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Linkage Map of *Escherichia coli* Strain K-12

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INTRODUCTION

Two years ago, the genetic map of *Escherichia coli* K-12 contained approximately 310 known gene loci (156). Since that time about 150 additional genes have been identified and mapped in this bacterium. The aim of this review is to call attention to these many new gene loci in a manner which may help to facilitate the genetic mapping of other new genes in the future. As in past editions of the *E. coli* linkage map, we shall endeavor to do this both by illustrating the positions of genes on a scale drawing of the circular bacterial linkage map (Fig. 1) and by providing an alphabetical list of genes that shows the various specific enzyme activities or other phenotypic traits ascribed to these gene loci (Table 1). Table 1 also contains references to publications on genetic mapping which have appeared since March, 1970. Older references have been omitted because their inclusion would produce an excessively cumbersome bibliography containing more than 425 citations. Genes that were mapped prior to 1970 are identified by the letter A in Table 1, and additional references to the mapping of these genes can be found in the 1970 edition of the linkage map (156).

GENETIC NOMENCLATURE

The system of *E. coli* genetic nomenclature which has been used in previous reviews of the linkage map is continued in the present review. Each gene locus is identified by a three-letter mnemonic symbol, which in many cases is followed by a capital letter to distinguish individual cistrons, operator loci, and promoter or initiator sites. In those situations where two or more symbols have been coined to denote the same gene locus, only one of these is used in Fig. 1, and the alternate symbols appear as cross-referenced entries in Table 1. Certain familiar gene symbols have been modified over the past two years in an effort to define specific gene functions with greater precision. These modifications are summarized in the following paragraph.

The old symbol *apk* (for aspartokinase) has been changed to *lysC* to signify lysine aspartokinase III (J. C. Patte, *personal communication*). The carbohydrate transport locus (*ctr*) of Wang, Morse, and Morse (163) is now identified by the symbols *ptsI* and *ptsH* which denote the two components of the phosphotransferase system (99). The locus *dnaD* (165) has been deleted from the map on the recommendation of J. A. Wechsler (*personal communication*), who finds that *dnaD* mutants are in fact mutants of the *dnaC* cistron. The *dnaE* gene (58, 165) is now designated *polC* for deoxyribonucleic acid (DNA) polymerase III (H. Shizuya and C. C. Richardson, *personal communication*). Fuchs et al. (56) have proposed that the *dnaF* locus (165) be renamed *nrd* for ribonucleoside diphosphate reductase. The provisional symbol for host specificity determinants, *hsp* (156), has been replaced by three specific symbols, *hsm*, *hsr*, and *hss*, which serve to distinguish the individual components of the host restriction and modification system (5). The symbol *old* (for oleate degradation) has been changed to *fad* (for fatty acid degradation) on the recommendation of J. E. Cronan, Jr., and P. Overath (*personal communication*). The old tentative designation for determinants of somatic antigens, *som*, has been dropped in favor of the symbol *rfb* (57). Morse and Primakoff (115) used the symbol *SuA* to identify the interesting class of suppressor mutations that relieve the polar effects of nonsense codons in polycistronic messages. As it now appears that the *SuA* suppressor locus determines a specific ribonuclease activity (94), the symbol *rnsC* is proposed as a standard designation for this gene. The symbol for the aspartokinase I-homoserine dehydrogenase I enzyme complex has been changed from *thrD* to *thrA* because these enzymes catalyze the

first steps in threonine biosynthesis (J. Theze, *personal communication*). It should be noted that the genes which code for ribosomal ribonucleic acid molecules are not shown on Fig. 1. These important genes, for which no symbol has yet been proposed, have been located approximately in the 75 to 78 min region of the linkage map by Yu et al. (180) and by Birnbaum and Kaplan (11).

RECENT ADJUSTMENTS IN THE POSITIONS OF GENETIC MARKERS

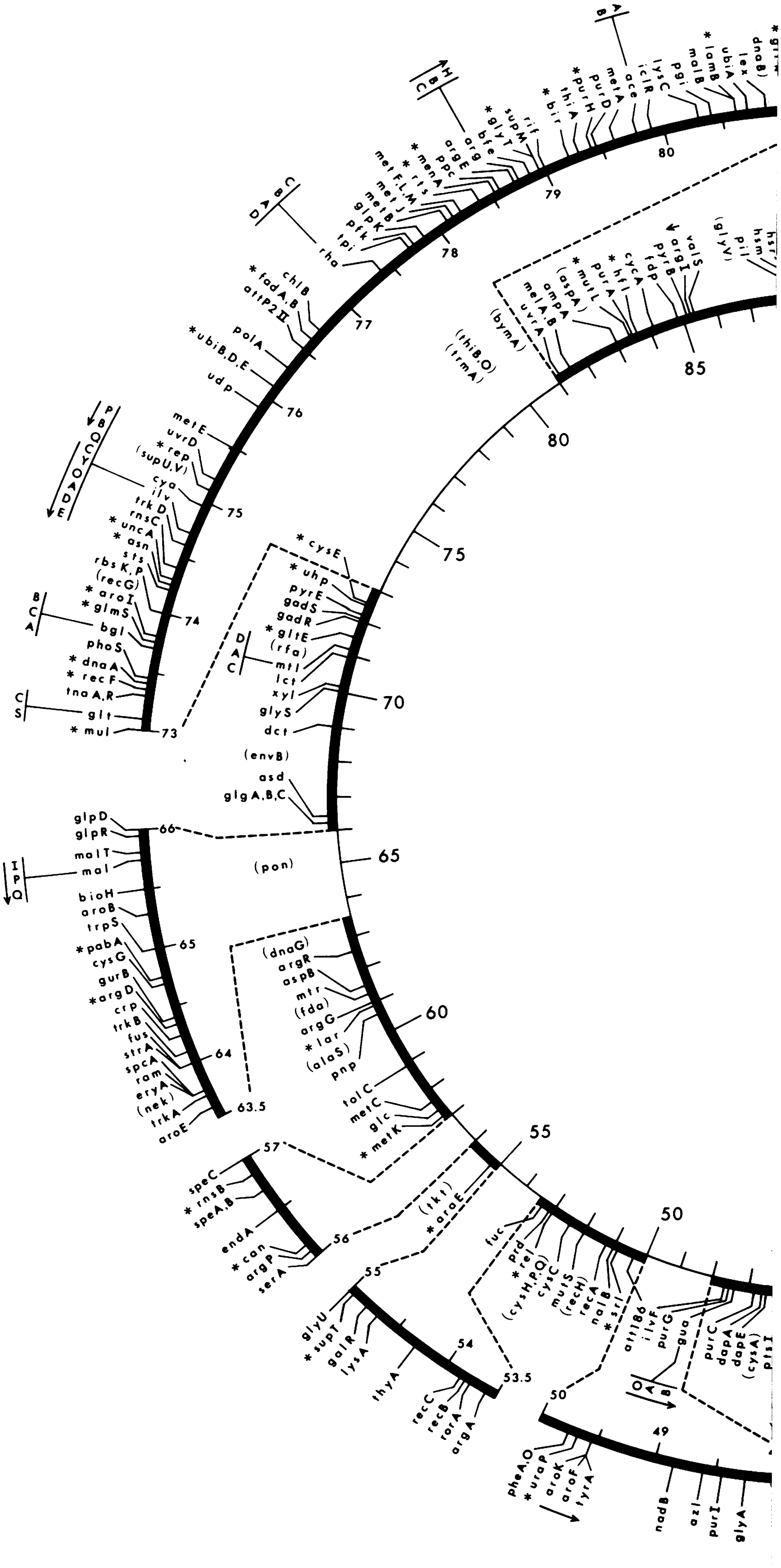
We estimate that 90% or more of the new mapping data reported in the past two years is based on the analysis of multifactor transduction crosses mediated by phage P1. The resulting large body of data on the frequency of joint transduction of closely linked markers has enabled us to make several adjustments in the positions of markers on the map depicted in Fig. 1. An especially useful device for making such adjustments is the mapping function derived by Wu (173), which relates joint transduction of markers to the distance, in time units, between the markers: frequency of joint transduction = $(1 - [\text{distance between two markers/length of transducing fragment}])^3$. The length of a transducing fragment is taken to be 2.0 min (173) for computation of the adjusted map intervals which are described in the paragraphs below.

