Modified Nucleosides of Nuclear and Nucleolar Low Molecular Weight Ribonucleic Acid*

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SUMMARY

Modified nucleosides have been found in some types of low molecular weight nuclear RNA of Novikoff hepatoma ascites cells in addition to 4 S RNA. The low molecular weight nuclear RNA species have been defined on the basis of their size as well as their content of uridylic acid as 4 S, 4.5 S, 5 S, U-1, U-2, and U-3 RNA (BUSCH, H., AND SMETANA, K. (1970) The Nucleolus, p. 285, Academic Press, New York). In particular, the U-2 RNA contained 11 pseudouridine residues and the unusual nucleoside, N7,N8-dimethyl 7-methyl guanosine, which was not found in transfer RNA or any other nuclear RNA except U-3. Nuclear 4.5 S RNAII contained 3 pseudouridine residues and 1 residue each of N6-methyl adenosine and N7-methyl guanosine. Nuclear 5 S RNAII contained 2 pseudouridine residues. Although the content of modified nucleosides in the 4 S RNAs from cytoplasm, ribosomes, and nuclei was the same, significantly lower amounts of dihydrouridine and N7-methyl guanosine were found in the nuclear 4 S RNA. No modified nucleosides were found in 4.5 S RNAI, 4.5 S RNAII, 5 S RNAI, 5 S RNAII, U-la RNA, and 5.5 S RNA.

Recently, a number of species of low molecular weight nuclear RNAs (1-10) have been purified from Novikoff hepatoma ascites cells and the sequence of one, the nuclear 4.5 S RNA1 has been completely defined (11). Although the functions of these RNA molecules are still unknown, the intranuclear distribution of these RNAs and some of their characteristics have been studied (12). In approaches to the sequences of other types of these RNA molecules, several 2'-O-methylated nucleotides were identified (12). To determine more about the presence or quantities of modified nucleosides in these RNA species, the recently described (13-15) micromethods of Randerath and Randerath were employed because of their demonstrated value in determining the minor nucleoside content of RNA of various tissues (14). The results obtained on the base-modified nucleotides agreed well with previous studies by Holley et al. (16) and others (17). The high sensitivity of the method allows detection of quantities of modified bases in samples of 50 μg of RNA. With this method, the presence and content of base-modified nucleosides have been defined for most of the low molecular weight nuclear and nucleolar RNA.

MATERIALS AND METHODS

Animals—Male albino rats, weighing 200 to 300 g, obtained from Holtzman Company (Madison, Wisconsin), were fed Purina laboratory chow ad libitum. The Novikoff hepatoma ascites cells were transplanted 7 days prior to killing. After the rats were killed by cervical dislocation, the cells were collected from the peritoneal fluid by centrifugation at 900 x g for 10 min in a Sorval centrifuge.

Preparation of Nuclei and Nucleoli—The citric acid procedure employed for the isolation of nuclei from tumor cells was essentially the same as that reported previously (8, 18, 19). The sonic disintegration method employed for the isolation of nucleoli was the same as that reported earlier (5, 20).

Extraction of RNA from Cell Fractions—RNA was extracted from the various cellular fractions by the phenol-sodium dodecyl sulfate method employed previously (4, 5, 8, 20). Ribosomes and the cytoplasmic supernatant were isolated from Novikoff hepatoma ascites cells as previously described (21). The isolation of 4 to 7 S RNA and preparative polyacrylamide gel electrophoresis were carried out as described previously (21).

