
Nucleotide sequence of bacteriophage fd DNA

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ABSTRACT

The sequence of the 6408 nucleotides of bacteriophage fd DNA has been determined. This allows to deduce the exact organisation of the filamentous phage genome and provides easy access to DNA segments of known structure and function.

INTRODUCTION

Small DNA viruses depend during their life cycle largely on host functions and are therefore preferred model systems for the analysis of the organisation, expression and replication of the more complex host genomes. To analyse viral genomes at the nucleotide level has become technically possible with the development of new rapid DNA sequencing techniques^{1, 2, 3}. Complete nucleotide sequences have been reported so far for coli phage $\phi\chi 174$ ^{4, 5} and Simian Virus SV40^{6, 7}. Here we report the sequence of bacteriophage fd DNA, strain 478 (Heidelberg).

Phage fd⁸ along with f1 and M13 belongs to a group of closely related filamentous, male-specific coli phages (for reviews see ref. 9, 10). Its genome is a single-stranded circular DNA of about 6000 nucleotides which is converted to a double-stranded form in the infected cell. Eight genes have been ordered by combined genetic and biochemical analysis within the phage genome. Its detailed organisation remained, however, relatively uncertain due to the lack of protein data for most gene products. Furthermore, analysis on the nucleotide level had concentrated mainly on DNA segments with regulatory functions^{10, 11}.

We have previously reported a preliminary nucleotide sequence of fd DNA (¹¹, and personal communications). The aim of this publication is the rapid communication of the final sequence. A more detailed account containing the experimental evidence will be published elsewhere.

RESULTS AND DISCUSSION

Restriction nucleases and cleavage maps. The enzymes used, their recognition sequences and the position of cleavage sites confirmed or newly established during this work are presented in Fig. 1. All cleavage sites shown have also been identified by DNA sequencing the ends of the respective restriction fragments. With one exception, all parts of double-stranded fd can be fragmented by digestion with several of these enzymes into pieces of less than 200 base-pairs.

DNA sequencing. The chemical method of Maxam and Gilbert² was used which allowed us to read sequences up to 150 (occasionally up to 220) nucleotides. Sequences obtained were stored and processed in a computer (G. Osterburg and R. Sommer, to be published) to yield the composite sequence of 6408 nucleotides presented in Fig. 2. About 75 % of this sequence was determined from both DNA strands in fd 478. Almost all of the missing 25 % have also been sequenced in the second strand, but in the closely related phage f1. Further information was obtained for about 1000 nucleotides by RNA sequencing¹² and for about 600 nucleotides by the plus/minus method of Sanger and Coulson¹. About 10 % of the fd sequence were also established as recognition sequences for restriction nucleases at known cleavage sites (Fig. 1 and unpublished results).

Nucleotide sequence. According to Fig. 2 fd DNA is composed of 6408 nucleotides (1578A, 2210T, 1325G, 1295C) corresponding to a molecular weight of 2.12×10^6 daltons (sodium salt). The sequence differs from that reported earlier¹¹ mainly by an insert of 18 nucleotides in the

