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 in Fig. 1 are estimates...
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, rRN, 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 mononics, 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 StockCenter: A. J. Clark (University of California, Berkeley), P. E. Hartman (Johns Hopkins University, Baltimore), K. E. Sanderson (University of California, 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 a lower case (italicized) letter to the (italized) 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), abcDl (leader), abcDa (attenuator), and abcDi (initiator). The terminator of transcription of this operon would be designated abcFl, 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., deoClp 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 involved naming the same sequence of deoxyribonucleic acid (DNA) twice, e.g., argEO and argEp and argCo and argCp in the argECB 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
| Gene symbol | Mnemonic | Map position (min) | Alternate gene symbols; phenotypic trait affected | References |
|------------|----------|-------------------|--------------------------------------------------|------------|
| aat        | Aminoacyl-tRNA-protein transferase (EC 2.3.2.6) | (54) | | 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 | aceE; acetate requirement; pyruvate dehydrogenase (decarboxylase component) | A, 345 |
| aceF       | Acetate | 3 | aceE2; acetate requirement; pyruvate dehydrogenase (dihydrolipoyltransacetylase component) | A, 345 |
| ack        | Aminoacyl-tRNA-protein transferase (EC 2.3.2.6) | 49 | Aminoacyl-tRNA-protein transferase (EC 2.3.2.6) | A |
| acrA       | Acridine | 10 | Mbt, mbl, mtr; sensitivity to acriflavin, phenethyl alcohol, sodium dodecyl sulfate | A |
| add        | Adenine | 36 | Adenine deaminase (EC 3.5.4.4) | 291, 92 |
| adh        | Adenine | 27 | Levels of alcohol dehydrogenase and nitrate reductase activity | A, 200, 508 |
| adk        | Adenine | 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; alanin-tRNA synthetase (EC 6.1.1.7) | A, 404, 619 |
| alaT       | Alanine | 86 | tala; alanine tRNA1B; in rnaA operon | 268, 424 |
| alaU       | Alanine | 70 | talD; alanine tRNA1B; in rnaD operon | 268, 424, 688 |
| alkB       | Alkaline | 43 | Sensitivity to alkylating agents | 678 |
| alnA       | Alanine | 1 | dad; D-alanine dehydrogenase | A, 170 |
| alnR       | Alanine | 99 | Regulatory gene | A |
| alc        | Alanine | 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        | Alanine | 27 | Reoxidation of reduced pyridine nucleotides | 36, 79 |
| apt        | Alanine | 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 | araG; 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 | 506, M |
| argA       | Arginine | 60 | argB, ArgI, ArgZ; amino acid acetyltransferase (EC 2.3.1.1) | A, 145 |
| argA0      | 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-g-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, ArgJ; 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 | argF, 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 | ArgR; 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) | Alternate gene symbols; phenotypic trait affected | References |
|-------------|----------|-------------------|--------------------------------------------------|------------|
| **aroC**    | Aromatic | 50                | Chorismate synthetase                             | A          |
| **aroD**    | Aromatic | 37                | 5-Dehydroquinase 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*, operon 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*, operon sequence for *aroH*                | A          |
| **aroI**    |          | 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, 462 |
| **asnB**    | Asparagine | 15               | Asparagine synthetase B (EC 6.3.1.1)               | 159, 264, 462 |
| **asnS**    | Asparagine | 21               | *lcr*; asparaginyl-tRNA synthetase                 | 455, 676  |
| **asnT**    | Asparagine | (43)             | *Asn* T; asparagine tRNA synthetase               | 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  |
| **ast**     | Aspartate | 84                | *tasC*; aspartate tRNA1; in *rrnC* operon         | 268, 423, 424, 425 |
| **attA**    |          | 47                | Acetate CoA-transferase (EC 2.8.3.-.)             | A          |
| **attB**    | Acetoacetate | 47              | Acetyl-CoA acetyltransferase (EC 2.3.1.9)         | A          |
| **attC**    | Acetate | 47                | Regulatory gene                                   | A          |
| **attP**    | 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        |
| **attP90**  | Attachment | 27               | Integration site for prophage *φ80*               | A, 489    |
| **attR2**   | Attachment | 17               | Integration site for prophage *ρ2*                | A          |
| **attR186** | Attachment | 57               | Integration site for prophage 186                 | A          |
| **attR434** | 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 *lev* genes; azaleucine resistance | A          |
| **bfr**     |          | 84                | Phage BP23 multiplication                          | A          |
| **bgI**     | β-Glucoside | 83            | *bgID*; phospho-β-glucosidase A                    | A, 223    |
| **bgIB**    | β-Glucoside | 83            | *bgIA*; phospho-β-glucosidase B                    | A, 223, 414, 642, 462 |
| **bgI**     | β-Glucoside | 83            | *bgIB*; β-glucoside transport                      | A, 414    |
| **bgIR**    | β-Glucoside | 83            | *bgIB*, *bgIC*; regulatory gene                    | A, 414    |
| **bgIS**    | β-Glucoside | 83            | *bgIC*; regulatory gene                            | A          |
| **bgIT**    | β-Glucoside | 84            | *bgIE*; regulatory gene for phospho-β-glucosidase A synthesis | A          |
| **bioA**    | Biotin    | 17               | Group II; 7KAP→DAPA                                 | A, 117, 608 |
| **bioA0**   | Biotin    | 17               | Operator sequence for *bioA*                      | 116, 117, 306, 462, 490, 608 |
| **bioAp**   | Biotin    | 17               | Promoter sequence for *bioA*                      | 116, 117, 306, 462, 608 |
| **bioB**    | Biotin    | 17               | Conversion of dethiobiotin to biotin               | A, 117, 608 |
| **bioBo**   | Biotin    | 17               | *bioO*; operator sequence for *bioBFCD*           | 116, 117, 306, 462, 490, 608 |
| **bioBp**   | Biotin    | 17               | *bioP*; promoter sequence for *bioBFCD*           | 116, 117, 306, 462, 608 |
| **bioC**    | Biotin    | 17               | Block before pimeloyl CoA                          | A, 117, 608 |
| **bioD**    | Biotin    | 17               | Dethiobiotin synthetase                            | A, 117, 608 |
| **bioE**    | 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    |
| **bioA**    | Biotin sulfoxide | 17          | Reduction of biotin-d-sulfoxide; may be *chlA*    | 95, 144   |
| **bioA**    | Biotin sulfoxide | 18          | Reduction of biotin-d-sulfoxide; may be *chlE*    | 95, 144   |
| **bioC**    | Biotin sulfoxide | 79          | Reduction of biotin-d-sulfoxide                    | 95, 144   |
| **bioD**    | Biotin sulfoxide | 0           | Reduction of biotin-d-sulfoxide; may be *chIG*    | 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) | Alternate gene symbols; phenotypic trait affected | References* |
|-------------|----------|-------------------|---------------------------------------------------|-------------|
| 
| **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 |
| **btaB** | B12 uptake | 89 | btaB, tnaA; epr, receptor for vitamin B12, E. coli, and bacteriophage BFP23 | A, 53, 56, 57, 84, 270, 398 |
| **btaC** | B12 uptake | 37 | Vitamin B12 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 |
| **cct** | 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 |
| **chIA** | Chlorate | 17 | narA; nitrate reductase and formate dehydrogenase activity; molybdenum-containing factor | A, 381 |
| **chIB** | Chlorate | 86 | narB; nitrate reductase and formate dehydrogenase activity; molybdenum-containing factor | A, 78, 305, 381 |
| **chIC** | Chlorate | 27 | narC; nitrate reductase (EC 1.7.99.4) A- (<a>), subunit, structural gene | A, 128, 381 |
| **chID** | Chlorate | 17 | narD; nitrate reductase and formate dehydrogenase activity; insertion of molybdenum-containing factor | A, 584 |
| **chIE** | Chlorate | 18 | narE; nitrate reductase (EC 1.7.99.4) C- (<gamma>), subunit, cytochrome b1 | A, 381 |
| **chIF** | Chlorate | (27) | Formate dehydrogenase (EC 1.2.2.1) structural gene | A |
| **chIG** | Chlorate | 0 | Nitrate reductase and formate dehydrogenase activity | A |
| **cir** | Colicin I resistance | 44 | fuaA; production of colicin I receptor affected | A, 120, 494, 582 |
| **cls** | 27 | Cardiolipin synthase activity | 485 |
| **cmIA** | 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<sup>++</sup> transport, system I | 473 |
| **corB** | Cobalt resistance | 96 | Mg<sup>++</sup> transport, system I | 473 |
| **crp** | 73 | cap; cyclic AMP receptor protein | A |
| **crr** | 52 | Catabolite repression resistance | 297, 523 |
| **cxt** | 6 | ccr; 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** | 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 synthetase (EC 4.2.99.3) | 161 |
| **cysR** | 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 |