The recent transduction experiments of Epstein and Kim (48), together with older data on markers in the *thr-leu* region at 0 to 1 min in Fig. 1, strongly suggest that the distance between *thr* and *leu* must be greater than 1.0 min. The best fit of all available data for this region is now obtained by moving the *leu* locus from its former location at 1.0 min to a new position at 1.5 min, as shown in Fig. 1. This change also causes a slight clockwise shift of the other markers in the 1- to 4-min segment of the map.

New transduction data on the mapping of *ent* genes (105, 177) at 13.5 min and of the *popA* locus at 11 min (H. P. Charles, *personal communication*) now permit a more precise placement of the old *purE* marker at 12.0 min, compared to its previous position at 13 min. This adjustment results in a counterclockwise shift of 1.0 min for all of the markers in the 6- to 12-min region of the map.

The only serious conflict that we encountered in this review concerns the mapping of the *proA* and *proB* genes at 6.5 and 8.3 min, respectively. Condamine (33) and W. Epstein (*personal communication*) have concluded that *proA* and *proB* must be very close to each other because the two markers recombine only at low frequency in genetic crosses. These investigators also found that neither *proA* nor *proB* is cotransducible with the *lac* locus at 9 min. Their results conflict with earlier studies (cited in 156) on the linkage of *proB* to *lac* and with the more recent data of Roberts and Reeve (134) who reported 27% cotransduction of these two markers. Moreover, a new marker, *strB*, was mapped between the two *pro* genes at distances of 0.6 and 1.2 min, respectively, from *proA* and *proB* (134). One possible explanation for these conflicting data is that different sublines of *E. coli* strain K-12 may vary in the amount or kind of DNA present in the *proA-lac* region. This view derives in part from the discovery by Glansdorff et al. (62), that the *pro* region of most K12 strains contains a second gene for ornithine transcarbamylase activity which is named *argF* to distinguish it from *argI* at 85 min. The *argF* activity is absent, however, in the K12 strain Hfr R4 and in *E. coli* strains B and W (62, 84, and N. Glansdorff, *personal communication*); in strain B, the absence of *argF* has been attributed to a chromosomal deletion (W. Epstein, *personal communication*). In addition, Charamella and Curtiss III (31) have postulated that some of the widely used sublines of strain K12 contain duplications of the *proA* or *proB* genes that are not present in other sublines. Their thesis is based on the observation that the variable proportion of $proA^-$ or $proB^-$ mutants obtained in different K12 sublines is strain specific. The foregoing results suggest that the *proA-lac* regions of different K12 strains may

FIG. 1. *Scale drawing of the circular linkage map of E. coli. The inner circle, which bears the time scale from 0 through 90 min, is based on the results of interrupted conjugation experiments reviewed by Taylor (156). The map is graduated in 1-min intervals beginning arbitrarily with zero at the thr locus. Certain parts of the map (e.g., the 9- to 10-min segment) are displayed on arcs of the outer circle to provide an expanded time scale for crowded regions. The genetic symbols in this figure are defined in Table 1. Markers in parentheses are only approximately mapped at the positions shown. A gene identified by an asterisk has been mapped more precisely than the markers in parentheses, but its orientation relative to adjacent markers is not yet known. The arrows which are placed next to the phoA and argI genes and next to certain operons show the direction of messenger RNA transcription for these loci. For a comparison of the strain K12 linkage map with the current genetic maps of E. coli strain C and Salmonella typhimurium, see Wiman et al. (168) and the companion article by Sanderson (137). (Figure on following pages.)*



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pgi
malB
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ubiA
lex
dnaB
metA
purD
*purH
thiA
*bir
rif
supM
*glyT
bfe
argE
ppc
*menA
*rts
metF,L,M
metJ
metB
glpK
pfk
tpi
rha
chlB
*fadA,B
attP2 II
polA
*ubiB,D,E
udp
metE
uvrD
*rep
(supU,V)
cya
ilv
trkD
rnsC
*uncA
*asn
sts
rbsK,P
(recG)
*aroI
*glmS
bgl
phoS
*dnaA
*recF
tnaA,R
glt
*mul
glpD
glpR
malT
mal
bioH
aroB
trpS
*pabA
cysG
gurB
*argD
crp
trkB
fus
strA
spcA
ram
eryA
(nek)
trkA
aroE
speC
*rnsB
speA,B
endA
*can
argP
serA
glyU
*supT
galR
lysA
thyA
recC
recB
rorA
argA
pheA,O
*uraP
aroK
aroF
tyrA
nadB
azl
purI
glyA
*cysE
*uhp
pyrE
gadS
gadR
*gltE
(rfa)
mtl
lct
xyl
glyS
dct
(envB)
asd
glgA,B,C
(pon)
(dnaG)
argR
aspB
mtr
(fda)
argG
*lar
(alaS)
pnp
tolC
melC
glc
*metK
(tkt)
*araE
fuc
prd
*rel
(cysH,P,Q)
cysC
mutS
(recH)
recA
nalB
*srl
attl186
ilvF
purG
gua
purC
dapA
dapE
(cysA)
ptsI
(thiB,O)
(trmA)
(bymA)
uvrA
metA,B
ampA
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pyrB
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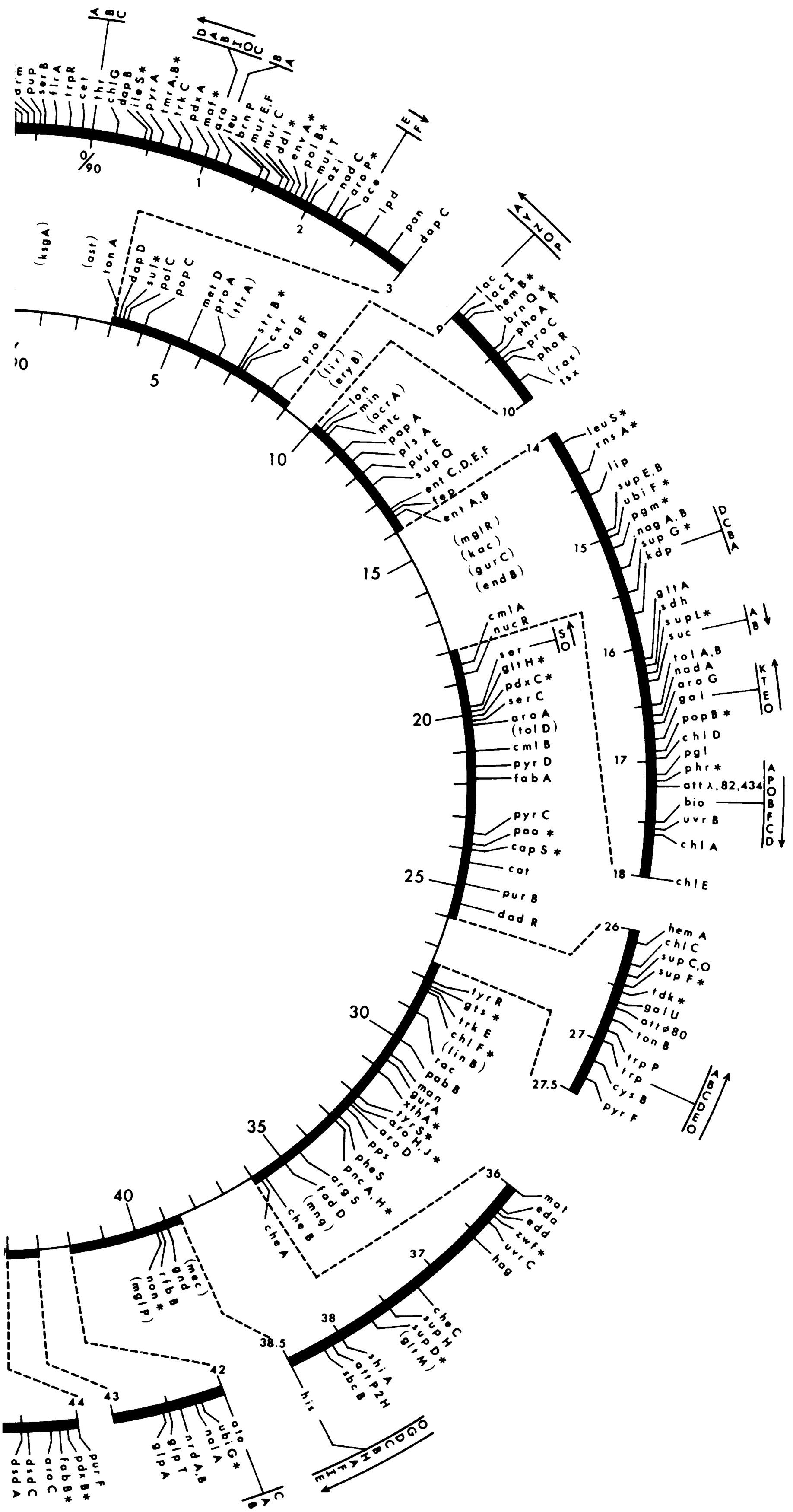
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tmrA,B*
trkC
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maf*
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leu
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murE,F
murC
ddl*
envA*
polB*
mutT
azi
nadC
aroP*
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lpd
pan
dapC
serB
flrA
trpR
cet
(ksgA)
(ast)
tonA
dapD
sul*
polC
popC
metD
proA
(tfrA)
strB*
cxr
argF
proB
lacI
hemB*
brnQ*
phoA
proC
phoR
(ras)
tsx
(lir)
(eryB)
lon
min
(acrA)
mtc
popA
plsA
purE
supQ
entC,D,E,F
fep
entA,B
(mglR)
(kac)
(gurC)
(endB)
leuS*
rnsA*
lip
supE,B
ubiF*
pgm*
nagA,B
supG*
kdp
gltA
sdh
supL*
suc
tolA,B
nadA
aroG
gal
popB*
chlD
pgl
phr*
attλ,82,434
bio
uvrB
chlA
chlE
cmlA
nucR
ser
gltH*
pdxC*
serC
aroA
(tolD)
cmlB
pyrD
fabA
pyrC
poa*
capS*
cat
purB
dadR
hemA
chlC
supC,O
supF*
tdk*
galU
attφ80
tonB
trpP
trp
cysB
pyrF
tyrR
gts*
trkE
chlF*
(linB)
rac
pabB
man
gurA
xthA*
tyrS*
aroH,J*
aroD
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pheS
pncA,H*
argS
fadD
(mng)
cheB
cheA
mot
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zwf*
uvrC
hag
cheC
supH
supD*
(glrM)
shiA
attP2H
sbcB
his
gnd
rfbB
non*
(mglP)
(mec)
ato
ubiG*
nalA
nrdA,B
glpT
glpA
purF
pdxB*
fabB*
aroC
dsdC
dsdA

