EVOLUTION OF *E. coli* tRNA\textsuperscript{Trp}

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Abstract. Earlier studies (1) have shown there are direct correlations between the hydrophobicity ranking of most amino acids and their anticodonic nucleotides. However, four anticodonic assignments, i.e. those for Trp, Tyr, Ile and the XGA anticodons for Ser, did not correlate. It was our proposal that this failure to correlate was due to the fact that these assignments were made late, relative to the bulk of the assignments, in evolution through the mutation of existing tRNAs. We have shown (2) that *E. coli* tRNA\textsuperscript{Ile\textsuperscript{1}} and tRNA\textsuperscript{Ile\textsuperscript{2}} were likely derived from tRNA\textsuperscript{Val\textsuperscript{1}} and tRNA\textsuperscript{Ile\textsuperscript{3}} respectively and *E. coli* tRNA\textsuperscript{Trp\textsuperscript{2}} was possibly derived from *E. coli* 5s rRNA or a common precursor with 5s rRNA (3). The fact that quite high homologies were observed in these comparisons is consistent with the late evolution of the tRNAs in question. We now examine the evolution of *E. coli* tRNA\textsuperscript{Trp} by comparing its homology with other *E. coli* tRNAs. The data suggest a possible evolutionary relationship with *E. coli* tRNA\textsuperscript{Gly} or tRNA\textsuperscript{Arg}. The data support the idea of the late assignment of anticodons to Trp.

1. Introduction

Study of the genetic code has revealed several features which suggest that its origin is based on relationships between amino acids and their anticodonic nucleotides. These relationships include selective affinities (4–7); which in turn are reflected in selectivities in chemical reactions between amino acids and nucleotides (8–10). A guiding principle in these studies that we have adhered to has been that the genetic code and the process of protein synthesis must have co-originated and coevolved. A major observation which supports the idea that the relationship between the amino acids and their anticodons is the important one, is that there exist significant correlations of properties between amino acids and their anticodonic nucleotides, Figure 1 (1, 11–13). Even though these correlations are significant, four of the assignments do not correlate. These assignments are for Trp, Tyr, Ile and the XGA anticodonic assignments for Ser. Now, because the bulk of the assignments do correlate (with a correlation coefficient of 0.97) there is reason to question whether or not the basis for the origin of these particular non-correlating assignments was the same as the basis for the bulk of the amino acids. In fact a systematic appraisal of the character of all sixteen possible dinucleotides shows that there is considerable

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Fig. 1. The average ranked hydrophobicity of the amino acids as a function of the average ranked hydrophobicity of their corresponding anticodonic dinucleoside monophosphates. The standard single letter abbreviations for the amino acids were used. Amino acids with accompanying numbers are those which possess two anticodonic assignments. The correlation coefficient for those points within the outlined band is 0.97. (See Lacey and Mullins, (1) for further details.)

Overlap in the hydrophobicity ratings of some (Figure 2). The major overlaps include the non-correlating assignments in addition to those dinucleotides which are still the anticodonic equivalents of the terminator codons. Thus, it has been suggested that some dinucleotides had properties insufficiently unique to allow their early use as anticodons (1). This would mean that early in the evolution of the process of protein synthesis there were more terminator codons than there are today. This large number of terminators would have represented a pool of unused codons (anticodons) which could later be assigned to proteinaceous amino acids on a basis quite different from that for the original assignments.

We have previously reported data which suggest that Ile was incorporated relatively late among the proteinaceous amino acids (2). The evidence is, first that Ile is relatively unreactive in several reactions (9, 10) which are highly relevant to protein synthesis. This fact might suggest it would not be used early in evolution. A second point which we have not previously mentioned is that Ile is one of the two