Table 18-1. The functions and mutant phenotypes of T4 gene products

Gene	A. Function of Gene Product	Size (kDa)	B. Mutant Phenotype	C. Restrictive Host or Condition
rIIA	Membrane-associated protein; affect host membrane ATPase	82.9	Rapid lysis; suppress T4 *30* and some *32* mutations	*rex*$^+$ λ lysogens; P2-like HK239 lysogen; *tabR*
60	DNA topoisomerase subunit	18.6	DNA delay; *rc* = acriflavine resistance	25°C or below
mobA	Pseudogene of Mob site-specific DNA endonuclease	4.2		Nonessential
39	DNA topoisomerase subunit; DNA-dependent ATPase; membrane-associated protein	58.0	DNA delay; *rc* = acriflavine resistance	25°C or below; synthetic lethal with T4 *49* and *17* mutations, or when host topoisomerase IV is poisoned with novobiocin
*pla*CTr5x				CTr5x
goF = *com*C-α = *go9*H	Affects mRNA metabolism	16.7	Allows T4 growth in NusD *rho* hosts	Auxiliary
cef = *m b*= *M1~motC*	Processing of T4 tRNAs	8.5		Auxiliary; CT439; *roc*$^-$ hosts
*pse*F = plaCTr5x?	5'phosphatase			Auxiliary
motB		18.2	Affects middle transcription	Auxiliary
dexA	Exonuclease A	26.0		Auxiliary; restricted on *optA*$^-$ hosts
dda = *sud*	DNA helicase; DNA-dependent ATPase	49.9	Suppress certain T4 *32* mutations	Auxiliary; synthetic lethal with T4 59 mutations
srd = *dda.2*	Postulated decoy of host σ^{70} or σS	29.0		Auxiliary
modA	Adenylribosylating enzyme	23.4	α subunits of host RNA polymerase are incompletely modified	Auxiliary
modB	Adenylribosylating enzyme	24.2		Auxiliary
srh = *modA*.5	Postulated decoy of host σ^{32}	8.1	Delays early T4 Gene Expr.ession at high temperatures	Auxiliary
mrh	Affects phosphorylation of host σ^{32}	18.5	Allows T4 growth in a σ^{32}-host	Auxiliary
soc	Small outer capsid protein	9.1	Unstable T4 capsids	Auxiliary
segF = *69*	Intron-like endonuclease. A probable fusion protein, generated from *56* and *69* by hopping of ribosomes across a pseudoknot , is larger	26.2		Nonessential
56	dCTPase; dUTPase; dCDPase; dUDPase	20.4	Little DNA synthesis; unstable DNA	Essential
oriA	several sequences in *56*, *69*, and *soc* required in *cis*; primer transcript same as transcripts for these genes		No replication from origin A	Auxiliary

dam	DNA adenine methylase	30.4	No DNA adenine methylation	Auxiliary
61 = 58	Primase; requires interaction with gp41 helicase for priming at unique sequence	39.8	DNA delay	Auxiliary; 25°C or below; synthetically lethal with T4 *49* or *17* mutations
sp = 61.3~ rIV	Periplasmic protein	11.0	Rapid lysis; suppresses *e* lysozyme mutations	Auxiliary
dmd = 61.5	Discriminator of mRNA degradation	7.0	Excessive mRNA degradation	Nonessential; suppressed by *motA* mutations
41	Replicative and recombination DNA helicase; GTPase; ATPase; dGTPase; dATPase	53.6	DNA arrest; little DNA displacement synthesis	Essential
40	Membrane-associated protein initiator of head vertex	13.3	polyheads	Auxiliary; high temperatures
uvsX = fdsA	RecA-like recombination protein; DNA-ATPase	44.0	UV- and X-ray sensitive; Recombination deficient; Suppress *49* mutations	Auxiliary
segA	Site-specific intron-like DNA endonuclease	25.3		Nonessential
β-gt	β-glucosyltransferase	40.7	No β-glucosylation of HMC DNA	Auxiliary; *Shigella*
42	dCMP hydroxymethylase	28.5	Little or no DNA synthesis	Essential
imm	Inner membrane protein	9.3	No immunity to superinfection, Membrane protein	Auxiliary
43	DNA polymerase; 3' to 5' exonuclease	103.6	No DNA synthesis; Mutator or antimutator activities of conditional lethals under semipermissive conditions	Essential; nonessential *dsd* mutants do not grow in *optA* hosts
regA	Translational repressor of several early genes	14.6	Extended synthesis of several early proteins	Auxiliary; restricted in *rpoB5081* at 42°
62	Clamp-loader subunit	21.4	No DNA synthesis	Essential
44	Clamp-loader subunit	35.8	No DNA synthesis	Essential
45	Processivity enhancing sliding clamp of DNA polymerase; and mobile enhancer of late promoters	24.9	No DNA synthesis; no late transcription	Essential
rpbA	RNA polymerase binding protein	14.7		Auxiliary
46	Recombination protein and nuclease subunit	63.6	Recombination deficient; DNA arrest; no host DNA degradation	Essential in B strains; mutants are "leaky" in some K strains
47	Recombination protein and nuclease subunit	39.2	Recombination deficient; DNA arrest; no host DNA degradation	Essential in B strains; mutants are "leaky" in some K strains
α-gt	α–glucosyl-transferase	46.7	No α glucosylation of HMC	Auxiliary
mobB	Putative site-specific intron-like DNA endonuclease	30.4		Nonessential
55	σ factor recognizing late T4 promoters	21.5	No late transcription	Essential
nrdH = 55.7	Anaerobic nucleotide reductase subunit	11.7		Auxiliary
nrdG = 55.9	Anaerobic nucleotide reductase subunit	18.2		Auxiliary
mobC = 55.10	Putative site-specific intron-like DNA endonucleasee	24.0		Auxiliary
nrdD = sunY	Anaerobic ribonucleotide reductase subunit; RNA contains a self-splicing intron	68.064		Anaerobic growth
I-Tev II	Endonuclease for *nrdD*-intron homing	30.4		Auxiliary