References: *A, 27; A, 120; A, 297, 305, 473; A, 397, 476, 477, 569; A, 584; A, 78, 305, 381; A, 128, 381; A, 310; A, 204, 303; A, 162, 628; A; A; A; A; A; A, 120, 494, 582; 485; 473; 297, 523; A, 310; A, 284; A, 204, 303; A, 162, 628; A; A; A; A, 120, 494, 582; 485; 473; 297, 523; A, 310; A, 284; A; A; A; A; A; A; A; A.
### Table 1—Continued

| Gene symbol | Mnemonic                      | Map position (min) | Alternate gene symbols; phenotypic trait affected | References
|-------------|-------------------------------|-------------------|---------------------------------------------------|-----------
| dacB        | d-Alanine carboxypeptidase, fraction B; penicillin-binding protein 4 | 69                | 395, 502                                          | A, 28, 288 |
| dadR        | Regulatory gene for d-amino acid deaminases | 26                |                                                   | A, 571    |
| dam         | DNA adenine methylation       | 74                |                                                   | A, 28, 388 |
| dapA        | Diaminopimelate               | 53                |                                                   | A         |
| dapB        | Diaminopimelate               | 0                 |                                                   | A         |
| dapC        | Diaminopimelate               | 3                 |                                                   | A         |
| dapD        | Diaminopimelate               | 4                 |                                                   | A         |
| dapE        | Diaminopimelate               | 53                |                                                   | A         |
| dcd         | (45) 2'-Deoxyctydine 5'-triphosphate deaminase (EC 3.5.4.-) activity |                | 179, 444a                                         | A         |
| dcm         | mec; DNA cytosine methylation | 43                |                                                   | A, 28     |
| dcp         | Dipeptidyl carboxypeptidase    |                  |                                                   | 134       |
| dctA        | Uptake of C, dicarboxylic acids | 79               |                                                   | A         |
| dctB        | Uptake of C, dicarboxylic acids | 16               |                                                   | A         |
| ddi         | d-Alanine:d-alanine ligase    | 2                 |                                                   | A, 164    |
| del         | Frequency of IS1-mediated deletion | 61            |                                                   | 445       |
| deoA        | Deoxyribose                   | 99                |                                                   | A, 6, 300 |
| deoB        | Deoxyribose                   | 99                |                                                   | A, 6, 300 |
| deoBo       | OP3; operator sequence for deoBD, regulator unknown | 99             |                                                   | 6, 69, 70 |
| deoBp       | P3; promoter sequence for deoBD | 99                |                                                   | 6, 69, 70 |
| deoC        | Deoxyribose                   | 94                |                                                   | 6, 300    |
| deoCl        | cytO; operator sequence for deoCABD regulated by cytR | 99            |                                                   | 6, 300    |
| deoC2o      | deoO; operator sequence for deoCABD regulated by deoR | 99            |                                                   | 6, 300    |
| deoC1p      | cytP; promoter sequence for deoCABD | 99            |                                                   | 6, 300    |
| deoC2p      | deoP; promoter sequence for deoCABD | 99            |                                                   | 6, 300    |
| deoD        | ppu; purine-nucleoside phosphorylase (EC 2.4.2.1) | 99            |                                                   | A, 6, 300 |
| deoDp       | P5; promoter sequence for deoD | 99                |                                                   | 70        |
| deoR        | NucR; regulatory gene for deo operon | 18              |                                                   | A, 630    |
| dgd         | d-Galactose dehydrogenase production | 69            |                                                   | A         |
| dgk         | D-galactonate                  | 91                |                                                   | 502       |
| dgoA        | d-Galactonate                  | 82                |                                                   | 102       |
| dgoD        | Galactonate dehydratase (EC 4.2.1.6) | 82            |                                                   | 102       |
| dgoK        | 2-Oxo-3-deoxygalactonate 6-phosphate aldolase (EC 4.1.2.21) | 82            |                                                   | 102       |
| dgoR        | Regulatory gene                | 82                |                                                   | 102       |
| dgoT        | Galactonate transport          | 82                |                                                   | 102       |
| divE        | Membrane protein biosynthesis  | 22                |                                                   | 539       |
| dnaA        | DNA biosynthesis; initiation and chain elongation | 82            |                                                   | A, 2, 233, 338, 419 |
| dnaB        | exB, groP, grpA; DNA biosynthesis; chain elongation | 91            |                                                   | A, 408, 527, 541, 654, 696, R |
| dnaC        | dnaD; DNA biosynthesis; initiation and chain elongation | 99            |                                                   | A         |
| dnaE        | 4polC; DNA biosynthesis; DNA polymerase III component; mutator activity | 4              |                                                   | A, 261, 325 |
| dnaG        | DNA biosynthesis; primase      | 66                |                                                   | A, 87, 521 |
| dnaI        | DNA biosynthesis               | 39                |                                                   | A         |
| dnaJ        | DNA biosynthesis; primase      | 39                |                                                   | A         |
| dnaK        | groPAB, groPC; DNA biosynthesis | 0              |                                                   | 527, 528, 601, 684 |
| dnaL        | DNA biosynthesis; DNA biosynthesis | 28            |                                                   | |
| dnaM        | DNA biosynthesis; initiation | 85                |                                                   | A         |
| dnaQ        | Mutator activity and DNA biosynthesis; may be mutD | 5              |                                                   | 261       |
| dnaT        | DNA biosynthesis; termination | 99                |                                                   | 346       |
| dnaW        | DNA biosynthesis               | 10                |                                                   | 50        |
| dnaX        | DNA biosynthesis               | 10                |                                                   | 248       |
| dnaY        | DNA biosynthesis               | 10                |                                                   | 248       |
| dnaZ        | DNA biosynthesis; DNA elongation factor II | 10          |                                                   | A, 653, 655 |
| dpp         | Transport of dipeptides        | (13)              |                                                   | A, L      |
| dsdA        | d-Serine deaminase             | 50                |                                                   | A, 238    |
| dsdAi       | Initiator sequence for dsdA    | 50                |                                                   | 238       |
| dsdAo       | Operator sequence for dsdA     | 50                |                                                   | 238       |
| dsdC        | Regulatory gene for dsdA       | 51                |                                                   | A         |
| dsi         | dUTPase                        |                    |                                                   |          |
| dso         | Resistance or sensitivity to methylene blue | 100           |                                                   | A, 8, 255, 629 |

References:
- A: 87, 521, 28, 288, 419, 654, 696, R
- B: 408, 527, 541, 654, 696, R
- C: 195, 527, 528, 684
- D: 527, 528, 601, 684
- E: 527, 528, 684
- F: 554
- G: 669
- H: 346
- I: 539
- J: 261
- K: 541
- L: 325
- M: 653, 655
- N: 261
- O: 346
- P: 28, 288
- Q: 654
- R: 261
- S: 346
- T: 28, 288
- U: 654
- V: 696
- W: 261
- X: 325
- Y: 653, 655
- Z: 238
### Table 1—Continued

| Gene symbol | Mnemonic | Map position (min) | Alternate gene symbols; phenotypic trait affected | References |
|-------------|----------|-------------------|-------------------------------------------------|------------|
| ebgA        |          | 67                | Second β-galactosidase activity appears as result of mutations | A, 20, 220 |
| ebgR        |          | 67                | Regulatory gene                                  | 220        |
| ecFA        |          | 65                | Pleiotropic effects on active transport coupling to metabolic energy; may be metC | 364, 365, 626 |
| ecFB        |          | 87                | Generalized resistance to aminoglycoside antibiotics; coupling of metabolic energy to active transport | 624        |
| edA         |          | 41                | kdgA, kga; 2-keto-3-deoxyglucuronic 6-phosphate aldolase (EC 4.1.2.14) | A          |
| fend        |          | 41                | Phosphogluconate dehydrogenase (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-dihydroxybenzolate dehydrogenase | A, 662, O  |
| entB        | Enterochelin | 13               | 2,3-Dihydro-2,3-dihydroxybenzolate synthetase     | A, 662, O  |
| entC        | Enterochelin | 13               | Isocitrate 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, 286, 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 to sensitivity to colicins | A, 120, 495 |
| exbC        |          | 58                | Uptake of enterochelin; resistance to 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 dehydrogenase (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 2.3.1.14) | J          |
| fabA        | Fatty acid degradation | 86       | oldA; thiolase I (EC 2.3.1.16) | A          |
| fabB        | Fatty acid degradation | 86       | oldB; 3-hydroxyacyl-CoA dehydrogenase (EC 1.1.1.35) | A          |
| fabD        | Fatty acid degradation | 40       | oldD; acyl-CoA synthetase (EC 6.2.1.3) | A, 652     |
| fabE        | Fatty acid degradation | 5        | Electron transport flavoprotein of beta-oxidation | A          |
| fabL        | Fatty acid degradation | 50       | Transport of long-chain fatty acids | 454        |
| fabR        | 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                | Fructose-1,6-diphosphatase (EC 3.1.3.11)          | A          |
| fec         | Iron     | 7                 | Citrate-dependent iron transport                 | 661        |
| fep         | Iron     | 13                | cbr, ctb, feuB; receptor for ferrienterochelin and colicins | A, 120, 406, 492, 494, 495, 662, 664, O |
| fes         | Iron     | 13                | Enterochelin-dependent iron transport            | A, 120, 495, 662, 664, O |
| fex         | Iron     | 100               | Expression of F factor                           | 362        |
| firA        | RNA polymerase function | 4        |                                                   | 350        |
| Gene symbol | Mnemonic | Map position (min) | Alternate gene symbols; phenotypic trait affected | References |
|-------------|----------|-------------------|--------------------------------------------------|------------|
| 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         |
| 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                 | 318        |
| 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        |
| fbaA        | Flagella | 24                | Flagellar synthesis                             | 318        |
| fbaB        | Flagella | 42                | Flagellar synthesis                             | 318        |
| fbaC        | Flagella | 43                | Flagellar synthesis                             | 318        |
| ffrA        | Fluorelocine | 100            | Metastable gene affecting surface properties, pilation, and colonial morphology | 135a       |
| flu         | Flurfing | 43                | Metastable gene affecting surface properties, pilation, and colonial morphology |            |
| fnr         |          | 29                | frdB, nirR; fumarate, nitrate, and nitrite reductases, hydrogenase, and cytochrome c_{55} activities affected | A, 344     |
| folA        | Folate   | 1                 | tmra; dihydrofolate reductase (EC 1.5.1.3); trimethoprim resistance | A, 556, 557 |
| folB        | Folate   | 1                 | tmraB; 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     |
| ftaA        |          | 2                 | Anomalous filamentous growth                    | A, 164, 380, 646, 656 |
| ftaE        |          | 73                | Anomalous filamentous growth                    | 598        |
| ftaH        |          | 69                | Anomalous filamentous growth                    | 536        |
| fus         | Fucose   | 60                | prd; l-fucose utilization                      | A, 218     |
| fusA        | Fusic acid | 73               | FrdA; protein chain elongation factor G         | 73, 184, 367 |
| fusB        | Fusic 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-amino butyrate                   | 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     |
| galElp      | Galactose | 17                | Promoter sequence for galETK, cyclic AMP dependent | 137, 436   |
| galElp2     | 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                | Fgal; galactose permease activity               | 513        |
| galR        | Galactose | 61                | Rgal; regulatory gene; represor of galETK operon | A         |
| galT        | Galactose | 17                | galB; galactose-1-phosphate uridylyltransferase  | 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 |
| Gene symbol | Mnemonic | Map position (min) | Alternate gene symbols; phenotypic trait affected | References |
|-------------|----------|-------------------|-----------------------------------------------|------------|
| guaC        | Galactitol | 46                | Regulatory gene                                | 359, 361   |
| guaD        | Galactitol | 46                | Galactitol-1-phosphate dehydrogenase           | 359, 361   |
| gdh         |          | 27                | Glutamate dehydrogenase                        | 467        |
| glc         | Glycolate | 64                | Utilization of glycolate; maltase synthase G   | 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 dehydrogenase (EC 2.7.7.27)| A, 352     |
| gik         |          | 51                | Guanine kinase (EC 2.7.1.2)                    | A          |
| glnS        | Gluconamine | 92               | Glucoamminephosphate isomerase (EC 5.3.1.19)   | A, I       |
| gltA        | Glutamine | 82                | Guanamine synthetase (EC 6.3.1.2)              | A, 305     |
| gltD        | Glutamine | 4                 | Uridyltransferase                              | 51         |
| glnF        | Glutamine | 69                | Regulation of glutamine synthetase production  | 467        |
| glnS        | Glutamine | 15                | Glutaminyl-tRNA synthetase (EC 6.1.1.12)       | A          |
| glnT        | Glutamine | 77                | Affects levels of glutamine tRNA1 and glutamine synthetase | 426        |
| glpU        | Glutamine | 15                | supE, Su2, suH; glutamine tRNA2                | 269, S     |
| glpV        | 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          |
| glpR        | Glycerol phosphate | 48            | Glycerol-3-phosphate transport system          | A, 413, 566|
| glnA        | Glutamate | 16                | glut; citrate synthase                         | A          |
| glnB        | Glutamate | 69                | aspB; glutamate tRNA1                          | A, 467     |
| glnE        | Glutamate | 80                | Glutamyl-tRNA synthetase; possible regulatory subunit | A          |
| glnH        | Glutamate | 22                | Requirement                                    | A          |
| glnM        | Glutamate | 43                | Guanamyl-tRNA synthetase                       | A          |
| glnR        | Glutamate | 92                | Regulatory gene for glutamate permease         | A          |
| glnS        | Glutamate | 82                | Glutamate permease                             | A          |
| glnT        | Glutamate | 82                | glnT; operator sequence for glnT; growth on glutamate as sole source of carbon | A          |
| glnU        | Glutamate | 89                | tglB; glutamate tRNA2; in rnrB operon          | 268, 368, 379, 424, 672, 675 |
| glnV        | Glutamate | 84                | tglC; glutamate tRNA2; in rnrC operon          | 268, 368, 424 |
| glnW        | Glutamate | 80                | tglE; glutamate tRNA2; in rnrF operon          | 268, 424   |
| glnX        | Glutamate | 82                | 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                | suA36, sumA, sup158; glycine tRNA2              | A, 82, 113, 515, 517, 518, 675 |
| glyU        | Glycine  | 61                | suA36, suD, sumB, sup7; glycine tRNA1           | A          |
| glyV        | Glycine  | 96                | suA58, suA78; glycine tRNA3 (duplicate gene)   | A, 434     |
| glyW        | Glycine  | 41                | suA38, suA78; glycine tRNA3 (duplicate gene)   | A          |
| gntM        | Glucanone | 75                | Glucose-6-phosphate dehydrogenase (EC 1.1.1.43)| A          |
| gntR        | Glucanone | 75                | usgA; transport and phosphorylation of glucanone | A, 23     |
| gntS        | Glucanone | 96                | Second system for transport, and possibly phosphorylation, of glucanone | 23         |
| gpp         |          | 84                | Guanine pentaphosphatase activity              | 581        |
| gpaA        | Guanaine | 81                | is-Glycerol-3-phosphate dehydrogenase [NAD(P)*] (EC 1.1.1.94) | A, 91     |
| gpt         |          | 6                 | gpp, gpx; guanine-hypoxanthine                 | A, 257, 260|
| grpD        |          | 71                | Phosphoribosyltransferase (EC 2.4.2.8)         | A          |
| grpE        |          | 56                | Phosphoribosyltransferase (EC 2.4.2.8)         | A          |
| gsa         |          | 13                | Guanine kinase                                 | 291        |
| gsaA        | Guanine  | 53                | guaA; GMP synthetase (EC 6.3.4.1)              | A, 474, 560, 631 |
| gsaB        | Guanine  | 53                | Promoter sequence for gsaA                     | 181        |
| gsaBr       | Guanine  | 53                | guaA; IMP dehydrogenase (EC 1.2.1.14)          | A, 474, 560, 631 |
| gsaBo       | Guanine  | 53                | Operator sequence for gsaBA                    | A          |

