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Abbreviations and Symbols

All contributors to this Series are asked to use the terminology (abbreviations and symbols) recommended by the IUPAC–IUB Commission on Biochemical Nomenclature (CBN) and approved by IUPAC and IUB, and the Editor endeavors to assure conformity. These Recommendations have been published in many journals *(1, 2)* and compendia *(3)* in four languages and are available in reprint form from the NAS–NRC Office of Biochemical Nomenclature (OBN), as stated in each publication, and are therefore considered to be generally known. Those used in nucleic acid work, originally set out in section 5 of the first Recommendations *(1)* and subsequently revised and expanded *(2, 3)*, are given in condensed form (I–V) below for the convenience of the reader. Authors may use them without definition, when necessary.

I. Bases, Nucleosides, Mononucleotides

1. *Bases* (in tables, figures, equations, or chromatograms) are symbolized by Ade, Gua, Hyp, Xan, Cyt, Thy, Oro, Ura; Pur = any purine, Pyr = any pyrimidine, Base = any base. The prefixes S–, H_2, F–, Br, Me, etc., may be used for modifications of these.

2. *Ribonucleosides* (in tables, figures, equations, or chromatograms) are symbolized, in the same order, by Ado, Guo, Ino, Xao, Cyd, Thd, Ord, Urd (Ψrd), Puo, Pyd, Nuc. Modifications may be expressed as indicated in (1) above. Sugar residues may be specified by the prefixes r (optional), d (=deoxyribo), a, x, l, etc., to these, or by two three-letter symbols, as in Ara-Cyt (for aCyd) or dRib-Ade (for dAdo).

3. *Mono-, di-, and triphosphates of nucleosides* (5′) are designated by NMP, NDP, NTP. The N (for "nucleoside") may be replaced by any one of the nucleoside symbols given in II-1 below. 2′-, 3′-, and 5′- are used as prefixes when necessary. The prefix d signifies "deoxy." [Alternatively, nucleotides may be expressed by attaching P to the symbols in (2) above. Thus: P-Ado = AMP; Ado-P = 3′-AMP.] cNMP ′-cyclic 3′ : 5′-NMP; Bt_2cAMP = dibutyryl cAMP, etc.

II. Oligonucleotides and Polynucleotides

1. Ribonucleoside Residues

(a) Common: A, G, I, X, C, T, O, U, Ψ, R, Y, N (in the order of I-2 above).

(b) Base-modified: sI or M for thioinosine = 6-mercaptopurine ribonucleoside; sU or S for thiouridine; brU or B for 5-bromouridine; hU or D for 5,6-dihydrouridine; i for isopentenyl; f for formyl. Other modifications are similarly indicated by appropriate *lower-case* prefixes (in contrast to I-1 above) *(2, 3)*.

(c) Sugar-modified: prefixes are d, a, x, or l as in I-2 above, alternatively, by *italics* or **boldface** type (with definition) unless the entire chain is specified by an appropriate prefix. The 2′-*O*-methyl group is indicated by *suffix* m (e.g., -Am- for 2′-*O*-methyladenosine, but -mA- for *N*-methyladenosine).

(d) Locants and multipliers, when necessary, are indicated by superscripts and subscripts, respectively, e.g., -m^6_2A- = 6-dimethyladenosine; -s^4U- or -^{4}S- = 4-thiouridine; -ac^4Cm- = 2′-*O*-methyl-4-acetylcytidine.

(e) When space is limited, as in two-dimensional arrays or in aligning homologous sequences, the prefixes may be placed *over the capital letter*, the suffixes *over the phosphodiester symbol*.

2. Phosphoric Acid Residues [left side = 5′, right side = 3′ (or 2′)]

(a) Terminal: p; e.g., pppN . . . is a polynucleotide with a 5′-triphosphate at one end; Ap is adenosine 3′-phosphate; C > p is cytidine 2′ : 3′-cyclic phosphate (*1, 2, 3*); p < A is adenosine 3′ : 5′-cyclic phosphate.

