A Novel Wobble Rule Found in Starfish Mitochondria

PRESENCE OF 7-METHYL GUANOSINE AT THE ANTICODON WOBBLE POSITION EXPANDS DECODING CAPABILITY OF tRNA*

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In the starfish mitochondrial (mt) genome, codons AGA and AGG (in addition to AGU and AGC) have been considered to be translated as serine. There is, however, only a single candidate mt tRNA gene responsible for translating these codons and it has a GCT anticodon sequence, but guanosine at the first position of the anticodon should base pair only with pyrimidines according to the conventional wobble rule. To solve this enigma, the mt tRNA<sub>AGCU</sub> was purified, and sequence determination in combination with electrospray liquid chromatography/mass spectrometry revealed that 7-methylguanosine is located at the first position of the anticodon. This is the first case in which a tRNA has been found to have 7-methylguanosine at the wobble position. It is suggested that methylation at N-7 of wobbling guanosine endows the tRNA with the capability of forming base pairs with all four nucleotides, A, U, G, and C, and expands the repertoire of codon-anticodon interaction. This finding indicates that a nonuniversal genetic code in starfish has been generated by base modification in the tRNA anticodon.

An unusual mode of wobble base interaction with mRNA codons exists in mitochondria (1, 2). Uridine at the wobble position base pairs with all four nucleotides, while modification from uridine to 5-carboxymethylaminomethyluridine (cmnm<sup>5</sup>U)<sup>1</sup> prevents pairing with pyrimidines. Codons with a pyrimidine in the third position are translated by tRNAs having unmodified guanosine at the first anticodon position. This rule was first proposed for fungal mitochondria (3, 4) and has been considered to hold for most codon boxes in animal mitochondria. However, a few exceptional codon-anticodon pairings have been observed in this organelle.

In most animal mitochondria, the methionine codons AUG and AUA are translated by a single methionine tRNA which has 5-formylethyridine (f<sup>5</sup>C) in the first anticodon position, indicating that f<sup>5</sup>C plays a role similar to cmm<sup>5</sup>U (5). In starfish and sea urchin mitochondria, however, AUA is restored to the isoleucine codon as in the universal genetic code (6–9), while AAA and AGR (R = A, G) are presumably translated as lysine and serine, respectively (6–9); these codon assignments are different from those in other known animal mitochondrial systems. For example, AGR codons are utilized for the termination and glycine codon in mammalian (10) and ascidian (11) mitochondria, respectively. In Drosophila, AGA is the serine codon but the other AGR codon, AGG, is absent from the mitochondrial genome (12–14). In contrast, both AGA and AGG appear in reading frames encoded on starfish and sea urchin mt DNAs and are presumably assigned to serine judging from the sequence alignment (6–9). In nematodes, AGN codons are translated with a serine tRNA whose gene possesses a TCT anticodon sequence (15). We have shown that unmodified uridine is located at the wobble position of the tRNA (16), indicating that the codon-anticodon interaction definitely follows the wobble rule. In contrast, the mitochondrial gene encoding the tRNA that translates all AGN codons in starfish and sea urchin has the anticodon GCT (6–9). The question that arises from this is how the GCT anticodon can recognize the AGA and AGG codons, in addition to AGY (Y = U, C), in echinoderms.

We have previously speculated on possible answers to this question (1, 2, 17). One possibility is that G at the first anticodon position of the starfish mt tRNA<sub>AGCU</sub> might be modified so as to allow it to pair with all four AGN codons. Alternatively, it might be that a region(s) in the tRNA other than the anticodon influences the decoding ability of AGR codons, because most metazoan mt tRNA<sub>AGCU</sub> have unusual secondary structures in which the D arm is lacking or incomplete (2, 17). This truncated D arm could be responsible for G-R pairing, in addition to G-Y pairing, between the anticodon and codons. Another feature is the G-C pair at the bottom of the anticodon stem, which is present in the tRNA<sub>AGCU</sub> of mitochondria of invertebrates, but not in those of most vertebrates, in which its place is taken by A-U pairs (2, 17, 18). Since tRNA<sub>AGCU</sub> of all metazoan mitochondria except for that of nematode have identical anticodon loops (15), there could be some structural differences in regions other than the anticodon loop, depending on which codons, AGY (vertebrates) or AGN (N = A, G, C, or U) (invertebrates), are translated as serine.

