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Functions of the Gene Products of *Escherichia coli*

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INTRODUCTION

A substantial fraction of the genes and open reading frames of *Escherichia coli*, in the neighborhood of half the estimated whole, have been identified and mapped to either a genetic map (76) or a physical map (163, 1058a, 1377, 1378, 1380, 1381). The products of most of these genes have been identified, and main cellular functions of many products are known. Sequencing projects are yielding sequences of large continuous segments of the genome (see, e.g., references 331 and 1810). Some of the genes defined by sequence as open reading frames are presumed to have functions similar to those of known genes of similar sequence. These presumptions of function will have to be tested by experiment. Other open reading frames have unique sequence not similar to other sequences in current data banks (331, 1810). Therefore there are overlapping sets of genes of *E. coli*, some mapped, some sequenced, some with known function, and some not.

The sequence of the entire *E. coli* genome is expected to be in hand in a few years. It may be useful, then, at this intermediate juncture to step back and look with perspective at the sum of what we know today about the genetic determination of the *E. coli* cell and its physiological functions. This compilation essentially updates an earlier classification of *E. coli* genes and gene products by metabolic and physiological categories (710).

When all of the genes of the *E. coli* chromosome and the function of each gene product are known, we will have before us a list of all the genetic and biochemical ingredients that together make up a functioning and self-perpetuating free-living organism. Further in the future, we will understand all of the complex interrelated regulation systems that allow the genes and gene products to carry out their functions in a coordinated way, making it possible for the cell not only to live and perpetuate itself but also to adapt appropriately to changing circumstances.

For the present, we can ask, "How far have we come, and how far have we yet to go in the task of understanding completely the genetic determination of the biology of a single cell?" *E. coli* is a useful tool in this connection not because it is among the simplest of free-living organisms (other bacteria have smaller genomes and more limited biochemistry) but because more is known both genetically and biochemically about *E. coli* than about any other single-celled organism.

The aim of this article is to summarize present knowledge of the gene products of *E. coli* and their functions in the cell. Three sources were used as the starting point for this compilation. One is the listing and bibliography of *E. coli* genes, phenotypes, and gene products prepared by Barbara Bachmann and based on the literature through mid-1988 (76). Another is a set of data on genes kindly provided by Kenneth E. Rudd and his associate, Gerard Bouffard, constituting a subset of the physical map and sequence data assembled in the course of constructing data bases of the genome of *E. coli* (163, 1377, 1380). Finally, the primary literature was consulted directly, often with the aid of the Medline data base, with emphasis on the last 6 years.

DATA BASE OF GENES AND GENE PRODUCTS

I have assembled a database, EcoGeneFunction, in Microsoft Foxpro2 (MS-DOS) with the following information: gene name, synonyms, gene product (or a phenotype), for enzymes the EC number for the class of enzyme and the reaction catalyzed, the categories of cellular function(s) of the gene product, the type of gene (e.g., regulatory, coding

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for an enzyme), literature references, and information on duplicate or redundant gene products. An electronic version of the data base suitable for distribution will be prepared and will be available either on a DOS diskette or at the gopher of the Marine Biological Laboratory on crane.mbl.edu. Kindly contact me for more information.

Selection of Genes

All of the genes and gene products listed in the most recent Bachmann genetic map (76) are included in this data base (although some of the names are now synonyms). To maintain continuity with past compilations, all genes listed in the 1990 Bachmann map are retained. No entry in that work is excluded, even though information on the products of some of the genes was limited to a description of a mutant phenotype. In time, no doubt many of the early descriptions will be replaced by more precise definitions. Added to the Bachmann list are new genes identified after that compilation. These genes are treated differently. In this case new genes are included only if their gene products or cellular roles have been delineated well enough to support classification of the cellular function of the gene product. Thus recently reported open reading frames and genes whose products have not yet been well defined are not included here.

There were 1,403 listings in the 1990 Bachmann compilation. Some of the entries were redundant, such as some suppressor genes and the corresponding tRNA designations. In the data base described here, these double entries are reduced to one entry each. Also, *rrn* loci are not listed; only their component RNA genes are given. Some genes do not appear in their original position in the list because they have been renamed or redefined, and two genes, *pyrS* and *guaR*, have been removed. After these revisions, the Bachmann compilation was reduced to 1,356 genes of which 23 represent sites that generate no gene product (2 Ori, 4 Ter, 4 Rhs, and 13 phage attachment sites).

To this group were added 361 newly characterized genes, some derived from Rudd's EcoGene6 data base (1379, 1380) and some derived from recent literature. The new genes that were added were those for which the gene product has been, at least in gross terms, identified. No open reading frames whose function was identified only through sequence similarity were included. A total of 1,717 gene products are listed in Table 2, collected through 1992.

Gene Names

For the sake of consistency, the gene names used in Table 2 are the same as those used by Rudd (1377–1379). Older, synonymous gene names are given, including the cumulative list of designations given in the most recent genetic map (76).

Functional Categories

The gene products were categorized according to their function, by using the classification system of cell functions shown in Table 1. (The right-hand column of numbers of genes in Table 1 does not apply to the immediate discussion but will be covered in the section, Apportionment of Resources.) This classification scheme is arbitrary; there is of course no single, correct way to catalog cellular functions and structures as they relate to gene products. What is presented here is only one version from many possible. However flawed it may be, the scheme will serve the purpose of providing an interim overview. The categories are sufficiently small that rearrangement into other schemes for other purposes should not be too difficult.

Some of the arbitrary elements of the scheme stem from the fact that some categories emphasize structure and some emphasize function, leading to some imprecision and overlap. For instance, the outer and inner membranes and the murein sacculus are structural elements of the cell, classified in the category Cell Structure. However, some of the enzymes for synthesis of peptidoglycans could have been put instead into the category of Macromolecule Synthesis. In the opposite direction, there are constituents of the cell membrane that could have been classified as structural elements but, since they carry out important cell processes, were classified by function instead. Some of these are porins that function as channels for traverse of small molecules in and out of the cell, outer membrane proteins that respond to the osmotic strength of the surrounding mileu, or components of the electron transport system. Such membrane components were placed in various categories for cellular processes and metabolic function rather than in the category Cell Structure. Clearly, the classification scheme used in this exercise did not avoid such ambiguities, and the assignments of gene products were arbitrary, perhaps even idiosyncratic.

Ambiguity of classification also occurs with all enzymes that perform more than one metabolic role. Some enzymes play several quite different metabolic roles. Carbamyl phosphate synthase, for example, catalyzes a reaction used in both pyrimidine synthesis and arginine synthesis. The product of the *trxB* gene, the enzyme ribonucleotide reductase, not only reduces ribonucleotides to deoxyribonucleotides but also reduces sulfate ions and methionine sulfoxide and carries out general sulfide reduction. Therefore, in classifying gene products, it was sometimes necessary to make arbitrary decisions. In the data base EcoGeneFunction, up to four different roles for gene products were assigned when appropriate. One role was arbitrarily chosen as the primary assignment, and others were defined as subsidiary. Only one of these assignments of function was used to establish the organization of the data that is presented in Table 2.

Another factor of complexity is that the metabolic role of a reaction may depend on environmental and nutritional conditions. As an example, glycerol kinase can function as the first enzyme in the utilization of externally supplied glycerol as a carbon source, but in another context glycerol kinase carries out an essential early step in the pathway of fatty acid synthesis, supplying glycerol 3-phosphate as a needed intermediate. Therefore, whether the role of glycerol kinase is catabolic or synthetic depends on whether the cell is growing on glycerol as a carbon source and whether it is actively synthesizing fatty acids de novo. Similarly, the reaction catalyzed by acetate kinase can be a reaction in the final steps of metabolism of glucose fermentation or can be an early step in the utilization of acetate as a carbon source. In the first case we would call this a reaction of fermentation, whereas in the second case it would be a degradative reaction.

To determine the major function of a gene product, one might look to the regulatory organization of genes in the cell as a true measure of the relatedness of gene functions and the primary cellular function of gene products. However, this approach is not used for this data base since some operons are composed of member genes that seem only

TABLE 1. Classification of *E. coli* gene products

Category of function	No. of genes
I. Intermediary metabolism	
A. Degradation	175
B. Central intermediary metabolism	54
C. Respiration (aerobic and anaerobic)	55
D. Fermentation	39
E. ATP-proton motive force interconversion	9
F. Broad regulatory functions	43
II. Biosynthesis of small molecules	
A. Amino acids	
1. Glutamate family/nitrogen assimilation	23
2. Aspartate family, pyruvate family	53
3. Glycine-serine family/sulfur metabolism	17
4. Aromatic amino acid family	24
5. Histidine	9
B. Nucleotides	
1. Purine ribonucleotides	20
2. Pyrimidine ribonucleotides	11
3. 2′-Deoxyribonucleotides	7
4. Salvage and interconversions	19
C. Sugars and sugar nucleotides	13
D. Cofactors, prosthetic groups, electron carriers	
1. Biotin	8
2. Folic acid	9
3. Lipoate	2
4. Molybdopterin	5
5. Pantothenate	4
6. Pyridoxine	4
7. Pyridine nucleotides	5
8. Thiamine	11
9. Riboflavine	3
10. Thioredoxin, glutaredoxin, and glutathione	5
11. Menaquinone and ubiquinones	15
12. Heme and porphyrins	11
E. Fatty acids and lipids	35
F. Polyamines	6
III. Macromolecule metabolism	
A. Synthesis and modification	
1. Ribosomal and "stable" RNAs	25
2. Ribosomal proteins and their modification	64
3. Ribosomes and their maturation and modification	8
4. tRNAs, aminoacyl-tRNA synthetases and their modification	133
5. RNA synthesis, modification, and DNA transcription	19
6. Basic proteins	4
7. DNA replication, restriction/modification, recombination, and repair	99
8. Proteins (translation and modification)	22
9. Polysaccharides (cytoplasmic)	5
B. Degradation of macromolecules	
1. RNA	12
2. DNA	8
3. Proteins	20
IV. Cell structure	
A. Membrane components	20
B. Murein sacculus	36
C. Surface polysaccharides and antigens	35
D. Surface structures	50
V. Cellular processes	
A. Transport/binding proteins	216
B. Cell division	33
C. Chemotaxis and mobility	15
D. Protein secretion	19
E. Osmotic adaptation	21
VI. Other functions	
A. Cryptic genes	31
B. Phage-related functions and prophages	31
C. Colicin-related functions	16
D. Plasmid-related functions	5
E. Drug/analog sensitivity	35
F. Radiation sensitivity	4
G. DNA sites	20
H. Adaptations to atypical conditions	20

remotely connected in metabolic terms. One example is the operon containing *pdxA*, which codes for an enzyme in the pathway of pyridoxine synthesis; *ksgA*, which codes for a methyltransferase that acts on RNA; *apaG*, a gene of unknown function; and *apaH*, the gene for diadenosine tetraphosphatase (1344). Another mixed operon contains the *pdxB* gene; *asd'* (a homolog of an aspartate semialdehyde dehydrogenase gene); *his*T, the gene which codes for a tRNA modification enzyme pseudouridine synthase; and *dedA*, a gene which codes for a membrane protein (1440). Yet another example is the operon containing *serC*, which codes for 3-phosphoserine aminotransferase, an enzyme in the pathway of serine synthesis; and *aroA*, which codes for 5-enolpyruvylshikimate 3-phosphate synthase, an enzyme in the pathway of synthesis of aromatic amino acids (412). A goal for information systems will be to connect information on regulatory relationships among genes and gene products with representations of the biochemistry of *E. coli*. The classification scheme of Table 1 does not yet make use of regulatory relationships.

Gene Products and Phenotypes

The information available in the cited literature for the genes in Table 2 is not all of the same type. The level of our understanding of *E. coli* gene products is extremely variable from gene to gene. For some, the gene product has been well characterized physically and biochemically and the function in the cell is well understood. For others, the gene product has been identified but its role in the cell is not fully understood. For some, tentative function assignments have been made on the basis of sequence similarities. For still others, a gene is defined only broadly by a mutant phenotype. Phenotypic descriptions of organisms carrying either mutant or wild-type alleles do not always reveal the identity of the underlying gene product. For instance, drug resistance can be conferred by a mutant ribosomal protein, a mutant RNA polymerase subunit, or a mutant transport component. The root cause of radiation sensitivity or resistance or high rates of spontaneous mutation can reside in any one of several DNA repair processes. Complex phenotypes are often difficult to penetrate. Clearly, as mutants and gene products are defined more precisely and information on the metabolic function of gene products becomes more exact,

some of the assignments of category of function made in this compilation will have to be changed to be more nearly correct.

Citations

The focus of the bibliography provided here is the gene product rather than the gene. Primary literature citations have been collected in the cumulative lists compiled by Bachmann over the years (75, 76) for many *E. coli* genes, with a focus on their genetic map positions. More recently, citations have been collected on physical maps and sequences of *E. coli* genes in a number of data bases, including the review by Danchin (1058a) and in the work of Rudd (163, 1377, 1378, 1380, 1381) and others. In Table 2 the citations focus on the function of the gene product. There is some overlap with other bibliographies, as when the sequence gives most of the information we have on the function of the gene product and in the cases when little work has been reported since isolation and mapping of mutant alleles many years ago.

There is great unevenness in the extent and depth of knowledge of the many gene products of *E. coli*. The present state of knowledge about any given gene product ranges from having full biochemical characterization and X-ray patterns of the molecular structure to the other extreme, having only a phenotype connected to the gene with no indication of the nature of the gene product. Between these extremes are many states. For some enzymes, known for decades, the catalyzed reactions have been studied in detail and activators and inhibitors and their sites of action are known; for some other enzymes, sequences have been determined and directed mutagenesis has given information on biochemical interactions of individual amino acid residues at catalytic sites, binding sites, and regulatory sites. Other enzymes have not yet been isolated or purified, and the main source of information about the properties of the protein is the nucleotide sequence of the gene and its translated amino acid sequence. For still others, neither gene nor enzyme has been isolated, and a metabolic or cellular process has been assigned to the gene by reasoning from the properties of mutants. The same uneveness in the state of knowledge is found for other cellular components.

In some cases, little research as been done over the years and the citations collected in cumulative reviews by Bachmann (75, 76) remain the most pertinent. In other cases, there is a large literature and the few citations in Table 2 (arbitrarily no more than three per entry) constitute only a sample of a large literature and are not intended to be inclusive.

APPORTIONMENT OF *E. COLI* GENETIC RESOURCES

Table 2 shows the broad outlines of the apportionment of *E. coli* genetic resources to different kinds of cellular activities or cell substance (keeping in mind that there is a degree of ambiguity and arbitrary choice in the classification system applied). The numbers of genes located in each category are shown in the righthand column of Table 1. The percentage of genes listed here that are devoted to each of the main categories of functions is summarized in Table 3.

In the category of small-molecule metabolism, the number of gene products concerned with degradation and with interconversion of metabolites is relatively large. This seems to reflect the versatility of *E. coli* in its ability to derive energy and building blocks from many different starting compounds by using separate specialized pathways that each feed into the main central degradation pathways. As to biosynthesis, the number of genes required to specify enzymes for biosynthesis of small molecules is of the same order as the number of genes used in degradative pathways and intermediary metabolism (Table 3).

The number of gene products devoted to the metabolism of macromolecules is larger than the number devoted to any one of the small-molecule categories but smaller than the sum of the two major small-molecule categories (Table 3). On the whole there are no surprises here in the balance of genetic resources devoted to small and large molecules, even though the sample of *E. coli* genes and gene products analyzed here may constitute only half or less of the total number.

Within the category of metabolism of macromolecules, tRNAs and their amino acid synthetases require relatively large proportions of the coding functions of *E. coli* so far identified. The size of the tRNA category is a consequence of the redundancy of the code and also of many instances of replicate tRNA genes. The next largest component in macromolecule metabolism is that of DNA replication, recombination, repair and restriction/modification, reflecting the importance of the care, maintenance, and promulgation of hereditary material.

As this catalog has been arranged, a smaller number of genes encode structural materials of the cell, although, as noted above, some structural elements have been classified by their function; therefore the category of genes encoding components of cell structure is reduced in size. In the category of cellular functions as defined here, a large fraction is that of transport proteins (including a few other binding proteins of various functions). The size of this group emphasizes the importance of the gateways between the exterior environment and the interior of the cell. This group of genes encodes the molecules that transport specific molecules into the cell, excrete other molecules, and maintain a balance of such critical ions as sodium and potassium.

The last group in Table 1 is a catchall. Only modest numbers of genes have been assigned to these "other-function" categories. Genes of cryptic operons are listed here, as are genes related to external genetic elements such as phages and plasmids and also the DNA sites for which there is no gene product. The genes described as conferring sensitivity to drugs or radiation or as being involved in adaptation to atypical conditions are genes that may well be reclassified into more definitive categories when the identity and mechanism of action of their gene products are more clearly defined.

DISTRIBUTION OF TYPES OF GENES

Table 4 classifies the genes listed here by type of gene product, if that has been determined, or notes them as known at the level of phenotype only if the gene product has not been determined. Despite the massive research attention *E. coli* receives from a large number of scientists, the category of genes known only by phenotype remains very large, about 15% of the total. One hopes that members of this class will receive concentrated attention in the future so that their cellular functions can be better understood and the category of genes defined only by phenotypes can shrink toward zero.

Among the various types of gene products that have been

TABLE 2. *E. coli* genes grouped by function

Gene	Synonym	Gene product and description	Reference(s)
I. Intermediary metabolism			
A. Degradation			
aceE	*aceE1*	Pyruvate dehydrogenase (decarboxylase component) (EC 1.2.4.1)	556
aceF	*aceE2*	Pyruvate dehydrogenase (dihydrolipoyltransacetylase component) (EC 2.3.1.12)	1389, 1447, 1448
ackA		Acetate kinase activity (EC 2.7.2.1)	1037, 1714
ackB		Acetate kinase activity (EC 2.7.2.1)	1233
adi		Arginine decarboxylase, degradative periplasmic glucose-1-phosphatase (EC 3.1.3.10)	1544 1286
agp			
amyA		α-Amylase (EC 3.2.1.1)	1308
ansA		Cytoplasmic L-asparaginase I (EC 3.5.1.1); isozyme	743
ansB		Cytoplasmic L-asparaginase II (EC 3.5.1.1); isozyme	154, 742
appA		pH 2.5 acid phosphatase (EC 3.1.3.2); exopolyphosphatase (EC 3.6.1.11)	337, 338
araA		L-Arabinose isomerase (EC 5.3.1.4)	898, 946
araB		Ribulokinase (EC 2.7.1.16)	898, 946
araC		Activator and repressor protein for *ara*	897, 975, 1069
araD		L-Ribulosephosphate 4-epimerase (EC 5.1.3.4)	898
asu		Asparagine utilization, as sole nitrogen source	258
atoA		Acetyl-CoA:acetoacetyl-CoA transferase (EC 2.8.3.-) β-subunit	741, 1237
atoB		Acetyl-CoA acetyltransferase (EC 2.3.1.9)	741, 1237
atoC		Positive regulator of *ato*	740, 741, 1237
atoD		Acetyl-CoA:acetoacetyl-CoA transferase (EC 2.8.3.-) α-subunit?	741, 1237
cadA		Lysine decarboxylase (EC 4.1.1.18)	1066, 1720
cadC		Transcriptional activator of *cad* operon	1720
cxm	*cxr*	Methylglyoxal biosynthesis	806
cynR		*cyn* operon positive regulator	40, 1571
cynS	*cnt*	Cyanate aminohydrolase (EC 3.5.5.3), cyanase	40, 578, 959
dadA	*dadR*	D-Amino acid dehydrogenase subunit (EC 1.4.99.1)	1752
dadB	*alnA*	D-Amino acid dehydrogenase subunit (EC 1.4.99.1)	481
dadQ	*alnR*	Regulator of *dad* regulon	481
dgd		D-Galactose dehydrogenase (EC 1.1.1.48)	967
dgoA		2-Oxo-3-deoxygalactonate 6-phosphate aldolase (EC 4.1.2.21)	298
dgoD		Galactonate dehydratase (EC 4.2.1.6)	298
dgoK		2-Oxo-3-deoxygalactonate kinase (EC 2.7.1.58)	298
dgoR		Regulator of *dgo* operon	298
dgt		Deoxyguanosine triphosphate triphosphohydrolase (EC 3.1.5.1)	1305, 1306, 1780
dsdA		D-Serine deaminase (EC 4.2.1.14)	1018–1020
dsdC		Activator for *dsdA*	1216
eda	*kdgA*, *kga*	2-Keto-3-deoxygluconate 6-phosphate aldolase (EC 4.1.2.14); 2-keto-4-hydroxyglutarate aldolase (EC 4.1.3.16)	419, 1235
edd		Phosphogluconate dehydratase (EC 4.2.1.12)	419
eno		Enolase (EC 4.2.1.11)	714
eutB		Ethanolamine-ammonia lyase heavy chain (EC 4.3.1.7)	749, 750, 1177
eutC		Ethanolamine-ammonia lyase light chain (EC 4.3.1.7)	749, 750, 1177
exuR		Negative regulator of *exu* regulon, *exuT*, *uxaAC*, and *uxuB*	142
fadA		Thiolase I (EC 2.3.1.16)	1796
fadB	*oldA*, *oldB*	3-Hydroxydroxyacyl-CoA dehydrogenase (EC 1.1.1.35), 3-hydroxyacyl-CoA epimerase (EC 5.1.2.3), δ(3)-*cis*-δ(2)-*trans*-enoyl-CoA isomerase (EC 5.3.3.8) Enoyl-CoA-hydratase (crotonase) (EC 4.2.1.17)	1795, 1797
fadD	*oldD*	Acyl-CoA synthetase (EC 6.2.1.3)	135
fadE		Electron transport flavoprotein (ETF) of β-oxidation	270, 1204
fadH		2,4-Dienoyl-CoA reductase (EC 1.3.1.34)	1806
fatA		Utilization of *trans*-unsaturated fatty acids	378
fba	*ald*, *fda*	Fructose-bisphosphate aldolase, class II (EC 4.1.2.13)	17, 592, 1138
fruK	*fpk*	Fructose-1-phosphate kinase (EC 2.7.1.56)	1194
fruL		*fruR* leader peptide	736
fruR	*fruC*, *shl*	Repressor of *fru* operon	513, 736, 890
fruS		Regulator of *fruA* and *fruF*	153
fucA	*fucC*, *prd*	L-Fuculose-1-phosphate aldolase (EC 4.1.2.17)	250, 1827
fucI		L-Fucose isomerase (EC 5.3.1.-)	250
fucK		L-Fuculokinase (EC 2.7.1.51)	250
fucO		L-1,2-Propanediol oxidoreductase (EC 1.1.1.77)	295
fucR		Positive regulator of the *fuc* operon	251, 987