TABLE 1—Continued

**Gene symbol**: Symbol used to represent the gene in the linkage map.

**Mnemonic**: A mnemonic is a word or phrase that is used as a memory aid.

**Map position (min)**: The map position of the gene in minutes.

**Alternate gene symbols; phenotypic trait affected**: Additional gene symbols or the phenotype affected by the gene.

**References**: A list of references that support the information provided in the table.
| Gene symbol | Mnemonic | Map position (min) | Alternate gene symbols; phenotypic trait affected | References |
|-------------|----------|-------------------|--------------------------------------------------|------------|
| guaB        | Guanine  | 53                | Promoter sequence for guaBA                      | 560        |
| guaC        | Guanine  | (99)              | GMP reductase (EC 1.6.6.5)                       | A          |
| gyrB        | Gyrase   | 73                | Utilization of methyl-β-d-glucuronic; possibly identical to crp | A          |
| gyrC        | Gyrase   | (18)              | Utilization of methyl-β-d-glucuronic              | A          |
| gyrD        | Gyrase   | (67)              | Utilization of methyl-β-d-glucuronic              | 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                | 8-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; Uroporphyrin I synthase (EC 4.3.1.8) activity | 401        |
| hemD        | Hemin    | 84                | Uroporphyrin III cosynthase                       | 85         |
| hemE        | Hemin    | 90                | hemC; Uroporphyrin decarboxylase (EC 4.1.1.37) activity | A          |
| hemF        | Hemin    | 17                | popB, sec; coproporphyrin III oxidase (EC 1.3.3.3) activity | A          |
| hemH        | Hemin    | 11                | hemG, popA; ferrochelatase (EC 4.99.1.1) activity | A          |
| hisO        | Histidine| 44                | N-(5'-Phospho-L-ribosylformimino)-5-amino-1-(5'-phosphoribosyl)-4-imidazolecarboxamide isomerase (EC 5.3.1.16) activity | 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) activity | A          |
| hisE        | Histidine| 44                | Phosphoribosyl-ATP pyrophosphohydrolase            | A          |
| hisF        | Histidine| 44                | Cyclase                                           | A          |
| hisG        | Histidine| 44                | ATP phosphoribosyltransferase (EC 2.4.2.17) activity | A          |
| hisGa       | Histidine| 44                | Attenuator sequence in hisG leader region         | 29, 138    |
| hisGe       | Histidine| 44                | Leader region; regulation of transcription of his operon activity | 29, 138    |
| hisGo       | Histidine| 44                | hisG; operator sequence for his operon            | A          |
| hisH        | Histidine| 44                | Amido transferase                                 | A          |
| hisI        | Histidine| 44                | Phosphoribosyl-AMP cyclohydrolase (EC 3.5.4.19) activity | A          |
| hisR        | Histidine| (84)              | hisT; histidine tRNA                               | 269        |
| hisS        | Histidine| 54                | Histidyl-tRNA synthetase (EC 6.1.1.21) activity    | 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              | his, 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              | his; specificity determinant for hsdM and hsdR activities | A          |
| hyd         |          | 57                | Hydrogenase activity                              | 478        |
| iap         |          | 59                | Altered isozyme pattern of alkaline phosphatase   | 440        |
| icsR        |          | 25                | Inositol dehydrogenase, NADP" specific (EC 1.1.1.42) activity | 18         |
| ileS        | Isoleucine| 0                 | Isoeucyl-tRNA synthetase (EC 6.1.1.5) activity    | A, 176     |
| ileT        | Isoleucine| 86                | tiiA; isoleucine tRNA1; in rrnA operon            | 268, 424   |
| ileU        | Isoleucine| 70                | tiiD; isoleucine tRNA1; in rrnD operon            | 268, 424, 688 |
| iloA        | Isoleucine-valine | 84               | ile; threonine deaminase (EC 4.2.1.16) activity | A, 26, 96, 402, 577 |
| iloB        | Isoleucine-valine | 82               | Acetolactate synthase I (EC 4.1.3.18), valine sensitive | A, 213, 448 |
| iloC        | Isoleucine-valine | 84               | iloA; ketol-acid reductoisomerase (EC 1.1.1.86) activity | A, 26, 402, 578, 648 |
| iloD        | Isoleucine-valine | 84               | iloB; dihydroxyacid dehydratase (EC 4.2.1.9) activity | A, 26, 96, 402, 577 |
| iloE        | Isoleucine-valine | 84               | iloC, iloJ; branched-chain-amino-acid aminotransferase (EC 2.6.1.42) activity | A, 26, 96, 357, 402, 577 |
| iloF        | Isoleucine-valine | 54               | Affects production of valine-resistant acetolactate synthase activity | A          |
| iloG        | Isoleucine-valine | 84               | Acetolactate synthase II (EC 4.1.3.18), valine insensitive | A, 26, 125, 213, 479, 576 |
| iloH        | Isoleucine-valine | 84               | Acetolactate synthase III (EC 4.1.3.18), valine sensitive | A, 213     |
| iloI        | Isoleucine-valine | 84               | Acetolactate synthase III (EC 4.1.3.18), valine sensitive | A, 213     |
| iloO        | Isoleucine-valine | 84               | Locus affecting expression of iloG activity       | A, 26, 96, 479, 576 |
| iloY        | Isoleucine-valine | 84               | Positive regulatory locus for iloC activity       | 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)* | Alternate gene symbols; phenotypic trait affected | References* |
|-------------|----------|---------------------|--------------------------------------------------|-------------|
| kbA         | K-polysaccharide | 61 Acidic polysaccharide capsule (K) antigen | A, B, N |
| kagA        | Kasugamycin | 1 RNA methylase for tRNA | A, B, N |
| kagB        | Kasugamycin | 34 Second-step (high-level) resistance to kasugamycin | A, B, N |
| kagC        | Kasugamycin | 12 Kasugamycin resistance; affects ribosomal protein S2 | 685 |
| lacA        | Lactose | 8 | a, lacA; galactose 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 |
| lacIp       | Lactose | 8 | y; galactoside permease (M protein) | A, 171, 254 |
| lacZ        | Lactose | 8 | z; β-β-galactosidase (EC 3.2.1.23) | A, 169 |
| lacZo       | Lactose | 8 | lacO; operator sequence for lac operon | A, 37, 135, 382 |
| lacZp       | Lactose | 8 | lacZp; promoter sequence for lac operon | A, 135, 382 |
| lamB        | Lambda | 91 | maltB; 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-Isopropylmalyl synthase (EC 4.1.3.12) | A |
| leuB        | Leucine | 2 | 2-Isopropylmalyl dehydrogenase (EC 1.1.1.85) | A |
| leuC        | Leucine | 2 | α-Isopropylmalyl isomerase subunit | A |
| leuD        | Leucine | 2 | α-Isopropylmalyl isomerase subunit | A |
| leuK        | Leucine | 18 | Regulation of biosynthetic enzymes for leucine, isoleucine-valine, histidine, and tryptophan | A, 64 |
| leuR        | Leucine | 78 | Level of leucyl-tRNA synthetase affected | 620 |
| leuS        | Leucine | 15 | Leucyl-tRNA synthetase (EC 6.1.1.4) | A, C |
| leuSc        | 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         | Levallophan | (9) | Resistance to levallophan | 111 |
| lexA        | Leucine | 91 | extrA, spr, tsd, umuA; resistance or sensitivity to X rays and UV | A, 304, 465 |
| ligA        | Ligase | 52 | dnaA, pdeC; DNA ligase | A, 204, 262, 538 |
| ligAo       | Ligase | 52 | lap; possibly operator sequence for ligA | A |
| ligAp       | Ligase | 52 | lap; possibly promoter sequence for ligA | A |
| linB        | Lincomycin | (28) | High-level resistance to lincomycin | A |
| lip         | Lipoate | 14 | Requirement | A |
| irr         | Lipoate | (12) | Increased sensitivity to lincomycin, to erythromycin, or to both | A |
| lit         | Phage T4 late gene expression | 25 | | 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 | leu; regulatory gene, high-affinity branched-chain amino acid transport system | 10, 498 |
| Gene symbol | Mnemonic | Map position (min) | Alternate gene symbols; phenotypic trait affected | References |
|-------------|----------|-------------------|--------------------------------------------------|------------|
| lon         | Long form | 10                | capR, deg, dir, muc; filamentous growth; radiation, sensitivity; regulation of gal operon; capsular polysaccharide synthesis | A, 42, 188, 205 |
| lipA        | Lipopolysaccharide core | 6               | tfrA; lipopolysaccharide core synthesis; resistance to phages T4, T7, and P1; deficiency in conjugation | A, 232 |
| lipB        | Lipopolysaccharide core | (65)            | pon; lipopolysaccharide core synthesis | A |
| lpp         | Lipoprotein | 3               | dhli; lipopide dehydrogenase (NADH) (EC 1.6.4.3) | A, 345 |
|              |           | 36               | mIgA; murein lipoprotein structural gene | 252, 277, 366, 519, 602, 667, 682, 683 |
| latR        |          | 20               | Leucine-specific transport | 10 |
| lysA        | Lysine    | 61               | Diaminopimelate decarboxylase (EC 4.1.1.20) | A |
| lysC        | Lysine    | 91               | apty; aspartokinase III | A |
| lysCo       | Lysine    | 91               | Operator sequence for lysC | 77 |
| lysT        | Lysine    | 16               | sulf, sup L; lysine tRNA | 269, S |
| lysX        | Lysine    | 60               | Lysine excretion | A |
| mac         | Macrolide | (26)             | Erythromycin growth dependence | A |
| majA        |          | 1                | Maintenance of F-plasmids | A, 643, 644 |
| majB        |          | 2                | Maintenance of F-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, 564 |
| malP        | Maltose   | 75               | malA; maltodextrin phosphorylase (EC 2.4.1.1) | A |
| malP1       | Maltose   | 75               | malP, malA: initiation sequence for malPQ | A, 123 |
| malQ        | Maltose   | 75               | malA; amylo maltase (EC 2.4.1.23) | A |
| malT        | Maltose   | 75               | malA; positive regulatory gene for malPQ, malEFG, and malK BamB | A, 123 |
| manA        | Mannose   | 36               | Mannosephosphate isomerase (EC 5.3.1.8) | A |
| manC        | Mannose   | (87)             | mni; d-mannose isomerase regulation; utilization of D-mannose | 596 |
| mdh         |          | 70               | Malate dehydrogenase (EC 1.1.1.37) | A |
| metA        | Melibiose | 93               | met-7; a-galactosidase (EC 3.2.1.22) | A |
| metB        | Melibiose | 93               | met-4; thiomethylgalactoside permease II | A |
| menA        | Menaquinone | 88             | Conversion of 1,4-di-hydroxy-2-naphthoate to demethylmenaquinone | A, 687 |
| menB        | Menaquinone | 48             | Conversion of 2-succinylbenzoate to 1,4-di-hydroxy-2-naphthoate | 687, K |
