The product of the selB gene from Escherichia coli is required for co-translational insertion of selenocysteine into protein. To make the SELB protein accessible to biochemical analysis, the protein was purified from cells that overexpressed the selB gene from a phage T7 promoter plasmid. It was calculated that the overproduced SELB protein was purified 20-fold. The N-terminal amino acid sequence of the purified protein was determined, and it confirmed that the initiation codon of selB mRNA translation overlaps the stop codon of the preceding selA gene by 4 bases. Structural similarity between SELB and elongation factors was demonstrated by limited proteolysis of SELB by trypsin. The cleavage sites within SELB were identified by N-terminal sequencing of the two proteolytic products. The position in the SELB protein of the major cleavage site was homologous to a tryptic cleavage site which is characteristic for elongation factors. Immunological analysis showed that the levels of SELB are equivalent in aerobically and anaerobically grown cells; the amount of the protein was estimated to be approximately 1100 copies/E. coli cell. Upon fractionation of cell extracts, SELB was found to be partially associated with the ribosomes. The results therefore indicate that SELB is the first known elongation factor-like protein that has specificity for a particular charged tRNA.

Selenoprotein synthesis requires a special translational step in which a specific UGA codon directs the incorporation of selenocysteine (1). In Escherichia coli, we could identify four genes, termed selA, selB, selC and selD, whose products are required for selenocysteine biosynthesis and incorporation (2). The gene product of selC is a tRNA species (tRNA^Seleno^) that is aminoacylated with L-serine (3). The products of the selA and selD genes are required for the subsequent conversion of serine to selenocysteine, which occurs on the tRNA (4, 5). A functional selB gene product is not required up to this step. In contrast, mutations in selB cause an accumulation of preformed selenocysteyl-tRNA^Seleno^ in vivo (4). Therefore, in the absence of SELB, selenocysteyl-tRNA^Seleno^ cannot participate in translation.

DNA sequence analysis of the cloned selB gene revealed an open reading frame coding for a protein of 614 amino acids, corresponding to an M, of 68,800 (6). The derived amino acid sequence reveals that the N-terminal half of the SELB protein shares extensive sequence similarity with the translation factors EF-Tu and initiation factor eIF2 (6). In this paper we report on the initial characterization of the SELB protein. The protein was purified and characterized both biochemically and immunologically. The data presented are consistent with our hypothesis that SELB is a special translation factor that is essential for the insertion of selenocysteine into protein.

EXPERIMENTAL PROCEDURES

Materials—Restriction enzymes, Klenow fragment of DNA polymerase I, and T4 DNA ligase were purchased from Boehringer Mannheim. [35]S]Methionine and [125]I-protein A from Staphylococcus aureus were obtained from Du Pont-New England Nuclear. TPCK-treated trypsin and poloxoyethylene 9 lauryl ether (Polydocanol) were purchased from Sigma. Coomassie Brilliant Blue R-250 was from Serva (Heidelberg, FRG). The Nucleosil 300-7C4 HPLC column was obtained from Macherey and Nagel (Düren). Protein G-Sepharose 4 Fast Flow and CNBr-activated Sepharose 4B were obtained from Pharmacia LKB Biotechnology Inc.

DNA Cloning Techniques—Standard procedures were used for plasmid preparations, restriction endonuclease digestions, ligations, transformations, and gel electrophoresis of DNA (7).

Expression of the selB Gene in the T7 Promoter Polyomerase System—For overproduction of SELB protein, the selB gene was cloned into the phase T7 promoter expression plasmid pT7-6 (8). Briefly, pT7-6 DNA was linearized with restriction endonuclease HindIII and the 5' protruding ends were filled in with DNA polymerase (Klenow fragment). After cleavage with SalI the vector DNA was ligated with the 2.3-kilobase EcoRV-SalI fragment of plasmid pWL144 which harbors the complete selB gene (Fig. 1) (2). The resulting plasmid, pWL194, carries selB under the control of the phase T7 promoter. For expression of selB, pWL194 was transformed into E. coli strain K38 (9), which had already been transformed with plasmid pGPl-2 (8). Synthesis of SELB protein was followed by labeling with [35]S]Methionine according to Tabor and Richardson (8).

