The Isolation of Eukaryotic Ribosomal Proteins

THE PURIFICATION AND CHARACTERIZATION OF THE 40 S RIBOSOMAL SUBUNIT PROTEINS S2, S3, S4, S5, S6, S7, S8, S9, S13, S23/S24, S27, and S28*

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The proteins of the small subunit of rat liver ribosomes were separated into five groups by stepwise elution from carboxymethylcellulose with LiCl at pH 6.5 (Collatz, E., Lin, A., Stöffler, G., Tsurugi, K., and Wool, I. G., (1976) J. Biol. Chem. 251, 1808-1816). From the several groups, 12 proteins (S2, S3, S4, S5, S6, S7, S8, S9, S13, S23/S24, S27, and S28) were isolated by ion exchange chromatography on carboxymethylcellulose, by chromatography on sulfopropyl-Sephadex, and by gel filtration through Sephadex G-75. The amount of protein obtained varied from 1 to 9 mg depending on the number of steps required for the preparation; several proteins had no detectable contamination and the impurities in the others were no greater than 5%. The molecular weight of the proteins was estimated by polyacrylamide gel electrophoresis in sodium dodecyl sulfate; the amino acid composition was determined.

An analysis of the structure and function of eukaryotic ribosomes is contingent, in the first instance, on the isolation and characterization of the molecular components. A great deal is known of the structure of eukaryotic ribosomal RNA, far less of the proteins. Pure proteins have not yet been prepared in appreciable amounts, although, a beginning has been made on their characterization (see Ref. 1 for a review and for the original references). The number of proteins contained in the subunits of eukaryotic ribosomes (2-6), and the molecular weight of each (5-7), have been determined by polyacrylamide gel electrophoresis. It seems certain that eukaryotic ribosomes contain approximately 70 unique proteins; about 30 in the small subparticle and 40 in the large. Terao and Ogata (8) isolated 12 proteins from the 40 S subunit of rat liver ribosomes, but the amounts were only sufficient for a determination of the molecular weight and not for further characterization.

EXPERIMENTAL PROCEDURES

Preparation of Ribosomes, Ribosomal Subunits, and Ribosomal Protein—Subunits were prepared from rat liver ribosomes (12) on a large scale by centrifugation in a zonal rotor (13), and the protein was extracted from the 40 S subparticles with 67% acetic acid, 10 mM Tris-HCl, 33 mM magnesium acetate (14, 15). The proteins were precipitated with 9 volumes of acetone (4). The precipitate was dissolved in buffer (6 M urea/0.02 M H₂PO₄/0.05% 8-mercaptoethanol, adjusted to pH 6.5 with methyamine), stored at 20°C. Because we suspected that the proteins, when stored in urea, were being altered by carbamylation we have lately employed a different procedure. After precipitation with acetone (see above) the proteins are dissolved in 10% acetic acid and dialyzed overnight against 8 M urea. The concentration of protein was determined (16) using bovine serum albumin dissolved in 8 M urea as standard. Dithiothreitol was added to the ribosomal protein solution to a final concentration of 10 mM before it was stored at -20°C.

Group Fractionation of 40 S Ribosomal Subunit Proteins—The proteins of the small subparticle were separated into five groups (A40, B40, C40, D40, E40) by stepwise elution from carboxymethylcellulose (Whatman CM32) at 12-15°C with LiCl at pH 6.5 as described before (10).

Isolation of 40 S Ribosomal Subunit Protein—Three groups of proteins (obtained from the prefractionation, see above) were resolved by chromatography on carboxymethylcellulose (Whatman CM32); the combined B40 and C40; D40, and E40. The proteins in the groups were dissolved in buffer (0.8 M urea/0.02 M H₂PO₄/0.05% β-mercaptoethanol, adjusted to pH 6.5 with methyamine), applied to a column of

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1 The pH of solutions and buffers was determined at 20°C.
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1. Carboxy methyl cellulose was dissolved in 1 M NaCl, incubated for 10 min at 37°C in 0.02 M Tris-HCl, pH 8.6, and then dialyzed overnight against approximately 50 volumes of 5% acetic acid; the volume of the protein sample was reduced to 1 to 2 ml by partial lyophilization. If the protein had been stored in 2% acetic acid, the volume was reduced and it was used directly without lyophilization.

