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Recalibrated Linkage Map of *Escherichia coli* K-12[1]

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INTRODUCTION

A radical revision of the genetic map of *Escherichia coli* K-12 has been desirable for some time. Since the last review of mapping data (672), 200 new loci have been reported in the literature. In addition, an evaluation of the time-of-entry data now available indicates that the lengths of several major intervals on the map are significantly different from those that had been given in previous maps. In this review, the results of a basic recalibration of the map, derived mainly from time-of-entry and cotransductional data, are presented. Over 650 loci have been reviewed and assigned map locations. In addition, problems encountered in evaluation of the available data are discussed and changes in nomenclature are tabulated. We also include a discussion of the possible significance of the nonrandom distribution of gene loci on the map.

SOURCES OF MAPPING DATA

Potential sources of information concerning gene positions and gene order in *E. coli* include: (i) interrupted matings (348, 435); (ii) generalized transduction with phage P1 (416, 736); (iii) physical measurements of suitably defined deoxyribonucleic acid (DNA) segments on plasmids (327, 511); (iv) gradient of transmission (160, 348); (v) genetic linkage in Hfr × F^- crosses (161, 348, 691, 707); (vi) complementation or recombination with: (a) F′ factors (431) and (b) specialized transducing phages (735); (vii) deletion analysis using: (a) spontaneous mutants (446), (b) survival of induced lysogens (2), (c) eduction (661), and (d) transductional shortening of F′ factors (457, 510, 512); (viii) linkage analysis by transformation (W. P. M. Hoekstra, personal communication); and (ix) in vivo or in vitro detection of gene products from plasmids that carry chromosomal genes (354, 354b, 355, 420a, 495).

Although it is most desirable to obtain physical measurements of the positions of genetic loci, at the present time this is not feasible for most genes. In the great majority of cases, gene positions are first approximated by means of Hfr crosses, which can in some cases be accomplished rapidly (431), and then localized more precisely by cotransduction using phage P1. The genetic map assembled in this review was constructed chiefly by converting published P1 cotransduction frequencies into map distances (see below) and then comparing the additivity of these distances with those obtained from interrupted mating experiments.

The data we have used were obtained from a survey of the published literature through June 1975 and from personal communications.

REVISION OF MAJOR INTERVALS AND TOTAL MAP LENGTH

The metric of the *E. coli* map used at present is the minute, determined from the time intervals between transfer of markers in interrupted mating experiments carried out at 37 C (348, 672). It has been observed that some of the distances given on earlier versions of the map are at variance with the results of certain of these time-of-entry experiments. Therefore, a review of such data has been carried out, and a series of new time-of-entry experiments has been completed (K. B. Low, unpublished data). From these results, which are drawn from a total of 45 experiments, new averages for major map distances have been determined.

As an example of one such major map interval, consider the distance between *trp* and *his*. In previous versions of the map, this interval (in minutes) has been variously given as 27

[1] Reprints of this paper may be obtained from the authors. Those wishing to have a wall chart consisting of a circular drawing of the *E. coli* linkage map (together with a reprint) suitable for teaching and laboratory use may obtain one for $4 from the ASM Publications Office.

(348), 15.6 (670), 13.5 (669, 671), and 11.5 (672). These variations had accrued partly on the basis of changes in measured times-of-entry and partly because one of the markers (*trp*) was moved clockwise on the basis of cotransductional linkages without regard to time-of-entry data. A survey of what appear to be the most "accurate" (see below) measures of the *trp-his* distance shows that most values obtained are in the range of 15 to 18 min (283, 429, 430, 456; K. B. Low, unpublished data). An example of one such result is shown in Fig. 1, from which a distance of 16 min is obtained. On this revision of the map, we have used an average value of 16.8 min. In a similar fashion, all other major map distances have been reexamined by averaging both published data (65, 66, 253, 283, 284, 429, 430, 456, 670, 671, 730) and new unpublished data. The genetic markers for which the most time-of-entry information is available are *thr, leu, proA, lac, purE, trp, his, aroC, thy, argG, malT, xyl, pyrE, ilv,* and *argE*. Using the revised map intervals, the total contiguous map length was found to be 100 ± 2 min, in contrast to the value of 90 min used in several previous

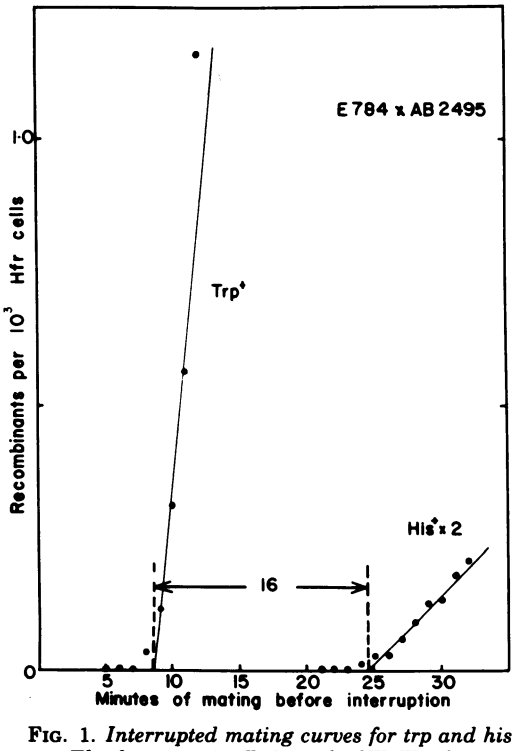

FIG. 1. *Interrupted mating curves for trp and his genes. The donor strain, E784 (gift of W. Woods), is a λ⁻ derivative of Hfr KL19 (see Fig. 2). The F⁻ strain, AB2495, is a Trp⁻, Thy⁻ derivative of AB1157 (26). Experimental conditions have been described (429, 435, 470).*

maps. Therefore, we have decided that it is important at this time to change the overall length of the map and we have chosen the value of 100 min as the most accurate and useful figure. It is of interest that the published value for the total map length of *E. coli* C (726) is 101 min.

A few words should be said about the problems involved in determining genetic distances by interrupted mating (i.e., time-of-entry) experiments. The determination of entry times by extrapolation of interrupted mating curves has been discussed before (431, 435, 671). In addition, one is faced with substantial variations in measured transfer times depending on the particular Hfr and F⁻ strains used and on experimental conditions (728). Hfr Ra-2, for example, transfers markers approximately 15% faster than do several other Hfr strains that transfer the same region of the chromosome early in conjugation (429, 430). Somewhat similar differences were observed when different F⁻ strains were crossed with the same Hfr strain for comparison. In arriving at the best estimate of a revised major map interval, results from at least three different crosses involving different Hfr and F⁻ strains and different directions of transfer were averaged. Occasionally, values were obtained that were given less weight because they differed markedly (usually being 10 to 20% larger) from the results of several other crosses. Results from the literature that were used in this survey are given in the references listed above in this section, and copies of the unpublished experiments are on file at the *E. coli* Genetic Stock Center at the Yale University School of Medicine.

INTERPRETATION OF TRANSDUCTION MAPPING DATA

As noted in a preceding section, generalized transduction crosses mediated by bacteriophage P1 comprise the principal source of new genetic mapping data in the literature. In the last edition of the linkage map (672), it was noted that all of the mapped genes of *E. coli* could be assigned to a series of 10 transductional "linkage groups." That is, each group contained a set of genes that were known to be continuously linked to each other on overlapping transducing fragments of phage P1. Analysis of all transduction data now available shows that nearly all of the 615 precisely mapped genes of *E. coli* are continuously linked by P1 cotransduction and can be assigned to one of two transductional "linkage groups." The gaps that separate these two groups occur at min 28.5 to 35.5 and at min 95 to 98.5 on the

genetic map. These gaps are shown in the circular reference map of Fig. 2.

As in the past, we use the equation derived by Wu (736) to compute map intervals in minutes (Fig. 3) from gene cotransduction frequency data: frequency of cotransduction = $(1 - d/L)^3$, where d is the distance between markers in minutes and L is the length of the transducing fragment in minutes. In Wu's original derivation, the numerical value of L was set at 2.0 min. As explained in the next section, the molecular length of 1 min of genetic map corresponds to approximately 41 kilobases (kb, a unit of DNA length corresponding to 10^3 base pairs). The best current estimate for the molecular length of phage P1 DNA (and hence of a transducing fragment as well) is about 97 kb (E. Ohtsubo and M.-T. Hsu, personal communimunication), which corresponds to about 2.3 min of genetic map length. We have noted in many cases that a map interval calculated for a long distance (i.e., corresponding to a very low cotransduction frequency) is less than the value obtained when the distances calculated for shorter intervals within that region are summed. If it is assumed that markers located close to the ends of a linear transducing fragment are less likely to be integrated due to decreased probability of synapsis and recombination, the effective length of a transducing fragment would be somewhat less than 2.3 min. We will continue to use $L = 2.0$ min for the purposes of this review.

Genetic markers have been assigned to positions in Fig. 3 on the basis of best fit with all available cotransduction and interrupted mating data. We wish to emphasize, however, that marker placements are subject to many sources of error and that the positions of gene loci will need to be revised as more mapping data become available. In the following paragraphs we discuss some of the principal sources of uncer-

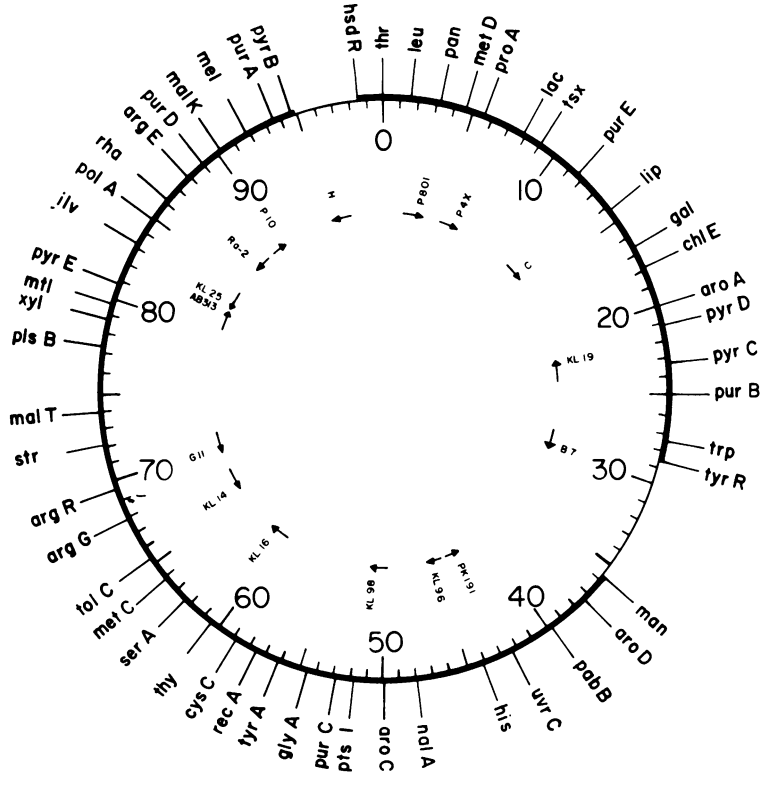

FIG. 2. *Circular reference map of E. coli K-12. The large numbers refer to map position in minutes, relative to the thr locus. From the complete linkage map (Fig. 3), 52 loci were chosen on the basis of greatest accuracy of map location, utility in further mapping studies, and/or familiarity as long-standing landmarks of the E. coli K-12 genetic map. The two thin portions of the circle represent the only two map intervals that are not spanned by a continuous series of P1 cotransduction linkages. Inside the circle, the leading transfer regions of a number of Hfr strains are indicated. For more complete information on Hfr points of origin and Hfr derivatives of particular use in mapping, see references 151, 431, and 431a.*

tainty in the interpretation of transduction mapping data.

One example of the possible extent of variation in cotransduction frequencies encountered in the literature is seen in Table 1, which lists values obtained for the *thr-leu* interval. The table shows results obtained by direct cotransduction and also by summation of smaller internal intervals. As can be seen, the distances calculated using the Wu equation vary between 0.83 and 2.14 min. In the cases where summation of small segments was carried out, the range of values could presumably be due to large marker-specific effects (445, 497, 650, 746), as well as statistical variation and differences in experimental conditions from laboratory to laboratory. Almost all of the results obtained for the *thr-leu* interval involved the same *thr*$^-$ and *leu*$^-$ alleles, *thr-1* (= *4*) and *leu-6* (= *8*) (26), and so the variations observed for direct *thr-leu* cotransduction are presumably due to factors other than marker-specific effects.

Another potential source of mapping error can be found in the large differences in the reported cotransduction frequencies for a pair of markers when selection is shifted from one member of the pair to the other. A good example is the marker pair *ilv-metE*, where the data from five different laboratories yield mean cotransduction frequencies of 7.5 ± 2.3% for *metE* when *ilv* is the selected marker and 36.7 ± 6.1% for *ilv* when *metE* is the selected marker. Similar results have been noted for reciprocal crosses with numerous other marker pairs in *E. coli*. In this review, we have taken the average of the reciprocal cotransduction frequencies (when both values are reported) for computing the map distance between such marker pairs. Unfortunately, we often find that only the values for single selections are reported in the literature. It is evident from the preceding example that map intervals that are computed from such single determinations may vary substantially from distances based on the averaged data from reciprocal crosses.

