) mutations	A
supO	Suppressor	27	Suppressor of ochre (UAA) and amber (UAG) mutations; may be *supC*	A
supP	Suppressor	96	*Su-6;* suppressor of amber (UAG) mutations	H
supQ	Suppressor	12	Suppressor	A
supT	Suppressor	61	Suppressor; see *glyU*	
supU	Suppressor	84	*su7;* suppressor of amber (UAG) mutations; see *trpT*	
supV	Suppressor	(84)	*su8;* suppressor of ochre (UAA) and amber (UAG) mutations	A
tabC		85	Affects development of phage T4	612
tag		47	3-Methyl-adenine DNA glycosylase activity	V
tar		42	*cheM;* chemotactic response; methyl-accepting chemotaxis protein II	397, 569, 570, 587
tdi		(4)	Transduction, transformation, and rates of mutation reduced	593
tdk		27	Thymidine kinase (EC 2.7.1.75)	A, 79
terC	Terminus	(32)	*tre;* terminus of replication of chromosome	336, 337, 375
thiA	Thiamine	90	Thiamine thiazole requirement	A
thiB	Thiamine	90	Thiaminephosphate pyrophosphorylase (EC 2.5.1.3)	A
thiC	Thiamine	90	Thiamine pyrimidine requirement	A
thi-o	Thiamine	90	*thiO;* probable operator sequence for *thiA,B,C*	A
thrA	Threonine	0	*HS, thrD;* aspartokinase I-homoserine dehydrogenase I	A
thrAa	Threonine	0	Attenuator sequence in leader region of *thrABC* operon	186
thrAe	Threonine	0	Leader region of *thrABC* operon	186
thrAo	Threonine	0	Operator sequence for *thrABC* operon	187, 524, 525
thrAp	Threonine	0	Promoter sequence for *thrABC* operon	187, 525
thrB	Threonine	0	Homoserine kinase (EC 2.7.1.39)	A
thrC	Threonine	0	Threonine synthase (EC 4.2.99.2)	A
thrS	Threonine	38	Threonyl-tRNA synthetase (EC 6.1.1.3)	242, 588
thrT	Threonine	89	Threonine tRNA3	A, 82, 113, 517, 518, 675
thrU	Threonine	89	Threonine tRNA4	517, 518, 675
thyA	Thymine	60	Thymidylate synthetase	A
tkt		(62)	Transketolase (EC 2.2.1.1)	A
tnaA		83	*ind;* tryptophanase (EC 4.1.99.1)	A, 223, 338, 392, 414, 439
tnaAp		83	Promoter sequence for *tnaA*	647
tnaR		83	Regulatory gene	A, 618
tolA	Tolerance	16	*cim, tol-2;* tolerance to colicins E2, E3, A, and K	A
tolAp	Tolerance	16	*tolP;* promoter sequence for *tolAB*	A
tolB	Tolerance	16	*tol-3;* tolerance to colicins E1, E2, E3, A, and K	A
tolC	Tolerance	66	*colE1-i, mtcB, refI, tol-8;* specific tolerance to colicin E1	A
tolD	Tolerance	(23)	Tolerance to colicins E2 and E3; ampicillin resistance	A
tolE	Tolerance	(23)	Tolerance to colicins E2 and E3; ampicillin resistance	A
tolI	Tolerance	(0)	Tolerance to colicins Ia and Ib	A
tolJ	Tolerance	0	Resistance to colicins L, A, and S4; partial resistance to colicins E and K	121
tonA	T-one	3	*T1, T5rec;* receptor for ferrichrome, bacteriophages T1, T5, and ϕ80, and colicin M	A, 119, 226, 227, 494, 664
tonB	T-one	27	*exbA; T1rec;* uptake of chelated iron and cyanocobalamin; sensitivity to phages T1 and ϕ80 and colicins	A, 31, 120, 178, 226, 227, 489, 495, 664

TABLE 1—*Continued*

Gene symbol	Mnemonic	Map position (min)[b]	Alternate gene symbols; phenotypic trait affected	References[c]
tpiA		88	Triosephosphate isomerase (EC 5.3.1.1)	A, 466
tre	Trehalose	26	Utilization of trehalose	36
trg		(30)	Chemotactic response; methylation of methyl-accepting chemotaxis protein III	228, 323
trkA		72	Transport of potassium	A
trkB		73	Transport of potassium	A
trkC		1	Transport of potassium	A
trkD		84	Transport of potassium	A, 642
trkE		28	Transport of potassium	A
trmA	tRNA methyltransferase	89	tRNA (uracil-5)-methyltransferase (EC 2.1.1.35)	A, 47
trmB	tRNA methyltransferase	(7)	tRNA (guanine-7)-methyltransferase (EC 2.1.1.33)	A
trmC	tRNA methyltransferase	(55)	Deficiency of 5-methylaminomethyl-2-thio-uridine in tRNA	A, 48
trmD	tRNA methyltransferase	(58)	tRNA (guanine-1)-methyltransferase (EC 2.1.1.31)	48
trpA	Tryptophan	27	*tryp-2;* tryptophan synthase (EC 4.2.1.20), A protein	A, 214, 420, 666
trpAt	Tryptophan	27	Terminator sequence of *trpEDCBA* operon	214, 420, 666
trpB	Tryptophan	27	*tryp-1;* tryptophan synthase (EC 4.2.1.20), B protein	A
trpC	Tryptophan	27	*tryp-3; N*-(5-phosphoribosyl)anthranilate isomerase-indole-3-glycerolphosphate synthetase	A, 428
trpCp	Tryptophan	27	Promoter sequence for *trpCBA*	428
trpD	Tryptophan	27	*tryE;* glutamine amidotransferase-phosphoribosyl anthranilate transferase	A
trpE	Tryptophan	27	*anth, tryp-4, tryD;* anthranilate synthase (EC 4.1.3.27)	A, 40, 41, 45, 355, 418, 591, 595, 695
trpEa	Tryptophan	27	Attenuator sequence in leader region of *trpEDCBA* operon	45, 355, 591, 595, 695
trpEe	Tryptophan	27	*trpL;* leader region of *trpEDCBA* operon	45, 355, 418, 591, 595, 695
trpEo	Tryptophan	27	*trpO;* operator sequence for *trpEDCBA* operon	A, 40, 41
trpEp	Tryptophan	27	Promoter sequence for *trpEDCBA* operon	A, 40, 41
trpR	Tryptophan	100	*Rtry;* regulation of *trpEDCBA* operon and *aroH*	A, 516
trpS	Tryptophan	74	Tryptophanyl-tRNA synthetase (EC 6.1.1.2)	A, 52
trpT	Tryptophan	84	*su7, supU;* tryptophan tRNA gene at distal end of *rrnC* operon	A, 423, 425
trxA	Thioredoxin	85	*tsnC;* thioredoxin deficiency	389, 390
tsf		4	Protein chain elongation factor Ts	175, 677
tsr		99	*cheD;* chemotactic response; methyl-accepting chemotaxis protein I	570, 587, T
tsx	T-six	9	*nupA, T6rec;* nucleoside uptake; receptor for phage T6 and colicin K	A, 225, 386, 407
tufA		73	Protein chain elongation factor Tu (duplicate gene)	A, 37, 182, 183, 184, 189, 289, 367, 415, 633
tufB		89	Protein chain elongation factor Tu (duplicate gene)	A, 37, 39, 182, 183, 189, 368, 370, 415, 481, 633, 675
tynA		(27)	Tyramine oxidase (EC 1.4.3.4)	435
tyrA	Tyrosine	56	Chorismate mutase T (EC 5.4.99.5)-prephenate dehydrogenase (EC 1.3.1.12)	A
tyrB	Tyrosine	91	Tyrosine aminotransferase (EC 2.6.1.5), tyrosine repressible	190, 191, R
tyrR	Tyrosine	29	Regulation of *arof, aroG,* and *tyrA* and aromatic amino acid transport systems	A, 148, 651
tyrS	Tyrosine	36	Tyrosyl-tRNA synthetase (EC 6.1.1.1)	A, G
tyrT	Tyrosine	27	su_{III}, *Su-3, supF;* tyrosine tRNA1 (tandemly duplicated gene)	A, 146, 517, 550
tyrTp	Tyrosine	27	Promoter sequence for *tyrT*	550
tyrU	Tyrosine	89	*supM;* tyrosine tRNA2	A, 113, 517, 518, 550, 675
tyrUp	Tyrosine	89	Promoter sequence for *tyrU*	550
tyrV	Tyrosine	27	su_{III}, *Su-3, supF;* tyrosine tRNA1 (tandemly duplicated gene)	146, 339, 517, 550
tyrVt	Tyrosine	27	Terminator sequence for *tyrV*	146, 339