(b) Internal: hyphen (for known sequence), comma (for unknown sequence); unknown sequences are enclosed in parentheses. E.g., pA-G-A-C(C_2,A,U)A-U-G-C > p is a sequence with a (5′) phosphate at one end, a 2′ : 3′-cyclic phosphate at the other, and a tetranucleotide of unknown sequence in the middle. **(Only codon triplets are written without some punctuation separating the residues.)**

3. Polarity, or Direction of Chain

The symbol for the phosphodiester group (whether hyphen or comma or parentheses, as in 2b) represents a 3′-5′ link (i.e., a 5′ . . . 3′ chain) unless otherwise indicated by appropriate numbers. "Reverse polarity" (a chain proceeding from a 3′ terminus at left to a 5′ terminus at right) may be shown by numerals or by right-to-left arrows. Polarity in any direction, as in a two-dimensional array, may be shown by appropriate rotation of the (capital) letters so that 5′ is at left, 3′ at right when the letter is viewed right-side-up.

4. Synthetic Polymers

The complete name or the appropriate group of symbols (see II-1 above) of the repeating unit, **enclosed in parentheses if complex or a symbol,** is either (a) preceded by "poly," or (b) followed by a subscript "n" or appropriate number. **No space follows "poly"** (*2, 5*).

The conventions of II-2b are used to specify known or unknown (random) sequence, e.g.,

polyadenylate = poly(A) or $(A)_n$, a simple homopolymer;

poly(3 adenylate, 2 cytidylate) = poly(A_3C_2) or $(A_3,C_2)_n$, an *irregular* copolymer of A and C in 3 : 2 proportions;

poly(deoxyadenylate-deoxythymidylate) = poly[d(A-T)] or poly (dA-dT) or $(dA\text{-}dT)_n$ or $d(A\text{-}T)_n$, an *alternating* copolymer of dA and dT;

poly(adenylate,guanylate,cytidylate,uridylate) = poly(A,G,C,U) or $(A,G,C,U)_n$, a random assortment of A, G, C, and U residues, proportions unspecified.

The prefix copoly or oligo may replace poly, if desired. The subscript "n" may be replaced by numerals indicating actual size, e.g., $(A)_n \cdot (dT)_{12-18}$.

III. Association of Polynucleotide Chains

1. *Associated* (e.g., H-bonded) chains, or bases within chains, are indicated by a *center dot* (not a hyphen or a plus sign) separating the *complete* names or symbols, e.g.:

poly(A) · poly(U) or $(A)_n \cdot (U)_m$
poly(A) · 2 poly(U) or $(A)_n \cdot 2(U)_m$
poly(dA-dC) · poly(dG-dT) or $(dA\text{-}dC)_n \cdot (dG\text{-}dT)_m$.

2. *Nonassociated* chains are separated by the plus sign, e.g.:

$2[\text{poly(A)} \cdot \text{poly(U)}] \xrightarrow{\Delta}$ poly(A) · 2 poly (U) + poly(A)
or $2[A_n \cdot U_m] \rightarrow A_n \cdot 2U_m + A_n$.

3. Unspecified or unknown association is expressed by a comma (again meaning "unknown") between the completely specified chains.

Note: In all cases, each chain is completely specified in one or the other of the two systems described in II-4 above.

IV. Natural Nucleic Acids

RNA	ribonucleic acid or ribonucleate
DNA	deoxyribonucleic acid or deoxyribonucleate
mRNA; rRNA; nRNA	messenger RNA; ribosomal RNA; nuclear RNA
hnRNA	heterogeneous nuclear RNA
D-RNA; cRNA	"DNA-like" RNA; complementary RNA
mtDNA	mitochondrial DNA
tRNA	transfer (or acceptor or amino-acid-accepting) RNA; replaces sRNA, which is not to be used for any purpose
aminoacyl-tRNA	"charged" tRNA (i.e., tRNA's carrying aminoacyl residues); may be abbreviated to AA-tRNA
alanine tRNA or $tRNA_?^{Ala}$, etc.	tRNA normally capable of accepting alanine, to form alanyl-tRNA
alanyl-tRNA or $alanyl\text{-}tRNA^{Ala}$	The same, with alanyl residue covalently attached. [*Note:* fMet = formylmethionyl; hence $tRNA^{fMet}$, identical with $tRNA_f^{Met}$]

Isoacceptors are indicated by appropriate subscripts, i.e., $tRNA_1^{Ala}$, $tRNA_2^{Ala}$, etc.

