Reference List

1. **Adhya, S. and M. Gottesman**. 1978. Control of transcription termination. Ann. Rev. Biochem. **47**:967-996.

2. **Adhya, S., M. Gottesman, and B. De Crombrugghe**. 1974. Release of polarity in *Escherichia coli* by gene N of phage lambda: termination and antitermination of transcription. Proc. Natl. Acad. Sci. U.S.A. **71**:2534-2538.

3. **Altieri, A.S., M.J. Mazzulla, D.A. Horita, R.H. Coats, P.T. Wingfield, A. Das, D.L. Court, and R.A. Byrd**. 2000. The structure of the transcriptional antiterminator NusB from *Escherichia coli*. Nat. Struct. Biol. **7**:470-474.

4. **Antao, V.P., S.Y. Lai, and I. Tinoco Jr**. 1991. A thermodynamic study of unusually stable RNA and DNA hairpins. Nucleic Acids Res. **19**:5901-5905.

5. **Atkinson, B.L. and M.E. Gottesman**. 1992. The *Escherichia coli rpoB60* mutation blocks antitermination by coliphage HK022 Q-function. J. Mol. Biol. **227**:29-37.

6. **Banik-Maiti, S., R.A. King, and R.A. Weisberg**. 1997. The antiterminator RNA of phage HK022. J. Mol. Biol. **272**:677-687.

7. **Barik, S. and A. Das**. 1990. An analysis of the role of host factors in transcription antitermination in vitro by the Q protein of coliphage lambda. Mol. Gen. Genet. **222**:152-156.

8. **Barik, S., B. Ghosh, W. Whalen, D. Lazinski, and A. Das**. 1987. An antitermination protein engages the elongating transcription apparatus at a promoter-proximal recognition site. Cell **50**:885-899.

9. **Borukhov, S., V. Sagitov, and A. Goldfarb**. 1993. Transcript cleavage factors from *E. coli*. Cell **72**:459-466.

10. **Brennan, C.A., A.J. Dombroski, and T. Platt**. 1987. Transcription termination factor rho is an RNA-DNA helicase. Cell **48**:945-952.

11. **Burns, C.M., L.V. Richardson, and J.P. Richardson**. 1998. Combinatorial effects of NusA and NusG on transcription elongation and Rho-dependent termination in *Escherichia coli*. J. Mol. Biol. **278**:307-316.

12. **Burova, E. and M.E. Gottesman**. 1995. NusG overexpression inhibits Rho-dependent termination in *Escherichia coli*. Mol. Microbiol. **17**:633-641.

13. **Bycroft, M., T.J.P. Hubbard, M. Proctor, S.M.V. Freund, and A.G. Murzin**. 1997. The solution structure of the S1 RNA binding domain: A member of an ancient nucleic acid-binding fold. Cell **88**:235-242.

14. **Cai, Z., A. Gorin, R. Frederick, X. Ye, W. Hu, A. Majumdar, A. Kettani, and D.J. Patel**. 1998. Solution structure of P22 transcriptional antitermination N peptide-boxB RNA complex. Nat. Struct. Biol. **5**:203-212.

15. **Campbell, A.M.** 1961. Sensitive mutants of bacteriophage lambda. Virology **14**:22-32.

16. **Chan, C.L. and R. Landick**. 1989. The *Salmonella typhimurium* his operon leader region contains an RNA hairpin-dependent transcription pause site. Mechanistic implications of the effect on pausing of altered RNA hairpins. J. Biol. Chem. **264**:20796-20804.

17. **Chan, C.L. and R. Landick**. 1993. Dissection of the his leader pause site by base substitution reveals a multipartite signal that includes a pause RNA hairpin. J. Mol. Biol. **233**:25-42.

18. **Chattopadhyay, S., J. Garcia-Mena, J. DeVito, K. Wolska, and A. Das**. 1995. Bipartite function of a small RNA hairpin in transcription antitermination in bacteriophage lambda. Proc. Natl. Acad. Sci. USA **92**:4061-4065.

19. **Chattopadhyay, S., S.C. Hung, A.C. Stuart, A.G. Palmer 3rd, J. Garcia-Mena, A. Das, and M.E. Gottesman**. 1995. Interaction between the phage HK022 Nun protein and the nut RNA of phage lambda. Proc. Natl. Acad. Sci. USA **92**:12131-12135.

20. **Chou, S.H., L. Zhu, and B.R. Reid**. 1997. Sheared purine x purine pairing in biology. J .Mol. Biol. **267**:1055-1067.

21. **Cilley, C.D. and J.R. Williamson**. 1997. Analysis of bacteriophage N protein and peptide binding to boxB RNA using polyacrylamide gel coelectrophoresis (PACE). RNA. **3**:57-67.

22. **Clerget, M., D.J. Jin, and R.A. Weisberg**. 1995. A zinc-binding region in the β' subunit of RNA polymerase is involved in antitermination of early transcription of phage HK022. J. Mol. Biol. **248**:768-780.

23. **Conaway, J.W., A. Shilatifard, A. Dvir, and R.C. Conaway**. 2000. Control of elongation by RNA polymerase II. Trends in Biochem. Sci. **25**:375-80.

24. **Court, D.** 1993. RNA Processing and Degradation by RNase III, p. 71-116. In G. Brawerman and J. Belasco (eds.), Control of mRNA Stability. Academic Press, New York.

25. **Court, D.L., T.A. Patterson, N. Baker, N. Costantino, C. Mao, and D.I. Friedman**. 1995. Structural and functional analysis of the transcription-translation proteins NusB and NusE. J. Bacteriol. **177**:2589-2591.

26. **Craven, M.G. and D.I. Friedman**. 1991. Analysis of the *Escherichia coli nusA10* (Cs)

allele: relating nucleotide changes to phenotypes. J. Bacteriol. **173**:1485-1491.