The mapping function derived by Wu (736) assumes that transducing fragments are cut at random from the bacterial genome. This theoretical frequency of cotransduction of two markers is thus simply a function of the physical distance between the markers and of the consequent probability that both markers will be contained in the same fragment. However, the differing values obtained for reciprocal cotransduction frequencies suggest that transducing fragments may not be produced randomly. Unequal reciprocal cotransduction frequencies have been noted also in generalized transduction crosses mediated by phage P22 in *Salmonella typhimurium* (377). Chelala and Margolin (112) have studied this problem in detail and their findings strongly support the idea that transducing fragments in phage P22 are not cut at random from the host chromosome. They have developed an elegant model which suggests that transducing fragments of P22 headfull length are packaged into phage heads sequentially, starting from specific initiation sites in the bacterial DNA. The genetic composition of individual transducing fragments is thus determined by the position of genes relative to packaging initiation sites, rather than by the position of random cuts in host DNA sequences. It seems likely that the basic elements of this model will apply equally well to other generalized transducing phages such as P1. If so, the model offers a plausible explanation for the *ilv-metE* results described above. Preferred recognition sites for the cutting and packaging of *E. coli* DNA are distributed in such a way that fragments which contain *ilv*, but not *metE*, are packaged much more frequently than fragments which contain either *metE* alone or *metE* and *ilv* together. The interesting observations of Harriman (286), who found that a single P1-infected cell can produce transducing particles that collectively span very long host DNA segments, are also consistent with the sequential DNA packaging model.

Although we employed the averaged data from reciprocal crosses to compute the map intervals shown in Fig. 3, the possibility remains that this may not be an entirely valid procedure. Despite all of the uncertainties mentioned in this section, we find that many of the map intervals derived from genetic data agree satisfactorily with direct length measurements of the corresponding DNA sequences. Some of these physical correlations are described in the next section.

PHYSICAL MAPPING STUDIES

This edition of the linkage map contains, for the first time, several genetic markers whose map coordinates were determined by physical rather than genetic techniques. For example, three of the structural gene clusters for 16*S* and 23*S* ribosomal ribonucleic acid (RNA) (*rrnA, rrnB, rrnC*) and their associated 5*S* RNA genes (*cqsA, cqsB*) were mapped by a variety of physicochemical techniques (42, 170, 177, 353, 420, 755). The mapping of new genes for 30*S* and 50*S* ribosomal subunit proteins (*rps, rpl*), for the α, β, and β' subunits of RNA polymerase (*rpoA, rpoB, rpoC*) and for protein elongation factor Tu (*tufA, tufB*) was also achieved by physico-

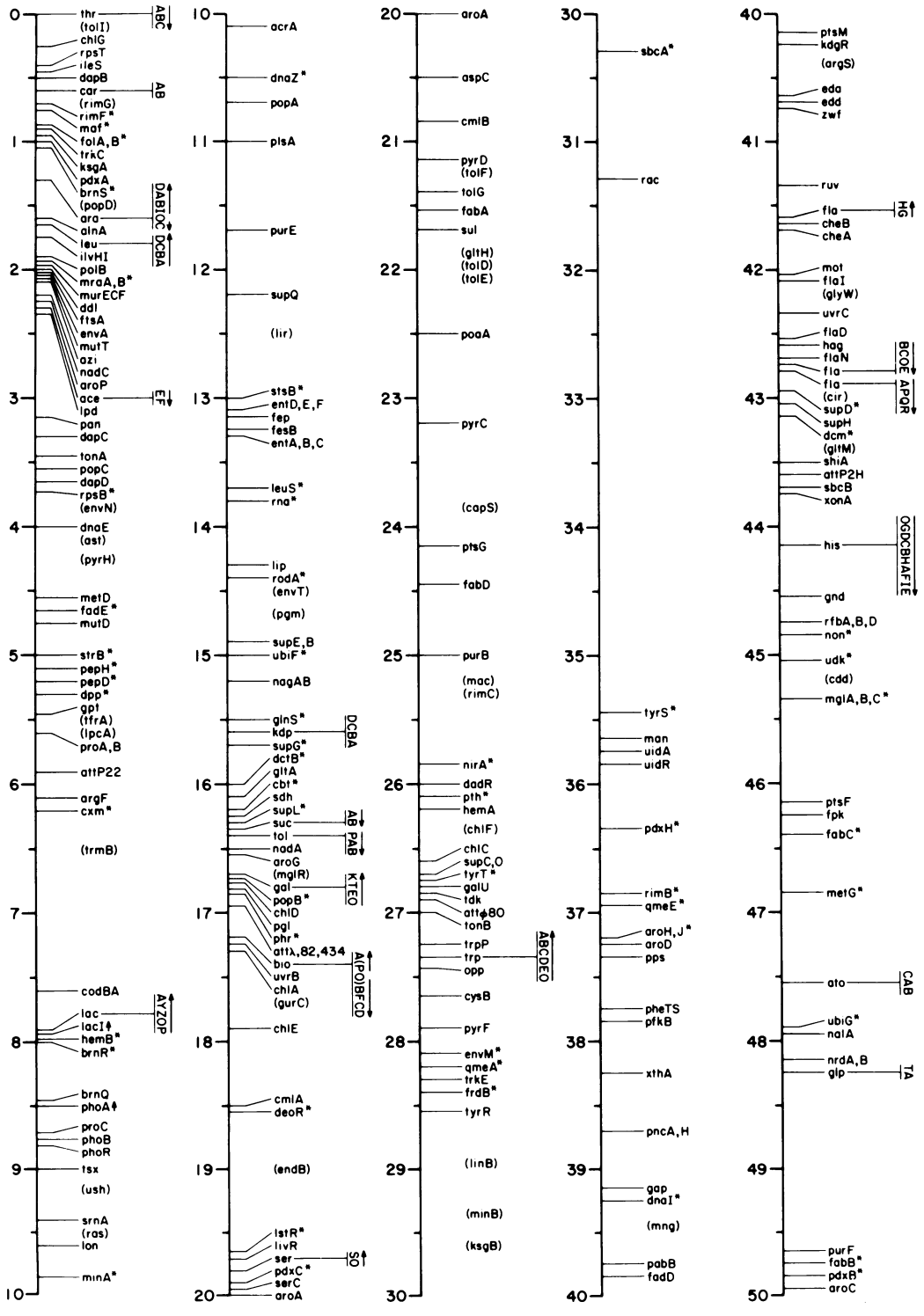

FIG. 3. *Linear scale drawings representing the circular linkage map of E. coli K-12. The time scale of 100 min, beginning arbitrarily with zero at the thr locus, is based on the results of interrupted conjugation experiments, as discussed in the text. The genetic symbols used in this figure are defined in Table 2. Parentheses around a gene symbol indicate that the location of that marker is not well known, sometimes having been determined only within very wide limits. An asterisk indicates that a marker has been mapped more precisely but that its position with respect to adjacent markers is not known. Arrows above genes and operons indicate the direction of messenger RNA transcription of these loci. For a comparison of the E. coli K-12 linkage map with the genetic maps of E. coli strain C and Salmonella typhimurium, see Wiman et al. (726), and Sanderson (594) and Casse et al. (105).*

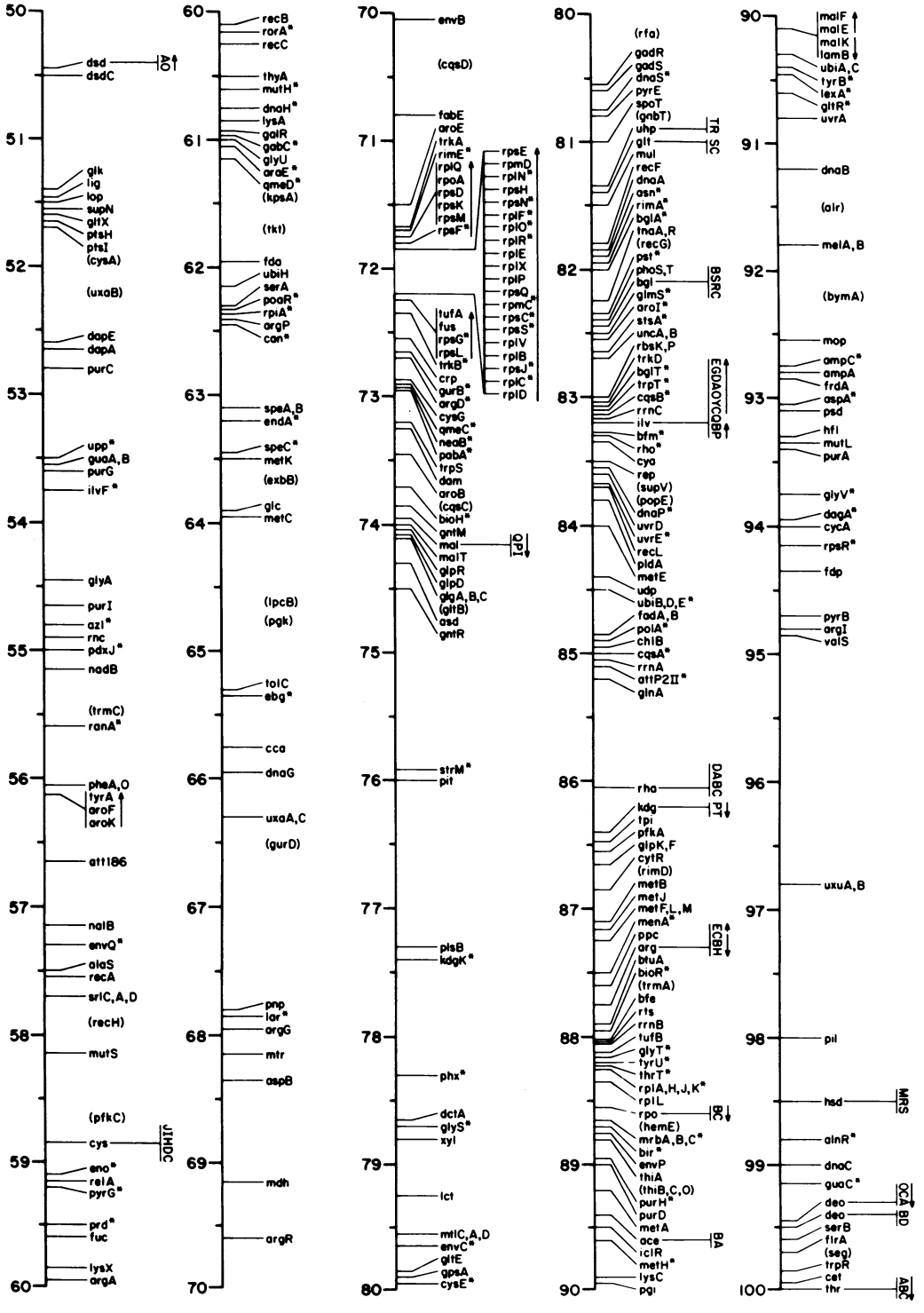

FIG. 3.—*continued*

TABLE 1. *Determinations of the thr-leu map distance using Wu's formula and published cotransduction frequencies*

Cotransduction frequency (%)	Calculated *thr-leu* distance (min)	Reference
By direct *thr-leu* cotransduction		
7, 3	1.29	671
2	1.44	201
1.5, 2	1.47	51
20	0.83	33
1.6, 2.8	1.44	641
0.75, 0.75, 1.7	1.55	537
2.5	1.35	155
3	1.37	737
By summation of subintervals		
17, 24 + 56, 21	0.8 + 0.55 = 1.35	671
25 + 32 + 68 + 66	0.73 + 0.63 + 0.24 + 0.26 = 1.86	671
6 + 15	1.21 + 0.93 = 2.14	201
10 + 75 + 66 + 43	1.05 + 0.18+ 0.26 + 0.49 = 1.98	201
5 + 43	1.25 + 0.49 = 1.74	201
10 + 12	1.05 + 1.0 = 2.05	201
60 + 10	0.31 + 1.08 = 1.39	256
50 + 2.3	0.42 + 1.43 = 1.85	51
27 + 3	0.7 + 1.37 = 2.07	537
4.3 + 68	1.28 + 0.25 = 1.53	641
7 + 95 + 74 + 68	1.16 + 0.05 + 0.19 + 0.25 = 1.65	641
6.9 + 47	1.17 + 0.45 = 1.62	641
7 + 32.5	1.16 + 0.61 = 1.77	641
4 + 40	1.31 + 0.53 = 1.84	269
29 + 19	0.67 + 0.84 = 1.51	269

chemical methods (205, 354, 355, 420, 420a).

Recent advances in the electron microscope analysis of heteroduplex DNA molecules of known genetic composition now make it possible to correlate physical distances, expressed in kilobases, directly with genetic map distances, expressed in minutes. In their extensive collection of heteroduplex mapping data for bacterial genes in the F′ factor F14, Deonier et al. (170) and Ohtsubo et al. (511) report molecular lengths of 161 and 25.5 kb for the DNA sequences between *ilvD* and *metB* and between *metB* and *argC*, respectively. The corresponding genetic intervals, as they appear in Fig. 3, are 3.9 min for *ilvD* (83.2 min) to *metB* (87.1 min) and 0.65 min for *metB* to *argC* (87.75 min). The combined data for the interval from *ilvD* to *argC* yield a conversion factor of 41 kb per min of map length. On this basis, the total molecular length of the 100-min genome is 4.1×10^6 base pairs, corresponding to a molecular weight of 2.7×10^9. These values are still in good agreement with those computed by Ohtsubo et al. (511) on the basis of earlier genetic mapping data (672), andwith other estimates of the size of the *E. coli* genome (91, 128).

