The transducing phages λDarOE and λDlv5, which carry the Escherichia coli ribosomal RNA operons rrnD and rrnX, respectively, have been mapped with the restriction endonucleases BamHI, EcoRI, HindIII, and SmaI. Using hybridization techniques, we have located the ribosomal RNA genes on these phage DNAs.

The DNA sequence of the 437-base-pair 16 S-23 S ribosomal RNA intergenic spacer in the two rRNA operons rrnD and rrnX has been determined. The nucleotides examined exhibit only one base pair change between rrnD and rrnX. Both spacer regions contain the genes for tRNA18S and tRNA15Ala; the gene sequences are identical with the previously deduced tRNA sequences and are clustered within the first 60% of the spacer DNA. The most striking feature of the 16 S-23 S intergenic region in these two operons is the disparity in G-C content between the tRNA gene sequences (60% G-C) and the remaining spacer DNA (37% G-C). Spacer sequences are known to be involved in the processing of the ribosomal RNA transcript by RNase III and RNase P.

In addition, we report the sequence of the first 108 base pairs of the 23 S rRNA gene.

In Escherichia coli, the genes for 16 S, 23 S, and 5 S ribosomal RNA are co-transcribed from seven operons into 30 S pre-rRNA. In addition to sequences destined to become mature rRNAs, the rRNA transcript contains regions whose functions are less well understood. Such “spacer” regions flank all three rRNA genes and are presumed to be crucial to the precise and efficient processing of the mature rRNAs from a single precursor molecule.

Using hybridization and RNA fingerprinting techniques, several investigators (2, 5-8) recently identified the genes for certain tRNA species in two of the rrr spacer regions. Between 16 S and 23 S rRNA sequences are found either the gene for tRNA18S (in the rrnD operons) or the genes for tRNA15Ala and tRNA15Ala (in the remaining three operons). Other tRNA genes exist near the distal end of three rRNA operons and are presumed to be involved in the processing of the ribosomal RNA transcript by RNase III.

We report here the DNA sequence of the 16 S-23 S rRNA spacer in the two E. coli rRNA operons rrnD and rrnX. Our sequence reveals the presence of the two rRNA genes predicted by hybridization studies (tRNA18S and tRNA15Ala) surrounded by relatively A-T-rich sequences. In addition, the data extend into the initial 108 base pairs of the 23 S rRNA gene. We previously reported that sequences appearing within the first 48 nucleotides of this 16 S-23 S spacer are complementary to the region preceding the 16 S gene and are involved in processing of the 30 S pre-rRNA by RNase III.
The 16 S-23 S rRNA Spacer Region

activity about 3000 Ci/mmol) or prepared at a specific activity of about 1500 Ci/mmol by the method of Glynn and Chappell (22). The desired fragments were finally purified by polyacrylamide gel electrophoresis; all acrylamide gels contained 45 mM Tris/borate, pH 8.3, and 1.25 mM EDTA. Complementary DNA strands were separated as described by Maxam and Gilbert (21).

DNA Sequencing—DNA fragments were sequenced using the chemical modification procedure of Maxam and Gilbert (21). Six base-specific reactions were generally used to give cleavage at A > C; G, A and hdilv5 DNAs with the restriction endonucleases Sma I.

RESULTS

Mapping Restriction Enzyme Cleavage Sites—Agarose-gel fractionation of products generated by digestion of λdarO E and λdilv5 DNAs with the restriction endonucleases Sma I,

**FIG. 1.** Pattern of λ, λdarO E, and λdilv5 DNA digestion products. One microgram each of λ, λdarO E, and λdilv5 DNAs were cleaved with the restriction endonucleases BamHI (Gel A), Sma I (Gel B), EcoRI (Gel C), and HindIII (Gel D) for 1 h at 37°C in 50 μl of digestion buffer and subjected to electrophoresis on a 1.4% agarose gel as described under "Experimental Procedures." Fragment sizes were determined relative to the mobility of λ-DNA fragments and are given in percentage of λ-DNA. (1% λ = 465 base pairs (25).) The large fragments (>5% λ-DNA) were also sized on 0.8 and 1.0% agarose gels. The pattern, but not the photograph, of EcoRI cleavage products of λ is given.