TABLE 1. *List of genetic markers of E. coli*

Gene symbol	Mnemonic	Map position (min)[a]	Alternate gene symbols; phenotypic trait affected	References[b]
aceA	Acetate	80	*icl;* utilization of acetate: isocitrate lyase	A
aceB	Acetate	80	*mas;* utilization of acetate: malate synthetase A	A
aceE	Acetate	2	*aceE1;* acetate requirement; pyruvate dehydrogenase (decarboxylase component)	A
aceF	Acetate	2	*aceE2;* acetate requirement, pyruvate dehydrogenase (lipoic reductase-transacetylase component)	A
acrA	Acridine	(10)	Sensitivity to acriflavine, phenethyl alcohol, sodium dodecyl sulfate	A
alaS	Alanine	(61)	*ala-act;* alanyl-transfer RNA synthetase	A
ampA	Ampicillin	83	Resistance or sensitivity to penicillin	A
araA	Arabinose	1	L-arabinose isomerase	A
araB	Arabinose	1	L-ribulokinase	A
araC	Arabinose	1	Regulatory gene	A
araD	Arabinose	1	L-ribulose 5-phosphate 4-epimerase	A
araE	Arabinose	55	L-arabinose permease	A
araI	Arabinose	1	Initiator locus	A
araO	Arabinose	1	Operator locus	A
argA	Arginine	54	*argB, Arg1, Arg$_2$;* *N*-acetylglutamate synthetase	A
argB	Arginine	79	*ArgC;* α-*N*-acetyl-L-glutamate-5-phosphotransferase	A, 8, 39
argC	Arginine	79	*argH, Arg2;* *N*-acetylglutamic-γ-semialdehyde dehydrogenase	A, 8, 39
argD	Arginine	64	*argG, Arg$_1$;* acetylornithine-δ-transaminase	A
argE	Arginine	79	*argA, Arg4;* L-ornithine-*N*-acetylornithine lyase	A, 8, 39
argF	Arginine	7	*argD, Arg5;* ornithine transcarbamylase	A, 62, 97, I
argG	Arginine	61	*argE, Arg6;* argininosuccinic acid synthetase	A
argH	Arginine	79	*argF, Arg7;* L-argininosuccinate arginine lyase	A, 8, 39
argI	Arginine	85	Ornithine transcarbamylase	62, 84, 97
argP	Arginine	56	Arginine permease	A
argR	Arginine	63	*Rarg;* regulatory gene	A, 86
argS	Arginine	35	Arginyl-transfer RNA synthetase	A
aroA	Aromatic	20	3-enolpyruvylshikimate-5-phosphate synthetase	A
aroB	Aromatic	65	Dehydroquinate synthetase	A
aroC	Aromatic	44	Chorismic acid synthetase	A
aroD	Aromatic	32	Dehydroquinase	A, 123
aroE	Aromatic	64	Dehydroshikimate reductase	A
aroF	Aromatic	50	3-deoxy-D-arabinoheptulosonic acid-7-phosphate (DHAP) synthetase, (tyrosine-repressible isoenzyme)	A, 112
aroG	Aromatic	17	DHAP synthetase, (phenylalanine-repressible isoenzyme	A
aroH	Aromatic	32	DHAP synthetase, (tryptophan-repressible isoenzyme)	A
aroI	Aromatic	74	Function unknown	A
aroJ	Aromatic	32	Probable operator locus for *aroH*	26
aroK	Aromatic	50	Operator locus for *aroA, tyrA*	112
aroP	Aromatic	2	General aromatic amino acid transport	17, 18
asd		66	*dap + hom;* aspartic semialdehyde dehydrogenase	A
asn		74	Asparagine synthetase	A
aspA		(83)	Aspartase	A
aspB	Aspartate	62	*asp;* aspartate requirement	A
ast	Astasia	(3)	Generalized high mutability	A
atoA	Acetoacetate	42	Coenzyme A transferase	128
atoB	Acetoacetate	42	Thiolase II	128
atoC	Acetoacetate	42	Regulatory gene	128
attλ	Attachment	17	Integration site for prophage λ	A

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

[b] Numbers refer to Literature Cited. The letter A identifies genes for which additional citations to older mapping data may be found in reference 156. The other letters refer to *personal communications* from the following individuals: (B) M. Belfort; (C) R. S. Buxton and I. B. Holland; (D) F. Casse; (E) H. P. Charles; (F) T. Cox and G. E. Degnen; (G) J. E. Cronan, Jr., D. F. Silbert, and D. L. Wulff; (H) R. Dahl and M. L. Morse; (I) W. Epstein; (J) J. R. Guest and I. T. Creaghan; (K) Z. I. Horii and A. J. Clark; (L) J. Kirschbaum; (M) B. Konrad; (N) B. Low, S. Clarke, and W. Konigsberg; (O) W. K. Maas; (P) C. Milcarek and B. Weiss; (Q) J. C. Patte; (R) G. Pauli and P. Overath; (S) C. C. Richardson; (T) R. R. B. Russell; (U) R. Schmitt; (V) H. Shizuya and C. C. Richardson; (W) A. Silverston, M. Goman, and J. Scaife; (X) K. Stacey; (Y) A. L. Taylor, *unpublished data;* (Z) A. Templin, S. R. Kushner, and A. J. Clark; (A') J. Theze; (B') H. E. Umbarger; (C') J. A. Wechsler; (D') H. J. W. Wijsman and E. J. J. Lugtenberg.

