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"The" Genetic Code?

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The DNA-based code for protein through messenger and transfer RNA is widely regarded as the code of life. But genomes are littered with other kinds of coding elements as well, and all of them probably came after a supercode for the tRNA system itself.

Evolution and the diversification of organisms are made possible by codes, or arbitrary assignments of "meaning," in multiple ways. Many are not widely appreciated. Codes allow the same system of components to be used for multiple purposes. These can be open-ended, the way the alphabet and vocabulary make this column possible, but the flexibility of a code can become constrained once a system with many components that must work in concert, if an organism is to develop and survive—or evolve—is in place. Codes are highly efficient ways to carry uncorrupted information from one place to enable *indirect* action elsewhere. But this requires a decryption system at the receiving end.

Fidelity at both ends is vital. In World War II, the Germans had their Enigma encryption machine, whose use by U-boats caused chaos for British shipping, until the eccentric computer pioneer Alan Turing learned how to break the code. That led to doom for Germany. For organisms, the price for code breakdown in the Battle of Life is similarly unremorseful.

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Everyone knows of "the" genetic code, by which nucleotide triplets in DNA in the nucleus of cells specify the amino acid (aa) sequence of proteins. This is the code described in textbooks as the heart of the genetic theory of life and its evolution. Discoveries in recent years have made things more complicated by showing that genomes are littered with all sorts of other kinds of coding elements. An example is DNA sequences located near to protein-coding segments—"genes" proper—that are chemically recognized by regulatory proteins, which bind there to cause the nearby gene to be expressed (or repressed) in specific cells or under specific conditions.[1,2] This gene-expression mechanism is as fundamental as the classical genetic code, because it allows cells to differentiate into organs and tissues, enabling organisms from plants to people to exist. The cells in the eyes you're reading with and in the fingers that hold this page all have the same genome, but eyes and fingers are different because they use different subsets of those genes. This is specified by tissue-specific developmental codes.

Other DNA sequence elements are used to package, protect, or copy DNA. Embryos develop and adult organisms respond to their environments by using extensive arbitrary codes in the form of combinations of chemical signaling molecules that are produced by specific genes and are released to be detected by other cells whose gene expression they alter. These are codes because it is the combination of factors, not the factors themselves, that carry the information.

Your life depends on the fidelity of these many codes. Aberrant codes related to cell behavior can lead to dysgenesis or various metabolic diseases. Anomalous cell-surface proteins can cause autoimmune destruction, and viruses are the Alan Turings of life that evolve ways to break their receptor codes to gain illicit entry into cells (Fig. 1).

But there is an additional code, a code of codes, that makes all of this possible, including "the" genetic code itself, and may be the oldest and most fundamental one of all. Protein-coding (Figure 2) works via two intermediaries: messenger RNA (mRNA), a complementary copy of code transcribed from a coding region of DNA, and transfer RNA (tRNA), which carries aa's to ribosomes to be linked together to form a chain (polypeptide) that becomes a protein, thus translating "the" genetic code. If mRNA takes a message to ribosomes, tRNA is the Enigma decrypter that turns the code into action (a protein). As important as the genetic protein code itself is, this decryption system may be the most deeply fundamental aspect of the coding system, itself a kind of code, and probably the first code.

In 1953 Watson and Crick solved the basic structure of DNA as a set of parallel chains connected by specific pairing of nucleotides, A with T and C with G, the famous double helix. It was not until 1967 that the use of DNA to code for aa sequences—our friend the protein code, shown in Table 1—was deciphered (see[3]). Remarkably, this protein-coding process was found to be based on the same Watson-Crick complementary base-pairing phenomenon that made DNA itself. Experiments that synthesized

Figure 1. Alan Turing.

template RNA strings in bacterial extracts to see what aa strings were produced showed that specific nucleotide triplets in DNA, that we now call *codons*, through a mRNA copy, bind with nucleotide triplet *anticodons* in tRNA (i.e., the anticodon is a string of 3 nucleotides complementary to those at the corresponding codon position in the mRNA).