**FIG. 2.** Restriction maps of λdarO E and λdilv5 DNAs and the 16 S-23 S rRNA intergenic DNA spacer. A, cleavage sites on the two transducing phage DNAs were mapped for the enzymes BamHI, Sma I, EcoRI, and HindIII as described in the text. The EcoRI map for λdilv5 DNA was not fully elucidated and is taken from Ref. 10. λ-DNA; — E. coli DNA; ⬇ rDNA. B, cleavage sites in the 16 S-23 S spacer DNA are shown for the restriction endonucleases Alu I, Hae III, Hha I, Hinfl, Hph I, Mnl I, Mbo I, and Taq I. These were determined by the technique of Smith and Birnstiel (27) which is described in the legend to Fig. 4. Cleavage sites are numbered according to their distance (in base pairs) from the end of the 16 S rRNA gene; sites within the 16 S rRNA gene have negative numbers, those outside have positive numbers. ⬇ genes for mature RNA.
BamHI, EcoRI, and HindIII are shown in Fig. 1. We mapped cleavage sites for these enzymes (Fig. 2A) by determining: 1) cleavage product sizes, 2) which products are common to both λ and the λ transducing phage DNAs, 3) those fragments which contain the “ends” of the λ genome, and 4) the order of the remaining fragments through partial and secondary digestion experiments.

The sizes of DNA fragments were determined from their electrophoretic mobility relative to standards generated by digestion of λ-DNA with BamHI, Sma I, EcoRI, and HindIII (23-25) (Fig. 1). Our size estimates for the cleavage products of λdaroE and λdilv5 are given in percentage of λ in Figs. 1 and 2A. Several fragments from each endonucleolytic digest were common to λ phage and λ transducing phage DNAs. For both λdaroE and λdilv5 DNAs, the following fragments co-migrated with λ-DNA fragments: Sma I, 17.2 and 17.3; BamHI, 11.4, 13.3, 14.8, and 13.9; HindIII, 1.0, 13.5, and 9.1; and EcoRI, 15.2, 11.8, and 7.5. We therefore assume that these fragments are derived from the λ portion of the transducing phage DNAs. Moreover, with the exception of BamHI 11.4, which is located at the extreme left end of λ-DNA, these fragments can all be assigned to the right arm of the λ genome (23-25). Hence, the λdaroE and λdilv5 transducing phage genomes are of the standard λGal type (26): they contain bacterial DNA in the left arm of the λ chromosome.

To determine which cleavage fragments contain the termini of the transducing phage DNAs, we exploited the existence of “sticky ends” on λ-DNA. In this type of experiment, one aliquot of digested DNA is incubated at 80°C for 3 min, then rapidly chilled; a second aliquot remains unheated after digestion. Subsequent comparison of the patterns when these two samples are fractionated on an agarose gel reveals a band composed of the two sticky end fragments in the untreated sample, while this band is resolved by two smaller ones in the heated sample. Thus, we ascertained (data not shown) that the Sma I 22.8, BamHI 11.4, EcoRI 23.1, and HindIII 23.5 fragments of λdaroE DNA appear at the left end of the linear map. Similarly, the Sma I 26.4, BamHI 11.4, EcoRI 25.5, and HindIII 21.1 fragments of λdilv5 are located at the left end.

The above information sufficed to order the Sma I, HindIII, and EcoRI cleavage products of λdaroE (Fig. 2A) according to the following reasoning. The Sma I 17.2 and 17.3 fragments originate from the right arm of λ-DNA, and the Sma I 22.8 and 17.5 fragments contain the sticky ends of λ; thus, since the 17.2 and 17.3 products account for only 34.5% of the right arm of λ-DNA, and the 15.2 and 7.5 are end fragments; therefore, because the 15.2, 11.8, and 7.5 fragments account for only 34.5% of the right arm of λ-DNA, only 28.8 can neighbor fragment 15.2. Finally, the HindIII 10.0, 13.5, and 9.1 fragments belong in λ’s right arm: 23.5 and 9.1 are end fragments; and 23.5 and 24.5 must be adjacent to one another since only these two HindIII fragments hybridize ribosomal RNA (see below), leaving 20.1 to lie between 24.5 and 1.0.