TABLE 1.—*Continued*

Gene symbol	Mnemonic	Map position (min)[a]	Alternate gene symbols; phenotypic trait affected	References[b]
attP2H	Attachment	38	Phage P2 integration site H	25
attP2II	Attachment	77	Phage P2 integration site II	25
attφ80	Attachment	27	Integration site for prophage φ80	A
att82	Attachment	17	Integration site for prophage 82	A, 144
att186	Attachment	50	Integration site for prophage 186	169
att434	Attachment	17	Integration site for prophage 434	A, 144
azi	Azide	2	*pea, fts;* resistance or sensitivity to sodium azide or phenethyl alcohol; filament formation at 42 C	A
azl	Azaleucine	49	Regulation of *leu* and *ilv* genes	B′
bfe		79	*cer;* resistance or sensitivity to phage BF23 and colicins E1, E2, E3	24, 85, L, M
bglA	β-glucoside	74	*β-glA;* aryl β-glucosidase	A
bglB	β-glucoside	74	*β-glB;* β-glucoside permease	A
bglC	β-glucoside	74	*β-glC;* regulatory gene	A
bioA	Biotin	18	Group II; 7-oxo-8-aminopelargonic acid (7KAP) → 7,8-diaminopelargonic acid (DAPA)	A, 46
bioB	Biotin	18	Conversion of dethiobiotin to biotin	A
bioC	Biotin	18	Block prior to pimeloyl coenzyme A	A, 32
bioD	Biotin	18	Dethiobiotin synthetase	A
bioF	Biotin	18	Pimeloyl coenzyme A → 7KAP	A, 32
bioH	Biotin	66	*bioB;* block prior to pimeloyl coenzyme A	A, 32
bioO	Biotin	18	Operator for genes *bioB* through *bioD*	32
bioP	Biotin	18	Promoter site for genes *bioB* through bioD	32
bir	Biotin retention	79	Biotin uptake, retention, and regulation	27
brnP	Branched-chain	2	Transport of isoleucine, leucine, and valine	70
brnQ	Branched-chain	9	Transport of isoleucine, leucine, and valine	70
bymA		(81)	Bypass of maltose permease at *malB*	76
can	Canavanine	56	Canavanine resistance	107, 108
cap			See *crp*	
capS	Capsule	24	Regulatory gene for capsular polysaccharide synthesis	A
cat		24	*CR;* catabolite repression	A
cet		90	*ref, refII;* tolerance to colicin E2	A, 158, C
cheA	Chemotaxis	36	*motA;* chemotactic motility	A
cheB	Chemotaxis	36	*motB;* chemotactic motility	A
cheC	Chemotaxis	37	Chemotactic motility	A
chlA	Chlorate	18	*narA;* pleiotropic mutations affecting nitrate-chlorate reductase and hydrogen lyase activity	A, 109, 159
chlB	Chlorate	77	*narB;* pleiotropic mutations affecting nitrate-chlorate reductase and hydrogen lyase activity	A, 109, 159, D
chlC	Chlorate	26	*narC;* structural gene for nitrate reductase	A, 109
chlD	Chlorate	17	*narD, narF;* nitrate-chlorate reductase	A, 109
chlE	Chlorate	18	*narE;* nitrate reductase	A, 109, 159
chlF	Chlorate	28	Structural gene for formate dehydrogenase	63
chlG	Chlorate	0	Formate-nitrate reductase	63
cmlA	Chloramphenicol	19	Resistance or sensitivity to chloramphenicol	A
cmlB	Chloramphenicol	21	Resistance or sensitivity to chloramphenicol	A
crp		64	*cap;* cyclic adenosine monophosphate receptor protein	47, 48, R, W
ctr			See *ptsI, ptsH*	A, 163
cxr		7	Synthesis of methylglyoxal	I
cya		75	Adenyl cyclase	48, 176, H
cycA	Cycloserine	84	First-step resistance to D-cycloserine	A, 135, 164
cysA	Cysteine	(47)	Requirement	I
cysB	Cysteine	27	Pleiotropic mutations affecting cysteine biosynthesis	A
cysC	Cysteine	52	Adenosine 5′-sulphatophosphate kinase	A
cysE	Cysteine	73	Apparently pleiotropic	A
cysG	Cysteine	65	Sulphite reductase	A
cysH	Cysteine	(53)	Adenosine 3′-phosphate 5′-sulphatophosphate reductase	A
cysP	Cysteine	(53)	Sulphate permease and sulphite reductase	A
cysQ	Cysteine	(53)	Sulphite reductase	A
dadR		26	Regulatory gene for D-amino acid deaminases	91
dapA	Diaminopimelate	47	Dihydrodipicolinic acid synthetase	A, 20
dapB	Diaminopimelate	0	Dihydrodipicolinic acid reductase	A, 20
dapC	Diaminopimelate	3	Tetrahydrodipicolinic acid → *N*-succinyl-diaminopimelate	A, 20

TABLE 1.—*Continued*

Gene symbol	Mnemonic	Map position (min)[a]	Alternate gene symbols; phenotypic trait affected	References[b]
dapD	Diaminopimelate	3	Tetrahydrodipicolinic acid → *N*-succinyl diaminopimelate	A, 20
dapE	Diaminopimelate	47	*dapB*; *N*-succinyl-diaminopimelic acid deacylase	A, 20
darA			See *uvrD*	A
dct		69	Uptake of C_4-dicarboxylic acids	A
ddl		2	D-alanine: D-alanine ligase	D′
deo	Deoxythymidine		See *dra*, *drm*, *pup*, and *tpp*	A
dnaA		73	DNA synthesis: initiation-defective	140, 165
dnaB		(81)	*groP*; DNA synthesis	30, 60, 165, C′
dnaC		89	*dnaD*; DNA synthesis: initiation-defective	30, 165, C, C′
dnaE			See *polC*	58, 133, V
dnaF			See *nrdA*	56, 165
dnaG		(63)	DNA synthesis	165
dra		89	*deoC*, *thyR*; deoxyriboaldolase	A, 14
drm		89	*deoB*, *thyR*; deoxyribomutase	A, 14
dsdA	D-serine	45	D-serine deaminase	A
dsdC		44	Regulatory gene	A
eda	D-serine	36	*kga*, *kdg*; 2-keto-3-deoxygluconate-6-phosphate aldolase	51, 55, 129, 130
edd		36	Entner-Doudoroff dehydrase (gluconate-6-phosphate dehydrase)	A, 51, 55
endA		57	DNA-specific endonuclease I	A, 170
endB		(16)	DNA-specific endonuclease I	170
entA	Enterochelin	14	2,3-dihydro-2,3-dihydroxybenzoate dehydrogenase	35, 177
entB	Enterochelin	14	2,3-dihydro-2,3-dihydroxybenzoate synthetase	177
entC	Enterochelin	13	Isochorismate synthetase	177
entD	Enterochelin	13	Unknown step in conversion of 2,3-dihydroxybenzoate to enterochelin	35, 105
entE	Enterochelin	13	Unknown step in conversion of 2,3-dihydroxybenzoate to enterochelin	105
entF	Enterochelin	13	Unknown step in conversion of 2,3-dihydroxybenzoate to enterochelin	105
envA	Envelope	2	Anomalous cell division involving chain formation	A, 122
envB	Envelope	(68)	Anomalous spheroid cell formation	A
eps	Episome stability		See *spc*	175
eryA	Erythromycin	64	50-8 protein of 50*S* ribosomal subunit	A, 42, 121, 154
eryB	Erythromycin	(10)	High level resistance to erythromycin	A
exbA			See *tonB*	71
exr			See *lex*	
fabA		22	β-hydroxydecanoylthioester dehydrase	37, G
fabB		44	Fatty acid biosynthesis	A, 37
fadA	Fatty acid degradation	77	*oldA*; thiolase I	A, R
fadB	Fatty acid degradation	77	*oldB*; hydroxyacyl-coenzyme A dehydrogenase	A, R
fadD	Fatty acid degradation	35	*oldD*; acyl-coenzyme A synthetase	A, R
fda		(61)	*ald*; fructose-1,6-diphosphate aldolase	A
fdp		85	Fructose diphosphatase	A
fep		13	Defect of enterochelin-dependent iron transport system	35, 105, 177
flrA	Fluoroleucine	90	Regulation of *leu* and *ilv* genes	90
ftsA			See *azi*	A
fuc	Fucose	53	Utilization of L-fucose	A
fus	Fusidic acid	64	*far*; protein chain elongation factor EF G	68, 95, 121, 155
gadR		72	Regulatory gene for *gadS*	106
gadS		72	Glutamic acid decarboxylase	A, 106
galE	Galactose	17	*galD*; uridinediphosphogalactose 4-epimerase	A
galK	Galactose	17	*galA*; galactokinase	A
galO	Galactose	17	*galC*; operator locus	A
galT	Galactose	17	*galB*; galactose 1-phosphate uridyl transferase	A
galR	Galactose	55	*Rgal*; regulatory gene	A
galU	Galactose	27	*UDPG*; uridine diphosphoglucose pyrophosphorylase	A
glc	Glycolate	57	Utilization of glycolate; malate synthetase G	A
glgA	Glycogen	66	Glycogen synthetase	A
glgB	Glycogen	66	α-1,4-glucan: α-1,4-glucan 6-glucosyltransferase	A
glgC	Glycogen	66	Adenosine diphosphate glucose pyrophosphorylase	A
glmS	Glucosamine	74	L-glutamine: D-fructose-6-phosphate amino transferase	172
glpA	Glycerol phosphate	43	L-α-glycerophosphate dehydrogenase (anaerobic)	89