Purification of RNAs Obtained from Polyacrylamide Gel Electrophoresis—Obtained by fractionation of 4.5 S RNA on DEAE-Sephadex A-50 columns as described previously (21) were 4.5 S RNAI, 4.5 S RNAII, and 4.5 S RNAIII. Obtained by fractionating 5 S RNA on a DEAE-Sephadex A-50 column as described previously (22) were 5 S RNAIII, 5 S RNAI, and 5 S RNAII. U-la RNA was obtained from U-1 RNA as described below. U-1 RNA was adsorbed on a benzoylated DEAE (BD)-cellulose column and eluted with 1 M NaCl and subsequently with 25% ethanol. The portion eluting with ethanol is U-la RNA (12). U-2 RNA was obtained by fractionating U-2 RNA from preparative polyacrylamide gel electrophoresis on a column (1.5 x 30 cm) of DEAE-Sephadex A-50 at room temperature. The linear gradient employed was sodium chloride from 0.3 to 0.0 M in 0.02 M Tris-HCl, pH 7.6, containing 7 M urea. U-2 RNA was eluted at 0.46 M sodium chloride. U-3 RNA obtained from

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polyacrylamide gel electrophoresis was fractionated again on a shorter (2.5 cm) gel to remove any aggregation products.

Analysis of RNA for Nucleosides—This was carried out by the tritium derivative method as described by Randerath (13-15). The method essentially consists of degrading the RNA to nucleosides with ribonuclease A, snake venom phosphodiesterase, and alkaline phosphatase. The nucleosides were oxidized with sodium periodate and reduced subsequently in the presence of tritiated borohydride. The labeled nucleoside derivatives were separated by cellulose thin layer chromatography using a mixture of acetonitrile, ethyl acetate, 1-butanol, 2-propanol, and 6 N ammonia in a ratio of 7:2:1:2:2.7 (v/v) in the first dimension and a solvent mixture of t-amyl alcohol, methyl ethyl ketone, acetonitrile, ethyl acetate, water, and formic acid in a ratio of 4:2:1:5:2:1:5:0.18 (v/v) in the second dimension. The fluorographs were prepared by the method of Randerath and Randerath and the radioactivity was measured by eluting the nucleoside derivatives from thin layer chromatography sheets with 2 N ammonia and counting in the presence of Omnifluor (New England Nuclear, Boston, Mass.).

Synthesis of $N^2,N^2$-Dimethyl 7-Methyl Guanosine—$N^2,N^2$-Trimethyl guanosine was prepared according to the method described by Saponara and Enger (23). Twenty milligrams of $N^2,N^2$-dimethyl guanosine (obtained from Cycle Chemical) were suspended in 400 µl of dimethyl acetamide containing 10 µl of concentrated ammonia and then was placed on a phosphocellulose column (1 × 50 cm) at pH 7 (0.001 M ammonium acetate). A linear gradient of 0.001 M to 0.3 M of ammonium acetate was used to elute the samples. One major peak of the product was found between two minor peaks (corresponding to $N^2,N^2$-di- methyl-G and 7-methyl-G). The product was lyophilized and was identified as $N^2,N^2$-dimethyl, 7-methyl guanosine by mass spectroscopy.

RESULTS

4 S RNA—For comparison of the nucleoside distribution of 4 S RNA and other low molecular weight RNA, fluorographs of two-dimensional thin layer chromatography separations were prepared of the 1H-labeled triazole derivatives of the nucleosides of 4 S RNAs from the cell sap, ribosomes, nuclei, and nucleoli (Fig. 1). Less than 0.5% of the radioactivity remained at the origin. The nucleosides were identified by their position compared with maps reported earlier by Randerath and Randerath (13-15). Table I shows that the compositions of 4 S RNA from nuclei, ribosomes, and the cell sap are essentially the same for both the major and modified nucleosides. Of the total nucleosides of the nuclear, cytoplasmic, and ribosomal 4 S RNAs, 11.5% were modified. The nucleolar 4 S RNA differed markedly from these RNAs in its higher content of U and A. In the nucleolar 4 S RNA, the modified nucleosides only accounted for 9.5% of the total and there was significantly less dihydro-U and $N^2$-methyl-G.