This system entirely depends on the fact that, when activated, distinct tRNA molecules bind a specific aa which they carry to the mRNA during translation, and that the aa they carry corresponds to their anticodon sequence. As the mRNA moves through a ribosome, each of its triplets is sequentially bound, again by base-pairing, to a tRNA with the complementary anticodon; this juxtaposes the tRNA's aa to the end of the building string of aa's (Figure 2B).

The 64 nucleotide triplets made possible by four options (A,C,T,G) in each of three successive positions, code for only 20 aa's because most amino acids are represented by more than one codon, and hence more than one type of tRNA specifies a given aa, as shown in Table 1. The table also shows that the genome has many copies of most types of tRNA (each coded for and transcribed from its own location in the genome). It is crucial that the code and its supporting tRNA system be degenerate. Were this not so, more than 40 nucleotide triplets would code for nothing, and it would be much more difficult to maintain or modify the code by natural selection. Too many mutations would change a codon's specification from an aa to "nothing," causing a skip in the mRNA, and translating into nothing.

A TALE WITHIN, OR UPON A TALE

So far so good. But if genes code for proteins by specifying their aa sequence, then the translation mechanism has to be just as specific! Surprisingly, *how* this codon-tRNA-aa specifity, with its multiplicities of codons and tRNA genes with the same specificity, is managed and maintained has little to do with the protein code. Instead, there is an independent tRNA "supercode" (known in the literature as the second genetic code or the RNA code). Like the protein code, the supercode involves RNA-aa associations, but unlike the protein code, the supercode is far from universal and includes aspects of tRNA that have nothing to do with its nucleotide sequence or base-pairing. Instead, enzymes called *aminoacyl-tRNA synthetases* (aaRS's) first "charge," or *aminoacylate* the tRNA by attaching its cognate aa, and then accompany it to the ribosomes where the aa is discharged to the growing aa string. There are specific aaRS's for each aa.

tRNA's are small molecules 73 to 95 nucleotides in length that use complementary base-pairing to fold into a four-armed cloverleaf structure (Figure 3A), the D stem-loop, the central arm containing the anticodon, the

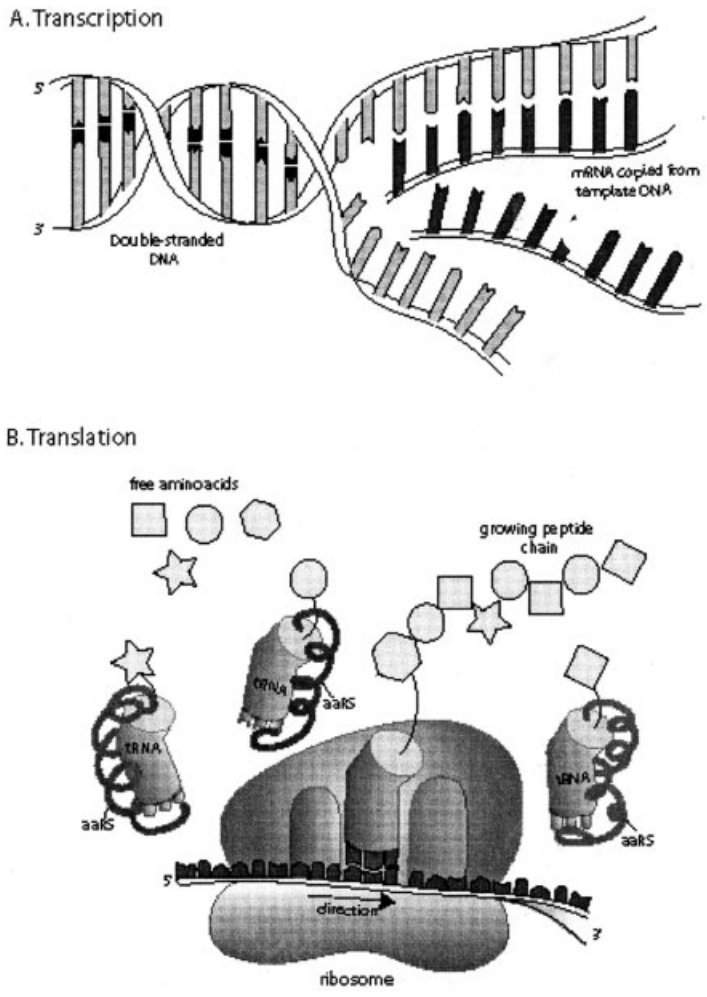

Figure 2. The main steps in DNA as a protein code. **A.** Transcription: mRNA copied from the template DNA. **B.** Translation: amino acids carried to the ribosome by tRNAs for incorporation into the growing polypeptide chain, with mRNA as template. The aaRS's are explained below.