TABLE 1—*Continued*

Gene symbol	Mnemonic	Map position (min)[b]	Alternate gene symbols; phenotypic trait affected	References[c]
ubiA	Ubiquinone	91	4-Hydroxybenzoate → 3-octaprenyl 4-hydroxybenzoate	A
ubiB	Ubiquinone	85	2-Octaprenylphenol → 2-octaprenyl-6-methoxy-phenol	A
ubiC	Ubiquinone	91	Chorismate lyase	A
ubiD	Ubiquinone	85	3-Octaprenyl-4-hydroxybenzoate → 2-octaprenylphenol	A
ubiE	Ubiquinone	85	2-Octaprenyl-6-methoxy-1,4-benzoquinone → 2-octaprenyl-3-methyl-6-methoxy-1,4-benzoquinone	A
ubiF	Ubiquinone	15	2-Octaprenyl-3-methyl-6-methoxy-1,4-benzoquinone → 2-octaprenyl-3-methyl-5-hydroxy-6-methoxy-1,4-benzoquinone	A
ubiG	Ubiquinone	48	2-Octaprenyl-3-methyl-5-hydroxy-6-methoxy-1,4-benzoquinone → ubiquinone-8	A, 329
ubiH	Ubiquinone	62	2-Octaprenyl-6-methoxyphenol → 2-octaprenyl-6-methoxy-1,4-benzoquinone	A
udk		45	Uridine kinase (EC 2.7.1.48)	A
udp		85	Uridine phosphorylase (EC 2.4.2.3)	A
uhpR		82	Regulation of hexose phosphate transport	A, 223, 392
uhpT		82	Hexose phosphate transport	A, 223, 392
uidA		36	*gurA;* β-D-glucuronidase (EC 3.2.1.31)	A, 452
uidAo		36	Operator sequence for *uidA*	452
uidR		36	Regulatory gene	A, 452
umuC		25	Induction of mutations by UV; sensitivity to UV	304
uncA	Uncoupling	83	F_1-component of ATP-synthesizing system, α-subunit	A, 139, 143, 199, 301, 551, 641, 642
uncB	Uncoupling	83	F_0-component of ATP-synthesizing system	A, 107, 139, 199, 230, 641, 642
uncC	Uncoupling	83	F_1-component of ATP-synthesizing system, ε-subunit	139, 198, 199, 641, 642, E
uncD	Uncoupling	83	F_1-component of ATP-synthesizing system, β-subunit	106, 139, 158, 199, 552, 641, 642
uncE	Uncoupling	83	F_0-component of ATP-synthesizing system	139, 140
uncG	Uncoupling	83	F_1-component of ATP-synthesizing system, λ-subunit	F
ung		56	Uracil-DNA-glycosidase	142
upp		53	*uraP;* uracil phosphoribosyltransferase (EC 2.4.2.9)	A, 474
ups		26	Efficiency of nonsense suppressors	122
ush		11	UDP-glucose hydrolase (5′-nucleotidase)	A, 35
uvrA	UV	92	*dar;* repair of UV damage to DNA; UV endonuclease	A, 427, 532
uvrB	UV	17	*dar-1,6;* repair of UV damage to DNA; UV endonuclease	A, 427, 457, 608
uvrC	UV	42	*dar-4,5;* repair of UV damage to DNA	A
uvrD	UV	85	*dar-2, mutU, pde, rad, recL, uvrE, uvr502;* repair of UV damage to DNA	A, 341, 520, 573
uxaA		67	Altronate hydrolase (EC 4.2.1.7)	A, 393, 443
uxaB		(52)	Altronate oxidoreductase (EC 1.1.1.58)	A, 443
uxaC		67	Uronate isomerase (EC 5.3.1.12)	A, 393, 443
uxuA		98	Mannonate hydrolase (EC 4.2.1.8)	A, 284
uxuB		98	Mannonate oxidoreductase (EC 1.1.1.57)	A, 284
uxuR		98	Regulatory gene	453
valS	Valine	96	*val-act;* valyl-tRNA synthetase (EC 6.1.1.9)	A, 309, 310
valT	Valine	(16)	Valine tRNA1	269
xthA		38	Exonuclease III	A, 652
xseA		53	Exonuclease VII	86, 631
xyl	Xylose	79	Utilization of D-xylose	A
zwf	Zwischenferment	41	Glucose-6-phosphate dehydrogenase (EC 1.1.1.49)	A

[a] Abbreviations: DAHP, 3-deoxy-D-arabinoheptulosonate-7-phosphate; 7KAP, 7-oxo-8-aminopelargonate; DAPA, 7,8-diaminopelargonate; CoA, coenzyme A; tRNA, transfer ribonucleic acid; DNA, deoxyribonucleic acid; ATP, GTP, and CTP, adenosine, guanosine, and cytosine 5′-triphosphate, respectively; UDP and TDP, uridine and thymidine 5′-diphosphate, respectively; IMP, UMP, and GMP, inosine, uridine, and guanosine 5′-monophosphate, respectively; cyclic AMP, cyclic adenosine 3′,5′-monophosphate; ATPase, adenosine triphosphatase; dUTPase, deoxyuridine triphosphatase; NAD, nicotinamide adenine dinucleotide; NADH, reduced NAD; NADP, NAD phosphate; UV, ultraviolet light.

[b] Numbers refer to time scale shown in Fig. 1. Parentheses indicate approximate map locations.

[c] Numbers refer to Literature Cited. The letter A refers to Literature Cited in Table 2 of reference 24. The other letters refer to personal communications from the following persons; (B) S. D. Barbour; (C) J. Calvo; (D) A. J. Clark; (E) E. C. Cox; (F) G. B. Cox; (G) B. Diderichsen; (H) G. E. Eggertsson; (I) J. Felton and A. Wright; (I′) J. Foulds; (J) J. Garwin and J. E. Cronan, Jr.; (K) J. R. Guest; (L) P. E. Hartman; (M) R. W. Hogg; (N) P. Kuempel; (O) A. J. Laird; (P) A. B. Lenny and P. Margolin; (Q) A. Ohta and W. Dowhan; (R) D. Mount and J. Little; (S) H. Ozeki; (T) J. S. Parkinson; (U) C. H. R. Raetz; (V) E. Seeberg, I. Øfseng, T. Lindahl, and P. Karran; (W) B. G. Spratt; (X) R. T. Vinopal; (Y) J. R. Walker; (Z) I. Young.

with that of *S. typhimurium*, we have adopted here the *Salmonella* nomenclature used for naming genes involved in the utilization of amino acids: these locus symbols consist of a single letter coding for the amino acid, followed by the letters *ut* (for "utilization"). Thus, the old symbol *poaA* on the *E. coli* map for the locus coding for proline oxidase has been changed to *putA* as used in *Salmonella*, where this locus is better understood. The symbol *strB* on the *E. coli* map has been changed herein to *strC*, to avoid confusion with the better-known locus called *strB* in *Salmonella*.