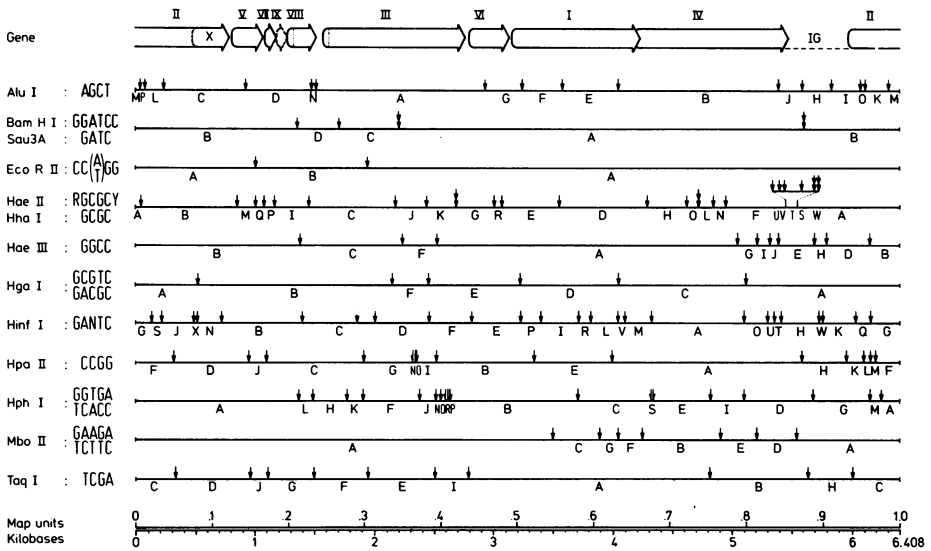


Fig. 1: Fragment maps of restriction nucleases used in the sequence analysis of fd DNA, strain 478. The known maps for HpaII, HgaI, HaeII (HinfI), HaeIII, Alu^{10,11} were confirmed and refined. Maps for HhaI, HinfI, TaqI, BamHI, Sau3A (DpnI, MboI), EcoRII, MboII, and HphI were newly established (E.A. Auerswald et al., M. Takanami et al., both unpublished). The first nucleotide of the recognition sites for the various restriction nucleases are listed below. An additional Hinf site has been detected in fragment HinfC (position 1858) in the DNA from fd ATCC (M. Takanami, unpublished). The circular phage DNA is opened at the unique HindII (HpaI) cleavage site. The map includes the positions and the orientation of the phage genes. IG is the intergenic space.

AluI	AGCT	39	63	229	934	1488	1517	2963	3277	3613	4097	5427	5631
		5888	6108	6135	6336								
BamHI	GGATCC	2220	5645										
Sau3A	GATC	1382	1714	2221	5646								
EcoRII	CCTGG	1014	1966										
HaeII	RGCGCY	2710	4743	5560	5568								
HhaI	GCGC	44	873	1011	1085	1177	1470	2195	2467	2711	3040	3096	3599
		4313	4642	4744	4886	4996	5491	5504	5513	5535	5561	5569	
HaeIII	GGCC	1396	2245	2554	5082	5240	5346	5415	5726	5829	6181		
HgaI	GACGC	526	2164	2479	3238								
	GCGTC	4084	5159										
HinfI	GANTC	136	216	490	511	723	1403	2011	2497	2845	3259	3419	3743
		3839	4073	4118	4350	5121	5330	5376	5439	5767	5789	6043	6199
HpaII	CCGG	314	966	1095	1924	2378	2390	2396	2552	3371	4019	5615	5996
		6119	6179	6221									
HphI	GGTGA	1376	1774	1909	2398	2542	2581	2620	2626	3740	4347	4848	5118
	TCACC	5707	6163										
		1503	2635	4365	6189	6286							
MboII	GAAGA	3913											
	TC TTC	3529	4076	4272	4938	5256	5588						
TaqI	TCGA	336	988	1127	1508	1949	2528	2815	4834	5684	6041		

repetitive sequence around position 2380. Except for a G → A transition in position 1859 the identical sequence was obtained in 2000 nucleotides from another fd strain (ATCC).

The nucleotide sequence of the related phage f1 has been determined to about 90 % (E. Beck, unpublished). It differs from the fd sequence by deletion of a single nucleotide (position 3195) and by about 160 base changes. Except for seven, these are all silent mutations which do not alter the amino acid sequence of the fd gene products.

Genome organisation. By analysing the fd DNA sequence for continuous translational reading frames - combined with the information obtained from the sequence of amber mutations in f1 and M13 (E. Beck, unpublished; J. Schoenmakers, personal communication) and from the silent base changes in f1 - allows to deduce the exact sizes and positions of the eight known gene products and of known regulatory signals. The DNA sequence predicts the amino acid sequences of known and unknown gene products, and the existence of a new gene (gene IX) in the intergenic space between genes VII and VIII¹¹.

According to our analysis (Fig. 2) the overall organisation of the filamentous phage genome differs markedly from that of icosahedral single-stranded DNA phages, like $\phi\chi 174^4$: Although genes are generally closely spaced there is only one single short overlap of genes in different reading frames (at the junction of genes I and IV). In addition there is an intergenic region (IG) of 508 nucleotides which harbours the origins of DNA replication^{13, 14}. Recent experiments show that this space can be further expanded by insertion of foreign DNA¹⁶.