TABLE 1.—*Continued*

Gene symbol	Mnemonic	Map position (min)[a]	Alternate gene symbols; phenotypic trait affected	References[b]
glpD	Glycerol phosphate	66	*glyD;* D-α-glycerophosphate dehydrogenase (aerobic)	A, 89
glpK	Glycerol phosphate	78	Glycerol kinase	A, 3
glpT	Glycerol phosphate	43	L-α-glycerophosphate transport system	A, 89, 128
glpR	Glycerol phosphate	66	Regulatory gene	A
gltA	Glutamate	16	*glut;* requirement for glutamate; citrate synthase	A
gltC	Glutamate	73	Operator locus	A
gltE	Glutamate	72	Glutamyl-transfer RNA synthetase	A, 118
gltH	Glutamate	20	Requirement	A
gltM	Glutamate	(38)	Glutamyl-transfer RNA synthetase	118
gltR	Glutamate	81	Regulatory gene for glutamate permease	A
gltS	Glutamate	73	Glutamate permease	A
glyA	Glycine	48	Serine hydroxymethyl transferase	A
glyS	Glycine	70	*gly-act;* glycyl-transfer RNA synthetase	A, 54
glyT	Glycine	79	*supA36, su36, sumA;* glycine transfer RNA II	74, 126, M
glyU	Glycine	55	*sumB;* glycine transfer RNA I	74
glyV	Glycine	(86)	Glycine transfer RNA III	29
gnd		39	Gluconate-6-phosphate dehydrogenase	A, 57
groN			*See rif*	59
groP			*See dnaB*	60
gts		28	Uncharacterized membrane defect	167
guaA	Guanine	47	gua_b; xanthosine-5′-monophosphate aminase	A
guaB	Guanine	47	gua_a; inosine-5′-monophosphate dehydrogenase	A
guaC	Guanine	89	Guanosine-5′-monophosphate reductase	A, 41
guaO	Guanine	47	Operator locus	A
gurA	Glucuronide	31	β-glucuronidase	123, 124
gurB	Glucuronide	64	Utilization of methyl-β-D-glucuronide	124
gurC	Glucuronide	(16)	Utilization of methyl-β-D-glucuronide	124
hag	H antigen	37	*H;* flagellar antigens (flagellin)	A
hemA	Hemin	26	Synthesis of δ-aminolevulinic acid	A
hemB	Hemin	9	*ncf;* synthesis of catalase and cytochromes	A
hfl		84	High frequency of lysogenization by phage λ	9, B
hisA	Histidine	39	Isomerase	57, 67
hisB	Histidine	39	Imidazole glycerol phosphate dehydrase: histidinol phosphatase	57, 67
hisC	Histidine	39	Imidazole acetol phosphate transaminase	57, 67
hisD	Histidine	39	Histidinol dehydrogenase	57, 67
hisE	Histidine	39	Phosphoribosyl-adenosine triphosphate-pyrophosphohydrolase	57
hisF	Histidine	39	Cyclase	57, 67
hisG	Histidine	39	Phosphoribosyl-adenosine triphosphate-pyrophosphorylase	57, 67
hisH	Histidine	39	Amido transferase	57, 67
hisI	Histidine	39	Phosphoribosyl-adenosine monophosphate-hydrolase	57, 67
hisO	Histidine	39	Operator locus	57
hsm	Host specificity	89	*hs, rm, hsp;* host modification activity: DNA methylase M	A, 5
hsr	Host specificity	89	*hs, rm, hsp, por;* host restriction activity: endonuclease R	A, 5
hss	Host specificity	89	Specificity determinant for *hsm* and *hsr* activities	5
icl			*See aceA*	A
iclR		80	Regulation of the glyoxylate cycle	A
ileS	Isoleucine	1	Isoleucyl-transfer RNA synthetase	79
ilvA	Isoleucine-valine	75	*ile;* threonine deaminase	A
ilvB	Isoleucine-valine	75	Acetohydroxy acid synthetase I	A
ilvC	Isoleucine-valine	75	*ilvA;* α-hydroxy-β-keto acid reductoisomerase	A
ilvD	Isoleucine-valine	75	*ilvB;* dehydrase	A
ilvE	Isoleucine-valine	75	*ilvC;* transaminase B	A
ilvF	Isoleucine-valine	48	Possibly acetohydroxy acid synthetase II	B′
ilvO	Isoleucine-valine	75	Operator locus for genes *ilvA, D, E*	A
ilvP	Isoleucine-valine	75	Operator locus for gene *ilvB*	A
ilvQ	Isoleucine-valine	75	Induction recognition site for *ilvC*	B′
ilvY	Isoleucine-valine	75	Positive control element for *ilvC* induction	B′
kac	K-accumulation	(16)	Defect in potassium ion uptake	A
kdpA-D	K-dependent	16	Requirement for a high concentration of potassium	A
kga			See *eda*	51

TABLE 1.—*Continued*

Gene symbol	Mnemonic	Map position (min)[a]	Alternate gene symbols; phenotypic trait affected	References[b]
ksgA	Kasugamycin	(1)	RNA methylase for 16*S* ribosomal RNA	A, 73
lacA	Lactose	9	*a, lacAc;* thiogalactoside transacetylase	A
lacI	Lactose	9	*i;* regulator gene	A
lacO	Lactose	9	*o;* operator locus	A
lacP	Lactose	9	*p;* promoter locus	A
lacY	Lactose	9	*y;* galactoside permease (M protein)	A
lacZ	Lactose	9	*z;* β-galactosidase	A
lamB	Lambda	81	*malB;* phage λ receptor site	157
lar	Large	61	Large cells and radiation resistance	96
lct	Lactate	71	L-lactate dehydrogenase	A, 147
leuA	Leucine	2	α-isopropylmalate synthetase	A
leuB	Leucine	2	β-isopropylmalate dehydrogenase	A
leuS	Leucine	14	Leucyl-transfer RNA synthetase	102
lex		81	*exr;* resistance or sensitivity to X-rays and ultraviolet light	A, 116
linB	Lincomycin	(29)	High level resistance to lincomycin	A
lip	Lipoic acid	15	Requirement	A
lir		(9)	Increased sensitivity to lincomycin and/or erythromycin	A
lon	Long form	10	*capR, dir, muc;* filamentous growth, radiation sensitivity, and regulation of capsular polysaccharide synthesis	A, 110, 153
lpd		3	Lipoyldehydrogenase	J
lps	Lipopolysaccharide		See *rfa*	50
lysA	Lysine	55	Diaminopimelic acid decarboxylase	A, 21
lysC	Lysine	80	*apk;* lysine aspartokinase III	A, Q
maf		1	Maintenance of autonomous sex factor	161
malB	Maltose	81	*mal-5;* maltose permease	A, 157
malI	Maltose	66	Initiator site	76
malP	Maltose	66	*malA;* maltodextrin phosphorylase	A, 77
malQ	Maltose	66	*malA;* amylomaltase	A, 77
malT	Maltose	66	*malA;* positive regulatory gene for the *malPQ* and *malB-lamB* operons	A, 77, 157
man	Mannose	31	Phosphomannose isomerase	A, 123
mec		(39)	DNA methylase for cytosine	111
melA	Melibiose	81	*mel-7;* α-galactosidase	A, U
melB	Melibiose	81	*mel-4;* thiomethylgalactoside permease II	A, U
menA	Menaquinone	79	Requirement	120
metA	Methionine	80	met_3; homoserine *O*-transsuccinylase	A
metB	Methionine	78	*met-1*, met_1; cystathionine synthetase	A
metC	Methionine	58	Cystathionase	A, 166
metD	Methionine	6	Utilization of D-methionine	34, I
metE	Methionine	76	*met-*B_{12}; N^5-methyltetrahydropteroyl triglutamate-homocysteine methylase	A
metF	Methionine	78	*met-2*, met_2; N^5,N^{10}-methyltetrahydrofolate reductase	A
metJ	Methionine	78	Possible regulatory gene	151
metK	Methionine	57	*S*-adenosylmethionine synthetase activity	69, 107
metL	Methionine	78	Methionine aspartokinase II	Q
metM	Methionine	78	Homoserine dehydrogenase II	Q
mglP	Methyl-galactoside	(40)	*P-MG;* methyl-galactoside permease and galactose binding protein	A, 15
mglR	Methyl-galactoside	(16)	*R-MG;* regulatory gene	A
min	Mini-cell	10	Formation of minute cells containing no DNA	A
mng	Manganese	(35)	Resistance or sensitivity to manganese	143
mot	Motility	36	Flagellar paralysis	A
mtc	Mitomycin C	10	*Mb, mbl;* sensitivity acridines, methylene blue and mitomycin C	A
mtlA	Mannitol	71	Mannitol-specific enzyme II of the phosphotransferase (*pts*) system	147
mtlC	Mannitol	71	Regulatory gene or site	147
mtlD	Mannitol	71	Mannitol-1-phosphate dehydrogenase	A, 147
mtr	Methyl tryptophan	61	Resistance to 5-methyltryptophan	A
mul		73	Mutability of ultraviolet-irradiated phage λ	160
murC	Murein	2	L-alanine adding enzyme	103, D'
murE	Murein	2	*meso*-diaminopimelic acid adding enzyme	103, 104, D'

