

zone contain appreciable quantities of coral fragments.

Prograding and upbuilding, similar to that illustrated by profiles 80 and 81, can also be seen in profiles 79 and 77. The isolated mounds west of Little Bahama Bank (*B*, profile 79) may be coral mounds, but this has not been verified by sampling. The sediment rise, midway along profile 77 (*C*), is the tip of the northwesterly trending slope off Great Bahama Bank. Profile 76 in Northwest Providence Channel, between Little and Great Bahama Banks, indicates that the present slopes of the channel were formed by sediments prograding toward its axis. The other profiles (74 and 75, 73, 71, 69, 67) show a terrace in various stages of burial. In profiles 74 and 75, and 73, the sediments have partially buried the terrace along its western edge. Extensions of stratigraphic data from wells near Miami (*I1*) suggest that the core of this terrace, known as Miami Terrace, may consist of shallow water Suwanee limestone (Oligocene strata) or the Hawthorn formation of Lower Miocene age. Along profiles 75 and 74 (*D*) sediments have completely buried the slope flanking the terrace on its seaward side. In this profile, deposition from the Bahamas side of the Straits of Florida is as great as that from Florida.

Farther south (see profiles 73 and 71), the slope flanking Miami Terrace on the east is covered by a thin veneer of sediments and is separated from a broad sedimentary ridge to the east by a narrow depression (*E*, 73 and 71). This sedimentary ridge, between the 800-m contours, extends to latitude 26°N where it grades into the western side slope of the Straits of Florida (Fig. 1). It appears to have been formed by sediment progradation in a southward direction with some outbuilding to the east and west. Profiles 73 and 71 clearly show that the depression west of the ridge is non-depositional in origin, not erosional as suggested by Kofoed and Malloy (9).

Along profile 71, Miami Terrace consists of a prominent ridge on the east (*F*) without any internal reflectors, and a filled trough to the west. Due to its high reflectivity, and from considerations of the regional geology, Rona and Clay (12) suggested that the ridge consists of limestone; possibly it is a coral reef. The filled basin west of the ridge is partially capped by sediments prograding toward the ridge. In profile 69 both the inner basin and

the ridge are buried under a thick sedimentary prism. South of the Florida Keys (profile 67), the terrace (Pourtales Terrace) is again exposed. Irregularities on the surface of this terrace appear to be due to folding and faulting. There is also some indication of drag folding along the slope, flanking the terrace on its seaward side. This slope is covered by a thick mantle of sediments, most of which appears to have been deposited from the mainland side of the Straits of Florida.

Dredge samples (9, 13) suggest that country rock, forming the foundation of this terrace (as of the Miami Terrace), may be the shallow-water limestones of the Hawthorn formation of Lower Miocene age. Profiles 69, 70, and 71 clearly show that Pourtales and Miami Terraces were once continuous, but became separated recently by the emplacement of a large volume of sediments southwest of Miami. Kofoed and Malloy (9) suggested that the Miami Terrace was downdropped in relation to the Pourtales Terrace. Evidence cited by them for the existence of a fault is the north-south linearity of the bottom contours southwest of Miami (Fig. 1). Seismic profiles across the location of this proposed fault (profiles 69, 70, 71) reveal no indication of faulting. On the contrary, the surface of the terrace can be traced across the location of the fault zone without any disruption.

Although stratigraphic well data are available from both sides of the Straits of Florida, the wells are too far apart to allow one to attempt to decipher the structure of the straits solely on well data. Consequently, the following speculations on the origin of the straits are based on the seismic profiles. These profiles show that north of 26°30'N the Straits of Florida appear to be the result of differential upbuilding along the margins. No evidence of the fault postulated by Sheridan *et al.* (5) has been found in this area. Instead, the lower elevation in the center of the trough may be related to a decrease in sedimentation beneath the Gulf Stream. In contrast, faulting may have played a role in molding the Straits of Florida south of 26°30'N. The steepness of the slopes flanking Miami and Pourtales terraces along their seaward sides, and the presence of drag folds along the slope south of Pourtales Terrace suggest that these features may be fault-line scarps. If faulting produced the slopes flanking

the terraces, it probably occurred in Miocene or post-Miocene time, as the cores of both terraces consist of Lower Miocene limestones. It is tentatively suggested that the Straits of Florida were formed on a subsiding basement and that the formation was accompanied by upbuilding along the margins, with sedimentation toward the center restricted by the Gulf Stream.

