The gene for the yeast *Saccharomyces cerevisiae* glutamine tRNA synthetase is shown here to encode a protein of 808 amino acids. This contrasts with the 551 amino acids of the *Escherichia coli* glutamine tRNA synthetase. The yeast GLN4 transcripts have 5’ termini that start approximately 25 nucleotides in front of the long open reading frame. Much of the extra size of the yeast enzyme is due to a large amino-terminal extension. At codon 225, the yeast enzyme aligns with the amino terminus of the *E. coli* protein. From this point on, the two sequences have an average of 40% identity, with a few small gaps for alignment, until their respective carboxyl termini. At codon 254 of the yeast and codon 30 of the *E. coli* enzyme, however, there starts an exact 15-amino acid match between the two proteins. This match encompasses and is partially the same as a short sequence which is a signature sequence for the amino acid group of the bacterial aminoacyl-tRNA synthetases which are specific for different amino acids. This is the strongest sequence match found between any yeast cytoplasmic or mitochondrial aminoacyl-tRNA synthetase with its bacterial homologue. This region of the structure is associated with a nucleotide fold. The result provides strong validation of the signature sequence, especially for sequences where the homology relationships are less dramatic than in this example. Because the 224-amino acid extension of the yeast enzyme does not align with any part of the *E. coli* enzyme, we propose that it is not associated directly with the catalytic function of the enzyme. Its possible function is investigated in the accompanying paper.

Aminoacyl-tRNA synthetases catalyze the esterification of an amino acid with the cognate tRNA (1). Although they exist in a variety of subunit sizes and quaternary arrangements, recent investigations suggest that there is a common motif underlying their structural organization (2, 3). There is a catalytic core to which additional polypeptide sequences have been joined; these additional sequences are not essential for catalysis but may play a role in other cellular processes (4).

In bacteria, the catalytic region of some of the synthetases is positioned toward the amino-terminal portion of the protein; dispensable sequences are located on the carboxyl-terminal side of the catalytic core (2, 3). In eukaryotes, the cytoplasmic synthetases are typically larger than the prokaryotic homologues (1). One explanation is that the eukaryotic synthetases have additional domains, fused to the core structure, to perform physiological functions not required of the prokaryotic enzymes. Alternatively, the eukaryotic protein has acquired insertions at various sites of the core enzyme which provide subtle modulations of the catalytic functions. Although the aminoacyl-tRNA synthetases catalyze a common reaction and share a structural motif, recent investigations have established that there is little primary structure similarity among them. The most significant sequence element was discovered by Webster et al. (5) as a consequence of the determination of the sequence of *Escherichia coli* isoleucine tRNA synthetase. This element is a sequence of 10–15 amino acids which serves as a signature for a group within this class of enzymes. This sequence forms a critical part of the nucleotide fold that is known to be in the amino-terminal part of the bacterial methionine and tyrosine tRNA synthetases (6–9).

The presence of this sequence element may be questioned in some of the enzymes, however, because of the significant amino acid substitutions that occur among the putative signature sequences. While attempts have been made to find other more definitive common sequences in the primary structures of the enzymes, no better example has been found or proposed.

We previously reported the isolation of GLN4, the structural gene for Gln-tRNA synthetase in *Saccharomyces cerevisiae* (10). GLN4 is an essential gene which exists in single copy on chromosome XV. The size of the transcript, as determined by an RNA blot, is 2900 nucleotides. This suggests that the protein product is considerably larger than the 551 amino acids of the *E. coli* polypeptide (11).

We report the sequence of GLN4 and an analysis of the primary structure of the encoded enzyme. This sequence is of particular interest because the primary structure of the *E. coli* counterpart has been determined and a location for the putative signature sequence proposed (5). This proposed sequence element starts 30 amino acids from the amino terminus. Its identification is based upon partial, and in some cases weak, sequence similarities with several enzymes rather than a strong relationship with one particular enzyme. Identification of the putative signature sequence in the yeast enzyme

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The nucleotide sequence(s) reported in this paper has been submitted to the GenBank™/EMBL Data Bank with accession number(s) J02784.

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provides a further evaluation of its significance. Furthermore, alignment of the yeast sequence alongside the bacterial sequence enables us to investigate whether the anticipated greater length of the yeast enzyme arises from multiple insertions into the catalytic domain or from the presence of discrete domains fused to the core enzyme. This, in turn, provides a basis for future investigations on the structure of an eukaryotic aminoacyl-tRNA synthetase.