27. **Craven, M.G., A.E. Granston, A.T. Schauer, C. Zheng, T.A. Gray, and D.I. Friedman**. 1994. *Escherichia coli-Salmonella typhimurium* hybrid *nusA* genes: Identification of a short motif required for action of the λ N transcription antitermination protein. J. Bacteriol. **176**:1394-1404.

28. **Dambly, C., M. Couturier, and R. Thomas**. 1968. Control of development in temperate bacteriophages. II. Control of lysozyme synthesis. J. Mol. Biol. **32**:67-81.

29. **Das, A.** 1992. How the phage lambda N gene product suppresses transcription termination: communication of RNA polymerase with regulatory proteins mediated by signals in nascent RNA. J. Bacteriol. **174**:6711-6716.

30. **Das, A.** 1993. Control of transcription termination by RNA-binding proteins. Ann. Rev. Biochem. **63**:893-930.

31. **Das, A., S. Barik, B. Ghosh, and W. Whalen**. 1996. Immunoprinting: a technique used to study dynamic protein-nucleic acid interactions within transcription elongation complex. Methods Enzymol. **274**:363-374.

32. **Das, A., M.E. Gottesman, J. Wardwell, P. Trisler, and S. Gottesman**. 1983. A mutation in the *Escherichia coli* rho gene that inhibits the N protein activity of phage lambda. Proc. Natl. Acad. Sci. U.S.A. **80**:5530-5534.

33. **Das, A., M. Pal, J.G. Mena, W. Whalen, K. Wolska, R. Crossley, W. Rees, P.H. von Hippel, N. Costantino, D. Court, M. Mazzulla, A.S. Altieri, R.A. Byrd, S. Chattopadhyay, J. DeVito, and B. Ghosh**. 1996. Components of multiprotein-RNA complex that controls transcription elongation in Escherichia coli phage lambda. Methods in Enzymology **274**:374-402.

34. **Das, A. and K. Wolska**. 1984. Transcription antitermination in vitro by lambda N gene

product: requirement for a phage nut site and the products of host *nusA*, *nusB*, and *nusE* genes. Cell **38**:165-173.

35. **Dasgupta, S., L. Fernandez, L. Kameyama, T. Inada, Y. Nakamura, A. Pappas, and D.L. Court**. 1998. Genetic uncoupling of the dsRNA-binding and RNA cleavage activities of the *Escherichia coli* endoribonuclease RNase III--the effect of dsRNA binding on gene expression. Mol. Microbiol. **28**:629-660.

36. **De Crombrugghe, B., M. Mudryj, R. DiLauro, and M. Gottesman**. 1979. Specificity of the bacteriophage lambda N gene product (pN): nut sequences are necessary and sufficient for antitermination by pN. Cell **18**:1145-1151.

37. **DeVito, J. and A. Das**. 1994. Control of transcription processivity in phage lambda: Nus factors strengthen the termination-resistant state of RNA polymerase induced by N antiterminator. Proc. Natl. Acad. Sci. U.S.A. **91**:8660-8664.

38. **Doelling, J.H. and N.C. Franklin**. 1989. Effects of all single base substitutions in the loop of boxB on antitermination of transcription by bacteriophage lambda's N protein. Nucleic Acids Res. **17**:5565-5577.

39. **Dove, W.F.** 1966. Action of the lambda chromosome. I. Control of functions late in bacteriophage development. J. Mol. Biol. **19**:187-201.

40. **Echols, H., D. Court, and L. Green**. 1976. On the nature of cis-acting regulatory proteins and genetic organization in bacteriophage: the example of gene Q of bacteriophage lambda. Genetics. **83**:5-10.

41. **Faber, C., M. Scharpf, T. Becker, H. Sticht, and P. Rosch**. 2001. The structure of the coliphage HK022 Nun protein-lambda-phage boxB RNA complex. Implications for the mechanism of transcription termination. J. Biol. Chem. **276**:32064-32070.

42. **Farnham, P.J., J. Greenblatt, and T. Platt**. 1982. Effects of NusA protein on

transcription termination in the tryptophan operon of *Escherichia coli*. Cell **29**:945-951.

43. **Forbes, D. and I. Herskowitz**. 1982. Polarity suppression by the Q gene product of bacteriophage lambda. J. Mol. Biol. **160**:549-569.

44. **Franklin, N.C.** 1985. Conservation of genome form but not sequence in the transcription antitermination determinants of bacteriophages lambda, phi 21 and P22. J. Mol. Biol. **181**:75-84.

45. **Franklin, N.C.** 1993. Clustered arginine residues of bacteriophage lambda N protein are essential to antitermination of transcription, but their locale cannot compensate for *boxB* loop defects. J. Mol. Biol. **231** :343-360.

46. **Franklin, N.C. and G.N. Bennett**. 1979. The N protein of bacteriophage lambda, defined by its DNA sequence, is highly basic. Gene. **8**:107-119.

47. **Franklin, N.C. and J.H. Doelling**. 1989. Overexpression of N antitermination proteins of bacteriophages lambda, 21, and P22: loss of N protein specificity. J. Bacteriol. **171**:2513-2522.

48. **Friedman, D.I.** 1988. Regulation of Phage Gene Expression by Termination and Antitermination of Transcription, p. 263-319. In Calendar R. (ed.), The Bacteriophage Vol. 2. Plenum Publishing Corporation, New York.

49. **Friedman, D.I., M. Baumann, and L.S. Baron**. 1976. Cooperative effects of bacterial mutations affecting lambda N gene expression. I. Isolation and characterization of a *nusB* mutant. Virology. **73**:119-127.

50. **Friedman, D.I. and D.L. Court**. 1995. Transcription antitermination: the lambda paradigm updated. Mol. Microbiol. **18**:191-200.

51. **Friedman, D.I. and D.L. Court**. 2001. Bacteriophage lambda: alive and well and still doing its thing. Curr. Opin. Microbiol. **4**:201-207.

52. **Friedman, D.I. and M. Gottesman**. 1983. Lytic Mode of Lambda Development, p. 21-51. In R.W. Hendrix, J.W. Roberts, F.W. Stahl, and R.A. Weisberg (eds.), Lambda II. Cold Spring Harbor Laboratory, New York.