Purification of SELB Protein—E. coli strain K38 harboring plasmids pGPl-2 and pWL194 was grown in a 10-liter Biostat fermenter (B. Braun, Melsungen, FRC) at 30 °C in a medium containing (w/v) 0.2% glucose, 0.1% glycerol, 1% peptone, 0.5% yeast extract, 25 mM NaCl, 2 mM MgCl₂, 60 mM potassium phosphate (pH 7.1), and asparagin and kanamycin sulfate, 50 μg/ml each, to select for maintenance of the plasmids. When the optical density (OD₆₀₀) had reached a value of 2.5, the temperature was raised to 37 °C to induce expression of selB. It was subsequently lowered to 33 °C, and aeration was continued for 60 min. The culture then was chilled to 0 °C, and the cells were harvested with the aid of a continuous flow centrifuge. The harvested cells were washed once with buffer A (50 mM Tris-Cl, pH 7.4, 10 mM MgCl₂, 50 mM KCl, 2 mM diithiothreitol (DTT), and 0.5 mM EDTA) and then resuspended in 1 volume of buffer A containing phenylmethylsulfonyl fluoride at

1 The abbreviations used are: EF, elongation factor; TPCK, L-l-

tosylamide-2-phenylthyl chloromethyl ketone; HPLC, high pressure liquid chromatography; DTT, dithiothreitol; SDS, sodium dodecyl sulfate.
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Figure 1. Insert of plasmid pWL144 and nucleic acid sequence of selA-selB overlap. The open box indicates the extent of the selB structure that is sequenced in this work along with the black line that represents the insert DNA and the thin line, part of the vector pACYC184. The nucleic acid sequence and derived amino acid sequence of the selA-selB open reading frame overlap are illustrated below the insert. The sequence of the noncoding strand is given in the 5' to 3' direction. The ATG start codon of selB mRNA translation is boxed, and the putative Shine-Dalgarno sequence is underlined. The termination codon (TGA) of the selA gene is indicated by asterisks. C, Csl; EV, EcoRV; Su, Sau3A; M, MluI; S, Sall; x, restriction is possible only in strain W3A321 (30 kbp, kilobase).

0.1 mg/ml and DNase I at 20 mg/ml. Cells were broken by two passages through a French press cell (16,000 psi), and the cell debris was removed by two consecutive centrifugations (30 min each at 30,000 x g). The supernatant fraction was subjected to centrifugation at 150,000 x g for 60 min, and the resulting sediment containing the ribosomes was washed twice with buffer A containing 100 mM NH₄Cl and finally with buffer A containing 1 M NH₄Cl. The SELB protein can be extracted from the ribosomal fraction by washing in the presence of 1 M NH₄Cl. The ribosomes were removed by ultracentrifugation (60 min at 150,000 x g), and the high salt wash fraction was subjected to fractionation on a ammonium sulfate precipitation. The high salt wash was first adjusted to 45% ammonium sulfate saturation, and the precipitate formed was removed by centrifugation. The supernatant then was brought to 63% saturation, the resulting precipitate containing SELB was again collected by centrifugation and afterward dissolved in 30 ml of buffer B (potassium phosphate, pH 7.0 (at the concentration indicated), 2 mM magnesium acetate, 1 mM DTT, and 0.5 mM EDTA) containing 100 mM potassium phosphate and dialyzed for 6 h against two changes, each of 2 liters, of the same buffer. Following a further centrifugation step (10 min at 30,000 x g), the solution was applied to a hydroxyapatite column (Bio-Gel HTP, 20 x 100 mm) equilibrated with buffer B (100 mM potassium phosphate). The column was developed with 500 ml of a linear gradient (100-200 mM potassium phosphate in buffer B) at a flow rate of 20 ml/h. SELB eluted at a concentration of approximately 180 mM phosphate. The peak fractions containing SELB were pooled and concentrated by ultrafiltration (Amicon cell, PM-10 membrane) to an approximate protein concentration of 6 mg/ml. The concentrated solution was dialyzed once against 2 liters of buffer B containing 10 mM potassium phosphate. During dialysis, pure SELB protein precipitated because of its low solubility in low salt/low phosphate buffers. The precipitate was collected by centrifugation and redissolved in buffer C (100 mM potassium phosphate, pH 7.0, 5 mM MgCl₂, 1 mM DTT, and 0.5 mM EDTA) which was supplemented with 1 mM GDP to enhance the solubility of SELB. The solution was dialyzed for three times, each time for a period of 12 h, against buffer C (2 liters) and finally against buffer C containing 50% glycerol. The purified protein was stored at -20 °C in small aliquots.