**MATERIALS AND METHODS**

**DNA Sequence Analysis**—DNA sequence analysis was conducted by the chain termination method of Sanger et al. (12). Fragments of GLN4 were subcloned into M13mp8 and M13mp9 (New England Biolabs). Sequencing was initiated using the 15- or 17-base universal primer (New England Biolabs).

**RNA Preparation**—Total RNA was isolated from haploid strain AM644-29 (10) harboring GLN4 bearing plasmid pSWL203. Cells were grown in minimal media to a Klett reading of 100, broken with glass beads and RNA was isolated by the method of Carlson and Botstein (13).

**Plasmids**—The isolation of GLN4 bearing plasmid pSWL203 has been previously described (10). Additional plasmids relevant to this work, obtained through subcloning the GLN4 insert of pSWL203 via standard techniques, are as follows: pSWL219, EcoRI (14 to 410) to HindIII (799) fragment of GLN4 ligated into the EcoRI and HindIII sites of M13 phage mp10w (New England Biolabs); pSWL220, EcoRI (1487) to ClaI (2737) fragment of GLN4 ligated into EcoRI and ClaI sites of M13 phage mp10w (New England Biolabs); and pSWL99-7, TacI (−385 to −286) fragment of GLN4 ligated into the Accl site of M13 phage mp8 (New England Biolabs). Nucleotide numbers have been designated relative to +1 as the start of the GLN4 coding sequence (see below).

**S1 Nuclease Mapping**—Fifty micrograms of total RNA was mixed with approximately 5-10^6 cpm of a gel-purified probe uniformly labeled with α-32P]dATP (Amersham Corp.), according to the method of Hsu and Schimmel (14). The mixture was ethanol precipitated and resuspended in 50 µl of hybridization buffer, which contained 40 mM PIPES (pH 6.4), 0.4 M NaCl, 1 mM EDTA, and deionized formamide. The optimum concentration of formamide was determined empirically for each hybridization and was generally obtained by virtue of its ability to restore the Gln⁺ phenotype to E. coli strain which harbors GLN4. Hybridization analysis established that the direction of transcription of this locus is as indicated in Fig. 1. With the exception of a small segment of about 100 base pairs at the 3'-end of this region (Fig. 1), the entire 5.0 kilobase pairs between the Sau3A sites were sequenced by the direct method of Hsu and Schimmel (14). Restriction fragments were cloned for sequencing into M13 vectors mp8 and mp9, and the entire sequence was determined in both orientations. All fragment junctions were also verified by sequencing to ensure proper alignment.

Computer analysis of the GLN4 DNA sequence shows a single long open reading frame encoding a protein of 809 amino acids. The location of this open reading frame is shown in Fig. 1. There are no other open reading frames longer than 65 codons on the strand previously determined to be the coding strand (10). This open reading frame encompasses and extends beyond both ends of the Hpal-BamHI fragment. Gene disruption experiments showed previously that this portion of the gene encodes an internal polypeptide sequence of the enzyme (10).

The 809-codon open reading frame shows strong homology to the E. coli Gln-tRNA synthetase (11). The alignment of the sequences is achieved with an amino-terminal extension of 224 amino acids of the yeast enzyme. This extension has no counterpart in the E. coli enzyme.

Fig. 2 shows the translated amino acid sequence of the long open reading frame of GLN4 and its alignment with the amino acid sequence of E. coli glutamine tRNA synthetase. With the exception of the amino-terminal extension of the yeast enzyme, the two sequences have an identity of 40%. The identity shared by the two enzymes is especially pronounced between the N-terminal half of the E. coli enzyme and that portion of the yeast enzyme which aligns to it. While the two sequences differ in size by 259 amino acids, only a few amino acids are inserted at scattered places in the parts that align. The remainder is entirely contained within the large amino-terminal extension and within a short carboxyl-terminal overhang of 23 amino acids of the yeast enzyme.

The putative signature sequence for the E. coli protein starts at codon 30 (5). At this position the sequence alignment, there is an exact match in 15 out of 16 amino acids that aligns amino acids 30-44 of the E. coli enzyme with amino acids 254-268 of the yeast enzyme. Given the overall sequence identity of 40%, the a priori random probability is vanishingly small that these two sequences would have an exact match of

![Fig. 1. Restriction map and location of the GLN4 coding sequence and transcript.](image)

**RESULTS**

**Coding Region for Glutamine tRNA Synthetase**—We established previously that GLN4 encodes glutamine tRNA synthetase (10). A recombinant plasmid with a 5-kilobase pair insert of genomic DNA from S. cerevisiae was shown to harbor GLN4 by virtue of its ability to restore the Gln⁺ phenotype to strains that are Gln⁻ due to a mutation in the gene and by its ability to confer an elevation in glutamine tRNA synthetase activity.