TABLE 1.—*Continued*

Gene symbol	Mnemonic	Map position (min)[a]	Alternate gene symbols; phenotypic trait affected	References[b]
murF	Murein	2	D-alanyl-D-alanine adding enzyme	103, D'
mutL	Mutator	83	Generalized high mutability	98
mutS	Mutator	52	Generalized high mutability	A, F
mutT	Mutator	2	Generalized high mutability; specifically induces AT → CG transversions	A
nadA	Nicotinamide adenine dinucleotide	17	*nicA;* nicotinic acid requirement	A
nadB	Nicotinamide adenine dinucleotide	49	*nicB;* nicotinic acid requirement	A
nadC	Nicotinamide adenine dinucleotide	2	Quinolinate phosphoribosyl transferase	A, J
nagA	*N*-acetylglucosamine	15	*N*-acetylglucosamine-6-phosphate deacetylase	78
nagB	*N*-acetylglucosamine	15	Glucosamine-6-phosphate deaminase	78
nalA	Nalidixic acid	42	Resistance or sensitivity to nalidixic acid	A, 89, 128
nalB	Nalidixic acid	51	Resistance or sensitivity to nalidixic acid	A, 169
nam			*See pncA*	44
nar	Nitrate reductase		*See chl*	
nek		(64)	Resistance to neomycin and kanamycin (30*S* ribosomal protein)	A
nic			*See nad*	
non	Nonmucoid	39	Block in capsule formation	132
nrdA		42	*dnaF;* ribonucleoside diphosphate reductase: subunit B1	56, 165
nrdB		42	Ribonucleoside diphosphate reductase: subunit B2	56
nucR	Nucleosides	19	*deoR;* regulatory gene for *pup*, *tpp*, and *dra*	2, 117
old			*See fadA, fadB, fadD*	
pabA	*p*-aminobenzoate	65	Requirement	A
pabB	*p*-aminobenzoate	30	Requirement	A
pan	Pantothenic acid	3	Requirement	A
pdxA	Pyridoxine	1	Requirement	A
pdxB	Pyridoxine	44	Requirement	A
pdxC	Pyridoxine	20	Requirement	A, N
pfk		78	Structural or regulatory gene for fructose 6-phosphate kinase	A, 3
pgi		80	Phosphoglucoisomerase	A
pgl		17	6-phosphogluconolactonase	A
pgm		15	Phosphoglucomutase	1
pheA	Phenylalanine	50	Chorismate mutase P-prephenate dehydratase	A
pheO	Phenylalanine	50	Operator locus	81
pheS	Phenylalanine	33	*phe-act;* phenylalanyl transfer synthetase	A, 136
phoA	Phosphatase	10	*P;* alkaline phosphatase	A, 119, 174
phoR	Phosphatase	10	*R1 pho, R1;* regulatory gene	A, 119, 174
phoS	Phosphatase	73	*R2 pho, R2;* regulatory gene	A
phr	Photoreactivation	17	Photoreactivation of ultraviolet-damaged DNA (K12-B hybrids)	A, 152
pil	Pili	88	*fim;* presence or absence of pili (fimbriae)	A
plsA	Phospholipid	12	Glycerol-3-phosphate acyltransferase	38
pncA	Pyridine nucleotide cycle	33	*nam;* nicotinamide deamidase	44, 127
pncH	Pyridine nucleotide cycle	33	Hyperproduction of nicotinamide deamidase	127
pnp		61	Polynucleotide phosphorylase	A
poa		24	Proline oxidase	33
polA	Polymerase	76	*resA;* DNA polymerase I	A, 10, 88
polB	Polymerase	2	DNA polymerase II	28, S
polC	Polymerase	4	*dnaE;* DNA polymerase III	58, 133
pon	P-one	(65)	Resistance or sensitivity to phages P1 and Mu-1	Y
popA	Porphyrin	11	Possibly ferrochelatase	E
popB	Porphyrin	17	Probably coproporphyrin oxidase	E
popC	Porphyrin	4	Synthesis of δ-aminolevulinic acid	E
por	P1 restriction		See *hsr*	
ppc		79	*glu, asp;* succinate, aspartate, or glutamate requirement; phosphoenolypyruvate carboxylase	A
pps		33	Utilization of pyruvate or lactate; phosphopyruvate synthetase	A
prd	Propanediol	53	1,2-propanediol dehydrogenase	A, F

TABLE 1.—*Continued*

Gene symbol	Mnemonic	Map position (min)[a]	Alternate gene symbols; phenotypic trait affected	References[b]
proA	Proline	7	pro_1; block prior to L-glutamate semialdehyde	A, 134, 31
proB	Proline	8	pro_2; block prior to L-glutamate semialdehyde	A, 134, 31
proC	Proline	10	pro_3; *Pro2;* probably Δ-pyrroline-5-carboxylate reductase	A, 119, 31
ptsH		46	*ctr, Hpr;* phosphotransferase system: protein cofactor	A, 40, 49, 99, 163
ptsI		46	*ctr;* phosphotransferase system: enzyme I	A, 40, 49, 99, 163
pup		90	Purine nucleoside phosphorylase	A
purA	Purine	84	ade_k, Ad_4; adenylosuccinic acid synthetase	A
purB	Purine	25	ade_h, adenylosuccinase	A
purC	Purine	47	ade_g; phosphoribosyl-aminoimidazole-succinocarboxamide synthetase	A, 49, T
purD	Purine	79	$adth_a$; phosphoribosylglycineamide synthetase	A, 85
purE	Purine	12	ade_3, ade_f, Pur_2; phosphoribosyl-aminoimidazole carboxylase	A
purF	Purine	44	*purC*, $ade_{u,b}$; phosphoribosyl-pyrophosphate amidotransferase	A
purG	Purine	47	$adth_b$; phosphoribosylformylglycineamidine synthetase	A
purH	Purine	79	ade_i; phosphoribosyl-aminoimidazole-carboxamide formyltransferase	A
purI	Purine	48	Aminoimidazole ribotide synthetase	A
pyrA	Pyrimidine	1	*cap, arg + ura;* glutamino-carbamoyl-phosphate synthetase	A
pyrB	Pyrimidine	85	Aspartate transcarbamylase	A
pyrC	Pyrimidine	24	Dihydroorotase	A
pyrD	Pyrimidine	21	Dihydroorotic acid dehydrogenase	A
pyrE	Pyrimidine	72	Orotidylic acid pyrophosphorylase	A
pyrF	Pyrimidine	27	Orotidylic acid decarboxylase	A
rac	Recombination activation	34	Suppressor of *recB* and *recC* mutant phenotype in merozygotes	A
ram	Ribosomal ambiguity	64	P4a protein of 30*S* ribosomal subunit	A, 181
ras	Radiation sensitivity	(10)	Sensitivity to ultraviolet and X-ray irradiation	A, 162
rbsK	Ribose	74	Ribokinase	4
rbsP	Ribose	74	D-Ribose permease	A, 4
recA	Recombination	51	Ultraviolet sensitivity and competence for genetic recombination	A
recB	Recombination	54	Ultraviolet sensitivity, genetic recombination; exonuclease V subunit	A, 66, 171
recC	Recombination	54	Ultraviolet sensitivity, genetic recombination; exonuclease V subunit	A, 66, 171
recF	Recombination	73	*uvrF;* ultraviolet sensitivity and competence for genetic recombination	149, K
recG	Recombination	(74)	Competence for genetic recombination	148
recH	Recombination	(52)	Competence for genetic recombination	148
rel	Relaxed	53	*RC;* regulation of RNA synthesis	A
rep	Replication	75	Inhibition of lytic replication of temperate phages	A
rfa	Rough	(71)	*lps;* lipopolysaccharide core defect	50, 139
rfbB	Rough	39	*som;* thymidine diphosphate-glucose oxidoreductase	57
rhaA	Rhamnose	77	L-rhamnose isomerase	A
rhaB	Rhamnose	77	L-rhamnulokinase	A
rhaC	Rhamnose	77	Regulatory gene	A
rhaD	Rhamnose	77	L-rhamnulose-1-phosphate aldolase	A
rif	Rifampicin	79	*stl, stv, groN, ron;* RNA polymerase: β subunit	A, 72, 83, 85, 113, 126, L, M
rne			*See rnsB*	170
rnsA	Ribonuclease	14	*rns;* ribonuclease I	A
rnsB	Ribonuclease	57	*rne;* ribonuclease II	170
rnsC	Ribonuclease	74	*SuA;* polarity suppressor; RNA endonuclease A	94, 114, 115
ron			*See rif*	61
rorA		54	Resistance to X-ray irradiation	64
rts		78	*ts-9;* altered electrophoretic mobility of 50*S* ribosomal	A
sbcB		38	Exonuclease I; suppressor of *recB, recC*	7, 92, 93, Z
sdh		16	Succinate dehydrogenase	36
serA	Serine	56	3-phosphoglyceric acid dehydrogenase	A