Continued on following page

TABLE 2—*Continued*

Gene	Synonym	Gene product and description	Reference(s)
galK	*galA*	Galactokinase (EC 2.7.1.6)	1691
galM		Aldose-1-epimerase (mutarotase) (EC 5.1.3.3)	1032
galR	*Rgal*	Repressor of *galETK* operon	326
galS		Second *gal* repressor	1727
gapA	*gad*	Glyceraldehyde-3-phosphate dehydrogenase A (EC 1.2.1.12)	638, 713
gapB		Glyceraldehyde 3-phosphate dehydrogenase B (EC 1.2.1.12)	18, 398
garA		Glucarate utilization	1349
garB		Glucarate utilization	1349
gatC		Regulator of gat	905
gatD		Galactitol-1-phosphate dehydrogenase	368, 905
gcd		Glucose dehydrogenase (EC 1.1.99.17)	278
gcl		Glyoxylate carboligase (EC 4.1.1.47)	236
gcvA		Positive regulator of *gcv*	1760
gcvH	*gcv*	H protein of glycine cleavage complex, carrier of aminomethyl moiety (EC 1.4.4.2)	1263, 1535, 1538
gcvP		Glycine decarboxylase, P protein of glycine cleavage system (EC 1.4.4.2)	1263, 1538
gcvT		T protein (tetrahydrofolate dependent) of glycine cleavage system	1263, 1538
glc		Malate synthase G (EC 4.1.3.2)	1670
glk		Glucokinase (EC 2.7.1.2)	318
glpQ		Glycerophosphodiester diesterase (EC 3.1.4.46)	881, 1628
gntR		Regulator of *edd*; transport and phosphorylation of gluconate	74, 280
gntV		Gluconokinase, thermosensitive	280, 719
gpm		Phosphoglyceromutase (EC 2.7.5.3)	162
gurB	*crp*?	Utilization of methyl-β-D-glucuronide; *crp*?	1549
gurC		Utilization of methyl-β-D-glucuronide	1549
gurD		Utilization of methyl-β-D-glucuronide	1549
hga		2-Keto-4-hydroxyglutarate aldolase (EC 4.1.3.16)	1235
kba		Ketose-bisphosphate aldolase (EC 4.1.2.13)	1243
kdgK		Ketodeoxygluconokinase (EC 2.7.1.45)	1285
kdgR		Regulator of *kdgK*, *kdgT*, and *eda*	1285
lacA	*a*, *lacAc*	Galactoside acetyltransferase (EC 2.3.1.18)	43
lacI	*i*	Repressor of the *lac* operon	805, 826
lacZ	*z*	β-D-Galactosidase (EC 3.2.1.23)	511
mac		Maltose acetyltransferase, broad specificity (EC 2.3.1.-)	173
malM	*molA*	Periplasmic protein of *mal* operon	536, 1370
malP	*malA*	Maltodextrin phosphorylase (EC 2.4.1.1)	1432
malQ	*malA*	Amylomaltase (EC 2.4.1.25)	1300
malS		α-Amylase (EC 3.2.1.1)	1435
malT	*malA*	Positive regulator of *mal* regulon	1435
malY		Enzyme that may degrade or block biosynthesis of endogenous *mal* inducer	1324
malZ		Maltodextrin glucosidase (EC 3.2.1.20)	1435
manC	*mni*	D-Mannose isomerase regulation; utilization of D-lyxose	1542
maoA	*tynA*	Tyramine oxidase (EC 1.4.3.4)	1131, 1791
melA	*mel-7*	α-Galactosidase (EC 3.2.1.22)	944, 1134, 1283
melR		Regulator of melibiose operon	1724
mtlC		Regulator for *mtl*906, 907, 1506	
mtlD		Mannitol-1-phosphate dehydrogenase (EC 1.1.1.17)	1608
nlp	*sfs7*	*crp**-dependent stimulation of *malPQ* and *lacZ*, similar to Ner protein of phage Mu?	265
pac		Penicillin acylase, detaches phenylacetate residue	104, 1072
pat		Putrescine aminotransferase activity	1293
pfkA		6-Phosphofructokinase I (EC 2.7.1.11)	379, 380, 851
pfkB		6-Phosphofructokinase II; suppressor of *pfkA* (EC 2.7.1.11)	73, 579
pga		Penicillin G acylase (EC 3.5.1.11)	261, 1182
pgi		Glucosephosphate isomerase (EC 5.3.1.9)	488
pgk		Phosphoglycerate kinase (EC 2.7.2.3)	1151
pgm		Phosphoglucomutase (EC 5.4.2.2)	1286
phnD	*psiD*	Carbon-phosphorus lyase	1009, 1075, 1713
phnF		Utilization of phosphorus-containing compounds	1075, 1713
phnG		Utilization of phosphorus-containing compounds	1009, 1075, 1713
phnH		Utilization of phosphorus-containing compounds, C-P lyase component?	1009, 1075, 1713
phnI		Utilization of phosphorus-containing compounds	1009, 1075, 1713
phnJ		Utilization of phosphorus-containing compounds, C-P lyase component?	1009, 1075, 1713

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TABLE 2—*Continued*

Gene	Synonym	Gene product and description	Reference(s)
phnK		Utilization of phosphorus-containing compounds, C-P lyase component?	1009, 1075, 1713
phnL		Utilization of phosphorus-containing compounds, probable regulator	1009, 1075, 1713
phnM		Utilization of phosphorus-containing compounds	1009, 1075, 1713
phnN		Utilization of phosphorus-containing compounds	1009, 1075, 1713
phnO		Utilization of phosphorus-containing compounds, probably a regulator	1009, 1075, 1713
phnP		Utilization of phosphorus-containing compounds, C-P lyase component?	1009, 1075, 1713
phoA		Alkaline phosphatase (EC 3.1.3.1)	372
phoP		Response regulator for *phoA* (sensor, *phoQ*)	570, 783
phoQ		Sensor for *phoP*, histidine protein kinase	783
poaR		Regulation of proline oxidase production	290
poxA		Regulator for *poxB*	1671
poxB		Pyruvate oxidase (EC 1.2.2.2)	554, 1706
prp		Propionate metabolism	1518
psiF		Induced by phosphate starvation	1074, 1712
pta		Phosphotransacetylase (EC 2.3.1.8) activity	580, 1296
putA	*poaA*	Proline dehydrogenase (EC 1.5.99.8)	1767
pykA		Pyruvate kinase II, glucose stimulated (EC 2.7.1.40)	1059, 1664
pykF		Pyruvate kinase I (formerly F), fructose stimulated (EC 2.7.1.40)	1183, 1514
rbsK		Ribokinase (EC 2.7.1.15)	37, 662
rbsR		Regulator for *rbs*	983
rhaA		L-Rhamnose isomerase (EC 5.3.1.14)	78
rhaB		Rhamnulokinase (EC 2.7.1.5)	78
rhaD		Rhamnulosephosphate aldolase (EC 4.1.2.19)	78
rhaR	*rhaC*	Positive regulator for *rha*	1623, 1624
rhaS	*rhaC*	Positive regulator for *rha*	1623
rpiA		Ribosephosphate isomerase (EC 5.3.1.6), constitutive	1498
sdaA		L-Serine deaminase (EC 4.2.1.13)	1018, 1562, 1563
sdaB		L-Serine deaminase, L-SD2 (EC 4.2.1.13)	1562
srlD	*gutD*, *sbl*	Glucitol (sorbitol)-6-phosphate dehydrogenase (EC 1.1.1.140)	1788
srlM	*gutM*	Glucitol operon activator	1788
srlR	*gutR*	Regulator for *srl*	1788
tdcA	*tdc*	Threonine dehydratase (EC 4.2.1.16)	1452
tdcB		Threonine dehydratase, catabolic (EC 4.2.1.16)	549, 650, 1452
tdcR		Threonine dehydratase operon activator protein	1451
tdh		Threonine dehydrogenase (EC 1.1.1.103)	62, 307, 441
thdA		Sulfone and sulfoxide oxidase activity	754
thdC		Protection against furans and thiophenes	754
thdD		Protection against furans and thiophenes	754
thdF		Thiophene and furan oxidation	14
tnaA	*ind*	Tryptophanase (EC 4.1.99.1)	1625
tnaL		Tryptophanase leader peptide	544
treC		Amylotrehalase	155
udk		Uridine/cytidine kinase (EC 2.7.1.48)	1662
udp		Uridine phosphorylase (EC 2.4.2.3)	183, 1082
uidA	*gurA*	β-D-Glucuronidase (EC 3.2.1.31)	140
uidR		Regulator for *uid*	140
uxaA		Altronate hydrolase (EC 4.2.1.7)	1275
uxaB		Altronate oxidoreductase (EC 1.1.1.58)	141
uxaC		Uronate isomerase (EC 5.3.1.12)	1170
uxuA		Mannonate hydrolase (EC 4.2.1.8)	142
uxuB		Mannonate oxidoreductase (EC 1.1.1.57)	142
uxuR		Regulator of *uxuBA* operon	142
xapA	*pndA*	Xanthosine phosphorylase (EC 2.4.2.1)	124
xapR	*pndR*	Regulator for *xapA*	210
xylA		D-Xylose isomerase (EC 5.3.1.5)	96, 1366
xylB		Xylulokinase (EC 2.7.1.17)	156, 1366
xylR		Regulator for *xyl*	1366
B. Central intermediary metabolism			
aceA	*icl*	Isocitrate lyase (EC 4.1.3.1)	3, 821, 1375
aceB	*mas*	Malate synthase A (EC 4.1.3.2)	211, 212, 1036
aceK		Isocitrate dehydrogenase kinase/phosphatase (EC 2.7.1.116)	700, 819, 878

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TABLE 2—*Continued*

Gene	Synonym	Gene product and description	Reference(s)
acn		Aconitase (EC 4.2.1.3)	1296
ahpC		Alkyl hydroperoxide reductase, C22 subunit; detoxification of hydroperoxides	1552
ahpF		Alkyl hydroperoxide reductase, F52a subunit; detoxification of hydroperoxides	1552
appY		Regulatory protein affecting *appA* and other genes	68
cynT		Carbonic anhydrase (EC 4.2.1.1)	40, 578
dprA		Dihydropteridine reductase (EC 1.6.99.7)	567, 1678
fbp	*fdp*	Fructose-1,6-bisphosphatase (EC 3.1.3.11)	592
fumA		Fumarase A, aerobic isozyme (EC 4.2.1.2)	1656, 1769
fumB		Fumarase B, anaerobic isozyme (EC 4.2.1.2)	109, 575, 1769
fumC		Fumarase C, isozyme (EC 4.2.1.2)	956, 1656, 1769
gabC		Regulator for *gabPDT*	1076
gabD		Succinate-semialdehyde dehydrogenase (EC 1.2.1.24), NADP-dependent activity	95, 1076
gabT		Aminobutyrate aminotransferase (EC 2.6.1.19) activity	95, 1076
gadA	*gadS*	Glutamate decarboxylase isozyme (EC 4.1.1.15)	1500
gadB		Glutamate decarboxylase isozyme (EC 4.1.1.15)	1500
glmS		L-Glutamine:D-fructose-6-phosphate aminotransferase (EC 2.6.1.16)	77, 468, 1655
gltA	*glut*	Citrate synthase (EC 4.1.3.7)	38, 392, 1013
gnd		Gluconate-6-phosphate dehydrogenase, decarboxylating (EC 1.1.1.44)	224
gpsA		*sn*-Glycerol-3-phosphate dehydrogenase [NAD(P)$^+$] (EC 1.1.1.94)	416
grx		Small dithiol protein required for glutathione-dependent ribonucleotide reductase	1254, 1387, 1407
hdhA		NAD-dependent 7-α-hydroxysteroid dehydrogenase (EC 1.1.1.159), dehydroxylation of bile acids	1804
icdC'	*icd*	Isocitrate dehydrogenase, NADP$^+$ specific (EC 1.1.1.42), chromosomal fragment	218, 684, 685
icdE	*icd*	Isocitrate dehydrogenase, NADP$^+$ specific (EC 1.1.1.42), chromosome-e14 hybrid	636, 684, 685
iclR		Repressor of *aceBA* operon	300, 1150, 1572
kbl		2-Amino-3-ketobutyrate CoA ligase (glycine acetyltransferase) (EC 2.3.1.29)	1115, 1116
lpdA	*lpd, dhl*	Lipoamide dehydrogenase (NADH) (EC 1.8.1.4); component of pyruvate and 2-oxodehydrogenase complexes; L-protein of glycine cleavage complex	26, 1538
maeA	*sfc*	NAD-linked malic enzyme? (EC 1.1.1.38)	296
mdh		Malate dehydrogenase (EC 1.1.1.37)	1685
metK		Methionine adenosyltransferase (EC 2.5.1.6) (AdoMet synthetase); methyl and propylamine donor, corepressor of *met* genes	143, 1420
mog	*chlG, bisD*	Required for the efficient incorporation of molybdate in molybdoproteins	644
nadR		Probable *nadAB* transcriptional regulator	1379
nanA		*N*-Acetylneuraminate lyase (aldolase) (EC 4.1.3.3)	10, 11
pckA	*pck*	Phosphoenolpyruvate carboxykinase (EC 4.1.1.49)	541
pgl	*blu*	6-Phosphogluconolactonase (EC 3.1.1.31)	855
ppa		Inorganic pyrophosphatase (EC 3.6.1.1)	865, 866
ppc	*asp, glu*	Phosphoenolpyruvate carboxylase (EC 4.1.1.31)	1606, 1607
ppsA	*pps*	Phosphoenolpyruvate synthase (EC 2.7.9.2)	1236
prr		γ-Aminobutyraldehyde (pyrroline) dehydrogenase activity	1293
sad		Succinate-semialdehyde dehydrogenase (EC 1.2.1.16), NAD dependent	1024
snoB		Reduces activity of *Rhizobium* NifA in *E. coli*, probably by increased rate of degradation and by inactivation	675
snoC		Increases rate of degradation of *Rhizobium* NifA in *E. coli*	675
sucA	(*lys* + *met*)	2-Oxoglutarate dehydrogenase (decarboxylase component) (EC 1.2.4.2)	628
sucB	(*lys* + *met*)	2-Oxoglutarate dehydrogenase (dihydrolipoyltranssuccinase component) (EC 2.3.1.61)	628, 1209
sucC		Succinyl-CoA synthetase (EC 6.2.1.5), β subunit	1007
sucD		Succinyl-CoA synthetase (EC 6.2.1.5), α subunit	1007
tesB		Thioesterase II (EC 3.1.2.-)	1137
tkt		Transketolase (EC 2.2.1.1)	752
tpiA		Triosephosphate isomerase (EC 5.3.1.1)	136, 1271
trxB		Thioredoxin reductase	856, 1297

Continued on following page

TABLE 2—*Continued*

Gene	Synonym	Gene product and description	Reference(s)
ugpQ		Glycerophosphodiester phosphodiesterase, cytosolic (EC 3.1.4.46)	1628
zwf		Glucose-6-phosphate dehydrogenase (EC 1.1.1.49)	1372, 1373
C. Respiration (aerobic and anaerobic)			
appB		Probable third cytochrome oxidase, subunit	337
appC		Probable third cytochrome oxidase, subunit	337
cybB		Cytochrome b_{561}	1090, 1142, 1160
cybC		Cytochrome b_{562}	1090, 1142, 1160
cydA		Cytochrome *d* terminal oxidase, polypeptide subunit I (EC 1.10.3.-)	303, 605, 1156
cydB		Cytochrome *d* terminal oxidase, polypeptide subunit II (EC 1.10.3.-)	303, 605, 1156
cydC		Cytochrome *d* terminal oxidase, possible heme *d* component	363, 522
cydD		Cytochrome *d* activity, Zn sensitive	411, 1156, 1272
cyoA		Cytochrome *o* ubiquinol oxidase subunit II (EC 1.10.3.-)	257, 303, 1143
cyoB		Cytochrome *o* ubiquinol oxidase subunit I (EC 1.10.3.-)	255, 1091, 1143
cyoC		Cytochrome *o* ubiquinol oxidase subunit III (EC 1.10.3.-)	255, 257, 1091
cyoD		Cytochrome *o* ubiquinol oxidase operon protein CyoD	255, 257, 1091
cyoE		Cytochrome *o* ubiquinol oxidase operon protein CyoE	255, 257, 1091
dmsA		Anaerobic dimethyl sulfoxide reductase chain A	216, 1403
dmsB		Anaerobic dimethyl sulfoxide reductase chain B	1369, 1402, 1403
dmsC		Anaerobic dimethyl sulfoxide reductase chain C	1403
fdx		[2Fe-2S] ferredoxin, electron carrier protein	1582
fldA		Flavodoxin	1198
fre	*flrD*, *fadI*, *fsrC*	Ferrisiderophore reductase; flavin reductase (NADPH:flavin oxidoreductase) (EC 1.6.8.1)	1521
glpA		*sn*-Glycerol-3-phosphate dehydrogenase (anaerobic), large subunit (EC 1.1.99.5)	282, 724, 881
glpB		*sn*-Glycerol-3-phosphate dehydrogenase (anaerobic), membrane anchor subunit (EC 1.1.99.5)	282, 724, 881
glpC		*sn*-Glycerol-3-phosphate dehydrogenase (anaerobic), small subunit (EC 1.1.99.5)	282, 724, 881
glpD	*glyD*	*sn*-Glycerol-3-phosphate dehydrogenase (aerobic) (EC 1.1.99.5)	71, 724
glpE		Protein of *glp* regulon	724
glpG		Protein of *glp* regulon	1450
glpR		Repressor of the *glp* operon	264, 724, 881
hmp	*frsB*	Hemoprotein (EC 1.6.99.7); ferrisiderophore reductase activity	46, 466, 1677
hyaA		Hydrogenase-1 small subunit (EC 1.18.99.1)	1070, 1071, 1298
hyaB		Hydrogenase-1 large subunit (EC 1.18.99.1)	1070, 1071, 1298
hyaC		Membrane-spanning protein of *hya* operon?	1070, 1071, 1298
hyaD		Processing of HyaA and HyaB proteins	1070, 1071, 1298
hyaE		Processing of HyaA and HyaB proteins	1070, 1071, 1298
hyaF		Nickel incorporation into hydrogenase-1 proteins	1070, 1071, 1298
hydA		Hydrogenase 1 activity	945
katC		Catalase activity	922
katE		Catalase hydroperoxidase HPII(III) (EC 1.11.1.6)	5, 349, 1690
katG		Catalase-peroxidase hydroperoxidase HPI(I) (EC 1.11.1.6)	5, 979, 1636
narG	*chlC*, *narC*	Nitrate reductase (EC 1.7.99.4), α subunit	144, 408
narH	*chlC*	Nitrate reductase (EC 1.7.99.4), β subunit	144, 408
narI	*chlI*	Cytochrome *b*(NR), nitrate reductase (EC 1.7.99.4), γ subunit	144, 408
narJ	*chlC*	Nitrate reductase (EC 1.7.99.4), δ subunit, assembly function	144, 408
ndh		Respiratory NADH dehydrogenase (EC 1.6.99.3)	591, 707, 1516
nirB	*nirD*	Nitrite reductase [NAD(P)H] subunit (EC 1.6.6.4)	599
nirC		Nitrite reductase activity	599
nirD		Nitrate reductase [NAD(P)H] subunit (EC 1.6.6.4)	599
pntA		Pyridine nucleotide transhydrogenase (EC 1.6.1.1), α subunit	8, 1629
pntB		Pyridine nucleotide transhydrogenase (EC 1.6.1.1), β subunit	8, 1629
sdhA		Succinate dehydrogenase (EC 1.3.99.1), flavoprotein subunit	1084, 1765
sdhB		Succinate dehydrogenase (EC 1.3.99.1), iron sulfur protein	335, 1084
sdhC	*cybA*	Succinate dehydrogenase (EC 1.3.99.1), cytochrome b_{556}	1084, 1126
sdhD		Succinate dehydrogenase (EC 1.3.99.1), hydrophobic subunit	1084, 1765
sodA		Superoxide dismutase, manganese (EC 1.15.1.1)	122, 458, 1295
sodB		Superoxide dismutase, iron (EC 1.15.1.1)	122, 458, 1295
torA		Trimethylamine *N*-oxide reductase (EC 1.6.6.9)	1493, 1494
torR		Regulator for *torA*	1234

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TABLE 2—*Continued*

Gene	Synonym	Gene product and description	Reference(s)
D. Fermentation			
acd		Acetaldehyde-CoA dehydrogenase	272
act		Pyruvate formate-lyase-activating enzyme	1424
adhE	*ana*	CoA-linked acetaldehyde dehydrogenase and alcohol dehydrogenase; pyruvate-formate-lyase deactivase (EC 1.1.1.1)	546, 580, 803
adhR		Regulator for *acd* and *adhE*	273
ald		Aldehyde dehydrogenase, NAD linked (EC 1.2.1.3)	252, 634
aldH		Aldehyde dehydrogenase, prefers NADP over NAD (EC 1.2.1.3)	616
dld	*ldh*	D-Lactate dehydrogenase, NADH independent (EC 1.1.1.28)	1642
fdhF		Selenopolypeptide subunit of formate dehydrogenase H (part of formate hydrogen-lyase complex) (EC 1.2.1.2)	244, 615, 1830
fdnG		Formate dehydrogenase-N, nitrate inducible, major subunit (EC 1.2.1.2)	117, 118, 931
fdnH		Formate dehydrogenase-N, nitrate inducible, iron-sulfur subunit (EC 1.2.1.2)	118, 931
fdnI		Formate dehydrogenase-N, nitrate inducible, cytochrome b_{556}(Fdn) subunit (EC 1.2.1.2)	118, 931
fhlA		Formate hydrogen-lyase transcriptional activator for *fdhF*, *hyc*, and *hyp* operons	1041, 1367, 1433
fhlB		Regulator for formate hydrogen-lyase (FHL complex)	1041, 1367
frdA		Fumarate reductase (EC 1.3.99.1), flavoprotein subunit	291
frdB		Fumarate reductase (EC 1.3.99.1), iron-sulfur protein subunit	291, 1016, 1738
frdC		Fumarate reductase (EC 1.3.99.1), membrane anchor polypeptide	291
frdD		Fumarate reductase (EC 1.3.99.1), membrane anchor polypeptide	291
hybA		Small subunit of hydrogenase-2, probable iron-sulfur protein (EC 1.18.99.1)	149, 1297
hybB		Hydrogenase-2 activity	1297
hybC		Large subunit, hydrogenase-2 (EC 1.18.99.1)	1297
hybD		Hydrogenase-2 activity	1297
hybG		Pleiotrophic regulator of hydrogenase genes	1297
hycA		Transcriptional repression of *hyc* and *hyp* operons	1297, 1423
hycB		Probable small subunit of hydrogenase-3, iron-sulfur protein (part of formate hydrogen-lyase [FHL] complex) (EC 1.18.99.1)	1297, 1423
hycC		Membrane-spanning protein of hydrogenase 3 (part of FHL complex) (EC 1.18.99.1)	1297, 1423
hycD		Membrane-spanning protein of hydrogenase 3 (part of FHL complex) (EC 1.18.99.1)	1297, 1423
hycE		Probable large subunit of hydrogenase 3 (part of FHL complex) (EC 1.18.99.1)	945, 1297, 1423
hycF		Probable iron-sulfur protein of hydrogenase 3 (part of FHL complex) (EC 1.18.99.1)	1297, 1423
hycG		Hydrogenase activity	1297, 1423
hycH		Processing of large subunit (HycE) of hydrogenase 3 (part of the FHL complex)	1297, 1423
hydG		Regulation of hydrogenase 3 activity	945, 1550
hydH		Regulation of hydrogenase 3 activity	945, 1550
hydL	*hup?*	Probable member of *hyb* operon; pleiotrophic effects	
hypA		Pleiotrophic effects on three hydrogenase isozymes	945, 997, 1297
hypB	*hydB hydE*	Pleiotrophic effects on three hydrogenase isozymes	945, 997
hypC		Pleiotrophic effects on three hydrogenase isozymes	945, 997
hypD		Pleiotrophic effects on three hydrogenase isozymes	945, 997
lctD	*lct*	L-Lactate dehydrogenase (EC 1.1.1.27)	393
pfl		Pyruvate formate-lyase (EC 2.3.1.54)	820, 1426
E. ATP-proton motive force interconversion			
atpA	*unc*	Membrane-bound ATP synthase (EC 3.6.1.34), F1 sector, α subunit	925, 1683
atpB	*unc*	Membrane-bound ATP synthase (EC 3.6.1.34), F0 sector, subunit a	926, 1682
atpC	*unc*	Membrane-bound ATP synthase (EC 3.6.1.34), F1 sector, ε subunit	879, 1065
atpD	*unc*	Membrane-bound ATP synthase (EC 3.6.1.34), F1 sector, β subunit	899
atpE	*unc*	Membrane-bound ATP synthase (EC 3.6.1.34), F0 sector, subunit c; DCCD[a]-binding protein	464, 478, 537
atpF	*unc*	Membrane-bound ATP synthase (EC 3.6.1.34), F0 sector, subunit b	1051
atpG	*unc*	Membrane-bound ATP synthase (EC 3.6.1.34), F1 sector, γ subunit	681
atpH	*unc*	Membrane-bound ATP synthase (EC 3.6.1.34), F1 sector, δ subunit	438
atpI	*unc*	Membrane-bound ATP synthase (EC 3.6.1.34), subunit?	1436