1 The abbreviation used is: PIPES, 1,4-piperazinediethanesulfonic acid.
FIG. 2. Amino acid sequence of S. cerevisiae glutamine tRNA synthetase. The amino acids are deduced from the nucleotide sequence of GLN4. The E. coli tRNA synthetase sequence is shown beneath as a series of dots, except where there is a difference between the two sequences. A dash indicates a gap. The alignment was determined by a computer sequence alignment method (37).

Fig. 3. The nucleotide sequence of the noncoding regions of GLN4. The sequences were established by the dyeox sequencing strategy of Sanger et al. (12) as described in the text. A, B, and respectively, display the 5' and 3' noncoding sequences. In A, the approximate center of the location of the 5'-ends of transcripts, as indicated by arrows at −15 and −28; the position of a potential TATA box, located in the 5' flanking region at nucleotide −410. This site is located in the 5' flanking region at nucleotide −410. We have mapped the 5'-end of the GLN4 transcripts with special concern for whether the transcripts initiate in front of the ATG of the long open reading frame. A previously reported gene disruption experiment showed that the HpaI site, which encompasses codons 74 and 75, is a restriction site internal to the transcript, lies within a nontranslated region. We also explored whether GLN4 encodes two or more overlapping transcripts which are distinguished by the locations of their 5'-ends and which possibly utilize alternate ATG codons for translation initiation. If the size difference of these transcripts is less than 75 nucleotides, we may not have detected them in the previously determined RNA blots which demonstrated a single mRNA species of 2900 nucleotides (10).
probe is designated as pSWL219 in Fig. 1. The probe encompasses all of the potential initiating ATG codons upstream of the aforementioned signature sequence.

Hybridization and S1 nuclease mapping were conducted with total RNA from a strain which overproduces the GLN4 transcript by virtue of carrying GLN4 on autonomously replicating plasmid pSWL203 (10). The S1 nuclease-protected products were separated by size on a 6% denaturing polyacrylamide gel and analyzed by autoradiography. Probe fragments of known molecular weight were run in adjacent lanes as size standards.

Autoradiography of the gel shows the presence of closely spaced bands of approximately 710 nucleotides in length (data not shown). This places the transcriptional start near the ATG located at nucleotide position +1. Because this probe detects no other set of bands, we doubt the possibility that GLN4 produces two overlapping transcripts which utilize different ATGs for translational initiation.

The nuclease protection experiment was repeated with another probe which begins closer to the transcriptional start so as to refine the location of the 5'-end of the GLN4 transcript. The probe, designated as pSWL99-7 (Fig. 1), begins at a TaqI site located at nucleotide +266 and extends to a TaqI site at -385. With this probe, we detect two sets of bands (Fig. 4A). Each set consists of several sub-bands, and each of these is separated from its neighbor by a single nucleotide. The two sets of bands map to close, but distinct, places. One is centered at nucleotide -28, and the other is centered at -15. These transcripts have 5'-ends that lie just upstream of the ATG codon at position +1. There is no ATG in any reading frame positioned between these 5'-ends and the ATG codon of the GLN4 open reading frame. The multiplicity of these sets of bands is possibly due (at least in part) to melting at the ends of the probe-RNA hybrids and subsequent S1 nuclease digestion of the frayed ends of the duplexes.

The consensus sequence TATA A, the Goldberg-Hogness box, is a signal for transcriptional initiation (15). In yeast it is generally found between 39 and 150 nucleotides upstream of the transcriptional start. GLN4 contains the sequences TATAAA and TATAATA at nucleotide positions -93 and -23, respectively. The latter falls between the two mapped transcriptional starts at -28 and -15. The -93 TATA box, which exactly matches the consensus sequence, lies -65 and -78 nucleotides, respectively, in front of the two major GLN4 transcriptional starts. Given its strong similarity to the consensus TATA sequence and that it is located at what is considered to be the general locale for yeast TATA sequences, we consider this sequence as likely to serve the role of the TATA element for GLN4.