TABLE 1.—*Continued*

Gene symbol	Mnemonic	Map position (min)[a]	Alternate gene symbols; phenotypic trait affected	References[b]
serB	Serine	90	Phosphoserine phosphatase	A
serC	Serine	20	*pdxF;* 3-phosphoserine-2-oxoglutarate aminotransferase	43, N
serO	Serine	20	Operator locus	N
serS	Serine	20	Seryl-transfer RNA synthetase	A, 102, N
shiA	Shikimic acid	38	Shikimate and dehydroshikimate permease	A
spcA	Spectinomycin	64	*eps;* P4 protein of 30*S* ribosomal subunit	A, 42, 121, 175
speA	Spermidine	57	Arginine decarboxylase	107
speB	Spermidine	57	Agmatine ureohydrolase	A, 107, 108
speC	Spermidine	57	Ornithine decarboxylase	O
srl	Sorbitol	51	Utilization of sorbitol	I
stl	Streptolydigin		*See rif*	61, 72, 138, 146
strA	Streptomycin	64	P10 protein of 30*S* ribosomal subunit	A, 16, 42, 121
strB	Streptomycin	7	Low-level streptomycin resistance	134
sts		74	Altered ribonuclease II activity	100
stv	Streptovaricin		*See rif*	A
SuA			See *rnsC*	94, 114, 115
sucA	Succinate	16	*suc, lys* + *met;* succinate requirement; α-ketoglutarate dehydrogenase (decarboxylase component)	A
sucB	Succinate	16	*suc, lys* + *met;* succinate requirement; α-ketoglutarate dehydrogenase (dihydrolipoyltransuccinylase component)	A
sul		3	Suppressor of *lon* mutation	45
supA36			*See glyT*	
supB	Suppressor	15	su_B; suppressor of *ochre* mutations (not identical to *supL*)	A
supC	Suppressor	26	su_C; suppressor of *ochre* mutations (possibly identical to supO)	A
supD	Suppressor	38	su_I, *Su-1;* suppressor of *amber* mutations	A, 75
supE	Suppressor	15	su_{II}; suppressor of *amber* mutations	A
supF	Suppressor	26	su_{III}, *Su-3; amber* suppressor: tyrosine transfer RNA	A, 65
supG	Suppressor	16	*Su-5;* suppresor of ochre mutations	A
supH	Suppressor	38		A
supL	Suppressor	16	Suppressor of *ochre* mutations	A
supM	Suppressor	79	*sup15B; ochre* suppressor: tyrosine.transfer RNA	A, 126
supN	Suppressor	45	Suppressor of *ochre* mutations	A
supO	Suppressor	26	Suppressor *ochre* mutations (possibly identical to *supC*)	A
supQ	Suppressor	13		136
supT	Suppressor	55		A
supU	Suppressor	(75)	*su7; amber* suppressor: glutamine transfer RNA	A, 74
supV	Suppressor	(75)	*su8;* suppressor of *ochre* mutations	A
tdk		27	Deoxythymidine kinase	A
tfrA	T-four	(7)	ϕ^r; resistance or sensitivity to phages T4, T3, T7, and λ	A
thiA	Thiamine	79	*thi;* synthesis of thiazole	A, 85, 126
thiB	Thiamine	(78)	Thiamine phosphate pyrophosphorylase	A
thiO	Thiamine	(78)	Probable operator locus for *thiA thiB* genes	A
thrA	Threonine	0	*HS, thrD;* aspartokinase I-homoserine dehydrogenase I complex	A, 52, A′
thrB	Threonine	0	Homoserine kinase	A, A′
thrC	Threonine	0	Threonine synthetase	A′
thyA	Thymine	54	Thymidylate synthetase	A
tkt		(55)	Transketolase	A
tmrA		1	Trimethoprim resistance; dihydrofolate reductase activity	X
tmrB		1	Trimethoprim resistance; dihydrofolate reductase activity	X
tnaA		73	*ind;* tryptophanase	A
tnaR		73	R_{tna}; regulatory gene	A
tolA	Tolerance	17	*cim; tol-2;* tolerance to colicins E2, E3, A, and K	A
tolB	Tolerance	17	*tol-3;* tolerance to colicins E1, E2, E3, A, and K	A
tolC	Tolerance	59	*colE1-i, tol-8, refI;* specific tolerance to colicin E1	A, 166
tolD	Tolerance	(20)	Tolerance to colicins E2 and E3; ampicillin resistance	22
tonA	T-one	3	*T1, T5 rec;* resistance or sensitivity to phages T1 and T5	A

TABLE 1.—*Continued*

Gene symbol	Mnemonic	Map position (min)[a]	Alternate gene symbols; phenotypic trait affected	References[b]
tonB	T-one	27	*T1 rec, exb;* resistance to phages T1, ϕ80, colicins B, I, V; transport of Fe; enterochelin excretion	A, 71
tpi		78	Triosephosphate isomerase	3
tpp		89	*deoA, TP;* thymidine phosphorylase	A, 14
trkA		64	Transport of potassium	48
trkB		64	Transport of potassium	48
trkC		1	Transport of potassium	48
trkD		75	Transport of potassium	48
trkE		28	Transport of potassium	48
trmA		(79)	Methylase for 5-methyluracil in transfer RNA	12, 13
trpA	Tryptophan	27	*tryp-2;* tryptophan synthetase, A protein	A
trpB	Tryptophan	27	*tryp-1;* tryptophan synthetase, B protein	A
trpC	Tryptophan	27	*tryp-3; N*-(5-phosphoribosyl) anthranilate isomerase-indolyl-3-glycerol phosphate synthetase	A
trpD	Tryptophan	27	*tryE;* phosphoribosyl anthranilate transferase	A
trpE	Tryptophan	27	*tryD, anth, tryp-4;* anthranilate synthetase	A
trpO	Tryptophan	27	Operator locus	A
trpP	Tryptophan	27	Tryptophan permease	91
trpR	Tryptophan	90	*Rtry;* regulatory gene for the *trp* operon and *aroH*	A, 26, 82, C
trpS	Tryptophan	65	Tryptophanyl-transfer RNA synthetase	A, 82
tsx	T-six	10	*T6 rec;* resistance or sensitivity to phage T6 and colicin K	A
tyrA	Tyrosine	50	Chorismate mutase T-prephenate dehydrogenase	A
tyrR	Tyrosine	28	Regulation of *aroF, aroG,* and *tyrA* genes	A, 19, 80
tyrS	Tyrosine	32	Tyrosyl-transfer RNA synthetase	A
ubiA	Ubiquinone	83	4-hydroxybenzoate → 3-octaprenyl 4-hydroxybenzoate	A, 178
ubiB	Ubiquinone	76	2-octaprenylphenol → 2-octaprenyl-6-methoxy-1,4-benzoquinone	A, 150
ubiD	Ubiquinone	76	3-octaprenyl-4-hydroxybenzoate → 2-octaprenylphenol	A
ubiE	Ubiquinone	76	2-octaprenyl-6-methoxy-1,4-benzoquinone → 2-octaprenyl-3-methyl-6-methoxy-1,4-benzoquinone	179
ubiF	Ubiquinone	15	2-octaprenyl-3-methyl-6-methoxy-1,4-benzoquinone → 2-octaprenyl-3-methyl-5-hydroxy-6-methoxy-1,4-benzoquinone	78, 179
ubiG	Ubiquinone	42	2-octaprenyl-3-methyl-5-hydroxy-6-methoxy-1,4-benzoquinone → ubiquinone-8	150
udp		76	Uridine phosphorylase	131
uhp		72	Uptake of hexose phosphates	A, 53
uncA	Uncoupling	74	Membrane-bound Mg, calcium adenosine triphosphatase uracil permease	23, 87
uraP	Uracil	50		A
uvrA	Ultraviolet	81	*dar-3;* repair of ultraviolet radiation damage to DNA	A
uvrB	Ultraviolet	18	*dar-1,6;* repair of ultraviolet radiation damage to DNA	A
uvrC	Ultraviolet	36	*dar-4,5;* repair of ultraviolet radiation damage to DNA	A
uvrD	Ultraviolet	75	*uvr-502, dar-2, rad;* repair of UV radiation damage to DNA	A, 125, 142, 145
uvrF			*See recF*	149
valS	Valine	85	*val-act;* valyl-transfer RNA synthetase	A
xthA	Exo-three	31	Exonuclease III	P
xyl	Xylose	70	Utilization of D-xylose	A
zwf	Zwischenferment	36	Glucose-6-phosphate dehydrogenase	A