To map these fragments, λdaroE DNA was 5'-
end-labeled as described under “Experimental Procedures” and cleaved with Xho I, which makes one cut (in the right half of the DNA) to produce a 60% and a 31% fragment from λdaroe. (Note from Fig. 2A that λdaroe DNA totals about 90% λ, whereas λdiltDNA is about 105% λ.) The longer fragment was isolated and subjected to limited digestion with BamHI according to Smith and Birnstiel (27). Since only partial products containing the extreme left end of the DNA were labeled, we could map the cleavage sites by subjecting the BamHI partial digest to agarose-gel electrophoresis and measuring the mobility difference of the partial products relative to DNA size markers. This analysis ordered the BamHI fragments as shown in Fig. 2A (data not shown). BamHI digestion of Sma I fragments 22.8 and 32 confirmed the locations of the similarly sized BamHI fragments 2.2 and 2.8, and 7.2 and 7.9.

The cleavage sites for Sma I, BamHI, and HindIII in λdiltDNA were determined in a somewhat different manner. We first ordered the Sma I products by isolating partial digestion products and then cleaving each with Sma I to determine which limit digestion fragments were generated. Four partial fragments were isolated: a 22% fragment containing 9.5 and 12.8; a 24% fragment containing 1.4, 12.8, and 9.5; a 31% fragment containing 9.5 and 21.2; and a 35% partial containing 21.2 and 17.2 (data not shown). Because the Sma I end fragments were determined to be 26.4 and 17.3, and since 17.2 and 17.3 are λ-DNA fragments, we could unambiguously align these fragments as shown in Fig. 2A. The BamHI and HindIII cleavage sites in λdiltDNA were determined by comparing the products from a digest of each λdiltDNA Sma I cleavage fragment by BamHI or HindIII (Table I) with all the products generated by cleavage with that enzyme alone. In this manner, we were able to assign unambiguously all cleavage sites for BamHI and HindIII.

The Sma I and EcoRI cleavage maps for λdaroe were previously reported by Jorgensen (9) and the EcoRI cleavage map for λdiltDNA by Collins et al. (10). We have confirmed the location of all λdiltDNA EcoRI fragments except 2.3, 0.6, 1.5, and 1.4 and have incorporated the data of Collins et al. (10) for these small fragments into Fig. 2A.

**Location and Direction of Transcription of rRNA Genes**

Fig. 3 shows the results of an experiment in which 32P-labeled 16 S and 23 S rRNAs were hybridized to DNA fragments on nitrocellulose filters according to Southern (18). These data reveal which fragments contain template DNA for the two rRNA species and also give the approximate location and the direction of transcription for both rRNA operons in the two translating phage DNAs (Fig. 2A). Specifically, the Sma I 1.4 fragment from λdaroe and λdiltDNA arises exclusively from the 16 S gene since it and both the Sma I cleavage fragments which flank it hybridize 16 S RNA. The two Sma I sites were predicted by the 16 S rRNA sequence reported by Ehresmann et al. (28); recent DNA sequencing confirms that the Sma I 1.4% fragment contains the central portion of the 16 S gene (11, 29). In both λdaroe and λdiltDNA, 23 S rRNA hybridizes to fragments which map to the right of the Sma I 1.4 fragment, indicating that the direction of rRNA transcription is from left to right in our maps.

**Mapping of the 16 S-23 S Spacer Region**

To map the 16 S-23 S spacer region in greater detail, we isolated the Sma I half of h-DNA to produce a 60% and a 31% fragment from λdiltDNA. Each fragment was 5’-end-labeled (see “Experimental Procedures”) and digested with HindIII to reveal a common fragment of 1100 base pairs, as determined by its mobility relative to the products of

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3 R. Young, unpublished data.