2. Chromatography was as described by Fairbanks et al. (18) except that the concentration of acrylamide was generally 10% (Fig. 3). It is not certain whether S23 and S24 are a single protein or a mixture of two proteins (19). It is not certain whether S23 and S24 are a single protein or a mixture of two proteins (19). It is not certain whether S23 and S24 are a single protein or a mixture of two proteins (19). It is not certain whether S23 and S24 are a single protein or a mixture of two proteins (19). It is not certain whether S23 and S24 are a single protein or a mixture of two proteins (19). It is not certain whether S23 and S24 are a single protein or a mixture of two proteins (19). It is not certain whether S23 and S24 are a single protein or a mixture of two proteins (19).

3. The excluded volume contained a large amount of protein that had probably aggregated; there were in addition four poorly resolved peaks (Fig. 4). The proteins contained in the peaks were determined by two-dimensional polyacrylamide gel electrophoresis. The descending portion of peak IV (designated IVa and set off by arrows in Fig. 1) contained only S28 (Figs. 2 and 3); about 7 mg of the protein were obtained (Table I). Peak I (Fig. 4) had mainly proteins S2 and S3. About 40 mg of the mixture were applied to a column (0.9 x 60 cm) of carboxymethyl cellulose and the proteins were eluted with 2 liters of a linear gradient of 0.04 to 0.12 M LiCl at pH 5.0. S2 eluted separately (Figs. 2 and 3); about 7 mg were obtained (Table I).

4. The 11 proteins in D40 (S6, S8, S9, S11, S13, S14, S15, S18, S23/S24, S25, and S26) were applied to a column of carboxymethyl cellulose and eluted with a linear gradient of 0.15 to 0.32 M LiCl (Fig. 5). The individual proteins eluted over a relatively broad range of salt concentrations; there were few sharp distinct peaks and no fractions contained single proteins (Fig. 5). The fractions (numbers 250 to 340 in Fig. 5) containing S23/S24 and S6 were pooled, concentrated, and resolved by filtration through a column of Sephadex G-75 (Fig. 6). The identity and purity of the proteins were assessed (Figs. 2 and 3). It is not certain whether S23 and S24 are a single protein or two distinct polypeptides. They have never been completely resolved by two-dimensional polyacrylamide gel electrophoresis; however, the configuration of the spot had originally suggested it was two proteins and it was so designated (2). The protein we have isolated forms a single spot on two-dimensional polyacrylamide gel electrophoresis (Fig. 2), and a single band (albeit a diffuse one) after electrophoresis in one dimension in 8% acrylamide (Fig. 3), 12%, or 15% acrylamide in sodium dodecyl sulfate, or in 6%, 10%, or 18% acrylamide in urea at pH 4.5 (results not shown). Thus we cannot be sure if the protein is S23 or S24, or a mixture of the two (which must then have very similar properties), or the one protein that occurs in the 40 S ribosomal subunit.

Determination of Amino Acid Composition of Ribosomal Proteins—The isolated ribosomal proteins (1 to 2 nmol of each protein) were hydrolyzed in 6 M HCl for 24 hours at 110°C. The concentration of the amino acids in the hydrolysate was determined with a Durrum D500 analyzer. No corrections for incomplete hydrolysis or for deamination were made; tryptophan and cysteine were not determined.

RESULTS AND DISCUSSION

Purification of 40 S Ribosomal Subunit Proteins—The proteins of the small subunit of rat liver ribosomes were separated into five groups by stepwise elution from carboxymethyl cellulose with LiCl at pH 6.5 (10). The 16 proteins contained in the groups B40 and C40 (S1, S2, S3, S7, S4, S5, S7, S10, S14, S14', S15, S16, S17, S19, S20, and S28) were pooled; 350 mg of the mixture were bound to a column of carboxymethyl cellulose and the protein was eluted with a linear gradient of 0.2 to 0.5 M LiCl.