| menC        | Menaquinone | 48             | Conversion of chorismate to 2-succinylbenzoate | 216 |
| metA        | Methionine | 90               | metC; homoserine acetyltransferase (EC 2.3.1.31) | A |
| metB        | Methionine | 88               | met-1, met-1; cystathionine y-synthase (EC 4.2.99.9) | A |
| metC        | Methionine | 65               | Cystathionine y-lyase (EC 4.4.1.1) | A |
| metD        | Methionine | 5                | High-affinity uptake of D- and L-methionine | A, 261 |
| metE        | Methionine | 85               | met-B12; tetrahydropropylglycylaminate methyltransferase (EC 2.1.1.14) | A |
| metF        | Methionine | 88               | met-2, met-7; 5,10-methylene tetrahydrofolate reductase (EC 1.1.1.68) | A |
| metG        | Methionine | (46)             | Methionyl-tRNA synthetase | A, 79a, 509 |
| metH        | Methionine | 90               | B2-dependent homocysteine-N7-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 | 269, S |
| metY         | Methionine | (68)             | Methionine tRNA2 | 269 |
| metZ         | Methionine | (61)             | Methionine tRNA1 | 269 |
| mglA        | Methyl-galactoside | 45             | mglP; methyl-galactoside transport and galactose taxis | A, 514 |
| mglB        | Methyl-galactoside | 45             | methylgalactose-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             | Mg2+ transport, system II | 473 |
| minA        | Minicell  | 10               | Formation of minute cells containing no DNA | A |
| Gene symbol | Mnemonic | Map position (min) | Alternate gene symbols; phenotypic trait affected | References |
|------------|----------|-------------------|-------------------------------------------------|------------|
| 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   | A          |
| mraB       | Murein   | 2                 | biogenesis                                       | A          |
| mtaB       | Murein   | 3                 | ponA; penicillin-binding protein 1A              | 602        |
| map        | Male-specific phage | 100 | Sensitivity or resistance of male strains to male-specific phages R17 and μ2 | 70        |
| mtaA       | Mannitol | 80                | Mannitol-specific enzyme II of phophotransferase system | A, 359, 360 |
| mtaC       | Mannitol | 80                | Regualtory locus                                | A, 359     |
| mtdD       | Mannitol | 80                | Mannitol-1-phosphate dehydrogenase (EC 1.1.1.17) | A, 359     |
| mtr        | Methyltrypotphan | 68 | Resistance to 5-methyltrypotphan                | A, 311     |
| murC       | Murein   | 2                 | L-Alanine-adding enzyme                          | A          |
| murE       | Murein   | 2                 | meso-Diaminopimelate-adding enzyme               | A, 164     |
| murF       | Murein   | 2                 | d-alanine-l-amine-adding enzyme                  | A, 184     |
| 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, 875, 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          |
| naiA       | Nalidixic acid | 48 | See gyrA                                         | A          |
| naiB       | Nalidixic acid | 57 | Resistance or sensitivity to nalidixic acid     | A          |
| naiC       | Nalidixic acid | 82 | nald; resistance or sensitivity to nalidixic and piromidic acids | 275       |
| ndh        | NAD dehydrogenase complex | 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 |
| nfaA       | Nitrofurazone sensitivity | (22) | Nitrofurazone reductase I activity              | 399        |
| nfaB       | Nitrofurazone sensitivity | (11) | Nitrofurazone reductase I activity              | 399        |
| nirA       | Nitrite reductase | 29 | NADH-nitrite reductase (EC 1.6.6.4) activity and cytochrome c552 | 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          |
| Gene symbol | Mnemonic | Map position (min) | Alternate gene symbols; phenotypic trait affected | References |
|-------------|----------|-------------------|-------------------------------------------------|------------|
| nrdA        | dnaF; ribonucleoside diphosphate reductase (EC 1.17.4.1), subunit B1 | 48 | | A, 179 |
| nrdB        | Ribonucleoside diphosphate reductase (EC 1.17.4.1), subunit B2 | 48 | | A, 179 |
| nupC        | Transport of nucleosides, except guanosine | 52 | | 432 |
| nupG        | Transport of nucleosides | 65 | | 432 |
| nusA        | Expression of phase λ N gene function | 68 | | 172 |
| nusB        | Expression of phase λ N gene function | 10 | | 173 |
| nuvA        | 9 | Uridine thiolation factor A activity | 372, 621 |
| nuvC        | 9 | 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, 284, 385 |
| ompB        | Outer membrane protein | 74 | cry, kmt; production of outer membrane proteins 1a and 1b (a and b; c) | 34, 80, 221, 246, 496, 537, 639 |
| ompC        | Outer membrane protein | 47 | meoA, par; outer membrane protein 1b (b; c), structural gene | 32, 167, 246, 266, 496, 546, 632, 638 |
| ompF        | Outer membrane protein | 21 | cmIB, coa, cry, tolF; outer membrane protein 1a (a; b, F), structural gene | 32, 80, 165, 166, 167, 266, 353, 540, 546, 639, 639, 1 |
| opp         | Oligopeptide transport | 83 | het, poh; origin of replication of chromosome | 157, 251, 391, 392, 400, 410, 414, 599, 641 |
| oriC        | Origin of replication | 83 | 642, 645, 680 |
| pabA        | p-Aminobenzoate | 74 | Requirement | A |
| pabB        | p-Aminobenzoate | 40 | Requirement | A, 652 |
| panA        | Pantothenate | 3 | Ketopantoate hydroyxymethyl 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 |
| phbA        | Penicillin-binding protein | 14 | Penicillin-binding protein 2 | 285, 586, 285 |
| pphB        | Penicillin-binding protein | 2 | ftsI, sep; penicillin-binding protein 3; septum formation | 164, 586, 602, 2Y |
| pcsA        | Pyridoxine | 81 | Cell division; chromosome segregation | 333, 335 |
| pdsA        | Pyridoxine | 1 | Requirement | A, 256 |
| pdsB        | Pyridoxine | 50 | Requirement | A, 91 |
| pdsC        | Pyridoxine | 20 | Requirement | A |
| pdsH        | Pyridoxine | 36 | Pyridoxine phosphate oxidase | A, 561 |
| pdsJ        | Pyridoxine | 55 | Requirement | A, 17 |
| pepD        | Peptides | 6 | pepH (carnosinase); peptide D, a dipeptidase | A, L |
| pepN        | Peptides | 21 | Peptidase N, an aminopeptidase | 351 |
| pfkA        | 6-Phosphofructokinase I (EC 2.7.1.11) | 88 | | A, 22, 466, 623 |
| pfkB        | Level of 6-phosphofructokinase II production; suppressor of pfkA | 38 | | A, 22 |
| pfkC        | Modifier of 6-phosphofructokinase activity | (58) | | A |
| plf         | Pyruvate formate lyase | 20 | | 637 |
| pg1         | Gluconeophosphatase isomerase (EC 5.3.1.9) | 91 | | A |
| pgk         | Phosphoglycerate kinase (EC 2.7.2.3) | 63 | | A, 278, 623 |
| pgl         | bld, 6-phosphogluconolactonase (EC 3.1.1.31) | 17 | | A |
| pglA        | Phosphoglucomutase (EC 2.7.5.1) | (15) | | A |
| pglB        | Phosphatidylglycerophosphate synthetase | 42 | | 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 phoshatase (EC 3.1.3.1) | A, 62, 276 |
| phoB        | Phosphate | 9 | phoC, phoT; positive regulatory gene for phoA and phoS | A, 62, 330, 491, 657 |
| phoR        | Phosphate | 9 | phoRa, R1pho; negative regulatory gene for phoA and phoS | A, 62, 330, 491, 657 |
| phoS        | Phosphate | 83 | phoR2A, R2pbo; periplasmic phosphate-binding protein | A, 338, 657, 670, I |
| phoT        | Phosphate | 83 | phoS; inorganic phosphate transport | A, I |
| phr         | Photoreactivation | 16 | Deoxyribodipryrimidine photolase (EC 4.1.99.3) | A, 531, 690 |
| Gene symbol | Mnemonic | Map position (min) | Alternate gene symbols; phenotypic trait affected | References |
|-------------|----------|-------------------|--------------------------------------------------|------------|
| *phxB* | Phi-X | 17 | Adsorption of φX174 | 433 |
| *pldB* | Pili | 98 | fm; formation of type 1 somatic pili | A, 604, 605 |
| *plcC* | Pili | 98 | fm; formation of type 1 somatic pili | A, 604, 605 |
| *pit* | Inorganic phosphate transport | 76 | Inorganic phosphate transport system | A |
| *pldA* | Phospholipid synthesis | 85 | | A |
| *psbA* | Phospholipid synthesis | 91 | Glycerol phosphate acyltransferase activity | A, 579, U |
| *pncA* | Pyridine nucleotide cycle | 39 | nac; nicotinamide deamidase (EC 3.5.1.19) | A, 652 |
| *pncH* | Pyridine nucleotide cycle | 39 | Hyperproduction of nicotinamide deamidase | A |
| *ppx* | Phosphoenolpyruvate | 89 | glu, asp; phosphoenolpyruvate carboxylyase (EC 4.1.1.31) | A, 56, 84, 110, 389 |
| *ppa* | Phosphoenolpyruvate | 37 | Phosphoenolpyruvate synthase | A |
| *prmB* | Pmr-1; methylation of 50S ribosomal subunit protein L1 | 71 | | |
| *proA* | Proline | 6 | proA; block before l-glutamate semialdehyde reductase | A |
| *proB* | Proline | 6 | proB; block before l-glutamate semialdehyde reductase | A |
| *proC* | Proline | 9 | proC, proA; probably Δ-pyrroline-5-carboxylate reductase | A |
| *proT* | Proline | 83 | Proline transport | 430 |
| *psd* | Phosphatidylserine | 94 | Phosphatidylserine decarboxylase | A, 234 |
| *psl* | Phosphatidylserine synthetase | 56 | Phosphatidylserine synthetase | 456, 500, 501 |
| *pts* | Inorganic phosphate transport system | 83 | Inorganic phosphate transport system | A, 642 |
| *pta* | Phosphotransacetylase | 49 | Phosphotransacetylase (EC 2.3.1.8) activity | 65 |
| *pth* | Peptidyl-tRNA hydrolase | 26 | Peptidyl-tRNA hydrolase | A |
| *pts* | Phosphotransferase system | 46 | Fructosephosphotransferase enzyme II | A, 7, 514 |
| *ptsG* | Phosphotransferase system | 24 | cat, CR, gpt, gptA, tgl, umg; glucosolphosphotransferase enzyme II | A, 152 |
| *ptsH* | Phosphotransferase system | 52 | cr, Hpr; phosphohistidineprotein-hexose phophotransferase (EC 2.7.1.69) | A, 204 |
| *ptsI* | Phosphotransferase system | 52 | cr; phosphotransferase system enzyme I | A, 204 |
| *ptsM* | Phosphotransferase system | 40 | gptB, mpi, pel, ptsX; mannosephosphotransferase enzyme II; penetration of phage λ | A, 147, 296 |
| *purA* | Purine | 94 | ades, Ades; adenylosuccinate synthetase (EC 6.3.4.4) | A |
| *purB* | Purine | 25 | ades; adenylosuccinate lyase (EC 4.3.2.2) | A |
| *purC* | Purine | 53 | ades; phosphoribosylaminomimidazole-succinocarboxamidine synthetase (EC 6.3.2.6) | A |
| *purD* | Purine | 89 | adth; phosphoribosylglycinamidine synthetase (EC 6.3.4.13) | A |
| *purE* | Purine | 12 | ades, ades, PurA; phosphoribosylaminomimidazolecarboxylase (EC 4.1.1.21) | A |
| *purF* | Purine | 49 | ades, purC; amidophosphoribosyltransferase (EC 2.4.1.14) | A |
| *purG* | Purine | 53 | adth; phosphoribosylformylglycinamidine synthetase (EC 6.3.5.3) | A, 474, 631 |
| *purH* | Purine | 89 | ades; phosphoribosylaminomimidazolecarboxamidine formyltransferase (EC 2.1.2.3) | A |
| *purI* | Purine | 55 | Phosphoribosylaminomimidazole synthetase (EC 6.3.3.1) | A |
| *putA* | Purine | 22 | | A, 204, 309, 310, 482 |
| *pyrA* | Pyrimidine | 9 | | A |
| *pyrB* | Pyrimidine | 96 | Aspartate carbamoyltransferase (EC 2.1.3.2), catalytic subunit | A |