4.5 S and 5 S RNA—Fig. 2 shows the fluorographs of the separations of nucleoside derivatives of nuclear 4.5 S RNA, 4.5 S RNA1, 4.5 S RNA11, 5 S RNA, 5 S RNA1, and 5 S RNA11. As shown in Table II, no modified nucleosides were found in nuclear 4.5 S RNA, 4.5 S RNA1, 5 S RNA, and 5 S RNA11 (12). The compositions with respect to the major nucleosides were essentially the same as those determined earlier by $^3$P and ultraviolet absorbance (12, 21, 22, 24). However, 4.5 S RNA11 contains $T$, $N^3$-methyl-G, and $N^4$-methyl-A, which accounted for 2.0%, 0.8%, and 0.8% of the total nucleosides, respectively.

The abbreviations used in the tables and figures are: No, nuclei; Nu, nucleoli; Rib, ribosomes; B, enzyme blank; gly, glycerol; $A'$, adenine hydroxymethyl diethyleneglycol; $C'$, cytosine hydroxymethyl diethyleneglycol; $G'$, guanine hydroxymethyl diethyleneglycol; $U'$, uracil hydroxymethyl diethyleneglycol; $\Phi'$, pseudouracil hydroxymethyl diethyleneglycol; m$A'$, 1-methyl adenine hydroxymethyl diethyleneglycol; m$A''$, $N^3$-methyl adenine hydroxymethyl diethyleneglycol; m$C'$, 3-methyl cytosine hydroxymethyl diethyleneglycol; m$G'$, 5-methyl cytosine hydroxymethyl diethyleneglycol; m$G''$, 1-methyl guanine hydroxymethyl diethyleneglycol; m$G''''$, $N^2$-methyl guanine hydroxymethyl diethyleneglycol; m$G''''''$, 7-methyl guanine hydroxymethyl diethyleneglycol; $T''$, thymine hydroxymethyl diethyleneglycol.

Since partial (15 to 25%) conversion of m$A$ to m$A''$ occurs during the hydrolysis of RNA to nucleosides (15), the values of m$A$ in Table I are probably derived from m$A''$. The sum of m$A$ and m$A''$ is similar to the reported values for m$A$ in mammalian RNA (14). However, Fig. 2C and Table II show that 4.5 S RNA11 contains no m$A$, whereas m$A''$ accounted for 1 residue per molecule. These results indicate that the m$A$ of 4.5 S RNA11 is unique to this molecular species and is not derived from m$A$.  

Fig. 1. Fluorographs of two-dimensional thin layer chromatography. Separation of pH nucleoside derivatives from 4 S RNA of Novikoff hepatoma ascites cells. A, cell sap; B, ribosomes; C, nuclei; and D, nucleoli. See Footnote 2 for definitions of symbols appearing on figure.
Since the approximate chain length of this RNA is 93 (25), the number of residues of \( N^2 \)-methyl guanine hydroxymethyl diethylene glycol, and \( N^2 \)-methyl adenine hydroxymethyl diethylene glycol is 3, 1, and 1, respectively. Interestingly, 4.5 S RNA contains four alkali-stable dinucleotides, previously found to be AmpAp, GmpAp, and two GmpGp (25). The RNA contains four alkali-stable dinucleotides, previously found to be AmpAp, GmpAp, and two GmpGp (25). The contents of inosine were included in guanosine because trialcohol derivative of inosine was not well separated from the trialcohol derivative of guanosine.

### Table I

Nucleoside composition of 4S RNAs from nucleoli, nuclei, ribosomes, and cell sap.