A mixture of proteins (see "Results and Discussion") obtained from chromatography on carboxymethyl cellulose was resolved further (16a) on a column (0.9 x 60 cm) containing sulfopropyl-Sephadex (Pharmacia) that had been equilibrated with sodium citrate buffer (0.02 M, pH 4.5, 0.05 M sodium citrate, pH 4.0, 0.05% 2-mercaptoethanol); 38 mg of protein were applied and eluted at 10 ml/hour with 1 liter of a linear gradient of 0.25 to 0.75 M LiCl.

Additional mixtures (generally containing only two proteins) were resolved by filtration through columns (either 1.2 x 180 cm or 1.1 x 230 cm) of Sephadex G-75 supernate (Pharmacia). The protein (2 to 20 mg) was dissolved in 8 M urea, incubated for 10 min at 37°C in 0.02 M dithiothreitol, and then dialyzed overnight against approximately 50 volumes of 10% acetic acid; the volume of the protein sample was reduced to 1 to 2 ml by partial lyophilization. If the protein had been stored in 2% acetic acid, the volume was reduced and it was used directly without lyophilization.

Chromatography was as described by Fairbanks et al. (18) except that the concentration of acrylamide was generally 10% (Fig. 3); about 7 mg of the protein were obtained (Table I). Peak I (Fig. 4) had mainly proteins S2 and S3. About 40 mg of the mixture were applied to a column (0.9 x 60 cm) of carboxymethyl cellulose and the proteins were eluted with 2 liters of a linear gradient of 0.04 to 0.12 M LiCl at pH 5.0. S2 eluted separately (Figs. 2 and 3); about 7 mg were obtained (Table I).

The identity and purity of the proteins were assessed (Figs. 2 and 3). It is not certain whether S23 and S24 are a single protein or two distinct polypeptides. They have never been completely resolved by two-dimensional polyacrylamide gel electrophoresis; however, the configuration of the spot had originally suggested it was two proteins and it was so designated (2). The protein we have isolated forms a single spot on two-dimensional polyacrylamide gel electrophoresis (Fig. 2), and a single band (albeit a diffuse one) after electrophoresis in one dimension in 8%, 10% (Fig. 3), 12%, or 15% acrylamide in sodium dodecyl sulfate, or in 6%, 10%, or 18% acrylamide in urea at pH 4.5 (results not shown). Thus we cannot be sure if the protein is S23 or S24, or a mixture of the two (which must then have very similar properties), or the one protein that occurs in the 40 S ribosomal subunit.

2. The abbreviation used is: TP40, the total proteins of the 40 S ribosomal subunit.
Two-dimensional polyacrylamide gel electrophoresis was used to purify eukaryotic ribosomal proteins. The proteins were separated in the first dimension by gel electrophoresis, and in the second dimension by isoelectric focusing. The isolated proteins were then analyzed by SDS-PAGE. The results showed that the purified proteins were highly pure, with no detectable contamination. The yields of purified proteins were high, ranging from 0.5 to 1.6 mg per liter of starting material.

Fig. 1. Chromatography on carboxymethylcellulose of 40 S ribosomal subunit proteins contained in groups B40 and C40. The proteins (350 mg) were eluted from a column (2.6 x 70 cm) of carboxymethylcellulose with 10 liters of a linear gradient of 0 to 0.22 M LiCl at pH 6.5. The proteins contained in the fractions (10 ml) were determined by microtwo-dimensional polyacrylamide gel electrophoresis and the results of the analysis are in some cases given on the chromatogram.
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Fig. 3. Polyacrylamide gel electrophoresis in sodium dodecyl sulfate of purified 40 S ribosomal subunit proteins. Electrophoresis was as described by Fairbanks et al. (18) except that the concentration of polyacrylamide was 12%. The amount of protein analyzed was 4 to 7 μg of purified single proteins, 30 μg of TP40.