The conversion factor of 41 kb per min can be employed to evaluate the degree of coincidence of physical and genetic maps in several other parts of the *E. coli* genome. For example, Sharp et al. (611) reported a minimum length of 6 kb for the interval between *nadA* (16.5 min) and *gal* (16.7). This molecular length corresponds to 6/41 or 0.15 min of map length and agrees well with the 0.2-min distance inferred from transduction data (Fig. 3). M. Fiandt, W. Szybalski, F. Blattner, S. R. Jaskunas, L. Lindahl, and M. Nomura (personal communication; 420a, 495) have characterized a transducing phase, λ *spc1*, that carries the markers *aroE* (71.5 min) through *rpsE* (formerly *spc*, at 71.85 min). The length of the bacterial sequence in this phage is 19.3 kb. The genetic map interval of 0.35 min for *aroE* to *rpsE* is within the 0.47-min upper limit set by the molecular length of the bacterial sequence in λ *spc1*. Hu et al. (327) have constructed a partial physical map of *E. coli* DNA sequences in the F′ factor F13. Their measurements suggest an upper limit of 134.6 kb (3.3 min) for the distance between *lac* (7.9 min) and *purE* (11.7 min), but the corresponding genetic map distance is somewhat longer at 3.8 min. Palchaudhuri, E. Ohtsubo, and W. K. Maas (personal communication) find a molecular length of 126 kb (3.3 min) for the DNA sequence in F′ factor KLF5, which contains the genes *polA* (84.9 min) through *rpoB* (88.5 min). Again, the genetically determined interval of 3.6 min is somewhat longer than the reported physical length. A possible explanation for

these last-mentioned discrepancies is that the F13 or KLF5 plasmids may contain unsuspected deletions of DNA segments that are normally present in the bacterial chromosome. However, it seems unlikely that F14 contains any large deletions of its bacterial sequence (511).

We would like to call attention to one of the limitations of Fig. 3, where groups of contiguous genes have been assigned to map positions at discrete points on the time scale. Although this format is a convenient one for recording the results of genetic mapping experiments, it has the drawback of failing to show the true physical dimensions of the gene clusters. The *ilv* operon at 83.2 min, for example, has an overall molecular length of about 7 kb, corresponding to 0.17 min of map length (512a). Similarly, each of the *rrn* clusters at 83.2, 85.0, and 88.1 min occupies 5.3 kb or 0.13 min of map length (170), and the *rpoB,C* genes at 88.5 min occupy approximately 8.8 kb or 0.21 min (205, 420a). It is therefore possible that the map position for a given marker in Fig. 3 can deviate from its true physical position by as much as 0.2 min on this basis alone. We anticipate that it will soon be possible to redraw certain portions of the linkage map in a format that illustrates both the relative order and the linear dimensions of individual genes.

CLUSTERING OF GENE LOCI

It is readily evident in Fig. 3 that the mapped genes of *E. coli* are distributed along the chromosome in a nonrandom fashion. This is shown more clearly in Fig. 4, where the number of gene loci per 1-min interval of map length is plotted as a function of map location. The total number of genes plotted is only 606 because promoter sites, prophage attachment sites, and markers displayed in parentheses are excluded. The figure reveals major peaks of high gene density, or gene clustering, at min 43 to 45, 72, 84, 89, 2, 17, and 28, and major troughs of low gene density at min 65, 77, 86, 97, 12, 24, and 30 to 35 on the map. The nonrandom distribution is statistically significant, as it deviates from the random expectation of 6.06 genes per min with a significance level of $P < 0.01$ in a Kolmogorov-Smirnov one-sample test for goodness of fit. Most of the major peaks rise and fall sharply, a feature that indicates that very crowded regions of the genome tend to be flanked on both sides by relatively silent regions. It is conceivable that this alternating pattern of genetically crowded and silent regions may be functionally and topologically related to the folded structure of the condensed bacterial nucleoid (652, 731). For example, it may be that the major clusters represent physi-

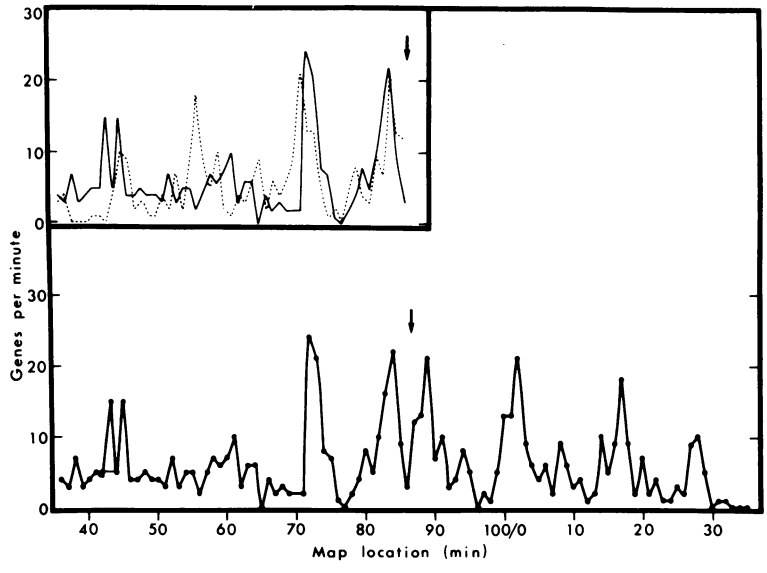

FIG. 4. *Distribution of known gene loci on the genetic map. The total number of mapped genes (excluding prophage attachment sites, promoter-initiator sites, and markers in parentheses in Fig. 3) in each 1-min interval of map length is plotted against map location, starting at min 35 and proceeding in a clockwise direction. The arrows placed at min 87 indicate an axis of symmetry for positions of gene clusters on the chromosome (see text). Inset: The continuous line represents the number of genes per minute in the 36- to 86-min map segment, proceeding clockwise from left to right. The dashed line represents the number of genes per min in the 37- to 87-min map segment, proceeding counterclockwise left to right. Another possible axis of symmetry lies at min 82 (see text).*

ologically active segments of DNA that gain accessibility to RNA and protein-synthesizing components by being located on the surface of the nucleoid. Conversely, the flanking silent regions of DNA would be embedded in the interior of the nucleoid.

In support of this hypothesis, we note that the major peaks do in fact contain most of the genes that are required for balanced macromolecular syntheses. The cluster at min 72 contains genes for 30S and 50S ribosomal subunit proteins, for the α-subunit of RNA polymerase, for protein elongation factors G and Tu, and for cyclic adenosine 5'-monophosphate receptor protein. The min 84 cluster includes genes for ribosomal RNA species, termination factor ρ, adenyl cyclase, DNA polymerase I, DNA initiation, and oxidative phosphorylation. The min 89 cluster contains genes for 50S ribosomal subunit proteins, ribosomal RNA, elongation factor Tu, β and β' subunits of RNA polymerase, and several genes affecting envelope structure and function. The cluster around min 2 includes more genes for envelope structure and function, for nucleoside catabolism, for modification of ribosomal proteins, for DNA elongation, and for DNA polymerases II and III.

It is difficult to predict at this time what the role of the relatively silent DNA regions might be. If these regions are confined to the interior of the nucleoid, it may be that some of this DNA plays a structural role in forming the condensed nucleoid. A further possibility is that the silent regions do contain functional genes that can be transcribed, but that few of these genes produce mutant phenotypes that can be recognized by current methods.

In addition to clustering of gene loci, the plot in Fig. 4 reveals a certain degree of symmetry in the positions where clusters appear on the map. The pairs of major peaks at min 84 and 89, 72 and 2, 43 to 45 and 28, and the two major troughs at min 77 and 97, are all approximately equidistant from an axis of symmetry located at min 87. If the gene distribution map is divided into two halves at min 87 and rearranged so that the right half is superimposed in reverse sequence onto the left half (see inset of Fig. 4), one observes a substantial degree of coincidence of major peaks and troughs in the two halves. The most serious deviation from this apparent symmetry occurs at min 17 in the right half where a major peak has no mirror image at min 56 in the left half. Although the symmetrical distribution of gene clusters around a point at min 87 is thus imperfect, the data nonetheless suggest that the two halves of the genome that are defined by this point may be topologically organized in a complementary way. A different symmetrical distribution is seen if the axis of symmetry is placed at 82 min.

In recent years, several laboratories have shown that DNA replication in *E. coli* strains K-12 and B/r proceeds bidirectionally from a replication origin in the vicinity of the *ilv* genes. For example, Louarn et al. (428) have shown that the *ilv* and *rha* genes, located at min 83 and 86, respectively, are among the first genes to be replicated in synchronized cells. Hohlfeld and Vielmetter (315) employed sequential mutagenesis of specific gene loci in synchronized cells to determine the map positions of the replication origin and terminus. Their data, when replotted on the recalibrated map, suggest that the origin and terminus are located at min 86 and 32, respectively. The axis of symmetry defined by estimates of the bidirectional replication origin thus lies close to two possible axes of symmetry that we discern solely from the map positions of gene clusters. The coincidence of these two independent parameters further strengthens the conjecture that the chromosome of *E. coli* may be divided into two half-genomes that are functionally and topologically complementary to each other in the condensed nucleoid structure.

Interestingly, the terminus of DNA replication at min 32 is located in the longest silent region of the map. Perhaps a large proportion of the DNA in this region is utilized for maintaining the structural organization of the dividing nucleoid-membrane complex. It is also noteworthy that nearly half (47%) of all the mapped genes of *E. coli* and virtually all of the genes required for macromolecular synthesis are clustered in the 72- to 5-min segment around the replication origin at min 86. This seems to be a reasonable evolutionary development as it is precisely this part of the genome that will be present in the most copies per nucleoid during rapid growth and multiple initiation of DNA replication cycles.

GENETIC NOMENCLATURE

The system of genetic nomenclature used in this, as in previous editions of the linkage map, is based upon the recommendations of Demerec et al. (165). Within the past 3 years, many new gene symbols have been assigned and a number of old ones have been changed. Some of these changes have been made for the purpose of describing gene functions and relationships more clearly. Other changes have been made so that the nomenclature used in *E. coli* genetics will correspond more closely to that used in *Salmonella* genetics (594). A reciprocal effort is planned (K. Sanderson and P. E. Hartman, manuscript in preparation) which, it is hoped,

TABLE 2. *List of genetic markers of E. coli*

Gene symbol	Mnemonic	Map position (min)[a]	Alternate gene symbols; phenotypic trait affected	References[b]
aceA	Acetate	89	*icl;* utilization of acetate; isocitrate lyase	64, 687
aceB	Acetate	89	*mas;* utilization of acetate; malate synthase A	687
aceE	Acetate	2	*aceE1;* acetate requirement; pyruvate dehydrogenase (pyruvate:cytochrome b_1 oxidodoreductase)	296, 297
aceF	Acetate	2	*aceE2;* acetate requirement; pyruvate dehydrogenase (pyruvate:lipoate oxidoreductase)	296, 297
acrA	Acridine	10	*mb, mbl, mtc;* sensitivity to acriflavine, phenethyl alcohol, sodium dodecyl sulfate	335, 486, 487, 519, 660
alaS	Alanine	57	*ala-act;* alanyl-transfer RNA synthetase	490, 584, W
alnA	Alanine	2	Utilization of D- or L-alanine; D-alanine: pyruvate deaminase	33
alnR	Alanine	99	Regulatory gene	33
alr		92	Alanine racemase	719
ampA	Ampicillin	93	Penicillin resistance; regulation of *ampC*	80, 202
ampC	Ampicillin	93	Penicillin resistance; penicillinase structural gene	80
araA	Arabinose	1	L-Arabinose isomerase	412
araB	Arabinose	1	Ribulokinase	412
araC	Arabinose	1	Regulatory gene; activator and repressor protein	117, 612, 613, 721
araD	Arabinose	1	L-Ribulose-5-phosphate 4-epimerase	412
araE	Arabinose	61	L-Arabinose permease	196, 506
araI	Arabinose	1	Initiator locus	612, 613
araO	Arabinose	1	Operator locus	378
argA	Arginine	60	*argB, Arg1, Arg$_2$;* *N*-acetyl-glutamate synthetase	262, 337, 671, 696
argB	Arginine	88	*argC;* α-*N*-acetyl-L-glutamate-5-phosphotransferase	29, 147, 192, 252, 253, 352, 444, 546, 696
argC	Arginine	88	*argH, Arg2;* *N*-acetyl-γ-glutamyl-phosphate reductase	29, 147, 192, 252, 253, 352, 444, 546, 696
argD	Arginine	73	*argG, Arg$_1$;* acetylornithine aminotransferase	338, 696
argE	Arginine	88	*argA, Arg4;* acetylornithine deacetylase	29, 147, 192, 252, 253, 352, 444, 546, 696
argF	Arginine	6	*argD, Arg5;* ornithine carbamoyltransferase (duplicate gene)	254, 262, 413, 444, 696
argG	Arginine	68	*argE, Arg6;* argininosuccinate synthetase	444, 670, 671, 696
argH	Arginine	88	*argF, Arg7;* argininosuccinate lyase	29, 147, 192, 252, 253, 352, 444, 546, 696
argI	Arginine	95	Ornithine cabamoyltransferase (duplicate gene)	254, 351, 413
argP	Arginine	62	Transport of arginine, ornithine, and lysine	108, 441, 442
argR	Arginine	70	*Rarg;* regulatory gene	262, 350, 367, 444, 696
argS	Arginine	(40)	Arginyl-transfer RNA synthetase	126
aroA	Aromatic	20	3-Enolpyruvylshikimate-5-phosphate synthetase	540, 562, 670
aroB	Aromatic	73	Dehydroquinate synthetase	329, 540, 712
aroC	Aromatic	50	Chorismic acid synthetase	540, 670
aroD	Aromatic	37	5-Dehydroquinate dehydratase	501, 540, 670
aroE	Aromatic	71	Dehydroshikimate reductase	72, 540, 671, 712
aroF	Aromatic	56	DAHP[c] synthetase (tyrosine-repressible isoenzyme)	461, 702, B′
aroG	Aromatic	17	DAHP synthetase (phenylalanine-repressible isoenzyme)	2, 68, 702
aroH	Aromatic	37	DAHP synthetase (tryptophan-repressible isoenzyme)	702
aroI	Aromatic	83	Function unknown	251
aroJ	Aromatic	37	Propable operator locus for *aroH*	95
aroK	Aromatic	56	Operator locus for *aroF, tyrA*	461, B′
aroP	Aromatic	2	General aromatic amino acid transport	69, 70, 273
asd		74	*dap + hom;* aspartate semialdehyde dehydrogenase	121, 288, 606