The sequence ANNAUGG is considered an efficient eukaryotic signal for translational initiation (16). For yeast transcripts this sequence has been refined to read ANNAUGNNU (17). A purine at -3 and the absence of a U at -1 are considered necessary for a high efficiency of translational initiation. The ATG at position +1, the first ATG codon to appear on the GLN4 transcript, contains the necessary alignment for efficient translation initiation (see also the accompanying manuscript (18)).

We examined the 5'-untranslated region of GLN4 for sequences that might be associated with gene regulation or control. While the gene for isoleucine tRNA synthetase is subject to general amino acid control, there is no evidence that GLN4 is affected by this regulatory pathway (19, 20). A consensus sequence 5'-AAGTGACTC-3' has been implicated as affecting expression of genes in this regulatory circuit (21, 22). The core sequence TGACTC is considered the most critical region of the consensus sequence; conformity to this part of the consensus sequence is generally high. Genes under general amino acid control usually contain several copies of the consensus sequence. They are located 50-150 nucleotides upstream from the transcriptional start (21, 22).

We found three stretches of nucleotides which fit the six-base consensus sequence in four out of six positions. In contrast, genes under general amino acid control frequently show a perfect fit to this six-base consensus sequence. Our failure to find compelling similarities to general amino acid control sequences is consistent with the lack of a response of levels of glutamine tRNA synthetase to general amino acid supply.

The 3'-End of GLN4 Transcripts—To map the 3'-end of
the GLN4 transcript, a probe (pSWL220) was constructed that extends from the EcoRI site at nucleotide +1987 to the ClaI site at +2737 (Fig. 1). When hybridized against the GLN4 transcript, this probe gives three fragments that are protected from S1 nuclease digestion (Fig. 4B). The ends of these fragments are positioned at approximately nucleotides +2501, +2532, and +2559. The coding sequence of the GLN4 open reading frame ends at +2427 and thus is encompassed by all three of the 3'-ends that are found by this analysis.

Zaret and Sherman (23) have proposed the consensus sequence TAG...TATGG...TTT as a signal for transcriptional termination and polyadenylation of yeast transcripts. This consensus sequence is generally located within 140 bases of the 3'-side of the stop codon.

The 3'-end of the GLN4 coding sequence reads TGAATGATTTAATGTGCATATATGTAATT. The GLN4 stop codon is indicated by boldface, and a sequence homologous to the tripartite consensus sequence is underlined. The signature sequence defined by Webster et al. (5) TATG...TTT as a signal for transcriptional termination sequences of typically 100-200 nucleotides would increase the mRNA to a size of 2500-2600 nucleotides. This is within 10% of the previously reported size of 2900 nucleotides, as estimated from RNA blots.

DISCUSSION

Functional domains in aminoaoyl-tRNA synthetases have been demonstrated by analysis of protein fragments generated by gene deletions of bacterial aminoaoyl-tRNA synthetase genes (4, 24). The gene for a eukaryote synthetase affords, in principle, the opportunity to investigate the locations of functional domains within the polypeptide through a determination of the exon/intron structure of the DNA. However, the sequence analysis and the S1 nuclease digestion patterns with specific probes give no evidence for the presence of introns at any point in the long open reading frame of GLN4.

There are 21 reported sequences of aminoaoyl-tRNA synthetases (3). These include sequences for 12 different amino acid-specific enzymes from E. coli, Bacillus stearothermophilus, Bacillus caldotenax, and the yeast S. cerevisiae. The strongest homology between enzymes specific for different amino acids is that between E. coli isoleucine and methionine tRNA synthetases (5). In a sequence of 11 amino acids, these two enzymes share 10 identities and one conservative change. This part of the methionine enzyme's structure has been determined, and it corresponds to a segment of the nucleotide fold associated with the ATP/adenylate binding site (8).

From investigations of the primary structure of other aminoaoyl-tRNA synthetases, several have been identified to have a sequence that is similar to this segment of the isoleucine and methionine enzymes (5, 25). None, however, has the near perfect match that is found for these two enzymes. In the case of the B. stearothermophilus tyrosine tRNA synthetase, for example, there are only five identities with the isoleucine or methionine sequence in this 11-amino acid segment (5). The structure of the polypeptide backbone of the tyrosine enzyme, however, is superimposable on that of the methionine enzyme over this segment. This confirms, in this instance, the significance of the partial sequence similarity. The E. coli glutamine, tyrosine, and glutamic tRNA synthetases also have segments that are similar to the aforementioned region in isoleucine and methionine tRNA synthetases (2, 5, 25). On the basis of these observations, this segment is a signature sequence for a group of the aminoaoyl-tRNA synthetases.

