Nucleic Acids Research, 1994, Vol. 22, No. 12 2183–2196

Summary: the modified nucleosides of RNA

Patrick A.Limbach, Pamela F.Crain and James A.McCloskey*
Departments of Medicinal Chemistry and Biochemistry, University of Utah, Salt Lake City, UT 84112, USA

Received April 11, 1994; Accepted May 20, 1994

ABSTRACT

A comprehensive listing is made of posttranscriptionally modified nucleosides from RNA reported in the literature through mid-1994. Included are chemical structures, common names, symbols, Chemical Abstracts registry numbers (for ribonucleoside and corresponding base), Chemical Abstracts Index Name, phylogenetic sources, and initial literature citations for structural characterization or occurrence, and for chemical synthesis. The listing is categorized by type of RNA: tRNA, rRNA, mRNA, snRNA, and other RNAs. A total of 93 different modified nucleosides have been reported in RNA, with the largest number and greatest structural diversity in tRNA, 79; and 28 in rRNA, 12 in mRNA, 11 in snRNA and 3 in other small RNAs.

Posttranscriptional processing of RNA produces an exceptional number and structural diversity of modified nucleosides, properties long recognized as characteristic features of RNA (1,2). In parallel with steadily increasing knowledge of the array of functional roles of modification (3,4), and indeed of the multiple roles of RNA itself (5), the continuing discovery of new nucleosides mandates a need for a comprehensive listing of RNA nucleosides, and a means for access to the substantial body of relevant literature. The present compilation consists of all reported modified ribonucleosides of known structure, including those from established sequence positions as well as those derived from enzymatic or chemical hydrolysates of RNA. Included are nucleosides from mutant organisms as well as compounds considered to be undermodified (a somewhat ambiguous term) as a result of metabolic or physiological stress. Excluded are those known to be artifactual, for example as a consequence of degradation, or those having clearly incorrect structures. If the basis of structure assignment or identification is considered to be inconclusive, this is indicated under the Notes column.

There are two notable examples of modification that have not been included in the compilation. The covalently bonded adduct between the tRNA nucleoside N^6-threonylcarbamoyladenosine (structure ***11***) and the base Tris, is a complex nucleoside isolated and characterized from *E.coli* tRNA (6) (Chemical Abstracts registry number 61172-41-6), and is presently believed to be formed *in vitro* during tRNA isolation (6), and is thus not a fully natural nucleoside. Second, posttranscriptional methylation in some small nuclear RNAs results in a 5′-CH_3pppN... structure, rather than the more common $m^{2,2,7}$GpppN... cap in which the terminus is a nucleoside (7).

Entries are categorized primarily by type of RNA, although in early work total cellular RNA was often isolated with no clear distinction made between tRNA ('soluble RNA'), the various rRNAs ('microsomal') or others. In such cases the listing given may correspond to contemporary knowledge of distribution of the nucleoside within certain types of RNA. Some of the earlier literature concerning modification in rRNA is of questionable accuracy, and this particular problem is addressed in a later section. Many entries in the list were acquired by systematic examination of certain parts of the earlier literature, as well as through computer-based literature searches using Chemical Abstracts registry numbers for the nucleoside or (less commonly) the base. Registry numbers for both the nucleoside, and base (if assigned), are provided in the present listing. Their use is recommended for effective access to the modified nucleoside literature, including such topics as chemical synthesis (which for some compounds is extensive), biosynthesis, modification enzymes, function, and occurrence in specific biological sources.

Earlier listings and reviews of modification in RNA, including sequence placement in some cases, include the following: chemical synthesis (8), general distribution (9), tRNA distribution (10) and sequences (11), mitochondrial tRNA (12), archaeal tRNA (13), eukaryotic rRNA (14), mRNA cap structures (15,16) and small nuclear RNA (17,18).

DESCRIPTION OF ENTRIES

Structure number

Structures of the ribonucleosides are given on accompanying pages, even though in a minority of cases the structure assignment or principal literature may deal with the corresponding base. Side chain stereochemical assignments are not shown but are indicated in some cases in the Chemical Abstracts Index Name.

Common name

The most commonly used or preferred name is listed. For some nucleosides, additional alternate names are in common use, for example, 5-methyluridine in lieu of ribosylthymine (structure ***52***), or 'Q nucleoside' instead of queuosine (structure ***43***).

*To whom correspondence should be addressed at: 311A Skaggs Hall, University of Utah, Salt Lake City, UT 84112, USA

Symbol

The symbols listed follow convention and usage in the literature, even though some of the notations are idiosyncratic. In general, terms preceding the principal symbol (A, C, G, U) designate modification in the base, while methylation or ribosylation at O-2′ of ribose (the only known ribose modifications in RNA) are designated by 'm' or 'r', respectively, following the principal symbol. Numerous symbols, many of them inconsistent, have been used for the 'Y' family of nucleosides and bases (structures ***37–42***). The recommended symbols for those nucleosides are shown in the table; further comments are made in the Notes entries, including recommended symbols for the corresponding bases.

In general, the symbol 'N' is preferred for modified nucleosides of unknown structure, or 'Nm' if ribose methylation of O-2′ has been established. If the heterocyclic moiety is known or assumed, for example from the corresponding gene sequence, the designation A*, U*, etc. is recommended. The use of 'X' for an unknown nucleoside is not recommended because of confusion with the nucleoside acp^{3}U (see Note 34). The superscript 'x' is useful to indicate a form of modification without designation of position; for example 'm^{x}C' for cytidine monomethylated in the base at an unknown or unspecified position. Likewise 'x' is sometimes used in the fashion 'x^{5}s^{2}U', as to generically designate 5-substituted derivatives of 2-thiouridine. The use of 'm' for 'modified', as in 'mA' (occasionally used in the rRNA literature) is strongly discouraged because of the ambiguity associated with use of 'm' for methylation.

Chemical Abstracts registry number

Registry numbers are listed for the ribonucleoside and base (if assigned). The registry numbers may be used in combination with other search terms to allow selective computer-based literature retrievals. For instance, use of registry number 24719-82-2 (for t^{6}A) in combination with 'synthesis' produces eight citations dealing with the chemical synthesis of t^{6}A.

Chemical Abstracts index name

The name given is that assigned to the ribonucleoside. It is noted that in a limited number of cases, stereochemical assignment in the name was (correctly) made based on an early literature report, but was then automatically assigned without verification in all subsequent reports. For example the amino acid moiety for structure *11* is designated by index name and registry number as L-threonine, with the implication that all later reports of t^{6}A in tRNA deal specifically with the L-enantiomer of threonine.

Source

For each entry the known occurrence for each nucleoside within the type of RNA is listed as: A, archaea (archaebacteria); B, bacteria (eubacteria); E, eukarya (eukaryotes). Although organelle rRNAs have not been cataloged, mt (mitochondrial) is used when initial characterization was from this source. V (viral) designations are used in the mRNA section. For tRNA, specific literature citations are not given for occurrence in each of the three basic phylogenetic domains because much of this information was earlier cataloged and is readily available. The tRNA source distributions indicated have been determined from the sequence databank (9), the Structure column citations, or from specific citations retrieved using registry numbers. For all other RNA classes, citations are given to the first reported identification of the nucleoside in the source indicated. For example, the occurrence of N^2-methylguanosine (structure *30*) was reported in snRNA in 1972 (ref. 193), but the nucleoside structure had been established in 1958 using material isolated from tRNA (ref. 6). Therefore, in the snRNA category the Source listing is 'E (193)' and the Structure listing is '(6)'. In the case of rRNA, because only limited attempts have been previously made to catalog such data (9,14), an effort has been made to subclassify the Source entries in greater detail by providing literature citations for occurrence in specific rRNAs designated by size, if known. For example, under structure ***86***, the entry for nucleoside m^{1}acp$^3\Psi$ reported in eukaryal 17S rRNA (ref. 178) and 18S rRNA (ref. 179) is listed as 'E 17 (178)' and 'E 18 (179)'. The citation given thus corresponds to the first reports of occurrence of m^{1}acp$^3\Psi$ in those RNAs, and subsequent reports of occurrence specifically in other 17S and 18S eukaryal rRNAs are not further tabulated. Notations such as '16+23' indicate that a mixture of 16S and 23S rRNAs, free of 5S and tRNA, was studied.

Structure

The citation given is usually to the first report of structure assignment for the nucleoside, regardless of RNA source. Two primary citations are listed if the second one further refines the structure (e.g., side chain stereochemistry) or addresses ambiguities in the first report. Citations to incorrect structures, as opposed to incomplete ones, are not listed. Reference to structural characterization of the base rather than the nucleoside has been given in the case of some early studies in which chemical hydrolysis to the base was often employed prior to identification, and for some of the Y nucleosides which were isolated as bases (structures ***37–42***) as a consequence of the unusual acid lability of the glycosidic bond.

Synthesis

In each case the citation listed is to the first reported chemical synthesis of the ribonucleoside, or in limited cases, of the base. The chemical synthesis literature for many nucleosides is extensive, and no attempt has been made to cite additional syntheses even though they often represent improvements over the first reported synthesis. Access to the synthesis literature can be made effectively through Chemical Abstracts registry numbers. In general, many physical and spectroscopic data of interest (UV and mass spectra, chromatographic properties) are available from the first synthesis and structure characterization citations listed. The absence of a citation indicates the finding that no chemical synthesis has been reported.

Notes

Additional literature citations, alternate nomenclature, or further comments on entries in the preceding columns are provided.

NUCLEOSIDE MODIFICATION IN RIBOSOMAL RNA

Posttranscriptional modification in rRNA was recognized and reported in the early literature, but has received far less attention than for tRNA because of limited sequence studies carried out at the RNA level (which was a historically a frequent means of discovery of new nucleosides in tRNA), coupled with

considerably less understanding of modification structure–function relationships compared with tRNA. In compiling a comprehensive and reliable listing of modified nucleosides in rRNA, several problems arose that were common to all of the RNAs but were perhaps more prevalent for rRNAs. First, some early work predated an understanding of the structures of rRNAs and of methods to isolate them without cross-contamination from other rRNAs, or from tRNA. Second, methods of structural identification prior to about 1965 were inadequate in the event that structurally new or unexpected nucleosides were encountered, and some identifications based principally on chromatographic behavior must be regarded as inconclusive even though no outright assignment error is apparent. In addition, RNA hydrolysis using acid or base (rather than nucleases) must have inevitably led to some formation of degraded or rearranged products, and loss of labile substituents, which were not readily recognized as such. As a consequence of these problems, some of the assignments listed in the rRNA section of the database are tenuous (as indicated under Notes) and should be verified using rigorous experimental methods.

Because of the relatively greater extent to which modifications in *E.coli* rRNA have been studied, it is possible to compare earlier reports with more recent work (19), and thereby exclude one-time or unusual assigments that have not been subsequently verified by independent methods. On this basis, the following reported nucleoside occurrences in *E.coli* rRNA have not been listed in the table: m_2^2G (20), and D (21) and I (21) in 16S, and I (21), m^4C (22) and m^3U (22) in 23S. In spite of the problems outlined above, and because of the absence of any previous attempt to compile a comprehensive listing of rRNA modifications, the view has been adopted that the rRNA list should be published at this time, even though uncertainties remain.

SUMMARY

A total of 93 modified nucleosides for which structures have been assigned have been reported in RNA. The largest number, 79, with the greatest structural diversity, are found in tRNA, with 28 in rRNA, 12 in mRNA and 12 in other RNA species, most notably snRNA. Based on lessons learned primarily from tRNA, it is clear that many modification motifs and their sequence locations tend to be conserved, although distinct differences among the three primary phylogenetic domains are observed. The fewer number of modifications reported from the archaeal RNAs, to a limited extent, reflects fewer investigations compared with bacteria and eukarya. In any event, it is clear that present knowledge of the structural diversity of RNA nucleosides, and certainly of their distribution, is somewhat narrowly confined to relatively few organisms. It is the authors' judgement that the total number of RNA nucleosides listed, and the chemical structures reported, are very accurate. However, the distributions listed are in some cases a matter of concern, due primarily to the possibility of RNA inhomogeneity and the use of methods of nucleoside identification that are not sufficiently rigorous. Reinvestigation of some of the unusual or single-report source distributions is warranted, and will likely lead to future refinements in the listings.

It is the authors' intention to maintain this compilation as a continuously updated database. Comments concerning format, omissions or newly published material are solicited.

ACKNOWLEDGEMENTS

The authors are indebted to Richard T.Walker and numerous colleagues who offered advice and information on construction of the database, and to Steven C.Pomerantz for structural drawings. We are especially grateful to Byron Bossenbroek, Chemical Abstracts Service, American Chemical Society, for his invaluable advice concerning Chemical Abstracts registry numbers and index names. Compilation of this Summary was supported by grants GM21584 and GM29812 from the National Institute of General Medical Sciences.