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- 17 May 1966

Nucleotide Sequence of a Yeast Tyrosine Transfer RNA

Abstract. *The nucleotide sequence of a tyrosine transfer ribonucleic acid is described and compared to the known sequence of an alanine transfer RNA. It is possible to construct very similar base-paired models for the two molecules in spite of only limited similarities in sequences. The evidence indicates that the sequence containing guanosine, pseudouridine, and adenosine in the middle of the polynucleotide chain is the anticodon.*

The determination of the structure of alanine tRNA of yeast (1) proved that present techniques are adequate to define the sequence of an RNA molecule the size of tRNA. Since the description of the nucleotide sequence of alanine tRNA left a number of questions unanswered about the relation of

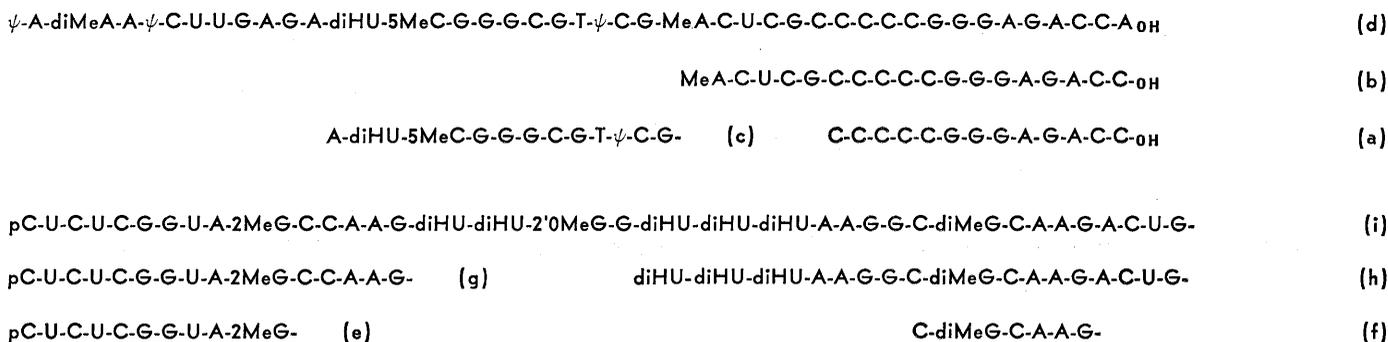


Fig. 1. Large fragments obtained from partial ribonuclease T1 digestion of the tyrosine RNA.

structure to functional sites in tRNA molecules, it was thought that the determination of the structure of a different tRNA molecule might contribute to the understanding of some of these questions.

This report culminates work on the structure of one of the two tyrosine tRNA's (tyrosine RNA 1) from baker's yeast (2), with the description of a unique nucleotide sequence.

Our procedures were the same as those used previously (1); the RNA was purified by countercurrent distribution, the fragments produced by digestion with pancreatic ribonuclease and ribonuclease T1 (3) were separated by chromatography on DEAE-cellulose in 7M urea (4), their base compositions determined, and the nucleotide sequences assigned (5). Then, partial digestion with ribonuclease T1 was used to give large fragments (6) which, when analyzed, provided sufficient information to allow a sequence to be defined.

Table 1 shows the products obtained when tyrosine tRNA 1 was digested by pancreatic ribonuclease and by ribonuclease T1. The two sets of fragments are generally in good agreement, with any discrepancies considered to be due to impurities present in the RNA. The presence of cytidine indicates that, as was the case for the alanine RNA, the terminal pA is missing from the tyrosine RNA as it is isolated. The pA residue is added prior to the attachment of the amino acid (7). The modified nucleotides were identified by their chromatographic and spectral properties (8). The tentative identification of MeA as 1-methyladenosine was based on its conversion to *N*⁶-methyladenosine by alkaline hydrolysis (9); it also has a *pK_a* near 7 (10).