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4 The abbreviation used is: b.p., base pair.
and 2) RNA (28) and DNA (11, 29) sequence data indicate that less than 200 nucleotides of the 16 S gene follow the *Sma* I 1.4 fragment.

We mapped restriction endonuclease cleavage sites in the 1100-base-pair fragment from both transducing phages by the method of Smith and Birnstiel (27). Fig. 4 shows the products of a partial digest of the *AdaroE* 1100-base-pair fragment with the endonucleases *Alu I*, *Hae III*, *Hpa II*, *Mbo I*, *Hph I*, *Mnl I*, and *Hha I*. We performed similar experiments with the enzymes *Hinfi* and *Taq I* (data not shown). The *AdaroE* 1100-base-pair fragment was examined in duplicate experiments with identical results. The final map of the 1100-base-pair fragment is presented in Fig. 2B.

**DNA Sequence Analysis of the 16 S–23 S Spacer Region**—Both strands of *rrnD* (*AdaroE*) and at least one of *rrnX* (*Adaro5*) DNA were sequenced through the 16 S–23 S intergenic region using the techniques developed by Maxam and Gilbert (21). The following fragments were sequenced from the designated restriction endonuclease sites through the indicated regions (see Fig. 2B): *Hae III* (b.p. 138 to b.p. 78) from *rrnD* and *X*, *Hae III* (b.p. 138 to b.p. 241) from *rrnD* and *X*, *Taq I* (b.p. 241 to b.p. 138) from *rrnD*, *Taq I* (b.p. 241 to b.p. 390) from *rrnD*, *HinfI* (b.p. 390 to b.p. 241) in *rrnD* and *X*, *HinfI* (b.p. 390 to b.p. 555) in *rrnD*, and *Taq I* (b.p. 560 to b.p. 390) in *rrnD* and *X*. Sequencing gels covering the single sequence difference in the spacer are shown in Fig. 5; the 16 S–23 S spacer sequence is shown in Fig. 6.

**Fig. 5.** DNA sequencing gels. DNA was prepared for sequencing as described under “Experimental Procedures.” These gels show the region of the spacer in which the one-nucleotide difference between these two operons was observed (residue 374). The numbering is described in the legend to Fig. 2B. Sequences designated are: A: *rrnD*, residues 388 → 367; and B: *rrnX*, residues 388 → 367. Gels are 20% polyacrylamide, 7 M urea as described under “Experimental Procedures.”

**DISCUSSION**

We have mapped the ribosomal RNA operons *rrnX* and *rrnD* carried on λ transducing phages and have determined the DNA sequence of the spacer region between the 16 S and 23 S genes in these two operons. Both spacers are 437 base pairs long and contain the genes for tRNA^{16}_{ile} and tRNA^{16}_{ile} genes. The spacer sequences are identical except for 1 base pair located at position 374.

Since *rrnX* is a hybrid operon (2), it is conceivable that the 16 S–23 S spacer regions of both *Adaro5* and *AdaroE* were derived from the same region of the *E. coli* chromosome during construction of the two transducing phages. However, the following points argue that the two spacer sequences we have examined are distinct, but highly conserved. 1) Studies of ColE1 plasmids (2, 31) carrying tRNA genes demonstrate that of the seven *E. coli* *rrn* operons, three contain both tRNA^{16}_{ile} and tRNA^{16}_{ile} genes and appear otherwise homologous in their 16 S–23 S spacers. 2) The distal portion of *rrnX* has been identified as *rrnC*, based on the presence of tRNA^{16}_{ile} and tRNA^{16}_{ile} (2) and on the location of the *ile* genes on *Adaro5* DNA (10). Since the *rrnC* 16 S–23 S spacer contains tRNA^{16}_{ile} (2) rather than tRNA^{16}_{ile} and tRNA^{16}_{ile} genes, the *rrnX* spacer region must have been derived from another *rrn* operon via a crossover occurring somewhere between the spacer and the distal tRNA genes. We further know that *rrnX* and *rrnD* sequences diverge in the promoter region,\(^5\) making multiple crossovers necessary in order to insert the *rrnD* 16 S–23 S spacer into *rrnX*. Such events seem unlikely in light of the fact that *rrnD* and *rrnC* have opposite orientation on the *E. coli* chromosome (31).