| Nucleolus | Nuclei | Ribosomes | Cell sap | \( p \) values |
|-----------|--------|-----------|----------|----------------|
| Major nucleosides | | | | |
| U | 18.80 ± 0.23 | 16.90 ± 0.32 | 17.10 ± 0.20 | 16.90 ± 0.30 | <0.02 |
| A | 20.30 ± 0.32 | 18.90 ± 0.15 | 18.80 ± 0.15 | 18.80 ± 0.25 | <0.05 |
| C | 24.40 ± 0.42 | 25.90 ± 0.14 | 25.80 ± 0.14 | 25.80 ± 0.32 | <0.02 |
| G | 27.00 ± 0.03 | 27.10 ± 0.02 | 27.00 ± 0.02 | 27.00 ± 0.22 | <0.02 |
| Total | 90.5 | 88.8 | 88.7 | 88.5 |
| Modified nucleosides | | | | |
| mA | 0.75 ± 0.06 | 0.90 ± 0.08 | 0.90 ± 0.10 | 0.90 ± 0.08 | <0.02 |
| mA | 0.16 ± 0.02 | 0.17 ± 0.02 | 0.17 ± 0.02 | 0.17 ± 0.02 | <0.05 |
| mC | 0.18 ± 0.01 | 0.20 ± 0.01 | 0.20 ± 0.01 | 0.20 ± 0.01 | <0.02 |
| mC | 1.22 ± 0.05 | 1.25 ± 0.10 | 1.20 ± 0.02 | 1.20 ± 0.12 | <0.02 |
| mG | 0.65 ± 0.03 | 0.65 ± 0.03 | 0.65 ± 0.03 | 0.65 ± 0.04 | <0.01 |
| mG | 0.41 ± 0.04 | 0.49 ± 0.01 | 0.49 ± 0.01 | 0.49 ± 0.05 | <0.01 |
| mG | 0.59 ± 0.05 | 0.57 ± 0.05 | 0.54 ± 0.05 | 0.54 ± 0.05 | <0.05 |
| T | 2.80 ± 0.01 | 2.90 ± 0.02 | 2.90 ± 0.02 | 2.90 ± 0.05 | <0.01 |
| hU | 1.64 ± 0.15 | 2.31 ± 0.21 | 2.31 ± 0.21 | 2.31 ± 0.21 | <0.01 |
| Total | 9.5 | 11.1 | 11.2 | 11.6 |

The probability (p) value for differences between nucleolar RNA and RNA of other cell fractions was calculated according to

\[
t = \frac{(\bar{x}_1 - \bar{x}_2) \sqrt{n_1 n_2 (n_1 + n_2 - 2)}}{\sqrt{\sum(x_i - \bar{x})^2/n(n - 1)}}
\]

The probability (\( p \)) value for differences between nucleolar RNA and RNA of other cell fractions was calculated according to

\[
t = \frac{(\bar{x}_1 - \bar{x}_2) \sqrt{n_1 + n_2}}{\sqrt{(\sum(x_i - \bar{x})^2/n(n - 1))}}
\]

All the values from cell sap, nuclear, and ribosomal RNAs were included in group \( \bar{x} \) and the values of nucleolar RNA were included in the other group, \( \bar{x}_2 \). The content of inosine was included in guanosine because trialcohol derivative of inosine was not well separated from the trialcohol derivative of guanosine.

U-1 RNA—a U-1 RNA which is localized to the cell nucleus consists of two major components which are U-1a and U-1b RNA. U-1a RNA was purified from the mixture by BD-cellULOSE column chromatography (12). Purified by preparative gel electrophoresis was 5.5 S RNA from the nucleolus and ribosomes. Neither U-1a RNA nor 5.5 S RNA from either nucleoli or ribosomes contained modified nucleosides (Fig. 3, Table I). Since the nucleoside compositions were essentially the same for the nucleolar 5.5 S RNA and ribosomal 5.5 S RNA, it is likely that the former is the precursor of the latter. However, U-1a RNA had a somewhat different composition from that of 5.5 S RNA and its localization to the extranucleolar portion of the cell nucleus showed it is a distinctive type of nuclear low molecular weight RNA.

U-2 and U-3 RNAs—Fluorographs of the separation of the nucleosides obtained from nuclear U-2 and nuclear U-3 RNA are shown in Fig. 4. An unusual spot which was not present in 4S RNA (Fig. 1), but was found in both U-2 and U-3 RNA, was identified as a trialcohol derivative of N\(^2\),N\(^2\)-dimethyl 7-methyl guanosine. Trimethyl guanosine first found in low molecular weight RNA from Chinese hamster ovary cells by Zapisek et al.