REFERENCES

1. Hall, R.H. (1971) The Modified Nucleosides in Nucleic Acids. Columbia University Press, New York.
2. Nishimura, S. (1979) In Schimmel, P.R., Söll, D. and Abelson, J.N. (eds.), Transfer RNA: Structure, Properties and Recognition. Cold Spring Harbor Laboratory, Cold Spring Harbor, New York, pp. 59–79.
3. Björk, G.R., Ericsson, J.U., Gustafsson, C.E.D., Hagervall, T.G., Jönsson, Y.H., and Wikström, P.M. (1987) *Ann. Rev. Biochem.*, **56**, 263–287.
4. Björk, G.R. (1992) In Hatfield D.L., Lee, B.J. and Pirtle, R.M. (eds.), Transfer RNA in Protein Synthesis. CRC Press, Boca Raton, FL, pp. 23–85.
5. Gesteland, R.F. and Atkins, J.F., (eds.) (1993) The RNA World. Cold Spring Harbor Laboratory Press, Plainview, New York.
6. Kasai, H., Murao, K., Liehr, J.G., Crain, P.F., McCloskey, J.A. and Nishimura, S. (1976) *Eur. J. Biochem.* **69**, 435–444.
7. Singh, R., and Reddy, R. (1989) *Proc. Natl. Acad. Sci. USA* **86**, 8280–8283.
8. Adamiak, R.W. and Gornicki, P. (1985) *Prog. Nucl. Acid Res. Mol. Biol.* **32**, 27–74.
9. Björk, G. (1984) In Apirion, D. (ed.) Processing of RNA. CRC Press, Boca Raton, FL, pp. 291–330.
10. Dirheimer, G. (1983) *Recent Results Cancer Res.* **84**, 15–46.
11. Steinberg, S., Misch, A. and Sprinzl, M. (1993) *Nucleic Acids Res.* **21**, 3011–3015.
12. Dirheimer, G. and Martin, R.P. (1990) In Gehrke, C.W. and Kuo, K.C., (eds.) Journal of Chromatography Library. Chromatography and Modification of Nucleosides. Elsevier, Amsterdam, Vol. 45B, pp. B197–B264.
13. Edmonds, C.G., Crain, P.F., Gupta, R., Hashizume, T., Hocart, C.H., Kowalak, J.A., Pomerantz, S.C., Stetter, K.O. and McCloskey, J.A. (1991) *J. Bacteriol.* **173**, 3138–3148.
14. Maden, B.E.H. (1990) In Gehrke, C.W. and Kuo, K.C., (eds.) Journal of Chromatography Library. Chromatography and Modification of Nucleosides. Elsevier, Amsterdam, Vol. 45B, pp. B265–B301.
15. Banerjee, A.K. (1980) *Microbiol. Rev.* **44**, 175–205.
16. Reddy, R., Singh, R. and Shimba, S. (1992) *Pharmaceut. Ther.* **54**, 249–267.
17. Reddy, R. and Busch, H. (1988) In Birnstiel, M.L. (ed.) Structure and Function of Major and Minor Small Nuclear Ribonucleoprotein Particles. Springer-Verlag, Berlin, pp. 1–37.
18. Solymosy, F. and Pollak, T. (1993) *Crit. Rev. Plant Sci.* **12**, 275–369.
19. Kowalak, J.A., Pomerantz, S.C., Crain, P.F., and McCloskey, J.A. (1993) *Nucleic Acids Res.* **21**, 4577–4585.
20. Starr, J.F. and Fefferman, R. (1964) *J. Biol. Chem.* **239**, 3457–3461.
21. Johnson, J.D. and Horowitz, J. (1971) *Biochim. Biophys. Acta* **247**, 262–279.
22. Gehrke, C.W. and Kuo, K.C. (1989) *J. Chromatogr.* **471**, 3–36.

Table

tRNA

Structure Number	Common Name	Symbol	Chemical Abstracts Registry Number: Ribonucleoside	Chemical Abstracts Registry Number: Base	Chemical Abstracts Index Name	Source	Structure	Synthesis	Notes
1	1-methyladenosine	m^1A	15763-06-1	5142-22-3	Adenosine, 1-methyl-	A,B,E	(1)	(2)	1
2	2-methyladenosine	m^2A	16526-56-0	1445-08-5	Adenosine, 2-methyl-	B	(4)	(5)	
3	N^6-methyladenosine	m^6A	1867-73-8	443-72-1	Adenosine, *N*-methyl-	A,B	(4,6)	(7)	
4	2'-*O*-methyladenosine	Am	2140-79-6	73-24-5	Adenosine, 2'-*O*-methyl-	A,E	(8,9)	(10)	2,3
5	2-methylthio-N^6-methyladenosine	ms^2m^6A	13406-51-4	102170-15-0	Adenosine, *N*-methyl-2-(methylthio)-	B	(11)	(12)	4
6	N^6-isopentenyladenosine	i^6A	7724-76-7	2365-40-4	Adenosine, *N*-(3-methyl-2-butenyl)-	E	(13,14)	(15)	5
7	2-methylthio-N^6-isopentenyladenosine	ms^2i^6A	20859-00-1	20758-33-2	Adenosine, *N*-(3-methyl-2-butenyl)-2-(methylthio)-	B	(17)	(17)	6
8	N^6-(*cis*-hydroxyisopentenyl)-adenosine	io^6A	15896-46-5	32771-64-5	Adenosine, *N*-(4-hydroxy-3-methyl-2-butenyl)-, (*Z*)	E	(19)	(20)	7
9	2-methylthio-N^6-(*cis*-hydroxyisopentenyl)adenosine	ms^2io^6A	52049-48-6	52020-11-8	Adenosine, *N*-(4-hydroxy-3-methyl-2-butenyl)-2-(methylthio)-, (*Z*)	E	(21)	(21)	
10	N^6-glycinylcarbamoyladenosine	g^6A	29902-55-4	32459-91-9	Glycine, *N*-[[(9-β-D-ribofuranosyl-9*H*-purin-6-yl)amino]carbonyl]-	E	(22)	(22)	
11	N^6-threonylcarbamoyladenosine	t^6A	24719-82-2	33422-66-1	L-Threonine, *N*-[[(9-β-D-ribofuranosyl-9*H*-purin-6-yl)amino]carbonyl]-	A,B,E	(23)	(24)	8
12	2-methylthio-N^6-threonylcarbamoyladenosine	ms^2t^6A	70333-82-3	132603-04-4	L-Threonine, *N*-[[[2-(methylthio)-9-β-D-ribofuranosyl-9*H*-purin-6-yl]amino]carbonyl]-	A,B,E	(25)		
13	N^6-methyl-N^6-threonylcarbamoyladenosine	m^6t^6A	39667-81-7	132603-03-3	L-Threonine, *N*-[[methyl(9-β-D-ribofuranosyl-9*H*-purin-6-yl)amino]carbonyl]-	B	(26)	(27)	9
14	N^6-hydroxynorvalylcarbamoyl-adenosine	hn^6A	146426-20-2		Norvaline, 3-hydroxy-*N*-[[(9-β-D-ribofuranosyl-9*H*-purin-6-yl)amino]carbonyl]-	A,B	(28)	(28)	
15	2-methylthio-N^6-hydroxy-norvalylcarbamoyladenosine	ms^2hn^6A	146426-21-3		Norvaline, 3-hydroxy-*N*-[[[2-(methylthio)-9-β-D-ribofuranosyl-9*H*-purin-9-yl]amino]carbonyl]-	A,B	(28)		
16	2'-*O*-ribosyladenosine (phosphate)	Ar(p)	28050-13-7	73-24-5	Adenosine, 2'-*O*-(5-*O*-phosphono-β-D-ribofuranosyl)-	E	(29,30)	(31)	10
17	inosine	I	58-63-9	68-94-0	Inosine	A,B,E	(34)	(35)	
18	1-methylinosine	m^1I	2140-73-0	1125-39-9	Inosine, 1-methyl-	A,E	(34)	(36)	
19	1,2'-*O*-dimethylinosine	m^1Im	65150-69-8	1125-39-9	Inosine, 1-methyl-2'-*O*-methyl-	A	(37)	(38)	
20	3-methylcytidine	m^3C	2140-64-9	4776-08-3	Cytidine, 3-methyl-	B,E	(39)	(40)	
21	5-methylcytidine	m^5C	2140-61-6	554-01-8	Cytidine, 5-methyl-	A,E	(41)	(42)	
22	2'-*O*-methylcytidine	Cm	2140-72-9	71-30-7	Cytidine, 2'-*O*-methyl-	A,B,E	(8,43)	(44)	11
23	2-thiocytidine	s^2C	13239-97-9	333-49-3	Cytidine, 2-thio-	A,B	(45)	(46)	12
24	N^4-acetylcytidine	ac^4C	3768-18-1	14631-20-0	Cytidine, *N*-acetyl-	A,B,E	(48)	(49)	
25	5-formylcytidine	f^5C	148608-53-1		Cytidine, 5-formyl-	Emt	(50)	(50)	
26	5,2'-*O*-dimethylcytidine	m^5Cm	113886-70-7	554-01-8	Cytidine, 5-methyl-2'-*O*-methyl-	A	(51)	(51)	13
27	N^4-acetyl-2'-*O*-methylcytidine	ac^4Cm	113886-71-8	14631-20-0	Cytidine, *N*-acetyl-2'-*O*-methyl-	A	(51)	(51)	13
28	lysidine	k^2C	116120-47-9		Pyrimidinium, 4-amino-2-[(5-amino-5-carboxypentyl)amino]-1-β-D-ribofuranosyl-, chloride, (*S*)-	B	(52)	(52)	14
29	1-methylguanosine	m^1G	2140-65-0	938-85-2	Guanosine, 1-methyl-	A,B,E	(6)	(53)	
30	N^2-methylguanosine	m^2G	2140-77-4	10030-78-1	Guanosine, *N*-methyl-	A,E	(6)	(54)	
31	7-methylguanosine	m^7G	20244-86-4	578-76-7	1*H*-Purinium, 2-amino-6,9-dihydroxy-7-methyl-6-oxo-9-β-D-ribofuranosyl-	A,B,E	(1)	(55)	1
32	2'-*O*-methylguanosine	Gm	2140-71-8	73-40-5	Guanosine, 2'-*O*-methyl-	A,B,E	(8,9,56)	(57)	3
33	N^2,N^2-dimethylguanosine	m^2_2G	2140-67-2	1445-15-4	Guanosine, *N*,*N*-dimethyl-	A,E	(58)	(54)	
34	N^2,2'-*O*-dimethylguanosine	m^2Gm	135023-21-1	10030-78-1	Guanosine, *N*-methyl-2'-*O*-methyl-	A	(59)		15
35	N^2,N^2,2'-*O*-trimethylguanosine	m^2_2Gm	113886-73-0	24391-36-4	Guanosine, *N*,*N*-dimethyl-2'-*O*-methyl-	A	(51)	(51)	13,16
36	2'-*O*-ribosylguanosine (phosphate)	Gr(p)	131293-20-4	73-40-5	Guanosine, 2'-*O*-(5-*O*-phosphono-β-D-ribofuranosyl)-	E	(61,62)		17
37	wybutosine	yW	55196-46-8	35693-91-5	3*H*-Imidazo[1,2-*a*]purine-7-butanoic acid, 4,9-dihydro-α-[(methoxycarbonyl)amino]-4,6-dimethyl-9-oxo-3-β-D-ribofuranosyl-, methyl ester, (*S*)-	E	(63,64)	(64)	18,19,20
38	peroxywybutosine	o_2yW	78355-49-4	36238-44-5	3*H*-Imidazo[1,2-*a*]purine-7-butanoic acid, 4,9-dihydro-β-hydroperoxy-α-[(methoxycarbonyl)amino]-4,6-dimethyl-9-oxo-3-β-D-ribofuranosyl-, methyl ester	E	(67)		18,20,21,22