It behooves authors who are thinking of coining a new locus symbol to attempt to determine whether or not the symbol that they are considering has been, or is about to be, used to designate another locus in either one of these organisms. Previous use of a gene symbol can be determined by consulting the literature and the most recent genetic maps for the two organisms, including the tables of outmoded gene symbols that have been reduced to synonymy. Often the intent to use a gene symbol is registered with the keepers of the Genetic Stock Centers for these organisms: B. J. Bachmann for *E. coli* and K. E. Sanderson, Department of Biology, University of Calgary, Calgary, Alberta, Canada T2N 1N4, for *Salmonella*. Numbers for the designation of mutant alleles are also registered in the two Stock Centers. Blocks of allele numbers are assigned to research workers for the designation of mutations that are to be described in publications or distributed to other laboratories.

COMMENTS ON THE LINKAGE MAP

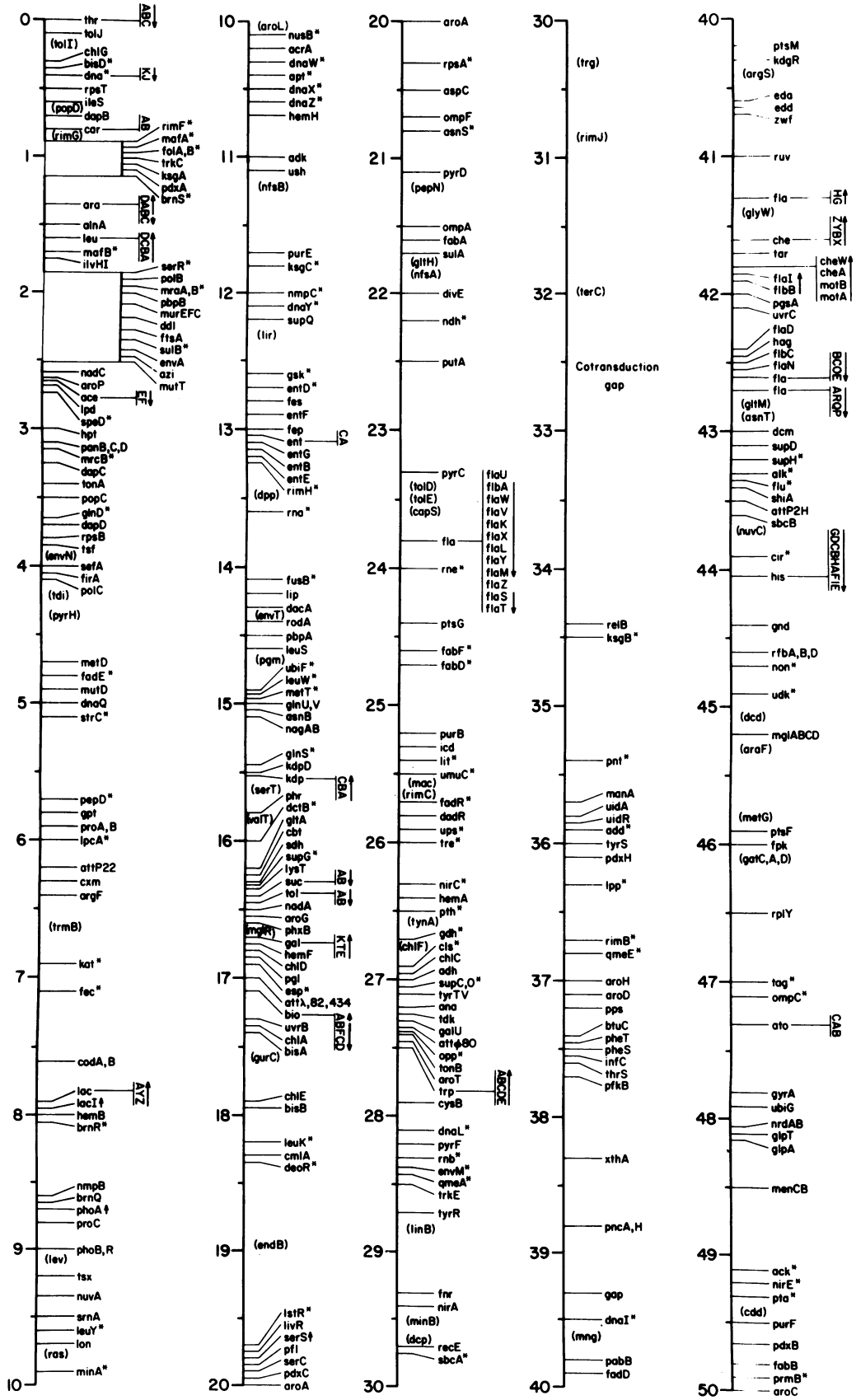
The many minor changes in gene order, map distances, and nomenclature for individual markers on the map are now too numerous to discuss individually. The experimental basis for these changes can be found in Literature Cited. Four markers that were on the 1976 map have been removed altogether from the map drawing and the tables: *ast* and *lar*, which have not been found in *E. coli* K-12; *dnaH* (32); and *rplH* (483). Some markers have been found to be identical to other genes that had been placed on the map earlier. The symbols for these markers are now given in Table 1 as synonyms for the earlier mapped loci: e.g., *recL* and *uvrE* are now synonyms for *uvrD* (341, 520, 573).

An outmoded gene designation can be found by first scanning in Table 1 the synonyms given for loci having that same gene symbol. Thus, *uvrE* will be found as a synonym under *uvrD*. If the designation is not found in this way, then the gene symbol is now different and the outmoded designation will be found in Table 2. Thus, *recL* is listed in Table 2, although *uvrE* is not.

Some of the major changes and outstanding problems encountered in drawing the linkage map require discussion. One of the two cotransduction gaps that remained on the 1976 map has been closed. Cotransduction has been obtained between markers across the gap between *valS* and the *hsd* operon in the 90-min region (284). These data, some of which involved cotransduction with an uncharacterized and undesignated temperature-sensitive mutation not placed on the linkage map herein, indicate that this region is over 1 min shorter than it was thought to be in 1976. New time-of-entry data for this region support the shorter map distance (K. B. Low, unpublished data).