53. **Friedman, D.I. and E.R. Olson**. 1983. Evidence that a nucleotide sequence, "boxA," is involved in the action of the NusA protein. Cell **34**:143-149.

54. **Friedman, D.I., E.R. Olson, C. Georgopoulos, K. Tilly, I. Herskowitz, and F. Banuett**. 1984. Interactions of bacteriophage and host macromolecules in the growth of bacteriophage lambda. Microbiol. Rev. **48**:299-325.

55. **Friedman, D.I., E.R. Olson, L.L. Johnson, D. Alessi, and M.G. Craven**. 1990. Transcription-dependent competition for a host factor: the function and optimal sequence of the phage lambda *boxA* transcription antitermination signal. Genes & Dev. **4**:2210-2222.

56. **Friedman, D.I., A.T. Schauer, M.R. Baumann, L.S. Baron, and S.L. Adhya**. 1981. Evidence that ribosomal protein S10 participates in control of transcription termination. Proc. Natl. Acad. Sci. U.S.A. **78**:1115-1118.

57. **Ghosh, B. and A. Das**. 1984. nusB: a protein factor necessary for transcription antitermination in vitro by phage lambda N gene product. Proc. Natl. Acad. Sci. U.S.A. **81**:6305-6309.

58. **Ghosh, B., E. Grzadzielska, P. Bhattacharya, E. Peralta, J. DeVito, and A. Das**. 1991. Specificity of antitermination mechanisms. Suppression of the terminator cluster T1-T2 of *Escherichia coli* ribosomal RNA operon, *rrnB*, by phage lambda antiterminators. J. Mol. Biol. **222**:59-66.

59. **Ghysen, A. and M. Pironio**. 1972. Relationship between the N function of bacteriophage lambda and host RNA polymerase. J. Mol. Biol. **65**:259-272.

60. **Gibson, T.J., J.D. Thompson, and J. Heringa**. 1993. The KH domain occurs in a diverse set of RNA-binding proteins that include the antiterminator NusA and is probably involved in binding to nucleic acid. FEBS Lett. **324**:361-366.

61. **Gill, S.C., S.E. Weitzel, and P.H. von Hippel**. 1991. *Escherichia coli* sigma 70 and NusA proteins. I. Binding interactions with core RNA polymerase in solution and within the transcription complex. J. Mol. Biol. **220**:307-324.

62. **Gill, S.C., T.D. Yager, and P.H. von Hippel**. 1991. *Escherichia coli* sigma 70 and NusA proteins. II. Physical properties and self-association states. J. Mol. Biol. **220**:325-333.

63. **Goda, Y. and J. Greenblatt**. 1985. Efficient modification of *E. coli* RNA polymerase in vitro by the N gene transcription antitermination protein of bacteriophage lambda. Nucleic Acids Res. **13**:2569-2582.

64. **Gopal, B., L.F. Haire, R.A. Cox, M. Jo Colston, S. Major, J.A. Brannigan, S.J. Smerdon, and G. Dodson**. 2000. The crystal structure of NusB from Mycobacterium tuberculosis. Nat. Struct. Biol. **7**:475-478.

65. **Gopal, B., L.F. Haire, S.J. Gamblin, E.J. Dodson, A.N. Lane, K.G. Papavinasasundaram, M.J. Colston, and G. Dodson**. 2001. Crystal structure of the transcription elongation/anti-termination factor NusA from Mycobacterium tuberculosis at 1.7 A resolution. J. Mol. Bio. **314**:1087-1095.

66. **Gopal, B., K.G. Papavinasasundaram, G. Dodson, M.J. Colston, S.A. Major, and A.N. Lane**. 2001. Spectroscopic and thermodynamic characterization of the transcription antitermination factor NusE and its interaction with NusB from

Mycobacterium tuberculosis. Biochemistry **40**:920-928.

67. **Gottesman, M.E. and R.A. Weisberg**. 1995. Termination and antitermination of transcription in temperate bacteriophage. Seminars in Virol. **6**:35-42.

68. **Gottesman, S., M. Gottesman, J.E. Shaw, and M.L. Pearson**. 1981. Protein degradation in *E. coli*: the lon mutation and bacteriophage lambda N and cll protein stability. Cell **24**:225-233.

69. **Grayhack, E.J., X.J. Yang, L.F. Lau, and J.W. Roberts**. 1985. Phage lambda gene Q antiterminator recognizes RNA polymerase near the promoter and accelerates it through a pause site. Cell **42**:259-269.

70. **Greenblatt, J.** 1992. Protein-protein interactions as critical determinants of regulated initiation and termination of transcription, p. 203-226. In S.L. McKnight and K.R. Yamamoto (eds.), Transcriptional Regulation. Cold Spring Harbor Laboratories, Cold Spring Harbor, N.Y.

71. **Greenblatt, J. and J. Li**. 1981. Interaction of the sigma factor and the *nusA* gene protein of *E. coli* with RNA polymerase in the initiation-termination cycle of transcription. Cell **24** :421-428.

72. **Greenblatt, J. and J. Li**. 1982. Properties of the N gene transcription antitermination protein of bacteriophage lambda. J. Biol. Chem. **257**:362-365.

73. **Greenblatt, J., T.F. Mah, P. Legault, J. Mogridge, J. Li, and L.E. Kay**. 1998. Structure and mechanism in transcriptional antitermination by the bacteriophage lambda N protein. Cold Spring Harb. Symp. Quant. Biol. **LXIII**:327-336.

74. **Greenblatt, J., J.R. Nodwell, and S.W. Mason**. 1993. Transcriptional antitermination. Nature **364**:401-406.

75. **Gross, C.A., C. Chan, A. Dombroski, T. Gruber, M. Sharp, J. Tupy, and B. Young**. 1998. The functional and regulatory roles of sigma factors in transcription. Cold Spring Harb. Symp. Quant. Biol. **LXIII**:141-155.