With the aim of determining which of these speculations is actually the case, the starfish mt tRNA<sub>AGCU</sub> responsible for the noncanonical decoding in the AGN codon box was purified and sequenced, and the modified nucleoside content was determined by electrospray liquid chromatography-mass spectromet-
etry (ES-LC/MS). The results showed the first of the speculations posited above to be correct; guanosine at the wobble position of starfish mt tRNAGCU_Ser has been completely converted to 7-methylguanosine (m7G). This strongly suggests that m7G is capable of base pairing with all four nucleotides, thus resulting in a genetic code change in echinoderm mitochondria. Based on the primary structure of the mt tRNAGCU_Ser, we also present a scenario that could explain evolutionary changes in the genetic code that have occurred in animal mitochondria.

**EXPERIMENTAL PROCEDURES**

**Purification of tRNA from Asterina amurensis**—The starfish A. amurensis was harvested at Miyako, Iwate prefecture, Japan. The ovaries were removed, immediately frozen on dry ice, and stored until RNA preparation. Crude ovary RNA was prepared by phenol extraction and precipitated by ethanol. It was purified further by DE52-cellulose column chromatography using an elution solvent containing 0.7 M NaCl, 20 mM Tris-HCl (pH 7.5), and 10 mM magnesium acetate. The RNA was recovered by ethanol precipitation and applied onto a Q-Sepharose column to eliminate residual polysaccharides. RNA was eluted by the same buffer used for the DE52 column chromatography. Serine tRNA was purified by hybridization methods using the 3’ biotinylated oligonucleotide CGAAAACTCTATGGATTGAAACCAGATT, immobilized on a streptavidin-agarose matrix as described previously (16, 19, 20). This 30-mer oligonucleotide complementary to the sequence of the 3’ region of the tRNA was designed based on our unpublished DNA sequence data (DDBJ accession no. is D17543).

**Sequence Determination of Starfish mt tRNAGCU_Ser**—The purified tRNAGCU_Ser was subjected to sequencing by the methods of Donis-Keller (21) and Kuchino et al. (22). RNase T1, RNase PhyM, and T4 RNA ligase were purchased from Pharmacia Biotech Inc., RNase T2 and RNase CL3 from Seikagaku Kogyo, and *Escherichia coli* alkaline phosphatase from Takara Shuzo. T4 polynucleotide kinase and other chemical reagents of analytical grade were from Wako Pure Chemicals. [32P]pCp and [γ-32P]ATP were obtained from Amersham, Japan. In Kuchino’s method, nucleotides in the tRNA were analyzed by two-dimensional TLC utilizing two different development systems. System A consisted of isobutyric acid/concentrated ammonia/water (66:1:33 by volume), in the first dimension, and 2-propanol/HCl/water (75:15:15 by volume) in the second dimension. In system B, the first dimension was the same as that for system A, but 0.1 M sodium phosphate (pH 6.8)/ammonium sulfate/1-propanol (100 ml:60 g:2 ml) (22, 23) was used for the second dimension. The base numbering conforms to the literature...
Sequence Location of Modified Nucleotides in mt tRNA$_{GCU}$—Starfish mt tRNA$_{GCU}$ was hydrolyzed completely to nucleo-
ides (24) and analyzed by electrospray LC/MS. The peak elut-
ing at 3.9 min contains dihydrouridine and pseudouridine (Fig.
2a). Based on sequencing by Kuchino's method, these nucleo-
tides are located in the D loop, the anticodon stem and the T loop.
The peak at 10.6 min contains two different methylcyti-
dines, m$^3$C and m$^5$C, which are assigned to position 32 of the
anticodon loop. The peak around 12.7 min is assigned as m$^7$G,
and to that of N$^5$-methyl-N$^8$-threonylcarbamoyladenosine (ms2t6A) in solvent system B (Fig. 2c). The mobilities of ms2t6A
in solvent system B and that of m$^6$t6A in solvent A have not been reported to date (23). However, ES-LC/MS analysis (see
below) showed that the A-37 derivative is m$^6$t6A. This tRNA
also contains dihydrouridine at position 14 in the D loop and
two pseudouridines at position 40 in the anticodon stem and at
position 55 in the T loop. The uridine at position 48 is partially
modified to an unknown form (data not shown).