The *pC_p* found in the pancreatic ribonuclease digest is the 5'-terminus. This is the first time that any nucleotide ex-

cept pGp has been found at the non-acceptor terminus of a purified tRNA.

The large fragments produced by partial ribonuclease T1 digestion that were used to establish the sequence are shown in Fig. 1. Fragment *a* gave C-C-C-C-G-, A-C-C_{OH}, A-G- and 2 G- when completely digested with ribonuclease T1. Fragment *b* upon T1 digestion gave the same products as well as MeA-C-U-C-G- and upon pancreatic ribonuclease digestion gave G-G-G-A-G-A-C-. Since fragment *a* contains only one A-C- sequence, the A-C-C_{OH} must overlap with G-G-G-A-G-A-C-. Since the 3'-hydroxyl group on A-C-C_{OH} must be the right-hand terminus, C-C-C-C-G- must go to the left. To complete fragment *b*, MeA-C-U-C-G- can only go to the left of fragment *a*.

Fragment *c* upon digestion with ribonuclease T1 gave A-diHU-5MeC-G-, T- ψ -C-G-, C-G-, and 2 G-. Pancreatic ribonuclease digestion produced G-G-G-C-. Treatment of fragment *c* with alkaline phosphatase, followed by complete digestion with ribonuclease T1, produced some T- ψ -C-G_{OH}, so that T- ψ -C-G- must be on the right. The only DiHU containing oligonucleotide produced by pancreatic ribonuclease in this half of the molecule (see below) is G-A-G-A-diHU-. Since this pentanucleotide is not part of fragment *c*, it must be directly to the left of fragment *c*. The only possible sequence for *c*, then, is that shown, and G-A-G- is immediately to the left of *c*.

The only oligonucleotide in this half of the molecule remaining to be placed is the nonanucleotide, ψ -A-diMeA-A- ψ -C-U-U-G-. It could go either to the left of fragment *c*, or between *c* and *b*. Since another large fragment was found which contained the components of *b* and *c*, but not the nonanucleotide, this nonanucleotide must go on the left of the G-A-G-. Adding the -A_{OH} to the acceptor terminus (7) gives the se-

quence of the acceptor half of the molecule shown as *d*.

Fragment *e* contained pC-U-C-U-C-G-, U-A-2MeG-, and G-. The 5'-phosphate identifies pC-U-C-U-C-G- as the nonacceptor terminus. To accommodate the sequences G-G-U- and A-2MeG-C- found in the pancreatic ribonuclease digests the sequence must be as shown.

Under the conditions used, the only other large fragment detected in partial digests with ribonuclease T1 of the intact tRNA that came from the nonacceptor half of the molecule was fragment *f* which contained C-diMeGp! and C-A-A-G-. Since A-A-G-C- is not found in pancreatic ribonuclease digests, the sequence of *f* must be as shown.

As with alanine tRNA (11), brief treatment of the tyrosine tRNA with ribonuclease T1, in the presence of 0.02M MgCl₂ at 0°C, split it into approximately equal halves. Partial digestion of the nonacceptor half produced fragments *g* and *h*. Fragment *g* contained the ribonuclease T1 oligonucleotides that were in *e*, as well as C-C-A-A-G-. The latter can only go to the right of *e*, so that *g* must have the structure shown.

Fragment *h* upon complete digestion with ribonuclease T1 gave DiHU-diHU-diHU-A-A-G-, G-, C-diMeGp!, C-A-A-G-, and A-C-U-G-. The DiHU-diHU-diHU-A-A-G- must go on the left since it is the only T1 product that can provide the DiHU for the 2'-OMeG-G-diHU- found in the pancreatic ribonuclease digest. Now A-C-U-G- could go either on the right or between DiHU-diHU-diHU-A-A-G- and C-diMeG-C-A-A-G-. The first alternative is the proper arrangement, since neither G-C- nor G-G-C- is found in pancreatic ribonuclease digests, as would be required by the second possibility. The remaining G- must be

placed to the right of DiHU-diHU-diHU-A-A-G- to provide for the A-A-G-G-C- produced by pancreatic ribonuclease.