TABLE 2—*Continued*

Gene symbol	Mnemonic	Map position (min)[a]	Alternate gene symbols; phenotypic trait affected	References[b]
asn	Asparagine	82	Asparagine synthetase	107
aspA	Aspartate	93	Aspartase	452, N
aspB	Aspartate	68	*asp;* aspartate requirement	348, 564
aspC	Aspartate	20	Aspartate aminotransferase	L
ast	Astasia	(4)	Generalized high mutability	759, 760
atoA	Acetoacetate	48	Coenzyme A transferase	535
atoB	Acetoacetate	48	Thiolase II	535
atoC	Acetoacetate	48	Regulatory gene	535
attλ	Attachment	17	Integration site for prophage λ	348, 579
attP2H	Attachment	44	Phage P2 integration site H	46, 93, 376, 661
attP2II	Attachment	85	Phage P2 integration site II	93
attP22	Attachment	6	*ata;* integration site for prophage P22	319
attφ80	Attachment	27	Integration site for prophage φ80	332, 621
att82	Attachment	17	Integration site for prophage 82	348, 579, 627
att186	Attachment	57	Integration site for prophage 186	730
att434	Attachment	17	Integration site for prophage 434	348, 579, 627
azi	Azide	2	*pea;* resistance or sensitivity to sodium azide or phenethyl alcohol; filament formation at 42 C	347, 445, 685, 757
azl	Azaleucine	55	Regulation of *leu* and *ilv* genes	542
bfe		88	*btuB, cer;* resistance or sensitivity to phage BF23 and colicins E1, E2, E3; membrane receptor for site for B_{12} (cyanocobalamin)	87, 356, 366, 383
bfm		83	Phage BF23 multiplication	614
bglA	β-Glucoside	82	*bglD;* phospho-β-glucosidase A	553, 554, 598
bglB	β-Glucoside	82	*bglA;* phospho-β-glucosidase B	553, 554, 598
bglC	β-Glucoside	82	*bglB;* β-glucoside transport	553, 554, 598
bglR	β-Glucoside	82	*bglB, bglC;* regulatory gene	553, 554, 598
bglS	β-Glucoside	82	*bglC;* regulatory gene	553, 554
bglT	β-Glucoside	83	*bglE;* regulatory gene for phospho-β-glucosidase A synthesis	553, 554
bioA	Biotin	17	Group II; 7KAP → DAPA[c]	2, 116, 164, 190, 276, 379, 576, 191
bioB	Biotin	17	Conversion of dethiobiotin to biotin	2, 116, 164, 190, 276, 576
bioC	Biotin	17	Block prior to pimeloyl coenzyme A	2, 116, 164, 190, 276, 576
bioD	Biotin	17	Dethiobiotin synthetase	2, 115, 116, 164, 188, 190, 276, 576
bioF	Biotin	17	Pimeloyl coenzyme A → 7KAP	2, 116, 164, 190, 276, 576
bioH	Biotin	74	*bioB;* block prior to pimeloyl coenzyme A	115, 288, 576, 606
bioO	Biotin	17	Operator for genes *bioB* through *bioD*	115, 276, 379
bioP	Biotin	17	Promoter site for genes *bioB* through *bioD*	115
bioR	Biotin	88	*dhbB;* regulatory gene	189, 523, 524
bir	Biotin retention	89	Biotin uptake, retention, and regulation	96
brnQ	Branched chain	8	Transport system 1 for isoleucine, leucine, and valine	269, 270
brnR	Branched chain	8	Component of transport systems 1 and 2 for isoleucine, leucine, and valine	269
brnS	Branched chain	1	Transport system 2 for isoleucine, leucine, and valine	269
btuA	B_{12} uptake	88	Energy-dependent transport of B_{12} (cyanocobalamin); (possibly identical to *bfe*)	366
bymA		(92)	Bypass of maltose permease at *malB*	313
can	Canavanine	62	Canavanine resistance	442, 443
capS	Capsule	(24)	Regulation of *galU* and of capsular polysaccharide synthesis	74, 455
carA		1	*arg + ura, cap, pyrA;* carbamoylphosphate synthetase: glutamine (light) subunit	31, 467, 670, 671
carB		1	*arg + ura, cap, pyrA;* carbamoylphosphate synthetase: ammonia ,(heavy) subunit	31, 467, 670, 671
cbt		16	Uptake of carboxylic acids	424, 425
cca		66	Transfer RNA nucleotidyltransferase	224
cdd		45	Cytidine deaminase	480
cet	Colicin E2	100	*ref, refII;* tolerance to colicin E2	89, 90, 317, 677
cheA	Chemotaxis	42	*motA;* chemotactic motility	20, 21
cheB	Chemotaxis	42	*motB;* chemotactic motility	20, 21

TABLE 2—*Continued*

Gene symbol	Mnemonic	Map position (min)[a]	Alternate gene symbols; phenotypic trait affected	References[b]
chlA	Chlorate	17	*narA;* pleiotropic effects on nitrate-chlorate reductase and hydrogen lyase activity	2, 446, 557, 558, 689, 690
chlB	Chlorate	85	*narB;* F_A factor of nitrate-bound membranous respiratory system	446, 557, 568, 672, 689
chlC	Chlorate	27	*narC;* structural gene for nitrate reductase	272, 446, 557, 585
chlD	Chlorate	17	*narD, narF;* nitrate reductase, activation by molybdate	2, 446, 644, 690
chlE	Chlorate	18	*narE;* nitrate reductase activity	446, 558, 689, 690
chlF	Chlorate	(26)	Structural gene for formate dehydrogenase	256
chlG	Chlorate	0	Formate-nitrate reductase activity	256
cir	Colicin I resistance	(43)	Receptor for colicins Ia and Ib	102
cmlA	Chloramphenicol	18	Resistance or sensitivity to chloramphenicol	562
cmlB	Chloramphenicol	21	Resistance or sensitivity to chloramphenicol	562
codA		8	Cytosine deaminase	159, 419
codB		8	Cytosine transport	419
cqsA	Sequence	85	5*S* RNA containing sequence UCUCCUCAUG; locus in strain MRE600	177, 535
cqsB	Sequence	83	5*S* RNA containing sequence CCUUAG; locus in strain MRE600	177, 353
cqsC	Sequence	74	5*S* RNA containing sequence CCUUAG; locus in strain MRE600	177, 353
cqsD	Sequence	70	5*S* RNA containing sequence CCUUAG; locus in strain MRE600	177, 353
crp		73	*cap;* cyclic AMP receptor protein[c]	194, 201, 672
cxm		6	*cxr;* synthesis of methyl glyoxal	H
cya		83	Adenyl cyclase	201, 672, 749
cycA	Cycloserine	94	Resistance to D-cycloserine and D-serine; transport of D-alanine, D-serine, and glycine	150, 587, 708
cysA	Cysteine	(52)	Requirement	H
cysB	Cysteine	28	Pleiotropic effects on cysteine biosynthesis	359, 622, 748
cysC	Cysteine	59	ATP-adenylylsulfate 5′-phosphotransferase[c]	359, 360, 465, 671
cysD	Cysteine	59	ATP:sulfate adenylyltransferase	360
cysE	Cysteine	80	Pleiotropic effects on cysteine biosynthesis	569, 369, 389, I
cysG	Cysteine	73	Sulfite reductase	671
cysH	Cysteine	59	Adenosine 3′-phosphate 5′-sulfatophosphate reductase	359, 360
cysI	Cysteine	59	*cysQ;* sulfite reductase	359, 360
cysJ	Cysteine	59	*cysP;* sulfite reductase	359, 360
cytR		87	Regulatory gene for *deo* operon and *udp, cdd* operon	282, 480
dadR		26	Regulatory gene for D-amino acid deaminases	394
dagA		94	Transport of D-alanine, D-serine, and glycine; D-serine and D-cycloserine resistance	130, 570
dam		73	DNA adenine methylation	453, X
dapA	Diaminopimelate	53	Dihydrodipicolinate synthetase	76, 121
dapB	Diaminopimelate	0	Dihydrodipicolinate reductase	76, 211
dapC	Diaminopimelate	3	Tetrahydrodipicolinate → *N*-succinyl diaminopimelate	76
dapD	Diaminopimelate	4	Tetrahydrodipicolinate → *N*-succinyl diaminopimelate	76
dapE	Diaminopimelate	53	*dapB; N*-succinyl-diaminopimelate deacylase	76, 121
dcm		43	*mec;* DNA cytosine methylation	448, 453, X
dctA		79	Uptake of C_4-dicarboxylic acids	375, 424
dctB		16	Uptake of C_4-dicarboxylic acids	375, 424, 425
ddl		2	D-Alanyl:D-alanine ligase	438, 473, 718

TABLE 2—*Continued*

Gene symbol	Mnemonic	Map position (min)[a]	Alternate gene symbols; phenotypic trait affected	References[b]
deoA	Deoxyribose	99	*tpp, TP;* thymidine phosphorylase	6, 53, 210, 426, 663
deoB	Deoxyribose	99	*drm, thyR;* phosphodeoxyribomutase	6, 53, 426, 513, 663
deoC	Deoxyribose	99	*dra, thyR;* phosphodeoxyriboaldolase	6, 53, 426, 513, 663
deoD	Deoxyribose	99	*pup;* purine nucleoside phosphorylase	6, 663
deoO	Deoxyribose	99	Operator for *dra* and *tpp* genes	8, 88
deoR	Deoxyribose	19	*nucR;* regulatory gene for *deo* operon	7, 282, 480
dnaA	DNA	82	DNA synthesis; initiation defective	306, 711, I
dnaB	DNA	91	*exrB; groP;* DNA synthesis	103, 247, 711, 716, P, E′
dnaC	DNA	99	*dnaD;* DNA synthesis; initiation defective	103, 534, 605, 710, 711, 715, 727
dnaE	DNA	4	*polC;* DNA polymerase III and mutator activity	244, 280, 421, 566, 648, 711, V
dnaG	DNA	66	DNA synthesis	490, 427, 711, D
dnaH	DNA	61	DNA synthesis; initiation defective	593
dnaI	DNA	39	DNA synthesis	41, D, K′
dnaP	DNA	84	DNA synthesis; initiation defective	699
dnaS	DNA	81	DNA synthesis; accumulation of small DNA fragments	389
dnaZ	DNA	10	DNA synthesis	217, J′
dpp	Dipeptides	5	Transport of dipeptides	156, O
dsdA	D-Serine	50	D-Serine deaminase	465, 466
dsdC	D-Serine	50	Regulatory gene for *dsdA*	465, 466
dsdO	D-Serine	50	Initiator-operator locus for *dsdA*	45
ebg		65	Mutation leading to second enzyme with β-galactosidase activity	97
eda		41	*kdgA, kga;* 2-keto-3-deoxygluconate-6-phosphate aldolase	207, 226, 228, 547, 549
edd		41	Gluconate-6-phosphate dehydrase	207, 226, 228, 536
endA		63	DNA-specific endonuclease I	182, 732
endB		(19)	DNA-specific endonuclease I	732
eno		59	Enolase	302, 336
entA	Enterochelin	13	2,3-Dihydro-2,3-dihydroxybenzoate dehydrogenase	750
entB	Enterochelin	13	2,3-Dihydro-2,3-dihydroxybenzoate synthetase	750
entC	Enterochelin	13	Isochorismate synthetase	750
entD	Enterochelin	13	Unknown step in conversion of 2,3-dihydroxybenzoate to enterochelin	135, 439
entE	Enterochelin	13	Unknown step in conversion of 2,3-dihydroxybenzoate to enterochelin	439
entF	Enterochelin	13	Unknown step in conversion of 2,3-dihydroxybenzoate to enterochelin	439
envA	Envelope	2	Anomalous cell division involving chain formation	499, 500
envB	Envelope	70	*mon*; anomalous spheroid cell formation	498, 713
envC	Envelope	80	Anomalous cell division involving chain formation	574, 575
envM	Envelope	28	Osmotically remedial envelope defect	184
envN	Envelope	(4)	Osmotically remedial envelope defect	184
envP	Envelope	89	Osmotically remedial envelope defect	184
envQ	Envelope	57	Osmotically remedial envelope defect	184
envT	Envelope	(14)	Osmotically remedial envelope defect	184
exbB		(64)	Insensitivity to colicins B and I; enterochelin excretion	278
fabA	Fatty acid biosynthesis	22	β-Hydroxydecanoylthioester dehydrase	142, 146, 608
fabB	Fatty acid biosynthesis	50	β-Ketoacyl acyl carrier protein synthetase	142, 199, 577
fabC	Fatty acid biosynthesis	46	Biosynthesis of unsaturated fatty acids	67
fabD	Fatty acid biosynthesis	24	Malonyl coenzyme A-acyl carrier protein transacylase	285, 608
fabE	Fatty acid biosynthesis	71	Acetyl-coenzyme A carboxylase	H′
fadA	Fatty acid degradation	85	*oldA*; thiolase I	522
fadB	Fatty acid degradation	85	*oldB*; hydroxyacyl-coenzyme A dehydrogenase	522
fadD	Fatty acid degradation	40	*oldD*; acyl-coenzyme A synthetase	522, L′
fadE	Fatty acid degradation	5	Possibly electron transport flavoprotein for acyl-coenzyme A dehydrogenase(s)	386