N-terminal Amino Acid Sequence Analysis—A solution containing 250 μg of purified SELB protein was saturated with urea, dialyzed against 0.1 M acetic acid, spotted on a glass fiber filter, and washed with 40% methanol, 10% acetic acid (v/v). N-terminal Edman degradation (10) were carried out by the gas phase method (11) in a noncommercial sequencer (12), and the phenylthiohydantoin derivatives of the amino acids were identified by isotopic HPLC (13).

Limited Trypsinolysis of SELB—SELB protein was subjected to limited proteolysis by following the procedure given by Möller and co-workers (14). 20 μg of SELB protein dissolved in 100 μl of 50 mM Tris-Cl, pH 7.4, containing 100 mM KCl, 10 mM MgCl₂, 1 mM CaCl₂, and 1 mM DTT was incubated at 28 °C with 0.2 μg of TPCK-treated trypsin. 20-μl samples were removed before and 5, 10, 20, and 40 min after trypsin addition and mixed with 20 μl of sample buffer (15). After boiling for 3 min the samples were subjected to denaturing electrophoresis in 10% polyacrylamide gels in the presence of sodium dodecyl sulfate (SDS) (16). Gels were stained with Coomassie Brilliant Blue R-250.

Purification of Tryptic Fragments—500 μg of purified SELB protein was treated with trypsin for 15 min as described above. The reaction was stopped by acidification to pH 3.5. Separation of tryptic fragments was achieved by reversed-phase HPLC on an RP-C4 column (Nucleosil 300-7 C4; 250 x 4 mm). Elution was carried out with a 50-min linear gradient of 55% buffer A (0.1% aqueous trifluoroacetic acid), 45% buffer B (acetonitrile containing 0.08% trifluoroacetic acid) to 30% buffer A, 70% buffer B. The flow rate was 1 ml/min. Fractions containing the cleavage products were dried under a stream of nitrogen, and the N-terminal sequences of the fragments were determined as described above.

Immunological Procedures—Antibodies directed against SELB were raised in a rabbit by intradermal injection at multiple sites with 80 μg of purified protein mixed with 1 ml of Freund's complete adjuvant. After 3 weeks, two booster injections of 100 μg of SELB protein, each made up in 1 ml of Freund's incomplete adjuvant, were given with an interval of 7 days. Blood was collected from the ear vein 8 days after the second injection. Immunoglobulin G fraction was isolated from the crude serum by affinity chromatography on a protein G-Sepharose 4 Fast Flow column. Nonspecifically reacting IgGs were removed by two passages of a 10-mg aliquot of the IgG fraction over a Sepharose 4B column (3 ml bed volume) to which 10 mg of protein of a crude extract from strain WL300 (selB) was coupled. The column was equilibrated with 50 mM Tris-Cl, pH 8.0, 250 mM NaCl, 0.01% polyoxyethylene 9 lauryl ether, and the flow-through was pooled. Bound IgGs were eluted from the column with 0.1 M glycine HCl, pH 2.7. The immunoglobulins of the final flowthrough (6 mg) were adjusted to a protein concentration of 5 mg/ml and stored at -20 °C. Dilutions of 1:100 were used in immunoblotting experiments (16).

Fractionation of Cell Extracts—A crude extract from cells of strain FM420 (17), grown anaerobically in buffered rich medium (2) at pH 7.1 and harvested in TMNK buffer (50 mM Tris-Cl, pH 7.4, 10 mM MgCl₂, 150 mM NH₄Cl, 50 mM KCℓ, 10% glycerol, 0.5 mM EDTA, 1 mM DTT) as described above (protein purification). 1.5 ml of the supernatant of the 30,000 x g centrifugation was layered on 4.5 ml of a 40% sucrose cushion in TMNK buffer and centrifuged for 16 h at 100,000 x g. The supernatant fraction (S100) of this centrifugation was diluted to 30% (w/v) sucrose cushion and re-centrifuged for 16 h at 100,000 x g. The high salt wash was removed, and the ribosomal fraction was resuspended in 1.5 ml of TMNK buffer. The fractionation was carried out at 0-4 °C throughout.