![FIG. 2. Fluorographs of two-dimensional thin layer chromatography. Separation of m1 nucleoside derivatives from nuclear low molecular weight RNAs. A, 4.5 S RNA, B, 4.5 S RNA; C, 4.5 S RNA; D, 5 S RNA; E, 5 S RNA; and F, 5 S RNA. See Footnote 2 for definitions of symbols appearing on figure.](http://www.jbc.org/)
### Table II

**Nucleoside composition of low molecular weight RNAs from nuclei, nucleoli, and ribosomes**

|         | U   | A   | C   | G   | m7A | m2G | m3G   |
|---------|-----|-----|-----|-----|-----|-----|-------|
| **Nuclei** |     |     |     |     |     |     |       |
| 4.5 SI. | 24.1±0.3 | 24.7±0.4 | 24.7±0.1 | 26.4±0.1 | 0.1±0.02 |       |       |
| 4.5 SII | 26.2±0.4 | 25.0±0.3 | 24.7±0.5 | 24.2±0.4 |       |       |       |
| 4.5 SIII | 23.2±0.2 | 25.3±0.3 | 21.3±0.2 | 25.6±0.4 | 2.9±0.02 | 0.8±0.05 | 0.77±0.03 |
| 5 SI.   | 24.4±0.3 | 19.2±0.2 | 25.3±0.1 | 30.7±0.2 | 0.4±0.10 |       |       |
| 5 SII | 23.5±0.1 | 20.1±0.5 | 26.3±0.4 | 30.1±0.3 |       |       |       |
| 5 SIII | 30.9±0.2 | 23.6±0.1 | 20.3±0.3 | 23.3±0.3 | 1.7±0.10 |       |       |
| U-1A   | 24.6±0.2 | 19.2±0.1 | 26.6±0.4 | 29.6±0.4 |       |       |       |
| U-2    | 25.8±0.1 | 21.6±0.1 | 23.8±0.2 | 22.8±0.1 | 5.5±0.10 |       |       |
| U-3    | 24.8±0.2 | 20.2±0.1 | 25.1±0.6 | 28.5±0.5 | 0.9±0.10 |       |       |
| **Nucleoli** |     |     |     |     |     |     |       |
| 5 S    | 24.0±0.5 | 19.5±0.3 | 26.6±0.4 | 29.9±0.1 |       |       |       |
| 5.5 S  | 22.9±0.1 | 20.7±0.1 | 26.8±0.2 | 29.6±0.6 | 0.35±0.10 |       |       |
| U-3    | 24.4±0.3 | 20.1±0.3 | 25.4±0.4 | 28.7±0.5 | 1.1±0.20 |       |       |
| **Ribosomes** |     |     |     |     |     |     |       |
| 5 S    | 23.7±0.5 | 19.8±0.6 | 26.5±0.4 | 30.2±0.2 |       |       |       |
| 5.5 S  | 22.6±0.3 | 20.2±0.4 | 26.9±0.2 | 30.3±0.1 | 0.38±0.10 |       |       |

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**Fig. 3.** Fluorographs of two-dimensional thin layer chromatography. Separation of [3H]nucleoside derivatives from 5 S, U-1a, and 5.5 S (28 S) RNAs. A, nuclear 5 S RNA; B, nucleolar 5 S RNA; C, ribosomal 5 S RNA; D, nuclear U-1a RNA; E, nucleolar 5.5 S RNA; and F, ribosomal 5.5 S RNA. See Footnote 2 for definitions of symbols appearing on figure.