There are still at least two cotransduction gaps on the map, however. The removal of *plsB* from the 70-min region of the map has left a gap between the *pit* and *kdgK* loci. The large gap in the 30-min region containing the terminus of replication (*terC*) is still a mystery. Two markers of the Rac prophage (*recE* and *sbcA*) have been mapped by cotransduction around 2 min clockwise from *trp* (P. Kuempel, personal communication); *relB* (139, 149) and *ksgB* (S. Barbour and P. Kuempel, personal communications) have been mapped by cotransduction around 1 min counterclockwise from *man*. This leaves, between these two pairs of markers, a gap of over 4.5 min, by time-of-entry, in which no markers have been mapped by cotransduction. It is still not known whether this region of the map accurately represents a segment of the genome (i.e., DNA) or is only an artifact resulting

FIG. 1. *Linear-scale drawings representing the circular linkage map of E. coli K-12. The time scale of 100 min, beginning arbitrarily with zero at the thr locus, is based on the results of interrupted-conjugation experiments. The genetic symbols used in this figure are defined in Table 1. The outmoded gene symbols malA, malB, rrnA, rrnB, rrnC, rrnD, rrnE, rrnF, and rrnG have been used for the operons formerly so-designated as a matter of convenience, because of their wide usage in the past. Parentheses around a gene symbol indicate that the position of that marker is not well known and may have been determined only within 5 to 10 min. An asterisk indicates that a marker has been mapped more precisely but that its position with respect to nearby markers is not known. Arrows above genes and operons indicate the direction of transcription of these loci. For a comparison with the linkage map of Salmonella typhimurium, see reference 535. NOTE: The rrnD operon is placed incorrectly in Fig. 1. The correct position of this operon is at approximately 71.7 min on the linkage map.*


0
thr
ABC
tolJ
(tolI)
chlG
bioD*
dna*
KJ
rpsT
ileS
(popD)
dapB
car
AB
(rimG)
rimF*
mafA*
folA,B*
trkC
ksgA
pdxA
brnS*
ara
DABC
alnA
leu
DCBA
mafB*
ilvHI
serR*
polB
mraA,B*
pbpB
murEFC
ddl
ftsA
sulB*
envA
azi
mutT
nadC
aroP
ace
EF
lpd
speD*
hpt
panB,C,D
mrcB*
dapC
tonA
popC
glnD*
dapD
rpsB
tsf
(envN)
sefA
firA
(tdi)
polC
(pyrH)
metD
fadE*
mutD
dnaQ
strC*
pepD*
gpt
proA,B
lpcA*
attP22
cxm
argF
(trmB)
kat*
fec*
codA,B
lac
AYZ
lacI
hemB
brnR*
nmpB
brnQ
phoA
proC
phoB,R
(lev)
tsx
nuvA
srnA
leuY*
lon
(ras)
minA*
10
(aroL)
nusB*
acrA
dnaW*
apt*
dnaX*
dnaZ*
hemH
adk
ush
(nfsB)
purE
ksgC*
nmpC*
dnaY*
supQ
(lir)
gsk*
entD*
fes
entF
fep
ent
CA
entG
entB
entE
rimH*
(dpp)
rna*
fusB*
lip
dacA
(envT)
rodA
pbpA
leuS
(pgm)
ubiF*
leuW*
metT*
glnU,V
asnB
nagAB
glnS*
kdpD
kdp
CBA
(serT)
phr
dctB*
(valT)
gltA
cbt
sdh
supG*
lysT
suc
AB
tol
AB
nadA
aroG
(argR)
phxB
gal
KTE
hemF
chlD
pgl
ssp*
attλ,82,434
bio
ABFGD
uvrB
chlA
bisA
(gurC)
chlE
bisB
leuK*
cmlA
deoR*
(endB)
lstR*
livR
serS
pfl
serC
pdxC
aroA
20
aroA
rpsA*
aspC
ompF
asnS*
pyrD
(pepN)
ompA
fabA
sulA
(gltH)
(nfsA)
divE
ndh*
putA
pyrC
flaU
(tolD)
flbA
(tolE)
flaW
(capS)
flaV
flaK
fla
flaX
flaL
rne*
flaY
flaM
flaZ
flaS
flaT
ptsG
fabF*
fabD*
purB
icd
lit*
umuC*
(mac)
(rimC)
fadR*
dadR
ups*
tre*
nirC*
hemA
pth*
(tynA)
gdh*
(chlF)
cls*
chlC
adh
supC,O*
tyrTV
ana
tdk
galU
attφ80
opp*
tonB
aroT
ABCDE
trp
cysB
dnaL*
pyrF
rnb*
envM*
qmeA*
trkE
tyrR
(linB)
fnr
nirA
(minB)
(dcp)
recE
sbcA*
30
(trg)
(rimJ)
(terC)
Cotransduction
gap
relB
ksgB*
pnt*
manA
uidA
uidR
add*
tyrS
pdxH
lpp*
rimB*
qmeE*
aroH
aroD
pps
btuC
pheT
pheS
infC
thrS
pfkB
xthA
pncA,H
gap
dnaI*
(mng)
pabB
fadD
40
ptsM
kdgR
(argS)
eda
edd
zwf
ruv
fla
HG
(glyW)
ZYBX
che
tar
cheW
cheA
motB
motA
flaI
flbB
pgsA
uvrC
flaD
hag
flbC
flaN
BCDE
fla
ARGP
fla
(gltM)
(asnT)
dcm
supD
supH*
alk*
flu*
shiA
attP2H
sbcB
(nuvC)
GDCBAFIE
cir*
his
gnd
rfbA,B,D
non*
udk*
(dcd)
mglABCD
(araF)
(metG)
ptsF
fpk
(gatC,A,D)
rplY
tag*
ompC*
CAB
ato
gyrA
ubiG
nrdAB
glpT
glpA
menCB
ack*
nirE*
pta*
(cdd)
purF
pdxB
fabB
prmB*
aroC