39	hydroxywybutosine	OHyW	84270-21-3	70363-52-9	1*H*-Imidazo[1,2-*a*]purine-7-butanoic acid, 4,9-dihydro-β-hydroxy-α-[(methoxycarbonyl)amino]-4,6-dimethyl-9-oxo-1-β-D-ribofuranosyl-, methyl ester	E	(68)		18,20,23
40	undermodified hydroxywybutosine	OHyW*	84270-20-2	70363-41-6	1*H*-Imidazo[1,2-*a*]purine-7-butanoic acid, α-amino-4,9-dihydro-β-hydroxy-4,6-dimethyl-9-oxo-1-β-D-ribofuranosyl-	E	(69)	(68)	18,20,24
41	wyosine	imG	52662-10-9	33359-03-4	9*H*-Imidazo[1,2-*a*]purin-9-one, 3,4-dihydro-4,6-dimethyl-3-β-D-ribofuranosyl-	E	(70)	(71)	18,20,25
42	methylwyosine	mimG	108274-04-0	96881-39-9	9*H*-Imidazo[1,2-*a*]purin-9-one, 3,4-dihydro-4,6,7-trimethyl-3-β-D-ribofuranosyl-	A	(72)	(73,74)	18
43	queuosine	Q	57072-36-3	72496-59-4	4*H*-Pyrrolo[2,3-*d*]pyrimidin-4-one, 2-amino-5-[[(4,5-dihydroxy-2-cyclopenten-1-yl)amino]methyl]-1,7-dihydro-7-β-D-ribofuranosyl-, [1*S*-(1α,4β,5β)]-	B,E	(75)	(76)	26
44	epoxyqueuosine	oQ	107865-20-3		4*H*-Pyrrolo[2,3-*d*]pyrimidin-4-one, 2-amino-5-[[(3,4-dihydroxy-6-oxobicyclo[3.1.0]hex-2-yl)amino]methyl]-1,7-dihydro-7-β-D-ribofuranosyl-	B	(78)		
45	galactosyl-queuosine	galQ	60426-58-6	90581-15-0	4*H*-Pyrrolo[2,3-*d*]pyrimidin-4-one-, 2-amino-5-[[[5-(β-D-galactopyranosyloxy)-4-hydroxy-2-cyclopenten-1-yl]amino]methyl]-1,7-dihydro-7-β-D-ribofuranosyl-, [1*S*-(1α,4β,5β)]	E	(79)		27
46	mannosyl-queuosine	manQ	60398-20-1	90501-23-8	4*H*-Pyrrolo[2,3-*d*]pyrimidin-4-one-, 2-amino-1,7-dihydro-5-[[[4-hydroxy-5-(β-D-mannopyranosyloxy)-2-cyclopenten-1-yl]amino]methyl]-7-β-D-ribofuranosyl-, [1*S*-(1α,4β,5β)]	E	(79)		27
47	7-cyano-7-deazaguanosine	$preQ_0$	61210-21-7	69205-79-4	1*H*-Pyrrolo[2,3-*d*]pyrimidin-5-carbonitrile, 2-amino-4,7-dihydro-4-oxo-7-β-D-ribofuranosyl-	B	(80)	(81)	28
48	7-aminomethyl-7-deazaguanosine	$preQ_1$	66048-70-2	69251-45-2	4*H*-Pyrrolo[2,3-*d*]pyrimidin-4-one, 2-amino-5-(aminomethyl)-1,7-dihydro-7-β-D-ribofuranosyl-	B	(82)	(82)	28
49	archaeosine	none	148608-52-0		1*H*-Pyrrolo[2,3-*d*]pyrimidine-5-carboximidamide, 2-amino-4,7-dihydro-4-oxo-7-β-D-ribofuranosyl-	A	(83)	(83)	29
50	pseudouridine	Ψ	1445-07-4	66-22-8	2,4(1*H*,3*H*)-Pyrimidinedione, 5-β-D-ribofuranosyl-	A,B,E	(84,85)	(86)	30
51	dihydrouridine	D	5627-05-4	34283-02-8	Uridine, 5,6-dihydro-	A,B,E	(87)	(88)	
52	ribosylthymine	m^5U	1463-10-1	65-71-4	Uridine, 5-methyl-	A,B,E	(89)	(90)	31
53	2'-*O*-methyluridine	Um	2140-76-3	66-22-8	Uridine, 2'-*O*-methyl-	A,B,E	(8,9)	(44)	3
54	5,2'-*O*-dimethyluridine	m^5Um	55486-09-4	65-71-4	Uridine, 5-methyl-2'-*O*-methyl-	B,E	(92)	(92)	32
55	1-methylpseudouridine	$m^1\Psi$	13860-38-3	615-77-0	2,4(1*H*,3*H*)-Pyrimidinedione, 1-methyl-5-β-D-ribofuranosyl-	A	(93)	(94,95)	
56	2'-*O*-methylpseudouridine	Ψm	2140-68-3	66-22-8	2,4(1*H*,3*H*)-Pyrimidinedione, 5-(2-*O*-methyl-β-D-ribofuranosyl)-	A,E	(96)	(97)	
57	2-thiouridine	s^2U	20235-78-3	141-90-2	Uridine, 2-thio-	A,E	(98)	(99)	
58	4-thiouridine	s^4U	13957-31-8	591-28-6	Uridine, 4-thio-	A,B	(100)	(42)	
59	5-methyl-2-thiouridine	m^5s^2U	32738-09-3	636-26-0	Uridine, 5-methyl-2-thio-	A,B	(101)	(99)	33
60	2-thio-2'-*O*-methyluridine	s^2Um	113886-72-9	141-90-2	Uridine, 2'-*O*-methyl-2-thio-	A	(51)	(51)	13
61	3-(3-amino-3-carboxypropyl)uridine	acp^3U	52745-94-5		1(2*H*)-Pyrimidinebutanoic acid, α-amino-3,6-dihydro-2,6-dioxo-3-β-D-ribofuranosyl-	B	(102,103)	(102)	34
62	5-hydroxyuridine	ho^5U	957-77-7	20636-41-3	Uridine, 5-hydroxy-	B,E	(104)	(105)	
63	5-methoxyuridine	mo^5U	35542-01-9	6623-81-0	Uridine, 5-methoxy-	B	(106)	(107)	
64	uridine 5-oxyacetic acid	cmo^5U	28144-25-4		Acetic acid, [(1,2,3,4-tetrahydro-2,4-dioxo-1-β-D-ribofuranosyl-5-pyrimidinyl)oxy]-	B	(108)	(108)	35
65	uridine 5-oxyacetic acid methyl ester	$mcmo^5U$	66536-81-0		Acetic acid, [(1,2,3,4-tetrahydro-2,4-dioxo-1-β-D-ribofuranosyl-5-pyrimidinyl)oxy]-, methyl ester	B	(109)	(110)	36
66	5-(carboxyhydroxymethyl) uridine	chm^5U	89708-80-5		5-Pyrimidineacetic acid, 1,2,3,4-tetrahydro-α-hydroxy-2,4-dioxo-1-β-D-ribofuranosyl-, (*S*)-	E	(111,112)	(112)	37
67	5-(carboxyhydroxymethyl) uridine methyl ester	$mchm^5U$	89665-83-8		5-Pyrimidineacetic acid, 1,2,3,4-tetrahydro-α-hydroxy-2,4-dioxo-1-β-D-ribofuranosyl-, methyl ester, (*S*)-	E	(113)	(113)	38

68	5-methoxycarbonylmethyl-uridine	mcm^5U	29428-50-0	29571-45-7	5-Pyrimidineacetic acid, 1,2,3,4-tetrahydro-2,4-dioxo-1-β-D-ribofuranosyl-, methyl ester	E	(114)	(115)	
69	5-methoxycarbonylmethyl-2'-*O*-methyluridine	mcm^5Um	60197-31-1	29571-45-7	5-Pyrimidineacetic acid, 1,2,3,4-tetrahydro-1-(2-*O*-methyl-β-D-ribofuranosyl)-2,4-dioxo-, methyl ester	E	(116)	(117,118)	
70	5-methoxycarbonylmethyl-2-thiouridine	mcm^5s^2U	20299-15-4	29571-40-2	5-Pyrimidineacetic acid, 1,2,3,4-tetrahydro-4-oxo-1-β-D-ribofuranosyl-2-thioxo-, methyl ester	E	(119)	(120)	
71	5-aminomethyl-2-thiouridine	nm^5s^2U	109666-14-0		Uridine, 5-(aminomethyl)-2-thio-	B	(121)		39
72	5-methylaminomethyluridine	mnm^5U	72667-55-1	37454-51-6	Uridine, 5-[(methylamino)methyl]-	B	(122)	(123)	40
73	5-methylaminomethyl-2-thiouridine	mnm^5s^2U	32860-54-1	21263-85-4	Uridine, 5-[(methylamino)methyl]-2-thio-	B	(45)	(125)	41
74	5-methylaminomethyl-2-selenouridine	mnm^5se^2U	89314-80-7	114482-38-1	Uridine, 5-[(methylamino)methyl]-2-seleno-	A,B	(126)	(126)	42
75	5-carbamoylmethyluridine	ncm^5U	29569-30-0		Uridine, 5-(2-amino-2-oxoethyl)-	E	(128)	(115)	
76	5-carbamoylmethyl-2'-*O*-methyluridine	ncm^5Um	60197-30-0		Uridine, 5-(2-amino-2-oxoethyl)-2'-*O*-methyl-	E	(129)	(117,118)	43
77	5-carboxymethylaminomethyl uridine	$cmnm^5U$	69181-26-6	14886-75-0	Glycine, *N*-[(1,2,3,4-tetrahydro-2,4-dioxo-1-β-D-ribofuranosyl-5-pyrimidinyl)methyl]-	B,E	(130)	(131)	44
78	5-carboxymethylaminomethyl-2'-*O*-methyluridine	$cmnm^5Um$	110419-13-1	14886-75-0	Glycine, *N*-[[1,2,3,4-tetrahydro-1-(2-*O*-methyl-β-D-ribofuranosyl)-2,4-dioxo-5-pyrimidinyl]methyl]-	B	(132)	(132)	45
79	5-carboxymethylaminomethyl-2-thiouridine	$cmnm^5s^2U$	78173-95-2		Glycine, *N*-[(1,2,3,4-tetrahydro-4-oxo-1-β-D-ribofuranosyl-2-thioxo-5-pyrimidinyl)methyl]-	B	(134)	(131)	46

rRNA

Structure Number	Common Name	Symbol	Chemical Abstracts Registry Number: Ribonucleoside	Base	Chemical Abstracts Index Name	Source	Structure	Synthesis	Notes
1	1-methyladenosine	m^1A	15763-06-1	5142-22-3	Adenosine, 1-methyl-	B (135) E 16+25 (136) E 18,28 (137) E 26,28 (138)	(1)	(2)	1,47
2	2-methyladenosine	m^2A	16526-56-0	1445-08-5	Adenosine, 2-methyl-	B 16+23 (140) B 23 (141)	(4)	(5)	
3	N^6-methyladenosine	m^6A	1867-73-8	443-72-1	Adenosine, *N*-methyl-	B 16+23 (140) B 23 (142) E (4) E 17 (143) E 18,28 (137)	(4,6)	(7)	
4	2'-*O*-methyladenosine	Am	2140-79-6	73-24-5	Adenosine, 2'-*O*-methyl-	E (8) E 5.8 (144) E 17,26 (143) E 18+28 (145)	(8,9)	(10)	3
80	N^6,N^6-dimethyladenosine	m^6_2A	2620-62-4	938-55-6	Adenosine, *N*,*N*-dimethyl-	A 16 (146) B 16+23 (140) B 16 (141) B 23 (147) E (4) E 18 (148)	(4)	(149)	
81	2'-*O*-methylinosine	Im	3881-21-8	68-94-0	Inosine, 2'-*O*-methyl-	E (150)	(150)	(151)	48
20	3-methylcytidine	m^3C	2140-64-9	4776-08-3	Cytidine, 3-methyl-	E 17 (152) E 18,28 (137)	(39)	(40)	47
82	N^4-methylcytidine	m^4C	10578-79-7	6220-47-9	Cytidine, *N*-methyl	E 13mt (153)	(153)	(42)	49
21	5-methylcytidine	m^5C	2140-61-6	554-01-8	Cytidine, 5-methyl-	B 16,32 (142) E (154) E 17,18,25,28 (138)	(41)	(42)	
22	2'-*O*-methylcytidine	Cm	2140-72-9	71-30-7	Cytidine, 2'-*O*-methyl-	A 5 (155) B 23 (156) E (56) E 5.8 (157) E 18,28 (137) E 17 (158)	(8,43)	(44)	11
24	N^4-acetylcytidine	ac^4C	3768-18-1	14631-20-0	Cytidine, *N*-acetyl-	A 5 (155) E 17,18 (158)	(48)	(49)	