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TABLE 2—*Continued*

Gene	Synonym	Gene product and description	Reference(s)
F. Broad regulatory functions			
ada		Bifunctional gene product: *O*6-methylguanine-DNA methyltransferase (EC 2.1.1.-); transcription activator/repressor	12, 125, 1319
arcA	*dye, fexA, msp, cpxC, sfrA, seg*	Negative response regulator of genes in aerobic pathways, (sensor for *arcB* and *cpxA*)	304, 723, 726
arcB		Aerobic respiration sensor protein; histidine protein kinase/phosphatase, sensor for *arcA* (EC 2.7.1.-)	725, 728
barA		Sensor-regulator for an uncharacterized bacterial adaptive response	1135
cpxA	*ecfB, ssd, eup*	Probable inner membrane sensor protein (histidine protein kinase), acting on *arcA*, energy coupling factor, F-pilin formation (EC 2.7.1.-)	1723
creB	*yjjE, ORF2*	Catabolic regulation response regulator	966, 1223
creC	*phoN*	Catabolite repression sensor (histidine protein kinase); alternative sensor for *pho* regulon (EC 2.7.1.-)	1712
crp	*cap, csm*	Cyclic AMP receptor protein	631, 632, 1503
cyaA		Adenylate cyclase (EC 4.6.1.1)	1245
cytR		Regulator for *deo* operon, *udp, cdd, tsx, nupC*, and *nupG*	90, 1240, 1504
envZ	*ompB, perA, tpo*	Response regulator for *ompC* and *ompF* (protein kinase/phosphatase sensor; regulates outer membrane protein biosynthesis) (EC 2.7.1.-)	696, 1721
era		GTP-binding protein	545, 910
fexB		FexA (ArcA) phenotype affected	911
fnr	*nirA, nirR, frdB*	Regulatory gene for nitrite and nitrate reductases, hydrogenase, and fumarate reductase	437, 1515, 1634
fur		Ferric iron uptake; negative regulator	604, 1725
gppA	*gpp*	Guanosine pentaphosphatase activity	106
kdpD	*kac*	High-affinity potassium transport system; regulator (sensor)	1146, 1269, 1701
lctZ	*lct**	Pleiotrophic effects on components of respiratory chain	305
lexA	*spr, exrA, umuA tsl*	Regulator for SOS (*lexA*) regulon	949
lon	*capR, muc, deg, dir*	DNA-binding, ATP-dependent protease La; heat shock protein (EC 3.4.21.53)	373
narL	*frdR, narR*	Pleiotrophic regulation of electron transport and fermentation: *nar, frd, dms*, and *tor* genes (sensor for *narX*)	421, 727, 1212
narQ		Sensor for nitrate reductase system, putative protein histidine kinase	260
narX	*narR*	Nitrate sensor, probable histidine protein kinase acts on *narL* (EC 2.7.1.-)	260, 285, 420
ntrL		Nitrogen-regulatory protein	25
ompR	*ompB, cry, kmt*	Response regulator (sensor for *envZ*) affecting transcription of *ompC* and *ompF*; outer membrane protein synthesis	188, 696, 1721
oxyR	*momR*	Activator, hydrogen peroxide-inducible genes	152, 1602, 1603
oxyS		RNA, a pleiotropic regulator	737
phoB	R_c, *phoT*	Positive regulator for *pho* regulon, (sensor for *phoR*)	1010, 1712
phoR	*nmpB, phoR1, R1pho*	Positive and negative regulatory gene for *pho* regulon, sensor protein (2.7.1.-)	1010, 1712, 1786
pus		Effect of suppressors on *relB* mutations	384
relA	*RC*	Regulation of RNA synthesis; stringent factor; ATP:GTP 3′-pyrophosphotransferase (EC 2.7.6.5)	1442, 1782
relB	*RC*	Regulation of RNA synthesis; stringent factor	1107
relX		Control of synthesis of guanosine 5′-diphosphate 3′-diphosphate	1219
rpoD	*alt*	RNA polymerase (EC 2.7.7.6), σ^{70} subunit; regulation of proteins induced at high temperatures	502, 1700
rpoH	*fam, hin, htpR*	RNA polymerase (EC 2.7.7.6), σ^{32} subunit; regulation of proteins induced at high temperatures	739, 1133, 1658
rpoN	*ntrA, glnF*	RNA polymerase (EC 2.7.7.6), σ^{60} subunit, nitrogen and fermentation regulation	1326
rpoS	*katF, appR, csi2 otsX*	RNA polymerase (EC 2.7.7.6), putative sigma subunit; affects expression of pH 2.5 acid phosphatase, and biosynthesis of catalase hydroperoxidase HPII(III) and exonuclease III	622, 875, 1634
soxR		Regulation of superoxide response regulon	458, 562
soxS		Regulation of superoxide response regulon	458
spf		Spot 42 RNA, inhibition of DNA synthesis	1334
sspA	*pog, ssp*	Stringent starvation protein; affects gene expression, also expression of late genes of phage P1	491, 1755

Continued on following page

TABLE 2—*Continued*

Gene	Synonym	Gene product and description	Reference(s)
suhA		Induction of heat shock genes	1622
uspT		Putative histidine protein kinase (sensor) for universal stress protein	1176
II. Biosynthesis of small molecules			
A. Amino acids			
1. Glutamate family/nitrogen assimilation			
argA	*argB, arg1, arg2*	Amino acid acetyltransferase; *N*-acetylglutamate synthase (EC 2.3.1.1)	194
argB	*argC*	Acetylglutamate kinase (EC 2.7.2.8)	170, 432, 547
argC	*argH, arg2*	*N*-Acetyl-γ-glutamylphosphate reductase (EC 1.2.1.38)	170, 432, 547
argD	*argG, arg1*	Acetylornithine δ-aminotransferase (EC 2.6.1.11)	495, 1341, 1684
argE	*argA, arg4*	Acetylornithine deacetylase (EC 3.5.1.16)	1064
argF	*argD, arg5*	Ornithine carbamyltransferase (EC 2.1.3.3)	276, 547, 674
argG	*argE, arg6*	Argininosuccinate synthetase (EC 6.3.4.5)	547
argH	*argF, arg7*	Argininosuccinate lyase (EC 4.3.2.1)	170, 432
argI		Ornithine carbamoyltransferase (EC 2.1.3.3)	854, 1087, 1812
argR	*xerA, Rarg*	Repressor of *arg* regulon; *cer*-mediated site specific recombination	1546, 1618
gdhA		NADP-specific glutamate dehydrogenase (EC 1.4.1.4)	1055
glnR		Glutamine synthetase (EC 6.3.1.2)	67, 1327, 1487
glnB		Regulatory protein P-II for glutamine synthetase	67
glnG	*ntrC, glnT*	Response regulator for *gln* (sensor for *glnL*) (nitrogen regulator I [NRI])	1726
glnL	*ntrB, glnR*	Histidine protein kinase sensor for *glnG* regulator (nitrogen regulator II [NRII]) (EC 2.7.1.-)	67, 1327
gltB	*aspB*	Glutamate synthase, large subunit (EC 1.4.1.13)	227, 228, 550
gltD	*aspB*	Glutamate synthase, small subunit (EC 1.4.1.13)	227, 228, 550
gltF		Regulator	227, 228
gltH		Glutamate synthesis	1022
proA	*pro1*	γ-Glutamylphosphate reductase (EC 1.2.1.41)	610, 1455
proB	*pro2*	γ-Glutamate kinase (EC 2.7.2.11)	610, 1455
proC	*pro3, pro2*	Pyrroline-5-carboxylate reductase (EC 1.5.1.2)	374, 610
uspA		Universal stress protein	1176
2. Aspartate family, pyruvate family			
alr		Alanine racemase (EC 5.1.1.1); isozyme	1707, 1746
asd	(*dap* + *hom*)	Aspartate-semialdehyde dehydrogenase (EC 1.2.1.11)	782
asnA		Asparagine synthetase A (EC 6.3.1.1)	643
asnB		Asparagine synthetase B (EC 6.3.5.4)	682, 1453
asnC		Regulator for *asnA*, *asnC*, and *gidA*	827
aspA		Aspartate ammonia-lyase (aspartase) (EC 4.3.1.1)	453, 1128
aspC	*aat*	Aspartate aminotransferase (EC 2.6.1.1)	333, 770, 1798
avtA	*avt*	Alanine-α-ketoisovalerate transaminase, transaminase C (EC 2.6.1.66)	1710
azl		Regulation of *ilv* and *leu* genes; azaleucine resistance	1265
dapA		Dihydrodipicolinate synthase (EC 4.2.1.52)	863, 1337
dapB		Dihydrodipicolinate reductase (EC 1.3.1.26)	168
dapC		Tetrahydrodipicolinate succinylase	205
dapD		Succinyldiaminopimelate transaminase (EC 2.6.1.17)	205
dapE	*msgB, dapB*	*N*-Succinyldiaminopimelate deacylase (EC 3.5.1.18)	167, 1774
dapF		Diaminopimelate epimerase (EC 5.1.1.7)	635, 870, 1336
ileR	*avr, flrA*?	Negative regulator for *thr* and *ilv* operons	1730
ilvA	*ile*	Threonine deaminase (EC 4.2.1.16)	428, 676, 1585
ilvB		Acetolactate synthase I (EC 4.1.3.18), valine sensitive, large subunit	484, 1728, 1735
ilvC	*ilvA*	Ketol-acid reductoisomerase (EC 1.1.1.86)	1733
ilvD	*ilvE*	Dihydroxyacid dehydratase (EC 4.2.1.9)	676
ilvE	*ilvC, ilvJ*	Branched-chain amino acid aminotransferase (EC 2.6.1.42)	711, 769
ilvH	*brnP*	Acetolactate synthase III (EC 4.1.3.18), valine sensitive, small subunit	1332, 1333, 1728
ilvI		Acetolactate synthase III (EC 4.1.3.18), valine sensitive, large subunit	1332, 1728
ilvO		*ilvGEDA* operon leader peptide	246, 1735

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TABLE 2—*Continued*

Gene	Synonym	Gene product and description	Reference(s)
ilvN		Acetolactate synthase I (EC 4.1.3.18), valine sensitive, small subunit	484, 1728, 1735
ilvR		Positive regulator for *thr* and *ilv* operons	744
ilvY		Positive regulator for *ilvC*	1733, 1734
ivbL		*ilvB* operon leader peptide	485, 1735
leuA		α-Isopropylmalate synthase (EC 4.1.3.12)	517, 1507
leuB		β-Isopropylmalate dehydrogenase (EC 1.1.1.85)	853
leuC		α-Isopropylmalate isomerase subunit (EC 4.2.1.33)	492
leuD		α-Isopropylmalate isomerase subunit (EC 4.2.1.33)	492
leuJ	*flr*	Regulator for *leu* and *ilv* operons	1171
leuL		*leu* operon leader peptide	94, 798
leuO		Probable activator protein for *leuABCD* operon	623
lrp	*livR, lss, lstR, mbl, oppI*	Regulator for leucine (or *lrp*) regulon and high-affinity branched-chain amino acid transport system regulatory gene; binds upstream of *lysU*	449, 950, 951
lysA		Diaminopimelate decarboxylase (EC 4.1.1.20)	253, 1557
lysC	*apk*	Aspartokinase III (EC 2.7.2.4)	274
lysR		Positive regulator for *lys*	623
metA	met_3	Homoserine transsuccinylase (EC 2.3.1.46)	409, 1362
metB	*met-1*, met_1	Cystathionine γ-synthase (EC 4.2.99.9)	657, 1029, 1371
metC		Cystathionine γ-lyase (EC 4.4.1.1)	657, 1029, 1371
metE	$metB_{12}$	Tetrahydropteroyltriglutamate methyltransferase (EC 2.1.1.14)	267
metF	*met-2*, met_2	5,10-Methylenetetrahydrofolate reductase (EC 1.7.99.5)	1398
metH		B_{12}-dependent homocysteine-*N*5-methyltetrahydrofolate transmethylase, repressor of *metE* and *metF* (EC 2.1.1.13)	85
metJ		Repressor of all *met* genes but *metF*	1252
metL	*metM*	Aspartokinase II (EC 2.7.2.4), homoserine dehydrogenase II (EC 1.1.1.3)	1231
metR		Regulator for *metE* and *metH*	1043
mraA		D-Alanine carboxypeptidase	1094
thrA		Aspartokinase I (EC 2.7.2.4), homoserine dehydrogenase I (EC 1.1.1.3)	1252
thrB	*HS, thrD*	Homoserine kinase (EC 2.7.1.39)	302, 1400
thrC		Threonine synthase (EC 4.2.99.2)	1232
thrL		*thr* operon leader peptide	330, 504
3. Glycine-serine family/sulfur metabolism			
cysB		Positive regulator for cysteine regulon	1012, 1100
cysC		Adenosine 5′-phosphosulfate kinase (EC 2.7.1.25)	928, 929
cysD		ATP:sulfate adenyltransferase (EC 2.7.7.4), subunit	927–929
cysE		Serine acetyltransferase (EC 2.3.1.30)	1745
cysH		Phosphoadenylylsulfate reductase (EC 2.8.2.-)	845, 1201
cysI	*cysQ*	Sulfite reductase (EC 1.8.1.2), α subunit	1201
cysJ	*cysP*	Sulfite reductase flavoprotein (EC 1.8.1.2) β subunit	1200, 1201
cysK	*cysE*	*O*-Acetylserine sulfhydrolase A (EC 4.2.99.8)	1206
cysM		*O*-Acetylserine sulfhydrolase B (EC 4.2.99.8)	1206, 1495, 1496
cysN		ATP-sulfurylase (ATP:sulfate adenylyltransferase) (EC 2.7.7.4), subunit	927–929
cysP		Thiosulfate binding protein	671
cysQ	*amt, amtA*	Affects pool of 3′-phosphoadenoside 5′-phosphosulfate in pathway of sulfite synthesis; protein	1153, 1716, 1717
glyA		Serine hydroxymethyltransferase (EC 2.1.2.1)	48, 1555, 1556
sbaA		Regulation of serine and branched-chain amino acid metabolism	328
serA		D-3-Phosphoglycerate dehydrogenase (EC 1.1.1.95)	1440, 1443
serB		Phosphoserine phosphatase (EC 3.1.3.3)	1659
serC	*pdxC, pdxF*	3-Phosphoserine aminotransferase (EC 2.6.1.52)	412, 868
4. Aromatic amino acid family			
aroA		5-Enolpyruvylshikimate-3-phosphate synthetase (EC 2.5.1.19)	39, 1210, 1488
aroB		Dehydroquinate synthase (EC 4.6.1.3)	811
aroC		Chorismate synthase (EC 4.6.1.4)	239, 1741
aroD		5-Dehydroquinate dehydratase (EC 4.2.1.10)	242, 811, 812
aroE		Dehydroshikimate reductase (EC 1.1.1.25)	51
aroF		Phospho-2-dehydro-3-deoxyheptonate aldolase (DAHP synthetase, tyrosine repressible) (EC 4.1.2.15)	1317

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TABLE 2—*Continued*

Gene	Synonym	Gene product and description	Reference(s)
aroG		Phospho-2-dehydro-3-deoxyheptonate aldolase (DAHP synthetase, phenylalanine repressible) (EC 4.1.2.15)	345, 1539
aroH		Phospho-2-dehydro-3-deoxyheptonate aldolase (DAHP synthetase, tryptophan repressible) (EC 4.1.2.15)	678, 1316, 1317
aroI		Member of *aroI* operon	529
aroK		Shikimate kinase I (EC 2.7.1.71)	977
aroL		Shikimate kinase II (EC 2.7.1.71)	358, 613
aroM		Regulated by *aroR*	358
pheA		Chorismate mutase (EC 5.4.99.5) and P-prephenate dehydratase (EC 4.2.1.51)	508, 509, 1152
pheM		*phe* leader peptide	
pheR		Regulator for *pheA*	508
trpA	*try*, *tryp-2*	Tryptophan synthase (EC 4.2.1.20), A protein	200, 1179, 1391
trpB	*tryp-1*	Tryptophan synthase (EC 4.2.1.20), B protein	200, 414, 1391
trpC	*tryp-3*	*N*-(5-Phosphoribosyl)anthranilate isomerase (EC 5.3.1.24) and indole-3-glycerolphosphate synthetase (EC 4.1.1.48)	1758
trpD	*tryE*	Glutamine amidotransferase (EC 4.1.3.27) and phosphoribosylanthranilate transferase (EC 2.4.2.18)	665, 1484
trpE	*anth*, *tryD*, *tryp-4*	Anthranilate synthase (EC 4.1.3.27)	630, 1483
trpL		*trp* operon leader peptide	873, 1352
trpR	*Rtry*	Regulator for *trp* operon and *aroH*; *trp* aporepressor	63, 817, 849
tyrA		Chorismate mutase T (EC 5.4.99.5) and prephenate dehydrogenase (EC 1.3.1.12)	1030, 1652, 1653
tyrB		Tyrosine aminotransferase (EC 2.6.1.57), tyrosine repressible	1467
5. Histidine			
hisA		*N*-(5′-Phospho-L-ribosyl-formimino)-5-amino-1-(5′-phosphoribosyl)-4-imidazolecarboxamide isomerase (EC 5.3.1.16)	221
hisB		Imidazoleglycerolphosphate dehydratase (EC 4.2.1.19) and histidinol phosphate phosphatase (EC 3.1.3.15)	221
hisC		Histidinol-phosphate aminotransferase (EC 2.6.1.9)	221
hisD		L-Histidinol:NAD^+ oxidoreductase (EC 1.1.1.23)	221, 753
hisF		Cyclase	505, 542
hisG		ATP phosphoribosyltransferase (EC 2.4.2.17)	221
hisH		Amidotransferase (EC 2.4.2.-)	221
hisI	*hisE*	Phosphoribosyl-AMP cyclohydrolase (EC 3.5.4.19) and phosphoribosyl-ATP pyrophosphatase (EC 3.6.1.31)	221
hisL		*his* operon leader peptide	235
B. Nucleotides			
1. Purine ribonucleotides			
adk	*plsA*, *dnaW*	Adenylate kinase (EC 2.7.4.3) activity; pleiotropic effects on glycerol-3-phosphate acyltransferase activity	1364, 1365, 1399
fadR	*ole*, *thdB*	Negative regulator for *fad* regulon, and positive activator of *fabA*	54, 387, 626
gmk	*spoR*, *kguA*	Guanylate kinase (EC 2.7.4.8)	518, 1782
guaA	gua_b	GMP synthetase (EC 6.3.5.2)	1621
guaB	gua_a	IMP dehydrogenase (EC 1.1.1.205)	44
guaC		GMP reductase (EC 1.6.6.8)	44
ndk		Nucleoside diphosphate kinase (EC 2.7.4.6)	591
prs		Phosphoribosylpyrophosphate synthetase (EC 2.7.6.1)	169, 668
purA	ade_k, Ad_4	Adenylosuccinate synthetase (EC 6.3.4.4)	394, 960, 1502
purB	ade_h	Adenylosuccinate lyase (EC 4.3.2.2)	611
purC	ade_g	Phosphoribosylaminoimidazole-succinocarboxamide synthetase (EC 6.3.2.6) = SAICAR synthetase	1619
purD	$adth_a$	Phosphoribosylglycinamide synthetase (EC 6.3.4.13), = GAR synthetase	9, 1475
purE	ade_3, ade_f, Pur_2	Phosphoribosylaminoimidazole carboxylase, = AIR carboxylase (EC 4.1.1.21), catalytic subunit	1078, 1620, 1719
purF	$ade_{u,b}$, *purC*	Amidophosphoribosyltransferase (EC 2.4.2.14) = PRPP amidotransferase	1061, 1404
purH	ade_i	Phosphoribosylaminoimidazolecarboxamide formyltransferase (EC 2.1.1.3) = AICAR formyltransferase	9, 471
purK		Phosphoribosylaminoimidazole carboxylase = AIR carboxylase (EC 4.1.1.21), CO_2-fixing subunit	1078, 1620, 1719

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TABLE 2—*Continued*

Gene	Synonym	Gene product and description	Reference(s)
purL	*purI*	Phosphoribosylformyl-glycineamide synthetase = FGAM synthetase (EC 6.3.5.3); homologous to *purG* of *S. typhimurium*	1430
purM	*purG*	Phosphoribosylaminoimidazole synthetase = AIR synthetase (EC 6.3.3.1); homologous to *purI* of *S. typhimurium*	1501
purN		5′-Phosphoribosyl-glycinamide (GAR) transformylase (EC 2.1.2.2)	708, 709
purR		Repressor for *pur* regulon, *glyA*	808, 1537, 1759
2. Pyrimidine ribonucleotides			
carA	*pyrA*, *cap*, (*arg* + *ura*)	Carbamoyl-phosphate synthetase (EC 6.3.5.5), glutamine (light) subunit	178, 1120, 1376
carB	*pyrA*, *cap*, (*arg* + *ura*)	Carbamoyl-phosphate synthetase (EC 6.3.5.5), ammonia (heavy) subunit	178, 1278, 1376
pyrB		Aspartate carbamoyltransferase (EC 2.1.3.2), catalytic subunit	1248, 1781, 1822
pyrC		Dihydro-orotase (EC 3.5.2.3)	193, 262, 1759
pyrD		Dihydro-orotate oxidase (EC 1.3.3.1)	1759
pyrE		Orotate phosphoribosyltransferase (EC 2.4.2.10)	35, 1282
pyrF		Orotidine-5′-phosphate decarboxylase (EC 4.1.1.23)	1651
pyrG		CTP synthetase (EC 6.3.4.2)	1737
pyrH	*pyrR*	UMP kinase	240, 756
pyrI		Aspartate carbamoyltransferase (EC 2.1.3.2) regulatory subunit	391
pyrL		*pyrBI* operon leader peptide	918
3. 2′-Deoxyribonucleotides			
dcd	*paxA*	2′-Deoxycytidine 5′-triphosphate deaminase (EC 3.5.4.-)	1709
dut	*sof*, *dnaS*	Deoxyuridinetriphosphatase (EC 3.6.1.23)	230, 654, 1709
mutT		(Deoxy)nucleoside triphosphatase prefers dGTP, causes AT-GC transversions	13, 1008, 1428
nrdA	*dnaF*	Ribonucleoside diphosphate reductase (EC 1.17.4.1) subunit B1	2, 1559, 1570
nrdB	*ftsB*	Ribonucleoside-diphosphate reductase (EC 1.17.4.1) subunit B2	1559, 1570
thyA		Thymidylate synthetase (EC 2.1.1.45)	1080
tmk		Thymidylate kinase (EC 2.7.4.9)	131
4. Salvage and interconversions			
add		Adenosine deaminase (EC 3.5.4.4)	237
amn		AMP nucleosidase (EC 3.2.2.4)	913
apaH		Diadenosine tetraphosphatase (EC 3.6.1.4)	454, 747
apt		Adenine phosphoribosyltransferase (EC 2.4.2.7)	920
cdd		Cytidine/deoxycytidine deaminase (EC 3.5.4.5)	1794
codA		Cytosine deaminase (EC 3.5.4.1)	332
cpdB		2′:3′-Cyclic-nucleotide 2′-phosphodiesterase (EC 3.1.4.16)	961
deoA	*tpp*, *TP*	Thymidine phosphorylase (EC 2.4.2.4)	1704
deoB	*drm*, *thyR*	Phosphopentomutase (EC 5.4.2.7)	467
deoC	*dra*, *thyR*	2-Deoxyribose-5-phosphate aldolase (EC 4.1.2.4)	1663
deoD	*pup*	Purine-nucleoside phosphorylase (EC 2.4.2.1)	467
deoR	*nucR*	Regulator for *deo* operon, *tsx*, and *nupG*	32, 329, 1106
gpt	*glyD*, *gpp*, *gxu*	Guanine-hypoxanthine phosphoribosyltransferase (EC 2.4.2.22)	653, 920, 921
gsk		Inosine-guanosine kinase (2.7.1.73)	669
hpt		Hypoxanthine phosphoribosyltransferase (EC 2.4.2.8)	653, 920, 921
optA		Regulator for *dgt*	1306
spoT		Guanosine 3′,5′-bis(diphosphate) 3′-pyrophosphohydrolase (EC 3.1.7.1); synthesis and degradation of ppGpp	1270, 1414, 1782
tdk		Thymidine kinase (EC 2.7.1.21)	131
upp	*uraP*	Uracil phosphoribosyltransferase (EC 2.4.2.9)	36, 1314
C. Sugars and sugar nucleotides			
cpsB		Mannose-1-phosphate guanyltransferase (GDP-mannose pyrophosphorylase) (EC 2.7.7.22)	164, 552, 1637
cpsG		Phosphomannomutase (EC 5.4.2.8)	1027
galE	*galD*	UDP-galactose 4-epimerase (5.1.3.2)	97, 832, 1691
galT	*galB*	Galactose-1-phosphate uridylyltransferase (EC 2.7.7.10)	463, 1691
malI		Repressor of *mal* genes	1324, 1325
manA	*pmi*	Mannose-6-phosphate isomerase (EC 5.3.1.8)	1542