TABLE 2—*Continued*

Gene symbol	Mnemonic	Map position (min)[a]	Alternate gene symbols; phenotypic trait affected	References[b]
fda		62	*ald*; fructose-1,6-diphosphate aldolase	48, 583
fdp		94	Fructose diphosphatase	227, 229, 754
fep		13	Defect of enterochelin-dependent iron transport system	134, 439, 750
fesB		13	Component B of ferric enterochelin esterase	406
flaA	Flagella	43	*cheC*; defects in flagellar synthesis and in chemotactic motility	21, 624, 625, 626
flaB	Flagella	43	Defect in flagellar synthesis	624, 625, 626
flaC	Flagella	43	Defect in flagellar synthesis	624, 625, 626
flaD	Flagella	43	Defect in flagellar synthesis	624, 625, 626
flaE	Flagella	43	Defect in flagellar synthesis	624, 625, 626
flaG	Flagella	42	Defect in flagellar synthesis	624, 625, 626
flaH	Flagella	42	Defect in flagellar synthesis	624, 625, 626
flaI	Flagella	42	Defect in flagellar synthesis	624, 625, 626
flaN	Flagella	43	Defect in flagellar synthesis	626
flaO	Flagella	43	Defect in flagellar synthesis	625, 626
flaP	Flagella	43	Defect in flagellar synthesis	625, 626
flaQ	Flagella	43	Defect in flagellar synthesis	625, 626
flaR	Flagella	43	Defect in flagellar synthesis	625, 626
flrA	Fluoroleucine	100	Regulation of *ilv* and *leu* genes	387
folA	Folate	1	*tmrA*; dihydrofolate reductase; trimethoprim resistance	61, F′
folB	Folate	1	*tmrB*; regulatory gene; trimethoprim resistance	61, F′
fpk		46	Fructose-1-phosphate kinase	212, 213, 362
frdA	Fumarate reduction	93	Fumarate reductase	642, 643
frdB	Fumarate reduction	28	Anaerobic fumarate reduction	N
ftsA		2	Anomalous filamentous growth	685, 718
fuc	Fucose	60	L-Fucose utilizaton	209, 671
fus	Fusidic acid	72	*far*; protein chain elongation factor G	261, 400, 495, 668
gabC	γ-Aminobutyrate	61	Regulatory gene for *gabT*	180
gabT	γ-Aminobutyrate	81	γ-Aminobutyrate-α-ketoglutarate transaminase	180
gadR		81	Regulatory gene for *gadS*	440
gadS		81	Glutamic acid decarboxylase	109, 449, 451
galE	Galactose	17	*galD*; uridinediphosphogalactose 4-epimerase	5, 85
galK	Galactose	17	*galA*; galactokinase	5, 85
galO	Galactose	17	*galC*; operator locus	85, 86, 328, 610
galT	Galactose	17	*galB*; galactose-1-phosphate uridyl transferase	5
galR	Galactose	61	Rgal; regulatory gene	86, 592
galU	Galactose	27	Uridinediphosphoglucose pyrophosphorylase	74, 272, 332, 609
gap		39	*gad*; glyceraldehyde-3-phosphate dehydrogenase	302, 336, L′
glc	Glycolate	64	Utilization of glycolate; malate synthetase G	687
glgA	Glycogen	74	Glycogen synthetase	106, 620
glgB	Glycogen	74	α-1,4-Glucan:α-1,4-glucan-6-glucosyltransferase	106, 620
glgC	Glycogen	74	Adenosine diphosphate glucose pyrophosphorylase	106, 620
glk		51	Glucokinase	148
glmS	Glucosamine	82	L-Glutamine:D-fructose-6-phosphate aminotransferase	393, 734
glnA	Glutamine	85	Glutamine synthetase	462
glnS	Glutamine	15	Glutaminyl-transfer RNA synthetase	393
glpA	Glycerol phosphate	48	L-α-Glycerol-3-phosphate dehydrogenase (anaerobic)	233, 385
glpD	Glycerol phosphate	74	*glyD*; D-α-glycerol-3-phosphate dehydrogenase (aerobic)	137, 385, 606
glpF	Glycerol phosphate	87	Facilitated diffusion of glycerol	38
glpK	Glycerol phosphate	87	Glycerol kinase	12, 138
glpT	Glycerol phosphate	48	L-α-Glycerophosphate transport system	137, 233, 385, 535
glpR	Glycerol phosphate	74	Regulatory gene	137
gltA	Glutamate	16	*glut*; citrate synthase	22, 198, 298

TABLE 2—*Continued*

Gene symbol	Mnemonic	Map position (min)[a]	Alternate gene symbols; phenotypic trait affected	References[b]
gltB	Glutamate	(74)	Glutamate synthase	36
gltC	Glutamate	81	Operator locus	449, 450
gltE	Glutamate	80	Glutamyl-transfer RNA synthetase; possible regulatory subunit	143, 408, 481
gltH	Glutamate	(22)	Requirement	449
gltM	Glutamate	(43)	Glutamyl-transfer RNA synthetase	481
gltR	Glutamate	91	Regulatory gene for glutamate permease	450
gltS	Glutamate	81	Glutamate permease	450
gltX	Glutamate	52	Catalytic subunit for glutamyl-transfer RNA synthetase	408, 591
glyA	Glycine	54	Serine hydroxymethyl transferase	153, 671
glyS	Glycine	79	*gly-act*; glycyl-transfer RNA synthetase	49, 221, 569
glyT	Glycine	88	*supA36, sumA, sup15B*; glycine transfer RNA 2	301, 516, 735
glyU	Glycine	61	*suA36, sufD, sumB, supT*; glycine transfer RNA 1	220, 300, 301
glyV	Glycine	94	*suA58, suA78*; glycine transfer RNA 3 (duplicate gene)	101, 220, Z
glyW	Glycine	(42)	*suA58, suA78*; glycine transfer RNA 3 (duplicate gene)	220
gnd		45	Gluconate-6-phosphate dehydrogenase	240, 536
gntM	Gluconate	74	*usgA*; transport and phosphorylation of gluconate	206, 485
gntR	Gluconate	74	Regulatory gene for *edd*; transport and phosphorylation of gluconate	763
gpsA		80	sn-Glycerol-3-phosphate dehydrogenase	143
gpt		5	*gpp, gxu*; guanine-xanthine phosphoribosyltransferase	287, 316, 319
guaA	Guanine	54	gua_b; xanthosine-5′-monophosphate amidotransferase	403, 493, 494, 529, 655, 671
guaB	Guanine	54	gua_a; inosine-5′-monophosphate dehydrogenase	403, 493, 494, 655
guaC	Guanine	99	Guanosine-5′-monophosphate reductase	160, 493
gurB	Glucuronide	73	Utilization of methyl-β-D-glucuronide; possibly identical to *crp*	502, 504, 651
gurC	Glucuronide	(18)	Utilization of methyl-β-D-glucuronide	502, 504
gurD	Glucuronide	(66)	Utilization of methyl-β-D-glucuronide	502
hag	H antigen	43	*H*; flagellar antigens (flagellin)	21, 625, 626
hemA	Hemin	26	Synthesis of δ-aminolevulinic acid	272, 596, 597
hemB	Hemin	8	*ncf*; synthesis of catalase and cytochromes	597
hemE	Hemin	89	Uroporphyrinogen decarboxylase activity; uroporphyrin accumulation	595
hfl		93	High frequency of lysogenization by phage λ	34, 35, 243
hisA	Histidine	44	Isomerase	240, 259
hisB	Histidine	44	Imidazole glycerol phosphate dehydrase:histidinol phosphatase	240, 259
hisC	Histidine	44	Imidazole acetol phosphate transaminase	240, 259
hisD	Histidine	44	Histidinol dehydrogenase	240, 259
hisE	Histidine	44	Phosphoribosyl-adenosine triphosphate-pyrophosphohydrolase	240
hisF	Histidine	44	Cyclase	240, 259
hisG	Histidine	44	Phosphoribosyl-adenosine triphosphate-pyrophosphorylase	240, 259
hisH	Histidine	44	Amido transferase	240, 259
hisI	Histidine	44	Phosphoribosyl-adenosine monophosphate-hydrolase	240, 259
hisO	Histidine	44	Operator locus	240
hsdM	Host specificity	98	*hs, hsm, rm, hsp*; host modification activity; DNA methylase M	19, 57, 123, 279, 411, 688, 729
hsdR	Host specificity	98	*hs, hsr, rm, hsp*,; host restriction activity; endonuclease R	19, 57, 123, 279, 411, 688, 729, 737
hsdS	Host specificity	98	*hss*; specificity determinant for *hsdM* and *hsdR* activities	19, 57, 123, 279, 411, 688, 729
iclR		89	Regulation of glyoxylate cycle	64, 693
ileS	Isoleucine	0	Isoleucyl-transfer RNA synthetase	331, J

TABLE 2—*Continued*

Gene symbol	Mnemonic	Map position (min)[a]	Alternate gene symbols; phenotypic trait affected	References[b]
ilvA	Isoleucine-valine	83	*ile*; threonine deaminase	539, 561
ilvB	Isoleucine-valine	83	Acetolactate synthase I subunit	539, 561
ilvC	Isoleucine-valine	83	*ilvA*; α-hydroxy-β-ketoacid reductoisomerase	539, 561
ilvD	Isoleucine-valine	83	*ilvB*; dehydrase	539, 561
ilvE	Isoleucine-valine	83	*ilvC*; transaminase B	539, 561
ilvF	Isoleucine-valine	54	Valine-insensitive acetolactate synthase activity	542
ilvG	Isoleucine-valine	83	Acetolactate synthase I subunit	155, 268
ilvH	Isoleucine-valine	2	*brnP*; acetolactate synthase II subunit	155, 157, 270, 388
ilvI	Isoleucine-valine	2	Acetolactate synthase II, subunit	155
ilvO	Isoleucine-valine	83	Possible operator locus	560, 561
ilvP	Isoleucine-valine	83	Possible operator locus	560, 561
ilvQ	Isoleucine-valine	83	Induction recognition site for *ilvC*	543
ilvY	Isoleucine-valine	83	Positive control element for *ilvC* induction	543
kdgK		77	2-Keto-3-deoxygluconokinase	550
kdgP		86	Operator site for *kdgT*	548
kdgR		40	Regulator gene for *kdgK*, *kdgT*, and *eda*	550
kdgT		86	Transport of 2-keto-3-deoxygluconate	548
kdpA-D	K-dependent	16	*kac*; requirement for a high concentration of potassium	81, 198
kpsA	K-polysaccharide	(61)	Acidic polysaccharide capsular (K) antigen	517
ksgA	Kasugamycin	1	RNA methylase for 16S ribosomal RNA	295, 639, 641, 762
ksgB	Kasugamycin	(30)	Second-step (high-level) resistance to Kasugamycin	641
lacA	Lactose	8	*a*, *lacAc*; thiogalactoside transacetylase	32, 471, 758
lacI	Lactose	8	*i*; regulator gene	154, 470a, 471
lacO	Lactose	8	*o*; operator locus	154, 471
lacP	Lactose	8	*p*; promoter locus	154, 346, 471
lacY	Lactose	8	*y*; galactoside permease (M protein)	225, 347, 407, 471
lacZ	Lactose	8	*z*; β-galactosidase	347, 445, 471
lamB	Lambda	90	*malB*; phage λ receptor site	311, 312, 606, 607, 676
lar	Large	68	Large cells and radiation resistance	401
lct	Lactate	79	L-Lactate dehydrogenase	528, 536
leuA	Leucine	2	α-Isopropylmalate synthetase	347, 378, 445
leuB	Leucine	2	β-Isopropylmalate dehydrogenase	378
leuC	Leucine	2	α-Isopropylmalate isomerase subunit	378, 637
leuD	Leucine	2	α-Isopropylmalate isomerase subunit	378, 637
leuS	Leucine	14	Leucyl-transfer RNA synthetase	433
lexA		90	*exrA*, *tsl*; resistance or sensitivity to X rays and UV[c]	324, 478, 479
lig		51	*dnaL*, *pdeC*; DNA ligase	263, 322, 323, 482
linB	Lincomycin	(29)	High-level resistance to lincomycin	16
lip	Lipoate	14	Requirement	298, 695
lir		(12)	Increased sensitivity to lincomycin and/or erythromycin	16, 533
livR		20	Regulation of leucine, isoleucine, and valine transport	A
lon	Long form	10	*capR*, *dir*, *muc*; filamentous growth, radiation sensitivity, regulation of *gal* operon, and capsular polysaccharide synthesis	4, 20, 82, 326, 447, 664
lop		51	Probably operator or promoter site for *lig*	263
lpcA		(6)	Lipopolysaccharide core synthesis; resistance to phages T4, T7, and P1	667
lpcB		65	*pon*; lipopolysaccharide core synthesis	667, 672
lpd		2	*dhl*; lipoamide dehydrogenase	11, 273, 274, 275
lstR		20	Leucine-specific transport	A
lysA	Lysine	61	Diaminopimelate decarboxylase	77, 348, 670
lysC	Lysine	90	*apk*; aspartokinase III	530, 674
lysX	Lysine	60	Lysine excretion	357
mac	Macrolide	(25)	Erythromycin growth dependence	640
maf		1	Maintenance of autonomous sex factor	698, M′
malE		90	*malB*; maltose permeation; periplasmic maltose-binding protein	311, 312, 606, 607, 676
malF	Maltose	90	*malB*; maltose permeation	311, 312, 606, 607, 676