83	N^4,2'-*O*-dimethylcytidine	m^4Cm	13048-95-8	6220-47-9	Cytidine, *N*-methyl-2'-*O*-methyl-	B (159)	(159)		50
27	N^4-acetyl-2'-*O*-methylcytidine	ac^4Cm	113886-71-8	14631-20-0	Cytidine, *N*-acetyl-2'-*O*-methyl	A 5 (155)	(51)	(51)	13
84	5-hydroxymethylcytidine	hm^5C	19235-17-7	1123-95-1	Cytidine, 5-(hydroxymethyl)-	E 18+26 (160)	(160)	(161)	51
29	1-methylguanosine	m^1G	2140-65-0	938-85-2	Guanosine, 1-methyl-	B 16+23 (140) B 23 (141) E (154) E 18 (137)	(6)	(53)	47
30	N^2-methylguanosine	m^2G	2140-77-4	10030-78-1	Guanosine, *N*-methyl-	B 16+23 (140) B 16,23 (142) E (154) E 18 (137) E 17,25 (138)	(6)	(54)	47
31	7-methylguanosine	m^7G	20244-86-4	578-76-7	1*H*-Purinium, 2-amino-6,9-dihydroxy-7-methyl-6-oxo-9-β-D-ribofuranosyl-	A 16 (162) B (136) E 17,18 (158) E 17,26 (143) E 18,28 (137)	(1)	(55)	1,52
32	2'-*O*-methylguanosine	Gm	2140-71-8	73-40-5	Guanosine, 2'-*O*-methyl-	B 23 (156) E (56) E 5.8 (144,163,164) E 18+28 (145)	(8,9,56)	(57)	3
33	N^2,N^2-dimethylguanosine	m^2_2G	2140-67-2	24391-36-4	Guanosine, *N*,*N*-dimethyl-	B (165) E (154) E 18 (137)	(58)	(54)	
50	pseudouridine	Ψ	1445-07-4	66-22-8	2,4(1*H*,3*H*)-Pyrimidinedione, 5-β-D-ribofuranosyl-	A 16 (166) B 16,23 (141) E (154,167) E 5 (168) E 5.8 (144,169) E 18,28 (170)	(84,85)	(86)	30
51	dihydrouridine	D	5627-05-4	34283-02-8	Uridine, 5,6-dihydro-	B 23 (171)	(87)	(88)	
85	3-methyluridine	m^3U	2140-69-4	608-34-4	Uridine, 3-methyl-	B 16,23 (171) E 18,28 (137) E 25,28 (138)	(137)	(172)	53
52	ribosylthymine	m^5U	1463-10-1	65-71-4	Uridine, 5-methyl-	B 16,23 (142) B 23 (174)	(89)	(90)	54
53	2'-*O*-methyluridine	Um	2140-76-3	66-22-8	Uridine, 2'-*O*-methyl-	B 23 (156) E (8) E 5.8 (169) E 17mt (175) E 17,25 (138) E 18+28 (145)	(8,9)	(44)	3
55	1-methylpseudouridine	$m^1Ψ$	13860-38-3	615-77-0	2,4(1*H*,3*H*)-Pyrimidinedione, 1-methyl-5-β-D-ribofuranosyl-	E 17,18 (176)	(93)	(94,95)	55
56	2'-*O*-methylpseudouridine	Ψm	2140-68-3	66-22-8	2,4(1*H*,3*H*)-Pyrimidinedione, 5-(2-*O*-methyl-β-D-ribofuranosyl)-	E 18+26 (177) E 28 (139)	(96)	(97)	
86	1-methyl-3-(3-amino-3-carboxypropyl)pseudouridine	$m^1acp^3Ψ$	52777-29-4		1(2*H*)-Pyrimidinebutanoic acid, α-amino-3,6-dihydro-3-methyl-2,6-dioxo-5-β-D-ribofuranosyl-	E 17 (178) E 18 (179)	(179)		
87	5-carboxymethyluridine	cm^5U	20964-06-1	20763-91-1	5-Pyrimidineacetic acid, 1,2,3,4-tetrahydro-2,4-dioxo-1-β-D-ribofuranosyl-	E (160)	(180)	(180)	51

mRNA

Structure Number	Common Name	Symbol	Chemical Abstracts Registry Number: Ribonucleoside	Base	Chemical Abstracts Index Name	Source	Structure	Synthesis	Notes
3	N^6-methyladenosine	m^6A	1867-73-8	443-72-1	Adenosine, *N*-methyl-	E (181)	(4,6)	(7)	
4	2'-*O*-methyladenosine	Am	2140-79-6	73-24-5	Adenosine, 2'-*O*-methyl-	E (181)	(8,9)	(10)	3
88	N^6,2'-*O*-dimethyladenosine	m^6Am	57817-83-1	443-72-1	Adenosine, *N*-methyl-2'-*O*-methyl-	E (182)	(183)	(184)	56
89	N^6,N^6,*O*-2'-trimethyladenosine	m^6_2Am	30891-53-3	938-55-6	Adenosine, *N*,*N*-dimethyl-2'-*O*-methyl-	E (186)	(186)	(184,186)	57
21	5-methylcytidine	m^5C	2140-61-6	554-01-8	Cytidine, 5-methyl-	E (188) V (187)	(41)	(42)	
22	2'-*O*-methylcytidine	Cm	2140-72-9	71-30-7	Cytidine, 2'-*O*-methyl-	E (181)	(8,43)	(44)	11

31	7-methylguanosine	m^7G	20244-86-4	578-76-7	1*H*-Purinium, 2-amino-6,9-dihydroxy-7-methyl-6-oxo-9-β-D-ribofuranosyl-	E (189)	(1)	(55)	1,58
32	2'-*O*-methylguanosine	Gm	2140-71-8	73-40-5	Guanosine, 2'-*O*-methyl-	E (181)	(8,9,56)	(57)	3
90	N^2,7-dimethylguanosine	$m^{2,7}G$	62122-07-0		1*H*-Purinium, 6,9-dihydro-7-methyl-2-(methylamino)-6-oxo-9-β-D-ribofuranosyl-	V (190)	(190)	(190)	58
91	N^2,N^2,7-trimethylguanosine	$m^{2,2,7}G$	40027-70-1		1*H*-Purinium, 2-(dimethylamino)-6,9-dihydro-7-methyl-6-oxo-9-β-D-ribofuranosyl-	E (191) V (190)	(192)	(192)	58,59
53	2'-*O*-methyluridine	Um	2140-76-3	66-22-8	Uridine, 2'-*O*-methyl-	E (181)	(8,9)	(44)	3
92	3,2'-*O*-dimethyluridine	m^3Um	7103-27-7	608-34-4	Uridine, 3-methyl-2'-*O*-methyl-	E (186)	(186)	(44)	

snRNA

3	N^6-methyladenosine	m^6A	1867-73-8	443-72-1	Adenosine, *N*-methyl-	E (193)	(4,6)	(7)	
4	2'-*O*-methyladenosine	Am	2140-79-6	73-24-5	Adenosine, 2'-*O*-methyl-	E (195)	(8,9)	(10)	3,60
88	N^6,2'-*O*-dimethyladenosine	m^6Am	57817-83-1	443-72-1	Adenosine, *N*-methyl-2'-*O*-methyl-	E (185)	(183)	(184)	
22	2'-*O*-methylcytidine	Cm	2140-72-9	71-30-7	Cytidine, 2'-*O*-methyl-	E (185)	(8,43)	(44)	11
30	N^2-methylguanosine	m^2G	2140-77-4	10030-78-1	Guanosine, *N*-methyl-	E (193)	(6)	(54)	
32	2'-*O*-methylguanosine	Gm	2140-71-8	73-40-5	Guanosine, 2'-*O*-methyl-	E (195)	(8,9,56)	(57)	3
91	N^2,N^2,7-trimethylguanosine	$m^{2,2,7}G$	40027-70-1		1*H*-Purinium, 2-(dimethylamino)-6,9-dihydro-7-methyl-6-oxo-9-β-D-ribofuranosyl-	E (192)	(192)	(192)	58,59,60
50	pseudouridine	Ψ	1445-07-4	66-22-8	2,4(1*H*,3*H*)-Pyrimidinedione, 5-β-D-ribofuranosyl-	E (193)	(84,85)	(86)	30,60
51	dihydrouridine	D	5627-05-4	34283-02-8	Uridine, 5,6-dihydro-	E (196)	(87)	(88)	61
53	2'-*O*-methyluridine	Um	2140-76-3	66-22-8	Uridine, 2'-*O*-methyl-	E (195)	(8,9)	(44)	3
56	2'-*O*-methylpseudouridine	Ψm	2140-68-3	66-22-8	2,4(1*H*,3*H*)-Pyrimidinedione, 5-(2-*O*-methyl-β-D-ribofuranosyl)-	E (197)	(96)	(97)	62

chromosomal RNA

51	dihydrouridine	D	5627-05-4	34283-02-8	Uridine, 5,6-dihydro-	E (198)	(87)	(88)	63
93	dihydroribosylthymine	m^5D	23067-10-9	696-04-8	Hydrouracil, 5-methyl-1-β-D-ribofuranosyl-	E (200)	(200)	(201)	63,64

other small RNA

50	pseudouridine	Ψ	1445-07-4	66-22-8	2,4(1*H*,3*H*)-Pyrimidinedione, 5-β-D-ribofuranosyl-	E (202)	(84,85)	(86)	30,65,66

Notes

1 First characterized as the base (1) and later as the monoribonucleotide (3).
2 Occurrence is rare in eukaryotes.
3 First characterized as an O-2′ or O-3′ methyl derivative (8), and subsequently shown to be O-2′ (9).
4 Structure assigment is reported as a preliminary communication, without details (11).
5 Although i^6A is characteristically eukaryal rather than bacterial, it has been reported in unfractionated *E.coli* tRNA (16), a finding which is not reproducible (J.M. Peltier and J.A. McCloskey, unpublished) and could be due to undermodified ms^2i^6A. Symbol used in early literature is IPA.
6 Subsequently and independently characterized in *E.coli* $tRNA^{Tyr}$ (18).
7 Also known as *cis*-zeatin riboside (symbol cZ). The name zeatin riboside refers to the *trans*-isomer, a cytokinin (registry number 6025-53-2).
8 Ref. 23 reports characterization of the base of this nucleoside. The L configuration for threonine in t^6A was established in ref. 24.
9 Previously used symbol is mt^6A.
10 A nucleoside component of yeast tRNA was isolated and tentatively characterized as 2′(3′)-*O*-ribosyladenosine by Hall (32), but whether the source material was tRNA was later concluded to be uncertain (33). Substitution at O-2′ *vs.* O-3′ was not established in the reported synthesis (31). Ar registry number: 28269-89-8, Chemical Abstracts Index Name: Adenosine, 2′-*O*-β-D-ribofuranosyl-.
11 Cm was first characterized as an O-2′ or O-3′ methyl derivative (8), and subsequently shown to be O-2′ (43).
12 Initial structural and spectroscopic data are reported in ref. 47, without derivation of a final structure.
13 Preliminary communication of structural characterization and chemical synthesis is given in ref. 51.
14 The registry number and Chemical Abstracts Index Name listed are for the chloride salt. The registry number (144796-96-3) and Chemical Abstracts index name (L-Lysine, N^6-(1,4-dihydro-4-imino-1-β-D-ribofuranosyl-2-pyrimidinyl)-) assigned to the neutral nucleoside are less effective in retrieval of lysidine literature. Alternate symbols are L and acp^2C. The latter symbol is not recommended because the notation acp has a different structural definition, and is more commonly used in acp^3U (structure *61*). The common name 'lysidine' was previously assigned to 4,5-dihydro-2-methyl-1*H*-imidazole (registry number 534-26-9).
15 A preliminary report of characterization is given in ref. 59.
16 Unknown nucleoside N-26 in *Sulfolobus acidocaldarius* $tRNA_i^{Met}$ was postulated to be m_2^2Gm in ref. 60, without experimental evidence.
17 Structure *36* was initially reported in ref. 61; more extensive structural data are presented in ref. 62. Gr registry number: 148711-49-3, Chemical Abstracts Index Name: Guanosine, 2′-*O*-β-D-ribofuranosyl-.
18 Comments on nomenclature for the yW family of nucleosides are given in refs. 65 and 66.
19 Errata for structure determination of yW (63) are reported in ref. 64. Alternate commonly used name is 'Y nucleoside'. Commonly used symbol for the corresponding base is Y.
20 Structural characterization was made from the acid-liberated base. A Chemical Abstracts registry number was then assigned to the corresponding ribonucleoside.
21 Alternate name is wybutoxine. Common name for the corresponding base is peroxy-Y, symbol Yr.
22 Initial report in ref. 67 with complete characterization in ref. 65. Occurrence

of the peroxy function in the natural nucleoside has been questioned (68) and led to the confusing use of Yr as a symbol for the base of hydroxywybutosine in ref. 68.