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TABLE 2—*Continued*

Gene	Synonym	Gene product and description	Reference(s)
nagA		*N*-Acetylglucosamine-6-phosphate deacetylase (EC 3.5.1.25)	1267, 1268
nagB	*glmD*	Glucosamine-6-phosphate deaminase (EC 5.3.1.10)	29, 1267, 1268
nagR	*nagC*	Repressor for the *nag* regulon	1266, 1268
rfbA	*som*	TDP-glucose pyrophosphorylase	1149
rfbB		TDP-glucose oxidoreductase	1149
rfbD		TDP-rhamnose synthetase	1149
ushA		UDP-sugar hydrolase (5′-nucleotidase)	207
D. Cofactors, prosthetic groups, electron carriers			
1. Biotin			
bioA		7,8-Diaminopelargonic acid synthetase (EC 2.6.1.62)	1203
bioB		Biotin synthetase	1203
bioC		Biotin biosynthesis; reaction prior to pimeloyl-CoA	1203
bioD		Dethiobiotin synthetase (EC 6.3.3.3)	1203
bioF		7-Keto-8-aminopelargonic acid synthetase (EC 2.3.1.47)	1203
bioH	*bioB*	Biotin biosynthesis; reaction prior to pimeloyl-CoA	1195
birA	*bioR, dhbB*	Biotin-(acetyl-CoA carboxylase) holoenzyme synthetase; biotin operon repressor (EC 6.3.4.15)	206
bisC		Biotin sulfoxide reductase	1256
2. Folic acid			
folA	*tmrA*	Dihydrofolate reductase (EC 1.5.1.3); trimethoprim resistance	54, 213, 486
folC		Dihydrofolate:folylpolyglutamate synthetase (EC 6.3.2.17); dihydrofolate synthetase (EC 6.3.2.12)	148, 802, 809
folD		5,10-Methylene-tetrahydrofolate dehydrogenase (EC 1.5.1.5); 5,10-methylene-tetrahydrofolate cyclohydrolase (EC 3.5.4.9)	334
folE		GTP cyclohydrolase I (EC 3.5.4.16)	1304
folK		7,8-Dihydro-6-hydroxymethylpterin-pyrophosphokinase (EC 2.7.6.3)	1591, 1592
folP		7,8-Dihydropteroate synthase (EC 2.5.1.15)	325, 1591
pabA		*p*-Aminobenzoate synthetase, CoII	561
pabB		*p*-Aminobenzoate synthetase, CoII	561, 1703, 1800
pabC		Aminodeoxychorismate lyase	560, 561, 1800
3. Lipoate			
lipA	*lip*	Enzyme of lipoate biosynthesis, acts on octanoic acid	1321
lipB	*lip*	Enzyme of lipoate biosynthesis	1321
4. Molybdopterin			1468
moaA	*chlA, bisA, narA*	Molybdopterin biosynthesis	82, 644, 1312
moaD	*chlM*	Molybdopterin biosynthesis	644, 1312
mob	*chlB*	Molybdopterin-guanine dinucleotide biosynthesis	644, 745, 1312
moeA	*chlE, bisB*	Molybdopterin biosynthesis	644, 1165, 1312
moeB	*chlN*	Molybdopterin biosynthesis	644, 1165, 1312
5. Pantothenate			
coaA	*panK, rts*	Pantothenate kinase (EC 2.7.1.33)	1508, 1667
panB	*ts-9*	Ketopentoate hydroxymethyltransferase (EC 4.1.2.12)	310
panC		Pantothenate synthetase (EC 6.3.2.1)	310
panD		Aspartate 1-decarboxylase (EC 4.1.1.11)	310
6. Pyridoxine			
pdxA		Pyridoxine biosynthesis	1344
pdxB		Ecrythronate-4-phosphate dehydrogenase, placement of 5, 5′, and 6′ carbons into pyridine ring of pyridoxine (EC 1.1.1.-)	868, 1440
pdxH		Pyridoxinephosphate oxidase	869
pdxJ		Pyridoxine biosynthesis	867, 1590

Continued on following page

TABLE 2—*Continued*

Gene	Synonym	Gene product and description	Reference(s)
7. Pyridine nucleotides			
nadA	*nicA*	Quinolinate synthetase, A protein	470, 1458
nadB	*nicB*	Quinolinate synthetase, B protein (EC 1.4.3.16)	470, 1458
nadC	*nic*	Quinolinate phosphoribosyltransferase (EC 2.4.2.19)	1638
pncA	*nam*	Nicotinamide deamidase (EC 3.5.1.19)	1221
pncB		Nicotinate phosphoribosyltransferase (EC 2.4.2.1)	1779
8. Thiamin			
thiA		Thiamin thiazole requirement	796
thiB		Thiamin phosphate pyrophosphorylase (EC 2.5.1.3)	796
thiC		Thiamin biosynthesis, pyrimidine moiety	1668
thiD		Phosphomethylpyrimidine kinase activity	705
thiE		Thiamin biosynthesis, thiazole moiety	1668
thiF		Thiamin biosynthesis, thiazole moiety	1668
thiG		Thiamin biosynthesis, thiazole moiety	1668
thiH		Thiamin biosynthesis, thiazole moiety	1668
thiJ		Thiamin biosynthesis	
thiK		Thiamin kinase (EC 2.7.1.89)	706
thiL		Thiamin monophosphate kinase (EC 2.7.4.16)	706
9. Riboflavin			
ribA		GTP cyclohydrolase II (EC 3.5.4.25)	1304
ribB	*htrP*	3,4-Dihydroxy-2-butanone-4-phosphate synthase	1338
ribC		Riboflavine synthase (EC 2.5.1.9)	1264
10. Thioredoxin, glutaredoxin, and glutathione			
ggt		γ-Glutamyltranspeptidase (EC 2.3.2.2)	1574
gor		Glutathione oxidoreductase (EC 1.6.4.2)	370, 446, 852
gshA		γ-Glutamate-cysteine ligase (EC 6.3.2.2)	165
gshB		Glutathione synthetase (EC 6.3.2.3)	348, 790, 1599
trxA	*fipA*, *tsnC*	Thioredoxin	539, 843, 993
11. Menaquinone and ubiquinones			
ispA		Geranyltranstransferase (farnesyldiphosphate synthase) (EC 2.5.1.10)	116, 490
menA		1,4-Dihydroxy-2-naphthoate → dimethylmenaquinone	116
menB		1,4-Dihydroxy-2-naphthoate synthase	116, 1471
menC		Conversion of chorismate to 2-*o*-succinylbenzoate, step 2	116, 1060, 1469a
menD		Conversion of chorismate to 2-*o*-succinylbenzoate, step 1	1060, 1214a, 1273
menE		*o*-Succinylbenzoate-CoA synthase	116
ubiA		4-Hydroxybenzoate → 3-octaprenyl-4-hydroxybenzoate	116, 1157, 1489
ubiB		2-Octaprenylphenol → 2-octaprenyl-6-methoxyphenol	116
ubiC		Chorismate lyase	116, 1157, 1489
ubiD		3-Octaprenyl-4-hydroxy-benzoate → 2-octaprenylphenol	116, 909
ubiE		2-Octaprenyl-6-methoxy-1,4-benzoquinone → 2-octaprenyl-3-methyl-6-methoxy-1,4-benzoquinone	116
ubiF		2-Octaprenyl-3-methyl-6-methoxy-1,4-benzoquinone → 2-octaprenyl-3-methyl-5-hydroxy-6-methoxy-1,4-benzoquinone	116, 286
ubiG		2-Octaprenyl-3-methyl-5-hydroxy-6-methoxy-1,4-benzoquinone → ubiquinone 8	116, 528
ubiH		2-Octaprenyl-6-methoxyphenol → 2-octaprenyl-6-methoxy-1,4-benzoquinone	116
ubiX		Putative polyprenyl *p*-hydroxybenzoate carboxylase	1167
12. Heme and porphyrins			
cysG		Uroporphyrinogen III methylase; siroheme biosynthesis (EC 2.1.1.-)	1238, 1716, 1717
hemB	*ncf*	5-Aminolevulinate dehydratase (EC 4.2.1.24) activity	415, 933, 1191
hemC	*popE*	Porphobilinogen deaminase (hydroxymethylbilane synthase) (EC 4.3.1.8)	751, 872, 1086
hemD		Uroporphyrinogen III synthase (EC 4.2.1.75)	30

Continued on following page

TABLE 2—*Continued*

Gene	Synonym	Gene product and description	Reference(s)
hemE	*hemC*	Uroporphyrinogen decarboxylase (EC 4.1.1.37)	1416
hemF	*popB, sec*	Coproporphyrinogen III oxidase (EC 1.3.3.3)	306
hemG		Protoporphyrinogen oxidase activity	1415
hemH	*visA*?, *popA, hemG*	Ferrochelatase (EC 4.99.1.1)	1095
hemL	*popC*	Glutamate-1-semialdehyde aminotransferase (-2,1-aminomutase) (EC 5.4.3.8)	566, 702, 703
hemX		Putative uroporphyrinogen III methylase (EC 2.1.1.-)	1417
popD		5-Aminolevulinate dehydratase (EC 4.2.1.24) activity	1513
E. Fatty acids and lipids			
aas		2-Acylglycerophospho-ethanolamine acyltransferase, and acyl-acyl-carrier protein synthetase	672
accA		Acetyl-CoA carboxylase, carboxytransferase component, α subunit (EC 6.4.1.2)	937
accB	*fabE*	Acetyl-CoA carboxylase, BCCP[a] subunit (EC 6.4.1.2)	936
accC	*fabG*	Acetyl-CoA carboxylase, biotin carboxylase subunit (EC 6.3.4.14)	831, 1315
accD	*dedB, usg*	Acetyl-CoA carboxylase, carboxytransferase component, β subunit (EC 6.4.1.2)	937, 938
acpP		Acyl carrier protein	1315
acpS		CoA:apo-[acyl-carrier-protein] pantetheinephosphotransferase (EC 2.7.8.7) = holo-[acyl-carrier-protein] synthase	1292
cdh		CDP-diglyceride hydrolase (EC 3.6.1.26)	692
cdsA		CDP-diglyceride synthetase (CTP:phosphatidate cytidylyltransferase) (EC 2.7.7.41)	693
cdsS		Stability of CDP-diglyceride synthetase activity	499
cfa	*cdfA*	Cyclopropane fatty acid synthase (EC 2.1.1.79)	1706a
cls		Cardiolipin synthase activity (EC 2.7.8.-)	649, 1481
dgkA		Diglyceride kinase (EC 2.7.1.107)	1386
dgkR		Level of diglyceride kinase	1307
fabA		β-Hydroxydecanoyl thioester dehydrase (EC 4.2.1.60)	309, 1469
fabB	*fabC*	3-Oxoacyl-[acyl-carrier-protein] synthase I (EC 2.3.1.41)	793, 1490, 1645
fabD		Malonyl-CoA-[acyl-carrier-protein] transacylase (EC 2.3.1.39)	1002, 1680
fabF	*cvc, vtrB*	3-Oxoacyl-[acyl-carrier-protein] synthase II (EC 2.3.1.41)	731, 1490
fabH		3-Oxoacyl-[acyl-carrier-protein] synthase III (EC 2.3.1.41)	1644
glpK		Glycerol kinase (EC 2.7.1.30)	1250, 1731
lpxA		UDP-*N*-acetylglucosamine acetyltransferase (EC 2.4.1.-)	313, 496
lpxB	*pgsB*	Tetraacyldisaccharide-1-phosphate synthetase; early step in lipid A biosynthesis	313
pgpA		Phosphatidylglycerophosphate phosphatase, membrane bound (EC 3.1.3.27)	493, 690
pgpB		Phosphatidylglycerophosphate phosphatase, membrane bound (EC 3.1.3.27)	493
pgsA		Phosphatidylglycerophosphate synthetase (EC 2.7.8.5) = CDP-1,2-diacyl-*sn*-glycero-3-phosphate phosphatidyl transferase	1162, 1163
pldA		Detergent-resistant phospholipase A activity (EC 3.1.1.32)	1139
pldB		Lysophospholipase L_2 (EC 3.1.1.5), membrane protein	778, 822
pldC		Lysophospholipase L_1 (EC 3.1.1.5)	778
plsB		Glycerolphosphate acyltransferase activity (EC 2.3.1.15)	297, 1753
plsC		1-Acyl-*sn*-glycerol-3-phosphate acyltransferase (EC 2.3.1.51)	283
plsX		Glycerolphosphate auxotrophy in *plsB* background	882
psd		Phosphatidylserine decarboxylase (EC 4.1.1.65)	934, 935
pssA		Phosphatidylserine synthetase (EC 2.7.8.8)	356
pssR		Regulator of *pssA*	1511
sbm		Methylmalonyl-CoA mutase (MCM) (EC 5.4.9.2)	1374
F. Polyamines			
speA		Arginine decarboxylase (EC 4.1.1.19)	143, 1101, 1783
speB		Agmatinase (EC 3.5.3.11)	1580, 1581, 1783
speC		Ornithine decarboxylase isozyme (EC 4.1.1.17)	143, 1218
speD		*S*-Adenosylmethionine decarboxylase (EC 4.1.1.50)	1583, 1783
speE		Spermidine synthase = putrescine aminopropyltransferase (EC 2.5.1.16)	1783
speF		Ornithine decarboxylase isozyme, inducible (EC 4.1.1.17)	785

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TABLE 2—*Continued*

Gene	Synonym	Gene product and description	Reference(s)
III. Macromolecule metabolism			
A. Synthesis and modification			
1. Ribosomal and "stable" RNAs			889, 1524
ffs		Stable 4.5S RNA	195, 1239, 1274
rrfA		5S rRNA	422, 1199, 1742
rrfB		5S rRNA	422, 1199, 1742
rrfC		5S rRNA	422, 1199, 1742
rrfD		5S rRNA	422, 1199, 1742
rrfE		5S rRNA	422, 1199, 1742
rrfG		5S rRNA	422, 1199, 1742
rrfH		5S rRNA	53
rrlA		23S rRNA	185, 1093, 1604
rrlB		23S rRNA	185, 1093, 1604
rrlC		23S rRNA	185, 1093, 1604
rrlD		23S rRNA	185, 1093, 1604
rrlE		23S rRNA	185, 1093, 1604
rrlG		23S rRNA	185, 1093, 1604
rrlH		23S rRNA	185, 1093, 1604
rrsA		16S rRNA	316, 884, 1014
rrsB		16S rRNA	316, 884, 1014
rrsC		16S rRNA	316, 558, 884
rrsD		16S rRNA	316, 558, 884
rrsE		16S rRNA	316, 558, 884
rrsG		16S rRNA	316, 558, 884
rrsH		16S rRNA	316, 558, 884
rrvD	*rrfD*	Second copy of 5S rRNA in *rrnD* operon	410
ssr		Stable 6S RNA	673
ssrA		10Sa RNA, nonribosomal	1181
2. Ribosomal proteins and their modification			
ksgC		Kasugamycin resistance; affects ribosomal protein S2	1803
prmA	*prm-1*	Methylation of 50S ribosomal subunit protein L11	288
prmB	*prm-2*	Methylation of 50S ribosomal subunit protein L3	288
rimE		Modification of ribosomal proteins	858
rimK		Ribosomal protein S6 modification protein	773
rimG	*ramB*	Modification of 30S ribosomal subunit protein S4	1828
rimI		Modification of 30S ribosomal subunit protein S18; acetylation of N-terminal alanine (EC 2.3.1.-)	1801
rimJ		Modification of 30S ribosomal subunit protein S5; acetylation of N-terminal alanine (EC 2.3.1.-)	1801
rimL		Modification of 30S ribosomal subunit protein L7; acetylation of N-terminal serine (EC 2.3.1.-)	1598
rplA	*rpy*	50S ribosomal subunit protein L1, regulates synthesis of L1 and L11	423, 1396
rplB		50S ribosomal subunit protein L2	423, 1361
rplC		50S ribosomal subunit protein L3	1569
rplD	*eryA*	50S ribosomal subunit protein L4, regulates synthesis of S10 ribosomal protein operon	1818, 1819
rplE		50S ribosomal subunit protein L5	984
rplF		50S ribosomal subunit protein L6	1199
rplI		50S ribosomal subunit protein L9	557
rplJ		50S ribosomal subunit protein L10	1816
rplK	*relC*	50S ribosomal subunit protein L11	424, 777
rplL		50S ribosomal subunit protein L7/L12	1246, 1816
rplM		50S ribosomal subunit protein L13	1199
rplN		50S ribosomal subunit protein L14	1199, 1276
rplO		50S ribosomal subunit protein L15	479
rplP		50S ribosomal subunit protein L16	479, 1361
rplQ		50S ribosomal subunit protein L17	1199
rplR		50S ribosomal subunit protein L18	422
rplS		50S ribosomal subunit protein L19	1748
rplT	*pdzA*	50S ribosomal subunit protein L20, and regulator	912, 1569
rplU		50S ribosomal subunit protein L21	1199
rplV	*eryB*	50S ribosomal subunit protein L22	57

Continued on following page

TABLE 2—*Continued*

Gene	Synonym	Gene product and description	Reference(s)
rplW		50S ribosomal subunit protein L23	423
rplX		50S ribosomal subunit protein L24	1199
rplY		50S ribosomal subunit protein L25	477
rpmA	*rpz*	50S ribosomal subunit protein L27	1772
rpmB		50S ribosomal subunit protein L28	1199
rpmC		50S ribosomal subunit protein L29	557, 1199
rpmD		50S ribosomal subunit protein L30	1199
rpmE		50S ribosomal subunit protein L31	557
rpmF		50S ribosomal subunit protein L32	1600
rpmG		50S ribosomal subunit protein L33	1199
rpmH	*rimA, ssaF*	50S ribosomal subunit protein L34	677
rpmI		50S ribosomal subunit protein A (L35)	912
rpmJ		50S ribosomal subunit protein X	1657
rpsA	*rps, ssyF*	30S ribosomal subunit protein S1	883, 1280, 1348
rpsB		30S ribosomal subunit protein S2	33
rpsC		30S ribosomal subunit protein S3	174, 196, 397
rpsD	*ramA, sud2*	30S ribosomal subunit protein S4	23, 397
rpsE	*spcA, eps*	30S ribosomal subunit protein S5	397, 557
rpsF		30S ribosomal subunit protein S6	1541
rpsG		30S ribosomal subunit protein S7	397, 1014
rpsH		30S ribosomal subunit protein S8	1040, 1771
rpsI		30S ribosomal subunit protein S9	1744
rpsJ	*nusE*	30S ribosomal subunit protein S10	1033
rpsK		30S ribosomal subunit protein S11	1744
rpsL		30S ribosomal subunit protein S12	23, 126
rpsM		30S ribosomal subunit protein S13	1579
rpsN		30S ribosomal subunit protein S14	557
rpsO	*secC*	30S ribosomal subunit protein S15	1014, 1276
rpsP		30S ribosomal subunit protein S16	1748
rpsQ	*nea*	30S ribosomal subunit protein S17	557, 1744
rpsR		30S ribosomal subunit protein S18	1098
rpsS		30S ribosomal subunit protein S19	1732
rpsT	*supS20*	30S ribosomal subunit protein S20	299
rpsU		30S ribosomal subunit protein S21	174
strM		Control of ribosomal ambiguity	1406
3. Ribosomes and their maturation and modification			
fusB		Pleiotropic effects on RNA synthesis, ribosomes, and ribosomal protein S6	1589
rimB		Maturation of 50S ribosomal subunit	199
rimC		Maturation of 50S ribosomal subunit	199
rimD		Maturation of 50S ribosomal subunit	199
rimF	*res*	Modification of ribosome	507
rimH	*stsB*	Modification of ribosome	746
rit		Affects thermolability of 50S ribosomal subunit	1192
rmf		Ribosome modulation factor	1694
4. tRNAs and their modification, aminoacyl-tRNA synthetases			829, 1476, 1773
aat		Aminoacyl-tRNA-protein transferase (EC 2.3.2.6)	376
alaS	*lovB, ala-act*	Alanine tRNA synthetase (EC 6.1.1.7)	666, 1088
alaT	*talA*	Alanine tRNA 1B (duplicate of *alaU,V*)	1225, 1595, 1597
alaU	*talD*	Alanine tRNA 1B (duplicate of *alaT,V*)	1225, 1595, 1597
alaV		Alanine tRNA 1B (duplicate of *alaT,U*)	1225, 1595, 1597
alaW	*alaW*α	Alanine tRNA 2 (duplicate of *alaX*)	1225, 1595, 1597
alaX	*alaW*β	Alanine tRNA 2 (duplicate of *alaW*)	1225, 1595, 1597
argQ	*argV*δ	Arginine tRNA 2 (duplicate of *argV,Y,Z*)	1049
argS	*lov*	Arginine tRNA synthetase (EC 6.1.1.19)	121, 442, 952
argU	*dnaY, pin*	Arginine tRNA 4	243, 247, 1427
argV	*argV*α	Arginine tRNA 2 (duplicate of *argQ,Y,Z*)	1049
argW		Arginine tRNA 5	1049
argX		Arginine tRNA 3	1049
argY	*argV*β	Arginine tRNA 2 (duplicate of *argV,Q,Z*)	1049
argZ	*argV*γ	Arginine tRNA 2 (duplicate of *argV,Y,Q*)	1049
asnS	*lcs, tss*	Asparagine tRNA synthetase (EC 6.1.1.22)	49, 642, 1001
asnT		Asparagine tRNA	829

Continued on following page

TABLE 2—*Continued*

Gene	Synonym	Gene product and description	Reference(s)
asnU		Asparagine tRNA	829
asnV		Asparagine tRNA	829
aspS	*tls*	Aspartate tRNA synthetase (EC 6.1.1.12)	443, 642
aspT	*tasC*	Aspartate tRNA 1 (duplicate of *aspV, U*)	829
aspU		Aspartate tRNA 1 (duplicate of *aspT, V*)	829
aspV		Aspartate tRNA 1 (duplicate of *aspT, U*)	829
cca		tRNA nucleotidyl transferase (EC 2.7.7.25)	1825
cysS		Cysteine tRNA synthetase (EC 6.1.1.16)	444, 667, 1217
cysT		Cysteine tRNA	1217, 1495
divE		$tRNA^{Ser1}$, affects cell division	1421, 1594
fmt		10-Formyltetrahydrofolate:L-methionyl-$tRNA^{fMet}$ N-formyltransferase (EC 2.1.2.9)	576, 892
glnR		Affects level of glutaminyl-tRNA synthetase	259
glnS		Glutamine tRNA synthetase (EC 6.1.1.18)	439, 608, 735
glnT		Affects level of glutamine tRNA 1 and glutamine synthetase	
glnU	*glnUα, supB*	Glutamine tRNA 1 (duplicate of *glnW*), suppressor of ochre (UAA) and amber (UAG) mutations	439, 735, 1353
glnV	*glnVα, Su2, suII supE*	Glutamine tRNA 2 (duplicate of *glnX*), suppressor of amber (UAG) mutations	439, 735, 1353
glnW	*glnUβ*	Glutamine tRNA 1 (duplicate of *glnU*), suppressor of ochre (UAA) and amber (UAG) mutations	439, 735, 1353
glnX	*glnVβ*	Glutamine tRNA 2 (duplicate of *glnV*), suppressor of amber (UAG) mutations	439, 735, 1353
gltE		Glutamate tRNA synthetase activity	877, 1129
gltM		Level of glutamate tRNA synthetase activity	1129
gltT	*tgtB*	Glutamate tRNA 2 (duplicate of *gltU, V, W*)	829
gltU	*tgtC*	Glutamate tRNA 2 (duplicate of *gltT, V, W*)	829
gltV	*tgtE*	Glutamate tRNA 2 (duplicate of *gltT, U, W*)	829
gltW		Glutamate tRNA 2 (duplicate of *gltT, U, V*)	829
gltX		Catalytic subunit for glutamate tRNA synthetase (EC 6.1.1.17)	189, 550, 1172
glyQ		Glycine tRNA synthetase, α chain (EC 6.1.1.14)	1631, 1632
glyS	*gly-act*	Glycine tRNA synthetase, β chain (EC 6.1.1.14)	320
glyT	*supA36, sumA, sup15B*	Glycine tRNA 2, suppressor	1050
glyU	*suA36, sufD*	Glycine tRNA 1, suppressor	1050
	supT, sumB		1050
glyV	*glnVα, suA78, suA58, ins*	Glycine tRNA 3 (duplicate of *glyX, Y, W*)	1050
glyW	*suA58, suA78, ins*	Glycine tRNA 3 (duplicate of *glyV, X, Y*)	1050
glyX	*glyVβ*	Glycine tRNA 3 (duplicate of *glyV, W, Y*)	1050
glyY	*glyVγ*	Glycine tRNA 3 (duplicate of *glyX, Y, W*)	1050
hemM		Glutamate tRNA dehydrogenase	406, 701, 932
hisR	*hisT*	Histidine tRNA	640
hisS		Histidine tRNA synthetase (EC 6.1.1.21)	640
hisT	*leuK, asuC*	Pseudouridine synthase I (EC 4.2.1.70)	346, 771, 1649
ileS		Isoleucine tRNA synthetase (EC 6.1.1.5)	1172, 1754
ileT	*tilA*	Isoleucine tRNA 1 (duplicate of *ileU, V*)	829
ileU	*tilD*	Isoleucine tRNA 1 (duplicate of *ileT, V*)	829
ileV		Isoleucine tRNA 1 (duplicate of *ileT, U*)	829
ileX		Isoleucine tRNA 2	829
ilvU		Regulator for *ileS* and modifier of isoleucine tRNA 2 and valine tRNA 2	457
leuP	*leuVβ*	Leucine tRNA 1 (duplicate of *leuQ, T, V*)	829
leuQ	*leuVγ*	Leucine tRNA 1 (duplicate of *leuP, T, V*)	829
leuR		Level of leucine tRNA synthetase	1611
leuS		Leucine tRNA synthetase (EC 6.1.1.4)	1743, 1757
leuT		Leucine tRNA 1 (duplicate of *leuQ, P, V*)	829
leuU		Leucine tRNA 2	829
leuV	*leuVα*	Leucine tRNA 1 (duplicate of *leuQ, P, T*)	829
leuW		Leucine tRNA 3	829
leuX	*Su-6, supP*	Leucine tRNA 5, suppressor of amber (UAG) mutations	1168
leuY		Level of leucine tRNA synthetase	1102
leuZ		Leucine tRNA 4	829
lrs		Level of a single leucine tRNA	1661
lysS	*herC, asuD*	Lysine tRNA synthetase, constitutive; suppressor of ColE1 mutation in primer RNA (EC 6.1.1.6)	320