Table 1 tabulates the alignment of nine sequences for five different amino acid-specific enzymes in the region of the signature sequence. The 15 out of 16 identities of the yeast and E. coli glutamine enzymes contrast with the 6 identities over a stretch of 12 codons observed with the E. coli-S. cerevisiae sequence comparisons for either the isoleucine or methionine enzymes. Note that each glutamine enzyme has 8 of 12 identities with E. coli isoleucine tRNA synthetase. The latter enzyme has, in turn, only 6 of 12 identities with its yeast counterpart. Thus, the region of exact match between the two glutamine enzymes is also the section that matches the glutamine enzymes' sequences with those of noncognate aminoaoyl-tRNA synthetases.

There are a few other examples of yeast cytoplasmic aminoaoyl-tRNA synthetase genes which have been sequenced. These are the aspartyl- (26), histidyl- (27), methionyl- (28), and threonyl-tRNA synthetases (29). The methionine tRNA synthetase has an unequivocal signature sequence. The aspartyl-tRNA synthetase has not been investigated in bacteria so that comparisons of the type described here, between bacterial and yeast enzymes, cannot be made. In the case of HTS1, this locus encodes both the cytoplasmic and mitochondrial forms of His-tRNA synthetase (27). In contrast to the glutamine tRNA synthetase, the yeast histidine enzyme has little sequence similarity to its E. coli counterpart (27, 30). The genes for two yeast threonine tRNA synthetases (cytoplasmic and mitochondrial), in addition to the gene for the E. coli enzyme, have been investigated (29, 31, 32). The bacterial and yeast cytoplasmic enzymes are 642 and 734 amino acids, respectively, with almost all of the additional sequences of

| Reference | Table 1: A signature sequence for some aminoaoyl-tRNA synthetases |
|-----------|---------------------------------------------------------------|
| 11        | E. coli Glu-tRNA synthetase                                  |
| 25        | S. cerevisiae Ilε-tRNA synthetase                            |
| 20        | E. coli Ilε-tRNA synthetase                                  |
| 5         | S. cerevisiae Met-tRNA synthetase                            |
| 28        | E. coli Met-tRNA synthetase                                  |
| 33        | E. coli Tyr-tRNA synthetase                                  |
| 38        | S. cerevisiae Gln-tRNA synthetase                            |

This work refers to the signature sequence defined by Webster et al. (5) which is based upon an 11-amino acid sequence similarity between bacterial aminoaoyl-tRNA synthetases specific for different amino acids. This table shows the exact 15-amino acid match between E. coli and S. cerevisiae glutamine enzymes that encompasses the aforementioned 11 amino acids (shown as the last 11 amino acids of each sequence) and additional sequences from S. cerevisiae and E. coli.
the yeast cytoplasmic enzyme located in an amino-terminal extension. The mitochondrial enzyme is much shorter, 462 amino acids. The three sequences can be aligned, and in this alignment the shorter length of the mitochondrial protein is largely due to a missing amino-terminal section. While there are several blocks of identical amino acids shared by the three proteins, there are no instances in this system of a 15-amino acid identity between either of the two sequence pairs.

The E. coli and yeast methionine tRNA synthetases are 677 and 751 amino acids, respectively (28, 33). The two sequences share a region of several hundred amino acids over which they have approximately 30% identity (34). However, there is no region that has as much as a 15-out-of-15 match. The signature sequence region of the alignment is shown in Table I. Note that the two sequences are displaced with respect to each other. The yeast enzyme has an amino-terminal extension of 191 amino acids, relative to the E. coli protein, and the E. coli enzyme extends further at its carboxyl end by approximately 100 amino acids. The latter sequences are associated with a domain that is used to form dimers of the E. coli enzyme (the yeast enzyme is a monomer (34, 35)). The amino-terminal extension of the yeast methionine tRNA synthetase, which is close in size to that of the yeast glutamine tRNA synthetase, is a stable part of the mature enzyme. However, no elements of similar sequence exist between the two amino-terminal extensions. Because the long amino-terminal extensions are joined to what corresponds to the catalytic portions of the bacterial counterparts, we surmise that in each case these extra sequences are associated with a biological function other than catalysis.

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