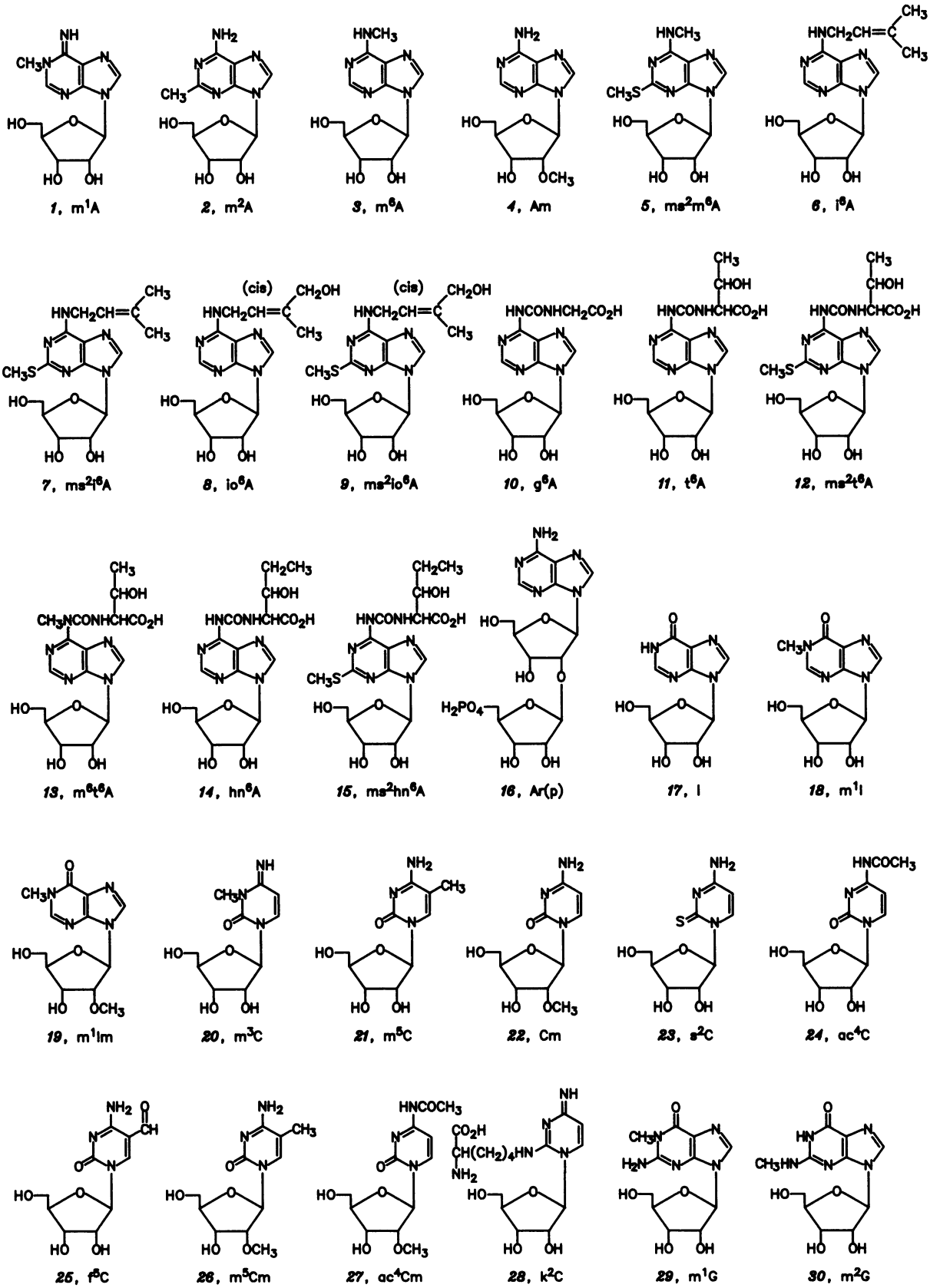
23 Common name for the corresponding base is hydroxy-Y.
24 Symbol for the corresponding base is Ye.
25 Symbol for the corresponding base is Yt.
26 Characterization of queuine, the base of queuosine, is reported in ref. 77.
27 Symbol Q* is also used for either manQ, galQ, or a mixture of the two.
28 $preQ_0$ and $preQ_1$ are undermodified Q nucleosides isolated from methyl-deficient mutant *E.coli* tRNA.
29 No symbol is presently assigned. Alternate name is 7-formamidino-7-deazaguanosine. The Chemical Abstracts index name is based on nomenclature for the 4(1*H*)-quinazolinone ring system.
30 The structure of pseudouridine was determined by Yu and Allen from material isolated from unfractionated yeast RNA (84), and was independently reported by Cohn (85) in a manuscript submitted eight days later.
31 Alternate commonly used symbol is T. Other common names are thymine riboside and 5-methyluridine. Occurrence is rare in archaeal tRNA. Enzymatic synthesis was reported in ref. 91 which preceeded the first report of chemical synthesis (90).
32 Alternate symbol is Tm.
33 Alternate symbol is s^2T.
34 Earlier symbols used were $4abu^3U$ and X. Symbol X for acp^3U has been confused in the literature with 'unknown nucleoside' and its use is therefore discouraged.
35 Alternate commonly used symbols are o^5U and V.
36 Alternate commonly used symbol is mV.
37 The Chemical Abstracts registry number listed is for the natural (*S*)-isomer; the (*R*)-isomer registry number is 127911-55-1.
38 The Chemical Abstracts registry number listed is for the natural (*S*)-isomer; the (*R*)-isomer registry number is 89665-84-9.
39 Observed as a component of unfractionated tRNA from *E.coli* mutants, as a biosynthetic precursor to mnm^5s^2U (121); not rigorously characterized by conventional means. No chemical synthesis reported.
40 Alternate symbol is mam^5U. More thorough characterization in ref. 124.
41 Alternate symbol is mam^5s^2U.
42 Earlier reports of se^4U in RNA cited in ref. 126 were discounted, as discussed in ref. 126. Although only one selenonucleoside, mnm^5se^2U, has been structurally characterized, it is likely that others exist but have not been detected due to oxidation, for example, in eukaryotic tRNA (127).
43 The first preparation of ncm^5Um was by conversion of cm^5Um which had been isolated from tRNA in the same study (117). Conventional chemical synthesis of ncm^5Um is reported in ref. 118.
44 Alternate symbol is $cmam^5U$.
45 Alternate symbol is $cmam^5Um$. The natural nucleoside from *E.coli* $tRNA^{Leu}$ has not been characterized except by comparison of its NMR spectrum with that of synthetic material (132). The discovery of $cmnm^5Um$ is cited in ref. 132 as a meeting abstract (133), in which, however, the compound is neither named nor structural data presented.
46 Alternate symbol is $cmam^5s^2U$.
47 This nucleoside is not reported in the sequence of 18S rRNA from HeLa cells (139).
48 More thorough characterization is reported in ref. 151.
49 The base (m^4Cyt) was previously reported in acid-treated HeLa rRNA, and was presumed to have originated from N^4,2′-*O*-dimethylcytidine (137).
50 More thorough characterization is reported in ref. 156.
51 5-(Hydroxymethyl)cytidine (structure ***84***) and 5-(carboxymethyl)uridine (structure *87*) were identified as the monophosphates by their UV spectra following separation by 2D-TLC (data not shown) (160); however, availability of authentic compounds or of previously cited properties was not addressed. These structure assignments are therefore considered inconclusive.
52 Although this nucleoside was reported in both 18S and 28S rRNA from HeLa cells (137), later studies showed it to be confined to the 18S rRNA (139).
53 Verification that the early report of m^3U synthesis (172) was correct was made much later (173). Although this nucleoside was reported present in both 18S and 28S rRNA from HeLa cells (137), later studies showed it to be confined to the 28S rRNA (138). In a recent examination of *E.coli* 23S rRNA, m^3U was not detected (J.A. Kowalak and J.A. McCloskey, unpublished).
54 Alternate commonly used symbol is T. Other common names are thymine riboside and 5-methyluridine. Enzymatic synthesis was reported in ref. 91 which preceeded the first report of chemical synthesis (90).
55 Detected as a biosynthetic precursor to structure ***86***.
56 The structure was announced in ref. 185 without data for characterization.
57 Presence of m^6_2Am in adenovirus mRNA was inferred from ^3H labeling data, but was not chemically characterized (187).
58 This 5′-cap nucleoside is joined to the RNA through a unique 3′-triphosphate bridge (GpppN...).
59 The structure was first assigned using material from 2-10S RNA from Chinese hamster ovary cells (192), and later from snRNA from Novikoff hepatoma ascites cells (193). More rigorous characterization of the synthetic nucleoside used for comparison is given in ref. 194. This nucleoside is rare in mRNA.
60 Am, Ψ, and the $m^{2,2,7}G$ cap nucleoside are also found in U3 RNA from the nucleolus. See Note 66.
61 Dihydrouridine is reported in a total enzymatic digest of nuclear 5S RNA from rat (196). However, this sole report of D in snRNA was not verified by sequencing of the RNA because pD could not be distinguished from pU (196).
62 Evidence for characterization of N-36 as Ψm in plant snRNA is inconclusive.
63 This RNA is reported as a chromatin-associated 3.2–3.8S species, with an unusual concentration of dihydropyrimidine nucleosides, but its occurrence as a separate class of RNA remains controversial. For review, see ref. 199.
64 Characterization of this nucleoside, not otherwise reported in RNA, was based on detection of 2-amino-isobutyric acid following treatment with alkali (200). Direct comparison with the authentic nucleoside was not made.
65 This is a 140 nt 3′-poly A-containing RNA from dinoflagellates. Presence of pseudouridine was concluded from characteristic absence of a sequencing gel band.
66 For the present listing, the 'other small RNA' category does not include small nucleolar RNA (snoRNA), which is grouped under snRNA.

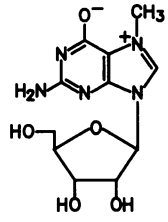
References

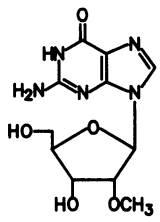
1. Dunn, D.B. (1961) *Biochim. Biophys. Acta*, **46**, 198–200.
2. Jones, J.W. and Robins, R.K. (1963) *J. Am. Chem. Soc.*, **85**, 193–201.
3. Dunn, D.B. (1963) *Biochem. J.*, **86**, 14–15.
4. Littlefield, J.W. and Dunn, D.B. (1958) *Nature*, **181**, 254–255.
5. Davoll, J. and Lowy, B.A. (1952) *J. Am. Chem. Soc.*, **74**, 1563–1566.
6. Adler, M., Weissmann, B. and Gutman, A.B. (1958) *J. Biol. Chem.*, **230**, 717–723.
7. Johnson, J.A., Thomas, H.J. and Schaeffer, H.J. (1958) *J. Am. Chem. Soc.*, **80**, 699–702.
8. Smith, J.D. and Dunn, D.B. (1959) *Biochim. Biophys. Acta*, **31**, 573–575.
9. Hall, R.H. (1963) *Biochim. Biophys. Acta*, **68**, 278–283.
10. Broom, A.D. and Robins, R.K. (1965) *J. Am. Chem. Soc.*, **87**, 1145–1146.
11. Crain, P.F., Hashizume, T., Reddy, D.M. and McCloskey, J.A. (1991) *Nippon Iyo Masu Supekutoru Gakkai Koenshu*, **16**, 15–26.
12. Gough, G. and Maguire, M.H. (1967) *J. Med. Chem.*, **10**, 475–478.
13. Hall, R.H., Robins, M.J., Stasiuk, L. and Thedford, R. (1966) *J. Am. Chem. Soc.*, **88**, 2614–2615.
14. Biemann, K., Tsunakawa, S., Sonnenbichler, J., Feldman, H., Dütting, D. and Zachau, H.G. (1966) *Angew. Chem. Int. Ed.*, **5**, 590–591.
15. Robins, M.J., Hall, R.H. and Thedford, R. (1967) *Biochemistry*, **6**, 1837–1848.
16. Gehrke, C.W. and Kuo, K.C. (1989) *J. Chromatogr.*, **471**, 3–36.
17. Burrows, W.J., Armstrong, D.J., Skoog, F., Hecht, S.M., Boyle, J.T.A., Leonard, N.J. and Occolowitz, J. (1968) *Science*, **161**, 691–693.
18. Harada, F., Gross, H.J., Kimura, F., Chang, S.H., Nishimura, S. and RajBhandary, U.L. (1968) *Biochem. Biophys. Res. Commun.*, **33**, 299–306.
19. Hall, R.H., Csonka, L., David, H. and McLennan, B. (1967) *Science*, **156**, 69–70.
20. Playtis, A.J. and Leonard, N.J. (1971) *Biochem. Biophys. Res. Commun.*, **45**, 1–5.
21. Hecht, S.M., Leonard, N.J., Burrows, W.J., Armstrong, D.J., Skoog, F. and Occolowitz, J. (1969) *Science*, **166**, 1272–1274.
22. Schweizer, M.P., McGrath, K. and Baczynskyj, L. (1970) *Biochem. Biophys. Res. Commun.*, **40**, 1046–1052.
23. Schweizer, M.P., Chheda, G.B., Baczynskyj, L. and Hall, R.H. (1969) *Biochemistry*, **8**, 3283–3289.
24. Chheda, G.B. and Hong, C.I. (1971) *J. Med. Chem.*, **14**, 748–753.
25. Yamaizumi, Z., Nishimura, S., Limburg, K., Raba, M., Gross, H.J., Crain, P.F. and McCloskey, J.A. (1979) *J. Am. Chem. Soc.*, **101**, 2224–2225.
26. Kimura-Harada, F., von Minden, D.L., McCloskey, J.A. and Nishimura, S. (1972) *Biochemistry*, **11**, 3910–3915.
27. Dutta, S.P., Hong, C.I., Murphy, G.P., Mittelman, A. and Chheda, G.B. (1975) *Biochemistry*, **14**, 3131–3144.
28. Reddy, D.M., Crain, P.F., Edmonds, C.G., Gupta, R., Hashizume, T., Stetter, K.O., Widdell, F. and McCloskey, J.A. (1992) *Nucleic Acids Res.*,