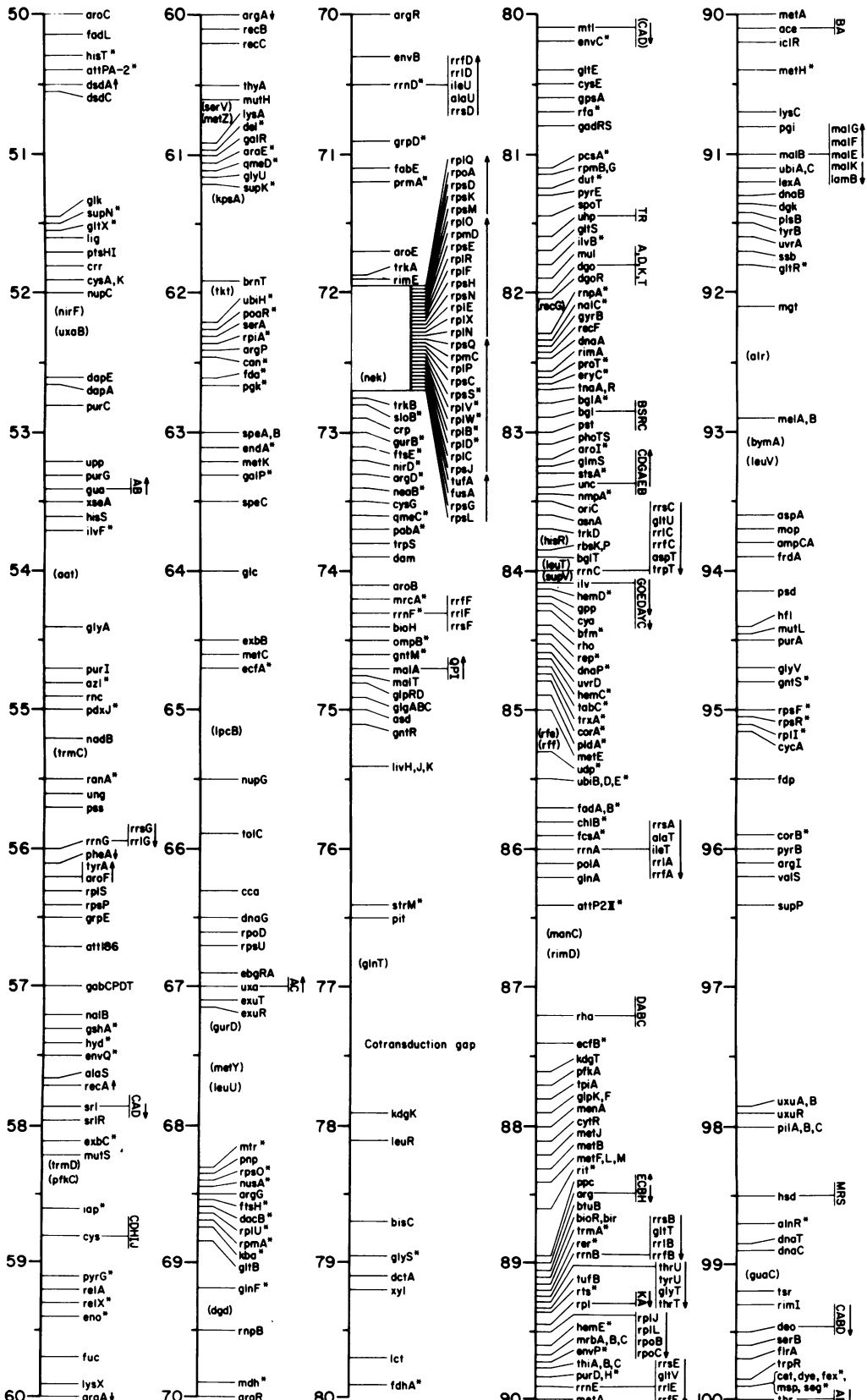

50
aroC
fadL
hisT*
attPA-2*
dsdA
dsdC
51
glk
supN*
gltX*
lig
ptsHI
crr
cysA,K
52
nupC
(nirF)
(uxaB)
dapE
dapA
purC
53
upp
purG
gua
xseA
hisS
ilvF*
54
(aat)
glyA
purI
azi*
rnc
55
pdxJ*
nadB
(trmC)
ranA*
ung
pss
56
rrnG
pheA
tyrA
aroF
rplS
rpsP
grpE
attI86
57
gabCPDT
nalB
gshA*
hyd*
envQ*
alaS
recA
58
srl
srlR
exbC*
mutS
(trmD)
(pfkC)
iap*
59
cys
pyrG*
relA
relX*
eno*
fuc
lysX
60
argA
60
argA
recB
recC
thyA
mutH
(serV)
(metZ)
lysA
del*
61
galR
araE*
qmeD*
glyU
supK*
(kpsA)
62
brnT
(tkt)
ubiH*
poaR*
serA
rpiA*
argP
can*
fdo*
pgk*
63
speA,B
endA*
metK
galP*
speC
64
glc
exbB
metC
ecfA*
65
(lpcB)
nupG
tolC
66
cca
dnaG
rpoD
rpsU
ebgRA
67
uxa
exuT
exuR
(gurD)
(metY)
(leuU)
68
mtr*
pnp
rpsO*
nusA*
argG
ftsH*
docB*
rplU*
rpmA*
kbo*
gltB
69
ginF*
(dgd)
rnpB
mdh*
70
argR
70
argR
envB
rrfD
rrlD
ileU
alaU
rrsD
rrnD*
grpD*
71
fabE
prmA*
rplQ
rpoA
rpsD
rpsK
rpsM
rplO
rpmD
rpsE
rplR
rplF
rpsH
rpsN
rplE
rplX
rplN
rpsQ
rpmC
rplP
rpsC
rpsS*
rplV*
rplW*
rplB*
rplD*
rplC
rpsJ
tufA
fusA
rpsG
rpsL
72
aroE
trkA
rimE
(nek)
73
trkB
sloB*
crp
gurB*
fliE*
nirD*
argD*
neoB*
cysG
qmeC*
pabA*
trpS
dam
74
aroB
mrcA*
rrnF*
bioH
ompB*
gntM*
malA
malT
glpRD
glgABC
asd
gntR
75
livH,J,K
76
strM*
pit
(glnT)
77
Cotransduction gap
78
kdgK
leuR
79
bisC
glyS*
dctA
xyl
80
lct
fdhA*
80
mtl
envC*
(CAD)
gltE
cysE
gpsA
rfa*
gadRS
81
pcsA*
rpmB,G
dut*
pyrE
spoT
uhp
TR
gltS
ilvB*
mul
A,D,K,T
82
dgo
dgoR
(recG)
rnpA*
nalC*
gyrB
recF
dnaA
rimA
proT*
eryC*
tnaA,R
bglA*
83
bgl
BSRC
pst
phoTS
aroI*
glmS
stsA*
CDGAEB
unc
nmpA*
oriC
asnA
84
(hisR)
trkD
rbsK,P
bglT
(leuT)
(supV)
rrnC
rrsC
gltU
rrlC
rrfC
aspT
trpT
ilv
hemD*
GOEDAYC
gpp
cya
85
bfm*
rho
rep*
dnaP*
uvrD
hemC*
tabC*
trxA*
corA*
pldA*
metE
udp*
(rfe)
(rff)
ubiB,D,E*
86
fadA,B*
chlB*
fcsA*
rrnA
rrsA
alaT
ileT
rrlA
rrfA
polA
glnA
attP2II*
(manC)
(rimD)
87
rha
DABC
ecfB*
kdgT
pfkA
tpiA
glpK,F
88
menA
cytR
metJ
metB
metF,L,M
rit*
ppc
arg
EGBH
btuB
bioR,bir
trmA*
rer*
rrnB
rrsB
gltT
rrlB
rrfB
89
tufB
rts*
rpl
thrU
tyrU
glyT
thrT
KA
rplJ
rplL
rpoB
rpoC*
hemE*
mrbA,B,C
envP*
thiA,B,C
purD,H*
rrnE
metA
rrsE
gltV
rrlE
rrfE
90
90
metA
ace
BA
iclR
metH*
lysC
pgi
malG
malF
91
malB
malE
ubiA,C
malK
lexA
lamB
dnaB
dgk
plsB
tyrB
uvrA
ssb
gltR*
92
mgt
(alr)
93
metA,B
(bymA)
(leuV)
aspA
mop
ampCA
frdA
94
psd
hfl
mutL
purA
glyV
gntS*
95
rpsF*
rpsR*
rplI*
cycA
fdp
96
corB*
pyrB
argI
valS
supP
97
uxuA,B
uxuR
98
pilA,B,C
hsd
MRS
alnR*
dnaT
dnaC
99
(guaC)
tsr
rimI
deo
CABD
serB
flrA
trpR
cet, dye, fex*,
msp, seg*
thr
ABC
100