The only ribonuclease T1 product that remains to be placed is DiHU-diHU-2'OMeG-G-. Fortunately, only by placing it between fragments *g* and *h* can requirements imposed by the pancreatic ribonuclease digest products be met. Fragment *i* then contains all the components detected in pancreatic ribonuclease and ribonuclease T1 digests of the nonacceptor half of the molecule.

By placing the half molecules together the complete sequence is obtained. As confirmation that this is the proper sequence at the junction of the halves, G- is formed by pancreatic ribonuclease digestion of the nonacceptor half, and G-ψ- is the only pancreatic ribonuclease product which is not obtained when the half molecules are digested.

The tyrosine tRNA has 78 nucleotides, whereas the alanine tRNA has 77. Regardless of where the additional nucleotide in the tyrosine RNA is positioned, there are only a few places where the same nucleotide occupies the same spot in the two molecules. Besides the A-C-C-A_{OH} at the acceptor terminus and the G-T-ψ-C-G-, which is com-

Table 1. Products obtained upon enzymic digestion of tyrosine tRNA.

Pancreatic ribonuclease products	
C _{OH}	G-MeA-C-
9 to 11 C-	A-2MeG-C-
5 to 6 U-	G-G-U-
2 DiHU-	2'OMeG-G-diHU-
5MeC-	A-diMeA-A-ψ-
ψ-	A-A-G-diHU-
pC-	G-G-G-C-
G-T-	A-A-G-A-C-
G-C-	A-A-G-G-C-
DiMeG-C-	G-A-G-A-diHU-
G-ψ-	G-G-G-A-G-A-C-
Ribonuclease T1 products	
8 G-	A-C-U-G-
C-diMeGp!	C-A-A-G-
A-C-C _{OH}	A-diHU-5MeC-G-
C-G-	MeA-C-U-C-G-
3 A-G-	C-C-A-A-G-
U-A-2MeG-	C-C-C-C-G-
DiHU-diHU-	DiHU-diHU-
2'OMeG-G-	diHU-A-A-G-
T-ψ-C-G-	pC-U-C-U-C-G-
	ψ-A-diMeA-A-ψ-C-U-U-G-

mon to many tRNA's (12), G-C-diMeG-C- is the only other sequence of four nucleotides that is present in the same position in both molecules. The sequence G-G-G-A-G-A- is found in both RNA's, but in different positions.

However, by placing the molecules in the clover-leaf arrangement shown in Fig. 2, strikingly similar structures result. The arrangements are based on achieving the maximum number of

hydrogen-bonded base pairs of the Watson-Crick type. The proposed secondary structure for the alanine RNA has 17 GC, two AU, and one GU (13) base pairs. The tyrosine tRNA in this arrangement gives 15 GC pairs, four AU pairs, and one GU pair.

In both cases the upper stem contains seven base pairs. In the alanine acceptor RNA, however, the opposing U-'s presumably do not form hydrogen bonds. In both structures the GU pair is in the upper stem. Both right-hand and lower limbs contain five base pairs terminated by a seven-residue loop. The tyrosine RNA left-hand limb has three hydrogen-bonded nucleotide pairs (assuming that 2MeG can form a hydrogen bond with C) and a 12-residue loop. The alanine RNA arrangement has four GC pairs and a ten-residue loop on the left side.

In addition, the transition regions between the limbs are very similar in the two structures. The transition from the upper to the right-hand limb in both models is made without having an unpaired nucleotide. The discrepancy in the number of nucleotides in the two molecules is accounted for by a difference in the number of nucleotides in the region between the right-hand and bottom limbs. The alanine scheme has four unpaired residues, whereas the