Applications. fd DNA is accessible in high yields in both its single-stranded and double-stranded form¹⁰. The knowledge of its nucleotide sequence and of the map positions of a great number of restriction sites provides therefore easy access to well defined DNA molecules which can be used in different investigations on DNA structure

5782 AATAGTG GACTCTTGT CCAAACTGGA **IG**

5809 ACAACACTCA CAAC~~T~~AACTC GGCCTATTCT TTTGATTTAT AAGGATTTT GTCATTTTCT GCTTACTGCT TAAAAATAA GTGATTTAA CAAATATTTA

5909 ACCCGAAAT TAACAAACA TTAACGTTA CAATTTAAAT ATTGCTTAT ACAATCATCC TGT~~TT~~TGGG C~~TTT~~TCTGA TTATCAACCG GGGTACATAT

6009 GATTGCATG CTAGTTTAC GATTACGGT CATCGATTCT CTGTGTTGCT CCAGACTTC AGGTAATGAC CTGATAGCCT TTGTAGACCT CTC~~AAAA~~ATA

6109 GCTACCCTC CCGGCATGAA TTTATCAGCT AGAACGGTTG AATATCATAT TGACGGTGTAT TTGACTGTCT CCGGCC~~TTTC~~ TCACC~~GGTTT~~ GAACTTTTGC

6209 CTACTCATT CTCGGGCATT GCATTTAAA TATATGAGGG TCTAAAAAT TTTATCCCT GCGTGA~~AAAT~~ TAAGC~~TTCA~~ CCAGC~~AAAA~~AG TATTACAGGG

6309 TCATAATGT TTGGTACAA CCGATTTAGC TTATGCTCT GAGC~~TTTAT~~ TGCTAA~~TTT~~ TGCTAACTCT CTGCCTTGTG TGTACGATTT ATTGGATGTT

II

1 AAGGCTACTA CCATTAGTAG AATTGATGCC ACC~~TTTT~~CAG C~~TC~~CGGCC~~CC~~ AAATGAAAT ATAGTAAAC AGGTTATTGA CCATTTGCCG AATGTATCTA

101 ATGGTCAAC TAAATCTACT CGTTCCGAGA ATTGGGAATC AACTGTTACA TGGAA~~TGAA~~ CTTCCAGACA CCGTACTTTA GTTG~~CATAT~~ TAAAA~~CATGT~~

201 TGAAC~~TACAG~~ CACCA~~GATTC~~ AGCAATTAAG C~~TC~~TAAGCCA TCCGCA~~AAAA~~ TGACCTTTA TCAAAAGSAG CAATTAAGG TACTGTCTAA TCCTGACCTG

301 TTGGAATTTG CTTCCGGTCT GGTTCGGCTT GAGGC~~TCGAA~~ TTGAAACGCG ATATTTGAAG TC~~TTT~~CGGGC TTCCTCTTAA TCTTTTGTAT GCAATTCGCT

401 TTGCTTCTGA CTATAATAGA CAGGTA~~AAAG~~ ACCTGATTTT TGATTTATGG TCATTTCTCGT TTTCTGAACT GTTTAAAGCA TTTGAGGGG ATTCAAATGAA

501 TATTTATGAC GATTCGGCAG TATTGGACGC TATCCAGTCT AACCATTTA CAATTACCC~~C~~ CTCTGGCAAA ACTTCC~~TTG~~ CAAAAGCCTC TCGCTATTTT

X

601 GGTTCATC GTCGCTGGT TAATGAGGGT TATGATAGTG TTGCTCTAC CATGCCCTGT AATCC~~TTTT~~ GCGGTTA~~GT~~ ATCTGCATTA GTTGAAGTGT

701 GTATTCCTAA ATCTCAATTG ATGAAT~~CTTT~~ CCACCTG~~TAA~~ TAATGTTGTT CCGTLAGITC GTTTTAT~~TAA~~ CGTAGATTTT TCC~~TCC~~CAAC GTCCTGACTG