V. Miscellaneous Abbreviations

P_i, PP_i	inorganic orthophosphate, pyrophosphate
RNase, DNase	ribonuclease, deoxyribonuclease
t_m (not T_m)	melting temperature (°C)

Others listed in Table II of Reference 1 may also be used without definition. No others, with or without definition, are used unless, in the opinion of the editor, they increase the ease of reading.

Enzymes

In naming enzymes, the 1972 recommendations of the IUPAC-IUB Commission on Biochemical Nomenclature (CBN)*(4)*, are followed as far as possible. At first mention, each enzyme is described *either* by its systematic name *or* by the equation for the reaction catalyzed *or* by the recommended trivial name, followed by its EC number in parentheses. Thereafter, a trivial name may be used. Enzyme names are not to be abbreviated except when the substrate has an approved abbreviation (e.g., ATPase, but not LDH, is acceptable).

References*

1. *JBC* **241,** 527 (1966); *Bchem* **5,** 1445 (1966); *BJ* **101,** 1 (1966); *ABB* **115,** 1 (1966), **129,** 1 (1969); and elsewhere.†
2. *EJB* **15,** 203 (1970); *JBC* **245,** 5171 (1970); *JMB* **55,** 299 (1971); and elsewhere.†
3. "Handbook of Biochemistry" (H. A. Sober, ed.), 2nd ed. Chemical Rubber Co., Cleveland, Ohio, 1970, Section A and pp. H130–133.
4. "Enzyme Nomenclature," Elsevier Scientific Publ. Co., Amsterdam, 1973, and Supplement No. 1, *BBA* **429,** (1976).

* Contractions for names of journals follow.

† Reprints of all CBN Recommendations are available from the Office of Biochemical Nomenclature (W. E. Cohn, Director), Biology Division, Oak Ridge National Laboratory, Box Y, Oak Ridge, Tennessee 37830, USA.

5. "Nomenclature of Synthetic Polypeptides," *JBC* **247**, 323 (1972); *Biopolymers* **11**, 321 (1972); and elsewhere.*

Abbreviations of Journal Titles

Journals	*Abbreviations used*
Annu. Rev. Biochem.	ARB
Arch. Biochem. Biophys.	ABB
Biochem. Biophys. Res. Commun.	BBRC
Biochemistry	Bchem
Biochem. J.	Bj
Biochim. Biophys. Acta	BBA
Cold Spring Harbor Symp. Quant. Biol.	CSHSQB
Eur. J. Biochem.	EJB
Fed. Proc.	FP
J. Amer. Chem. Soc.	JACS
J. Bacteriol.	J. Bact.
J. Biol. Chem.	JBC
J. Chem. Soc.	JCS
J. Mol. Biol.	JMB
Nature, New Biology	Nature NB
Proc. Nat. Acad. Sci. U.S.	PNAS
Proc. Soc. Exp. Biol. Med.	PSEBM
Progr. Nucl. Acid Res. Mol. Biol.	This Series

* Reprints of all CBN Recommendations are available from the NRC Office of Biochemical Nomenclature (W. E. Cohn, Director), Biology Division, Oak Ridge National Laboratory, Box Y, Oak Ridge, Tennessee 37830, USA.