76. **Gusarov, I. and E. Nudler**. 2001. Control of intrinsic transcription termination by N and NusA: the basic mechanisms. Cell **107**:437-449.

77. **Henthorn, K.S. and D.I. Friedman**. 1996. Identification of functional regions of the Nun transcription termination protein of phage HK022 and the N antitermination protein of phage gamma using hybrid *nun-N* genes. J. Mol. Biol. **257**:9-20.

78. **Herskowitz, I. and D. Hagen** . 1980. The lysis-lysogeny decision of phage lambda: explicit programming and responsiveness. Ann. Rev. Genet. **14**:399-445.

79. **Heus, H.A. and A. Pardi**. 1991. Structural features that give rise to the unusual stability of RNA hairpins containing GNRA loops. Science **253**:191-194.

80. **Hilliker, S. and D. Botstein**. 1975. An early regulatory gene of *Salmonella* phage P22 analogous to gene N of coliphage lambda. Virology **68**:510-524.

81. **Horwitz, R.J., J. Li, and J. Greenblatt**. 1987. An elongation control particle containing the N gene transcriptional antitermination protein of bacteriophage lambda. Cell **51**:631-641.

82. **Huang, A., J. Friesen, and J.L. Brunton**. 1987. Characterization of a bacteriophage that carries the genes for production of Shiga-like toxin I in *Escherichia coli*. J. Bacteriol. **169**:4308-4312.

83. **Hung, S.C. and M.E. Gottesman**. 1995. Phage HK022 Nun protein arrests transcription on phage λ DNA in vitro and competes with the phage λ N antitermination protein. J. Mol. Biol. **247**:428-442.

84. **Hung, S.C. and M.E. Gottesman**. 1997. The Nun protein of bacteriophage HK022 inhibits translocation of *Escherichia coli* RNA polymerase without abolishing its catalytic activities. Genes & Dev. **11**:2670-2678.

85. **Ito, K. and Y. Nakamura**. 1993. Pleiotropic effects of the *rpoC10* mutation affecting the RNA polymerase beta' subunit of *Escherichia coli* on factor-dependent transcription termination and antitermination. Mol. Microbiol. **9**:285-293.

86. **Jin, D.J., M. Cashel, D.I. Friedman, Y. Nakamura, W.A. Walter, and C.A. Gross**. 1988. Effects of rifampicin resistant *rpoB* mutations on antitermination and interaction with nusA in *Escherichia coli*. J. Mol. Biol. **204**:247-261.

87. **Joyner, A., L.N. Isaacs, H. Echols, and W.S. Sly**. 1966. DNA replication and messenger RNA production after induction of wild-type lambda bacteriophage and lambda mutants. J. Mol. Biol. **19**:174-186.

88. **Juhala, R.J., M.E. Ford, R.L. Duda, A. Youlton, G.F. Hatfull, and R.W. Hendrix**. 2000. Genomic sequences of bacteriophages HK97 and HK022: Pervasive mosaicism in the Lambdoid phages. J. Mol. Biol. **299**:27-51.

89. **Kainz, M. and J. Roberts**. 1992. Structure of transcription elongation complexes in vivo. Science **255**:838-841.

90. **Kameyama, L., L. Fernandez, D.L. Court, and G. Guarneros**. 1991. RNaselll activation of bacteriophage lambda N synthesis. Mol. Microbiol. **5**:2953-2963.

91. **Keppel, F., C.P. Georgopoulos, and H. Eisen**. 1974. Host interference with expression of the lambda N gene product. Biochimie. **56**:1505-1509.

92. **King, R.A., S. Banik-Maiti, D.J. Jin, and R.A. Weisberg**. 1996. Transcripts that increase the processivity and elongation rate of RNA polymerase. Cell **87**:893-903.

93. **King, R.A., P.L. Madsen, and R.A. Weisberg**. 2000. Constitutive expression of a transcription termination factor by a repressed prophage: promoters for transcribing the phage HK022 *nun* gene. J. Bacteriol. **182**:456-462.

94. **Ko, D.C., M.T. Marr, J. Guo, and J.W. Roberts**. 1998. A surface of *Escherichia coli* sigma 70 required for promoter function and antitermination by phage lambda Q protein. Genes & Dev. **12**:3276-3285.

95. **Komissarova, N. and M. Kashlev**. 1997. RNA polymerase switches between inactivated and activated states By translocating back and forth along the DNA and the RNA. J. Biol. Chem. **272**:15329-15338.

96. **Korzheva, N., A. Mustaev, E. Nudler, V. Nikiforov, and A. Goldfarb**. 1998. Mechanistic model of the elongation complex of *Escherichia coli* RNA polymerase. Cold Spring Harb. Sym. Quant. Biol. **LXIII**:337-435.

97. **Landick, R.** 1997. RNA polymerase slides home: pause and termination site recognition. Cell **88**:741-744.

98. **Lau, L.F. and J.W. Roberts**. 1985. Rho-dependent transcription termination at lambda tR1 requires upstream sequences. J. Biol. Chem. **260**:574-584.

99. **Lazinski, D., E. Grzadzielska, and A. Das**. 1989. Sequence-specific recognition of RNA hairpins by bacteriophage antiterminators requires a conserved arginine-rich motif. Cell **59**:207-218.

100. **Lecocq, J. and C. Dambly**. 1976. A bacterial RNA polymerase mutant that renders lambda growth independent of the N and *cro* functions at 42 degrees C. Mol. Gen. Genet. **145**:53-64.

101. **Legault, P., J. Li, J. Mogridge, L.E. Kay, and J. Greenblatt**. 1998. NMR structure of the bacteriophage lambda N peptide/boxB RNA complex: recognition of a GNRA

fold by an arginine-rich motif. Cell **93**:289-299.

102. **Lew, K. and S. Casjens**. 1975. Identification of early proteins coded by bacteriophage P22. Virology **68**:525-533.

103. **Li, J., R. Horwitz, S. McCracken, and J. Greenblatt**. 1992. NusG, a new *Escherichia coli* elongation factor involved in transcriptional antitermination by the N protein of phage lambda. J. Biol. Chem. **267**:6012-6019.