49	Recombination endonuclease VII	18.1	No resolution of recombination junctions; incomplete packaging of DNA; reduced heteroduplex repair, reduced DNA synthesis	Essential
49'	Internal translation initiation product	11.9		
pin	Inhibitor of host Lon protease	18.8	No degradation of amber peptides	Auxiliary
nrdC	Thioredoxin, glutaredoxin	10.1		Auxiliary
mobD	Putative site-specific DNA endonucleasee	30.5		Nonessential
rI = tk.-2	Membrane protein	11.1	No lysis inhibition	Auxiliary
tk	Thymidine kinase	21.6		Auxiliary
vs	Modifier of valyl-tRNA synthetase	13.1		Auxiliary
regB	Site-specific RNase	18.0	Misregulation of early genes	Auxiliary
denV	Endonuclease V; N-glycosidase	16.1	UV-sensitive	Auxiliary
ipII	Internal protein II	11.1--9.9		Auxiliary
ipIII	Internal protein III	21.7--20.4		Auxiliary
e	Soluble lysozyme; endolysin	18.7	No cell lysis	Essential, except when suppressed by *sp* and *5* mutations
nudE = e.1	Nudix hydrolase	17.0		Auxiliary
goF3			Allow T4 growth in *nusD rho* hosts	Auxiliary
rnaC = Species 1	Stable RNA			Auxiliary
rnaD = Species 2	Stable RNA			Auxiliary
$tRNA^{arg}$			psu_4 opal suppressor	CT439
segB	Probable site-specific intron-like DNA endonuclease	26.2		Nonessential
$tRNA^{ile}$				CT439
$tRNA^{thr}$				CT439
$tRNA^{ser}$			psu_a; psu_b; psu_1; amber suppressors	CT439
$tRNA^{pro}$				CT439
$tRNA^{gly}$				CT439
$tRNA^{leu}$			psu_3	CT439
$tRNA^{gln}$			psu_2; SB	CT439
ipI	Internal protein I	10.2--8.5		CT596
57B		17.2		?
57A	Chaperone of long and short tail fiber assembly	8.7	Defective tail fiber assembly	Essential; by-passed by certain host mutations
1	dNMP kinase	27.3	No DNA synthesis	Essential