TABLE 2—*Continued*

Gene symbol	Mnemonic	Map position (min)[a]	Alternate gene symbols; phenotypic trait affected	References[b]
malI	Maltose	74	Initiator site	313
malK	Maltose	90	*malB*; maltose permeation	311, 312, 606, 607, 676
malP	Maltose	74	*malA*; maltodextrin phosphorylase	288, 289, 314, 348, 606
malQ	Maltose	74	*malA*; amylomaltase	288, 289, 314, 348, 606
malT	Maltose	74	*malA*; regulatory gene for *malPQ* and *malEFK-lamB* operons	288, 289, 314, 348, 606, 676
man	Mannose	36	Phosphomannose isomerase	456, 501, 676
mdh		69	Malate dehydrogenase	292
melA	Melibiose	92	*mel-7*; α-galactosidase	604, E′
melB	Melibiose	92	*mel-4*; thiomethylgalactoside permease II	555, 604, E′
menA	Menaquinone	87	Requirement	492
metA	Methionine	89	met_3; homoserine *O*-transsuccinylase	325, 348, 582, 606
metB	Methionine	87	*met-1*, met_1; cystathionine synthetase	252, 348, 582, 670
metC	Methionine	64	Cystathionase	582, 671, 714
metD	Methionine	5	Uptake of D- and L-methionine	127, 365, 368
metE	Methionine	84	*met-*B_{12}; N^5-methyltetrahydropteroyl triglutamate-homocysteine methylase	187, 632, 670
metF	Methionine	87	*met-2*, met_2; N^5-N^{10}-methylenetetrahydrofolate reductase	252, 253, 348, 632, 674
metG	Methionine	47	Methionyl-transfer RNA synthetase	46
metH	Methionine	90	B_{12}-dependent homocysteine-N^5-methyltetrahydrofolate transmethylase	366
metJ	Methionine	87	Possible regulatory gene	659
metK	Methionine	63	*S*-adenosylmethionine synthetase activity	265, 330, 442
metL	Methionine	87	Aspartokinase II	674
metM	Methionine	87	Homoserine dehydrogenase II	674
mglA	Methyl-galactoside	45	*mglP*; methyl-galactoside transport and galactose taxis	54, 237, 514, 515, 581
mglB	Methyl-galactoside	45	*mglP*; galactose binding protein, structural gene	54, 237, 514, 515, 581
mglC	Methyl-galactoside	45	*mglP*; methyl-galactoside transport and galactose taxis	54, 237, 514, 515, 581
mglR	Methyl-galactoside	(17)	*R-MG*; regulatory gene	237
minA	Minicell	10	Formation of minute cells containing no DNA	119, 231, G
minB	Minicell	(29)	Formation of minute cells containing no DNA	119, 231, G
mng	Manganese	(39)	Resistance or sensitivity to manganese	623
mop	Morphogenesis of phages	93	*groE*, *tabB*; defect of head assembly in phages T4 and λ	129, 246, 649, 665
mot	Motility	42	Flagellar paralysis	21, 624, 625, 626
mraA	Murein	2	D-Alanine carboxypeptidase	473
mraB	Murein	2	D-Alanine requirement; cell wall peptidoglycan biosynthesis	473
mrbA	Murein	89	UDP-*N*-acetylglucosaminyl-3-enolpyruvate reductase activity[c]	473
mrbB	Murein	89	D-Alanine requirement; cell wall peptidoglycan biosynthesis	473
mrbC	Murein	89	Cell wall peptidoglycan biosynthesis	473
mtlA	Mannitol	80	Mannitol-specific enzyme II of phosphotransferase *(pts)* system	414, 636, 670
mtlC	Mannitol	80	Regulatory site or gene	414, 636
mtlD	Mannitol	80	Mannitol-1-phosphate dehydrogenase	414, 636
mtr	Methyltryptophan	68	Resistance to 5-methyltryptophan	304
mul		81	Mutability of UV-irradiated phage λ	697
murC	Murein	2	L-Alanine adding enzyme	436, 718
murE	Murein	2	*meso*-Diaminopimelate adding enzyme	436, 437, 473, 718
murF	Murein	2	*mra*; D-alanyl:D-alanine adding enzyme	436, 718
mutD	Mutator	5	Generalized high mutability; thymidine stimulated	158
mutH	Mutator	61	*mutR*, *prv*; increased rates of frameshift and base substitution mutations	308, 380, 491
mutL	Mutator	93	*mut-25*; high rates of AT ⇌ GC transitions	417, 619, G′
mutS	Mutator	58	High rates of AT ⇌ GC transitions	131, 618

TABLE 2—*Continued*

Gene symbol	Mnemonic	Map position (min)[a]	Alternate gene symbols; phenotypic trait affected	References[b]
mutT	Mutator	2	High rate of AT → GC transversion	132, 294, 618, 628
nadA	Nicotinamide adenine dinucleotide	16	*nicA*; quinolinate synthetase, A protein	2, 266, 671
nadB	Nicotinamide adenine dinucleotide	55	*nicB*; quinolinate synthetase, B protein	266, 348, 682
nadC	Nicotinamide adenine dinucleotide	2	Quinolinate phosphoribosyl transferase	248, 681
nagA	*N*-acetylglucosamine	15	*N*-acetylglucosamine-6-phosphate deacetylase	318
nagB	*N*-acetylglucosamine	15	*glmD*; glucosamine-6-phosphate deaminase	318, 734
nalA	Nalidixic acid	48	Resistance or sensitivity to nalidixic acid	284, 385, 535
nalB	Nalidixic acid	57	Resistance or sensitivity to nalidixic acid	284, 730
neaB	Neamine	73	Resistance to neamine	100
nirA	Nitrite reductase	26	Cytochrome c_{552} biosynthesis	122, 179
non	Nonmucoid	45	Block in capsule formation	559
nrdA		48	*dnaF*; ribonucleoside diphosphate reductase; subunit B1	235, 711
nrdB		48	Ribonucleoside diphosphate reductase: subunit B2	235
opp		27	Oligopeptide transport	27, 156
pabA	*p*-Aminobenzoate	73	Requirement	329, 712
pabB	*p*-Aminobenzoate	40	Requirement	329, L′
pan	Pantothenate	3	Requirement	69, 166, 671, 681
pdxA	Pyridoxine	1	Requirement	671
pdxB	Pyridoxine	50	Requirement	167
pdxC	Pyridoxine	20	Requirement	146, 669, 672
pdxJ	Pyridoxine	55	Pyridoxal requirement; possibly pyridoxol-5′-phosphate oxidase	I′
pdxH	Pyridoxine	36	Requirement	I′
pepD	Peptides	5	Peptidase (general) specific for dipeptides	O
pepH	Peptides	5	Carnosinase	O
pfkA		87	Fructose-6-phosphate kinase	12, 475, 692
pfkB		38	Suppressor of *pfkA* mutations	694
pfkC		(59)	Modifier of fructose-6-phosphate kinase activity	694
pgi		90	Phosphoglucoisomerase	227
pgk		65	Phosphoglycerate kinase	336
pgl		17	*blu*; 6-phosphogluconolactonase	395
pgm		(15)	Phosphoglucomutase	3
pheA	Phenylalanine	56	Chorismate mutase P-prephenate dehydratase	540, 670, 671, B′
pheO	Phenylalanine	56	Operator locus	334
pheS	Phenylalanine	38	*phe-act*; phenylalanyl-transfer RNA synthetase, α subunit	50, 591, E, L′
pheT	Phenylalanine	38	*pheS*; phenylalanyl-transfer RNA synthetase, β subunit	E
phoA	Phosphate	8	Alkaline phosphatase, structural gene	183, 489, 740
phoB	Phosphate	9	*phoT*; alkaline phosphatase	58, 474, 739
phoR	Phosphate	9	*R1pho, R1*; regulatory gene	183, 489, 740
phoS	Phosphate	82	*R2pho, R2*; inorganic phosphate transport	15, 183, 381, 724, 725
phoT	Phosphate	82	*phoS*; inorganic phosphate transport	724, 725
phx	Phi-X		Locus in *E. coli* C determining ϕX174 sensitivity	464
phr	Photoreactivation	17	Photoreactivation of UV-damaged DNA	662, 686
pil	Pili	98	*fim*; presence or absence of pili (fimbriae)	445
pit	P_i transport	76	Inorganic phosphate transport system	645, 725
pldA	Phospholipid degradation	84	Phospholipase A (detergent resistant)	1
plsA	Phospholipid synthesis	11	Glycerol-3-phosphate acyltransferase activity	145
plsB	Phospholipid synthesis	77	Glycerol-3-phosphate acyltransferase activity	144
pncA	Pyridine nucleotide cycle	39	*nam*; nicotinamide deamidase	173, 526, L′

TABLE 2—*Continued*

Gene symbol	Mnemonic	Map position (min)[a]	Alternate gene symbols; phenotypic trait affected	References[b]
pncH	Pyridine nucleotide cycle	39	Hyperproduction of nicotinamide deamidase	526
pnp		68	Polynucleotide phosphorylase	564
poaA		22	Proline oxidase	124, 608
poaR		62	Regulation of proline oxidase	125
polA	Polymerase	85	*resA*; DNA polymerase I	37, 163, 267, 372
polB	Polymerase	2	DNA polymerase II	98, 99, 305
polC	Polymerase	4	See *dnaE*	
popA	Porphyrin	11	Ferrochelatase	136, 551
popB	Porphyrin	17	*sec*; coproporphyrinogen oxidase	136, 551
popC	Porphyrin	4	Synthesis of δ-aminolevulinate	551, V
popD	Porphyrin	(1)	5-Aminolevulinic dehydratase	551
popE	Porphyrin	(84)	Porphobilinogen deaminase	551
ppc		88	*glu, asp*; phosphoenolpyruvate carboxylase	252, 253, 348
pps		37	Phosphopyruvate synthetase	63, L′
prd	Propanediol	59	1,2-Propanediol dehydrogenase	589, 738
proA	Proline	6	pro_1; block prior to L-glutamate semialdehyde	65, 111, 149, 319, 573, 670, H
proB	Proline	6	pro_2; block prior to L-glutamate semialdehyde	65, 111, 149, 319, 573, 670, H
proC	Proline	9	pro_3; Pro2; probably Δ-pyrroline-5-carboxylate reductase	111, 149, 489
psd		93	Phosphatidylserine decarboxylase	291
pst		82	Inorganic phosphate transport system	645, 724, 725
pth		26	Peptidyl-transfer RNA hydrolase	468
ptsF	Phosphotransferase system	46	Fructose phosphotransferase enzyme II	213, 362
ptsG	Phosphotransferase system	24	*cat, CR, gpt, gptA, tgl, umg*; glucosephosphotransferase enzyme II	56, 148, 197, 392, 608, 683
ptsH	Phosphotransferase system	52	*ctr, Hpr*; phosphotransferase system: protein cofactor	152, 197, 200, 418, 706
ptsI	Phosphotransferase system	52	*ctr*; phosphotransferase system: enzyme I	152, 197, 200, 418, 706
ptsM	Phosphotransferase system	40	*gptB, mpt, ptsX*; mannosephosphotransferase enzyme II	148, 197, 213, 362, 390, Q
purA	Purine	93	ade_k, Ad_4; adenylosuccinate synthetase	202, 348
purB	Purine	25	ade_h; adenylosuccinase	608, 622, 655, 670
purC	Purine	53	ade_g; phosphoribosyl-aminoimidazole-succinocarboxamide synthetase	200, 493, 655
purD	Purine	89	$adth_a$; phosphoribosylglycineamide synthetase	356, 655, 670
purE	Purine	12	ade_3, ade_f, Pur_2; phosphoribosyl-aminoimidazole carboxylase	175, 655
purF	Purine	50	$ade_{u,b}$, *purC*; phosphoribosyl-pyrophosphate amidotransferase	655, 670, 671
purG	Purine	54	$adth_b$; phosphoribosylformylglycineamidine synthetase	655, 681
purH	Purine	89	ade_i; phosphoribosyl-aminoimidazole-carboxamide formyltransferase	655
purI	Purine	55	Aminoimidazole ribotide synthetase	680, 681
pyrA	Pyrimidine	0	See *car*	
pyrB	Pyrimidine	95	Aspartate carbamyltransferase	31, 670
pyrC	Pyrimidine	23	Dihydroorotase	31, 608, 622
pyrD	Pyrimidine	21	Dihydroorotate dehydrogenase	31, 622
pyrE	Pyrimidine	81	Orotidylate pyrophosphorylase	598, 670, I
pyrF	Pyrimidine	28	Orotidylate decarboxylase	622
pyrG	Pyrimidine	59	Cytidinetriphosphate synthetase	K, M
pyrH	Pyrimidine	(4)	Uridinemonophosphate kinase	M
qmeA		28	*gts*; unspecified membrane defect	717, 720
qmeC		73	Unspecified membrane defect; tolerance to glycine and penicillin sensitivity	720
qmeD		61	Unspecified membrane defect; tolerance to glycine and penicillin sensitivity	720
qmeE		37	Unspecified membrane defect	720
rac	Recombination activation	31	Suppressor of *recB* and *recC* mutant phenotype in merozygotes	432
ranA		56	Defect in RNA metabolism	18