TABLE 1—Continued
| Gene symbol | Mnemonic | Map position (min) | Alternate gene symbols; phenotypic trait affected | References |
|-------------|----------|-------------------|--------------------------------------------------|------------|
| pyrC        | Pyrimidine | 23                | Dihydro- orotate (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                | g3t; 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 |
| rac         |           | 37                | Unspecified membrane defect                       | A          |
| ranA        | Radiation sensitivity | (9) | Sensitivity to UV and X rays | A |
| ras         |           | 55                | Defect in RNA metabolism                          | 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, umuA, zah; general recombination; repair of radiation damage; induction of phage lambda | A, 149, 215, 304, 372, 391, 403, 405, 422, 531, 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 Pac prophage; exonuclease VIII           | A, 153, N  |
| recF        | Recombination | 82               | aurF; 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-ribonucleotidase                               | A          |
| rfe         | Rough      | (85)              | Synthesis of enterobacterial common antigen and O antigen | 546 |
| rff         | Rough      | (85)              | Synthesis of enterobacterial common antigen       | 545        |
| rhaA        | Rhamnose   | 87                | L-Rhamnose isomerase (EC 5.3.1.14)                | A          |
| rhaB        | Rhamnose   | 87                | Rhamnolokinase (EC 2.7.1.5)                       | A          |
| rhaC        | Rhamnose   | 87                | Regulatory gene                                   | A          |
| rhaD        | Rhamnose   | 87                | Rhamnolosephosphate aldolase (EC 4.1.2.19)       | A          |
| rho         |            | 84                | nizA, psu, rnaC; SulA, sun, tsu; transcription termination factor rho; polarity suppressor | A, 66, 115, 214, 274, 273, 274, 326, 507, 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            | staB; ribosomal modification                      | A, 294     |
### Table 1—Continued