3	Head-proximal tip of tail tube	19.7	Unstable tails	Essential
2 = 64	Protein protecting DNA ends	31.6	Noninfectious particles with filled heads	Essential, except in *recBCD* hosts
4 = 50 = 65	Head completion protein	17.6	Noninfectious particles with filled heads but tails attached at wrong angles	Essential
53	Base plate wedge component	23.0	Defective tails	Essential
5	Base plate lysozyme; hub component	63.1--44 & 19	Defective tails	Essential
oriE	*cis*-acting sequences in genes *4*, *53*, *5*; primer transcript in opposite orientation of gene *5* transcripts		No DNA replication from *oriE*	Auxiliary
repEB	Protein required for initiation from *oriE*	5.48	No DNA replication from *oriE*	Auxiliary; synthetic lethal with *motA* mutation
repEA	Protein auxiliary for initiation from *oriE*	6.13	Anomalous DNA replication from *oriE*	Auxiliary
segC	Site-specific intron-like DNA endonuclease	22.2		Nonessential
6	Base plate wedge component	74.4	Defective tails; permit plating of fiberless phage	Essential
7	Base plate wedge component	119.2	Defective tails; permit plating of fiberless phage	Essential
8	Base plate wedge component	38.0	Defective tails	Essential
9	Base plate wedge component, tail fiber socket, trigger for tail sheath contraction	31.0	No attachment of tail fibers	Essential
10	Base plate wedge component, tail pin	66.2	Defective tails	Essential
11	Base plate wedge component, tail pin, interface with short tail fibers, gp12	23.7	Defective tails	Essential
12	Short tail fibers	56.2	Defective tails	Essential
wac	Whiskers, facilitate long tail fiber attachment	51.9	No whiskers	Auxiliary
13	Head completion	34.7	Inactive, but filled heads	Essential
14	Head completion	29.6	Inactive, but filled heads	Essential
15	Proximal tail sheath stabilizer, connector to gp3 and/or gp19	31.6	Defective tails	Essential
16	Terminase subunit, binds double-stranded DNA;	18.4	Empty heads	Nearly essential
16'	Truncated C-terminal end			
17	Terminase subunit with nuclease and ATPase activity; binds ss DNA, gp16 and gp20	69.8	Empty heads	Essential
17'A	Terminase subunits with nuclease and	59.2		
17'B	ATPase activity; internal transcription and translation in frame; does not bind ssDNA	57.1		
17''	Terminase subunit with nuclease and ATPase activity (transcript processing and internal initiation of translation in frame); does not bind ssDNA. Several additional proteins most likely initiated from internal ribosome binding sites of the *17* transcripts	46.8		
18	Tail sheath monomer	71.3	Defective tails	Essential

19	Tail tube monomer	18.5	Defective tails	Essential
20	Portal vertex protein of the head	61.0	Polyheads	Essential
pip = 67	Prohead core protein; precursor to internal peptides	9.1--small peptides	Defective heads	Essential
68	Prohead core protein	15.9	Isometric heads	Essential
21	Prohead core protein and protease	23.3--small peptides,	No or defective heads	Essential
21'	Prohead core protein and protease (internal initiation of translation)	20.8--small peptides	Defective heads	
22	Prohead core protein; precursor to internal peptides	29.9--small peptides	No or faulty heads	Essential
23	Precursor of major head subunit	56.0--48.7--43	No or faulty heads; *gol* mutations in gene *23* allow growth in *lit* hosts (CTR5x)	Essential; Gol peptide together with *E. coli* Lit, cleaves host EF Tu
segD	Probable site-specific intron-like DNA endonuclease	25.6		Nonessential
24 = os	Precursor of head vertex subunit	47.0----46, 48.4?	No or faulty heads, osmotic shock resistance	Essential; by-passed by certain gene *23* mutations
rnlB = 24.1	Second RNA ligase	37.6		?
hoc = eph	Large outer capsid protein	40.4	Unstable capsids	Auxiliary
inh = lip	Minor capsid protein; inhibitor of gp21 protease	25.6		Auxiliary
segE	Probable site-specific intron-like DNA endonuclease	22.9		Nonessential
uvsW = dar	RNA-DNA- and DNA-helicase; DNA-dependent ATPase	67.5	UV-sensitive; fail to unwind R-loops; suppress T4 *59* *uvsX*, *uvsY*, and *46* mutations	Auxiliary
uvsY = fdsB	ss DNA binding, recombination and repair protein; helper of UvsX, inhibitor of endoVII	15.8	UV-sensitive; recombination-deficient; repair-deficient, DNA arrest; suppress T4 *49* mutations	Auxiliary
oriF = oriuvsY	*cis* acting sequences in genes *uvsY*, *uvsY.-1* and *uvsY.-2*; primer transcript same as *uvsY*, *uvsY.-1* and *uvsY.-2* transcript		No DNA replication from *oriF*	Auxiliary
25	Base plate wedge subunit	15.1	Defective tails	Essential
26	Base plate hub subunit	23.9	Defective tails	Essential
26'	Internal in-frame translation initiation	12		?
26''	Internal out-of-frame translation initiation	10		?
51	Base plate hub assembly catalyst?	29.3	Defective tails	Essential
27	Base plate hub subunit	44.5	Defective tails; permit plating of fiberless phage	Essential
28	Base plate distal hub subunit	17.3	Defective tails	Essential
29	Base plate hub; determinant of tail length	64.4	Defective tails	Essential