TABLE 2. *Alternate gene symbols*

Alternate symbol	Symbol in Table 1	Alternate symbol	Symbol in Table 1
acrB	*gyrB*	*feuA*	*cir*
ade	*pur*	*feuB*	*fep*
ald	*fda*	*fim*	*pil*
adth$_a$	*purD*	*flaJ*	*motA, motB*
adth$_b$	*purG*	*flaF*	*hag*
ala-act	*alaS*	*frdB*	*fnr*
alt	*rpoD*	*ftsI*	*pbpB*
amk	*nek*	*gad*	*gap*
anth	*trpE*	*glmD*	*nagB*
apk	*lysC*	*glu*	*ppc*
arg + ura	*car*	*glut*	*gltA*
aroR	*aroT*	*gly-act*	*glyS*
asp	*ppc*	*glyD*	*gpt*
aspB	*gltB*	*gpp*	*gpt*
ata	*attP22*	*gpt*	*ptsG*
bfe	*btuB*	*gptB*	*ptsM*
blu	*pgl, pgm, malP*	*groE*	*mop*
brnP	*ilvH*	*groN*	*rpoB*
cap	*car, crp*	*groP*	*dnaB, dnaJ, dnaK*
capR	*lon*	*grpA*	*dnaB*
cat	*ptsG*	*grpC*	*dnaJ, dnaK*
cbr	*fep*	*grpF*	*dnaK*
cbt	*fep*	*gts*	*qmeA*
cer	*btuB*	*gurA*	*uidA*
cheC	*flaA*	*gut*	*srl*
cim	*tolA*	*gxu*	*gpt*
cmlB	*ompF*	*H*	*hag*
coa	*ompF*	*het*	*oriC*
colE1-i	*tolC*	*Hpr*	*ptsH*
con	*ompA, rfa*	*hs*	*hsd*
Cou	*gyrB*	*Hs*	*thrA*
cqsA	*rrnA*	*hsm*	*hsdM*
cqsB	*rrnC*	*hsp*	*hsd*
cqsC	*rrnF*	*hsr*	*hsdR*
cqsD	*rrnD*	*hss*	*hsdS*
CR	*ptsG*	*icl*	*aceA*
cru	*nupC*	*ile*	*ilvA*
cry	*ompB, ompF*	*ind*	*tnaA*
ctr	*ptsH, ptsI*	*ins*	*glyV, glyW*
cxr	*cxm*	*K12*	*rpsG*
dad	*alnA*	*kac*	*kdp*
dagA	*cycA*	*kdgA*	*eda*
dap + hom	*asd*	*kga*	*eda*
dar	*uvr*	*kmt*	*ompB*
deg	*lon*	*lcs*	*asnS*
dhbB	*bioR*	*lexB*	*recA*
dhl	*lpd*	*lexC*	*ssb*
dir	*lon*	*lop*	*ligAo*
dnaF	*nrdA*	*lps*	*rfa*
dnaL	*lig*	*lss*	*livR*
dnaS	*dut*	*lys + met*	*sucA, sucB*
dra	*deoC*	*mas*	*aceB*
drm	*deoB*	*Mb*	*acrA*
eps	*rpsE*	*mbl*	*acrA*
eryA	*rplD*	*mec*	*dcm*
eryB	*rplV*	*meoA*	*ompC*
exbA	*tonB*	*mlpA*	*lpp*
exrA	*lexA*	*mon*	*envB*
exrB	*ssb*	*mni*	*manC*
far	*fusA*	*mpt*	*ptsM*

TABLE 2—*Continued*

Alternate symbol	Symbol in Table 1	Alternate symbol	Symbol in Table 1
mra	*murF*	*sbl*	*srl*
mtcA	*acrA*	*sec*	*hemF*
mtcB	*tolC*	*sep*	*pbpB*
muc	*lon*	*sfiA*	*sulA*
mutU	*uvrD*	*sfiB*	*sulB*
nalA	*gyrA*	*sof*	*dut*
nam	*pncA*	*som*	*rfb*
nar	*chl*	*spcA*	*rpsE*
ncf	*hemB*	*spr*	*lexA*
neaA	*rpsQ*	*stl*	*rpoB*
nic	*nad*	*strA*	*rpsL*
nirR	*fnr*	*stsB*	*rimH*
nitA	*rho*	*stv*	*rpoB*
nitB	*rpoB*	*Su, su*	*sup*
nuc	*deo*	sud_2	*rpsD*
nupA	*tsx*	*sufD*	*glyU*
old	*fad*	*sumA*	*glyT*
ole	*fadR*	*sumB*	*glyU*
ompE	*nmpA*	*sun*	*rho*
par	*ompC*	sup_{s20}	*rpsT*
pdeB	*uvrD*	*T1rec*	*tonB*
pdeC	*lig*	*T1, T5rec*	*tonA*
pdxF	*serC*	*T6rec*	*tsx*
pea	*azi*	*tabB*	*mop*
pel	*ptsM*	*tabD*	*rpoB, rpoC*
phe-act	*pheS*	*talA*	*alaT*
phx	*rfa*	*talD*	*alaU*
PMG	*mgl*	*tasC*	*aspT*
poaA	*putA*	*tfrA*	*lpcA*
poh	*oriC*	*tgl*	*ptsG*
polC	*dnaE*	*tgtB*	*gltT*
pon	*lpcB, mrc*	*tgtC*	*gltU*
popA	*hemH*	*tgtE*	*gltV*
popB	*hemF*	*thyR*	*deoB, deoC*
popE	*hemC*	*tif*	*recA*
prd	*fuc*	*tilA*	*ileT*
prv	*mutH*	*tilD*	*ileU*
psuA	*rho*	*tmr*	*fol*
pup	*deoD*	*tolF*	*ompF*
pyrA	*car*	*tolG*	*ompA*
rad	*uvrD*	*TP*	*deoA*
ramA	*rpsD*	*tpp*	*deoA*
ramB	*rimF*	*tre*	*terC*
RC	*rel*	*trpP*	*aroT*
recL	*uvrD*	*try*	*trp*
refI	*tolC*	*tryp*	*trp*
refII	*cet*	*ts-9*	*rts*
relC	*rplK*	*tsnC*	*trxA*
res	*rimF*	*tsu*	*rho*
resA	*polA*	*tss*	*asnS*
RMG	*mglR*	*tut*	*ompA*
rm	*hsd*	*umg*	*ptsG*
rnsA	*rna*	*umuA*	*lexA*
rnsC	*rho*	*umuB*	*recA*
rodY	*envB*	*uraP*	*upp*
ron	*rpoB*	*usgA*	*gntM*
rorA	*recB*	*uvrF*	*recF*
rpx	*rps*	*val-act*	*valS*
rpy	*rpl*	*xonA*	*sbcB*
rpz	*rpm*	*zab*	*recA*

from a slowing of time-of-entry in this region. Experiments indicating a slowing of chromosomal replication across the terminus suggest that the latter may be the case but are not yet conclusive (336, 337).

There may be yet a third cotransduction gap on the map, in the 40-min region. Efforts to reproduce the cotransduction data which spanned the gap between *non* and the *ato* cluster at the time of the 1976 map, utilizing cotransduction between *his*, *ptsF*, *fpk*, and *nalA* (now *gyrA*), have not been successful (91). It is possible that a gap not spanned by cotransduction still remains between *udk* and the *mgl* cluster. Time-of-entry data do not indicate that this region is longer than shown on the present map; cotransduction of *udk* and the *mgl* cluster should be possible.

A very perplexing problem in this region concerns the map location of the *metG* marker. Efforts to obtain cotransduction of *metG* with *fpk* and *nalA* (now *gyrA*) have failed (91). In *E. coli* strain C, *metG* has been shown to lie roughly 2.5 min clockwise from *his*, and *metG* and *gat* can be cotransduced into *E. coli* C from strain K-12 at high frequency. *metG* cotransduces with *udk* in *Salmonella* (535). We have not included on the linkage map the loci *atl* and *rtl*, found in *E. coli* C but not in *E. coli* B or K-12, which map in this region when transduced into K-12 derivatives. Studies of these loci (509) indicate that there is nonhomology between strains C and K-12 in this region. Recent studies of *metG* (79a) have indicated that control of the expression of this locus is complex and is affected by other loci in this region.

The failure to obtain cotransduction of *metG* with other markers in this region and the possibility of a cotransduction gap between *udk* and the *mgl* cluster are suggestive but perhaps misleading coincidences. The problem cannot be solved by assuming that the gap is large and that *metG* is in the middle of it. P2 eductants which are thought to be deleted for the region including *udk* and the *mgl* cluster are not deleted for *metG*, although they are deleted for a locus which affects the expression of *metG* (79a). For lack of data satisfactorily positioning *metG*, we have placed this marker in parentheses at approximately 45 min on the map, next to genes with which it apparently cannot be cotransduced.