801 GTATAATGAG CCAGTIC~~TIA~~ AAATCGCA~~TA~~ AGGTAATICA AATGATTA~~A~~ AGTTGAAAT AAACCGTCTC AAGCGCAAT TACTACCCGT TCTGGTGT~~TT~~

V

901 CTGCTCAGGG CAAGCCTTAT TCACTGAATG AGCAGCTTTG TTACGTTGAT TTGGGTAATG AATATCCGGT CTTTGTCAAG ATTACTCTCG ACGAAGGTCA

1001 GCCAGGGTAT GGGCTG~~STC~~ TGACACCGT GCA~~TC~~GTCC CGATCGAGT GGGTIC~~CTT~~ ATGATGACC GTC~~TGG~~CTC GGTTC~~GGCT~~

1101 AAGTAAAGTG GAGCAGGTGC CCGATTTCGA CACAATTTAT CAGCGATGA TACA~~AAAT~~CTC C~~BTG~~TACTT TGT~~TT~~CGCG TTGGTATAAT CCGTGGGGGT

VII

1201 CAAAGT~~AG~~ TGAG TGT~~TT~~AGTG TATTC~~TTTT~~CG C~~CT~~TTTTCT TTAGGTTGG TGGCTTCGTA GTGGCATTAC GTATTTTACC C~~GT~~TTAATGG AAAC~~TTCTC~~T

IX

1301 ATGAAAAGT CTTTAGTCT CAAAGCCTCC GTAGCCGTTG CTAGCCTCGT TCGGATGCTG TCTTTCCGCTG CTAGGGTGA C~~BA~~TCCCGCA AAAGCGGCT

VIII

1401 TTGACTCCCT GCAAGCCTCA GCGACCGAAT ATATCGGTTA TGGTGGGGC ATGGTTGTTG TCAITGTCGG CCGCAACTATC GGTATGAAGC TGTITAAAGA

1501 LATTACCTCG AAAGCAAGCT GATAAACCGA TACAAT~~TAA~~ GGCTCCTTTT GGAGCCTTTT TTTTGGAGA TTTTCAACBT GAAAAAATTA TTATTCGCA

III

1601 TTCC~~TT~~AGT TGTTCCTTTC TATTC~~CACT~~ CCGCTGAAAC TGTGAAAGT TGTTAGCAA AACCTCATAC AGAAAATTC A TTTACTAAGC TCTGSAAGA

1701 CGACAAAAC~~T~~ ITAGT~~CGT~~ ACCTAACTA TGAGGGCTGT CTGTGGAA~~TG~~ CTACAGGCGT TGTGGTTGT ACTGGTGAGC AAAC~~T~~CAGTG TTACGGTACA