Electrospray LC/MS Analysis of Hydrolyzed tRNA$_{GCU}$—
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327 and 459, respectively as calculated), and on the retention time (25). In the sequence determination using Kuchino’s method (22), an unknown partially modified U derivative was observed at position 48. We were unable to identify the peak eluting just after the guanosine peak, which might correspond to this peak. Uridine derivatives are known to yield poor re-

Fig. 3. Electrospray LC/MS analysis of nucleosides from starfish mt tRNA\textsubscript{Ser}. a, chromatographic separation of nucleosides monitored at 266 nm. b, electrospray mass spectrum of the nucleoside component eluting at 12.7 min, marked by an arrow in a.
response to electrospray ionization (27). The peaks with retention
times of 14.7, 16.9, and 19.6 min are assigned from ES-LC/MS
data as deoxyguanosine, thymidine and deoxyadenosine,
respectively. The shoulder observed in the uridine peak (around
7.8 min) is deoxycytidine. These deoxynucleosides are presum-
ably contaminants from the oligodeoxynucleotide probes used
to purify the tRNA.

Alkali-induced Cleavage of mt tRNA\textsubscript{Ser} at the Location of
m\textsuperscript{7}G—

Since m\textsuperscript{7}G (identified from sequencing and ES-LC/MS
data) has not previously been reported to occur at the wobble
position in the anticodon of any tRNA (28), mt tRNA\textsubscript{GCU}
was subjected to aniline treatment to effect characteristic chain
cleavage at the m\textsuperscript{7}G site (26). As shown in Fig. 4, scission of mt
tRNA\textsubscript{GCU} at position 34 (the wobble position) by alkaline treat-
ment is clearly observed; yeast phenylalanine tRNA was like-
wise cleaved at the expected positions of nucleosides wyosine
(Y) and m\textsuperscript{7}G in a control experiment. Thus, this experiment,
together with sequence determination and ES-LC/MS analy-
ses, clearly shows that the wobble nucleotide of starfish
mt tRNA\textsubscript{GCU} is m\textsuperscript{7}G, leading to the sequence of starfish mt
tRNA\textsubscript{GCU} shown in Fig. 5.

DISCUSSION

We report here the first known occurrence of m\textsuperscript{7}G at the
wobble position of a tRNA. Even since we first discovered that
in starfish mitochondria AGN codons seem to be translated as
serine by the tRNAGCU from the sole corresponding gene lo-
cated on the mt genome (6), the question as to how tRNA GCU
possessing a GCU anticodon decodes all four AGN codons has
attracted our interest, especially with regard to the decoding
mechanism of mt tRNAs toward nonuniversal codons. This
long-pending puzzle has now been solved by the finding that a
modified residue (m\textsuperscript{7}G) exists at the wobble position of
tRNA\textsuperscript{GCU}, which is probably responsible for decoding AGN
codons. This solution seems to be the simplest one among the
speculations so far postulated (see Introduction) (1, 2, 17).

We thus consider that the occurrence of m\textsuperscript{7}G at the wobble
position, which has emerged uniquely in echinoderm mitochon-
dria, leads to non-canonical base pairing. This, together with
the results concerning codon-anticodon relationships obtained
so far for various animal mitochondria (3, 4, 29), enables us to
draw up a set of general rules for codon-anticodon interaction
in mitochondria. These are summarized in Fig. 6.