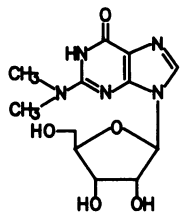
20, 5607–5615.
29. Desgres, J., Keith, G., Kuo, K.C. and Gehrke, C.W. (1989) *Nucleic Acids Res.*, **17**, 865–882.
30. Keith, G., Glasser, A.-L., Desgres, J., Kuo, K.C. and Gehrke, C.W. (1990) *Nucleic Acids Res.*, **18**, 5989–5993.
31. Lis, A.W. and Passarge, W.E. (1969) *Physiol. Chem. Phys.*, **1**, 68–71.
32. Hall, R.H. (1965) *Biochemistry*, **4**, 661–670.
33. Hall, R.H. (1971) The Modified Nucleosides in Nucleic Acids. Columbia University Press, New York, p. 111.
34. Hall, R.H. (1963) *Biochem. Biophys. Res. Commun.*, **13**, 394–398.
35. Levene, P.A. and Tipson, R.S. (1935) *J. Biol. Chem.*, **111**, 313–323.
36. Bredereck, H. and Martini, A. (1947) *Chem. Ber.*, **80**, 401–407.
37. McCloskey, J.A., Edmonds, C.G., Gupta, R., Hashizume, T., Hocart, C.H. and Stetter, K.O. (1988) *Nucleic Acids Symp. Series*, **20**, 45–46.
38. Yamauchi, K., Nakamura, K. and Kinoshita, M. (1978) *J. Org. Chem.*, **43**, 1593–1595.
39. Hall, R.H. (1963) *Biochem. Biophys. Res. Commun.*, **12**, 361–364.
40. Brookes, P. and Lawley, P.D. (1962) *J. Chem. Soc.*, 1348–1351.
41. Amos, H. and Korn, M. (1958) *Biochim. Biophys. Acta*, **29**, 444–445.
42. Fox, J.J., Van Praag, D., Wempen, I., Doerr, I.L., Cheong, L., Knoll, J.E., Eidinoff, M.L., Bendich, A. and Brown, G.B. (1959) *J. Am. Chem. Soc.*, **81**, 178–187.
43. Biswas, B.B. and Myers, J. (1960) *Nature*, **186**, 238–239.
44. Furukawa, Y., Kobayashi, K., Kanai, Y. and Honjo, M. (1965) *Chem. Pharm. Bull.*, **13**, 1273–1278.
45. Carbon, J., David, H. and Studier, M.H. (1968) *Science*, **161**, 1146–1147.
46. Ueda, T., Iida, Y., Ikeda, K. and Mizuno, Y. (1966) *Chem. Pharm. Bull.*, **14**, 666–667.
47. Carbon, J.A., Hung, L. and Jones, D.S. (1965) *Proc. Natl. Acad. Sci. USA*, **53**, 979–986.
48. Feldmann, H., Dutting, D. and Zachau, H.G. (1966) *Hoppe-Seylers Z. Physiol. Chem.*, **347**, 236–248.
49. Michelson, A.M. (1959) *J. Chem. Soc.*, 3655–3669.
50. Moriya, J., Yokogawa, T., Wakita, K., Ueda, T., Nishikawa, K., Crain, P.F., Hashizume, T., Pomerantz, S.C., McCloskey, J.A., Kawai, G., Hayashi, N., Yokoyama, S. and Watanabe, K. (1994) *Biochemistry*, **33**, 2234–2239.
51. Edmonds, C.G., Crain, P.F., Hashizume, T., Gupta, R., Stetter, K.O. and McCloskey, J.A. (1987) *J. Chem. Soc., Chem. Commun.*, 909–910.
52. Muramatsu, T., Yokoyama, S., Horie, N., Matsuda, A., Ueda, T., Yamaizumi, Z., Kuchino, Y., Nishimura, S. and Miyazawa, T. (1988) *J. Biol. Chem.*, **263**, 9261–9267.
53. Broom, A.D., Townsend, L.B., Jones, J.W. and Robins, R.K. (1964) *Biochemistry*, **3**, 494–500.
54. Gerster, J.F. and Robins, R.K. (1965) *J. Am. Chem. Soc.*, **87**, 3752–3759.
55. Haines, J.A., Reese, C.B. and Todd, L. (1962) *J. Chem. Soc.*, 5281–5287.
56. Morisawa, S. and Chargaff, E. (1963) *Biochim. Biophys. Acta*, **68**, 147–149.
57. Khwaja, T.A. and Robins, R.K. (1966) *J. Am. Chem. Soc.*, **88**, 3640–3643.
58. Smith, J.D. and Dunn, D.B. (1959) *Biochem. J.*, **72**, 294–301.
59. Edmonds, C.G., Crain, P.F., Gupta, R., Hashizume, T., Hocart, C.H., Kowalak, J.A., Pomerantz, S.C., Stetter, K.O. and McCloskey, J.A. (1991) *J. Bacteriol.*, **173**, 3138–3148.
60. Kuchino, Y., Ihara, M., Yabusaki, Y. and Nishimura, S. (1982) *Nature*, **298**, 684–685.
61. Kiesewetter, S., Ott, G. and Sprinzl, M. (1990) *Nucleic Acids Res.*, **18**, 4677–4682.
62. Glasser, A.-L., Desgres, J., Heitzler, J., Gehrke, C.W. and Keith, G. (1991) *Nucleic Acids Res.*, **19**, 5199–5203.
63. Nakanishi, K., Furutachi, N., Funamizu, M., Grunberger, D. and Weinstein, I.B. (1970) *J. Am. Chem. Soc.*, **92**, 7617–7619.
64. Funamizu, M., Terahara, A., Feinberg, A.M. and Nakanishi, K. (1971) *J. Am. Chem. Soc.*, **93**, 6706–6708.
65. Blobstein, S.H., Grunberger, D., Weinstein, I.B. and Nakanishi, K. (1973) *Biochemistry*, **12**, 188–193.
66. Kasai, H., Goto, M., Ikeda, K., Zama, M., Mizuno, Y., Takemura, S., Matsuura, S., Sugimoto, T. and Goto, T. (1976) *Biochemistry*, **15**, 898–904.
67. Nakanishi, M., Blobstein, S.H., Funamizu, M., Furutachi, N., Van Lear, G., Grunberger, D., Lanks, K. and Weinstein, I.B. (1971) *Nature (London)*, **234**, 107–109.
68. Kasai, H., Yamaizumi, Z., Kuchino, Y. and Nishimura, S. (1979) *Nucleic Acids Res.*, **6**, 993–999.
69. Kuchino, Y., Kasai, H., Yamaizumi, Z., Nishimura, S. and Borek, E. (1979) *Biochim. Biophys. Acta*, **565**, 215–218.
70. Kasai, H., Goto, M., Takemura, S., Goto, T. and Matsuura, S. (1971) *Tetrahedron Lett.*, **29**, 2725–2728.
71. Nakatsuka, S., Ohgi, T. and Goto, T. (1978) *Tetrahedron Lett.*, **29**, 2579–2582.
72. McCloskey, J.A., Crain, P.F., Edmonds, C.G., Gupta, R., Hashizume, T., Phillipson, D.W. and Stetter, K.O. (1987) *Nucleic Acids Res.*, **15**, 683–693.
73. Bazin, H., Zhou, X.X., Glemarec, C. and Chattopadhyaya, J. (1987) *Tetrahedron Lett.*, **28**, 3275–3278.
74. Itaya, T. (1987) *Chem. Pharm. Bull.*, **35**, 4372–4374.
75. Kasai, H., Ohashi, Z., Harada, F., Nishimura, S., Oppenheimer, N.J., Crain, P.F., Liehr, J.G., von Minden, D.L. and McCloskey, J.A. (1975) *Biochemistry*, **14**, 4198–4208.
76. Ohgi, T., Kondo, T. and Goto, T. (1977) *Tetrahedron Lett.*, **28** 4051–4054.
77. Crain, P.F., Sethi, S.K., Katze, J.R. and McCloskey, J.A. (1980) *J. Biol. Chem.*, **255**, 8405–8407.
78. Phillipson, D.W., Edmonds, C.G., Crain, P.F., Smith, D.L., Davis, D.R. and McCloskey, J.A. (1987) *J. Biol. Chem.*, **262**, 3462–3471.
79. Kasai, H., Nakanishi, K., Macfarlane, R.D., Torgerson, D.F., Ohashi, Z., McCloskey, J.A., Gross, H.J. and Nishimura, S. (1976) *J. Am. Chem. Soc.*, **98**, 5044–5046.
80. Noguchi, S., Yamaizumi, Z., Ohgi, T., Goto, T., Nishimura, Y., Hirota, Y. and Nishimura, S. (1978) *Nucleic Acids Res.*, **5**, 4215–4223.
81. Cheng, C.S., Hinshaw, B.C., Panzica, R.P. and Townsend, L.B. (1976) *J. Am. Chem. Soc.*, **98**, 7870–7872.
82. Okada, N., Noguchi, S., Nishimura, S., Ohgi, T., Goto, T., Crain, P.F. and McCloskey, J.A. (1978) *Nucleic Acids Res*, **5**, 2289–2296.
83. Gregson, J.M., Crain, P.F., Edmonds, C.G., Gupta, R., Hashizume, T., Phillipson, D.W. and McCloskey, J.A. (1993) *J. Biol. Chem.*, **268**, 10076–10086.
84. Yu, C.-T. and Allen, F.W. (1959) *Biochim. Biophys. Acta*, **32**, 393–405.
85. Cohn, W.E. (1959) *Biochim. Biophys. Acta*, **32**, 569–571.
86. Shapiro, R. and Chambers, R.W. (1961) *J. Am. Chem. Soc.*, **83**, 3920–3921.
87. Madison, J.T. and Holley, R.W. (1965) *Biochem. Biophys. Res. Commun.*, **18**, 153–157.
88. Green, M. and Cohen, S.S. (1957) *J. Biol. Chem.*, **225**, 397–407.
89. Littlefield, J.W. and Dunn, D.B. (1958) *Biochem. J.*, **70**, 642–651.
90. Fox, J.J., Yung, N., Davoll, J. and Brown, G.B. (1956) *J. Am. Chem. Soc.*, **78**, 2117–2122.
91. Lampen, J.O. (1952) In McElroy, W.D. and Glass, B. (eds.) Phosphorus Metabolites. The Johns Hopkins Press, Baltimore, Vol. II, pp. 368.
92. Gross, H.J., Simsek, M., Limburg, K., Heckman, J. and RajBhandary, U.L. (1974) *Nucleic Acids Res.*, **1**, 35–43.
93. Pang, H., Ihara, M., Kuchino, Y., Nishimura, S., Gupta, R., Woese, C.R. and McCloskey, J.A. (1982) *J. Biol. Chem.*, **257**, 3589–3592.
94. Scannell, J.P., Crestfield, A.M. and Allen, F.W. (1959) *Biochim. Biophys. Acta*, **32**, 406–413.
95. Cohn, W.E. (1960) *J. Biol. Chem.*, **235**, 1488–1498.
96. Hall, R.H. (1964) *Biochemistry*, **3**, 876–880.
97. Robins, M.J., Naik, S.R. and Alan, S.K. (1974) *J. Org. Chem.*, **39**, 1891–1899.
98. Chackalaparampil, I. and Cherayil, J.D. (1981) *Biochem. Int.*, **2**, 121–128.
99. Shaw, G., Warrener, R.N., Maguire, M.H. and Ralph, R.K. (1958) *J. Chem. Soc.*, 2294–2299.
100. Lipsett, M.N. (1965) *J. Biol. Chem.*, **240**, 3975–3978.
101. Kimura-Harada, F., Saneyoshi, M. and Nishimura, S. (1971) *FEBS Lett.*, **13**, 335–338.
102. Ohashi, Z., Maeda, M., McCloskey, J.A. and Nishimura, S. (1974) *Biochemistry*, **13**, 2620–2625.
103. Friedman, S., Li, H.J., Nakanishi, K. and Van Lear, G. (1974) *Biochemistry*, **13**, 2932–2937.
104. Lis, A.W. and Passarge, W.E. (1966) *Arch. Biochem. Biophys.*, **114**, 593–595.
105. Roberts, M. and Visser, D.W. (1952) *J. Am. Chem. Soc.*, **74**, 668–669.
106. Murao, K., Hasegawa, T. and Ishikura, H. (1976) *Nucleic Acids Res.*, **3**, 2851–2860.
107. Stout, M.G. and Robins, R.K. (1972) *J. Heterocycl. Chem.*, **9**, 545–549.
108. Murao, K., Saneyoshi, M., Harada, F. and Nishimura, S. (1969) *Biochem. Biophys. Res. Commun.*, **38**, 657–662.
109. Pope, W.T., Brown, A. and Reeves, R.H. (1978) *Nucleic Acids Res.*, **5**, 1041–1057.
110. Malkiewicz, A., Nawrot, B. and Sochacka, E. (1987) *Z. Naturforsch., B: Chem. Sci.*, **42**, 360–366.
111. Kawakami, M., Koji, N., Takemura, S., Kondo, T. and Goto, T. (1979)