48	Base plate; tail tube associated	39.7	Defective tails	Essential
54	Base plate-tail tube initiator	35.0	Defective tails	Essential
alt	Adenosylribosyltransferase (packaged and injected with DNA)	75.8	Synthetic defective with *modA* and *modB* deletions	Auxiliary
30 = lig	DNA ligase	55.3	DNA arrest; hyper-recombination	Essential; can be by-passed by functioning host ligase, when T4 *rII* is defective
rIII	unknown	9.3	Rapid lysis	Auxiliary
31	Co-chaperonin for GroEL	12.1	Head assembly; gp23 forms lumps; T4 topoisomerase is defective	Essential
cd	dCMP deaminase	21.2		Auxiliary
pseT	Deoxyribonucleotide3'phosphatase, 5' polynucleotide kinase	34.6		Auxiliary; CTr5x (*lit*$^-$)
alc = unf	RNA polymerase- and DNA-binding protein; transcription terminator on dC-DNA	19.0	Allow transcript elongation on C-DNA; no unfolding of host nucleoid	*E. coli* (pR386)
rnlA = 63	RNA ligase; catalyst of tail fiber attachment	43.5	Defective tail fiber attachment	Auxiliary
denA	Endonuclease II that restricts dC-containing DNA	16.7	Defective in host DNA degradation	Auxiliary; restricted in *E. coli* B *rpoB5081*
nrdB	Ribonucleotide reductase β subunit (contains intron)	45.3	Reduced DNA synthesis	Auxiliary; *nrd*-defective hosts
I-TevIII	Defective intron homing endonuclease	11.3		Nonessential
mobE	Putative mobile endonuclease	16.5		Nonessential
nrdA	Ribonucleotide reductase α subunit	86	Reduced DNA synthesis	Auxiliary; *nrd*-defective hosts
td	Thymidylate synthetase (contains intron)	33.1	Reduced DNA synthesis	Auxiliary; *td*-defective hosts
I-TevI	Intron homing endonuclease	28.2		Auxiliary
frd	Dihydrofolate reductase	21.7	Reduced DNA synthesis	Auxiliary
32	ss DNA binding protein, scaffold of DNA replication, recombination and DNA- precursor-synthesizing protein machines	33.5	DNA arrest, UV-sensitive, recombination and excision repair deficient	Essential; Tab32for *ts* mutants; *32 am* mutations in ochre-suppressor-containing hosts are suppressed by *dda* mutations.
segG = 32.1	Site-specific DNA endonuclease, leading to localized gene conversion, exclusion	24.6		Auxiliary
59	Loader of gene *41* DNA helicase, ss DNA binding protein	26.0	Fail to load gp41 helicase onto recombination intermediates, or ssDNA covered with gp32 or UvsX protein; DNA arrest	Omit:Auxiliary; Almost essential
33	Protein connecting gp45 and gp55, to allow transcription by RNA polymerase from late promoters	12.8	No late RNA synthesis	Essential
dsbA	Double-stranded DNA binding protein	10.4	Facilitates some late RNA synthesis	Auxiliary
rnh = das	RNaseH; 5' to 3' DNase; yeast FEN homologue	35.6	Defective processing of Okazaki fragments; *das* mutations suppress T4 *46*, *47* and *uvsX* mutations	Auxiliary

34	Proximal tail fiber subunit	140.4	Fiberless particles	Essential
oriG = ori34	Primer transcript in opposite orientation of *34* transcript			Auxiliary
35	Tail fiber hinge	40.1	Fiberless particles	Essential
36	Small distal tail fiber subunit	23.3	Fiberless particles	Essential
37	Large distal tail fiber subunit	109.2	Fiberless particles, host range	Essential
38	Assembly catalyst of distal tail fiber	22.3	Fiberless particles	Essential
t = rV~stII	Holin, inner membrane pore protein, affects lysis timing and inhibition	25.2	Affect lysis by *e* lysozyme; suppress T4 *rII* and *63* mutations	Essential
asiA	Protein that binds to host σ^{70}, inhibits interaction with –35 regions of classical promoters, and facilitates interaction with T4 MotA protein	10.6	Defective middle mode, and (indirectly) late transcription	Almost essential
arn	Inhibitor of MrcBC restriction nuclease	10.9		Auxiliary
motA = sip	Activator of middle promoters; dsDNA binding protein specific for mot boxes	23.6	Defective middle mode transcription; suppress *rII*-defects in λ lysogens;affects interaction with σ^{70} and AsiA	Almost essential
52	DNA topoisomerase subunit; membrane-associated protein	50.6	DNA delay	Temperatures below 25°C; inhibition of host topoisomerase IV with novobiocin
ac	Membrane protein	5.5	Acriflavine resistant	Auxiliary
ama~ rs		5.4	Acriflavine resistant	Auxiliary
stp	Peptide modulating host restriction system	3.7	Suppress *pseT* mutations	Auxiliary
ndd = D2b	Protein that disrupts host nucleoid; binds to host HU	16.9	Nucleoid disruption defective	Auxiliary; CT447
pla262	Unknown			CT262
denB	Endonuclease IV, single-strand specific endonuclease	21.2	Allow progeny production of T4 with dC-DNA	Auxiliary
rIIB	Membrane-associated protein; affects host membrane ATPase	35.5	Rapid lysis; suppresses T4 *30* and some *32* mutations	rex^+ λ lysogens; P2-like HK239 lysogen*; tabR*