TABLE 2—*Continued*

Gene symbol	Mnemonic	Map position (min)[a]	Alternate gene symbols; phenotypic trait affected	References[b]
ras	Radiation sensitivity	(9)	Sensitivity to UV and X rays	700, 701
rbsK	Ribose	83	Ribokinase	13
rbsP	Ribose	83	D-Ribose permease	13, 671
recA	Recombination	58	*recH, tif, zab*; competence for genetic recombination and repair of radiation damage	104, 271, 307, 653, 722, Y
recB	Recombination	60	Competence for genetic recombination and repair of radiation damage; exonuclease V subunit	195, 258, 324, 679, 722, 723, 733
recC	Recombination	60	Competence for genetic recombination and repair of radiation damage; exonuclease V subunit	195, 258, 679, 723, 733
recF	Recombination	82	*uvrF*; competence for genetic recombination and repair of radiation damage	320, 654
recG	Recombination	(82)	Competence for genetic recombination	653
recL	Recombination	84	Competence for genetic recombination and repair of radiation damage	320, T
relA	Relaxed	59	*RC*; regulation of RNA synthesis	9, 218
rep	Replication	83	Inhibition of replication of certain phages	92, 169, 405, 616
rfa	Rough	80	*lps*; lipopolysaccharide core biosynthesis	204, 602, 603
rfbA	Rough	45	Thymidinediphosphoglucose pyrophosphorylase	518, 661
rfbB	Rough	45	Thymidinediphosphoglucose oxidoreductase	240, 518, 661
rfbD	Rough	45	Thymidinediphosphorhamnose synthetase	518, 661
rhaA	Rhamnose	86	L-Rhamnose isomerase	253, 552
rhaB	Rhamnose	86	L-Rhamnulokinase	253, 552
rhaC	Rhamnose	86	Regulatory gene	253, 552
rhaD	Rhamnose	86	L-Rhamnulose-1-phosphate aldolase	253, 552
rho		83	*SuA, rnsC*; termination factor rho; polarity suppressor	73
rimA	Ribosomal modification	82	Defect in maturation of 50S ribosomal subunits	73
rimB	Ribosomal modification	37	Defect in maturation of 50S ribosomal subunits	73
rimC	Ribosomal modification	(25)	Defect in maturation of 50S ribosomal subunits	73
rimD	Ribosomal modification	(87)	Defect in maturation of 50S ribosomal subunits	73
rimE	Ribosomal modification	72	Modification of ribosomal proteins	U
rimF	Ribosomal modification	1	*res*; ribosomal modification	242
rimG	Ribosomal modification	(2)	*ramB*; modification of 30S ribosomal subunit S4	762
rna	Ribonuclease	14	*rns, rnsA*; ribonuclease I	18, 565, 658
rnc	Ribonuclease	55	Ribonuclease III	18, 658
rodA	Rod shape	14	Rounded morphology, radiation resistance, and drug sensitivities	460
rorA		60	Resistance to X rays	257
rpiA		62	Ribose-5-phosphate isomerase (constitutive)	629
rplA	Ribosomal protein, large	88	50S ribosomal subunit protein L1	420
rplB	Ribosomal protein, large	72	50S ribosomal subunit protein L2	354a, 495
rplC	Ribosomal protein, large	72	50S ribosomal subunit protein L3	354a, 495
rplD	Ribosomal protein, large	72	*eryA*; 50S ribosomal subunit protein L4	72, 162, 354a, 495, 527, 640, 666
rplE	Ribosomal protein, large	72	50S ribosomal subunit protein L5	354a, 495
rplF	Ribosomal protein, large	72	50S ribosomal subunit protein L6	354a, 495
rplH	Ribosomal protein, large	88	50S ribosomal subunit protein L8	420
rplJ	Ribosomal protein, large	88	50S ribosomal subunit protein L10	420

TABLE 2—*Continued*

Gene symbol	Mnemonic	Map position (min)[a]	Alternate gene symbols; phenotypic trait affected	References[b]
rplK	Ribosomal protein, large	88	50S ribosomal subunit protein L11	234, 420, 709
rplL	Ribosomal protein, large	88	50S ribosomal subunit protein L7/L12	219, 234, 420, 709
rplN	Ribosomal protein, large	72	50S ribosomal subunit protein L14	354a, 495
rplO	Ribosomal protein, large	72	50S ribosomal subunit protein L15	354a, 495
rplP	Ribosomal protein, large	72	50S ribosomal subunit protein L16	354a, 495
rplQ	Ribosomal protein, large	72	50S ribosomal subunit protein L17	354
rplR	Ribosomal protein, large	72	50S ribosomal subunit protein L18	354a, 495
rplV	Ribosomal protein, large	72	50S ribosomal subunit protein L22	72
rplX	Ribosomal protein, large	72	50S ribosomal subunit protein L24	354a, 495
rpmC	Ribosomal protein, large	72	50S ribosomal subunit protein L29	354a, 495
rpmD	Ribosomal protein, large	72	50S ribosomal subunit protein L30	354a, 495
rpoA	RNA polymerase	72	RNA polymerase: α-subunit	354, D′
rpoB	RNA polymerase	89	*groN, rif, ron, stl, stv*; RNA polymerase: β-subunit	25, 174, 245, 293, 343, 349, 356, 382, 383, 472, 516, 600, 633, 756, D′
rpoC	RNA polymerase	89	RNA polymerase: β'-subunit	205, 384, 488, 525, D′
rpsB	Ribosomal protein, small	4	30S ribosomal subunit protein S2	A′
rpsC	Ribosomal protein, small	72	30S ribosomal subunit protein S3	354a, 495
rpsD	Ribosomal protein, small	72	*ramA, sud2*; 30S ribosomal subunit protein S4	215, 216, 354, 354a, 354b, 420a, 578, 761
rpsE	Ribosomal protein, small	72	*eps, spcA, spc*; 30S ribosomal subunit protein S5	14, 17, 72, 162, 171, 219, 354a, 354b, 420a, 712
rpsF	Ribosomal protein, small	72	*nek*; possibly 30S ribosomal subunit protein S6	17, 72
rpsG	Ribosomal protein, small	72	*K12*; 30S ribosomal subunit protein S7	72, 354a, 355, 463, 495
rpsH	Ribosomal protein, small	72	30S ribosomal subunit protein S8	354a, 354b, 420a, M′
rpsJ	Ribosomal protein, small	72	30S ribosomal subunit protein S10	354a, 495
rpsK	Ribosomal protein, small	72	30S ribosomal subunit protein S11	354, 354a, 354b, 420a
rpsL	Ribosomal protein, small	72	*strA*; 30S ribosomal subunit protein S12	60, 72, 162, 219, 348, 354a, 355, 495, 521a, 578, 606
rpsM	Ribosomal protein, small	72	30S ribosomal subunit protein S13	354, 354a, 354b, 420a
rpsN	Ribosomal protein, small	72	30S ribosomal subunit protein S14	354a, 354b, 420a
rpsQ	Ribosomal protein, small	72	*neaA*; 30S ribosomal subunit protein S17	100, 354a, 495, C
rpsR	Ribosomal protein, small	94	30S ribosomal subunit protein S18	52, 172, 370
rpsS	Ribosomal protein, small	72	30S ribosomal subunit protein S19	354a, 495
rpsT	Ribosomal protein, small	0	*supS20*; 30S ribosomal subunit protein S20	51, K
rrnA	Ribosomal RNA	85	Gene cluster for 16SrRNA, spacer, and 23SrRNA	42, 170, 193, 458, 755
rrnB	Ribosomal RNA	88	Gene cluster for 16SrRNA, spacer, and 23SrRNA	42, 170, 193, 355, 420, 458, 755
rrnC	Ribosomal RNA	83	Gene cluster for 16SrRNA, spacer, and 23SrRNA	42, 170, 193, 355, 458, 755
rts		88	*ts-9*; uncharacterized growth defect	219, 709
ruv		41	Filament formation and sensitivity to UV radiation	344, 521

TABLE 2—*Continued*

Gene symbol	Mnemonic	Map position (min)[a]	Alternate gene symbols; phenotypic trait affected	References[b]
sbcA		30	Suppressor of *recB, recC*: control of exonuclease VIII	28, 397, 422, 423
sbcB		44	Suppressor of *recB, recC*: exonuclease I	28, 396, 398, 673
sdh		16	Succinate dehydrogenase	141
seg	Segregation	(100)	Replication of F′ factors	290
serA	Serine	62	3-Phosphoglycerate dehydrogenase	670, 671, 684
serB	Serine	100	Phosphoserine phosphatase	671, 684
serC	Serine	20	*pdxF*; 3-phosphoserine-2-oxoglutarate aminotransferase	113, 168, 309
serO	Serine	20	Operator locus	113, 114
serS	Serine	20	Seryl-transfer RNA synthetase	113, 114, 453
shiA	Shikimate	43	Shikimate and dehydroshikimate permease	541
speA	Spermidine	63	Arginine decarboxylase	442
speB	Spermidine	63	Agmatine ureohydrolase	442, 443
speC	Spermidine	63	Ornithine decarboxylase	147a
spoT	Spotless	81	Guanosine polyphosphate metabolism	402, 647
srlA	Sorbitol	58	*sbl*; sorbitolphosphotransferase enzyme II	414, Y
srlC	Sorbitol	58	*sbl*; regulatory gene	414, Y
srlD	Sorbitol	58	*sbl*; sorbitol-6-phosphate dehydrogenase	414, Y
srnA	Stable RNA	9	Degradation of stable RNA	509
strB	Streptomycin	5	Low-level streptomycin resistance	573
strM	Streptomycin	76	Control of ribosomal ambiguity	593a
stsA		83	Altered ribonuclease II activity	415
stsB		13	Starvation sensitivity: ribosome biosynthesis	B
sucA	Succinate	16	*lys + met, suc*; α-ketoglutarate dehydrogenase (decarboxylase component)	298, 299, 671
sucB	Succinate	16	*lys + met, suc*; α-ketoglutarate dehydrogenase (dihydrolipoyltranssuccinylase component)	298, 299
sul		22	Suppressor of *lon* mutation	176, 358
supB	Suppressor	15	su_B; suppressor of ochre mutations	62
supC	Suppressor	27	su_C; suppressor of ochre mutations	62, 236, 622, 656
supD	Suppressor	43	su_I, *Su-1*; suppressor of amber mutations	239, 310, 622, 656
supE	Suppressor	15	su_{II}, *Su-2*; suppressor of amber mutations	198, 239, 622
supG	Suppressor	16	*Su-5*; suppressor of ochre mutations	236
supH	Suppressor	43	Suppressor	185, 187
supL	Suppressor	16	Suppressor of ochre mutations	186, 187
supN	Suppressor	52	Suppressor of ochre mutations	186, 187, 465
supO	Suppressor	27	Suppressor of ochre mutations (possibly identical to *supC*)	186, 187
supQ	Suppressor	12	Suppressor	590
supV	Suppressor	(84)	*su8*; suppressor of ochre mutations	634
tdk		27	Deoxythymidine kinase	303, 332
tfrA	T-four	(6)	Resistance or sensitivity to phages T3, T7, λ, and possibly T4	149, G
thiA	Thiamine	89	*thi*; thiamine thiazole requirement	356, 373, 516, 655
thiB	Thiamine	89	Thiaminephosphate pyrophosphorylase deficiency	373
thiC	Thiamine	89	Thiamine pyrimidine requirement	374
thiO	Thiamine	89	Probable operator locus for *thiA, B, C* genes	S
thrA	Threonine	0	*HS, thrD*; aspartokinase I-homoserine dehydrogenase I	208, 238, 255, 347, 445, 531, 532, 674, 675
thrB	Threonine	0	Homoserine kinase	238, 674, 675
thrC	Threonine	0	Threonine synthetase	238, 674, 675
thrT	Threonine	88	Threonine transfer RNA 3	738
thyA	Thymine	60	Thymidylate synthetase	10, 20, 671
tkt		62	Transketolase	363
tnaA		82	*ind*; tryptophanase	241, 538
tnaR		82	Regulatory gene	241
tolA	Tolerance	16	*cim, tol-2*; tolerance to colicins E2, E3, A, and K	39, 40, 483, 484, 496, 563

TABLE 2—*Continued*

Gene symbol	Mnemonic	Map position (min)[a]	Alternate gene symbols; phenotypic trait affected	References[b]
tolB	Tolerance	16	*tol-3*; tolerance to colicins E1, E2, E3, A, and K	39, 40, 483, 484, 496, 563
tolC	Tolerance	65	*colE1-i, mtcB, tol-8, refI*; specific tolerance to colicin E1	118, 317, 484, 520, 714
tolD	Tolerance	(22)	Tolerance to colicins E2 and E3; ampicillin resistance	79, 203
tolE	Tolerance	(22)	Tolerance to colicins E2 and E3; ampicillin resistance	203
tolF	Tolerance	(21)	Tolerance to bacteriocin JF246 and colicins A and K	223
tolG	Tolerance	21	Tolerance to bacteriocin JF246; specific membrane protein	109, 222
tolI	Tolerance	(0)	Tolerance to colicins Ia and Ib	102
tolP	Tolerance	16	Promoter locus for *tolA*	39, 40
tonA	T-one	3	*T1, T5rec*; resistance or sensitivity to phages T1 and T5	149, 166, 445
tonB	T-one	27	*exbA, T1rec*; resistance to phages T1, ϕ80, colicins B, I, V; transport of Fe; enterochelin excretion	264, 277, 278, 621, 704, 748
tpi		86	Triosephosphate isomerase	12
trkA		72	Transport of potassium	201
trkB		72	Transport of potassium	201
trkC		1	Transport of potassium	201
trkD		83	Transport of potassium	201
trkE		28	Transport of potassium	201
trmA		88	Methylase for 5-methyluracil in transfer RNA	43, 44
trmB		(6)	Synthesis of 7-methylguanosine in transfer RNA	454
trmC		(55)	Synthesis of 2-thio-5-methylaminomethyluridine in transfer RNA	454
trpA	Tryptophan	27	*tryp-2*; tryptophan synthetase, A protein	139, 339, 747, 748
trpB	Tryptophan	27	*tryp-1*; tryptophan synthetase, B protein	139, 339, 747, 748
trpC	Tryptophan	27	*tryp-3*; *N*-(5-phosphoribosyl) anthranilate isomerase–indole-3-glycerolphosphate synthetase	139, 339, 747, 748
trpD	Tryptophan	27	*tyrE*; glutamine amidotransferase–phosphoribosyl anthranilate transferase	139, 181, 339, 345, 459, 747
trpE	Tryptophan	27	*anth, tryp-4, tryD*; anthranilate synthetase, large subunit	139, 339, 747, 748
trpO	Tryptophan	27	Operator locus	139, 459, 638, 747
trpP	Tryptophan	27	Tryptophan permease	394
trpR	Tryptophan	100	*Rtry*; regulatory gene for the *trp* operon and *aroH*	95, 120, 340, 341
trpS	Tryptophan	73	Tryptophanyl-transfer RNA synthetase	178, 340, 342
trpT	Tryptophan	83	*su7, supU*; tryptophan transfer RNA	301, 512a, 634, 744
tsx	T-six	9	*T6rec*; resistance or sensitivity to phage T6 and colicin K	149, 175, 232, 445
tufA		72	Protein chain elongation factor Tu	355
tufB		88	Protein chain elongation factor Tu	355
tyrA	Tyrosine	56	Chorismate mutase T–prephenate dehydrogenase	540, 670, 671, B′
tyrB	Tyrosine	90	Tyrosine-repressible L-tyrosine:2-oxyglutarate aminotransferase activity	L
tyrR	Tyrosine	29	Regulation of *aroF, aroG,* and *tyrA* genes	71, 94, 333, 703
tyrS	Tyrosine	35	Tyrosyl-transfer RNA synthetase	78, 601
tyrT	Tyrosine	27	*supF*; tyrosine transfer RNA 1	239, 249, 260, 586
tyrU	Tyrosine	88	*supM*; tyrosine transfer RNA 2	516, 735
ubiA	Ubiquinone	90	4-Hydroxybenzoate → 3-octaprenyl 4-hydroxybenzoate	133, 751
ubiB	Ubiquinone	84	2-Octaprenylphenol → 2-octaprenyl-6-methoxy-1,4-benzoquinone	133, 135, 657
ubiC	Ubiquinone	90	Chorismate lyase	410, 753
ubiD	Ubiquinone	84	3-Octaprenyl-4-hydroxybenzoate → 2-octaprenylphenol	135
ubiE	Ubiquinone	84	2-Octaprenyl-6-methoxy-1,4-benzoquinone → 2-octaprenyl-3-methyl-6-methoxy-1,4-benzoquinone	752