Results and Discussion

Expression of the selB Gene in the T7 Promoter Polymase System—The plasmid pWL144 (Ref. 2, Fig. 1) contains a 2.1-kilobase chromosomal DNA insert that complements a selB deletion mutation (2). Its nucleotide sequence was determined by an open reading frame coding for a protein of 66.5 kDa (Fig. 2A), which is in agreement with the mass of 66.5 kilodaltons determined in vivo (8) to give plasmid pWL194 in which the deletion mutation (2) was restored. Its nucleotide sequence was determined and revealed an open reading frame for a protein of 614 amino acids with a calculated size of 68.8 kDa (6). The putative selB gene was cloned into the expression vector pT7-6 (8) to give plasmid pWL194 in which the selB gene is under the control of the phage T7 (α10 promoter (see "Experimental Procedures"). In an in vivo expression experiment, induction of the T7 promoter led to the specific synthesis of a protein of 66.5 kDa (Fig. 2A), which is in agreement with the size of SELB predicted from the nucleotide sequence.

Purification of SELB Protein—Purification of SELB was achieved by overproducing the protein using the T7 expression system described above. E. coli strain K38 carrying plasmids pWL194 and pGPP1-2 was grown in a 1-liter fermenter that had been induced to give high level expression of the selB gene. Since no activity assay was available for SELB quantitation, enrichment was followed by mixing the extract of these cells with a small amount of extract from cells that had been induced in the presence of [35S]methionine (incorporation was approximately 6.5 x 10⁶ cpm) and by determin-
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**N-terminal Amino Acid Sequence of SELB**—The nucleotide sequence that directly precedes the selB gene includes an open reading frame with a coding capacity for a protein of 463 amino acids (data not shown). It codes for the SELA protein, which has a function in the conversion of serine to selenocysteine (4, 5). The first potential ATG codon of the selB open reading frame overlaps by 4 base pairs with the TGA stop codon of the selA gene (Fig. 1). To determine exactly which codon initiates selB mRNA translation, the N-terminal amino acids of the purified protein were sequenced. The sequence obtained from 13 cycles was Met-Ile-Ile-Ala-Thr-Ala-Gly-His-Val-Asp-His-Gly-Lys. It is identical with the sequence derived from the DNA sequence of the selB gene starting with the first ATG codon as indicated in Fig. 1. This proves that (i) the ATG codon of selB, which overlaps with the TGA termination codon of the selA gene, is indeed used for initiation of selB mRNA translation; (ii) the N-terminal methionine is deformedylated but not processed; and (iii) no frameshifting event takes place at the selA/selB overlap.

**Limited Trypsinolysis of SELB**—By analyzing the derived amino acid sequence of SELB, a striking similarity in primary structure was found with EF-Tu (6). As an initial means of analyzing conformational similarities between SELB and EF-Tu, SELB was subjected to limited proteolysis by trypsin. This approach has been used successfully for EF-Tu and EF-1 to evaluate the conformational state of these proteins (14, 18–22). Proteolysis of EF-Tu and other elongation factors results in a typical degradation pattern whereby the predominant cleavage occurs in a flexible protein fold near the N terminus which is exposed at the surface of the protein (14, 18–23). The experiment depicted in Fig. 3 demonstrates that SELB is also highly susceptible to low trypsin concentrations, yielding first a 63-kDa cleavage product followed by a 46-kDa degradation product. To define the sites within SELB at which cleavage occurs, the tryptic fragments were purified by reversed-phase HPLC on a RPC4 column (Fig. 4), and the N-terminal amino acids were sequenced. For the 63-kDa protein the sequence Gly-Met-Thr-Asp-Leu-Gly-Tyr-Ala-Tyr-Asp-Pro-Gln-Pro-Asp was obtained, which results from a cleavage between Arg24 and Gly28 in SELB. This site is homologous to the cleavage site Arg27-Gly28 in E. coli EF-Tu (23) and to similar cleavage sites in other elongation factors (14) (Fig. 5). The N-terminal sequence of the 46-kDa tryptic fragment was Gly-Met-Asp-Leu-(?) -Glu-(?) -Leu-Leu, which is the result of a cleavage between Arg22 and Gly25 in SELB.