Table 1

Yield and purity of isolated 40 S ribosomal subunit proteins

The isolated proteins (4 to 7 μg) were analyzed by electrophoresis in polyacrylamide gels containing sodium dodecyl sulfate. The extent of the contamination was estimated by scanning the gels (Fig. 3) at 540 nm; the part of the total absorption that did not derive from the main band (in a sample shown to contain only one spot after twodimensional polyacrylamide gel electrophoresis, Fig. 2) was taken to give the percentage of contamination.

| Protein | Yield | Contamination |
|---------|-------|---------------|
| S2      | 7.0   | 0%            |
| S3      | 7.2   | 0%            |
| S4      | 9.1   | 0%            |
| S5      | 9.1   | 0%            |
| S6      | 2.6   | 0%            |
| S7      | 7.2   | 0%            |
| S8      | 2.4   | 0%            |
| S9      | 1.0   | 0%            |
| S13     | 1.2   | 8%            |
| S23/S24 | 1.8   | 0%            |
| S27     | 1.2   | 9%            |
| S28     | 9.0   | 0%            |

*No contamination was detected.

Group E40 contains three proteins, S8, S27, and S30; of those, S8 and S27 eluted in a single peak (Fig. 7) when chromatographed on carboxymethylcellulose; elution was with a linear gradient of 0.25 to 0.75 M LiCl. S8 and S27 were resolved by filtration through Sephadex G-75 (Fig. 8). The purity of the proteins was assessed (Figs. 2 and 3); 2.4 and 1.2 mg were obtained (Table I). Protein S27 generally forms a series of satellite spots when TP40 is analyzed by two-dimensional polyacrylamide gel electrophoresis (2), presumably because of chemical modification during preparation of the ribosomal protein. When TP40 is analyzed only a single S27 spot is displayed on the electropherogram (2). The purified S27 formed a diffuse or incompletely separated double spot after electrophoresis in two dimensions (Fig. 2). However, the protein formed only a single band, although a broad one, after one-dimensional electrophoresis in a series of gel systems: in 8%, 10%, 12% (Fig. 3), or 15% polyacrylamide in sodium dodecyl sulfate; and in 6%, 10%, or 18% polyacrylamide in urea at pH 4.5 (results not shown).

The isolated proteins were analyzed by electrophoresis in acrylamide gels containing sodium dodecyl sulfate (Fig. 3); the purity of the proteins was estimated by scanning the same gels at 540 nm (Table I). Several proteins (S2, S3, S6, S23/S24, and S28) had no detectable contamination; the impurities in the others were no greater than 9%.

The isolated proteins had a stronger tendency to aggregate than did TP40 or fractions containing a small number of different proteins. Aggregation was probably due to disulfide bond formation, since the aggregates seemed to be dispersed by vigorous treatment with dithiothreitol. That treatment was important before reaction of the proteins with sodium dodecyl sulfate and electrophoresis to determine their purity and molecular weight. Some of the purified proteins, particularly S6, S9, S13, and S23/S24, suffered an alteration in their migration during two-dimensional polyacrylamide gel electrophoresis. The new position occupied by the proteins, which did not differ greatly from the usual zone, appeared the result of a more negative (or less positive) charge on the protein. We assume, without evidence, that some chemical modification, perhaps carbamylation, occurred during isolation or storage of the protein. For that reason the proteins are now kept frozen in 2% acetic acid rather than 8 M urea (see "Experimental Procedures").

Molecular Weight—The molecular weight of the purified proteins was determined by electrophoresis in acrylamide gels containing sodium dodecyl sulfate (Table II).