Continued on following page

TABLE 2—*Continued*

Gene	Synonym	Gene product and description	Reference(s)
lysT	*lysTα, supG, supL, sua*	Lysine tRNA (duplicate of *lysW,V*), suppressor of ochre (UAA) and amber (UAG) mutations	197
lysU		Lysine tRNA synthetase, inducible; heat shock protein (EC 6.1.1.6)	274, 916, 1145
lysV	*supN*	Lysine tRNA (duplicate of *lysT,W*), suppressor of ochre (UAA) and amber (UAG) mutations	829
lysW	*lysTβ suβ*	Lysine tRNA (duplicate of *lysT,W*), suppressor of ochre (UAA) and amber (UAG) mutations	829
metG		Methionine tRNA synthetase (EC 6.1.1.10)	526, 1057, 1676
metT	*metTα*	Methionine tRNA (duplicate of *metU*)	1444
metU	*metTβ*	Methionine tRNA (duplicate of *metT*)	1444
metX	*metZβ*	Methionine $tRNA^{fMet1}$ (duplicate of *metZ*)	577, 1214, 1676
metV		Methionine $tRNA^{fMet2}$	801
metZ	*metZα*	Methionine $tRNA^{fMet1}$ (duplicate of *metX*)	577, 1214, 1676
miaA	*trpX*	2-Methylthio-*N*6-isopentyladenosine hypermodification (EC 2.7.7.-)	294
nuvA		Uridine thiolation factor A activity	958, 1614
nuvC		4-Thiouridine modification of tRNA; near-UV sensitivity and resistance	958, 1614
pheS	*phe-act*	Phenylalanine tRNA synthetase (EC 6.1.1.20), α subunit	508, 787, 1249
pheT		Phenylalanine tRNA synthetase (EC 6.1.1.20), β subunit	508, 787, 1249
pheU	*pheW, pheR*	Phenylalanine tRNA (duplicate of *pheV*)	1, 508, 1249
pheV	*pheC*	Phenylalanine tRNA (duplicate of *pheU,R,W*)	1, 1249, 1261
phtM		Leader, phenylalanine tRNA synthetase	1213, 1519
proK	*proV*	Proline tRNA 1	829
proL	*proW*	Proline tRNA 2	829
proM	*proU, osrA*	Proline tRNA 3	829
proS	*drpA*	Proline tRNA synthetase (EC 6.1.1.15)	320
pth	*rap*	Peptidyl-tRNA hydrolase (EC 3.1.1.29)	500, 1130
queA		tRNA modification, queine biosynthesis	1330
selA	*fdhA*	Selenocysteine synthase, step 1: L-seryl-tRNA dehydrated (EC 4.2.1.-)	473, 1425
selC	*fdhC*	Selenocystyl tRNA, when utilized, inserts at UGA	92, 940, 1425
selD	*fdhB*	Selenocysteine tRNA synthase, step 2, H_2Se added to acrylyl-tRNA (EC 4.2.1.-)	473, 1425
serR		Level of seryl-tRNA synthetase	320
serS		Serine tRNA synthetase (EC 6.1.1.11); also charges selenocystein tRNA with serine	319, 1429
serT	*divE*	Serine tRNA 1	641, 1168, 1354
serU	*supD, supH, suI, Su-1, ftsM*	Serine tRNA 2; suppressor of amber (UAG) mutations	891, 1354
serV		Serine tRNA 3	641, 1168, 1354
serW		Serine tRNA 5 (duplicate of *serX*)	641, 1168, 1354
serX		Serine tRNA 5 (duplicate of *serW*)	641, 1168, 1354
tgt		tRNA-guanine transglycosylase (EC 2.4.2.29)	483
thrS		Threonine tRNA synthetase (EC 6.1.1.3)	1099, 1358
thrT		Threonine tRNA 3	603, 1613
thrU		Threonine tRNA 4	603, 1613
thrV		Threonine tRNA 1	603, 1613
thrW		Threonine tRNA 2	603, 1613
trmA		tRNA methyltransferase; tRNA (uracil-5-)-methyltransferase (EC 2.1.1.35)	581, 1175, 1244
trmB		tRNA methyltransferase; tRNA (guanine-7-)-methyltransferase (EC 2.1.1.33)	1026
trmC		tRNA methyltransferase; 5-methylaminoethyl-2-thiouridine biosynthesis	129, 586
trmD		tRNA methyltransferase; tRNA (guanine-1-)-methyltransferase (EC 2.1.1.31)	214, 652, 1748
trmE	*asuE*?	tRNA methyltransferase; 5-methylaminoethyl-2-thiouridine biosynthesis	433
trmF		tRNA methyltransferase; 5-methylaminoethyl-2-thiouridine biosynthesis	433
trnA	*glnU*	Level of several tRNAs	259
trpS		Tryptophan tRNA synthetase (EC 6.1.1.2)	1073, 1353
trpT	*su8, su9, supU, supV, su7*	Tryptophan tRNA, suppressor of ochre (UAA) and amber (UAG) mutations	639, 1356
tyrS		Tyrosine tRNA synthetase (EC 6.1.1.1)	100, 102, 461

Continued on following page

TABLE 2—*Continued*

Gene	Synonym	Gene product and description	Reference(s)
tyrT	*tyrTα Su-3, su_c Su-4, supF, supE, tyrV, suIII, suI_3*	Tyrosine tRNA 1, duplicate of *tyrV*), suppressor of ochre (UAA) and amber (UAG) mutations; second gene product = rtT RNA, possible modulator	158, 641, 1081
tyrU	*supM*	Tyrosine tRNA 2, suppressor of ochre (UAA) and amber (UAG) mutations	641
tyrV	*tyrTβ*	Tyrosine tRNA 1 (duplicate of *tyrT*), suppressor of ochre (UAA) and amber (UAG) mutations	641
valS	*val-act*	Valine tRNA synthetase (EC 6.1.1.9)	268, 440
valT		Valine tRNA 1 (duplicate of *valU,X,Y*)	1596
valU	*valUα*	Valine tRNA 1 (duplicate of *valT,X,Y*)	197, 1596
valV		Valine tRNA 2B	1596
valW		Valine tRNA 2A	1596
valX	*valUβ*	Valine tRNA 1 (duplicate of *valT,U,Y*)	1596
valY	*valUγ*	Valine tRNA 1 (duplicate of *valT,U,X*)	1596
5. RNA synthesis, modification, and DNA transcription			
dbpA		Putative ATP-dependent RNA helicase	695
deaD		Putative ATP-dependent RNA helicase	1630
firA	*skp*?	Transcription factor	381, 382, 1615
hepA		Probable RNA helicase	924, 1810
nusA		Transcription termination; L factor	533, 955
nusB	*groNB*	Transcription termination; L factor	1033, 1578
nusG		Component in transcription antitermination	955, 1567
opr		Rate of degradation of aberrant subunit proteins of RNA polymerase	1465
pnp		Polynucleotide phosphorylase (EC 2.7.7.8)	1323, 1793
ranA		RNA metabolism	53
rhlB		Putative ATP-dependent RNA helicase	760
rho	*psu, nitA, rnsC, tsu, SuA, sun*	Transcription termination factor Rho; polarity suppressor	390, 516, 540
ridA		Transcription and translation; dependence on rifampin and kasugamycin	321
rne	*ams*	RNase E activity, RNA processing, alteration of mRNA stability	425, 1113, 1526
rpoA	*phs sez*	RNA polymerase (EC 2.7.7.6), α subunit	609, 715, 1340
rpoB	*nitB, rif, tabD, ron, groN, stv, stl*	RNA polymerase (EC 2.7.7.6), β subunit	874, 1466, 1776
rpoC	*tabD*	RNA polymerase (EC 2.7.7.6), β′ subunit	722, 994, 1247
rpoZ	*spoS*	DNA-directed RNA polymerase ω subunit (EC 2.7.7.6)	519, 520, 694
srmB		ATP-dependent RNA helicase (EC 2.7.7.-)	1161
6. Basic proteins			
hns	*bglY, drdX, fimG, topS, pilG, cur*	Histone-like protein HLP-II (HU, BH2, HD, NS); pleiotropic regulator	1044, 1520, 1785
hupA		DNA-binding protein HU-α (HU-2)	404, 548, 825
hupB	*hopD*	Histone-like protein HU-1 (HU-β, NS1)	404, 405, 548
tpr		A protaminelike protein	158
7. DNA (replication, restriction/modification, recombination, and repair)			
aidB		Induced by alkylating agents	1687
aidC		Induced by alkylating agents	1689
alkA	*aidA*	3-Methyl-adenine DNA glycosylase II, inducible (EC 3.2.2.-)	757, 1687, 1688
alkB	*aidD*	DNA repair system specific for alkylated DNA	830, 1687, 1688
cer		Site-specific recombinase	287
dam		DNA adenine methylase (EC 2.1.1.72)	83, 119, 1174
dcm	*mec*	DNA cytosine methylase (EC 2.1.1.73)	943
del		Frequency of IS*1*-mediated deletion	1154
dfp	*dnaS, dut*	Flavoprotein affecting synthesis of DNA and pantothenate metabolism	1517
dinF		Induced by UV and mitomycin C; subject to *recA* and *lexA* regulation	1616
dnaA		DNA biosynthesis; initiation of chromosome replication; global transcription regulator	311, 535, 659

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TABLE 2—*Continued*

Gene	Synonym	Gene product and description	Reference(s)
dnaB	*groP, grpA*	Chromosome replication; chain elongation	21, 1696, 1697
dnaC	*dnaD*	Chromosome replication; initiation and chain elongation	1028, 1696, 1697
dnaE	*polC*	DNA polymerase III, α chain (EC 2.7.7.7)	1561, 1775
dnaG	*dnaP, parB*	DNA biosynthesis; DNA primase (EC 2.7.7.-)	572, 1531
dnaI		DNA biosynthesis	824, 1601
dnaJ	*groPAB, grpC, groPC*	DNA biosynthesis; heat shock protein	497, 876, 1477
dnaK	*groPAB, grpC, grpF, groPC, groPF*	DNA biosynthesis; heat shock protein	876, 1558, 1750
dnaL	*dnaK*	DNA biosynthesis	1464
dnaN		DNA polymerase III holoenzyme, β subunit (EC 2.7.7.7)	563, 1561, 1775
dnaQ	*mutD*	DNA polymerase III holoenzyme, ε subunit; mutant alleles have mutator activity (EC 2.7.7.7)	1560, 1561, 1775
dnaT		DNA biosynthesis; primosomal protein i	1031
dnaX	*dnaZ*	DNA polymerase III holoenzyme, τ and γ subunits; DNA elongation factor III	1560, 1648, 1775
endA		DNA-specific endonuclease I	947
fis		Site-specific DNA inversion stimulation factor; DNA-binding protein; a transactivator for transcription	534, 841, 1202
fpg		Formamidopyrimidine DNA glycosylase	150, 151, 559
gidA		Glucose-inhibited division; chromosome replication?	65
gidB		Glucose-inhibited division; chromosome replication?	65
gyrA	*nalA*	DNA gyrase (EC 5.99.1.3), subunit A, resistance or sensitivity to nalidixic acid, DNA cleavage with transient covalent bonding	19, 1193, 1320
gyrB	*acrB, cou, pcbA, himB, nalC,D*	DNA gyrase (EC 5.99.1.3) subunit B, resistance or sensitivity to coumermycin, DNA cleavage with transient covalent bonding, ATPase activity	19, 1193, 1320
helD		DNA helicase IV (EC 3.6.1.-)	1766
het	*cop*	Binding of DNA sequences in OriC region to outer membrane; structural gene for DNA-binding protein?	1762
himA	*hid*	Integration host factor (IHF), α subunit; site-specific recombination	161, 775, 893
himD	*hip*	Integration host factor (IHF), β subunit; site-specific recombination	161, 548, 893
holA		DNA polymerase III, δ subunit (EC 2.7.7.7)	223, 395, 1775
holB		DNA polymerase III, δ′ subunit (EC 2.7.7.7)	395, 1775
holC		DNA polymerase III, χ subunit (EC 2.7.7.7)	1775
holD		DNA polymerase III, ψ subunit (EC 2.7.7.7)	1775
holE		DNA polymerase III, θ subunit (EC 2.7.7.7)	568, 1775
hsdM	*rm, hsm, hsp, hs*	Host modification; DNA methylase M (EC 2.1.1.72)	978, 1289
hsdS	*rm, hss, hsp, hs*	Specificity determinant for *hsdM* and *hsdR*	978, 1289
iciA		Inhibitor of replication replication	686
lig	*pdeC, dnaL, lop*	DNA ligase (EC 6.5.1.2)	902
mcrC		Component of methylcytosine restriction system	386, 846, 1823
mfd		Mutation frequency decline; transcription-repair coupling factor	506, 1460
mioC		Initiation of chromosome replication	976
mmrA		Recovery in rich medium following UV irradiation	998, 1470
mrr		Restriction of methylated adenine	1698
msp		Sensitivity or resistance of male strains to male-specific phages R17 and f2	209
mutA		Mutator, transversion specific	1079
mutC		Mutator, transversion specific	1079
mutH	*prv, mutR*	Methyl-directed mismatch repair	70, 1428, 1736
mutL	*mut-25*	Methyl-directed mismatch repair	111, 1428, 1778
mutS	*fdv*	Methyl-directed mismatch repair	70, 275, 942
mutY	*micA*	Adenine glycosylase; G · C→T · A transversions (EC 3.2.2.-)	69
ogt		*O*6-Alkylguanine-DNA/cysteine-protein methyltransferase (EC 2.1.1.63)	1281, 1319
parC		Topoisomerase IV subunit A (EC 5.99.1.-)	791, 792
parE		Topoisomerase IV subunit B (EC 5.99.1.-)	791
phr		Photoreactivation; deoxyribodipyrimidine photolyase (EC 4.1.99.3)	1790
polA	*resA*	DNA polymerase I (EC 2.7.7.7)	465, 1220, 1270
polB		DNA polymerase II (EC 2.7.7.7)	245, 679
priA		Primosomal protein N′ (= factor Y)	894, 1173, 1814
priB		Primosomal replication protein N	22, 1813
priC		Primosomal replication protein N″	1813

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TABLE 2—*Continued*

Gene	Synonym	Gene product and description	Reference(s)
recA	*lexB, tif, umuB, zab, rmmB, recH*	General recombination, DNA repair, and induction of phage λ (EC 3.4.99.37)	1114, 1118, 1809
recB	*rorA*	Recombination and DNA repair; exonuclease V (EC 3.1.11.5)	147, 1215
recC		Recombination and DNA repair; exonuclease V (EC 3.1.11.5)	147, 1215
recD		Recombination and DNA repair; exonuclease V (EC 3.1.11.5) α subunit	147, 1215
recF	*uvrF*	Recombination and DNA repair	564, 1409
recG		Probable ATP-dependent DNA helicase	767, 968, 971
recJ		Exonuclease specific for single-stranded DNA; recombination and DNA repair	970, 985, 986
recN	*radB*	Recombination and DNA repair	969, 1368
recO		Conjugational recombination and DNA repair	1104
recQ		ATP-dependent DNA helicase, conjugational recombination and DNA repair	1660
recR		*recB*- and *recC*-independent recombinational repair	1006
rep	*dasC*?, *mmrA*?	*rep* helicase, a single-stranded DNA-dependent ATPase (EC 3.6.1.-)	238, 980, 1763
rra		Reverses *recBC, sbcA* alleviation of RgI restriction of glucosyl-free DNA containing hydroxymethyl- and methylcytosine	774
ruvA		Branch migration of Holliday structures; repair	1230, 1480, 1643
ruvB		Branch migration Holliday structures; repair	1230, 1480, 1643
ruvC		Holliday junction nuclease; resolution of structures; repair	293, 968, 1586
sbcB	*xonA*	Exonuclease I; suppressor of *recB* and *recC* mutations (EC 3.1.11.1)	24, 1251
sbcC		Suppression of *recB* and *recC* mutations; recombination functions	1148
ssb	*exrB, lexC*	Single-stranded DNA-binding protein	204
tag		3-Methyl-adenine DNA glycosylase I, constitutive (EC 3.2.2.-)	128, 757
tdi		Transduction, transformation, and rates of mutation	1530
toc	*gyrB*?	Suppressor of *topA*	399
topA	*supX*	DNA topoisomerase I, ω protein (EC 5.99.1.2)	1096, 1833
topB	*mutR*	DNA topoisomerase III (EC 5.99.1.2)	385
tus	*tau*	DNA-binding protein; inhibition of replication at Ter sites	553, 633, 810
umuC	*uvm*	Induction of mutations by UV; error-prone repair; forms complex with UmuD and UmuD′	80, 823, 1768
umuD	*uvm*	Induction of mutations; error-prone repair; processed to UmuD′; forms complex with UmuC	80, 823, 1768
ung		Uracil-DNA-glycosylase (EC 3.2.2.-)	469, 1675
uup		Precise excision of insertion element	663
uvrA	*dar*	Repair of UV damage to DNA; excision nuclease	269, 833, 1045
uvrB	*visB, dar-1,6*	DNA repair; excision nuclease	1196, 1456, 1457
uvrC	*dar-4,5*	Repair of UV damage to DNA; excision nuclease	948, 1197, 1459
uvrD	*mutU, pdeB, rad, recL, dda, dar-2, uvrE, uvr 502*	DNA-dependent ATPase I and helicase II (EC 3.6.1.-)	238, 1718
vsr		DNA patch repair protein	624, 943, 1505
xerC		Site-specific recombinase of λ integrase family, acts on *cer* sequence of ColE1 and probably effects chromosome segregation at cell division	139, 287
8. Proteins (translation and modification)			
dsbA	*ppfA*	Required for disulfide bond formation	91, 768
frr		Ribosome-releasing factor	689, 1482
fusA	*far*	Protein chain elongation factor EF-G	1097
glnD		Uridylyltransferase acts on regulator of *glnA*	67
glnE		Adenylating enzyme for glutamine synthetase (EC 2.7.7.42)	27
greA		Elongation factor: cleaves 3′ nucleotide of paused mRNA	157, 1509, 1510
hha		Hemolysin expression-modulating protein	1158
iap		Alkaline phosphatase isozyme conversion, aminopeptidase	716, 1147
infA		Protein chain initiation factor IF-1	315
infB	*ssyG*	Protein chain initiation factor IF-2	861, 1105, 1393
infC	*fit*	Protein chain initiation factor IF-3	1127
map		Methionine aminopeptidase (EC 3.4.11.18)	110
pcm		L-Isoaspartate protein carboxylmethyltransferase type II (EC 2.1.1.77)	489

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TABLE 2—*Continued*

Gene	Synonym	Gene product and description	Reference(s)
ppiA		Peptidyl-prolyl *cis-trans* isomerase A (a rotamase) (EC 5.2.1.8)	607, 964
ppiB		Peptidyl-prolyl *cis-trans* isomerase B (a rotamase) (EC 5.2.1.8)	607, 964
prfA	*sueB*, *uar*, *asuA*?, *ups*?	Protein synthesis release factor 1	308
prfB	*supK*	Protein synthesis release factor 2	308, 1083
selB	*fdhA*	Selenocysteinyl-tRNA-specific translation factor	474, 1425
tsf		Protein chain elongation factor EF-Ts	33, 687
tufA		Protein chain elongation factor EF-Tu	810, 1097, 1255
tufB		Protein chain elongation factor EF-Tu	810, 1604
ups		Efficiency of nonsense suppressors	341
9. Polysaccharides (cytoplasmic)			
glgA		Glycogen synthase (EC 2.4.1.21)	1360
glgB		1,4-α-Glucan branching enzyme (EC 2.4.1.18)	1360
glgC		Glucose-1-phosphate adenylyltransferase (EC 2.7.7.27)	637, 901, 1077
glgP		Glycogen phosphorylase (EC 2.4.1.1)	1431, 1432, 1808
glgS		Glycogen biosynthesis, *rpoS* dependent	621
B. Degradation of macromolecules			
1. RNA			
rna	*rnsA*, *rns*	RNase I (EC 3.1.27.6)	1056, 1826
rnb		RNase II (EC 3.1.13.1)	396, 799
rnc		RNase III (EC 3.1.26.3)	249, 1322, 1527
rnd		RNase D (EC 3.1.26.3)	1820, 1821
rnhA	*dasF*, *herA*, *sin*, *sdrA*	RNase H (EC 3.1.26.4)	312, 721
rnhB		RNase HII (EC 3.1.26.4)	720
rnpA		RNase P, protein component (EC 3.1.26.5)	377, 1526, 1573
rnpB		RNase P, RNA component	377, 1526, 1573
rnt		RNase T, degradation of tRNA	1211
rph		RNase PH	377
srnA		Degradation of stable RNA	1185
stsA		RNase activity	908
2. DNA			
hsdR	*rm*, *hsr*, *hsp*, *hs*	Host restriction; endonuclease R (EC 3.1.21.3)	978, 1289
mcrA	*rglA*	Restriction of DNA at 5-methylcytosine residues (EC 3.1.21.-); locus of e14 element	645, 646
mcrB	*rglB*	Restriction of DNA at 5-methylcytosine residues (EC 3.1.21.-)	386, 846, 1824
nfo		Endonuclease IV (EC 3.1.21.2)	919
nth		Endonuclease III; a DNA *N*-glycosylase and phosphoric monoester lyase, specific for apurinic and/or apyrimidinic sites (EC 3.1.25.2)	64
xseA		Exonuclease VII, large subunit (EC 3.1.11.6)	241
xseB		Exonuclease VII, small subunit (EC 3.1.11.6)	1665, 1666
xthA		Exonuclease III (EC 3.1.11.2)	1401, 1410
3. Proteins			
clpA		ATP-dependent *clpA* protease, ATP-binding, regulatory subunit (EC 3.4.21.-)	551, 788, 1042
clpB		Similar to ATP-dependent *clp* protease ATP-binding subunit, heat shock proteins F84.1 and F68.5	1042, 1523, 1764
clpP		ATP-dependent protease, proteolytic subunit, heat shock protein F21.5 (EC 3.4.21.-)	551, 1042
dcp		Dipeptidyl carboxypeptidase	375
eco	*eti*	Ecotin, a serine protease inhibitor	1052, 1053
hlyA		Pro-hemolysin	658, 800, 1532
hlyC		Acyl carrier protein for processing prohemolysin	79, 718, 1705
htrA	*degP*	A periplasmic endopeptidase and heat shock protein	957
pepA	*xerB*	Aminopeptidase A/I (EC 3.4.11.1)	1545
pepD	*pepH*	Peptidase D, a dipeptidase (EC 3.4.13.3)	472, 625