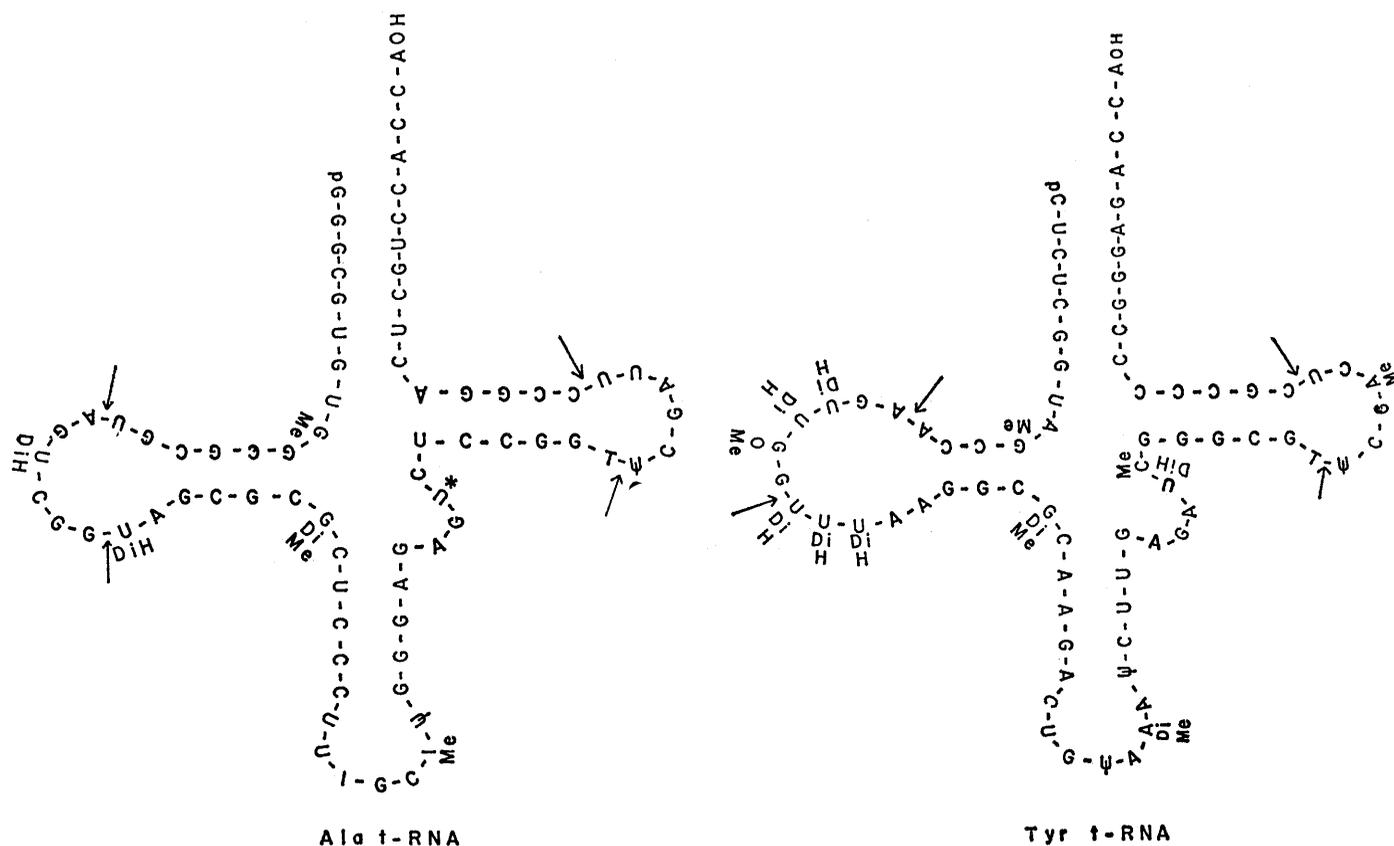


Fig. 2. Proposed structure for yeast tyrosine 1 and alanine tRNA's.

tyrosine structure has five residues unpaired. The transition to the left-hand limb is made in both cases by DiMeG. The transition from the left to the upper limb is made in an identical fashion in both structures—by two unbonded nucleotides.

In addition to the DiMeG and T- ψ -C-G residues being in homologous positions, it is apparent from the cloverleaf arrangements that ψ is found only in the lower and right-hand loops, while DiHU is found in the left-hand loop and in the transition from the right-hand to the lower limb.

The alanine tRNA has no unusual nucleotides in the regions that are proposed to be hydrogen-bonded. The tyrosine RNA, however, has 2MeG and ψ in locations that are presumably hydrogen-bonded.