The experiment was carried out as described under “Experimental Procedures.” Lane 1, 4 μg of purified SELB prior to the addition of trypsin; lanes 2–5, after the addition of trypsin; lane 2, 5 min; lane 3, 10 min; lane 4, 20 min; lane 5, 40-min treatment with trypsin; lane 6, 4 μg of SELB incubated for 40 min at 28 °C in the absence of trypsin. The apparent molecular mass of SELB is indicated as deduced from its mobility in SDS-polyacrylamide gels. The molecular mass, as calculated from the amino acid sequence, is about 2.5 kDa larger.

**FIG. 3. Limited tryptic digestion of SELB.** The experiment was carried out as described under “Experimental Procedures.” Lane 1, 4 μg of purified SELB prior to the addition of trypsin; lanes 2–5, after the addition of trypsin; lane 2, 5 min; lane 3, 10 min; lane 4, 20 min; lane 5, 40-min treatment with trypsin; lane 6, 4 μg of SELB incubated for 40 min at 28 °C in the absence of trypsin. The apparent molecular mass of SELB is indicated as deduced from its mobility in SDS-polyacrylamide gels. The molecular mass, as calculated from the amino acid sequence, is about 2.5 kDa larger.

**FIG. 2. A, expression of [35S]methionine-labeled selB gene product in the T7 promoter polymerase system (7).** Cell lysates were separated in a 10% polyacrylamide gel in the presence of sodium dodecyl sulfate (15), and the gel was dried and autoradiographed. Lane 1, strain K38 carrying plasmids pGPl-2 and pT7-5 (vector control). Lane 2, K38/pGPl-2/pWL194. B, purification of SELB as followed by SDS-polyacrylamide (10%) gel electrophoresis. Gels were stained with Coomassie Brilliant Blue R-250. Lane 1, molecular mass standards (β-galactosidase, bovine serum albumin, ovalbumin, and aldolase); lane 2, crude extract after 30,000 × g centrifugation; lane 3, supernatant of 150,000 × g centrifugation; lane 4, sediment of 150,000 × g centrifugation; lane 5, 1 M NH&l, wash of 150,000 × g sediment; lane 6, 45–63% ammonium sulfate fraction; lane 7, hydroxylapatite pool; lane 8, purified SELB.

In a typical experiment, 21 mg of purified SELB was obtained from 4,725 mg of protein in a 30,000 × g supernatant. An enrichment factor of approximately 20-fold could be calculated from experiments in which [35S]methionine-labeled extract was used; the final yield was 9%.

The A280/A260 absorbance ratio of purified SELB was 1.62, demonstrating that it is essentially free of nucleotides. Gel filtration through a TSK G3000SW column in the presence of 0.02% polyoxyethylene 9 lauryl ether revealed that SELB, in its native state, is present as a monomer (results not shown).
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Fig. 4. Purification of tryptic fragments of SELB. A, profile of preparative reversed-phase HPLC of the tryptic fragments of SELB. (For details see "Experimental Procedures.") B, gel electrophoretic analysis of the fragments separated in part A. Lanes 1, 2, and 3 correspond to the peaks 1, 2, and 3, respectively. The 46-kDa fragment of peak 1 and the 63-kDa fragment of peak 3 were used for sequencing.

Fig. 5. Alignment of the amino acid sequences of the common tryptic cleavage site in SELB and in EF-Tu from representatives of the three primary lines of descent: subbacterial \textit{(E. coli, EC)} (31), eukaryotic \textit{(Arthromonas salina, AS)} (14), and archaeabacterial \textit{(Methanococcus vanillii, MV)} (32). Identical amino acids, conserved in all four sequences, are boxed. The site of trypsin cleavage is indicated by the arrowhead.