**Anatomy of the 16 S–23 S Spacer**—To facilitate a discussion of various features of the 16 S–23 S spacer in *rrnX* and *rrnD*, we shall divide it into five segments as indicated in Fig. 6. **Segments II** and IV are the tRNA\(^{16}_{ile}\) and tRNA\(^{16}_{ile}\) genes, respectively. Segments I, III, and V separate these structural genes from the large ribosomal RNA genes and from each other.

Segment I (68 base pairs) spans the region between the 3′ terminus of the 16 S gene and the beginning of the first spacer tRNA gene, that for tRNA\(^{16}_{ile}\). We previously established that the first 48 nucleotides of Segment I are complementary to DNA beyond the other end of the 16 S gene, about 1700 nucleotides away (11). Apparently, these distant regions come together in the primary transcript to form an RNase III recognition site. (See Fig. 7 and below.) The first 48 nucleotides of the *rrnE* 16 S–23 S spacer (which contains the gene for tRNA\(^{16}_{ile}\)) are also complementary to DNA at the other end of the 16 S gene (34).

Segments II and IV are the tRNA\(^{16}_{ile}\) and tRNA\(^{16}_{ile}\) genes. Their sequences correspond exactly to those previously determined for the tRNAs by direct RNA sequencing methods (6, 35, 36). Moreover, our sequence for the tRNA\(^{16}_{ile}\) gene and surrounding regions is identical to that recently determined by Sekiya and Nishimura (37) who analyzed a cloned *E. coli* DNA fragment containing this tRNA gene. Like other tRNA genes of known sequence in *E. coli*, the tRNA\(^{16}_{ile}\) and tRNA\(^{16}_{ile}\) DNA sequences contain the CCA terminus required for functional tRNA; hence the products of these genes have no apparently requirement for CCA\(_{OUT}\) addition by tRNA nucleotidyltransferase.

The 42 base pairs which separate the two tRNA genes comprise Segment III. This space is considerably longer than the distance between tRNAs in the well characterized dimeric tRNA precursor molecules of phage T4\(^5\) (38, 39) or *E. coli* (40).

\(^5\) C. Guthrie, personal communication.
The 16 S-23 S rRNA Spacer Region

Although the sequence of rrrD 16 S-23 S spacer DNA is shown. Except for a C to T transition at position 374 (indicated by *), the sequence for rrrX is identical. Mature tRNA and rRNA gene sequences are un-

Segment V, between the end of the tRNA\textsubscript{Ile} gene and the beginning of the 23 S rRNA gene, is surprising includes 40% of the spacer DNA (174 residues). Of the five spacer segments, only this region is large enough to encode any of the small stable RNAs found in E. coli, yet it contains sequences dissim-

nucleases used. While we do not know whether the difference in G-C content is of biological significance, the fact that A-T-rich regions also occur in the intergenic spacers of at least some eukaryotic rRNA operons (44, 45) suggests an important function for A-T-rich spacers. One plausible explanation is that the low G-C content of the regions surrounding the tRNA genes prevents adjacent sequences from interfering with formation of the proper tRNA secondary and tertiary structure, which is required for recognition by RNase P and other enzymes whose action releases the tRNAs from the 30 S primary transcript.