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MARIANNE GRUNBERG-MANAGO AND FRANÇOIS GROS

Correlation of Biological Activities with Structural Features of Transfer RNA

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I. Biological Activities of tRNAs

Transfer RNA (tRNA), a class of small RNA molecules of molecular weight ratio (M_r) about 25,000, is becoming more and more intriguing as it is found to be implicated in many activities other than those associated with its traditional role in protein biosynthesis. There are of the order of 55 different species of tRNA in a particular cell type, and they appear to arise from longer precursor tRNA molecules. The precursor molecules are primary gene products synthesized by RNA polymerase under the direction of the DNA genome. One of the characteristics of tRNAs is their high content of modified bases compared with other RNA molecules. So far it is not clearly established at which step, and in what order during the maturation of tRNAs, the modified bases are formed.

Now that a three-dimensional structure for one tRNA species is known, there is interest in attempting to consider the functions of tRNA in terms of this structure. A summary of the current state of identification of functions or, more precisely, biological activities of tRNAs in prokaryotes and eukaryotes is given in Table I. Transfer RNA plays a central role in protein biosynthesis (activities 1–9), and much more is known about the biochemistry of the processes involved than in any other function. It is therefore probably more feasible to

TABLE I
ACTIVITIES OF tRNA

Protein biosynthesis

1. Activation of amino acids
2. Recognition by EF-Tu
3. Location in A-site
4. Decoding mRNA
5. Signal for "magic spot"[a]
6. Recognition of initiator tRNA by IF
7. Location in I-site (part of P-site)
8. Recognition by transformylase

(6–8: Special for Initiation)

9. Regulation
   a. Repressor
   b. Feedback inhibitor
   c. Suppression

RNA metabolism

10. As precursor by cleavase and maturation enzymes
11. Enzymes modifying bases
12. C-C-A repair enzyme
13. As peptidyl-tRNA by hydrolase
14. Nuclease degradation
15. Reverse transcriptase primer
16. Selection during viral encapsulation
17. Correlation with 3′ end of viral RNA
18. Alteration of *Escherichia coli* ENDO I specificity

Cell wall biosynthesis

19. Transfer of amino acids to wall structure

[a] ppGpp and pppGpp.

relate structure and function in this field. The additional activities or functions are listed for future interest.

In normal protein biosynthesis, each tRNA species is charged with an amino acid (activity 1) by an aminoacyl-tRNA synthetase ("activating enzyme"), and the charged species is then carried to the ribosome in the form of a ternary complex made with elongation-factor-Tu (EF-Tu) and GTP (activity 2). In similar fashion, the unique tRNA species, initiator tRNA, a special class of methionine tRNA, is thought to be carried to the ribosome by an initiation factor and GTP (activity 6). The aminoacyl-tRNA is located by an uncharacterized mechanism in the A-site of the ribosome (activity 3) where it decodes mRNA via its anticodon triplet (activity 4). In contrast, the initiator tRNA, formylmethionyl-tRNA^{fMet} in prokaryotes, and methionyl-tRNA^{fMet} (sometimes called Met-tRNA$_i$) in eukaryotes, is located in the initia-

tion (I)-site on the small ribosomal subunit (activity 7) for decoding the initiator triplet codon. This site becomes part of the ribosomal P-site. Since the prokaryotic Met-tRNA^{fMet} must be formylated, it is also recognized by a special enzyme for this, the transformylase (activity 8).

When prokaryotic cells are starved for amino acids, an unusual role may be detected for uncharged tRNA. The uncharged tRNA is bound to the ribosomal A-site as though in mRNA decoding, but sets off a signal for the formation, by the so-called stringent factor, of unusual guanosine nucleotide derivatives originally called "magic spots" (activity 5), now ppGpp and pppGpp.

A group of somewhat poorly defined (mechanistically) roles for tRNA in the regulation of protein biosynthesis has been collected as "function" 9. These include bacterial roles as a repressor, feedback inhibitor of the aromatic amino-acid pathway, and the well-characterized role as suppressor of nonsense mutations. Additionally in eukaryotes, there are uncharacterized roles relating to the binding to tryptophan pyrrolase (in *Drosophila*) and the inhibition of protein synthesis in virally infected animal cells by the degradation of one or more essential tRNA species, a process that seems to accompany interferon production.