1801 TTGGGTTCCATA TTGGGCTTGC TATCCCTGAA AATGAGGGTG GTGGCTCTGA GGGTGGCGGT TCTGAGGGTG GCGGTTCCTGA GGGTGGCGGT ACTAAACCTC
 1901 CTGAGTACGG TGATACACCT ATTCGGGCT ATACTTAT CAACCCCTC EGAGGCACCT ATCCGCCTGG TACTGAGCAA AACCCCGCTA ATCCCTAACTC
 2001 TTCTCTTTGAG GAGTCTCAGC CTCITTAATAC TTTCATGTTT CAGAATAATA GGTTCGGAAA TAGGCAGGGT GCATTAAGT TTTATACGGG CACTGTTACT
 2101 CAAGGCACTG ACCCCGTTAA AACTTATTAC CAGTACACTC CTGTATCATC AAAGCCATG TATGACGCTT ACTGGAACGG TAAATTCAGA GACTGCGCTT
 2201 TCCATTCTGG CTTTAATGAG GATCCATTCC TTGTGAATA TCAAGGCCAA TCGTCTGACC TGCCTCAACC TCCGTGCAAT GCTGGCGGGC GCTCTGGTGG
 2301 TGGTCTGGT GCGGCTCTG AGGTGGCGG CTCTGAGGGT GCGGGTCTG AGGTGGCGG CTCTGAGGGT GCGGGTCCG GTGGCGGGCTC GGGTCCCGT
 2401 GATTTGATT ATGAANAAT GGCAAACGCT AATAAGGGGG CTATGACCGA AAATGCCGAT GAAAACGGC TACAGTCTGA CGCTAAAGC AAAC TTGATT
 2501 CTGTCCGTAC TGATTCAGGT GCTGCTATCG ATGGTTTCAT TGGTGACGTT TCCGGCCTTG CTAATGGTAA TGGTGCTACT GGTGATTTTG CTGGCTCTAA
 2601 TTCCCAAATG GCTCAAAGTGG GTGAGGGTGA TAATTCACCT TTAATGAATA ATTTCCGTCA ATATTTACCT TCTTTGCCCT AGTCGGTTGA ATGTGGCCCT
 2701 TATGCTTTG GCGCTGGTAA ACCATATGAA TTTTCTATTG ATTTGACAAA AATAAACITA TCCGIGGGT ICITTIATAT GTTGCACCT
 2801 TTATGTAIGT ATTTGGAGC TTTGCTAACA TACTGGGTAA TAAGGAGTCT TAATCATGCC AGTTCCTTTG GGTATTCCGT TATTATTGGG TTTCCCTCGG
 2901 TTCCCTCTGG TAACTTTGTT CGGCTATCTG CTTACTTTCC TTAANAAGGG CTTCGGTAAG ATAGCTATTG CTATTTCAAT GTTTCCTTGT CTTATTATTG
 3001 GGGTTAACTC AATTCCTTGT GGTATCTCT CTGATATTAG GGCACAATTA CCGCTGATT TTGTTACAGG CGTTCAGTTA ATTCTCCCGT CTAATGCCCT
 3101 TCCCTGTTTJ TATGTTAIC ICCTGTAAA GCGTGTATT TCAITTTTG ACGTTAACA AAAAATCGTT ICITTIITGG AITGGATAA ATAAATGG
 3201 CTGTTTATTT TGTAACTGGC AAATFAGGCT CTGGAAGAC GCTCGTTAGC GTTGTAGA TTCAGGATAA AATTTAGCT GGGTGCAAAA TAGCAACTAA
 3301 TCTTGATTA AGGCTTCAAA ACCTCCCGCA AGTCGGGAGG TTGCTAAAA CCGCTCGGCT TCTTAGAATA CCGGATAAGC CTTCTATTTC TGATTTGCTT
 3401 GCTATTGGC GTGGTAATGA TTCCTACGAC GAAAAATAAA ACGGTTTGT TGTCTTAG GAATGCGGTA CTTGGITTA TACCCGTTCA TGGAAATGACA
 3501 AGSAAAGACA GCGGATTATT GATTTGGTTTC TTCATGCTCG TAAATTTGGA TGGGATATTA TTTTTCTGT TCAGGATTA TCTATTGTTG ATAAACAGGC
 3601 GCGTCTGCA TTAGCTGAAC ACGTTGTTTA TTGTGCGCGT CTGGACAGAA TFACTTTACC CTTTGTCCGC ACTTTATATT CTCTTGTAC TGGCTCAAAA
 3701 ATGCCCTGC CTAATATACA TSTTGGTGT GTTAAATATG GTGATCTCA ATTAAGCCCT ACTGTTGAGC GTTGGCTTTA TACTGTAAG AATTTATATA
 3801 ACGCATATGA CACTAAACAG GCTTTTCCCA GTAATTAGA TCCAGGTGT TATTCATATT TAACCCCTTA TTTATCACAC GGTGCGGTATT TCAAACCAT
 3901 AAATTTAGT CAGAAGATGA AATTAACATA AATATATTTG AAAAGTTTT CTGCGGTTCT TTGCTTTGCG ATAGGATTTG CATCAGCATT TACATATAG