RNA Processing Sites in the 16 S-23 S Spacer—RNase III, probably the first endonuclease to act on the 30 S rRNA primary transcript in wild type E. coli, has long been known to cleave at least once within the 16 S-23 S spacer (46, 47). Detailed analysis of the 16 S-containing RNase III digestion product revealed that the enzyme cleaves \textit{3'} to the sequence GCUCACACA (after position 33, Figs. 6 and 7) near the beginning of the spacer RNA. The 23 S\textsubscript{m} product was found to contain no additional large oligonucleotides relative to mature 23 S rRNA, suggesting that RNase III acts at a site very close to the distal end of the spacer. These data and the fact that RNase III cleaves completely double-stranded RNA in \textit{vitro} (48-50) correlate well with the potential of sequences

\textsuperscript{6} D. Charny, D. Goldberg, and J. A. Steitz, unpublished observations.
The 16 S–23 S rRNA Spacer Region

Fig. 7. Possible secondary structure of spacer RNA. The spacer sequence was searched for inverted repeats using the nucleic acid computer program of Korn et al. (32). All hairpin structures illustrated have calculated ΔG values less than −4.5 kcal/mol (33). Presumed sites of RNase P cleavage are indicated by P. RNase III scission (denoted by III) occurs after residue 33 of the spacer and, as indicated by the dotted arrows, 5' to one of the three UC sequences appearing within the complementary portion of the rRNA transcript preceding 16 S sequences (11); residues −105 to −132 prior to 16 S are pictured. A second site of RNase III recognition and cleavage of spacer RNA in vitro is located near position 290 (see text). A third scission apparently occurs near the 3' end of spacer RNA (not shown), within a region which is complementary to sequences distal to the 23 S gene (see text). Spacer residues are numbered as in Fig. 6; the two tRNA sequences are indicated schematically.

at the two ends of the 16 S–23 S spacer to form extensive secondary structures with distant portions of the 30 S pre-rRNA (see above). Moreover, oligonucleotides predicted by our DNA sequences near both ends of the spacer (Fig. 6) have recently been identified in small double-stranded RNAs isolated from E. coli; these are cleavable in vitro by RNase III⁷ (51). Finally, a third point of RNase III scission of the 30 S pre-rRNA has recently been identified⁸ near residue 290 (Figs. 6 and 7); it is not yet clear what structural features of the spacer RNA specify recognition and cleavage at this point.

RNase P, which specifically cleaves tRNA precursors to generate the 5' end of the mature molecule (52), is another endonuclease which presumably participates in the in vivo processing of the 30 S rRNA transcript. Indeed, some of the aberrant ribosomal RNA precursors appearing in cells lacking RNase III could be explained by RNase P action at the 5' end of spacer tRNAs (43). Note in Fig. 7 that the spacer sequences surrounding the tRNA genes predict that RNase P cleaves 5' to tRNA₁₅ and tRNA₁₈₁₆ within a double-stranded region, while the comparable site in tRNA₁²₆ is single-stranded. Both types of structures at RNase P cleavage sites have been previously noted in E. coli or phage T4 tRNA precursor molecules (see Ref. 53).

The in vitro processing of spacer RNA by RNase P has also been recently studied by Lund et al.⁹ who used RNase III-produced fragments of 30 S pre-rRNA as substrates. Surprisingly, they find that the RNase P site 5' to tRNA₁₅ is much less susceptible to cleavage than the site 5' to tRNA₁₆. Perhaps this differential activity can be explained by inaccessibility of the tRNA₁₆ acceptor stem due to formation of the unusual RNA secondary structure pictured in Fig. 7. By contrast, in vivo both in normal cells and in chloramphenicol-treated cells containing CoEI plasmids carrying the Ile-Ala tRNA spacer region (7), approximately equal amounts of the mature tRNAs are formed. A similar discrepancy in the in vitro compared to in vivo processing of a phage T4 dimeric tRNA precursor has recently been documented (54).

Finally, in addition to RNase III and P, other enzymes responsible for trimming the 3' ends of nascent tRNA molecules must process spacer RNA. However, although active in crude extracts (6), the nucleases which perform these functions remain obscure.

23 S rRNA Gene Sequences—The sequences we determine for the initial 108 base pairs of the 23 S rRNA gene from rrnD and rrnX are included in Fig. 6. These sequences contain all of the RNase T1 oligonucleotides found near the 5' terminus of 23 S rRNA (55) but align many of these oligonucleotides differently than suggested by Branlant et al. (55).

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⁷ H. D. Robertson, personal communication.
⁸ E. Lund, J. E. Dahlberg, and C. Guthrie, personal communication.

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