In addition to their role in protein synthesis, tRNAs have activities concerned with a number of reactions conveniently classified as being concerned with RNA metabolism (activities 10–18). The tRNA is trimmed to size and matured from the precursor molecule by a series of as yet poorly characterized enzymes presumably linked to other metabolic roles (activities 10–12). The C-C-A-repair enzyme (activity 12) certainly repairs tRNAs with incomplete 3′ ends and probably is concerned with maturation as well. If peptidyl-tRNA should fall off the ribosome, there is a peptidyl-tRNA hydrolase (activity 13) that can remove the peptide, thus permitting the tRNA to be recycled for use in protein biosynthesis. Little is known about tRNA turnover, but specific nucleases (activity 14) must be involved.

Recently some interesting properties of eukaryotic tRNAs have been identified (activities 15–17) with regard to virus metabolism. Reverse transcriptase from RNA tumor viruses uses a specific tRNA^{Trp} as a primer during synthesis of virally coded DNA. Furthermore, a certain number of selected tRNA species (perhaps ten to fifteen) are incorporated noncovalently into RNA tumor virus particles during encapsulation from the cell membrane.[1] It is also well established that many viruses, especially plant viruses, have elements of tRNA structure that permit their 3′ ends to be charged specifically with an amino

[1] See article by Waters and Mullin in this volume.

acid (activity 17), e.g., turnip yellow mosaic viral RNA with valine. Activity 18 is not well-defined, but the specificity of bacterial endonuclease I for double-stranded cuts in DNA is altered to a "nicking" property (single-strand cleavage) when it binds tRNA.

Finally, there is a special class of tRNAs that is chargeable and that transfers amino acids into cell-wall structures (activity 19). These tRNAs, best characterized for a series of staphylococcal $tRNA^{Gly}$ species, do not contain all the constant features of the general cloverleaf structure, presumably including those for ribosome binding. However, their primary structures can be arranged in normal cloverleaf structures *(1)*.

II. Subclassification and Generalized Primary Structure of tRNAs

The information from 77 different tRNA sequences known in July 1976 and listed in Table II (Barrell and Clark *(1)*, Clark and Klug *(2)*, plus 14 new structures) has been conveniently incorporated into standard "cloverleaf" forms as shown in Fig. 1. This remarkable feature of all the primary structures was first proposed by Holley *et al. (3)* and is based on Watson–Crick base-pairing. The simple classification shown in Fig. 1 is based on size (see Table II for species).

Thus we have small and large tRNAs dependent upon the size of the extra arm (see also Fig. 2 and Table II). The fourteen new structures are those for Ec Arg_2 y Arg_2, Ec Cys, T4 Gln, Ec Gly_2, Ec Lys, Rbl $Lys_{2A(2B)}$, Rbl Lys_3, An fMet, Bsu fMet, Sf fMet, Rl Ser_3, Bs Val_{2A}, y Val_{2A}.

In Fig. 2 (p. 6), I have incorporated the information from the small class 1 sequences into a standard generalized cloverleaf. For this information, 56 of the 63 class 1 species indicated in Table II have been

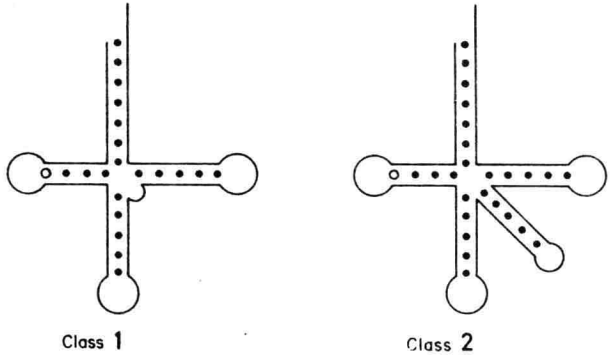

FIG. 1. Simplified classes of tRNA. The open circle indicates that a Watson–Crick base-pair is not always found in this position.