In conventional mitochondrial wobble rules so far elucidated
(3, 4, 29), tRNAs with unmodified guanosine in the first anti-
codon position are considered to translate only codons termin-
ating in a pyrimidine at the third position, while anticodons
with modified uridine at the same position translate codons having a purine at the third position (Fig. 6a).

In *Drosophila* mitochondria, alignment of mt genes suggests that AGA is a serine codon, whereas AGG is an unassigned codon (2), because AGG has never appeared in *Drosophila* mt genomes. We have isolated *Drosophila melanogaster* tRNA<sub>Glu</sub>, which presumably recognizes codons AGC, AGU, and AGA (15), and found that unmodified guanosine is the wobble nucleotide (unpublished observation). Based on the mt genomic sequence, it is unlikely that any tRNA competing with tRNA<sub>Glu</sub> with G, in addition to A, C, and U, at the third position of the translation system (Fig. 6b).

This hypothesis is supported by the following fact. In starfish mitochondria, AUA is an isoleucine codon, which differs from other known animal mitochondria in which AUA is used as a methionine codon (2). We found that isoleucine and methionine tRNAs of starfish have unmodified GAU and CAU anticodons, respectively (data not shown). Our observation that the wobble nucleoside of the sole mammalian mt methionine tRNA is 5-formylcytidine led us to propose the possibility that this modification allows decoding of AUA in addition to AUG (5). These codon-anticodon relationships for methionine and isoleucine in mammalian and starfish mitochondria support the above interpretation on the decoding properties of unmodified guanosine at the wobble position. Since the unmodified CAU anticodon of methionine tRNA has no capability of decoding AUA (1, 2) due to the lack of modification at the wobble position, the tRNA<sub>Met</sub> does not compete with tRNA<sub>Ile</sub> possessing the GAU anticodon in mammalian and starfish mitochondria support the above interpretation on the decoding properties of unmodified guanosine at the wobble position. Since the unmodified CAU anticodon of methionine tRNA has no capability of decoding AUA (1, 2) due to the lack of modification at the wobble position, the tRNA<sub>Met</sub> does not compete with tRNA<sub>Ile</sub> possessing the GAU anticodon in mammalian and starfish mitochondria.

In ascidian mitochondria, AGR codons are specific for glycine, while AGY codons are translated as serine (11). The corresponding mt tRNAs were isolated and sequenced; tRNA<sub>Glu</sub> was found to have unmodified G at the wobble position, whereas tRNA<sub>Glu</sub> specific for AGR has cmm<sup>5</sup>U at the same position (30). In this case, tRNA<sub>Glu</sub> may compete with tRNA<sub>Glu</sub> preventing AGR codons from being mistranslated as Ser. In mammalian mitochondria, only AGU and AGG codons are translated by tRNA<sub>Glu</sub> possessing the anticodon GCU, and there are no tRNAs that translate the AGA and AGG codons (1, 2). Although it is apparently in contradiction to the above-mentioned codon-anticodon rule, AGG and AGA are utilized as termination codons in mammalian mitochondria (10, 31). We propose here that a release factor (1, 2) recognizing these codons plays a role similar to that of the competitor tRNA (Fig. 6c). Thus, only AGY codons remain for assignment to serine.

The present finding that m<sup>5</sup>G is the wobble nucleotide in starfish mt tRNA<sub>Glu</sub> suggests that methylation of G at N7 expands codon-anticodon interaction to permit base pairing with G, in addition to A, C, and U, at the third position of the codon (Fig. 6d). Although the influence of the altered charge distribution (resulting from N7 methylation) on the base pairing of m<sup>5</sup>G with G is unknown, we are now carrying out experiments using an *in vitro* translation system to confirm the decoding properties of tRNA possessing m<sup>5</sup>G at the wobble position, and also to verify the ability of m<sup>5</sup>G to base pair with all four nucleotides with respect to the structural factors.

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