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TABLE 2—*Continued*

Gene	Synonym	Gene product and description	Reference(s)
pepN		Aminopeptidase N (EC 3.4.11.-)	84a
pepP		Aminopeptidase P II (EC 3.4.11.9)	1805
pepQ		Proline dipeptidase (EC 3.4.13.9)	772
prc	*tsp*	Carboxy-terminal protease for penicillin-binding protein 3 precursor	598
prlC		Oligopeptidase A	292
ptr		Protease III	87
sohB		*htrA* suppressor, a protease?	81
sppA		Protease IV, a signal peptide peptidase (EC 3.4.-.-)	688, 1575
sulA	*sfiA*, *suf*	Suppressor of *lon*	373
tlp		Protease II (EC 3.4.21.-)	772
IV. Cell structure			
A. Membrane components			
envD		Envelope protein	813
hlpA	*skp*	Outer membrane protein	651
mdoG	*mdoA*	Periplasmic membrane-derived oligosaccharide (MDO) synthesis	864
mdoH	*mdoA*	Membrane glycosyltransferase, membrane-derived oligosaccharide (MDO) synthesis	864
mvrC		Membrane protein	1103
nlpA	*skp*	Lipoprotein-28	1789
nlpB		Lipoprotein-34	166
ompA	*con*, *tolG*, *tut*	Outer membrane protein 3a (II*;G;d)	400, 818
ompT		Outer membrane protein 3b (a), a protease	86, 596
phoE	*ompE*	Outer membrane pore protein e (E, Ic, NmpAB), structural gene	98, 357, 738
qmeA	*gts*	Unspecified membrane defect	1747
qmeC		Unspecified membrane defect; tolerance to glycine; penicillin sensitivity	1747
qmeD		Unspecified membrane defect; tolerance to glycine; penicillin sensitivity	1747
qmeE		Unspecified membrane defect	1747
rfaD	*htrM*	ADP-L-glycero-D-mannoheptose-6-epimerase; permits growth at high temperature (EC 5.1.3.-)	1241, 1311, 1363
rlpA		A minor lipoprotein	1588
rlpB		A minor lipoprotein	1588
sipB		Suppressor of outer membrane mutant	1303
sipC		Suppressor of outer membrane mutant	1303
sipD		Suppressor of outer membrane mutant	1303
B. Murein sacculus			
amiA		*N*-Acetylmuramyl-L-alanine amidase activity	1627
bolA		Possible regulator of murein genes	16
dacA	*pfv*	D-Alanyl-D-alanine carboxypeptidase, fraction A; penicillin-binding protein 5 (EC 3.4.16.4)	103, 732, 1669
dacB		D-Alanyl-D-alanine carboxypeptidase, fraction B; penicillin-binding protein 4 (EC 3.4.16.4)	834, 1110, 1111
dacC		D-Alanyl-D-alanine carboxypeptidase; penicillin-binding protein 6 (EC 3.4.16.4)	192
dadX	*msuA*?	Alanine racemase (EC 5.1.1.1); isozyme	569, 1751
ddlA		D-Alanine-D-alanine ligase A (EC 6.3.2.4)	15, 1815
ddlB		D-Alanine-D-alanine ligase B (EC 6.3.2.4)	1815
ftsI	*pbp*, *sep*	Penicillin-binding protein 3	103, 104
hipA		Frequency of persistence following inhibition of murein biosynthesis	130
lpp	*mlpA*	Murein lipoprotein	712, 1112
mepA		Murein DD-endopeptidase	797
mlt		Murein transglycosylase (EC 2.4.99.-)	436
mraB		D-Alanine requirement; cell wall peptidoglycan biosynthesis	1094
mraY		Phospho-*N*-acetylmuramoyl-pentapeptide transferase? (EC 2.7.8.13)	699
mrbA		UDP-*N*-acetylglucosaminyl-3-enolpyruvate reductase activity	1094
mrbB		Cell wall peptidylglycan biosynthesis; mutation causes D-alanine auxotrophy	1094

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TABLE 2—*Continued*

Gene	Synonym	Gene product and description	Reference(s)
mrbC		Cell wall peptidylglycan biosynthesis	1094
mrcA	*ponA*	Peptidoglycan transglycosylase-transpeptidase; penicillin-binding protein 1A	191, 1807
mrcB	*pbpF*, *ponB*	Peptidoglycan transglycosylase-transpeptidase; penicillin-binding protein 1Bs	191, 1807
mrdA	*pbpA*	Cell shape; penicillin-binding protein 2	66
mrdB	*rodA*	Rod shape-determining protein; sensitivity to radiation and drugs	103, 698
mreB		Rod shape-determining protein	389
mreC		Rod shape-determining protein	1692
mreD		Rod shape-determining protein	1692
murB		UDP-*N*-acetylenolpyruvoylglucosamine reductase (EC 1.1.1.158)	115, 1299
murC		L-Alanine-adding enzyme (EC 6.3.2.8)	538, 1068
murD		UDP-*N*-acetylmuramoylalanine-D-glutamate ligase (EC 6.3.2.9)	538, 1067, 1068
murE		*meso*-Diaminopimelate-adding enzyme (EC 6.3.2.13)	538, 1067, 1068
murF	*mra*	D-Alanine:D-alanine-adding enzyme (EC 6.3.2.15)	413, 538, 1068
murG		Transferase in peptidoglycan synthesis	538, 1068
murH		Peptidoglycan biosynthesis, late stage	322, 538
murZ		Murein biosynthesis	538
pal	*excC*	Peptidoglycan-associated lipoprotein	248, 888
ponA		Peptidoglycan transglycosylase-transpeptidase, PBP 1A	
slt		Soluble lytic murein transglycosylase (EC 3.2.1.-)	435
C. Surface polysaccharides and antigens			
cpsA	*non**	Capsular polysaccharide biosynthesis, colanic acid	1637
cpsC		Capsular polysaccharide biosynthesis, colanic acid	1637
cpsD		Capsular polysaccharide biosynthesis, colanic acid	1637
cpsE		Capsular polysaccharide biosynthesis, colanic acid	1637
cpsF		Capsular polysaccharide biosynthesis, colanic acid	1637
kdsA		3-Deoxy-D-manno-octulosinic acid 8-phosphate synthase (EC 4.1.2.16)	1761
kdsB		CTP:CMP-3-deoxy-D-manno-octulosonate transferase (EC 2.7.7.38)	462
kdtA		3-Deoxy-D-manno-octulosonic-acid transferase (KDO transferase)	277, 1363
lpcA	*tfrA*	Lipopolysaccharide core biosynthesis; resistance to phages T4, T7, and P1; deficiency in conjugation	606, 1593
lpcB	*pon*	Lipopolysaccharide core biosynthesis	606, 1593
ops		Level of exopolysaccharide production	1829
rcsA		Positive regulator for *ctr* capsule biosynthesis	552, 1553, 1554
rcsB		Positive response regulator for *ctr* capsule biosynthesis (sensor for *rcsC*)	525, 552, 1553
rcsC		Negative regulator for *ctr* capsule biosynthesis, probable sensor acting on *rcsB* (EC 2.7.1.-)	184, 552, 1553
rfaB		UDP-D-galactose:(glucosyl)lipopolysaccharide-1,6-D-galactosyl-transferase	1287, 1363
rfaC		Lipopolysaccharide core biosynthesis; proximal heptose	1363
rfaF		Lipopolysaccharide core biosynthesis	1363
rfaG		Lipopolysaccharide core biosynthesis; glucosyltransferase I	1226, 1227, 1363
rfaH	*sfrB*, *hlyT*	Transcriptional activator affecting biosynthesis of lipopolysaccharide core, F pilin, and hemolysin	1288, 1363
rfaI		UDP-D-galactose:(glucosyl)lipopolysaccharide-α-1,3-D-galactosyl-transferase	1287, 1363
rfaJ		UDP-D-glucose:(galactosyl)lipopolysaccharide glucosyltransferase	1287, 1363
rfaK		Lipopolysaccharide core biosynthesis	816, 1363
rfaL		Lipopolysaccharide core biosynthesis	816, 1363
rfaM		Lipopolysaccharide core biosynthesis; glucosyltransferase II	1363
rfaP		Lipopolysaccharide core biosynthesis; phosphorylation of core heptose	1226, 1227, 1363
rfaQ		Lipopolysaccharide core biosynthesis	1227, 1363
rfaY		Lipopolysaccharide core biosynthesis	816, 1363
rfaZ		Lipopolysaccharide core biosynthesis	816, 1363
rfe		Synthesis of enterobacterial common antigen (ECA):UDP-GlcNAc:undecaprenylphosphate GlcNAc-1-phosphate transferase, O antigen (EC 2.4.1.-)	1062, 1186
rffA		Synthesis of enterobacterial common antigen (ECA):TDP-4-keto-6-deoxy-D-glucose:TDP-D-glucosamine transaminase	848, 1062, 1063

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TABLE 2—*Continued*

Gene	Synonym	Gene product and description	Reference(s)
rffC		Synthesis of enterobacterial common antigen (ECA):ECA chain elongation	848, 1062, 1063
rffD		Synthesis of enterobacterial common antigen (ECA):UDP-ManNAc dehydrogenase	848, 1062, 1063
rffE		Synthesis of enterobacterial common antigen (ECA):UDP-GlcNAc-2-epimerase	848, 1062, 1063
rffM		Synthesis of enterobacterial common antigen (ECA):UDP-ManNAcA:lipid I transferase	93, 848, 1062
rffT		Synthesis of enterobacterial common antigen (ECA):TDP-Fuc4NAc:lipid II transferase	848, 1062, 1063
D. Surface structures			
crl		DNA-binding protein affecting expression of cryptic *csgA* gene for surface fibers	61, 1189
csgA		Curlin subunit, coiled surface structures; cryptic	61, 1189
fimA	*pil, pilA, fimD*	Type 1 fimbrin (pilin)	1048, 1449
fimB	*pil*	Regulator for *fimA*	1048
fimC	*pil*	Putative chaperone for type 1 fimbriae	1610
fimD	*pil*	Cell surface localization of type 1 fimbriae	815
fimE		Regulator for *fimA*	146, 1048
fimF		Fimbrial morphology	844, 1390
fimG		Fimbrial morphology	844, 1390
fimH		Minor fimbrial subunit, adhesin, mannose specificity	844, 1610
flgA	*flaU*	Flagellar biosynthesis; assembly of basal-body periplasmic P ring	697, 999, 1184
flgB	*flbA*	Flagellar biosynthesis, cell-proximal portion of basal-body rod	697, 999
flgC	*flaW*	Flagellar biosynthesis, cell-proximal portion of basal-body rod	697, 999
flgD	*flaV*	Flagellar biosynthesis, initiation of hook assembly	697, 999
flgE	*flaK*	Flagellar biosynthesis, hook protein	697, 999
flgF	*flaX*	Flagellar biosynthesis, cell-proximal portion of basal-body rod	697, 999
flgG	*flaL*	Flagellar biosynthesis, cell-distal portion of basal-body rod	697, 999
flgH	*flaY*	Flagellar biosynthesis, basal-body outer membrane L (lipopolysaccharide layer) ring protein	697, 748, 999
flgI	*flaM*	Flagellar biosynthesis, basal-body periplasmic P ring protein	697, 748, 999
flgJ	*flaZ*	Flagellar biosynthesis	697, 999
flgK	*flaS*	Flagellar biosynthesis, hook-filament junction protein	697, 999
flgL	*flaT*	Flagellar biosynthesis; hook-filament junction protein	697, 999
flgM		Anti-FliA (anti-sigma) factor; also known as Rfl protein; active only when hook assembly not complete	697, 999
flhA	*flaH*	Flagellar biosynthesis; export of flagellar proteins?	697, 860, 999
flhB	*flaG*	Flagellar biosynthesis	697, 999
flhC	*flaA*	Regulator of flagellar biosynthesis acting on class 2 operons; transcription initiation factor?	697, 999
flhD	*flbB*	Regulator of flagellar biosynthesis, acting on class 2 operons; transcription initiation factor?	697, 999
flhE		Flagellar biosynthesis	697, 999
fliA	*flaD*	Flagellar biosynthesis; regulation of late gene expression (class 3a and 3b operons); sigma factor	697, 794, 999
fliB		Flagellar biosynthesis; in *Salmonella* spp., methylation of lysine residues on the filament protein, flagellin	697, 794, 999
fliC	*H, hag, flaF*	Flagellin; flagellar biosynthesis, filament structural protein	60, 697, 999
fliD	*flbC rfs*	Flagellar biosynthesis; filament-capping protein; enables filament assembly	60, 697, 999
fliE	*flaN*	Flagellar biosynthesis; basal-body component, possibly at (MS-ring)-rod junction	697, 999, 1119
fliF	*flaBI*	Flagellar biosynthesis; basal-body MS (membrane and supramembrane)-ring and collar protein	697, 794, 999
fliG	*flaBII*	Flagellar biosynthesis, component of motor switching and energizing, enabling rotation and determining its direction	804, 999, 1357
fliH	*flaBIII*	Flagellar biosynthesis; export of flagellar proteins?	697, 794, 999
fliI	*flaC*	Flagellar biosynthesis; export of flagellar proteins?	697, 794, 999
fliJ	*flaO*	Flagellar biosynthesis	697, 794, 999
fliK	*flaE*	Flagellar biosynthesis, hook length control	697, 794, 999
fliL	*flaAI*	Flagellar biosynthesis	697, 999, 1011
fliM	*flaAII*	Flagellar biosynthesis, component of motor switch and energizing, enabling rotation and determining its direction	804, 999, 1357

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TABLE 2—*Continued*

Gene	Synonym	Gene product and description	Reference(s)
fliN	*motD*	Flagellar biosynthesis, component of motor switch and energizing, enabling rotation and determining its direction	804, 999, 1357
fliO	*flbD*	Flagellar biosynthesis	697, 794, 999
fliP	*flaR*	Flagellar biosynthesis	697, 794, 999
fliQ	*flaQ*	Flagellar biosynthesis	697, 794, 999
fliR	*flaP*	Flagellar biosynthesis	697, 794, 999
fliS		Flagellar biosynthesis; repressor of class 3a and 3b operons (RflA activity)	697, 794, 999
fliT		Flagellar biosynthesis; repressor of class 3a and 3b operons (RflA activity)	697, 794, 999
flu		Metastable gene affecting surface properties, piliation, and colonial morphology	383
mor		Regulator of switching between two sets of surface properties	1715
V. Cellular processes			
A. Transport/binding proteins			
abpS		Low-affinity transport, arginine and ornithine; periplasmic binding protein	231, 232
araE		Low-affinity L-arabinose transport system; L-arabinose proton symport	190, 1000
araF		L-Arabinose-binding protein	664, 1679
araG		High-affinity L-arabinose transport system	664
araH		High-affinity L-arabinose transport system; membrane protein	664
argP		Transport of arginine, ornithine, and lysine	234
argT		Probable lysine-, arginine-, and ornithine-binding protein	1167
aroP		General aromatic amino acid transport	661
aroT	*aroR*, *trpP*	Transport of aromatic amino acids, alanine, and glycine	1617
bcp		Bacterioferritin comigratory protein	45
betT		High-affinity choline transport	871
bfr		Bacterioferritin	47
bioP	*birB*	Biotin transport	127, 1257
brnQ		Transport system 1 for isoleucine, leucine, and valine	1792
brnR		Component of transport systems 1 and 2 for isoleucine, leucine, and valine	1792
brnS		Transport system for isoleucine, leucine, and valine	574
brnT		Low-affinity transport system for isoleucine	574
btuB	*bfe*, *cer*, *btuA*	Receptor for vitamin B_{12}, E colicins, and bacteriophage BF23	108, 840
btuC		Vitamin B_{12} transport	1343
btuD		Vitamin B_{12} transport, membrane-associated protein	1343
btuR		Regulator for *btuB*	992
bymA		Bypass of maltose permease at *malB*	655
cadB		Transport of lysine/cadaverine	1066, 1720
calA		Calcium transport	181
calC		Calcium transport	181
calD		Calcium transport	181
cbt		Dicarboxylate-binding protein	974
codB		Cytosine transport	332
cog		Regulator of *ompG*	1092
corA		Mg^{2+} transport, system I	530, 1224
corB		Mg^{2+} transport, system I	530, 1224
crr	*treD*, *tgs*, *gsr*, *iex*	Glucose phosphotransferase system enzyme III^{glc}	371, 589, 1394
cup		Uptake of carbohydrates	1005
cutE		Copper homeostasis protein	1355
cycA	*dagA*	Resistance to D-cycloserine and D-serine; transport of D-alanine, D-serine, and glycine	301, 1346
cysA		Sulfate permease A protein; chromate resistance	1387, 1495
cysU	*cysT*	Sulfate permease T protein	1496
cysW	*cysT*	Sulfate permease W protein	1495
dctA		Uptake of C_4-dicarboxylic acids	973
dctB		Uptake of C_4-dicarboxylic acids	973
dgoT		Galactonate transport	298
dgsA		Enzyme IIA/IIB of phosphotransferase system	1351
dppA		Dipeptide transport protein	4, 1190
ecfA	*metC*?	Energy coupling factor; pleiotropic effects on active transport coupling to metabolic energy; may be *metC*	660

Continued on following page

TABLE 2—*Continued*

Gene	Synonym	Gene product and description	Reference(s)
entA		2,3-Dihydro-2,3-dihydroxybenzoate dehydrogenase (EC 1.3.1.28), enterochelin biosynthesis	962, 1650
entB	*entG*	2,3-Dihydro-2,3-dihydroxybenzoate synthetase (EC 3.3.2.1), enterochelin biosynthesis	1384, 1528
entC		Isochorismate synthetase (EC 5.4.99.6), enterochelin biosynthesis	763, 963, 1207
entD		Enterochelin synthetase, component D	59, 279, 1528
entE		Enterochelin synthetase, component E	1528, 1529
entF		Enterochelin synthetase, component F	1385, 1528
exbB		Uptake of enterochelin; resistance or sensitivity to colicins	176, 426
exbC		Uptake of enterochelin; resistance or sensitivity to colicins	1302
exbD		Uptake of enterochelin	426, 1279
exuT		Transport of hexuronates	1155
fadL	*ttr*	Transport of long-chain fatty acids; sensitivity to phage T2	133, 134, 1397
fecA		Citrate-dependent iron transport, outer membrane receptor	1533, 1673
fecB		Citrate-dependent iron transport, periplasmic protein	1533, 1673
fecC		Citrate-dependent iron(III) transport protein, cytosolic	1533, 1673
fecD		Citrate-dependent iron transport, membrane-bound protein	1533, 1673
fecE		Citrate-dependent iron(III) transport protein, membrane-bound protein	1533, 1673
fecI		Regulator for *fec* operon, membrane location	1673
fecR		Regulator for *fec* operon, periplasmic	1673
feo		Ferrous iron transport system	
fepA	*cbr*, *cbt*, *feuB*	Receptor for ferric enterobactin (enterochelin) and colicins B and D	58, 1132, 1208
fepB		Ferric enterobactin (enterochelin) uptake; periplasmic component	429, 1208
fepC		Ferric enterobactin (enterochelin) uptake; cytoplasmic membrane component	1208, 1474
fepD		Ferric enterobactin (enterochelin) uptake	1208, 1474
fepE		Ferric enterobactin (enterochelin) uptake	1208
fepG		Ferric enterobactin transport protein	1474
fes		Enterochelin esterase	182
fhuA	T1, T5*rec*, *tonA*	Outer membrane protein receptor for ferrichrome, colicin M, and phages T1, T5, and ϕ80	177, 222, 807
fhuB		Hydroxamate-dependent iron uptake, cytoplasmic membrane component	837, 838, 1446
fhuC		Hydroxymate-dependent iron uptake, cytoplasmic membrane component	837, 838, 1446
fhuD		Hydroxamate-dependent iron uptake, cytoplasmic membrane component	837–839
fhuE		Outer membrane receptor for ferric iron uptake	1422
fhuF		Ferric hydroxymate transport	597
fiu		Ferric iron uptake, outer membrane protein	317
fruA	*ptsF*	Fructose phosphotransferase enzyme II (EC 2.7.1.69)	1194, 1294
fruB		Fructose phosphotransferase enzyme III	512
fruF	*fpr*	Phosphohistidinoprotein-hexose phosphotransferase, fructose specific	573, 1194
fucP		Fucose permease	250
gabP		Transport of γ-aminobutyrate	620, 1076
galP	*Pgal*	Galactose permease	1342
gatA		Galactitol-specific enzyme II of phosphotransferase system	903–905
glnH		Periplasmic glutamine-binding protein	1166
glnP		Glutamine high-affinity transport system; membrane component	1166
glnQ		Glutamine high-affinity transport system	1166
glpF		Facilitated diffusion of glycerol	1576, 1731
glpT		*sn*-Glycerol-3-phosphate permease	427, 881
gltP		Glutamate-aspartate symport protein	359, 1626
gltR		Regulator for *gltS*	1023
gltS	*gltC*	Glutamate transport	402, 765
gntS	*gntM*, *usgA*	Second system for transport and possible phosphorylation of gluconate	74, 280
gntT	*gntM*, *usgA*	High-affinity transport of gluconate	451, 1136
hisJ		Histidine-binding protein of high-affinity histidine transport system	55
hisM		Histidine transport, membrane protein M	842
hisP		Histidine transport, inner membrane receptor protein P	842, 1089
kdgT		2-Keto-3-deoxy-D-gluconate transport system	1015
kdpA	*kac*	High-affinity potassium transport system; probable K^+-stimulated ATPase (EC 3.6.1.36)	1269

Continued on following page

TABLE 2—*Continued*

Gene	Synonym	Gene product and description	Reference(s)
kdpB	*kac*	High-affinity potassium transport system (EC 3.6.1.36)	1269
kdpC	*kac*	High-affinity potassium transport system (EC 3.6.1.36)	1269
kdpE		Regulator of *kdp* operon (effector)	1146, 1269, 1701
kefB	*trkB*	K^+ efflux; NEM^a-activable K^+/H^+ antiporter	431
kefC	*trkC*	K^+ efflux; NEM-activable K^+/H^+ antiporter	431, 1125
kgtP	*witA*	α-Ketoglutarate permease	1463
lacY	*y*	Galactoside permease (M protein)	190, 759, 1395
lctP		L-Lactate permease	393
lepA		GTP-binding membrane protein	1491
livF		Leucine transport protein	6
livG	*hrbBCD*	High-affinity branched-chain amino acid transport system	6
livH	*hrbBCD*	High-affinity branched-chain amino acid transport system; membrane component	6
livJ	*hrbBCD*	High-affinity branched-chain amino acid transport system; periplasmic binding protein for leucine, isoleucine, and valine	6
livK	*hrbBCD*	High-affinity branched-chain amino acid transport system; leucine-specific periplasmic binding protein	6
livL		High-affinity branched-chain amino acid transport	6
livM		High-affinity branched-chain amino acid transport	6
lysP	*cadR*	Lysine-specific permease; pleiotropic increase in lysine decarboxylase	1536
lysX		Lysine excretion	
malE	*malB*	Periplasmic maltose-binding protein; substrate recognition for transport and chemotaxis	101, 1534
malF	*malB*	Transport of maltose; cytoplasmic membrane protein	342, 350
malG	*malB*	Transport of maltose and maltodextrins	342, 350
malK	*malB*	Transport of maltose	351, 1325, 1331
malX		Phosphotransferase enzyme II, maltose and glucose specific (EC 2.7.1.69)	1324
manX	*ptsL, ptsM, gptB, mpt, ptsX*	Mannose phosphotransferase system, protein II-A(III)	447, 448
manY	*ptsM, pel, ptsP, ptsX*	Mannose phosphotransferase system: Pel protein II-P; penetration of phage λ (EC 2.7.1.69)	447, 448
manZ	*ptsM, ptsX, gptB, mpt*	Mannose phosphotransferase system, enzyme IIB(IIM) (EC 2.7.1.69)	447, 448
mdoA		Membrane-derived oligosaccharides; membrane-localized component of glucosyl transferase system	515, 864
mdoB		Membrane-derived oligosaccharides; phosphoglycerol transferase I activity	515, 864
melB	*mel-4*	Melibiose utilization; thiomethylgalactoside permease II	1283, 1284
metD		High-affinity uptake of D- and L-methionine	760, 761
mglD		Regulator for methyl-galactoside transport	1345
mglR	R-MG	*mgl* regulator	498
mgt		Mg^{2+} transport, system II	498
modA		Molybdate uptake	619, 644
modB	*tslJ*	Molybdate uptake	644
modC	*chlD*	Molybdate uptake	619, 644, 1454
modD		Molybdate uptake	644
molR		Molybdate transport	644, 895
mtlA		Mannitol-specific enzyme II of phosphotransferase system (EC 2.7.1.69)	1277, 1566
mtr		Tryptophan-specific transport protein	612, 1412, 1413
nagE	*ptsN*	*N*-Acetylglucosamine-specific enzyme II of phosphotransferase system *nalD* (EC 2.7.1.69)	1267, 1268, 1686
narK		Transport of nitrate	369
nhaA	*ant, antA*	Na^+/H antiporter activity	1258, 1584, 1612
nhaB		$Na^+/H+$ antiporter	1258, 1612
nhaR	*antO, yaaB*	Activator of *nhaA*	1309
nikA	*hydC*	Transport of Ni, essential for hydrogenases	1777
nikB	*hydD*	Transport of Ni, essential for hydrogenases	1777
nupC	*cru*	Transport of nucleosides except guanosine	1122
nupG		Transport of nucleosides	1121, 1739
ompG		Outer membrane porin protein	1092
oppA		Oligopeptide transport; periplasmic binding protein	41, 784, 786
oppB		Oligopeptide transport	42
oppC		Oligopeptide transport	42
oppD		Oligopeptide transport	42