TABLE II

CLASSES OF tRNA ACCORDING TO ARM SIZES AND STRUCTURE CORRELATIONS[a]

Class 1 (63)	
A(36)	4 base-pairs in b-stem (D stem) 5 bases in extra loop III and containing m^7G
(and with A9)	Ec Ala_1, Ec Arg_1, Ec Arg_2, Ec Asp_1, Ec Gly_3, Ec + Sal His_1, Ec Ile_1, Ec Lys, y Lys, Rbl $Lys_{2A(2B)}$, Rbl Lys_3, Svt Lys_4, An fMet, Ec Met, y Met_3, Mye + Rbl Met_4, Ec Phe, Mp Phe, Bs Phe, y Phe, Wg + Ps Phe, Rbl Phe, T4 Pro, Ec Trp, Ec Val_1, Ec Val_{2A}, Ec Val_{2B}, Bs Val_{2A}, Mye Val_1
(and with m^1G9 or G9)	y Cys, Ec fMet, Bsu fMet, y fMet, Mye + Rbl + St + Xl + Smg + Hup fMet, y Trp, Chi + Bl Trp
B(6)	4 base-pairs in b-stem (D stem) 5 bases in extra loop III without m^7G y Ala_1, Tu Ala_1, y Arg_3, Hay Lys, Sf fMet, Ec Thr
C(7)	4 base-pairs in b-stem (D stem) 4 bases in extra loop y Asp_1, Ec Glu_1, Ec Glu_2, Ec + Sal Gly_1, Sta Gly, Wg Gly, y Gly
D(14)	3 base-pairs in b-stem (D stem) Small extra arm with several bases (3–5) y Arg_2 (5), Ec Cys (4), Ec Gln_1 (5), Ec Gln_2 (5), T4 Gln (5), y Glu_3 (4), Ec Gly_2 (4), T4 Gly (4), Tu Ile (5), y Tyr (5), Tu Tyr (5), y Val_1 (5), y Val_{2A} (5), Tu Val (3)
Class 2 (14)	3 base-pairs in b-stem (D stem) Large extra arm with several bases (13–21) Ec + Sal Leu_1 (15), Ec Leu_2 (15), T4 Leu (14), y Leu_3 (13), y Leu_4 (13), Ec Ser_1 (16), Ec Ser_3 (21), T4 Ser (18), y Ser_1 (14), y Ser_2 (14), Rl Ser_1 (14), Rl Ser_3 (14), Ec Tyr_1 (13), Ec Tyr_2 (13)

[a] Abbreviations: An, *Anacystis nidulans;* Bl, Beef liver; Bs, *Bacillus stearothermophilus;* Bsu, *Bacillus subtilis;* Chi, chicken; Ec, *Escherichia coli;* Hay, haploid yeast Hup, human placenta; Mp, *Mycoplasma;* Mye, myeloma; Ps, *Pisum sativum;* Rbl rabbit liver; Rl, rat liver; Sal, *Salmonella typhimurium;* Sf, *Streptococcus faecalis* Smg, Sheep mammary gland; Sta, *Staphylococcus;* St, Salmon testis; Svt, Svt 2 cells Tu, *Torulopsis utilis;* Wg, wheat germ; Xl, *Xenopus laevis;* y, yeast.

used: clear exceptions, based on functions such as fMet species and St Gly, to the generalized form are omitted.

As shown in Fig. 2, the Watson–Crick base-pairs give rise to fou double-helical stem regions a, b, c, and e, three of which are closed by non-base-paired loop regions I, II and IV. Another point of nomencla ture illustrated in Fig. 2 is that a *stem* plus a *loop* is also called an *arm* Most of the tRNA cloverleaf forms have remarkably constant regions There is a phosphate at the 5′ end, whereas at the 3′ end, where the amino acid is attached, there is a common sequence C-C-A. In addi