(9, 23) was synthesized according to the method described by Saponara and Enger (23), who defined the structure of this nucleoside; it was labeled according to the method of Randerath and Randerath (13-15). Fig. 4F shows the fluorograph of the position of this labeled trimethyl G derivative, as well as its purity. After heating this derivative in 10% piperidine, all of the compound was degraded and glycerol was produced as shown in Fig. 4E. When labeled nucleoside derivatives from U-2 RNA were heated in piperidine, the unusual spot disappeared and a dark glycerol spot appeared. Chromatography of a mixture of nucleoside derivatives of U-2 RNA and trimethyl guanosine...
Ampip (12).

stable dinucleotides (6 residues of 2'-O-methylated nucleotides) which are UmpCp, CmpUp, AmpGp, GmpGp, UmpAp, and for 2 of the approximately 225 residues of U-3 RNA, U-3 RNA was found to contain 1 alkali-stable trinucleotide and 6 alkali-stable dinucleotides (6 residues of 2'-O-methylated nucleotides) which are UmpCp, CmpUp, AmpGp, GmpGp, UmpAp, and AmpAp (12).

In U-3 RNA, Ψ compositions 0.9% of the nucleosides and accounts for 2 of the approximately 225 residues of U-3 RNA, U-3 RNA also contained a 2'-O-methylated nucleotide in the 3'-terminal fragments produced by pancreatic and T1 RNase digestion (26). However, the U-2 and U-3 RNAs are structurally different, as shown by the differences in their nucleoside compositions (Table II).

**Discussion**

The present study provides evidence that several species of nuclear low molecular weight RNAs such as U-2 RNA, U-3 RNA, 4.5 S RNA, 4.5 S RNAIII and 5 S RNAIII, and nuclear 4 S RNA are unique with respect to their content of modified nucleosides. In particular, U-2 RNA and U-3 RNA are the only nuclear RNAs that contain N2,N4-dimethyl 7-methyl guanosine. The N4-methyl adenosine which was absent from mammalian tRNA (17) was found in nuclear 4.5 S RNAIII. The findings not only establish the uniqueness of these species but also shows that these RNAs are not degradation products of higher molecular weight RNAs. The presence of specific numbers and types of 2'-O-methylated nucleotides in 4.5 S RNAIII, 5 S RNAIII, U-2 RNA, and U-3 RNA (12, 22, 25, 26) also provides additional evidence for the uniqueness of these RNAs.

Although the function of these RNAs is not known at the present time, the specific localization of some of these RNAs in the nucleus and nucleolus and the presence of specific modified nucleosides of only some of these RNAs suggest that they have unique nuclear functions. Interestingly, Prestayko et al. (24) have shown that some of the U-3 RNA is bound to nucleolar 28 S RNA. These RNAs were also shown to be associated with proteins in small ribonucleoprotein particles (27–29).

Although dihydrouridine was found in the “low molecular weight chromosomal RNA” by Shih and Bonner (30), it was found only in 4 S RNA in this study. This result supports previous reports of Heyden and Zachau (31) and Artman and Roth (32). No lower molecular weight RNA than 4 S RNA was found in this study (12).

The reason for the differences between the nucleolar 4 S RNA and 4 S RNAs from ribosomes, cell sap or nucleoli is not clear (5, 8, 12, 33, 34). It is possible that the 4 S RNA from nucleoli contains RNA other than tRNA since nucleolar 4 S RNA has only 60% of the amino acid acceptor activity of nuclear or cytoplasmic 4 S RNA (34, 35). It is also possible that the modification of precursor nucleosides to dihydro-U and N2-methyl-G in nucleoli is a slower process compared with other modifications so that nucleolar 4 S RNA contains a greater proportion of immu-
tRNA. Whether the low content of dihydro-U and N2-methyl guanosine in nucleolar 4 S RNA is related to its low amino acid acceptor activity remains to be answered. There is evidence that in some tRNAs, the recognition site of aminoacyl-tRNA synthetases may reside at the dihydro-U loop and its stem (36–39). Interestingly, N2-methyl-G appears to be specifically localized in the dihydro-U stem in several tRNAs which were sequenced (40). In any event, nucleolar 4 S RNA is different from the 4 S RNA of other parts of the cell with respect to amino acid acceptor activity and content of modified nucleosides.

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