



**Fig. 3** Possible secondary structure of the dimeric tRNA precursor region as predicted from the corresponding DNA sequence of Fig. 2. The two tRNA cloverleaf structures are depicted without modifications of the bases except for the  $\text{TV}\Psi$  sequences in the T-arms. Bases different in the respective *E. coli* tRNA species<sup>10,11</sup> are indicated within boxes.

possible. The 16S–23S spacer DNA is thus represented by the 259 base pairs confined within positions 63 and (probably) 322. The analogous region in the *E. coli* rrnD operon is considerably larger with 437 nucleotide positions. In *E. coli* the spacer region is known to be transcribed as a part of the single transcriptional unit of the rrnD operon<sup>10</sup>. A large rRNA precursor containing both the 16S and 23S rRNA sequences was also observed in spinach<sup>25,26</sup> and *Chlamydomonas*<sup>27</sup> chloroplasts. A rRNA of similar large size has been observed also in *E. gracilis* chloroplasts<sup>28</sup> and therefore it is reasonable to assume that a similar situation exists in this case although direct experimental evidence for transcription of the intergenic spacer is lacking.

Screening for GTTC sequences, which are indicative for the  $\text{GT}\Psi\text{C}$  sequence present in the  $\Psi$  loop of all tRNA species<sup>29</sup>, and for homology with the *E. coli* rDNA spacer region reveals two tRNA genes coding for an isoleucine ( $\text{AU}_C^U$ -) and an alanine ( $\text{GC}_G^A$ -) accepting species, respectively. The tRNA primary structures deduced from the two tRNA genes allow folding to a cloverleaf model completely consistent with all other structural criteria of tRNAs<sup>29</sup> (see Fig. 3). The deduced cloverleaf models contain several compensating base changes in the stem regions in addition to changes in the unpaired regions, which excludes the possibility that the two genes are derivatives of the *E. coli* genome due to a cloning or recombinational artefact. Also, the two chloroplast tRNA genes lack the CCA termini found in the respective *E. coli* tRNA genes<sup>10,11</sup>. The two tRNA genes are separated from each other by only six base pairs, which is reminiscent of the clustering of tRNA genes on the phage T<sub>4</sub> genome<sup>30</sup>. Within the precursor transcript, the two acceptor stems together with their neighbouring sequences can form a continuous stack of 24 base pairs (plus  $2 \times 5$  base pairs of the two T-stems according to the tRNA tertiary model<sup>31,32</sup>) as drawn in

Fig. 3. A possible hairpin structure directly preceding the 5' end of the tRNA<sup>Ile</sup> is also depicted in Fig. 3, since its stem region could possibly also form an uninterrupted stack with the acceptor stem (and the T-stem<sup>31,32</sup>) of this tRNA within the precursor molecule. It is tempting to speculate that some of these possible secondary structures constitute at least part of the signal structures necessary for proper processing of the common precursor chain. Alternatively, or in addition to this, recognition of the sequence GGUUUUG, which is common to both the tRNA precursors immediately beyond the 3' ends, may act as a signalling step during the processing events.

A comparison of the rRNA and tRNA coding sequences with the intergenic regions (Fig. 2) shows that the former are highly conserved contrary to the latter which are subject to many alterations, mainly by deletions but including some base substitutions. The short homologous stretches in the intergenic regions may have some functional significance for processing steps. Furthermore it is interesting that, similar to *E. coli* rDNA<sup>10,11</sup>, the G+C content is high in the structural and low in the intergenic parts.