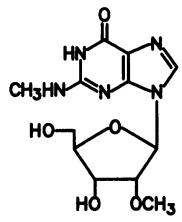
Nucleic Acids Symp. Ser., **6**, s53-s55.
112. Kondo, T., Fukami, T., Goto, T., Kawakami, M. and Takemura, S. (1983) *Nucleic Acids Symp. Ser.*, **12**, 127–130.
113. Kawakami, M., Takemura, S., Kondo, T., Fukami, T. and Goto, T. (1988) *J. Biochem. (Tokyo)*, **104**, 108–111.
114. Tumaitis, T.D. and Lane, B.G. (1970) *Biochim. Biophys. Acta*, **224**, 391–403.
115. Fissekis, J.D. and Sweet, F. (1970) *Biochemistry*, **9**, 3136–3142.
116. Diamond, A.M., Choi, I.S., Crain, P.F., Hashizume, T., Pomerantz, S.C., Cruz, R., Steer, C.J., Hill, K.E., Burk, R.F., McCloskey, J.A. and Hatfield, D.L. (1993) *J. Biol. Chem.*, **268**, 14215–14223.
117. Gray, M.W. and Thomas, C. (1976) *Biochemistry*, **15**, 3046–3051.
118. Sochacka, E. and Malkiewicz, A. (1990) *Nucleosides Nucleotides*, **9**, 793–802.
119. Baczynskyj, L., Biemann, K. and Hall, R.H. (1968) *Science*, **159**, 1481–1483.
120. Baczynskyj, L., Biemann, K., Fleysher, M.H. and Hall, R.H. (1969) *Can. J. Biochem.*, **47**, 1202–1203.
121. Hagervall, T.G., Edmonds, C.G., McCloskey, J.A. and Björk, G.R. (1987) *J. Biol. Chem.*, **262**, 8488–8495.
122. Yokoyama, S., Sakamoto, K., Muramatsu, T., Yamaizumi, Z., Nishimura, S. and Miyazawa, T. (1988) *Nucleic Acids Symp. Ser.*, **20**, 49–50.
123. Sierzputowska-Gracz, H., Sochacka, E., Malkiewicz, A., Kuo, K., Gehrke, C.W. and Agris, P.F. (1987) *J. Am. Chem. Soc.*, **109**, 7171–7177.
124. Sakamoto, K., Kawai, G., Niimi, T., Satoh, T., Sekine, M., Yamaizumi, Z., Nishimura, S., Miyazawa, T. and Yokoyama, S. (1993) *Eur. J. Biochem.*, **216**, 369–375.
125. Vorbruggen, H. and Krùlikiewicz, K. (1975) *Angew. Chem.*, **14**, 225–256.
126. Wittwer, A.J., Tsai, L., Ching, W.-M. and Stadtman, T.C. (1984) *Biochemistry*, **23**, 4650–4655.
127. Ching, W.-M. (1984) *Proc. Natl. Acad. Sci. USA*, **81**, 3010–3013.
128. Dunn, D.B. and Trigg, M.D. (1975) *Biochem. Soc. Trans*, **3**, 656–659.
129. Gray, M.W. (1975) *Can. J. Biochem.*, **53**, 735–746.
130. Murao, K. and Ishikura, H. (1978) *Nucleic Acids Res., Spec. Publ.*, **5**, 333–336.
131. Reese, C.B. and Sanghvi, Y.S. (1984) *J. Chem. Soc., Chem. Commun.*, 62–63.
132. Sekine, M., Peshakova, L.S., Hata, T., Yokoyama, S. and Miyazawa, T. (1987) *J. Org. Chem.*, **52**, 5060–5061.
133. Yokoyama, S., Watanabe, K., Yamaizumi, Z., Kuchino, Y., Nishimura, S. and Miyazawa, T. (1985) The 11th International tRNA Workshop. Banz, Germany, Abstract DII-3.
134. Yamada, Y., Murao, K. and Ishikura, H. (1981) *Nucleic Acids Res.*, **9**, 1933–1939.
135. Srivastava, R. and Gopinathan, K.P. (1987) *Biochem. Int.*, **15**, 1179–1188.
136. Isaksson, L.A. and Phillips, J.H. (1968) *Biochim. Biophys. Acta*, **115**, 63–71.
137. Iwanami, Y. and Brown, G. (1968) *Arch. Biochem. Biophys.*, **126**, 8–15.
138. Klagsbrun, M. (1973) *J. Biol. Chem.*, **248**, 2612–2620.
139. Maden, B.E.H. and Salim, M. (1974) *J. Mol. Biol.*, **88**, 133–164.
140. Starr, J.L. and Fefferman, R. (1964) *J. Biol. Chem.*, **239**, 3457–3461.
141. Dubin, D.T. and Günalp, A. (1967) *Biochim. Biophys. Acta*, **134**, 106–123.
142. Hayashi, Y., Osawa, S. and Miura, K. (1966) *Biochim. Biophys. Acta*, **129**, 519–531.
143. Cecchini, J.P. and Miassod, R. (1979) *Eur. J. Biochem.*, **98**, 203–214.
144. Lau, R.Y., Kennedy, T.D. and Lane, B.G. (1974) *Can. J. Biochem.*, **52**, 1110–1122.
145. Singh, H. and Lane, B.G. (1964) *Can. J. Biochem.*, **42**, 1011–1021.
146. Fox, G.E., Magrum, L.J., Balch, W.E., Wolfe, R.S. and Woese, C.R. (1988) *Proc. Natl. Acad. Sci. USA*, **74**, 4537–4541.
147. Lai, C.J., Dahlberg, J.E. and Weisblum, B. (1973) *Biochemistry*, **12**, 457–460.
148. Brown, G.M. and Attardi, G. (1965) *Biochem. Biophys. Res. Commun.*, **20**, 298–302.
149. Kissman, H.M., Pidacks, C. and Baker, B.R. (1955) *J. Am. Chem. Soc.*, **77**, 18–24.
150. Gray, M.W. (1974) *Biochim. Biophys. Acta*, **374**, 253–257.
151. Gray, M.W. (1976) *Nucleic Acids Res.*, **3**, 977–988.
152. Klootwijk, J. and Planta, R.J. (1973) *Eur. J. Biochem.*, **39**, 325–333.
153. Dubin, D.T., Taylor, R.H. and Davenport, L.W. (1978) *Nucleic Acids Res.*, **5**, 4385–4397.
154. Dunn, D.B. (1959) *Biochim. Biophys. Acta*, **34**, 286–287.
155. Bruenger, E., Kowalak, J.A., Kuchino, Y., McCloskey, J.A., Stetter, K.O. and Crain, P.F. (1993) *FASEB J.*, **7**, 196–200.
156. Nichols, J.L. and Lane, B.G. (1966) *Can. J. Biochem.*, **44**, 1633–1645.
157. MacKay, R.M. and Doolittle, W.F. (1981) *Nucleic Acids Res.*, **9**, 3321–3334.
158. Thomas, G., Gordon, J. and Rogg, H. (1978) *J. Biol. Chem.*, **253**, 1101–1105.
159. Nichols, J.L. and Lane, B.G. (1966) *Biochim. Biophys. Acta*, **119**, 649–651.
160. Rácz, I., Király, I. and Lásztity, D. (1978) *Planta*, **142**, 263–267.
161. Brossmer, R. and Röhm, E. (1966) *Z. Naturforsch. B: Anorg. Chem., Org.Chem., Biochem., Biophys., Biol.*, **21**, 942–952.
162. Zueva, V.S., Mankin, A.S., Bogdanov, A.A., Thurlow, D.L. and Zimmermann, R.A. (1985) *FEBS Lett.*, **188**, 233–238.
163. Maden, B.E.H. and Robertson, J.S. (1974) *J. Mol. Biol.*, **87**, 227–235.
164. Nazar, R., Sitz, T.O. and Busch, H. (1974) *FEBS Lett.*, **45**, 206–212.
165. Woese, C.R., Gutell, R., Gupta, R. and Noller, H.F. (1983) *Microbiol. Rev.*, **47**, 621–669.
166. Stahl, D.A. (1978) PhD Thesis. University of Illinois at Urbana-Champaign.
167. Brawerman, G. and Chargaff, E. (1959) *Biochim. Biophys. Acta*, **31**, 172–177.
168. Miyazaki, M. (1974) *J. Biochem.*, **75**, 1407–1410.
169. Rubin, G.M. (1974) *J. Biol. Chem.*, **248**, 3860–3875.
170. Amaldi, F. and Attardi, G. (1968) *J. Mol. Biol.*, **32**, 737–755.
171. Johnson, J.D. and Horowitz, J. (1971) *Biochim. Biophys. Acta*, **247**, 262–279.
172. Levene, P.A. and Tipson, R.S. (1934) *J. Biol. Chem.*, **104**, 385–393.
173. Miles, H.T. (1956) *Biochim. Biophys. Acta*, **22**, 247–253.
174. Fellner, P. (1969) *Eur. J. Biochem.*, **11**, 12–27.
175. Dubin, D.T. and Taylor, R.H. (1978) *J. Mol. Biol.*, **121**, 523–540.
176. Brand, R.C., Klootwijk, J., Planta, R.J. and Maden, B.E.H. (1978) *Biochem. J.*, **169**, 71–77.
177. Gray, M.W. and Keddy, G.M. (1974) *Biochemistry*, **13**, 5453–5463.
178. Maden, B.E.H., Forbes, J., de Jonge, P. and Klootwijk, J. (1975) *FEBS Lett.*, **59**, 60–63.
179. Saponara, A.G. and Enger, M.D. (1974) *Biochim. Biophys. Acta*, **349**, 61–77.
180. Gray, M.W. and Lane, B.G. (1968) *Biochemistry*, **7**, 3441–3453.
181. Desrosiers, R., Friderici, K. and Rottman, F. (1974) *Proc. Natl. Acad. Sci. USA*, **71**, 3971–3975.
182. Wei, C.-M., Gershowitz, A. and Moss, B. (1975) *Cell*, **4**, 379–386.
183. Crain, P.F., Choi, Y.C., Busch, H. and McCloskey, J.A. (1978) *Nucleic Acids Res.*, **5**, 771–778.
184. Robins, M.J., MacCoss, M. and Lee, A.S.K. (1976) *Biochem. Biophys. Res. Commun.*, **70**, 356–363.
185. Shibata, H., Ro-Choi, T.S., Reddy, R., Choi, Y.C., Henning, D. and Busch, H. (1975) *J. Biol. Chem.*, **250**, 3909–3920.
186. Bangs, J.D., Crain, P.F., Hashizume, T., McCloskey, J.A. and Boothroyd, J.C. (1992) *J. Biol. Chem.*, **267**, 9805–9815.
187. Sommer, S., Salditt-Georgieff, M., Bachenheimer, S., Darnell, J.E., Furuichi, Y., Morgan, M. and Shatkin, A.J. (1976) *Nucleic Acids Res.*, **3**, 749–765.
188. Dubin, D.T., Stollar, V., Hsu-Chen, C.C., Timko, K. and Guild, G.M. (1977) *Virology*, **77**, 457–470.
189. Rottman, F., Shatkin, A.J. and Perry, R.P. (1974) *Cell*, **3**, 197–199.
190. Hsu-Chen, C.C. and Dubin, D.T. (1976) *Nature*, **264**, 190–191.
191. Liou, R. and Blumenthal, T. (1990) *Mol. Cell Biol.*, **10**, 1764–1768.
192. Saponara, A.G. and Enger, M.D. (1969) *Nature*, **223**, 1365–1366.
193. Reddy, R., Ro-Choi, T.S., Henning, D., Shibata, H., Choi, Y.C. and Busch, H. (1972) *J. Biol. Chem.*, **247**, 7245–7250.
194. Ro-Choi, T.S., Choi, Y.C., Henning, D., McCloskey, J.A. and Busch, H. (1975) *J. Biol. Chem.*, **250**, 3921–3928.
195. Busch, H., Ro-Choi, T.S., Prestayko, A.W., Shibata, H., Crooke, S.T., El-Khatib, S.M., Choi, Y.C. and Mauritzen, C.M. (1971) *Perspect. Biol. Med.*, **15**, 117–139.
196. Krol, A., Gallinaro, H., Lazar, E., Jacob, M. and Branlant, C. (1981) *Nucleic Acids Res.*, **9**, 769–787.
197. Kiss, T., Antal, M. and Solymosy, F. (1987) *Nucleic Acids Res.*, **15**, 543–560.
198. Huang, R.C.C. and Bonner, J. (1965) *Proc. Natl. Acad. Sci. USA*, **54**, 960–967.
199. Naora, H. (1977) In Stewart, P.R. and Letham, D.S. (eds.) The Ribonucleic Acids. Springer-Verlag, Berlin, pp. 43–80.
200. Jacobson, R.A. and Bonner, J. (1968) *Biochem. Biophys. Res. Commun.*, **33**, 716–720.
201. Cline, R.E., Fink, R.M. and Fink, K. (1959) *J. Am. Chem. Soc.*, **81**, 2521–2527.
202. Reddy, R., Henning, D., Liu, M.-H., Spector, D. and Busch, H. (1985) *Biochem. Biophys. Res. Commun.*, **127**, 552–557.