not be precisely homologous, owing to the presence of deletions, duplications, or possibly even combinations of both in various ancestral lines. It follows that no valid comparison of *pro-lac* linkage data from different laboratories can be made without first investigating the ancestry of the parental strains employed. The companion article by Bachmann (6) on the genealogy of K12 strains will serve as a useful guide in such investigations. For the present review, we rely mainly on the transduction data of Roberts and Reeve (134) for determining the positions of *proA* and *proB* in Fig. 1.

The *pyrD* and *pyrC* loci near 22 min were shown to be separated by less than 1 min in the 1970 edition of the map. A reevaluation of older mapping data for this region, together with the recent findings of J. E. Cronan, Jr., D. F. Silbert, and D. L. Wulff (*personal communication*) who have mapped the *fabA* locus at 22 min, indicates that *pyrD* and *pyrC* are not cotransducible and that the distance

between them cannot be less than 2.0 min. This conclusion is reflected in Fig. 1 by shifting the position of *pyrC* clockwise to 23.5 min. In addition, the interval between *pyrC* and *purB* has been increased from 1.0 to 1.5 min by application of Wu's equation to the data available for this region (91). The cumulative effect of these adjustments is the clockwise shift of the *trp* operon and its nearest neighbors from their former position at 25 min to the new location at 27 min.

The *man* locus, which had been mapped close to *aroD* at 32 min, is now relocated at 30.5 min on the basis of transduction data reported by Novel and Novel (123). These authors also presented evidence that *man* is oriented counterclockwise to *aroD* on the linkage map, but this view has been challenged by C. Milcarek and B. Weiss (*personal communication*), who interpret their mapping data for the *xthA* locus at 31 min to mean that *man* and *xthA* may be situated clockwise to *aroD*.

Although seven of the nine genes which map in the 42- to 43-min interval have been ordered with respect to each other, it should be noted that current data do not permit a positive orientation of this gene cluster within the linkage map. It thus remains to be seen whether the clockwise gene sequence is from *ato* to *glpA*, as presently shown in Fig. 1, or the reverse of this.

One of the most crowded regions of the map is the segment from 72 to 81 min. About 30 new genes have been mapped in this interval, and our analysis of the large amount of new transduction data for this region has generated a number of small adjustments of marker positions. The cumulative effect of these changes is to produce a gradual clockwise shift of markers in this region such that the *malB* gene is now placed close to 81 min, as compared to its previous location near 79 min.

TRANSDUCTION LINKAGE IN E. COLI

The volume of information on joint transduction of *E. coli* markers has reached the point where it now becomes profitable to think of the genetic map in terms of individual transduction linkage groups. Each group consists of the markers in a given segment of the map which are known to be continuously linked to each other on successive overlapping transducing fragments of phage P1. There are ten such transductional linkage groups at the present time and these are listed in the left half of Table 2. Six of the linkage groups are quite large, ranging in length from 4.2 min to 17.0 min. Taken together, the ten groups account for 67.4 min or 75% of the bacterial genome if one accepts 90 min as the standard length of the map (156). The gaps that separate the ten linkage groups are correspondingly small, as shown in the right half of Table 2.

Our reason for introducing this view of the genetic map is that it helps to focus attention on a few specific regions where the indicated distances between markers may be in error. It can be reasonably assumed that the dimensions of the ten transductional linkage groups are quite accurate because they are generated from the results of numerous transduction crosses, which are for the most part reproducible and internally consistent. In contrast, the

TABLE 2. *Transductional linkage groups of E. coli K12*

Map segments continuously linked by transduction		Map segments presently unlinked by transduction	
Map segment[a]	Length in min	Map segment[a]	Length in min
88.5 (*hsm*) - 4.0 (*popC*)	5.5	4.0 (*popC*) - 5.5 (*metD*)	1.5
5.5 (*metD*) - 21.8 (*fabA*)	16.3	21.8 (*fabA*) - 23.6 (*pyrC*)	1.8
23.6 (*pyrC*) - 28.1 (*trkE*)	4.5	28.1 (*trkE*) - 30.5 (*man*)	2.4
30.5 (*man*) - 32.8 (*pheS*)	2.3	32.8 (*pheS*) - 35.0 (*fadD*)	2.2
35.0 (*fadD*) - 39.2 (*rfbB*)	4.2	39.2 (*rfbB*) - 41.9 (*ato*)	2.7
41.9 (*ato*) - 58.9 (*tolC*)	17.0	58.9 (*tolC*) - 61.0 (*argG*)	2.1
61.0 (*argG*) - 62.5 (*argR*)	1.5	62.5 (*argR*) - 63.6 (*aroE*)	1.1
63.6 (*aroE*) - 66.4 (*asd*)	2.8	66.4 (*asd*) - 70.0 (*glyS*)	3.6
70.0 (*glyS*) - 81.1 (*uvrA*)	11.1	81.1 (*uvrA*) - 83.0 (*ampA*)	1.9
83.0 (*ampA*) - 85.2 (*valS*)	2.2	85.2 (*valS*) - 88.5 (*hsm*)	3.3
Total	67.4	Total	22.6

[a] Map segments are designated by the first and last known markers of each segment, proceeding in a clockwise direction from the top of Fig. 1. The numbers show the exact positions of the markers as they appear in Fig. 1.

gaps between the linkage groups reflect the absence of demonstrated joint transduction, and the accuracy of their dimensions, therefore, remains indeterminate.

Some of the longest gaps listed in Table 2, for example, may not really be as large as they seem. If one considers that the genetic map now contains 460 genes, or an average of 5 genes per min of map length, and that most of these loci are randomly distributed, it seems increasingly improbable that the bacterial genome would contain genetically silent regions approaching 3.0 to 3.5 min in length. Accordingly, we would expect that future experimentation will lead to a shortening and perhaps total elimination of the longest gaps. Low (101) has described recent refinements of the interrupted mating technique of genetic mapping which should enable investigators to redetermine the lengths of chromosome segments near the longest gaps with greater precision than in the past. Experiments of this sort may reveal that some of the silent regions are shorter than presently indicated. As new gene loci continue to be discovered, some of the long gaps may also be closed by the extension and joining of the present transductional linkage groups. Of the smaller gaps listed in Table 2, those which appear to be shorter than the 2-min length of a transducing fragment will probably also disappear when the appropriate markers are tested for transductional linkage. Alternatively, failure to demonstrate joint transduction of such markers will require that the indicated distances between them be increased from present values.

Our overall impression of the current status of genetic mapping in *E. coli* is that the time is not far off when continuous transduction linkage of all known markers will be an accomplished fact. This achievement, in combination with the recent development of methods for measuring the physical length of genetically defined segments of bacterial DNA (141) means that it will soon be possible to translate genetic distance, measured as frequency of joint transduction, into physical units of map distance. Thus, we can look forward to a time when the linkage map of *E. coli* will be calibrated in micrometers of DNA length, or in kilobases (units of 1,000 nucleotide pairs) as proposed by Sharp et al. (141), rather than in minutes.

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