PHYSICAL LENGTH VERSUS LENGTH IN MAP UNITS

In the previous edition of the *E. coli* K-12 genetic map (24), an estimate of the length of DNA equivalent to 1 min of map length was given to be 41 kilobases (kb). This was derived from the lengths of chromosomal regions on F-prime factors relative to the length of the F factor, which was taken as 94.5 kb. New estimates of the number of kilobases per minute can be made using the lengths of intervals shown on the present map. Another correction factor arises from the standard of length used in the original electron microscopic measurements. Bacteriophage ϕX174 was assumed originally to be 5,250 bases long and, since its actual length has been determined to be 5,386 bases, an increase by a factor of 5,386/5,250 = 1.03 should be applied to all lengths reported using the original standard (N. Davidson, personal communication). Using two of the intervals discussed in the last map, therefore, amended values are:

on F-prime F14, *ilvD-argC*:

$$186.5\ (\times 1.03)\ \text{kb}/4.9\ \text{min} = 39\ \text{kb/min}$$

on F-prime KLF5, *polA-rpoB*:

$$126\ (\times 1.03)\ \text{kb}/3.4\ \text{min} = 38\ \text{kb/min}$$

Of these values, the one for the *ilvD-argC* interval, i.e., 39 kb/min, was derived using measurements of an F-prime factor (F14) that was less likely to have carried undetected deletions than in the other case (24), and for this reason the value of 39 kb/min may be the most accurate. Additional electron microscopic heteroduplex analysis (457) has indicated that the total amount of DNA between *lac* and *gal* is 412.9 (×1.03) kb, corresponding to 8.8 min of map length, or 48 kb/min. The somewhat higher value determined for this interval as compared with those discussed above might be due to some degree of position dependence of physical length per unit of recombinational length, as suggested by regional variations in transduction frequency (and thus cotransduction frequency) observed for *E. coli* K-12 (392). These results emphasize the fact that some uncertainty remains in the absolute lengths indicated on the map as a whole.

E. COLI GENETIC MECHANISMS AND TECHNIQUES

The continued proliferation of new powerful techniques for genetic and physical analyses of *E. coli* and related organisms is impressive. Representative examples of these techniques are listed in Table 3. Of particular note is the useful spectrum of manipulations made possible by insertion sequences and transposons, including bacteriophage Mu (154, 315, 555), and also the variety of methods for cloning regions of the *E. coli* DNA, a few of which are listed in Table 3.

TABLE 3. *Key or recent references to selected techniques in E. coli genetics*

Technique[a]	Reference(s)[b]
MUTANT ISOLATION	
General survey	A-470
Specificities of mutagens and mutators; distribution of nonsense mutations	28, 104, 105, 417
Mutations in *mut* strains	See *mut* loci
Mutagenesis by transposon insertions	
General aspects	228, 314, 315, 555
Random, using nonconjugative plasmids	532
Localized mutagenesis	
Using bacteriophage P1	628
Using bacteriophage Mu transfer by Hfr	610
Using nitrosoguanidine	454a
Mutant enrichment	
Penicillin selection, plate method	163
Penicillin selection, DNA repair mutants	531a
DAP starvation, plate method	112
Nalidixic acid selection	A-309
Auxotrophic mutations, in *polA* background	A-37
Mutations in essential genes	
Amber mutations	126, 274
Spontaneous mutations affecting protein or RNA synthesis	279
Mutations affecting lipid synthesis	499
Use of partial diploids	19, A-639
Large-scale automated procedure	554
Mass screening for CO_2 nonproducers	611
Mass replica plating, for non-UV-mutable mutants	304
Mutations affecting suppression and misreading of levels	A-193
Isolation of deletion mutants	
On F-primes	11
In *lacI*	544
On bacteriophage lambda	672
Operon analysis, using phages Mu and λ	413, 543, 560, 631, A-625
Eduction of *his* region	A-661
Isolation of promoter mutants, using gene fusion	44
GENETIC MAPPING	
Conjugation	
Time-of-entry	24, 376, 691, A-66, A-435
Rapid mapping	376
Gradient of transfer and genetic analysis	A-160, A-161, A-691
Early marker effects	A-253, A-429
Allele-specific effects; negative interference	104, A-445, A-497
Recombinational hot spots	60, 542
Radiation-induced recombination	A-707
Intergeneric crosses	509, 613, 614, 616
Transformation	
Mapping function	256
Transduction	
By bacteriophage P1	
Mapping function and position effects	392, A-416, A-736
Allele-specific effects	A-112, A-140
By bacteriophage Mu	25
By bacteriophage T1	141
By bacteriophage T4	658
Transductional shortening of F-primes; deletion analysis	A-457, A-510
Problems in transductional mapping of plasmids	419
Use of transposon pools, duplications (gene trapping)	315
Merodiploids, gene dosage	269, 377
Gene expression in regions near induced prophages	269
Mutation and transposition by bacteriophage Mu; analysis of gene sequence and transcriptional units	73, 154, 307, 423–425

TABLE 3—*Continued*

Technique[a]	Reference(s)[b]
In vitro synthesis of proteins coded for by transducing fragments	367, 369, 425
Deletion analysis, fine structure, deletions of prophages	104, 425, 466, 544, A-610
Physical versus recombinational lengths	131, 457, 469, 503
Physical mapping by RNA-DNA hybridization	668
TRANSPOSITION	
Using temperature-sensitive F-primes	A-32
By integrative suppression; review of related methods	267
By bacteriophage Mu	154
Transposon technology	313–315, 555
Transposon-mediated R factor integration	81, 114
FUSION	
R factor fusions with bacteriophage P1 or P22	419
Gene fusions, using λ-Mu hybrids	43, 75, 564, 565, 567, 578
F-prime fusions	469
Novel F-prime transductants; deletions on F-primes	239, 641
Fusion by deletion, other examples	420, A-379
CLONING	
Banks of E. coli fragments; cloning onto plasmids by poly(A)-poly(T) tailing or by restriction enzyme cleavage	54, 93, 97, 243, 305, 327, 350, 526, 532, 569, 684
Subcloning; maxicells	446, 533, 675
From an F-prime factor	568
Colony screening by nucleic acid hybridization	212
Transducing phages from abnormal attachment sites	
General method	398, 548a
Examples	176, 329, 387, 393, 510, 642
Directed integration of bacteriophage	62, 70, 270, 315, 693, 694, A-383
Cloning onto minichromosomes or λdv; selection for origins of replication	251, 409, 410, 431, 599, 642, 645
Fusions to orient genes near attachment sites	75, 267, 469, 564, 693, 694

[a] DAP, Diaminopimelic acid; poly(A), polyadenylate; poly(T), polythymidylate.
[b] Reference numbers preceded by "A-" refer to references in the previous edition of the map (24).

Increased evidence for the role of insertion sequences and transposons in normal *E. coli* biology has come from further analysis of the sites of recombination involved in Hfr formation (from F^+) and F-prime formation (from Hfr). In examples of both of these phenomena, the crossover is indicated to have occurred between preexisting insertion sequences (129, 131, 457, 458). The involvement of transposition events in mobilization of plasmids in conjugation has been recently discussed in a review of various stages in conjugal transmission of plasmids (90).

In a recent review of modes of gene transfer in bacteria, examples of potentially useful gene transfer systems can be found (378). Since that review, another potentially advantageous gene transfer system for *E. coli* has been reported, namely, generalized transduction using mutants of bacteriophage T4 (658). Although it is not yet clear whether or not all loci of *E. coli* are transducible by T4, the length of DNA carried in T4 transducing particles appears to be approximately twice that of the more commonly used bacteriophage, P1. Thus, T4 transduction may be of special use in detecting longer-range transductional linkages. For most basic techniques in genetic analysis involving gene transfer, we refer to previous reviews (376, 377, and references 151 and 470 contained in the last map review [24]). A convenient set of Hfr and F-prime strains for use in conjugational genetic analysis is shown in Fig. 2.