Continued on following page

TABLE 2—*Continued*

Gene	Synonym	Gene product and description	Reference(s)
oppE		Oligopeptide transport	42
oppF		Oligopeptide transport, ATP hydrolysis	42
panF		Pantothenate permease	730, 1328
pheP		Phenylalanine-specific transport system	1253
phnC		Utilization of phosphorus-containing compounds, probable transport	1009, 1075, 1713
phoU	*phoT*	Regulator for high-affinity phosphate-specific transport system	1313, 1712
pit		Low-affinity P_i transport	434
potA		Spermidine/putrescine transport protein	494
potB		Spermidine/putrescine transport protein	494
potA		Spermidine/putrescine transport protein	494
potB		Spermidine/putrescine transport protein	494
potC		Spermidine/putrescine transport protein	494
potD		Spermidine/putrescine transport protein	494
potE		Putrescine transport protein	785
proP		Low-affinity transport system for glycine betaine and proline; proline permease II	229, 314
proT		Proline transport	1108, 1109
proV	*proU*	High-affinity transport system for glycine betaine and proline; glycine betaine-binding protein	229, 340, 1547
proW	*proU*	High-affinity transport system for glycine betaine and proline	229, 340, 1547
pstA	*phoT*, *phoR2b*, $R2_{pho}$	High-affinity phosphate-specific transport system	1313
pstB	*phoT*	High-affinity phosphate-specific transport system, cytoplasmic membrane protein?	1313
pstC	*phoW*	High-affinity phosphate-specific transport system, cytoplasmic membrane component	1313
pstS	*nmpA phoR2a*, *phoST R2pho*	High-affinity phosphate-specific transport system; periplasmic phosphate-binding protein	1010
ptsG	*car*, *cat*, CR, *gpt*, *tgl*, *umg*, *gptA*	Glucosephosphotransferase enzyme II (EC 2.7.1.69)	203, 1382, 1392
ptsH	*ctr*, *Hpr*, *HPr*	Phosphohistidinoprotein-hexose phosphotransferase (EC 2.7.1.69)	371, 1382
ptsI	*ctr*	Phosphotransferase system enzyme I (EC 2.7.3.9)	371, 593, 1382
purP		High-affinity adenine transport	
putP		Major proline permease	314, 594, 1328
rbsA	*prlB*, *rbsP*, *rbsT*	D-Ribose high-affinity transport system; membrane-associated protein	202
rbsB	*rbsP*	D-Ribose periplasmic binding protein	568
rbsC	*rbsP*	D-Ribose high-affinity transport system; membrane-associated protein	107
rbsD	*rbsP*	D-Ribose high-affinity transport system; membrane-associated protein	107
rhaT		Rhamnose transport	84
rsgA	*gen-165*	Ferritin-like protein	729
sbp		Periplasmic sulfate-binding protein	733
shiA		Shikimate and dehydroshikimate permease	1262
srlA	*gutA*, *sbl*	D-Glucitol (sorbitol)-specific enzyme II of phosphotransferase system (EC 2.7.1.69)	1787
srlB	*gutB*	D-Glucitol (sorbitol)-specific enzyme III of phosphotransferase system	589, 1787
tdcC		Anaerobically inducible L-threonine, L-serine permease	549, 1452, 1568
tnaB	*tnaP*	Low-affinity tryptophan permease	538, 1799
tonB	*exbA*, T1*rec*	Membrane protein; uptake of chelated iron and cyanocobalimin; sensitivity to phages T1 and ϕ80 and colicins	52, 108, 177
treB		Enzyme II of PEP:CHO phosphotransferase system, trehalose specific	155, 814
trkA		Transport of potassium	159
trkD		Transport of potassium	160
trkE		Transport of potassium	401
trkG		Potassium uptake	401
trkH		Potassium uptake	401
trpP		Low-affinity tryptophan-specific permease	417
tsx	*nupA*, T6*rec*	Nucleoside channel; receptor of phage T6 and colicin K	179, 524
tyrP		Tyrosine-specific transport system	1770
tyrR		Regulation of *aroF*, *aroG*, and *tyrA* and aromatic amino acid transport systems	1260
ugpA	*psiB*, *psiC*	*sn*-Glycerol 3-phosphate transport system	1205, 1564

Continued on following page

TABLE 2—*Continued*

Gene	Synonym	Gene product and description	Reference(s)
ugpB	*psiB*, *psiC*	*sn*-Glycerol 3-phosphate transport system; periplasmic binding protein	1205
ugpC		*sn*-Glycerol 3-phosphate transport system	1205
ugpE		*sn*-Glycerol 3-phosphate transport system, membrane protein	1205
uhpA		Response regulator, positive activator of *uhpT* transcription (sensor for *uhpB*)	717
uhpB		Regulator of *uhp*, sensor for histidine protein kinase (EC 2.7.1.-)	717
uhpC		Regulator	717
uhpR		Regulation of hexose phosphate transport; outer membrane receptor for glucose 6-phosphate?	762, 1473
uhpT		Hexose phosphate transport protein	31
xylE		Xylose-proton symport	190, 347
xylF	*xylT*	Xylose binding protein transport system	7, 620
xylU		D-Xylose uptake protein	620, 857
B. Cell division			
dicA		Regulator of *dicB*	105
dicB		Inhibition of cell division	215
dicC		Regulator of *dicB*	105
dicF		RNA of 65 nucleotides, cell division inhibitor	456, 1609
envA		Cell envelope and cell separation; UDP-3-*O*-acyl-*N*-acetylglucosamine deacetylase	1359
envB	*mon*, *rodY*	Cell shape and sensitivity to antibiotics	50, 981, 1740
envC		Cell division; chain formation	813
fcsA		Cell division; septation	847
fic		Filamentation in presence of cyclic AMP in mutant	828
ftsA	*divA*	Cell division	1681
ftsE		Cell division	527, 531, 532
ftsH		Cell division; insertion of penicillin-binding protein 3 into membrane?	103, 1180
ftsQ		Cell division	1681
ftsW		Cell division; membrane protein involved in shape determination	698
ftsX		Cell division	527, 531, 532
ftsY		Cell division	527, 531, 532
ftsZ	*sfiB*, *sulB*	GTPase involved in cell division	323, 531, 1318
mbrA		Coupling of cell division and DNA replication	1639, 1640
mbrB		Link between growth rate and partitioning chromosomes	1639, 1640
mbrC		Partitioning chromosomes	1639, 1640
minB		Formation of minute cells containing no DNA; complex locus, position of division septum	1117
minC		Cell division inhibitor	354, 355
minD		Cell division inhibitor, a membrane ATPase, activates *minC*	353–355
minE		Cell division topological specificity factor	354, 355
mukB		Cell division protein involved in chromosome partitioning	647, 648, 1159
mukC		Cell division and chromosome partitioning	648
mukD		Cell division and chromosome partitioning	648
pcsA		Cell division; chromosome segregation	847
sdiA		Regulator of transcription of *ftsQAZ* gene cluster	1711
sefA		Septum formation	1169
sfiC		Cell division inhibition; locus of element e14	734, 1003, 1004
tig		Trigger factor; a molecular chaperone involved in cell division	582
weeA		Cell elongation	360, 361
C. Chemotaxis and mobility			
cheA		Sensor for *cheY* and *cheB* chemotactic response; histidine protein kinase (EC 2.7.1.-)	514, 1054, 1543
cheB		Response regulator for chemotaxis (*cheA* sensor); protein methylesterase (EC 3.1.1.61) demethylates receptors	514, 995, 1054
cheR	*cheX*	Response regulator for chemotaxis; protein glutamate methyltransferase activity (EC 2.1.1.80), methylates receptors	1388
cheW		Positive regulator of CheA protein activity	514, 965, 1054
cheY		Response regulator for chemotactic response (cheA sensor); switch regulator, placing it in counterclockwise state	989, 1357, 1408
cheZ		Chemotactic response; CheY protein phosphatase; antagonist of CheY as switch regulator	1548

Continued on following page

TABLE 2—*Continued*

Gene	Synonym	Gene product and description	Reference(s)
mglA	*mglP*	Methyl-galactoside transport and galactose taxis, cytoplasmic membrane protein	656
mglB	*mglP*	Galactose-binding protein; receptor for galactose taxis	656, 1442
mglC		Methyl-galactoside transport and galactose taxis	656
motA		Proton conductor component of motor; no effect on switching	137, 138, 1551
motB		Enables flagellar motor rotation, linking torque machinery to cell wall; no effect on switching	137, 138, 1551
tap		Methyl-accepting chemotaxis protein IV, peptide receptor	1017
tar	*cheM*	Ethyl-accepting chemotaxis protein II, chemoreceptor for aspartate	503, 896
trg		Methyl-accepting chemotaxis protein III, ribose receptor	208, 1222, 1784
tsr	*cheD*	Methyl-accepting chemotaxis protein I, serine receptor	510, 965
D. Protein secretion			
excD		Export of periplasmic proteins	887
expA		Expression of a group of export proteins	336
hlyB		Secretion protein for hemolysin	521, 755, 836
hlyD		Secretion protein for hemolysin	521, 836, 1532
lepB	*lep*	Leader peptidase (signal peptidase I)	132, 1021
lspA		Prolipoprotein signal peptidase (SPaseII) (EC 3.4.99.35)	1124
secA	*prlD*, *azi*, *pea*	Protein secretion	180, 1485, 1565
secB		Protein export; molecular chaperone	357, 850, 1750
secD		Protein secretion	1038, 1565
secE	*prlG*	Inner membrane protein, protein secretion (with *secY*)	198, 1164, 1565
secF		Membrane protein, protein secretion function	1038, 1565
secY	*prlA*	Membrane protein, protein secretion (with *secE*)	198, 1164, 1577
ssaD		Suppression of *secA* mutation	501, 1188, 1478
ssaE		Suppression of *secA* mutation	1188, 1478
ssaG		Suppression of *secA* mutation	1188, 1478
ssaH		Suppression of *secA* mutation	1186, 1478
ssyA		Suppressor of *secY* mutation	1478
ssyB		Suppressor of *secY* mutation	1479
ssyD		Suppressor of *secY* mutation	1479
E. Osmotic adaptation			
betA		Choline dehydrogenase (EC 1.1.99.1), a flavoprotein	871
betB		NAD^+-dependent betaine aldehyde dehydrogenase (EC 1.2.1.8)	452, 871
betI		Probably repressor of *bet* genes	871
envM		Osmotically remedial envelope defect	120, 1654
envN		Osmotically remedial envelope defect	418
envP		Osmotically remedial envelope defect	418
envQ		Osmotically remedial envelope defect	418
envT		Osmotically remedial envelope defect	448
envY		Envelope protein; thermoregulation of porin biosynthesis	990
micF	*stc*	Regulatory antisense RNA affecting *ompF* expression	34
ompC	*par*, *meoA*	Outer membrane protein 1b (Ib;c)	366, 1339, 1721
ompF	*cmlB*, *coa*, *tolF*, *cry*	Outer membrane protein 1a (Ia;b;F)	475, 555, 1461
osmB		Osmotically inducible lipoprotein	622
osmC		Osmotically inducible protein	584
osmY		Hyperosmotically inducible periplasmic protein	1801
otsA	*pexA*?	Trehalose phosphate synthase (EC 2.4.1.15)	622, 758, 871
otsB		Trehalose phosphate synthase (EC 2.4.1.15)	622, 758, 871
otsP	*treE*	Trehalose-6-phosphate phosphatase (EC 3.1.3.12)	814
otsR		Regulation of *ots*	814
proX	*proU*	Periplasmic glycine betaine-binding protein	229, 340, 1547
treA		Trehalase, periplasmic (EC 3.2.1.28)	583, 622
VI. Other functions			
A. Cryptic genes			
arbT		Phosphorylation and transport of arbutin; cryptic	1228
argM		A second acetylornithine transaminase; cryptic gene (EC 2.6.1.11)	1341
ascB	*sac*	6-Phospho-β-glucosidase (EC 3.2.1.86); cryptic	590, 1228

Continued on following page

TABLE 2—*Continued*

Gene	Synonym	Gene product and description	Reference(s)
ascF	*sac*	Phosphotransferase enzyme II (*asc*), cryptic, transports specific β-glucosides (EC 2.7.1.69)	590, 1228
ascG	*sac*	*asc* operon repressor	590, 1228
bglA	*bglD*	Phospho-β-glucosidase A (EC 3.2.1.86)	1439
bglB	*blgA*	Phospho-β-glucosidase B (EC 3.2.1.86)	1439
bglF	*bglB*, *bglC*	β-Glucoside transport, PEP^a-dependent enzyme II (EC 2.7.1.69), part of cryptic operon	172, 1438
bglG	*bglC*, *bglS*	Positive regulation of *bgl* operon	1437
bglT	*bglE*	Regulator for phospho-β-glucosidase A biosynthesis	1290, 1291
celA		PEP-dependent phosphotransferase transport system for cellobiose, arbutin, and salicin; enzyme IV	1229, 1329
celB		PEP-dependent phosphotransferase transport system for cellobiose, arbutin, and salicin; enzyme II (EC 2.7.1.69); part of cryptic operon	1229, 1329
celC		PEP-dependent phosphotransferase transport system for cellobiose, arbutin, and salicin; enzyme III (EC 2.7.1.69); part of cryptic operon	589, 1229, 1329
celD		Negative regulator of *cel* operon	1229
celF		Phospho-β-glucosidase (EC 3.2.1.86)	1229
citA		Cryptic gene of citrate transport system	587
citB		Cryptic gene of citrate transport system	587
ebgA		β-D-Galactosidase, α subunit; cryptic gene (EC 3.2.1.23)	588, 930
ebgB		Possible homolog of *lacY*	588
ebgC		β-D-Galactosidase, β subunit; cryptic gene (EC 3.2.1.23)	588, 930
ebgR		Regulator of *ebg* operon	991
ilvF		Acetolactate synthase activity (valine insensitive) (EC 4.1.3.18), probably a fifth isozyme	20
ilvG		Acetolactate synthase II (EC 4.1.3.18), valine insensitive, large subunit, silent in K-12	676
ilvM		Acetolactate synthase II (EC 4.1.3.18), valine insensitive, small subunit, silent in K-12	676, 1728
ilvJ		Acetolactate synthase IV (EC 4.1.3.18), valine insensitive, silent in K-12, a fourth isozyme	1350
narV		Cryptic nitrate reductase II (EC 1.7.99.4), γ subunit	145
narW		Cryptic nitrate reductase II, δ subunit, assembly function	145
narY		Cryptic nitrate reductase II (EC 1.7.99.4), β subunit	145
narZ		Cryptic nitrate reductase II (EC 1.7.99.4), α subunit	145
phnE		Utilization of phosphorus-containing compounds, gene cryptic in K-12, probably transport	1009, 1075, 1713
pqq		Redox cofactor, functions as cofactor of apoglucose dehydrogenase; cryptic in wild type	127
B. Phage-related functions and prophages			
bfm		Phage BF23 multiplication	1486
e14		Cryptic, excisable chromosomal element; contains *lit*, *mcrA*, *pin*, and *sfiC*	636
esp		Site for efficient packaging of phage T1	403
fipB		Morphogenesis of phage F1	982
fipC		Morphogenesis of phage F1	982
gprA		Replication of certain lambdoid phages	1178, 1405
gprB		Replication of certain lambdoid phages	1178, 1405
grpD		Initiation of phage lambda DNA replication; host DNA synthesis	1178, 1405
grpE		Phage λ replication; host DNA synthesis; heat shock protein	497, 876, 1558
hflB		Probable protease specific for phage λ *c*II repressor	89
hflC	*hflA*	Protease specific for phage λ *c*II repressor	88, 254
hflK	*hflA*	Protease specific for phage λ *c*II repressor	88, 254
hfq		Host factor I for bacteriophage Q β replication	764
int		Prophage DLP12 integrase	954
lamB	*malB*	Phage λ receptor protein; maltose high-affinity uptake system	482, 988
lit		Phage T4 late gene expression; locus of e14 element	636, 776
mopA	*groE*, *hdh*, *tabB*, *groEL*	Molecular chaperone affecting head assembly of phages T4 and λ	201, 523
mopB	*groE*, *hdh*, *tabB*, *groES*	Molecular chaperone affecting head assembly of phages T4 and λ	880
mul		Mutability of UV-irradiated phage λ	1693
nmpC		Outer membrane porin protein; locus of qsr prophage	143

Continued on following page

TABLE 2—*Continued*

Gene	Synonym	Gene product and description	Reference(s)
ogr		Regulator of late transcription in phage P2; part of cryptic P2 prophage	900, 1499
OriJ		Origin function in rac prophage	
phxB		Adsorption of φX174	1123
pin		Inversion of adjacent DNA; locus of e14 element	859
qin	*kim*	Cryptic lambdoid phage	941
qsr'		Defective prophage qsr'	954
rac	*sbcA*	Defective prophage rac; contains *recE* and *oriJ*	941
rap		Growth of phage λ	1242
recE	*rac*	A function of the Rac prophage: recombination and DNA repair; exonuclease VIII (EC 3.1.11.-)	266
tabC		Development of phage T4, related to Rho?	225, 1587
tnm		Transposition of Tn*9* and other transposons; development of phage Mu	704, 972
C. Colicin-related functions			
cet	*ref, refII*	Tolerance to colicin E2	407
cirA	*feuA*	Iron-regulated colicin I receptor; porin; requires *tonB* gene product	108, 565
cma		Colicin M	600
creD	*cet, refII*	Inner membrane protein involved in colicin E2-mediated killing	407
cvpA		Required for colicin V production	455
tolA	*cim, tol-2, excC, lky*	Tolerance to group A colicins and single-stranded filamentous DNA phage; leakage of periplasmic proteins	112, 914
tolB	*lky, tol-3*	Tolerance to colicins E2, E3, A, and K; leakage of periplasmic proteins	915
tolC	*colE1-i, mtcB, refI, tol-8*	Specific tolerance to colicin E1; expression of outer membrane proteins	399, 648, 1705
tolD		Tolerance to colicins E2 and E3; ampicillin resistance	445
tolE		Tolerance to colicins E2 and E3; ampicillin resistance	445
tolI		Tolerance to colicins Ia and Ib	219
tolJ		Resistance to colicins L, A, and S4; partial resistance to colicins E and K	343
tolM	*cmt*	Mutant phenotype: high-level tolerance to colicin M	600, 601
tolQ	*fii, tolP*?	Tolerance to group A colicins and single-stranded filamentous DNA phage	176, 426
tolR	*fii*	Tolerance to group A colicins and single-stranded filamentous DNA phage	426
tolZ		Tolerance to colicins E2, E3, D, 1a, and 1b; generation of chemical proton gradient	1039
D. Plasmid-related functions			
mafA		Maintenance of F-like plasmids	1695
mafB		Maintenance of F-like plasmids	1695
mprA		Regulator of plasmid *mcrB* operon (microcin B17)	364, 365
pcnB		Plasmid copy number control	1034
E. Drug/analog sensitivity			
abs		Sensitivity and permeability to antibiotics and dyes	271
acrA	*lir, Mb, mbl, mtcA*	Sensitivity to acriflavine, phenethyl alcohol, sodium dodecyl sulfate	284, 627, 1140
acrC		Sensitivity to acriflavine	1141
ampC	*ampA*	β-Lactamase; penicillin resistance (EC 3.5.2.6)	480
ampD		Regulates *ampC*	953
ampE		Regulates *ampC*	953
azaA		Resistance or sensitivity to azaserine	1756
azaB		Resistance or sensitivity to azaserine	1756
can		Canavanine resistance	233
cmlA		Resistance or sensitivity to chloramphenicol	99
dvl		Sensitivity to sodium dodecyl sulfate and toluidine blue plus light	1699
eryD	*mac*	Erythromycin growth dependence	1749
inm		Susceptibility to mutagenesis by nitrosoguanidine	1383
ksgA		*S*-Adenosylmethionine-6-*N'*,*N'*-adenosyl (rRNA) dimethyltransferase (EC 2.1.1.-); kasugamycin resistance	1672

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TABLE 2—*Continued*

Gene	Synonym	Gene product and description	Reference(s)
ksgB		Second-step (high-level) resistance to kasugamycin	476
ksgD		Kasugamycin resistance	476
lev		Resistance to levallorphan	327
linB		High-level resistance to lincomycin	683
lytA		Tolerance to β-lactams; autolysis defective?	602, 1484
marA		Multiple antibiotic resistance; tetracycline efflux system	585
mng		Resistance or sensitivity to manganese	1492
mvrA		Resistance to methyl viologen	1641
nalB		Resistance or sensitivity to nalidixic acid	595
nalD		Penetration of nalidixic acid through outer membrane	670
neaB		Resistance to neamine	367
nek	*amk*	Resistance to neomycin, kanamycin, and other aminoglycoside antibiotics	680
nfnA		Sensitivity to nitrofurantoin	1418, 1462
nfnB		Sensitivity to nitrofurantoin	1418, 1462
nfsA		Nitrofuran reductase I activity	1046
nfsB		Nitrofuran reductase I activity	1046
sbmA		Sensitivity to microcin B17	885
semA		Sensitivity to microcin E492	1301
sloB		Low growth rate; tolerance to amidinopenicillin and nalidixic acid	981
strC	*strB*	Low-level streptomycin resistance	1347
tlnA	*tlnI*	Resistance or sensitivity to thiolutin	1497
F. Radiation sensitivity			
ior		Radiation sensitivity, particularly gamma rays; recombination ability decreased	450
radA		Sensitivity to gamma and UV radiation and methyl methanesulfonate	388
radC		Sensitivity to radiation	459, 460
ras		Sensitivity to UV and X rays	1702
rer		Resistance to UV and gamma rays	1525
G. DNA sites[b]			
att186		Integration site for prophage 186	
att253		Integration site for prophage 253	
atte14		Integration site for element e14	
attHK139		Integration site for phage HK139	
attHK22	*attB-htt*	Integration site for phage HK022	
attλ	*att82* *att434*	Integration site for prophages λ, 82, and 434	
attP1,P7	*loxB*	Integration site for phages P1 and P7	
attP22	*ata*	Integration site for phage P22	
attP2H		Phage P2 integration site H	
attP2II		Phage P2 integration site II	
attP4		Integration site for phage P4	
attPA-2		Integration site for phage PA-2	
attφ80		Integration site for prophage φ80	
Dif		A recombination site in terminus region; resolves sister chromosomes	
OriC	*poh*?	Origin of replication of chromosome	
TerA	*tre*	Terminus; chromosomal DNA replication inhibition; site of Tus-mediated inhibition of DnaB helicase	
TerB		Terminus; chromosomal DNA replication termination; site of Tus-mediated inhibition of DnaB helicase	
TerC		Terminus; chromosomal DNA replication inhibition; site of Tus-mediated inhibition of DnaB helicase	
TerD		Terminus; chromosomal DNA replication inhibition; site of Tus-mediated inhibition of DnaB helicase	
TerE		Terminus; chromosomal DNA replication inhibition; site of Tus-mediated inhibition of DnaB helicase	
H. Adaptations to atypical conditions			
crg		Cold-resistant growth	795
cspA		Cold shock protein 7.4, transcriptional activator of *hns*	543

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TABLE 2—*Continued*

Gene	Synonym	Gene product and description	Reference(s)
cstA		Carbon starvation protein	1445
dps		Global regulator, starvation conditions	28
gef		Polypeptide destructive to membrane potential	364, 365
htgA		Protein required for high-temperature growth	352
htpG		Heat shock protein C 62.5	617, 1512
htpX		Heat shock protein	835
htrB		Protein required for growth at high temperature	779–781
htrC		Pleiotrophic effects on growth at high temperatures, radiation sensitivity, proteolysis	781, 1310
htrD		High temperature growth factor; probable regulator, cysteine transport	362
pspA		Shock protein, associated with inner membrane	186, 187
pspB		Shock protein B	186, 187
pspC		Shock protein activates *psp* operon expression	186, 187
pspD		Shock protein D	187
pspE		Shock protein E	186, 187
rdgA		Dependence of growth on *recA* gene product	487
rdgB		Dependence of growth and viability on *recA* function	487
relF		Polypeptide destructive to membrane potential	364, 365
uspA		Universal stress protein, regulator?	1176

[a] BCCP, biotin carboxyl carrier protein; CoA, coenzyme A; DCCD, *N,N'*-dicyclohexylcarbodiimide; NEM, *N*-ethylmaleimide; PEP, phosphoenol-pyruvate.
[b] DNA sites listed for completeness. No gene product is made.

defined, enzymes are by far the largest category, with transport proteins and regulatory proteins following. Among the genes presently known, genes that encode RNA molecules constitute only 7% of the whole.