TABLE 2—*Continued*

Gene symbol	Mnemonic	Map position (min)[a]	Alternate gene symbols; phenotypic trait affected	References[b]
ubiF	Ubiquinone	15	2-Octaprenyl-3-methyl-6-methoxy-1,4-benzoquinone → 2-octaprenyl-3-methyl-5-hydroxy-6-methoxy-1,4-benzoquinone	318, 752
ubiG	Ubiquinone	48	2-Octaprenyl-3-methyl-5-hydroxy-6-methoxy-1,4-benzoquinone → ubiquinone-8	657
ubiH	Ubiquinone	62	2-Octaprenyl-6-methoxyphenol → 2-octaprenyl-6-methoxy-1,4-benzoquinone	753
udk		45	Uridine kinase	281
udp		84	Uridine phosphorylase	556
uhpR		81	Regulation of hexose phosphate transport	364, 369
uhpT		81	Hexose phosphate transport	214, 369, 391, I
uidA		36	*gurA*; β-D-glucuronidase	501, 502, 504
uidR		36	Regulatory gene for *uidA*	503
uncA	Uncoupling	83	Membrane-bound (Mg^{2+}-Ca^{2+}) ATPase[c]	83, 371, 599
uncB	Uncoupling	83	Membrane-bound (Mg^{2+}-Ca^{2+}) ATPase	84
upp		53	*uraP*; uridine monophosphate phosphorylase	537, 658
ush		(9)	Uridine diphosphate-sugar hydrolase	30
uvrA	Ultraviolet	91	*dar-3*; repair of UV damage to DNA; UV endonuclease	59, 325, 686
uvrB	Ultraviolet	17	*dar-1, 6*; repair of UV damage to DNA; UV endonuclease	2, 59, 325, 686
uvrC	Ultraviolet	42	*dar-4, 5*; repair of UV damage to DNA	21, 325, 686
uvrD	Ultraviolet	84	*dar-2, rad*; repair of UV damage to DNA	23, 507, 508, 615, 616, 630, 631, 686, T
uvrE	Ultraviolet	84	*mutU, pdeB, uvr502*; UV sensitivity; generalized mutability; host cell reactivation	321, 616, 617, T
uxaA		66	Galacturonate metabolism; altronic hydrolase	545
uxaB		(52)	Altronate oxidoreductase	544
uxaC		66	Uronic isomerase	505, 544
uxuA		97	Glucuronate metabolism; mannonate hydrolyase	572
uxuB		97	Mannonate oxidoreductase	571
valS		95	*val-act*; valyl-transfer RNA synthetase	47, 654, 678, 745
xonA	Exonuclease I	44	Exonuclease I	741
xthA	Exonuclease III	38	Exonuclease III and endonuclease II	469, 742, L'
xyl	Xylose	79	Utilization of D-xylose	348, 670
zwf	Zwischenferment	41	Glucose-6-phosphate dehydrogenase	230, 536

[a] Numbers refer to time scale shown in Fig. 3. Parentheses indicate approximate map locations.

[b] Numbers refer to Literature Cited. Letters refer to personal communications from the following persons: (A) J. Anderson, S. Quay, and D. Oxender; (B) D. Apirion; (C) M. Cannon, T. Cabezon, and A. Bollen; (D) P. Carl; (E) M. M. Comer and A. Böck; (F) R. A. Cooper; (G) R. Curtiss III; (H) W. Epstein; (I) R. Essenberg; (J) J. Friesen; (K) J. Friesen and N. Fiil; (L) D. Gelfand; (M) N. Glansdorff, A. Pierard, and M. Crabeel; (N) J. R. Guest; (O) P. E. Hartman and M. Kirsch; (P) Y. Hirota; (Q) M. Jones-Mortimer; (R) R. Kadner; (S) T. Kawasaki; (T) S. Kushner; (U) S. Kushner and S. Champney; (V) R. Lathe; (W) K. B. Low and A. J. Clark, unpublished data; (X) M. Marinus; (Y) K. McEntee and W. Epstein; (Z) E. Murgola; (A') M. Nomura and M. Yamamoto; (B') A. J. Pittard, H. J. W. Wijsman, and D. Tribe; (C') D. Ratner; (D') J. G. Scaife and R. S. Hayward; (E') R. Schmitt; (F') R. Sheldon; (G') E. C. Siegel; (H') D. F. Silbert; (I') A. L. Taylor, unpublished data; (J') J. R. Walker; (K') J. Wechsler; (L') B. Weiss; (M') H. G. Wittman, G. Stöffler, D. Geyl, and A. Böck; (N') T. Yura.

[c] DAHP, 3-deoxy-D-arabinoheptulosonate-7-phosphate; 7KAP, 7-oxo-8-aminopelargonate; DAP, 7,8-diaminopelargonate; ATP, adenosine 5'-triphosphate; UDP, uridine 5'-diphosphate; ATPase, adenosine triphosphatase; cyclic AMP, cyclic adenosine 3',5'-monophosphate; UV, ultraviolet light.

will further reduce the confusion that has arisen due to the use of conflicting terminology for these two closely related organisms. A few changes in gene symbols appear to have been made arbitrarily or in ignorance of previously assigned designations, but have been accepted because of wide publication. We strongly urge that persons assigning new gene symbols attempt to avoid the reassignment of symbols that have already been used to designate gene loci in either *Salmonella* or *E. coli* (or in other organisms, if possible) and that they attempt to identify and use symbols already assigned to the loci in question unless these are clearly

TABLE 3. *Alternate gene symbols*

Alternate symbol	Symbol in Table 2	Alternate symbol	Symbol in Table 2
ade	*pur*	*hsp*	*hsd*
ald	*fda*	*hsr*	*hsdR*
$adth_a$	*purD*	*hss*	*hsdS*
$adth_b$	*purG*	*icl*	*aceA*
ala-act	*alaS*	*ile*	*ilvA*
anth	*trpE*	*ind*	*tnaA*
apk	*lysC*	*ins*	*glyV, glyW*
arg + ura	*car*	*K12*	*rpsG*
asp	*ppc*	*kac*	*kdp*
ata	*attP22*	*kdgA*	*eda*
blu	*pgl*	*kga*	*eda*
brnP	*ilvH*	*lps*	*rfa*
btuB	*bfe*	*lys + met*	*sucA, sucB*
cap	*car* and *crp*	*mas*	*aceB*
capR	*lon*	*Mb*	*acrA*
cat	*ptsG*	*mec*	*dcm*
cer	*bfe*	*mbl*	*acrA*
cheC	*flaA*	*mon*	*envB*
cim	*tolA*	*mot*	*che*
colE1-i	*tolC*	*mpt*	*ptsM*
CR	*ptsG*	*mra*	*murF*
ctr	*ptsH, ptsI*	*mtcA*	*acrA*
cxr	*cxm*	*mtcB*	*tolC*
dap + hom	*asd*	*muc*	*lon*
dar	*uvr*	*mutR*	*mutH*
dhbB	*bioR*	*mutU*	*uvrE*
dhl	*lpd*	*nam*	*pncA*
dir	*lon*	*nar*	*chl*
dnaF	*nrdA*	*ncf*	*hemB*
dnaL	*lig*	*neaA*	*rpsQ*
dra	*deoC*	*nek*	*rpsF*
drm	*deoB*	*nic*	*nad*
eps	*rpsE*	*nuc*	*deo*
eryA	*rplD*	*old*	*fad*
eryB	*rplV*	*pdeB*	*uvrE*
exbA	*tonB*	*pdeC*	*lig*
exrA	*lex*	*pdxF*	*serC*
exrB	*dnaB*	*pea*	*azi*
far	*fus*	*phe-act*	*pheS*
fim	*pil*	*PMG*	*mgl*
gad	*gap*	*polC*	*dnaE*
glmD	*nagB*	*pon*	*lpcB*
glu	*ppc*	*prv*	*mutH*
glut	*gltA*	*pup*	*deoD*
gly-act	*glyS*	*pyrA*	*car*
glyD	*glpD*	*rad*	*uvrD*
gpp	*gpt*	*ramA*	*rpsD*
gpt	*ptsG*	*ramB*	*rimG*
gptB	*ptsM*	*RC*	*rel*
groE	*mop*	*refI*	*tolC*
groN	*rpoB*	*refII*	*cet*
groP	*dnaB*	*relC*	*rplK*
gts	*qmeA*	*res*	*rimF*
gurA	*uidA*	*resA*	*polA*
gxu	*gpt*	*rif*	*rpoB*
H	*hag*	*RMG*	*mglR*
Hpr	*ptsH*	*rm*	*hsd*
hs	*hsd*	*rnsA*	*rna*
Hs	*thrA*	*rnsC*	*rho*
hsm	*hsdM*	*ron*	*rpoB*

TABLE 3—*Continued*

Alternate symbol	Symbol in Table 2	Alternate symbol	Symbol in Table 2
rpx	*rps*	sup_{S20}	*rpsT*
rpy	*rpl*	*supT*	*glyU*
rpz	*rpm*	*supU*	*trpT*
sbl	*srl*	*T1rec*	*tonB*
sec	*popB*	*T1, T5 rec*	*tonA*
som	*rfb*	*T6rec*	*tsx*
spcA	*rpsE*	*tabB*	*mop*
stl	*rpoB*	*tgl*	*ptsG*
strA	*rpsL*	*thyR*	*deoB, deoC*
stv	*rpoB*	*tif*	*recA*
Su, su	*sup*	*tmr*	*fol*
SuA	*rho*	*TP*	*deoA*
suA36	*glyU*	*tpp*	*deoA*
suA58	*glyV* or *glyW*	*try*	*trp*
suA78	*glyV* or *glyW*	*tryp*	*trp*
sud_2	*rpsD*	*ts-9*	*rts*
sufD	*glyU*	*tsl*	*lex*
sumA	*glyT*	*umg*	*ptsG*
sumB	*glyU*	*uraP*	*upp*
sup15B	*glyT*	*usgA*	*gntM*
supA36	*glyT*	*uvrF*	*recF*
supF	*tyrT*	*val-act*	*valS*
supM	*tyrU*	*zab*	*recA*

unsuitable. We would also like to suggest that the reshuffling of locus designations within a metabolic pathway, to make the gene designated A correspond to the first enzymatic step in that pathway and the gene designated B to the second step, may cost more in terms of the considerable confusion created by changing published designations than is gained by making it slightly easier to remember the designations.

The list of genetic markers is now so long that alternate gene symbols are not listed for the purpose of cross-reference in column 1 of Table 2. All previously used gene symbols of which we are aware are now listed in Table 3, alongside the symbols that have been used for the corresponding loci in Table 2. The bases for many of the changes in nomenclature will be found in the appropriate references to the Literature Cited, which are given in Table 2.

It is proposed that the genes which code for ribosomal proteins be designated by the symbols *rps* (for ribosomal proteins, small) and *rpl* and *rpm* (for ribosomal proteins, large). Thus the determinants for the 30S ribosomal subunit proteins S1, S2, etc., will be *rpsA, rpsB,* etc. The determinants for the 50S ribosomal subunit proteins L1 through L26 will be *rplA* through *rplZ* and those for proteins L27, L28, etc. will be *rpmA, rpmB,* etc. This system for naming these loci provides convenient mnemonics that require only the substitution of sequential capital letters for the numbers that have been used to identify these proteins. This maintains the existing system of genetic nomenclature and obviates the need for revising computer programs that handle genetic information coded by this system. It is proposed that all loci determining steps in ribosomal modification be designated *rim*. The determinants for RNA polymerase subunits will be called *pro* (J. G. Scaife and R. S. Hayward, personal communication). Thus, some of the most familiar old drug resistance markers now appear on the map under new symbols: *rif* is now *proB, spcA* is now *rpsE,* and *strA* is now *rpsL*. A number of suppressor loci have been renamed, as it has been established that they specify transfer RNA species. They have accordingly been given designations corresponding to the abbreviations for the appropriate amino acids followed by the capital letters T, U, etc.

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