REPEATED GENES: AN IMPORTANT ASPECT OF GENE ARRANGEMENT IN *E. COLI*?

In the past few years, increasing evidence has revealed the presence of duplications or near-

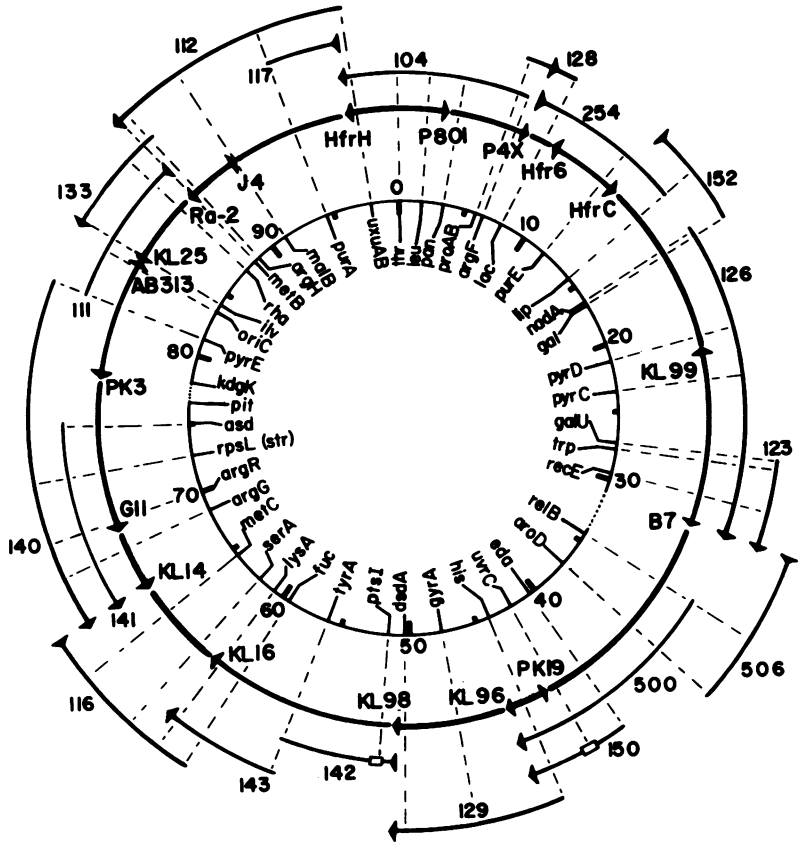


FIG. 2. *Revised map coordinates of the points of origin of some useful Hfr strains and F-prime factors. The dotted portions of the inner circle indicate gaps in transductional linkage. The point of the arrowhead for any Hfr indicates the point of origin. During conjugational transfer, this is immediately followed by transfer of the base of the arrowhead, etc. The small boxes on the lines for F142 and F150 indicate known deletions carried by these F-primes. The isolation of these strains is referred to as follows: Hfr P801, received by B. J. Bachmann in 1973 from the laboratory of F. Jacob; all other Hfr strains, references 376 and 377; F500, reference 452; F506, reference 430a; all other F-prime factors, reference 376. In addition, certain of the ancestral Hfr strains are lysogenic for bacteriophage λ, and λ- derivatives are available for more general use (see reference 376): AB259 (HfrH), BW113 (P4X), KL226 (HfrC), KL208 (B7), KL983 (KL98), KL228 (AB313), and KL209 (J4). PK19 is ColV+, and PK191 is a non-colicinogenic derivative (see reference 377).*

duplications on the *E. coli* K-12 chromosome. This is manifested in at least two ways. First, electron microscopic evidence indicates numerous inverted repeats of several discrete sizes, some of which have approximately the same lengths as known insertion sequences such as IS*1*, IS2, IS*3*, IS*4*, and γδ (89, 130). The lengths of DNA bracketed by these sets of inverted repeats are also nonrandom, and numerous examples of approximately 22, 28, and 69 kb were observed. In one study, approximately 14% of the entire chromosome was estimated to lie between such inverted repeats (89).

The second type of duplication alluded to above is the occurrence of more than one copy of genes whose products have known metabolic functions. The sequencing of two genes for $tRNA^{Tyr}$, i.e., *tyrT* and *tyrU*, shows that the DNAs corresponding to the mature tRNA's are identical except for two bases, although the adjoining base sequences are very different (517, 518). Furthermore, a sequence of 178 bases including the end of only one of these genes (*tyrT*) is repeated tandemly more than threefold, downstream from *tyrT* (146). *tyrT* and *tyrU* are located very far from each other on the map, at 27 and 89 min, respectively. Next to *tyrT* lies an apparent tandem duplication, *tyrV*. Another example of apparent gene duplication is the genes *argI* and *argF*, which both code for monomers of the same trimeric enzyme, ornithine carbamoyltransferase. These two genes are also well separated on the map, at 96 and 6 min, respectively, and their base sequences differ only by perhaps 5% (309, 310, 358). In spite of this divergence, the mature trimeric enzyme consists of

various combinations of monomers from the two genes. Pure trimers coded for by the two genes separately show very similar enzyme activities but differ significantly in thermal stabilities (358, 553). Since *argF* is not found in *E. coli* B, *E. coli* W, or several other closely related enteric bacterial species, it may be that *argF* evolved relatively recently in *E. coli* K-12 and is derived from a duplication of *argI*.

Other recently studied examples of multiple gene copies include in particular the seven rRNA operons *rrnA* through *rrnG*. Although located at seven different map locations, these operons include genes for 5S rRNA, 16S rRNA, and 23S rRNA, and the corresponding genes are nearly homologous but in general not identical (55, 124, 307, 424, 640). Another remarkable aspect of some of these operons is that the rRNA genes are coupled to tRNA genes, which differ in number and species from operon to operon (423, 424). Thus, not only have the rRNA genes undergone what appears to be gene duplication in the course of evolution, but also aspects of the organization of these genes appear to have been preserved as well. It is also interesting that in general the bulk of genes for tRNA are not either randomly distributed or all clustered, but lie in several regions corresponding to apparent high gene density on the map (269), and in many cases appear to exist as tandem repeats of the same tRNA gene, with up to five copies of a given tRNA gene per tRNA operon (271). One further example of duplication of a gene whose product is produced in large amounts is the case of *tufA* and *tufB*, each of which codes for a species of elongation factor Tu, which in total comprises over 5% of the cellular protein by weight (182, 367, 368). Here again, the base sequences of the duplicated genes, although located in different regions of the genetic map, are very nearly but not completely identical (183, 189).

The existence of many regions of the chromosome bounded by inverted repeats, mentioned earlier, indicates configurations that are at least topologically equivalent to transposons (313) and suggests that a major avenue for the generation of duplicate genes in *E. coli* has been via transposition of genetic material from one region to another, with retention of one copy at the original location. A detailed discussion of map position of related genes in *E. coli* K-12 and *S. typhimurium* suggests a number of possible insertions and deletions during evolutionary divergence of these closely related species (511), although any such conclusions must depend ultimately on accurate physical comparison of particular map regions. These authors also review the properties of numerous unstable genetic duplications that have been isolated in the laboratory. Genes involved in glucose catabolism have been found to be clustered at four regions separated by 90° on the map (512), and the authors suggest that two entire chromosome doublings could have led to evolution of related genes. This is to be contrasted with the examples of exact or near-exact gene duplication summarized above, in which the locations of duplicate genes seem to bear no regular relation to each other (see also 83). For these cases, the idea of transposition-like processes is at present the most attractive.

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