| Gene symbol | Mnemonic | Map position (min)* | Alternate gene symbols; phenotypic trait affected | References* |
|-------------|----------|---------------------|--------------------------------------------------|-------------|
| 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         |
| rnt         | Ribonuclease | 14                      | Affects thermolability of 50S ribosomal subunit rnt, rntA; 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        | Ribosomoprotein, large | 62                      | Ribose phosphate isomerase (EC 5.3.1.6) (constitutive) | A           |
| rpiA        | Ribosomoprotein, large | 89                      | 50S ribosomal subunit protein L1 | A, 160, 368, 370, 488, 675 |
| rpiB        | Ribosomoprotein, large | 72                      | 50S ribosomal subunit protein L2 | A, 288, 299, 367 |
| rpiC        | Ribosomoprotein, large | 72                      | 50S ribosomal subunit protein L3 | A, 288, 299, 367 |
| rpiD        | Ribosomoprotein, large | 72                      | eryA; 50S ribosomal subunit protein L4 | A, 73, 288, 289, 367 |
| rpiE        | Ribosomoprotein, large | 72                      | 50S ribosomal subunit protein L5 | A, 288, 290, 367 |
| rpiP        | Ribosomoprotein, large | 72                      | 50S ribosomal subunit protein L6 | A, 288, 290, 367 |
| rpiI        | Ribosomoprotein, large | 95                      | 50S ribosomal subunit protein L9 | 284         |
| rpiJ        | Ribosomoprotein, large | 89                      | 50S ribosomal subunit protein L10 | A, 160, 371, 488, 674, 675 |
| rpiJp       | Ribosomoprotein, large | 89                      | P; promoter sequence for rplJLrpoBC operon | 160, 371, 488, 674 |
| rpiK        | Ribosomoprotein, large | 89                      | relC; 50S ribosomal subunit protein L11 | A, 39, 160, 368, 370, 475, 488, 674, 675 |
| rpiKp       | Ribosomoprotein, large | 89                      | P,L1; promoter sequence for rplKA | 488         |
| rpiL        | Ribosomoprotein, large | 89                      | 50S ribosomal subunit protein L7/L12 | A, 160, 368, 371, 446, 488, 674, 675 |
| rpiN        | Ribosomoprotein, large | 72                      | 50S ribosomal subunit protein L14 | A, 288, 290, 367 |
| rpiNp       | Ribosomoprotein, large | 72                      | P, promoter sequence for rplN operon | 487         |
| rpiO        | Ribosomoprotein, large | 72                      | 50S ribosomal subunit protein L15 | A, 288, 299, 290, 367 |
| rpiP        | Ribosomoprotein, large | 72                      | 50S ribosomal subunit protein L16 | A, 288, 367, 487 |
| rpiQ        | Ribosomoprotein, large | 72                      | 50S ribosomal subunit protein L17 | A, 288, 367 |
| rpiR        | Ribosomoprotein, large | 72                      | 50S ribosomal subunit protein L18 | A, 73, 288, 290, 367 |
| rpiS        | Ribosomoprotein, large | 56                      | 50S ribosomal subunit protein L19 | 312, 526    |
| rpiU        | Ribosomoprotein, large | 69                      | 50S ribosomal subunit protein L21 | 311, 614, 616 |
| rpiV        | Ribosomoprotein, large | 72                      | 50S ribosomal subunit protein L22 | A, 288, 367 |
| rpiW        | Ribosomoprotein, large | 72                      | 50S ribosomal subunit protein L23 | 288, 289, 367 |
| rpx         | Ribosomoprotein, large | 72                      | 50S ribosomal subunit protein L24 | A, 72, 288, 290, 367 |
| rplY        | Ribosomoprotein, large | 46                      | 50S ribosomal subunit protein L25 | 547         |
| rpmA        | Ribosomoprotein, large | 69                      | 50S ribosomal subunit protein L27 | 311, 614    |
| rpmB        | Ribosomoprotein, large | 81                      | 50S ribosomal subunit protein L28 | 282         |
| Gene symbol | Mnemonic | Map position (min) | Alternate gene symbols; phenotypic trait affected | References |
|-------------|----------|-------------------|--------------------------------------------------|------------|
| 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, 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, str, 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, 236, 238, 368, 371, 446, 674, 675 |
| rpoD        | RNA polymerase | 67 | alt; RNA polymerase (EC 2.7.7.6), ε subunit | 210, 239, 236, 439, 493a, 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, 627 |
| rpsC        | Ribosomal protein, small | 72 | 30S ribosomal subunit protein S3 | A, 288, 367 |
| rpsD        | Ribosomal protein, small | 72 | rmaA, 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, 369, 659 |
| rpsI        | 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, 290, 367, 487, 660 |
| rpsLp       | Ribosomal protein, small | 72 | F. sub; 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 rrfB operon | 368, 672, 675 |
| rrfC        | rRNA, 5S | 84 | 5S rRNA gene of rrfC operon | 668 |
| rrlB        | rRNA, 23S | 89 | 23S rRNA gene of rrlB operon | 368, 672, 675 |
| rrlC        | rRNA, 23S | 84 | 23S rRNA gene of rrlC operon | 299, 668 |
| rrdD        | rRNA, 23S | 72 | 23S rRNA gene of rrdD operon | 686 |
| rrdG        | rRNA, 23S | 56 | 23S rRNA gene of rrdG operon | 694 |
| rnaA        | rRNA | 86 | cqsa; rRNA operon; see rfa, rla, rraA, ileT, and alaT | A, 55, 124, 288, 307, 640 |
| Gene symbol | Mnemonic | Map position (min) | Alternate gene symbols; phenotypic trait affected | References |
|-------------|---------|-------------------|-------------------------------------------------|------------|
| rrsB        | rRNA    | 89                | cqsE, rraB; rRNA operon; see rrfB, rrfB, rrsB, and gltT | A, 55, 307, 368, 640, 672, 675 |
| rrsC        | rRNA    | 84                | cqsB, rraB, rraB; rRNA operon; see rrfC, rrfC, rrsC, gltU, aspT, and trpT | A, 55, 299, 307, 423, 425, 640, 668 |
| rrsD        | rRNA    | 72                | cqsD; rRNA operon; see rrfD, rrfD, rrsD, ileU, and alaU | 55, 298, 307, 640, 688, 689 |
| rrsE        | rRNA    | 90                | rraD; rRNA operon, see rraE, rraE, rraE, and gltV | 55, 124, 673 |
| rrsF        | rRNA    | 74                | cqsC, rraC; rRNA operon; see rrfF, rrfF, and rrsF | 55, 640 |
| rrsG        | rRNA    | 56                | rRNA operon; see rraG and rrsG | 55, 694 |
| rrsA        | rRNA, 16S | 86              | 16S RNA gene of rraA operon | 124 |
| rrsA1p      | rRNA, 16S | 86              | Promoter sequence for rraA operon | 124 |
| rrsA2p      | rRNA, 16S | 86              | Promoter sequence for rraA operon | 124 |
| rrsB        | rRNA, 16S | 89              | 16S RNA gene of rraB operon | 63, 368, 672, 675 |
| rrsC        | rRNA, 16S | 84              | 16S RNA gene of rraC operon | 295, 668 |
| rrsD        | rRNA, 16S | 72              | 16S RNA gene of rraD operon | 688, 689 |
| rrsD1p      | rRNA, 16S | 72              | Promoter sequence of rraD operon | 689 |
| rrsD2p      | rRNA, 16S | 72              | Promoter sequence of rraD operon | 689 |
| rrsE        | rRNA, 16S | 90              | 16S RNA gene of rraE operon | 124 |
| rrsE1p      | rRNA, 16S | 90              | Promoter sequence for rraE operon | 124 |
| rrsE2p      | rRNA, 16S | 90              | Promoter sequence for rraE operon | 124 |
| rrsG        | rRNA, 16S | 56              | 16S RNA gene of rraG operon | 694 |
| rrs          | 89            |                   | ts-5; uncharacterized growth defect | A, 39, 370 |
| ruw         |          | 41              | filament formation and sensitivity to UV radiation | A |
| sboA        |          | 30              | Regulatory gene affecting recE; locus of Rac prophage | A, D |
| sboB        |          | 44              | sonA; 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 |
| serD        | Serine | 2              | Level of seryl-tRNA synthetase | 620 |
| serE        | Serine | 20              | Seryl-tRNA synthetase (EC 6.1.1.11) | A |
| serG        | Serine | 20              | serO; operator sequence for serS | A |
| serI        | Serine | 168             | Serine tRNA1 | 269 |
| serV        | Serine | 61              | Serine tRNA3 | 269 |
| shA         | Shikimate | 43            | Shikimate and dehydroshikimate permease | A |
| sloB        | Slow growth | 73            | Low growth rate; tolerance to amimidopenicillin and nalidixic acid | 374, 650 |
| speA        | Spermidine | 63          | Arginine decarboxylase (EC 4.1.1.19) | A |
| speB        | Spermidine | 63          | Arginase (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 |
| srA         | Sorbitol | 58              | gutA, sbl; d-glutol-specific enzyme II of phosphotransferase system | A, 359, 360, 404 |
| srtC        | Sorbitol | 58              | gutC, sbl; regulatory gene | A, 359, 404 |
| srtD        | Sorbitol | 58              | gutD, sbl; sorbitol-6-phosphate dehydrogenase (EC 1.1.1.140) | A, 359, 404 |
| srrR        | Sorbitol | 58              | Regulatory gene | D |
| srrA        | Sorbitol | 9               | Degradation of stable RNA | A |
| sss         | Single-strand binding | 92         | extrB, 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 |
| staA        | Sorbitol | 83              | Altered ribonuclease activity | A |
| sucA        | Succinate | 16            | lys + met, suc; succinate requirement; a-ketoglutarate dehydrogenase (decarboxylase component) | A |
| sucB        | Succinate | 16            | lys + met, suc; succinate requirement; a-ketoglutarate dehydrogenase (dihydrolipoamide succinyltransferase component) | A |
| sulA        | Suppressor | 22        | sfIA, sul; suppressor of lon | A, 188, 194, 293 |
| sulB        | Suppressor | 2            | sfIB; suppressor of lon | 188, 194, 293 |
| supB        | Suppressor | 15            | su; suppressor of ochre (UAA) and amber (UAG) mutations; see gltU | 188, 194, 293 |
| Gene symbol | Mnemonic      | Map position (min) | Alternate gene symbols; phenotypic trait affected | References\(^c\) |
|-------------|---------------|--------------------|--------------------------------------------------|------------------|
| supC        | Suppressor    | 27                 | **suc, Su-4:** suppressor of ochre (UAA) and amber (UAG) mutations | A                |
| supD        | Suppressor    | 43                 | **sua, Su-1:** suppressor of amber (UAG) mutations | A, 324           |
| supE        | Suppressor    | 15                 | **suc, Su-2:** suppressor of amber (UAG) mutations; see **glnV** | A                |
| supF        | Suppressor    | 27                 | **suc, Su-3:** suppressor of amber (UAG) mutations; see **bryT** | A                |
| supG        | Suppressor    | 16                 | **Su-5:** suppressor of ochre (UAA) and amber (UAG) mutations | A, H             |
| supH        | Suppressor    | 43                 | **Suppressor** | A                |
| supK        | Suppressor    | 61                 | **Suppressor** | X                |
| supL        | Suppressor    | 16                 | **Suppressor** | A                |
| supM        | Suppressor    | 89                 | Suppressor of ochre (UAA) and amber (UAG) mutations; see **bryU** | A                |
| supN        | Suppressor    | 51                 | **Suppressor** | A                |
| supO        | Suppressor    | 27                 | **Suppressor** | A                |