104. **Li, J., S.W. Mason, and J. Greenblatt**. 1993. Elongation factor NusG interacts with termination factor rho to regulate termination and antitermination of transcription. Genes & Dev. **7**:161-172.

105. **Liu, K. and M.M. Hanna**. 1995. NusA interferes with interactions between the nascent RNA and the C-terminal domain of the alpha subunit of RNA polymerase in *Escherichia coli* transcription complexes. Proc. Natl. Acad. Sci. USA **92**:5012-5016.

106. **Liu, K., Y. Zhang, K. Severinov, A. Das, and M.M. Hannah**. 1996. Role of *Escherichia coli* RNA polymerase alpha subunit in modulation of pausing, termination and antitermination by the transcription elongation factor NusA. EMBO J. **15**:150-161.

107. **Lozeron, H.A., J.E. Dahlberg, and W. Szybalski**. 1976. Processing of the major leftward mRNA of coliphage lambda. Virology **71**:262-277.

108. **Luttgen, H., R. Robelek, R. Muhlberger, T. Diercks, S.C. Schuster, P. Kohler, H. Kessler, A. Bacher, and G. Richter**. 2002. Transcriptional Regulation by Antitermination. Interaction of RNA with NusB Protein and NusB/NusE Protein Complex of *Escherichia coli*. J. Mol. Biol. **316**:875-885.

109. **Mah, T.F., J. Li, A.R. Davidson, and J. Greenblatt**. 1999. Functional importance of

regions in *Escherichia coli* elongation factor NusA that interact with RNA polymerase, the bacteriophage lambda N protein and RNA. Mol. Microbiol. **34**:523-537.

110. **Marr, M.T., S.A. Datwyler, C.F. Meares, and J.W. Roberts**. 2001. Restructuring of an RNA polymerase holoenzyme elongation complex by lambdoid phage Q proteins. Proc. Natl. Acad. Sci. U S A **98**:8972-8978.

111. **Marr, M.T. and J.W. Roberts**. 2000. Function of transcription cleavage factors GreA and GreB at a regulatory pause site. Mol. Cell **6**:1275-1285.

112. **Mason, S.W., J. Li, and J. Greenblatt**. 1992. Direct interaction between two *Escherichia coli* transcription antitermination factors, NusB and ribosomal protein S10. J. Mol. Biol. **223**:55-66.

113. **Mason, S.W., J. Li, and J. Greenblatt**. 1992. Host factor requirements for processive antitermination of transcription and suppression of pausing by the N protein of bacteriophage lambda. J. Biol. Chem. **267**:19418-19426.

114. **Mogridge, J., P. Legault, J. Li, M.D. Van Oene, L.E. Kay, and J. Greenblatt**. 1998. Independent ligand-induced folding of the RNA-binding domain and two functionally distinct antitermination regions in the phage lambda N protein. Mol. Cell **1**:265-275.

115. **Mogridge, J., T.-F. Mah, and J. Greenblatt**. 1995. A protein-RNA interaction network facilitates the template-independent cooperative assembly on RNA polymerase of a stable antitermination complex containing the λ N protein. Genes & Dev. **9**:2831-2844.

116. **Mogridge, J., T.F. Mah, and J. Greenblatt**. 1998. Involvement of boxA nucleotides in the formation of a stable ribonucleoprotein complex containing the bacteriophage

lambda N protein. J. Biol. Chem. **273**:4143-4148.

117. **Mooney, R.A., I. Artsimovitch, and R. Landick**. 1998. Information processing by RNA polymerase: recognition of regulatory signals during RNA chain elongation. J. Bacteriol. **180**:3265-3275.

118. **Nakamura, Y., S. Mizusawa, A. Tsugawa, and M. Imai**. 1986. Conditionally lethal *nusAts* mutation of *Escherichia coli* reduces transcription termination but does not affect antitermination of bacteriophage lambda. Mol. Gen. Genet. **204**:24-28.

119. **Neely, M.N. and D.I. Friedman**. 1998. Functional and genetic analysis of regulatory regions of coliphage H-19B: location of shiga-like toxin and lysis genes suggest a role for phage functions in toxin release. Mol. Microbiol. **28**:1255-1267.

120. **Neely, M.N. and D.I. Friedman**. 2000. N-mediated transcription antitermination in Lambdoid phage H-19B is characterized by alternative NUT RNA structures and a reduced requirement for host factors. Mol. Microbiol. **38**:1074-1085.

121. **Nehrke, K.W. and T. Platt**. 1994. A quaternary transcription termination complex. Reciprocal stabilization by Rho factor and NusG protein. J. Mol. Biol. **243**:830-839.

122. **Nodwell, J.R. and J. Greenblatt**. 1993. Recognition of boxA antiterminator RNA by the *E. coli* antitermination factors NusB and ribosomal protein S10. Cell **72**:261-268.

123. **Nudler, E.** 1999. Transcription elongation: structural basis and mechanisms. J. Mol. Biol. **288**:1-12.

124. **Oberto, J., M. Clerget, M. Ditto, K. Cam, and R.A. Weisberg**. 1993. Antitermination of early transcription in phage HK022. Absence of a phage-encoded antitermination factor. J. Mol. Biol. **229**:368-381.

125. **Obuchowski, M., A. Wegrzyn, A. Szalewska-Palasz, M.S. Thomas, and G. Wegrzyn**. 1997. An RNA polymerase alpha subunit mutant impairs N-dependent transcriptional antitermination in *Escherichia coli*. Mol. Microbiol. **23**:211-22.

126. **Olson, E.R., E.L. Flamm, and D.I. Friedman**. 1982. Analysis of *nutR*: a region of phage lambda required for antitermination of transcription. Cell **31**:61-70.

127. **Olson, E.R., C.S. Tomich, and D.I. Friedman**. 1984. The *nusA* recognition site. Alteration in its sequence or position relative to upstream translation interferes with the action of the N antitermination function of phage lambda. J. Mol. Biol. **180**:1053-1063.