SELB. This specific cleavage site is not found in EF-Tu; however, in the tertiary structure model of EF-Tu proposed by La Cour \textit{et al.} (24) and Jurnak (22), the homologous amino acids are situated in a small \(\alpha\)-helical region (helix E) extending from the surface of the protein. From the fact that in SELB this second cleavage occurs rapidly and specifically, it can be concluded that the amino acids in this position are also exposed on the surface of the protein. The 2 glycine residues neighboring Arg\(^{22}\) in SELB probably promote better accessibility for trypsin in comparison with EF-Tu. These results are not only in agreement with the finding that SELB and EF-Tu share extensive similarity at the primary structure level, but they also suggest strongly that both proteins share common features in tertiary structure.

\textit{Immunological Detection of SELB in E. coli Wild-type Cells—Antibodies directed against SELB were raised in rabbits and used to detect SELB protein in \textit{E. coli} cells of strain FM420 (17) which is wild-type for selB. SDS-lyses of cells grown to exponential phase under aerobic and anaerobic conditions were subjected to immunoblot analysis. An estimation of the amount of SELB in these extracts was achieved by running different amounts of purified SELB protein on the same gel (Fig. 6A). The experiment showed that (i) SELB protein produced under conditions of wild-type level gene expression has an identical electrophoretic migration behavior when compared with overproduced SELB protein; (ii) only a single gene product results from selB gene expression, which is consistent with the N-terminal sequence data; (iii) SELB synthesis is not subject to aerobic/anaerobic regulation since essentially equal amounts of SELB could be detected in aerobic and anaerobic cells; (iv) the total cell lysates of \(1.2 \times 10^8\) cells contains nearly 16 ng of SELB as determined by densitometric evaluation of the autoradiograph (using the Pharmacia LKB Ultrascan XL), which is equivalent to about 1100 molecules of SELB/cell under the particular growth conditions (25). Thus, the ratio of SELB molecules to ribosomes is approximately 1:18 and that to EF-Tu, 1:180.

The purification procedure had indicated that a major part of overproduced SELB protein co-sedimented with the ribosomes upon ultracentrifugation. In an attempt to determine the subcellular localization of SELB in cells of wild-type \textit{E. coli}, extracts (30,000 \(\times g\) supernatants) from strain FM420
were prepared and loaded on a 30% sucrose cushion. After centrifugation for 16 h at 100,000 × g, the ribosomal pellet was washed with buffer containing 1 m NH₄Cl, and the ribosomes were removed from the wash fluid by a further centrifugation step. Fig. 6B shows the distribution of SELB in the different fractions as determined by immunoblotting with anti-SELB antiserum. Approximately 50% of SELB was associated with the ribosomes and could be detached completely from the particulate fraction by washing with high salt. Whether this association reflects an intrinsic affinity of SELB to ribosomes remains to be demonstrated in vitro; however, such an observation is supportive of other data that favor the hypothesis that SELB is directly involved in translation (6).

The results presented in this study have shown that the selB gene, located at the 3′ side of selA, overlaps the 3′ end of selA by 4 bases. The formation of these gene products may therefore be translationally coupled (26). SELB protein exhibits features characteristic of proteins of the translational machinery. (i) It is sensitive to low trypsin concentrations to a characteristic cleavage site of all elongation factors. (ii) SELB is present constitutively under different growth conditions in amounts comparable to that of initiation factor 2p or release factors and is partially associated with the ribosomal fraction. Thus, the accumulated evidence presented in this study, together with the fact that SELB exhibits extensive sequence homology with EF-Tu, that it binds guanine nucleotides, and that it exclusively forms a complex with selenocysteyl-tRNA (6) is entirely consistent with SELB functioning as a special translation factor necessary for the decoding of the UGA codon of the fdhF mRNA which determines selenocysteinyl residue of a charged tRNA (6).

Proteins with sequence similarities to translation factor EF-Tu or EF-1 have been described recently in other systems. The nodQ gene of Rhizobium meliloti displays sequence similarity with EF-Tu and is essential for the nodulation process (27). Other examples have been reported for E. coli (28) and Saccharomyces cerevisiae (29). A distinct possibility is that some of these proteins, like SELB, may function as alternate translation factors being required for the synthesis of proteins involved in special biological processes.

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