| supP        | Suppressor    | 96                 | **Su-6:** suppressor of amber (UAG) mutations | H                |
| supQ        | Suppressor    | 12                 | **Suppressor** | A                |
| supT        | Suppressor    | 61                 | **Suppressor** | A                |
| supU        | Suppressor    | 84                 | **Suppressor** | A                |
| supV        | Suppressor    | (84)               | **Suppressor** | A                |
| tabC        | Terminus      | 85                 | Affects development of phage T4 | 612              |
| tag         | Thiamine      | 47                 | 3-Methyl-adenine DNA glycosylase activity | V                |
| tar         | Thymine       | 42                 | **cheM:** chemotaxis response; methyl-accepting chemotaxis protein II | 397, 569, 570, 587 |
| tdi         | (4)           | (4)                | Transduction, transformation, and rates of mutation reduced | 593              |
| tdk         | Thymine kinase (EC 2.7.1.75) | 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                 | Thiamine thiazole requirement | A                |
| thiC        | Thiamine      | 90                 | Thiamine thiazole requirement | A                |
| thi-o       | Thiamine      | 90                 | Thiamine thiazole requirement | A                |
| thrA        | Threonine     | 0                  | HS, thrD; aspartokinase I-homoserine dehydrogenase I | A                |
| thrB        | Threonine     | 0                  | Attenuator sequence in leader region of **thrABC** operon | 186              |
| thrC        | Threonine     | 0                  | Leader region of **thrABC** operon | 186              |
| thrD        | Threonine     | 0                  | Operator sequence for **thrABC** operon | 187, 524, 525    |
| thrE        | Threonine     | 0                  | Promoter sequence for **thrABC** operon | 187, 525         |
| thrF        | Threonine     | 0                  | Homoserine kinase (EC 2.7.1.39) | A                |
| thrG        | Threonine     | 0                  | Threonine synthase (EC 2.5.1.39) | A                |
| thrH        | Threonine     | 0                  | Threonine synthase (EC 2.5.1.39) | A                |
| thrI        | Threonine     | 38                 | Threonyl-tRNA synthetase (EC 6.1.1.3) | 242, 588         |
| thrJ        | Threonine     | 89                 | Threonyl-tRNA3 | A, 82, 113, 517, 518, 675 |
| thrU        | Threonine     | 89                 | Threonyl-tRNA4 | 517, 518, 675    |
| thyA        | Thymine       | 60                 | Thymidylate synthetase | A                |
| tkt         | Transketolase | (62)               | Transketolase (EC 2.2.1.1) | A                |
| tnaA        | Ind; tryptophanase (EC 4.1.99.1) | 83                 | A; 223, 338, 392, 414 | A                |
| tnaAp       | Promoter sequence for **tnaA** | 83                 | A; 223, 338, 392, 414 | 439              |
| tnaB        | Regulatory gene | 83                 | A; 618              |
| tolA        | Tolerance     | 16                 | **cim, tol-2:** tolerance to colicins E2, E3, A, and K | A                |
| tolB        | Tolerance     | 16                 | **cim, tol-2:** tolerance to colicins E2, E3, A, and K | A                |
| tolC        | Tolerance     | 16                 | **cim, tol-2:** tolerance to colicins E2, E3, A, and K | A                |
| tolD        | Tolerance     | (23)               | Speciﬁc tolerance to colicin E1 A | A                |
| tolE        | Tolerance     | (23)               | Speciﬁc tolerance to colicin E1 A | A                |
| tolI        | Tolerance     | (0)                | Speciﬁc tolerance to colicin E1 A | A                |
| tolJ        | Tolerance     | 0                  | Speciﬁc tolerance to colicin E1 A | A                |
| 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 |
| Gene symbol | Mnemonic     | Map position (min) | Alternate gene symbols; phenotypic trait affected                                                                 | References† |
|-------------|--------------|-------------------|-----------------------------------------------------------------------------------------------------------------|-------------|
| *tp*A       | Trehalose    | 88                | Triosephosphate isomerase (EC 5.3.1.1)                                                                         | A, 466      |
| *tre*       |              | 26                | Utilization of trehalose                                                                                        | 36          |
| *trg*       | (30)         |                   | Chemotactic response; methylation of methyl-accepting chemotaxis protein III                                  | 228, 323    |
| *trk*A      |              | 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          |
| *trp*A      | Tryptophan   | 27                | tryp-2; tryptophan synthase (EC 4.2.1.20), A protein termination sequence of *trpEDCBA* operon                   | A, 214, 420, 666 |
| *trpAt*     | Tryptophan   | 27                | Tryp-1; tryptophan synthase (EC 4.2.1.20), B protein tryp-3; N-(5-phosphoribosyl)anthranilate isomerase-     | A           |
| *trpB*      | Tryptophan   | 27                | Indole-3-glycerolphosphate synthetase                                                                         | A, 428      |
| *trpCp*     | Tryptophan   | 27                | Promoter sequence for *trpCBA*                                                                                 | 428         |
| *trpD*      | Tryptophan   | 27                | TrypE; glutamine amidotransferase-phosphoribosyl anthranilate synthase                                           | A           |
| *trpE*      | Tryptophan   | 27                | *anth*, tryp-4, tryD; anthranilate synthase (EC 4.1.3.27)                                                      | A, 40, 41, 45, 355, 418, 79, 585, 695 |
| *trpEd*     | 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 |
| *trpEs*     | 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               | *Rtyr*; 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*, *su8*; 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                 | *savA*, *savB*: 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, 182, 183, 189, 388, 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                | *su7*, *su8*, *su9*, *su10*, *su3*, *suF*; tyrosine tRNA1 (tandemly duplicated gene)                         | A, 146, 517, 550 |
| *tyrT*p      | Tyrosine     | 27                | Promoter sequence for *tyrT*                                                                                 | 550         |
| *tyrU*      | Tyrosine     | 89                | *supM*; tyrosine tRNA2                                                                                         | A, 113, 517, 518, 550, 675 |
| *tyrV*      | Tyrosine     | 27                | Promoter sequence for *tyrU*                                                                                 | 146, 339, 517, 550 |
| *tyrV*t      | Tyrosine     | 27                | Terminator sequence for *tyrV*                                                                               | 146, 339    |
| Gene symbol | Mnemonic | Map position (min) | Alternate gene symbols; phenotypic trait affected | References¹ |
|-------------|----------|-------------------|--------------------------------------------------|-------------|
| ubiA        | Ubiquinone| 91                | 4-Hydroxybenzotate → 3-octaprenyl 4-hydroxybenzotate | A, 329      |
| ubiB        | Ubiquinone| 85                | 2-Octaprenylphenol → 2-octaprenyl-6-methoxy-phenol| A            |
| ubiC        | Ubiquinone| 91                | Chorismate lyase                                  | A            |
| ubiD        | Ubiquinone| 85                | 3-Octaprenyl-4-hydroxybenzotate → 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            |
| udpR        |          | 82                | Regulation of hexose phosphate transport          | A, 223, 392  |
| udpT        |          | 82                | Hexose phosphate transport                        | A, 223, 392  |
| uidA         |          | 36                | gurA; β-d-glucuronidase (EC 3.2.1.31)              | A, 452      |
| uida         |          | 36                | Operator sequence for uidA                       | 452         |
| uidB         |          | 36                | Regulatory gene                                  | A, 452      |
| umuC         |          | 25                | Induction of mutations by UV; sensitivity to UV   | 304         |
| uncA         | Uncoupling| 83                | F₁-component of ATP-synthesizing system, α-subunit| A, 139, 143, 199, 305, 551, 641, 642 |
| uncB         | Uncoupling| 83                | F₁-component of ATP-synthesizing system           | A, 107, 139, 199, 230, 641, 642 |
| uncC         | Uncoupling| 83                | F₁-component of ATP-synthesizing system, ε-subunit| A, 139, 198, 199, 641, 660, E |
| uncD         | Uncoupling| 83                | F₁-component of ATP-synthesizing system, β-subunit| 106, 139, 158, 199, 552, 641, 642 |
| uncE         | Uncoupling| 83                | F₁-component of ATP-synthesizing system           | A, 139, 140 |
| uncG         | Uncoupling| 83                | F₁-component of ATP-synthesizing system, λ-subunit| F           |
| ung          |          | 56                | Uracil-DNA-glycosylase                            | 142         |
| upp          |          | 53                | uraF; uracil phosphoribosyltransferase (EC 2.4.2.9)| A, 474      |
| ups          |          | 26                | Efficiency of nonsense suppressors                | 122         |
| ush          |          | 11                | UDP-glucose-1-hydrolyase (5'-nucleotidase)        | A, 35       |
| wraA         | UV       | 92                | dAR; repair of UV damage to DNA; UV endonuclease  | A, 427, 532  |
| wraB         | UV       | 17                | dAR-1.6; repair of UV damage to DNA; UV endonuclease| A, 427, 457, 608 |
| wraC         | UV       | 42                | dAR-4.5; repair of UV damage to DNA               | A           |
| wraD         | UV       | 85                | dAR-2, mutU, pde, rad, recL, wraE, wraS20; repair of UV damage to DNA | A, 341, 520, 573 |
| uxaA         |          | 67                | Altrionate hydrolase (EC 4.2.1.7)                 | A, 393, 443  |
| uxaB         | (52)     |                    | Altrionate oxidoreductase (EC 1.1.1.58)           | A, 443      |
| uxaC         |          | 67                | Altrionate isomerase (EC 5.3.1.12)                | A, 393, 443  |
| uxaD         |          | 98                | Mannolte hydrolase                                | A, 284      |
| uxaE         |          | 98                | Mannolte oxidoreductase (EC 1.1.1.57)             | A, 284      |
| uxaR         |          | 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    | 70                | Utilization of D-xylose                         | A           |
| xylf         |          | 41                | Glucose-6-phosphate dehydrogenase (EC 1.1.1.49)  | A           |