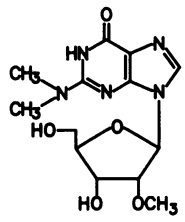

1, m¹A
2, m²A
3, m⁶A
4, Am
5, ms²m⁶A
6, i⁶A
7, ms²i⁶A
8, io⁶A
9, ms²io⁶A
10, g⁶A
11, t⁶A
12, ms²t⁶A
13, m⁶t⁶A
14, hn⁶A
15, ms²hn⁶A
16, Ar(p)
17, I
18, m¹I
19, m¹Im
20, m³C
21, m⁵C
22, Cm
23, s²C
24, ac⁴C
25, f⁵C
26, m⁵Cm
27, ac⁴Cm
28, k²C
29, m¹G
30, m²G

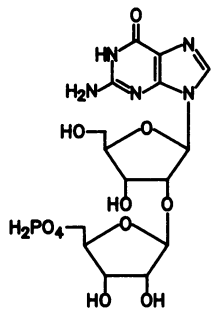

31, m^7G

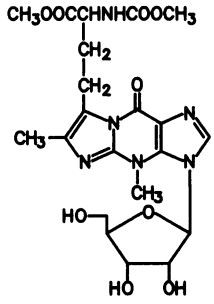

32, Gm

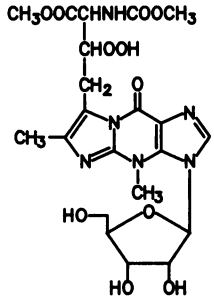

33, m^2_2G

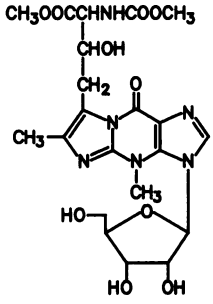

34, m^2Gm

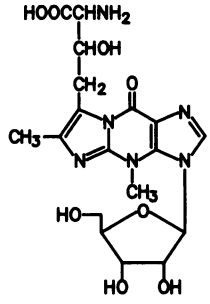

35, m^2_2Gm

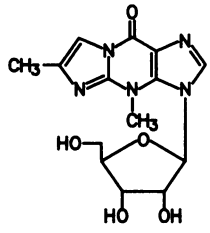

36, Gr(p)

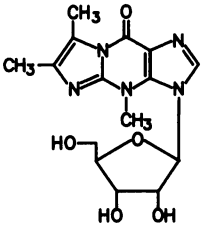

37, yW

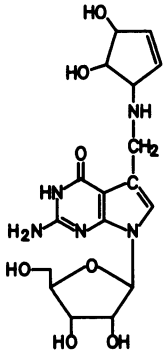

38, o_2yW

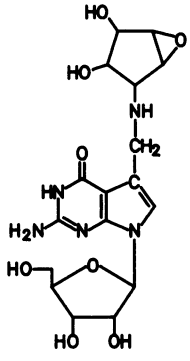

39, OHyW

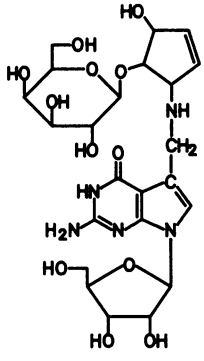

40, OHyW*

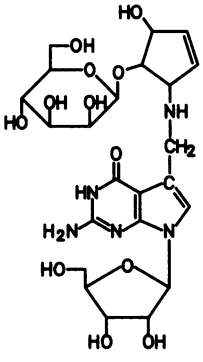

41, imG

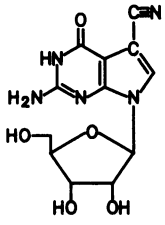

42, mimG

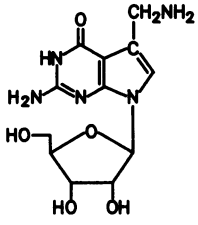

43, Q

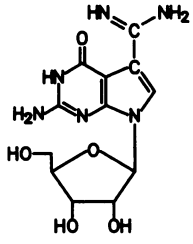

44, oQ

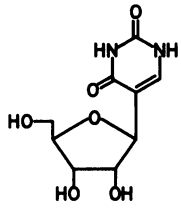

45, galQ

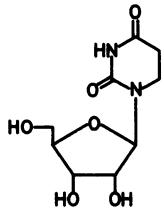

46, manQ

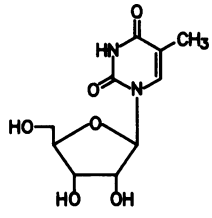

47, $preQ_0$

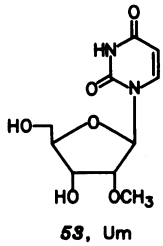

48, $preQ_1$

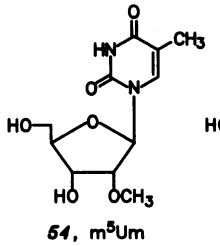

49

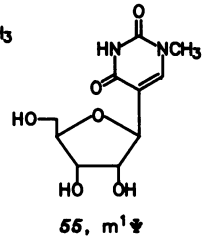

50, Ψ

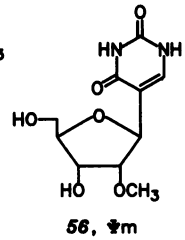

51, D

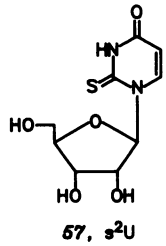

52, m^5U

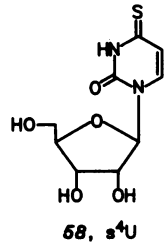

53, Um

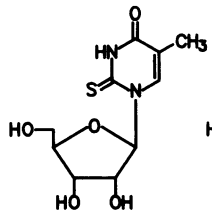

54, m^5Um

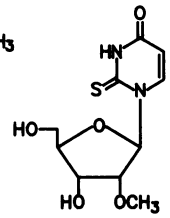

55, $m^1Ψ$

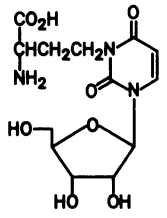

56, Ψm

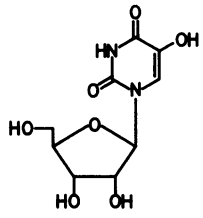

57, s^2U

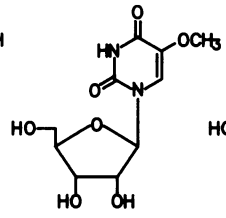

58, s^4U

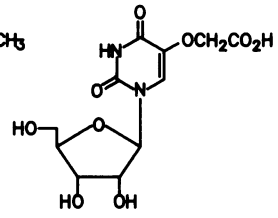

59, m^5s^2U

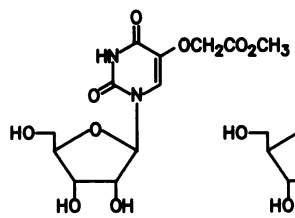

60, s^2Um

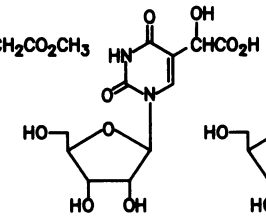

61, acp^3U

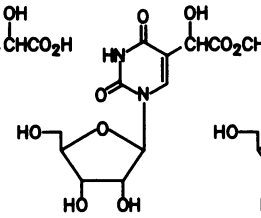

62, ho^5U

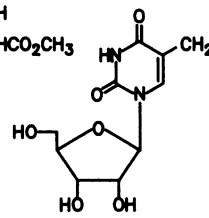

63, mo^5U

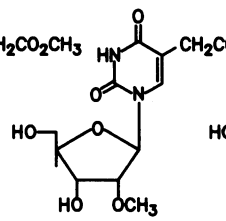

64, cmo^5U

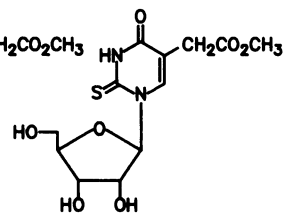

65, $mcmo^5U$

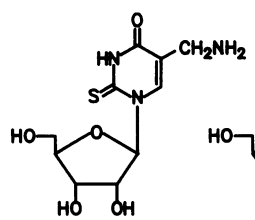

66, chm^5U

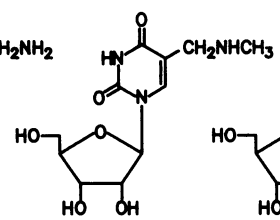

67, $mchm^5U$

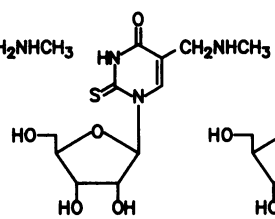

68, mcm^5U

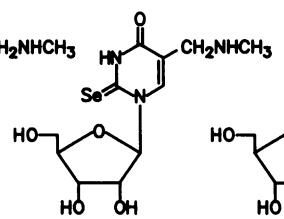

69, mcm^5Um

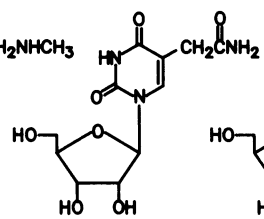

70, mcm^5s^2U

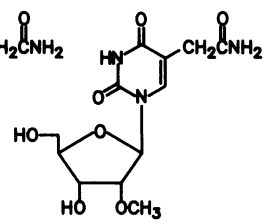

71, nm^5s^2U

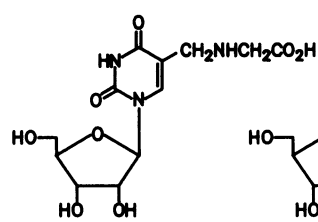

72, mnm^5U

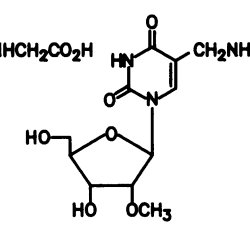

73, mnm^5s^2U

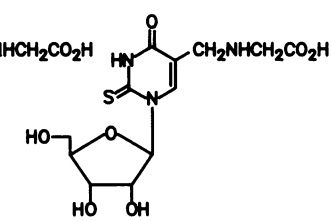

74, mnm^5se^2U

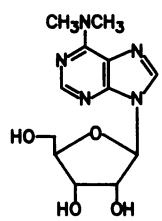

75, ncm^5U

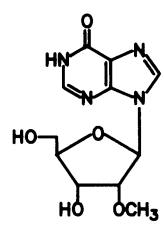

76, ncm^5Um

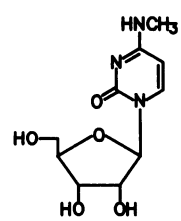

77, $cmnm^5U$

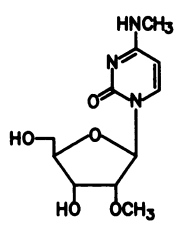

78, $cmnm^5Um$

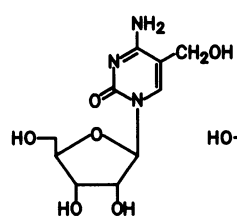

79, $cmnm^5s^2U$

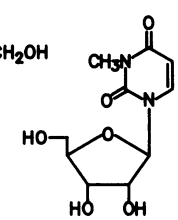

80, m_2^6A

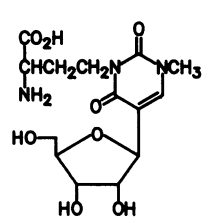

81, Im

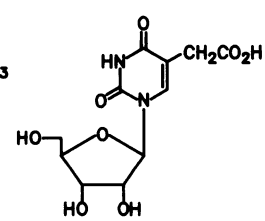

82, m^4C

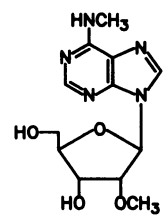

83, m^4Cm

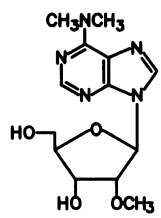

84, hm^5C

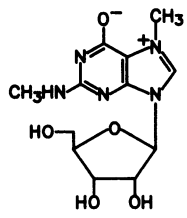

85, m^3U

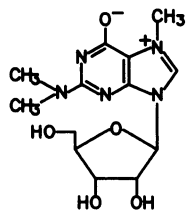

86, $m^1acp^3\Psi$

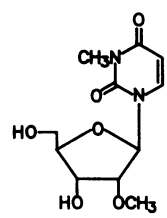

87, cm^5U

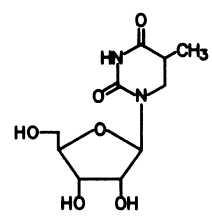

88, m^6Am


89, m_2^6Am


90, $m^{2,7}G$


91, $m^{2,2,7}G$


92, m^3Um


93, m^5D