128. **Pasman, Z. and P.H. von Hippel**. 2000. Regulation of rho-dependent transcription termination by NusG is specific to the *Escherichia coli* elongation complex. Biochemistry **39**:5573-5585.

129. **Patterson, T.A., Z. Zhang, T. Baker, L.L. Johnson, D.I. Friedman, and D.L. Court**. 1994. Bacteriophage lambda N-dependent transcription antitermination. Competition for an RNA site may regulate antitermination. J. Mol. Biol. **236**:217-228.

130. **Plunkett, G. 3rd, D.J. Rose, T.J. Durfee, and F.R. Blattner**. 1999. Sequence of Shiga toxin 2 phage 933W from *Escherichia coli* O157:H7: Shiga toxin as a phage late-gene product. J. Bacteriol. **181**:1767-1778.

131. **Ptashne, M.** 1992. A Genetic Switch (second edition). Cell Press, Blackwell Scientific Publications, Cambridge, Mass.

132. **Rees, W.A., S.E. Weitzel, T.D. Yager, A. Das, and P.H. von Hippel**. 1996. Bacteriophage lambda N protein alone can induce transcription antitermination in vitro. Proc. Natl. Acad Sci. U.S.A **93**:342-346.

133. **Richardson, J.P. and J. Greenblatt**. 1996. Control of RNA chain elongation and termination, p. 822-848. In F.C. Neidhardt (ed.), *Escherichia coli* and *Salmonella*: Cellular and Molecular Biology. American Society for Microbiology, Washington, D.C.

134. **Ring, B.Z. and J.W. Roberts**. 1994. Function of a nontranscribed DNA strand site in transcription elongation. Cell **78**:317-324.

135. **Ring, B.Z., W.S. Yarnell, and J.W. Roberts**. 1996. Function of E. coli RNA polymerase sigma factor sigma 70 in promoter-proximal pausing. Cell **86**:485-493.

136. **Robert, J., S.B. Sloan, R.A. Weisberg, M.E. Gottesman, R. Robledo, and D. Harbrecht**. 1987. The remarkable specificity of a new transcription termination factor suggests that the mechanisms of termination and antitermination are similar. Cell **51**:483-492.

137. **Roberts, J.** 1992. Antitermination and the control of transcription elongation, p. 389-406. In S.L. McKnight and K.R. Yamamoto (eds.), Transcription Regulation. Cold Spring Harbor Laboratory, Cold Spring Harbor N.Y.

138. **Roberts, J.W.** 1969. Termination factor for RNA synthesis. Nature **224**:1168-1174.

139. **Roberts, J.W.** 1975. Transcription termination and late control in phage lambda. Proc. Natl. Acad. Sci. U.S.A. **72**:3300-3304.

140. **Roberts, J.W.** 1976. Transcription termination and its control in *E. coli*, p. 247-271. In R. Losick and M. Chamberlin (eds.), RNA Polymerase. Cold Spring Harbor Laboratories, Cold Spring Harbor, N.Y.

141. **Roberts, J.W.** 1993. RNA and protein elements of E. coli and lambda transcription antitermination complexes. Cell **72**:653-655.

142. **Roberts, J.W., C.W. Roberts, S. Hilliker, and D. Botstein**. 1976. Transcription Termination and Regulation in Bacteriophages P22 and Lambda, p. 707-718. In R. Losick and M. Chamberlin (eds.), RNA Polymerase. Cold Spring Harbor Laboratories, Cold Spring Harbor, N.Y.

143. **Roberts, J.W., W. Yarnell, E. Bartlett, J. Guo, M. Marr, D.C. Ko, H. Sun, and C.W. Roberts**. 1998. Antitermination by bacteriophage Lambda Q protein. Cold Spring Harb. Symp. Quant. Biol. **LXIII**:319-325.

144. **Robledo, R., B.L. Atkinson, and M.E. Gottesman**. 1991. *Escherichia coli* mutations that block transcription termination by phage HK022 Nun protein. J. Mol. Biol. **220**:613-619.

145. **Robledo, R., M.E. Gottesman, and R.A. Weisberg**. 1990. λ nutR mutations convert HKO22 Nun protein from a transcription termination factor to a suppressor of termination. J. Mol. Biol. **212**:635-643.

146. **Rosenberg, M., D. Court, H. Shimatake, C. Brady, and D.L. Wulff**. 1978. The relationship between function and DNA sequence in an intercistronic regulatory region in phage lambda. Nature **272**:414-423.

147. **Ruteshouser, E.C. and J.P. Richardson**. 1989. Identification and characterization of transcription termination sites in the *Escherichia coli lacZ* gene. J. Mol. Biol. **208**:23-43.

148. **Salstrom, J.S. and W. Szybalski**. 1978. Coliphage lambda nutL-: a unique class of mutants defective in the site of gene N product utilization for antitermination of leftward transcription. J. Mol. Biol. **124**:195-221.

149. **Scharpf, M., H. Sticht, K. Schweimer, M. Boehm, S. Hoffmann, and P. Rosch**. 2000. Antitermination in bacteriophage lambda. The structure of the N36 peptide-boxB

RNA complex. Eur. J. Biochem. **267**:2397-2408.

150. **Schauer, A.T., D.L. Carver, B. Bigelow, L.S. Baron, and D.I. Friedman**. 1987. Lambda N antitermination system: functional analysis of phage interactions with the host NusA protein. J. Mol. Biol. **194**:679-690.

151. **Schauer, A.T., S.C. Cheng, C. Zheng, L. St.Pierre, D. Alessi, D.L. Hidayetoglu, N. Costantino, D.L. Court, and D.I. Friedman**. 1996. The alpha subunit of RNA polymerase and transcription antitermination. Mol. Microbiol. **21**:839-851.

152. **Sen, R., R.A. King, N. Mzhavia, P.L. Madsen, and R.A. Weisberg**. submitted. Sequence specific interaction of nascent antitermination RNA with the zinc finger motif of *E. coli* RNA polymerase.