III

VI

I

4001 TATATAACC AACCTAAGCC GGAGGTTAAA AAGGTAGTCT CTCAGACCTA TGATTTTGT AAATTCACCTA TTGACTCTTC TCAGCGTCTT AATCTAAGCT I
 4101 ATCGCTATGT TTTCAAGGAT TCTAAGGGAA AATTAATTA TAGCGACGAI ITACAGAAGC AAGGIIATTC CAICACATAI AITGAIITAI GIACIGTIIC
 4201 LAATTAAAAAA GGTAATTCAA ATGAAATIGI TAAATGTAAT TAATTTTGT TCTTTGATG TTGTTTCATC ATCTTCTTTT GCTCAAGTAA TTGAAATGAA
 4301 TAATTCGCCT CTGGCGGAT TCGTGACTTG GTATTCCAAG CAACAGAGTG AATCTGTTAT TGTCTCACCT GATGTTAAAG GTACAGTGAC TGTATATTCC
 4401 TCTGACGETTA AGCCTGAAAA TTTACGCCAT TTCTTTATCT CTGTTTTACG TGCTAATAA TTTGATATGG TTGGCTCAAT TCCTTCCATA ATTCAGAAAT
 4501 ATAACCCAA TAGTCAGGAT TATATTGATG AATTGCCATC ATCTGATAT CAGGAATAG ATGATAATTC CGCTCCTTCT GGTGGTTTTCT TGTTCGCCGA
 4601 AAATGATAAT GTTACTCAA CATTTAANAAT TAATAACGT GCGCAAAAG ATTTAATAAG GGTTGTAGAA TTGTTTGTTA AATCTAATAC ATCTAAATCC
 4701 TCAATGTAT TATCTGTTGA TGGTCTAAC TTATTAGTAG TTAGCGCCC TAAAGATATT TTAGATAACC TTCGCAATT TCITTTCTACT GTTGATTTGC IV
 4801 CAACTGACCA GATATTGATT GAAGGATTA TTTTGAGGT TCAGCAAGGT GATGCTTTAG ATTTTTCCIT TGCTGCTGGC TCTCAGGGCG GCACGTGTCG
 4901 TGGTGTGTT AACTGACC GCTAACCTC TGTTTTATCT TCTGGGGTG GTTCGTTCGG TATTTTTAAC GCGCATGTTT TAGGGCTATC AGTTCGGCA
 5001 TTAAGACTA ATAGCCATT CAAAAATTTG TCTGTGCCCT GTATTCTTAC GCTTTCAGGT CAGAAGGGT CTATTTCTGT TGGCCAGAAT GTCCCTTTTA
 5101 TTAAGACTA ATAGCCATT CAAAAATTTG TCTGTGCCCT GTATTCTTAC GCTTTCAGGT CAGAAGGGT CTATTTCTGT TGGCCAGAAT GTCCCTTTTA
 5201 AATGGCTGGC GGTAATATTG TTTTAGATAT AACCAGTAAG GCCGATAGT TGAGTTCTTC TACTCAGGCA AGTGATGTTA TTACTAATCA AAGAAGTATT
 5301 GCGACAACGG TTAATTTGCG TGATGGTCAG ACTTTTTTGC TCGGTGGCCT CACTGATTAC AAAAAACATT CTCAAGATTC TGGTGTGCGG TTCCCTGTCTA
 5401 AAATCCCTTT AAATCGGCCTC CTGTTTAGCT CCCGTTCTGA TTTAAGCGAG GAAAGCACGT TGTAGGTGCT CGTCAAAGCA ACCATAGTAC GCGCGCTGTA
 5501 GCGCGCGATT AAGCGCGCGG GGTGTGGTGG TTACGCGCAG CGTGACCGCT ACACTTGCCA GCGCCCTAGC GCCGCGTCCT TCGCTTTCT TCCTTCCTT IG
 5601 TCTCGGCACG TTTCTCGGCT TTCCCGTCA AGCTCTAAAT CGGGGGATCC CTTTAGGGT CCGATTTAGT GCITTAGGCG ACCTCGACCT CCAAAAACTT
 5701 GATTTGGGTT ATGGTTACG TAGTGGGCCA TCGCCCTGAT AGACGGTTTT TCGCCCTTTG ACGTTGGAGT CCACGTTCTT T