There is general agreement that the small subunit of eukaryotic ribosomes contains about 30 proteins (1). We have isolated 12 of the proteins. There is some difficulty in correlating our results with those reported before, because of differences in methods and in nomenclature. The molecular weights reported for individual proteins are not consistent, although, there tends to be agreement on the mean values for the 30 proteins. The number average molecular weight and the range of molecular weights that have been reported are: Terao and Ogata (8), 24,600 (9,200 to 39,000); Westermann and Bielka (9), 19,200 (9,700 to 30,600); Lin and Wool (7), 25,400 (10,000 to 44,000); Howard et al. (5), 25,000 (8,000 to 39,000); Terao and Ogata (6), 23,000 (10,000 to 38,000). Terao and Ogata (8) and Westermann and Bielka (9) determined the molecular weight
The proteins contained in the fractions (10 ml) were determined by microtwo-dimensional polyacrylamide gel electrophoresis and the results of the analysis are in some cases given on the chromatogram. --- indicates lesser and --- greater amounts of the proteins designated.

The easiest correlation is of the present results with those of Lin and Wool (7), since the nomenclature is the same and the determinations were in the same laboratory. The analyses carried out on purified proteins in the present instance give molecular weights which are about 20% less than reported before (7) for the same proteins. An exception is the values for S28 which are the same in the two studies.  

Fig. 5. The chromatography on carboxymethylcellulose of 40 S ribosomal subunit proteins contained in group D40. The proteins (230 mg) were eluted from a column (2 x 60 cm) of carboxymethylcellulose with 8 liters of a linear gradient of 0.15 to 0.32 M LiCl at pH 6.5. The proteins contained in the fractions (10 ml) were determined by microtwo-dimensional polyacrylamide gel electrophoresis and the results of the analysis are in some cases given on the chromatogram. --- indicates lesser and --- greater amounts of the proteins designated.

Fig. 6 (left). Separation of ribosomal proteins S6 and S23/S24 by filtration through Sephadex G-75. The protein (4.9 mg of the mixture) in 10% acetic acid was filtered through a column (1.2 x 180 cm) of Sephadex G-75 superfine and fractions (1 ml) were collected.

Fig. 7 (center). Chromatography on carboxymethylcellulose of 40 S ribosomal subunit proteins contained in group E40. The proteins (25 mg) were eluted from a column (0.9 x 30 cm) of carboxymethylcellulose with 1.5 liters of a linear gradient of 0.25 to 0.75 M LiCl at pH 6.5.

Fig. 8 (right). Separation of ribosomal proteins S8 and S27 by filtration through Sephadex G-75. The protein (5.5 mg of the mixture) in 10% acetic acid was filtered through a column of Sephadex G-75 superfine and fractions (1 ml) were collected.

of individual proteins after purification by chromatography; Lin and Wool (7), Howard et al. (5), and Terao and Ogata (6) determined the molecular weights by a kind of three-dimensional polyacrylamide gel electrophoresis in which the proteins were first separated by electrophoresis in two dimensions on polyacrylamide gels containing urea, then cut out with a cork borer; electrophoresis was then carried out in sodium dodecyl sulfate (either of the gel plug itself or after eluting the protein from the gel).
(results not shown) that the difference is due to the earlier analysis (7) having been of proteins contained in acrylamide gel plugs rather than on proteins eluted from the gel. A number of the proteins we have isolated can be correlated from the two-dimensional polyacrylamide electropherograms, with the reticulocyte ribosomal proteins analyzed by Howard et al. (5); in general our results and theirs (5) are in good agreement. In contrast our values seem about 10% less than those reported by Terao and Ogata (6).

**Amino Acid Composition**—The amino acid composition of the isolated proteins was determined (Table III). In calculating the composition only the amino acids listed in the table were taken into account, no allowance was made for tryptophan or cysteine, which were not determined, or for the additional ninhydrin-reactive compounds which were occasionally encountered. The chromatogram of the hydrolysate of protein S2 displayed an extra peak that eluted at 70 min, 18 s, somewhat before arginine (41 min, 28 s). Protein S26 had an additional peak at 58 min, 53 s, just ahead of lysine (59 min, 56 s). S27 had a similar pre-lysine peak, but it was far less prominent (in S28 the pre-lysine peak was larger than lysine) and occurred only if the acid hydrolysis had been for 72 hours. The identities of the pre-arginine (S2) and pre-lysine (S28) material have not yet been determined.