It might be significant, on the other hand, that bases that presumably cannot form a hydrogen-bonded base pair such as DiMeG, DiMeA, 1MeI, and 1MeG, are all located in regions depicted as being not hydrogen-bonded.

In both structures only the G- in the bottom loop is cleaved by ribonuclease T1 at 0°C and 0.02M MgCl₂. It is difficult to understand this specificity unless the other loops are rendered inaccessible. It is possible that the two lateral loops can form hydrogen bonds with each other. In both cases, the bases within the arrows could form two GC, two GU, and one or two AU type base pairs depending on whether the MeA in the right-hand loop of the tyrosine tRNA can form a base pair. The above also assumes that DiHU can form effective hydrogen bonds.

The activating enzyme recognition site is still not obvious. In addition to the anticodon (14), the DiHU containing left-hand limb and the unbonded residues between the lower and right-hand limbs might be likely candidates.

The sequences G- ψ -A in the lower loop and G-U-A between the left and upper limbs are the only sequences that satisfy all the requirements for the anticodon for tyrosine (15), since there is no A-U-A or A-U-G sequence in the molecule. It appears that of the two anticodons suggested for the alanine tRNA, 1-G-C and the C-G-G sequence between the two DiHU's (1), I-G-C is the correct one, since the region between the DiHU's in the tyrosine acceptor RNA is unlikely to be the anticodon. In serine tRNA, I-G-A has been found in a position similar to the I-G-C in the alanine RNA (16). G- ψ -A, then, is very probably the anticodon in the

tyrosine tRNA. Since it is possible that ψ forms better hydrogen bonds than U (17), its presence in the anticodon should not cause any problems. It might even be beneficial (18).

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18. After this was written, H. G. Zachau, D. Dütting, H. Feldmann, *Angew. Chem.* **78**, 392 (1966), reported the nucleotide sequences of two very closely related serine tRNA's from brewer's yeast. Most of the discussion in our report concerning probable secondary structures also applies to the serine RNA's.
19. We thank Dr. R. W. Holley without whose encouragement and assistance this work could not have been carried out, Drs. E. B. Keller and J. Apgar for consultation, and G. Teetor and M. Simonson for technical assistance.

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Deep-Sea Authigenic Calcite and Dolomite

Abstract. Crystals of calcite and, in one case, of dolomite up to 90 μ m in size are dispersed in pelagic red clay at several sites on the floor of the South Pacific Ocean. They were analyzed by microscopic, x-ray diffraction, electron x-ray microprobe, and oxygen isotopic techniques. These carbonates are authigenic and were probably precipitated from hydrothermal solutions connected with deep-sea volcanic activity.

The carbonate fraction of deep-sea pelagic sediments from the Pacific Ocean is generally composed of tests of Foraminifera and Coccolithophoridae. Such tests consist of microcrystalline aggregates of calcite; the size of the single crystals within the aggregates is usually about 1 μ m or less. Larger and apparently nonbiogenous carbonate crystals are dispersed in pelagic zeolitic clays at the following locations in the South Pacific.

1) 18°35'S, 126°25'W, 4030 m below sea level (Amph 39). Bathymetric survey of an area adjacent to a sea mount was carried out by R.S. *Argo* of the Scripps Institution of Oceanography. Basaltic and hyaloclastic rocks were dredged from the sea mount, and two cores of fine, dark brown sediment were recovered from the flat area west of the mount (1). Both sediment samples (Amph 39 and Amph 40) consist of

crystals of phillipsite, grains of hydrated basaltic glass, expandable smectitic clays, and black manganese oxide particles in addition to carbonates. The two samples differ greatly in carbonate content even though they were collected within several kilometers of each other and at similar depths. Volumetric determination gave 45.6 percent CaCO₃ for Amph 39 and 9.5 percent for Amph 40. Both samples contain very small amounts of microcrystalline calcitic tests of foraminifera and coccoliths. Sediment Amph 39 contains irregularly shaped, single-crystal grains of calcite up to 60 μ m long (Fig. 1a), which are absent from sample Amph 40.

2) 18°30'S, 124°30'W, 3860 m below sea level (Amph 38). An attempt to collect a gravity core at this location resulted in recovery of only a 5-cm layer of indurated brown material in the core nose. This rock consists essentially