How much will these relative proportions change as we approach complete knowledge of the genes and gene products of *E. coli*? As a guess, in the future one might expect to find genes for functions that are more difficult to dissect at the molecular level, such as genes for components of the cell structure and genes for the components of complex interrelated regulatory networks that govern cellular processes.

GENOME CONTENTS

Density of Information in the Genome

One gene, one enzyme, one catalyzed reaction? The density of biochemical information in terms of reactions catalyzed per kilobase of genetic material is highly variable in the bacterial genome because genes do not always have a one-to-one relationship with a biochemical reaction. By common usage, we hold to the principle that one gene encodes one polypeptide chain (or one cistron encodes one polypeptide). In the case of simple enzymes composed of one polypeptide, often one reaction is catalyzed per gene, but the composition and catalytic capabilities of enzymes in terms of polypeptide chains varies greatly. For enzymes made from multiple subunits (and often more than one chain of each subunit polypeptide), as many as four genes are needed to describe the enzyme and the reaction it catalyzes (e.g., the *sdhA*, *sdhB*, *sdhC*, and *sdhD* genes for succinic dehydrogenase) (211, 1152). At the other end of the spectrum there are polyfunctional polypeptides, where one gene encodes a polypeptide that has as many as four catalytic activities. The two-subunit fatty acid oxidation complex encoded by *fadA* and *fadB* catalyzes five reactions. The polypeptide of the *fadB* gene catalyzes four of the five. These are entirely separate reactions of some biochemical variety as reflected in the range of the EC numbers: 1.1.1.35, 5.1.2.3, 5.3.3.8, and 4.2.1.17 (1795, 1797). Clearly, the efficiency of biochemical information per kilobase of DNA or kilodalton of protein, if one can think of it that way, depends on the makeup of the catalytic proteins and varies over a wide range from the efficiency of very small RNase molecules encoded by single genes and highly efficient single polypeptides with multiple catalytic domains such as the *fadB*-encoded polypeptide to the other extreme, very large polypeptides with a single catalytic activity such as the *lacZ* β-galactosidase and huge multienzyme complexes such as pyruvate dehydrogenase requiring three genes, three enzyme components, and as many as 24 polypeptide chains per enzyme.

Density of code use in the genome. As more of the genome is sequenced and long stretches of continuous sequence are produced, including many instances of contiguous genes, it is not uncommon to find the promoter for one coding sequence placed within the C-terminal coding sequence of the upstream gene. Examples are legion. Adjacent genes such as *trpA-trpB*, *ilvA-ilvD*, *pdxA-ksgA*, *selA-selB*, *alkB-ada*, *mreC-mreD*, and the group *ddl-ftsQ-ftsA-ftsZ* all have short overlaps of part of the stop codon of the upstream gene and the first part of the initial methionine codon of the downstream gene, and the promoters for downstream genes are found in the coding region of the upstream gene. Other genes, such as *miaA* and *miaD*, overlap by several nucle-

TABLE 3. Distribution of cellular functions of *E. coli* gene products[a]

Function category	% of gene products in category
I. Intermediary metabolism	22
II. Biosynthesis of small molecules	19
III. Macromolecule metabolism	24
IV. Cell structure	8
V. Cellular processes	18
VI. Other functions	9

[a] Excludes 20 DNA sites with no gene product and 12 genes of independent genetic elements such as prophages.

otides (294), and still others, such as the EF-Tu gene, overlap even more. The promoters for transcription of the EF-Tu gene lie hundreds of base pairs into the coding region of the upstream *fus* gene (1817). The *thdF* gene involved in thiophene oxidation overlaps several hundred bases with regulatory and structural sequences of the *tnaA* gene on the opposite strand (14).

There are only a few examples of extensively overlapping coding regions. Two open reading frames in the *cysE* locus, *cysX* and *cysE*, are coded on opposite strands and overlap (1605). Coding sequences are used more than once in the *mcrB*, *trpR*, and *dnaX* genes. The *mcrB* gene of a restriction system produces two or possibly three proteins, one of 51 to 53 kDa and one or two additional polypeptides of about 34 kDa (386, 846). The N-terminal sequences of the large protein and one small protein differ, but their C-terminal sequences are the same; therefore the gene has at least two initiation sites and produces at least two polypeptides (1824). The C-terminal portion of the *trpR* gene is translated in both the 0 and the +1 frames. The two proteins produced have identical N-terminal sequences, but a translational frameshift produces different C-terminal sequences (113). The *dnaX* gene encodes two subunits of DNA polymerase III, the gamma and tau subunits. The gamma subunit is produced by translation in a frameshift mode relative to the tau translation (1646, 1647). These few genes are densely packed with information, actually doubling up their use of coding sequences. Although the *trpR* gene seems unremarkable in composition, the *mcrB* and *dnaX* genes are not typical *E. coli* genes. The G+C content of the *mcrB* gene is low (40.3%), and that of the *dnaX* gene is high (57.7%) (1379). It seems possible that these exceptional genes were acquired by *E. coli* from foreign sources.

There is a wide range in the density of genomic information. In contrast to these examples of close-packed coding information, other parts of the genome seem to be less densely packed. Within the long section of the genome sequenced by Blattner and colleagues were sections dubbed "gray holes" that had no recognized open reading frames and no known function and were apparently unexpressed DNA (331). Yura et al., who have sequenced another long section of the genome, postulate many short open reading frames in intragenic sequences (1810). If these short open reading frames are not expressed, some of these intergenic regions could also be gray holes.

Unexpressed DNA and cryptic genes. It has been known for some time that not all of the genes in the *E. coli* genome are expressible. Some of the DNA of the genome seems to be silent, carried along from generation to generation without expression. There are cryptic operons with recognizable genes that are unable to be expressed because they lack functional promoters or harbor several mutations or an insert of genetic material that prevents normal expression. Under severe selection, the faults can be reversed and cryptic operons can become active (430, 590, 1229). These unexpressed operons, in a manner of speaking, represent a class of zero density of code usage. Why are these nonexpressed genes carried in the genome? They carry functions that are nonessential for the cell under normal circumstances, but under particular conditions that are unfavorable to the wild type, the genes can be recalled to function by rare mutations. The ability to mutate a cryptic operon to full function could be a critical survival advantage for a population of bacteria (939), making it worth harboring dormant elements in the genome until a time of need.

Optional genetic elements. Some of the genetic elements in the *E. coli* genome derive from external sources, for instance phages and plasmids, and are adventitious (not a fundamental part of the *E. coli* genome). Since some *E. coli* strains do not have prophages or plasmids, evidently the prophages are not essential to the viability of the cell, but they may be an important part of the dynamics of gene exchange and gene enrichment in populations of *E. coli*. A possible benefit from harboring prophages could be the gain of an occasional function. Some prophage genes function from their prophage locations in the *E. coli* K-12 cell, or they may be silent but require only one or two mutations to gain function. For instance, the *mcrA* methyltransferase gene resides in prophage e14 (645), as do the *pin* invertase and the *lit* membrane protein (776). These genes are expressed in *E. coli* and provide seemingly useful functions. The *rac* prophage contributes a second origin of replication for the chromosome, *oriJ*, useful if *oriC* is not functioning. Also derived from *rac* are an exonuclease gene, *recE*, and a potassium transport gene, *trkG*, which does not even seem to belong to the lambda genome yet provides a function to the *E. coli* host (1434). A lambdoid phage, qsr', contributes the *nmpC* gene, and phage PA-2 contributes the *lc* gene; these are very similar membrane protein genes (143). Another potassium transport gene, *trkK*, resides in a lambda prophage. Therefore not all of a prophage genome is silent or of no value to the bacterial genome. Some phage functions seem to be useful.

TABLE 4. Classification of *E. coli* gene products and gene descriptions

Gene description	No. of genes
Enzymes, leader peptides, enzyme activity	748
Phenotypes	314
Transport, binding proteins	221
Regulators	164
Components of cell structure	113
RNA	104
Protein factors	36
DNA sites, no gene product	20
Total	1,720

Redundancy of Genes and Gene Products

For many cellular functions of *E. coli* there are two genes, as if the genetic program of *E. coli* calls for backup systems. Redundancy or repetition might seem an example of reduced density of genetic information and an unnecessary dilution of genetic information, but in at least some cases we understand that the seemingly redundant information is regulated differently and is used for different purposes in the cell.

What sort of genes are redundant? There are many examples. For instance, there are multiple genes for most tRNAs. There are of course genes that produce similar tRNAs that carry different anticodons for a given amino acid, but there are also exact duplicate genes for some tRNAs. There are also groups and pairs of genes that code for very similar proteins. There are very similar transport proteins, DNA-binding proteins, and sensor-regulator pairs of proteins, but perhaps the simplest to list are the redundant enzymes, such as, for instance, the three fumarase isozymes. There are many pairs and groups of genes for enzymes that carry out the same or closely similar reactions. The GeneFunction data base is sorted by EC number to identify multiple genes identified with a single reaction. Among these are examples

of redundant functions. Also, the literature was consulted to find cases in which two enzymes are known but only one has been associated with a gene. The result is shown in Table 5. There are 125 gene products that group into 58 pairs or clusters whose members have identical or very similar properties. In all but two of the pairs and groups the enzymatic reactions appear to be identical. In the exceptions, there are slight differences in a pair of enzymes (one may use NAD, and the other may use NADP), but the two enzymes of a pair carry out essentially the same biochemical reaction.

For some of these redundant genes and enzymes, we know that the regulation of the genes and gene products can be different, as for the isozymes encoded by the *aroF*, *aroG*, and *aroH* genes. All three enzymes are 3-deoxy-D-arabino-heptulosonate-7-phosphate synthases, but each is sensitive to different end product metabolites that exert a feedback inhibition type of control of enzyme activity (1259). The *aroF* enzyme is sensitive to tyrosine (1722), the *aroG* enzyme is sensitive to phenylalanine (344, 345), and the *aroH* enzyme is sensitive to tryptophan (1317). The same kinds of differential sensitivities affect the synthesis and activities of aspartokinase I-homoserine dehydrogenase I, aspartokinase II-homoserine dehydrogenase II, and aspartokinase III. The activity of each enzyme is inhibited by a different one or more amino acids, and the expression of the genes is repressed by different amino acids (281). Such subtleties of control mechanisms provide a rationale of regulatory fine tuning to account for what otherwise might seem to be supernumerary copies of some genes.

Another example of filling separate needs are the genes for glycerol-3-phosphate dehydrogenase. One enzyme is made and used under aerobic conditions (encoded by *glpD*) (71), and the other enzyme is part of a membrane-bound complex that is made and used under anaerobic conditions (by *glpA*, *glpB*, and *glpC*) (282). The advantages to the cell can easily be imagined in these cases. However, there are many other cases of doubled genes for which we have no explanation at the moment. Why does *E. coli* maintain more than one gene and gene product for so many functions?

In fact, to broaden the inquiry to more than enzymes, sequence similarities have been sought on a systematic basis among all *E. coli* protein gene products (862), by using the FASTA sequence comparison program, with the result that more than 30% of the *E. coli* protein sequences entered in the SwissProt data base version 23 have at least 20% and often much higher amino acid identity with one or more partner sequences and that these partner proteins almost always have a similar or related function. Further analysis of these sequence relationships may shed light on evolutionary processes as well as on the place of redundancy in *E. coli* cell physiology.

Most of the members of pairs or groups of redundant genes and enzymes listed in Table 5 are similar to one another in nucleotide and amino acid sequence. Perhaps these genes of similar sequence are the result of a process of duplication of genes followed by some divergence of sequence but little change in function. The duplications could have taken place within an ancestor *E. coli* genome or in an ancestral enteric bacterium prior to differentiation of species, as seems to be the case for the *tufA-tufB* gene pairs in *E. coli* and *S. typhimurium* (1472).

In contrast to the instances of sequence similarity, there are a few cases of redundancy in function but dissimilarity in the sequences of the genes and their gene products. These cases could be examples either of convergent evolution or of lateral transfer of genetic material from another source. With respect to lateral transfer, there are telltale characteristics that help identify genes acquired by *E. coli* from a foreign source. One characteristic is G+C content, especially in the third position of codons; another is codon usage.

The G+C content of sequenced E. coli genes has been tabulated (1379). A small fraction of the whole have extreme values of G+C content, below 43% G+C or above 58% G+C. Some of the genes of extreme composition are prophage genes, a few cryptic genes, the Rhs elements that resemble transposons, and the *phn* operon (phosphonate utilization); these are all plausible candidates for having been acquired from a foreign source. Some of the redundant genes listed in Table 5 are also atypical in G+C content, suggesting an external source. Genes with a high G+C content are *argF* (58.7%), *gabD* (58.3%), and *alkA* (55.6%). Genes with a low G+C content are *tdcA* (42.2%) and *glpA* (45.6%).

The sequences of the *argI* and *argF* genes, coding for two ornithine transcarbamylases, have been analyzed further (1674). When the three codon positions were examined separately, the G+C content of the third positions of the codons was found to be unusually high for *E. coli* (78%), giving strong support for the proposition that this extra gene was acquired from another source, perhaps from another enteric organism. (A similar situation exists for the *phoN* gene of *S. typhimurium*, which has a higher A+T content than most *S. typhimurium* genes [571].)

Codon usage also identifies groups of genes. Medigue et al. (1058) have shown that in addition to the previously recognized two categories of codon usage that reflect low and high rates of gene expression, there is a third category. Genes that fall into this third category may be genes of foreign origin. In this category are genes of external elements such as prophages and plasmids and also genes that one can easily imagine to have been acquired by *E. coli* from outside sources, such as genes that encode surface elements of the cell and are often found in the genomes of mobile elements (1058). The following members of redundant gene pairs (Table 5) have codon usage patterns that fall into this third class: *alkA*, *tdcA*, *aroL*, *pgpA*, and *ilvM*. These genes code respectively for a second 3-methyladenine DNA glycosylase, a second threonine dehydratase, shikimate kinase II, a second phosphatidylglycerophosphate phosphatase, and one of the several acetolactate synthase isozymes. These redundant genes seem likely to have been acquired from a foreign source, particularly the *alkA* and *tdcA* genes, which are aberrant both in G+C composition and in codon usage class.

Chromosomal locations of physiologically related genes. Many years ago, the observation was made that many groups of genes whose gene products were physiologically related were positioned on the genetic map in clusters that had a tendency to lie approximately 90° or 180° apart (1831). As more data on *E. coli* genes were amassed, reexamination of the question showed that only the genes encoding the enzymes of glucose catabolism seemed to occupy positions at four equidistant loci on the circular map, a juxtaposition not likely to have arisen by chance (1832). Now that even more information is available, the map positions of the genes that were grouped in the various categories of cellular function (Table 2) were examined for any tendency to be positioned nonrandomly on the map of the genome. None of the genes within the functional groupings used in Table 2 showed any such tendency, except possibly the genes of glucose catabolism. When one looks at the placement of genes for enzymes of glycolysis, the pentose shunt, the

TABLE 5. Redundancy in the *E. coli* genome

EC no.	Gene name	Enzyme name	Reference
1.1.1.3	*metL*	Homoserine dehydrogenase II	1811
	thrA	Homoserine dehydrogenase I	1231
1.1.99.5	*glpA*	Glycerol-3-phosphate dehydrogenase	282
	glpD	Glycerol-3-phosphate dehydrogenase	71
1.2.1.2	*fdnG*	Formate dehydrogenase-N	118
	fdhF	Formate dehydrogenase-H	72
1.2.1.12	*gapA*	Glyceraldehyde 3-phosphate dehydrogenase	175
	gapB	Glyceraldehyde 3-phosphate dehydrogenase	18
1.2.1.16	*gabD*	Succinate-semialdehyde dehydrogenase(NADP)	95
1.2.1.24	*sad*	Succinate-semialdehyde dehydrogenase(NAD)	1024
1.6.6.9	*tor*	Inducible trimethylamine N oxide reductase	1494
	—[a]	Constitutive trimethylamine N oxide reductase	
1.7.99.4	*narG*	Nitrate reductase alpha subunit	144
	narZ	Nitrate reductase alpha subunit	145
1.7.99.4	*narH*	Nitrate reductase beta subunit	144
	narY	Nitrate reductase beta subunit	145
1.7.99.4	*narI*	Nitrate reductase gamma subunit	144
	narV	Nitrate reductase gamma subunit	145
1.8.1.4	*lpd*	Lipoamide dehydratase	1540
	—[a]	Lipoamide dehydratase	1335
1.10.3.-	*cydA*	Cytochrome oxidase subunit I	303
	appB	Cytochrome oxidase subunit I	337
	cyoA	Cytochrome oxidase subunit	256
1.10.3.-	*cydB*	Cytochrome oxidase subunit II	303
	appC	Cytochrome oxidase subunit II	337
	cyoB	Cytochrome oxidase subunit	256
1.11.1.6	*katE*	Catalase HP I	1690
	katG	Catalase HP II	1635
1.15.1.1	*sodA*	Superoxide dismutase (Mn)	123
	sodB	Superoxide dismutase (Fe)	220
1.18.99.1	*hyaB*	Hydrogen lyase, beta subunit	1298
	hybC	Hydrogen lyase, beta subunit	1298
	hycE	Hydrogen lyase, beta subunit	1298
2.1.1.13	*metE*	Homocysteine transmethylase, vitamin B_{12} dependent	996
2.1.1.14	*metH*	Homocysteine transmethylase	1187
2.1.1.63	*ada*	6-Methylguanine-DNA methyltransferase	1047
	ogt	6-Methylguanine-DNA methyltransferase	1025
2.1.3.3	*argF*	Ornithine carbamoyl transferase	1674
	argI	Ornithine carbamoyl transferase	114
2.3.1.41	*fabB*	3-Oxoacyl-[acyl carrier protein]synthase	793
	fabF	3-Oxoacyl-[acyl carrier protein]synthase	731
	fabH	3-Oxoacyl-[acyl carrier protein]synthase	1644
2.4.1.1	*malP*	α-Glucan phosphorylase	1808
	glgP	α-Glucan phosphorylase	263
2.4.2.1	*xapA*	Purine-nucleoside phosphorylase II	124
	deoD	Purine-nucleoside phosphorylase I	629
2.4.99.-	—[a]	Murein lytic transglycosylase (*slt-35*)	436
	slt	Murein lytic transglycosylase (*slt-70*)	435
2.5.1.6	*metK*	*S*-Adenosylmethionine synthetase	1420
	—[a]	*S*-Adenosylmethionine synthetase	1419
2.7.1.11	*pfkA*	6-Phosphofructokinase	618
	pfkB	6-Phosphofructokinase	324
2.7.1.40	*pykA*	Pyruvate kinase	1059
	pykF	Pyruvate kinase	1183
2.7.1.71	*aroK*	Shikimate kinase I	977
	aroL	Shikimate kinase II	1085
2.7.2.4	*lysC*	Aspartate kinase III	226
	metL	Aspartate kinase II	1811
	thrA	Aspartate kinase I	789
3.1.1.5	*pldC*	Lysophospholipase L_1	778
	pldB	Lysophospholipase L_2	822
3.1.3.27	*pgpA*	Phosphatidylglycerophosphate phosphatase	690
	pgpB	Phosphatidylglycerophosphate phosphatase	691
	—[a]	Phosphatidylglycerophosphate phosphatase	493
3.1.4.-	*glpQ*	Glycerophosphodiester phosphodiesterase	1628
	ugpQ	Glycerophosphodiester phosphodiesterase	
3.1.26.4	*rnhA*	RNase HI	56
	rnhB	RNase HII	720
3.2.1.23	*ebgA*	β-Galactosidase, evolved	588
	lacZ	β-Galactosidase	614
3.2.1.86	*ascB*	6-Phospho-β-glucosidase	590
	celF	6-Phospho-β-glucosidase	1229
	bglB	6-Phospho-β-glucosidase	1439
3.2.2.21	*alkA*	3-Methyladenine DNA glycosylase I	757
3.2.2.20	*tag*	3-Methyladenine DNA glycosylase II	1035
3.4.16.4	*dacA*	Penicillin-binding protein 5	1669
	dacC	Penicillin-binding protein 6	191
3.4.21.-	*clpA*	ATP-dependent protease, ATP-binding subunit	551
	clpB	ATP-dependent protease, ATP-binding subunit	1764
3.5.1.1	*ansA*	Asparaginase I	743
	ansB	Asparaginase II	154
3.6.1.-	*helD*	DNA helicase IV	1766
	rep	DNA helicase	980
	uvrD	DNA helicase II	238
3.6.1.34	*atpA*	H^+-transporting ATP synthase, alpha subunit	1411
	atpD	H^+-transporting ATP synthase, beta subunit	1411
4.1.1.15	*gadA*	Glutamate decarboxylase	1500
	gadB	Glutamate decarboxylase	1500
4.1.1.17	*speC*	Ornithine decarboxylase, constitutive	785
	speF	Ornithine decarboxylase, inducible	171
4.1.2.13	*fba*	Fructose-bisphosphate aldolase class II	17
	—[a]	Fructose-bisphosphate aldolase class I	1235
4.1.2.15	*aroF*	DAHPase[b]	1722
	aroG	DAHPase[b]	1317
	aroH	DAHPase[b]	678
4.1.3.18	*ilvBN*	Acetolacetate synthase I	484
	ilvHI	Acetolacetate synthase III	1522
	ilvGM	Acetolacetate synthase II	886
	ilvJ	Possible acetolacetate synthase IV	1350
	ilvF	Possible acetolactate synthase V	20
4.2.1.13	*sdaA*	Serine dehydratase	1563
	sdaB	Serine dehydratase	1562
4.2.1.16	*tdcAB*	Threonine dehydratase	339
	ilvA	Threonine dehydratase	1585
4.2.1.51	*pheA*	Prephenate dehydratase	1152
	tyrA	Prephenate dehydratase	1030
4.2.1.2	*fumA*	Fumarate hydratase	109
	fumB	Fumarate hydratase	1769
	fumC	Fumarate hydratase	1656
4.2.99.8	*cysK*	Cysteine synthase A	923
	cysM	Cysteine synthase B	1495
5.1.1.1	*alr*	Alanine racemase	1708
	dadX	Alanine racemase	1751
5.2.1.8	*ppiA*	Peptidylprolyl-*cis-trans*-isomerase	289
	ppiB	Peptidylprolyl-*cis-trans*-isomerase	
5.4.99.5	*pheA*	Chorismate mutase	1152
	tyrA	Chorismate mutase	1030
5.99.1.3	*parC*	DNA topoisomerase IV, subunit A	791
	gyrA	DNA gyrase, subunit A	19
	parE	DNA topoisomerase IV, subunit B	791
	gyrB	DNA gyrase, subunit B	19
6.1.1.6	*lysS*	Constitutive lysine-tRNA synthetase	917
	lysU	Inducible lysine-tRNA synthetase	274
6.3.1.1	*asnA*	Asparagine synthetase A	1144
	asnB	Asparagine synthetase B	1453
6.3.2.4	*ddlA*	D-Alanine:D-alanine ligase	1815
	ddlB	D-Alanine:D-alanine ligase	413

[a] Gene has not been identified.
[b] DAHP, 3-deoxy-D-arabino-heptulosonate-7-phosphate synthase.

Entner-Doudoroff pathway, and the tricarboxylic acid cycle, a picture still emerges of four clusters of genes at around 16, 41, 66, and 91 map units, but in addition there are genes that group around 25, 88, and 93 map units, as well as a few singlets at other positions. With data from nearly all of the genes for the pertinent enzymes now available, the picture of the arrangement of the glucose-catabolizing genes no longer conforms to a simple picture of four equidistant gene clusters. If the map positions have any meaning at all, the clustering is more complex than that. It may be that in fact the map locations are random.

EPILOG

Inevitably there are errors of fact and of omission in this compilation of data, but one hopes that they are not so extensive as to interfere with the utility of the tables and bibliography. Corrections and suggestions for improvements will be most welcome. I would be pleased to incorporate both new information and corrections into the data base.

As the sequencing projects on *E. coli* DNA proceed and characterization of all the gene products and their functions is concluded, biologists will be able to answer a good many questions about how a simple cell works. How many functions and, specifically, what kinds of functions are sufficient to genetically determine a free-living cell that is able to derive energy and synthesize its own substance from a simple, defined medium? We will also be in a better position to answer other questions. For instance, how much of the information in the *E. coli* genome is represented more than once? Are redundant genes present as backup devices to fill in if one is lost or damaged, or are the seemingly duplicate gene products different from each other in some important way such as location in the cell or specificity of regulation, so that each gene is active and the gene products are utilized for different purposes under different circumstances? Ultimately, we will be in a position to understand the workings of all the interconnected regulatory circuits that manage the expression of all the genes of *E. coli* in an orchestrated way that allows the cell to respond appropriately to changing conditions. Even after all structural genes of *E. coli* are identified and characterized, unraveling the subtleties of interconnected regulation mechanisms will be a demanding enterprise.

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