153. **Sen, R., R.A. King, and R.A. Weisberg**. 2001. Modification of the properties of elongating RNA polymerase by persistent association with nascent antiterminator RNA. Mol. Cell. **7**:993-1001.

154. **Sharrock, R.A., R.L. Gourse, and M. Nomura**. 1985. Defective antitermination of rRNA transcription and derepression of rRNA and tRNA synthesis in the *nusB5* mutant of *Escherichia coli*. Proc. Natl. Acad. Sci. U.S.A. **82**:5275-5279.

155. **Sidorenkov, I., N. Komissarova, and M. Kashlev**. 1998. Crucial role of the RNA:DNA hybrid in the processivity of transcription. Mol. Cell **2**:55-64.

156. **Sigmund, C.D. and E.A. Morgan**. 1988. NusA protein affects transcriptional pausing and termination in vitro by binding to different sites on the transcription complex. Biochem. **27**:5622-5627.

157. **Sloan, S.B. and R.A. Weisberg**. 1993. Use of a gene encoding a suppressor tRNA as a reporter of transcription: analyzing the action of the Nun protein of bacteriophage HK022. Proc. Natl. Acad. Sci. U.S.A. **90**:9842-9846.

158. **Smith, H.W., P. Green, and Z. Parsell**. 1983. Vero cell toxins in *Escherichia coli* and related bacteria: transfer by phage and conjugation and toxic action in laboratory animals, chickens and pigs. J. Gen. Microbiol. **129**:3121-3137.

159. **Somasekhar, G. and W. Szybalski**. 1983. Mapping of the Q-utilization site (*qut*) required for antitermination of late transcription in bacteriophage lambda. Gene. **26**:291-294.

160. **Somasekhar, G. and W. Szybalski**. 1987. The functional boundaries of the Q-utilization site required for antitermination of late transcription in bacteriophage lambda. Virology. **158**:414-426.

161. **Squires, C.L., J. Greenblatt, J. Li, and C. Condon**. 1993. Ribosomal RNA antitermination in vitro: requirement for Nus factors and one or more unidentified cellular components. Proc. Natl .Acad. Sci. U.S.A. **90**:970-974.

162. **Su, L., J.T. Radek, L.A. Labeots, K. Hallenga, P. Hermanto, H. Chen, S. Nakagawa, M. Zhao, S. Kates, and M.A. Weiss**. 1997. An RNA enhancer in a phage transcriptional antitermination complex functions as a structural switch. Genes & Dev. **11**:2214-2226.

163. **Sullivan, S.L. and M.E. Gottesman**. 1992. Requirement for E. coli NusG protein in factor-dependent transcription termination. Cell **68**:989-994.

164. **Sullivan, S.L., D.F. Ward, and M.E. Gottesman**. 1992. Effect of *Escherichia coli* nusG function on lambda N-mediated transcription antitermination. J. Bacteriol. **174**:1339-1344.

165. **Tan, R. and A.D. Frankel**. 1995. Structural variety of arginine-rich RNA-binding peptides. Proc. Natl. Acad. Sci. U S A **92**:5282-5286.

166. **Taura, T., C. Ueguchi, K. Shiba, and K. Ito**. 1992. Insertional disruption of the *nusB*

(*ssyB*) gene leads to cold- sensitive growth of *Escherichia coli* and suppression of the *secY24* mutation. Mol. Gen. Genet. **234**:429-432.

167. **Van Gilst, M.R., W.A. Rees, A. Das, and P.H. von Hippel**. 1997. Complexes of N antitermination protein of phage lambda with specific and nonspecific RNA target sites on the nascent transcript. Biochemistry **36**:1514-1524.

168. **Van Gilst, M.R. and P.H. von Hippel**. 1997. Assembly of the N-dependent antitermination complex of phage lambda: NusA and RNA bind independently to different unfolded domains of the N protein. J. Mol. Biol. **274**:160-173.

169. **Vogel, U. and K.F. Jensen**. 1997. NusA is required for ribosomal antitermination and for modulation of the transcription elongation rate of both antiterminated RNA and mRNA. J. Biol. Chem. **272**:12265-12271.

170. **Wagner, P.L., M.N. Neely, X. Zhang, D.W. Acheson, M.K. Waldor, and D.I. Friedman**. 2001. Role for a phage promoter in Shiga toxin 2 expression from a pathogenic *Escherichia coli* strain. J. Bacteriol. **183**:2081-2085.

171. **Ward, D.F., A. DeLong, and M.E. Gottesman**. 1983. *Escherichia coli nusB* mutations that suppress *nusA1* exhibit lambda N specificity. J. Mol. Biol. **168**:73-85.

172. **Ward, D.F. and M.E. Gottesman**. 1981. The nus mutations affect transcription termination in *Escherichia coli*. Nature **292**:212-215.

173. **Warren, F. and A. Das**. 1984. Formation of termination-resistant transcription complex at phage lambda nut locus: effects of altered translation and a ribosomal mutation. Proc. Natl. Acad. Sci. U.S.A. **81**:3612-3616.

174. **Watnick, R.S. and M.E. Gottesman**. 1998. Escherichia coli NusA is required for efficient RNA binding by phage HK022 nun protein. Proc. Natl. Acad Sci. U S A. **95**:1546-1551.

175. **Watnick, R.S. and M.E. Gottesman**. 1999. Binding of transcription termination protein nun to nascent RNA and template DNA. Science **286**:2337-2339.

176. **Watnick, R.S., S.C. Herring, A.G. Palmer 3rd, and M.E. Gottesman**. 2000. The carboxyl terminus of phage HK022 Nun includes a novel zinc-binding motif and a tryptophan required for transcription termination. Genes & Dev. **14**:731-739.

177. **Weisberg, R.A. and M.E. Gottesman**. 1999. Processive antitermination. J. Bacteriol. **181**:359-367.