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1. Manning, J. E. & Richards, O. C. *Biochim. biophys. Acta* **259**, 285–296 (1972).
2. Scott, N. S. *J. molec. Biol.* **81**, 327–336 (1973).
3. Kopecka, H., Crouse, J. E. & Stutz, E. *Eur. J. Biochem.* **72**, 525–535 (1977).
4. Gray, P. W. & Hallick, R. B. *Biochemistry* **18**, 1820–1825 (1979).
5. Schwartzbach, S. D., Hecker, L. I. & Barnett, W. E. *Proc. natn. Acad. Sci. U.S.A.* **73**, 1984–1988 (1976).
6. Gray, P. W. & Hallick, R. B. *Biochemistry* **17**, 284–290 (1978).
7. Rawson, J. R. Y., Kushner, S. R., Vapnek, D., Alton, N. K. & Boerma, C. L. *Gene* **3**, 191–209 (1978).
8. Jenni, B. & Stutz, E. *Eur. J. Biochem.* **88**, 127–134 (1978).
9. Hallick, R. B., Gray, P. W., Chelman, B. K., Rushlow, K. E. & Orozco, E. M. Jr *Chloroplast Development* (eds Akyoyunoglu, G. et al.) 619–622 (Elsevier, Amsterdam, 1978).
10. Young, R. A., Makrilia, R. & Steitz, J. A. *J. biol. Chem.* **254**, 3624–3271 (1979).
11. Sekiya, T. & Nishimura, S. *Nucleic Acids Res.* **6**, 575–592 (1979).
12. Bohnert, H. J. et al. *FEBS Lett.* **103**, 52–56 (1979).
13. Schwarz, Z. & Kössel, H. *Nature* **283**, 739–742 (1980).
14. Schwarz, Z. & Kössel, H. *Nature* **279**, 520–522 (1979).
15. Knopf, U. C. & Stutz, E. *Molec. gen. Genet.* **163**, 1–6 (1978).
16. Graf, L., Schwarz, Z., Kössel, H. & Stutz, E. *Experientia* **36**, 34 (1980).
17. Brosius, J., Palmer, M. L., Kennedy, P. J. & Noller, H. F. *Proc. natn. Acad. Sci. U.S.A.* **75**, 4801–4805 (1979).
18. Carbon, P., Ehresmann, C., Ehresmann, B. & Ebel, J. P. *FEBS Lett.* **94**, 152–156 (1978).
19. Jenni, B. & Stutz, E. *FEBS Lett.* **102**, 95–99 (1979).
20. Maxam, A. & Gilbert, W. *Proc. natn. Acad. Sci. U.S.A.* **74**, 560–564 (1977).
21. Zablen, L. B., Kissil, M. S., Woese, C. R. & Buetow, D. E. *Proc. natn. Acad. Sci. U.S.A.* **72**, 2418–2422 (1975).
22. Woese, C. R. et al. *Nature* **254**, 83–86 (1975).
23. Shine, J. & Dalgarno, L. *Proc. natn. Acad. Sci. U.S.A.* **71**, 1342–1346 (1974).
24. Steitz, J. A. *Biological Regulation and Control* (ed. Goldberger, R.) 349–399 (Plenum, New York, 1979).
25. Hartley, M. R., Head, C. W. & Gardiner, J. *Acides Nucléiques et Synthèse des Protéines chez les Végétaux* (eds Bogorad, L. & Weil, J. H.) 419–423 (CNRS, Paris, 1977).
26. Bohnert, H.-J., Driesel, A. J. & Herrmann, R. G. *Acides Nucléiques et Synthèse des Protéines chez les Végétaux* (eds Bogorad, L. & Weil, J. H.) 213–218 (CNRS, Paris, 1977).
27. Rochaix, J. D. & Malnoe, P. *Cell* **15**, 661–670 (1978).
28. Wollgiehn, R. & Parthier, B. *Plant Sci. Lett.* **16**, 203–210 (1979).
29. Sprinzl, M., Grütter, F., Spelzhaus, A. & Gauss, D. H. *Nucleic Acids Res.* **8**, r1–r22 (1980).
30. Abelson, J. A. *Rev. Biochem.* **48**, 1035–1069 (1979).
31. Suddath, F. L. et al. *Nature* **248**, 20–24 (1974).
32. Robertus, J. D. et al. *Nature* **250**, 546–551 (1974).

## Erratum

In the letter 'Juvenile hormone mimics the photoperiodic apterization of the alate gynopara of aphid, *Aphis fabae*' by Jim Hardie, *Nature* **286**, 602–604, line 2 of paragraph 7 should read 'juvenile characters in the fifth instar. After scoring these alates' and line 5 of the same paragraph should read 'juvenilization are the second and third instars, an observation'.