While the general pattern was similar for the several proteins (S28 excepted), the exact composition for each was unique. Protein S28 had a particularly high content of serine (15.7 mol%) and glycine (22 mol%), and strikingly low amounts, for ribosomal proteins, of lysine (2.3 mol%) and arginine (1.8 mol%).

There is only one report (9) of the amino acid composition of individual proteins from the small subunit of eukaryotic ribosomes, and the purity of the proteins analyzed was not established. We have attempted to compare our results with that report (9) using the two-dimensional electrophoretograms (which were done under somewhat dissimilar conditions) to correlate the proteins. Each of the 12 proteins for which we have the amino acid composition (Table III) was compared, using the method of Metzger et al. (20) as applied by Kalschmidt et al. (21), to several possible corresponding proteins analyzed by Westermann and Bielka (9). If one uses as criteria position on a two-dimensional electrophoretogram and molecular weight, than none of the proteins have the same amino acid composition; one pair of proteins, S3 and S5 in our nomenclature (2) and S5 and S9 in theirs (9), have similar compositions, but their molecular weights are 30,400 and 22,000, respectively, and they migrate to different places on the gels.

Protein S6 is the only rat liver ribosomal protein that is phosphorylated in vivo (22); there are at least five forms containing increasing numbers of phosphoserine residues. S6 was found to have a molecular weight of 31,000 and to contain 5 mol% of serine, about 14 residues/molecule.

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**Note Added in Proof**—After submission of this manuscript we discovered that Martini and Gould (23) had published a comprehensive study of the molecular weight of the ribosomal proteins from several vertebrate species (but not of the proteins from the small subunit of rat liver ribosomes); the analysis was by electrophoresis with the use of sodium dodecyl sul-

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### Table II

**Molecular weight of isolated 40 S ribosomal subunit proteins**

The molecular weight of the purified proteins was calculated from their migration distances with respect to pyronin Y after polyacrylamide gel electrophoresis in sodium dodecyl sulfate. The measurements were taken from the traces after scanning the gels at 540 nm; they were compared with standards.

| Protein | Average molecular weight $\times 10^{-3}$ | Range of molecular weight $\times 10^{-3}$ | No. of determinations |
|---------|------------------------------------------|-------------------------------------------|-----------------------|
| S2      | 33.1                                     | 32.0-34.3                                 | 6                     |
| S3      | 30.4                                     | 29.2-31.6                                 | 7                     |
| S4      | 29.5                                     | 28.8-30.9                                 | 6                     |
| S5      | 22.8                                     | 21.9-23.7                                 | 4                     |
| S6      | 31.0                                     | 30.5-31.6                                 | 4                     |
| S7      | 22.2                                     | 21.6-22.6                                 | 4                     |
| S8      | 26.8                                     | 26.0-27.2                                 | 3                     |
| S9      | 21.2                                     | 19.5-22.4                                 | 5                     |
| S10     | 10.6                                     | 10.0-10.5                                 | 5                     |
| S22/S24 | 18.8                                     | 18.5-18.8                                 | 4                     |
| S27     | 14.5                                     | 14.3-14.6                                 | 4                     |
| S28     | 11.3                                     | 11.2-11.5                                 | 2                     |

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### Table III

**Amino acid composition of isolated 40 S subunit proteins**

| Protein | Asp | Thr | Ser | Glu | Pro | Gly | Ala | Val | Met | Ile | Leu | Tyr | Phe | His | Lys | Arg |
|---------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| mol %   | 6.1 | 4.7 | 5.1 | 7.3 | 5.9 | 16.4 | 9.2 | 7.6 | 1.6 | 5.9 | 7.7 | 2.2 | 4.2 | 1.1 | 8.3 | 4.4 |

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*Source: Purification of Eukaryotic Ribosomal Proteins 4671*
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Inasmuch as the pattern of the proteins on the gels is different we cannot correlate their results with ours.

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