178. **Weisberg, R.A., M.E. Gottesman, R.W. Hendrix, and J.W. Little**. 1999. Family values in the age of genomics: Comparative analysis of temperate bacteriophage HKO22. Ann. Rev. Genet. **33**:565-602.

179. **Whalen, W., B. Ghosh, and A. Das**. 1988. NusA protein is necessary and sufficient in vitro for phage lambda N gene product to suppress a rho-independent terminator placed downstream of nutL. Proc. Natl. Acad. Sci. U.S.A. **85**:2494-2498.

180. **Whalen, W.A. and A. Das**. 1990. Action of an RNA site at a distance: role of the nut genetic signal in transcription antitermination by phage-lambda N gene product. New Biol. **2**:975-991.

181. **Wilson, H.R., L. Kameyama, J.G. Zhou, G. Guarneros, and D.L. Court**. 1997. Translational repression by a transcriptional elongation factor. Genes & Dev. **11**:2204-2213.

182. **Wilson, H.R., D. Yu, H.K. Peters 3rd, J.G. Zhou, and D.L. Court**. 2002. The global regulator RNase III modulates translation repression by the transcription elongation factor N. EMBO J. **21**:4154-4161.

183. **Worbs, M., G.P. Bourenkov, H.D. Bartunik, R. Huber, and M.C. Wahl**. 2001. An extended RNA binding surface through arrayed S1 and KH domains in

transcription factor NusA. Mol. Cell **7**:1177-1189.

184. **Yager, T.D. and P.H. Von Hippel**. 1987. Transcript Elongation and Termination in *Escherichia coli*, p. 1241-1275. In F.C. Neidhardt, J.L. Ingraham, B. Magasanik, K.B. Low, M. Schaechter, and H.E. Umbarger (eds.), Escherichia coli and Salmonella typhimurium: Cellular and Molecular Biology. ASM, Washington, D.C.

185. **Yang, X.J., C.M. Hart, E.J. Grayhack, and J.W. Roberts**. 1987. Transcription antitermination by phage lambda gene Q protein requires a DNA segment spanning the RNA start site. Genes & Dev. **1**:217-226.

186. **Yang, X.J. and J.W. Roberts**. 1989. Gene Q antiterminator proteins of *Escherichia coli* phages 82 and lambda suppress pausing by RNA polymerase at a rho- dependent terminator and at other sites. Proc. Natl. Acad. Sci. U.S.A. **86**:5301-5305.

187. **Yarnell, W.S. and J.W. Roberts**. 1992. The phage lambda gene Q transcription antiterminator binds DNA in the late gene promoter as it modifies RNA polymerase. Cell **69**:1181-1189.

188. **Yarnell, W.S. and J.W. Roberts**. 1999. Mechanism of intrinsic transcription termination and antitermination. Science **284**:611-615.

189. **Zheng, C. and D.I. Friedman**. 1994. Reduced Rho-dependent transcription termination permits NusA-independent growth of *Escherichia coli*. Proc. Natl. Acad. Sci. USA **91**:7543-7547.

190. **Zhou, Y., J.J. Filter, D.L. Court, M.E. Gottesman, and D.I. Friedman**. 2002. A Requirement for NusG for Transcription Antitermination in vivo by the λ N Protein. J. Bacteriol. **184**:3416-3418.

191. **Zhou, Y., T.F. Mah, J. Greenblatt, and D.I. Friedman**. 2002. Evidence that the KH

RNA-binding domains influence action of the *E. coli* NusA protein. J. Mol. Biol. **318**:1175-1188.

192. **Zhou, Y., T.F. Mah, Y.T. Yu, J. Mogridge, E.R. Olson, J. Greenblatt, and D.I. Friedman**. 2001. Interactions of an Arg-rich region of transcription elongation protein NusA with NUT RNA: implications for the order of assembly of the lambda N antitermination complex in vivo. J. Mol. Biol. **310**:33-49.

Figure Legends

Figure 1. Genetic map of regulatory region of λ (not drawn to scale). Shown are relevant, promoters (*P*), operators (*O*), terminators (t, filled squares intrinsic and filled circles Rho-dependent), *nut* (*put*), and *qut*. Below are shown transcription patterns in the absence and presence of N and Nus factors and in the presence and absence of Q. Narrowing of lines provides an indication of reduced levels of transcription.

Figure 2. Features of antitermination sites in early operons of lambdoid phages. A. Comparison of *nut* regions (L and R) of λ and H-19B with components elements identified below (52,120). The arrows indicate regions of hyphenated dyad symmetry that are sources of stem-loop structures. B. The PUT stem-loop structures of phage HK022 (6). C. The GNRA fold-like structure formed by λ BOXB upon interaction with N, shown here for the NUTR-BOXB, is based on the structure determined for NUTL-BOXB (101,162). Bases, sugars, and phosphates are represented respectively by rectangles (with base indicated within), ovals, and squares. Dashed lines shows hydrogen bonds of Watson-Crick pairing and heavy dashed line shows sheared G(6)-A(10) base pair. Bases are numbered from 3’ end of upstream stem to 5’ end of downstream stem. The purine ring of adenine 7 stacks with the indole ring of Trp18 of N and adenine 9 is extruded from the structure.

Figure 3. The N-leader transcript beyond p_L. The sequence is shown starting at the BOXA sequence of NUTL; numbers indicate distance from RNA start of p_L. The structure of the RNaseIII site (RTS) is shown with the position of cleavage sites marked by arrows. The N ribosome-binding site (SD) and fMet codon are identified by underlines.

Figure 4. Assembly of transcription antitermination complex: N translation repression modes. RNA Pol is shown transcribing from the p_L promoter through *nutL* and the RNase III site (RTS) into the N gene. The antitermination complex is formed first at NUTL (to the right of step 1) and the RTS is transcribed and assembles beyond step 2. If RNaseIII is not immediately present the SD (Shine-Dalgarno) sequence is protected in some way (?) from ribosome binding. If RNaseIII is present, the RTS is processed and allows optimal translation of N. Note the antitermination complex may remain bound to RNA Pol.