¹ Abbreviations: DAHP, 3-deoxy-D-arabinohexulosonate-7-phosphate; KAP, 7-oxo-8-aminopelargonate; DAPA, 7,8-diamino-pelargonate; 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, NADP; phosphate; UV, ultraviolet light.

² Numbers refer to time scale shown in Fig. 1. Parentheses indicate approximate map locations.

³ 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. Didierichsen; (H) G. E. Eggertsson; (I) J. Felton and A. Wright; (J) J. Foulad; (J) J. Garwin and J. E. Cronan, Jr.; (K) J. R. Guest; (L) P. E. Hartman; (M) R. W. Hogg; (R) P. K. Krell; (O) A. J. Laird; (P) A. B. Lenney and P. Margolin; (Q) A. Ohta and W. Dowhan; (R) D. Mount and J. Little; (S) H. Osako; (T) J. S. Parkinson; (U) C. H. R. Raetz; (V) E. Seeberg; I. Seng, 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 renaming 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 *urrE* are now synonyms for *urrD* (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, *urrE* will be found as a synonym under *urrD*. 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 *urrE* 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*, *rnrA*, *rnrB*, *rnc*, *rmd*, *rnrE*, *rnf*, and *rnnG* 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 *rnnD* operon is placed incorrectly in Fig. 1. The correct position of this operon is at approximately 71.7 min on the linkage map.
| Alternate symbol | Symbol in Table 1 | Alternate symbol | Symbol in Table 1 |
|------------------|------------------|------------------|------------------|
| acrB             | gyrB             | feuA             | cir              |
| ade              | pur              | feuB             | fep              |
| aid              | fda              | fim              | pil              |
| add_h            | purD             | flaJ             | motA, motB       |
| add_h3           | purG             | flaF             | hag              |
| ala-act          | alaS             | frdD             | fns              |
| alt              | rpoD             | ftsi             | pbpB             |
| amk              | nkg              | gad              | nsp              |
| anth             | trpE             | glmD             | nagB             |
| aph              | lysC             | glu              | ppc              |
| arg + ural       | car              | glut             | gilA             |
| arO              | aroT             | gly-act          | glyS             |
| asp              | ppc              | glyD             | gpt              |
| aspB             | gilB             | gpp              | gpt              |
| ata              | attP22           | gpt              | ptsG             |
| bfe              | btuB             | gptB             | ptsM             |
| blu              | pgl, pgm, malP   | groE             | mop              |
| brnP             | iuH              | groN             | rpoB             |
| cap              | car, crp         | groP             | dnaB, dnaJ, dnaK |
| capR             | lon              | grpA             | dnaA             |
| cat              | ptsG             | grpC             | dnaJ, dnaK       |
| cbr              | fep              | grpF             | dnaK             |
| cby              | fep              | gts              | qmeA             |
| cer              | btuB             | gurA             | uID              |
| cheC             | tolA             | gut              | srl              |
| cim              | tolA             | gxu              | gpt              |
| cmlB             | ompF             | H                | hag              |
| coa              | ompF             | Hs               | hsd              |
| colEl-1i         | tolC             | Hs               | thrA             |
| con              | ompA, rfa        | hsm              | hsdM             |
| Cou              | gyrB             | hsp              | hsd              |
| cqsA             | rrrA             | hsr              | hsdR             |
| cqsB             | rrrC             | hss              | hsdS             |
| cqsC             | rrrF             | icl              | aceA             |
| cqsD             | rrrD             | ile              | ilcA             |
| CR               | ptsG             | ind              | tnaA             |
| cru              | nupC             | ins              | glyV, glyW       |
| cry              | ompB, ompF       | K12              | rpsG             |
| cte              | ptsH, ptsI       | kac              | kdp              |
| cxr              | ccm              | kgdA             | eda              |
| dad              | alnA             | kga              | eda              |
| dagA             | cycA             | kmt              | ompB             |
| dap + hom        | asd              | lcs              | asnS             |
| dar              | uvr              | lexB             | recA             |
| deg              | lon              | lexC             | sbb              |
| ddbB             | bioR             | lop              | ligAo            |
| dhl              | ldp              | lips              | rfa              |
| dir              | lon              | lps              | rfa              |
| dnaF             | nrdA             | lss              | libR             |
| dnaL             | lig              | lys + met        | sucA, sucB       |
| dnaS             | dut              | mas              | aceB             |
| dra              | deoC             | M6               | acaA             |
| drm              | deoB             | mbl              | acaA             |
| eps              | rpsE             | mec              | dcm              |
| eryA             | rplD             | meoA             | ompC             |
| eryB             | rplV             | mlpA             | lpp              |
| exbA             | tonB             | mon              | envB             |
| exprA            | lexA             | mni              | manC             |
| exprB            | ssb              | mpt              | ptsM             |
| Alternate symbol | Symbol in Table 1 | Alternate symbol | Symbol in Table 1 |
|------------------|------------------|------------------|------------------|
| mra              | murF             | sbl              | srl              |
| mtcA             | acrA             | sec              | hemF             |
| mtcB             | tolC             | sep              | phpB             |
| 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             | strA             | rpsL             |
| nic              | nad              | stsB             | rimH             |
| nIR             | fhr              | stv              | rpoB             |
| nitA             | rho              | su, su           | sup              |
| nitB             | rpoB             | sud2             | rpsD             |
| nuc              | deo              | sufD             | glyU             |
| nupA             | txs              | sun              | glyT             |
| old              | fad              | sumA             | sun               |
| ole              | fadR             | sumB             | rpoB             |
| ompE             | nmpA             | supV20           | glyU             |
| par              | ompC             | T1rec            | T1, T5rec        |
| pdeB             | uvrD             | tonB             | tonA             |
| pdeC             | pig              | T6rec            | tsx              |
| pdxF             | serC             | tabB             | tabA             |
| pea              | azi              | tD               | tA               |
| pel              | ptsM             | talA             | talD             |
| phe-act          | pheS             | talD             | alaU             |
| phx              | rfa              | tgi              | alaU             |
| PMG              | mgl              | tgtA             | lpcA             |
| poaA             | putA             | tgtB             | ptaG             |
| poh              | oriC             | tgtC             | gliT             |
| polC             | dnaE             | tgtE             | gliU             |
| pon              | lpcB, mrc        | thyR             | glyU             |
| popA             | hemH             | th0              | deoB, deoC       |
| popB             | hemF             | tabF             | mop              |
| popE             | hemC             | tabD             | rpoB, rpoC       |
| prd              | fuc              | tA               | rpoB             |
| prv              | mutH             | tI               | rpoB             |
| psuA             | rho              | tii               | rpoB             |
| pup              |deoD              | tiiD             | rpoB             |
| pyrA             | car              | toIF             | rpoB             |
| rad              | uvrD             | toIG             | rpoB             |
| ramA             | rpsD             | toP              | rpoB             |
| ramB             | rimF             | tsp              | rpoB             |
| RC               | rel               | tre              | rpoB             |
| recL             | uvrD             | trP              | rpoB             |
| refl             | tolC             | try              | rpoB             |
| refII            | cet               | tryp             | rpoB             |
| relC             | rplK             | ts-9             | rpoB             |
| res              | rimF             | tsnC             | rpoB             |
| resA             | polA             | tsu              | rpoB             |
| RMG             | mglR             | tss              | rpoB             |
| rm               | hsd               | ass              | rpoB             |
| rnsA             | rna               | umuA             | rpoB             |
| rnsC             | rho               | umuB             | rpoB             |
| rodY             | envB             | uraF             | rpoB             |
| ron              | rpoB             | usgA             | rpoB             |
| rorA             | recB             | uvrF             | rpoB             |
| rps             | rps               | val-act           | rpoB             |
| rpy             | rpl               | valS              | rpoB             |
| rps             | rpm               | xenA             | rpoB             |
|                   |                   | zab              | rpoB             |
|                   |                   | recA             | rpoB             |
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 for the last map, therefore, amended values are:

on F-prime F14, iluD-argC:

\[ \begin{align*}
186.5 \times (1.03) & = 92 \text{ kb/min} \\
& = 39 \text{ kb/min}
\end{align*} \]

on F-prime KLF5, polA-rpoB:

\[ \begin{align*}
126 \times (1.03) & = 81 \text{ kb/min} \\
& = 38 \text{ kb/min}
\end{align*} \]

Of these values, the one for the iluD-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 412.5 \times (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*                                                                 | Reference(s)* |
|----------------------------------------------------------------------------|----------------|
| **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 CO₂ 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                                                      | 508, 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* | 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 |

TRANPOSITION

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, 566, 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, 369, 387, 393, 526, 532, 599, 642, 644, 694, A-383 |
Subcloning; maxicells | 446, 533, 675 |
From an F-prime factor | 568 |
Colony screening by nucleic acid hybridization | 212 |
Transducing phages from abnormal attachment sites | 398, 548a |
General method | 176, 329, 387, 393, 516, 642 |
Examples | 62, 70, 270, 315, 694, A-383 |
Directed integration of bacteriophage | 251, 409, 410, 431, 587, 642, 645 |
Cloning onto minichromosomes or λadv; selection for origins of replication | 75, 267, 469, 564, 694, 695 |
Fusions to orient genes near attachment sites | 694 |

* DAP, Diaminopimelic acid; poly(A), polyadenylate; poly(T), polythymidylate.
* 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-
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 IS1, IS2, IS3, IS4, and γ6 (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<sup>tyr</sup>, i.e., tyr<sup>T</sup> and tyr<sup>U</sup>, 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 (tyr<sup>T</sup>) is repeated tandemly more than threefold, downstream from tyr<sup>T</sup> (146). tyr<sup>T</sup> and tyr<sup>U</sup> are located very far from each other on the map, at 27 and 89 min, respectively. Next to tyr<sup>T</sup> lies an apparent tandem duplication, tyr<sup>V</sup>. Another example of apparent gene duplication is the genes arg<sup>I</sup> and arg<sup>F</sup>, 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 \textit{argF} is not found in \textit{E. coli} B, \textit{E. coli} W, or several other closely related enteric bacterial species, it may be that \textit{argF} evolved relatively recently in \textit{E. coli} K-12 and is derived from a duplication of \textit{argI}.

Other recently studied examples of multiple gene copies include in particular the seven rRNA operons \textit{rrnA} through \textit{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 rRNA operon (271). One further example of duplication of a gene whose product is produced in large amounts is the case of \textit{tufA} and \textit{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 \textit{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 \textit{E. coli} K-12 and \textit{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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