Fig. 2: Nucleotide sequence of bacteriophage fd. The viral DNA single-strand is shown in 5' → 3' polarity. The circular DNA has been opened at the position of the origin of viral replication^{13,14}. Numbering of nucleotides starts at the unique HindII (HpaI) cleavage site. Genes are boxed, recognition sites for the restriction nucleases shown in Fig. 1 are overlined. The sequence is available on request on magnetic tape.

and function. For example they have been used as size markers in their intact or restricted form, for the search for recognition sequences of restriction nucleases¹⁷, in the site-specific modification of the fd genome for use as a cloning vehicle¹⁶, for the isolation and the cloning of regulatory signals from fd DNA, for the analysis of integration and loss of transposon Tn-5 (^{16,14}, E.A. Auerswald, to be published), and for the correlation of thermal denaturation profiles of DNA molecules with their nucleotide sequence¹⁸.

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REFERENCES

- 1 Sanger, F. and Coulson, A.R. (1975) *J. Mol. Biol.* 94, 441 - 448
- 2 Maxam, A.M. and Gilbert, W. (1977) *Proc. Natl. Acad. Sci. USA* 74, 560 - 564
- 3 Sanger, F., Nicklen, S., and Coulson, A.R. (1977) *Proc. Natl. Acad. Sci. USA* 74, 5463 - 5467
- 4 Sanger, F., Air, G.M., Barrell, B.G., Brown, N.L., Coulson, A.R., Fiddes, J.C., Hutchison III, C.A., Slocombe, P.M., and Smith, M. (1977) *Nature* 265, 687 - 695
- 5 Sanger, F. and Coulson, A.R. (1978) *FEBS Letters* 87, 107 - 110
- 6 Fiers, W., Contreras, W.R., Haegeman, G., Rogiers, R., van de Voorde, A., van Heuverswyn, H., van Herreweghe, J., Volckaert, G., and Ysebaert, M. (1978) *Nature* 273, 113 - 120
- 7 Reddy, V.B., Thimmappaya, B., Dhar, R., Subramanian, K.N., Zain, B.S., Pan, J., Ghosh, P.K., Celma, M.L., Weissman, S.M. (1978) *Science* 200, 494 - 502
- 8 Hoffmann-Berling, H., Marvin, D.A., and Dürwald, H. (1963) in *Zeitschrift für Naturforschung* Bd. 18b, Heft 11, 876 - 898
- 9 Marvin, D.A. and Hohn, B. (1969) *Bacteriol. Rev.* 33, 172 - 209

-
- 10 Ray, D.S. (1977) in *Comprehensive Virol.* 7, 105 - 178
eds. Fraenkel-Conrat, H. and Wagner, R.R., Plenum
Publ. Corp. N.Y. 10011 USA
 - 11 Schaller, H., Beck, E., and Takanami, M. (1978) in
Single Stranded DNA Phages, eds. Denhardt, D.T.,
Dressler, D., and Ray, D.S., Cold Spring Harbor Lab.,
Cold Spring Harbor, N.Y. 11724 USA
 - 12 Sugimoto, K., Sugisaki, H., Okamoto, T., and Takanami, M.
(1977) *J. Mol. Biol.* 111, 487 - 507, and unpublished
results
 - 13 Horiuchi, K. and Zinder, N.D. (1976) *Proc. Natl. Acad.
Sci. USA* 73, 2341 - 2345
 - 14 Schaller, H. (1978) in *Symp. on Quantitative Biol.*
Vol. XLIII, Cold Spring Harbor Lab., Cold Spring Harbor,
N.Y. 11724, USA
 - 15 Meyer, T., Geider, K., Kurz, Ch., and Schaller, H.
(submitted for publication)
 - 16 Herrmann, R., Neugebauer, K., Zentgraf, H., and Schaller,
H. (1978) in *Single Stranded DNA Phages*, eds. Denhardt,
D.T., Dressler, D., and Ray, D.S., Cold Spring Harbor
Lab., Cold Spring Harbor, N.Y. 11724 USA
 - 17 Sommer, R. and Schaller, H. (1979) *Molec. gen. Genet.*
(in press)
 - 18 Vologodskii, A.V. and Frank-Kamenetskii, M.D. (1978)
Nucleic Acids Res. 5, 2547 - 2556