TABLE 1. GENETIC CODE: CODON TRIPLETS, AA NAME FOR WHICH EACH TRIPLET CODES, AND IN PARENTHESES THE NUMBER OF GENES IN THE HUMAN GENOME THAT PRODUCE tRNA THAT USES THAT CODON

First Letter of Codon	Second Letter of Codon: T	C	A	G
T	TTT Phe (0)	TCT Ser (10)	TAT Tyr (1)	TGT Cys (0)
	TTC Phe (14)	TCC Ser (0)	TAC Tyr (11)	TGC Cys (30)
	TTA Leu (8)	TCA Ser (5)	TAA STOP (0)	TGA STOP (0)*
	TTG Leu (6	TCG Ser (4)	TAG STOP (0)	TGG Trp (7)
C	CTT Leu (13)	CCT Pro (11)	CAT His (0)	CGT Arg (9)
	CTC Leu (0)	CCC Pro (0)	CAC His (12)	CGC Arg (0)
	CTA Leu (2)	CCA Pro (10)	CAA Gln (11)	CGA Arg (7)
	CTG Leu (6)	CCG Pro (4)	CAG Gln (21)	CGG Arg (5)
A	ATT Ile (13)	ACT Thr (8)	AAT Asn (1)	AGT Ser (0)
	ATC Ile (1)	ACC Thr (0)	AAC Asn (33)	AGC Ser (7)
	ATA Ile (5)	ACA Thr (10)	AAA Lys (16)	AGA Arg (5)
	ATG Met (17)	ACG Thr (7)	AAG Lys (22)	AGG Arg (4)
G	GTT Val (20)	GCT Ala (25)	GAT Asp (0)	GGT Gly (0)
	GTC Val (0)	GCC Ala (0)	GAC Asp (10)	GGC Gly (11)
	GTA Val (5)	GCA Ala (10)	GAA Glu (14)	GGA Gly (5)
	GTG Val (19)	GCG Ala (5)	GAG Glu (8)	GGG Gly (8)

*An unusual tRNA carries this codon and it occasionally interprets TGA as selenocysteine instead of 'stop.'

TψC stem-loop, and the acceptor stem at the other end where its aa is attached. Due to base-pairing characteristics and chemical modification of the nucleotides, the folded tRNA forms a 3-dimensional L-shape that collapses the four cloverleaf arms into two domains: the acceptor and the anticodon (Figure 3B). It is important that forming its folded shape requires nucleotides in different places along the linear sequence code for the tRNA itself to be complementary, which we illustrate schematically in Figure 3C.

The appropriate aa binds to its tRNA where bases 1–7 in the acceptor stem pair with bases 72–66 at the other end, always terminating in a singled-stranded $N^{73}CCA^{76}$ string (N means that position 73 in the sequence can be any nucleotide, but all aa's in part require a CCA at the very end of the tRNA in order to attach properly). The numbers are the nucleotides reading from left to right, 5′ to 3′ as RNA sequences are usually written out. tRNA combines with its aaRS as part of the protein assembly system, that decrypts the original code (Figure 2).

These are universal aspects of tRNA's, and if that were all, the tRNA-aa part of the story would have nothing to do with coding. The triplet codes for each aa are identical in all species—there is only one codebook, that (with minor exceptions) preserves vital aspects of evolution and the coherence of all life. But the *way* in which tRNA's pair with aa's is not universal at all.

Gene duplication events are responsible for the multiple copies of genes specifying tRNA's that use each aa (Table 1). Like any other gene, each tRNA gene experiences mutation and varies. Similarly, the aaRS genes are also subject to mutation. Though all aaRSs have the same function, they are otherwise characterized by their diversity among species. Since there are only 20 aaRS genes, one for each aa, but the code is degenerate, an aaRS for a specific aa must recognize and charge the set of tRNAs (with different anticodons and multiple independent, varying copies in the ge-

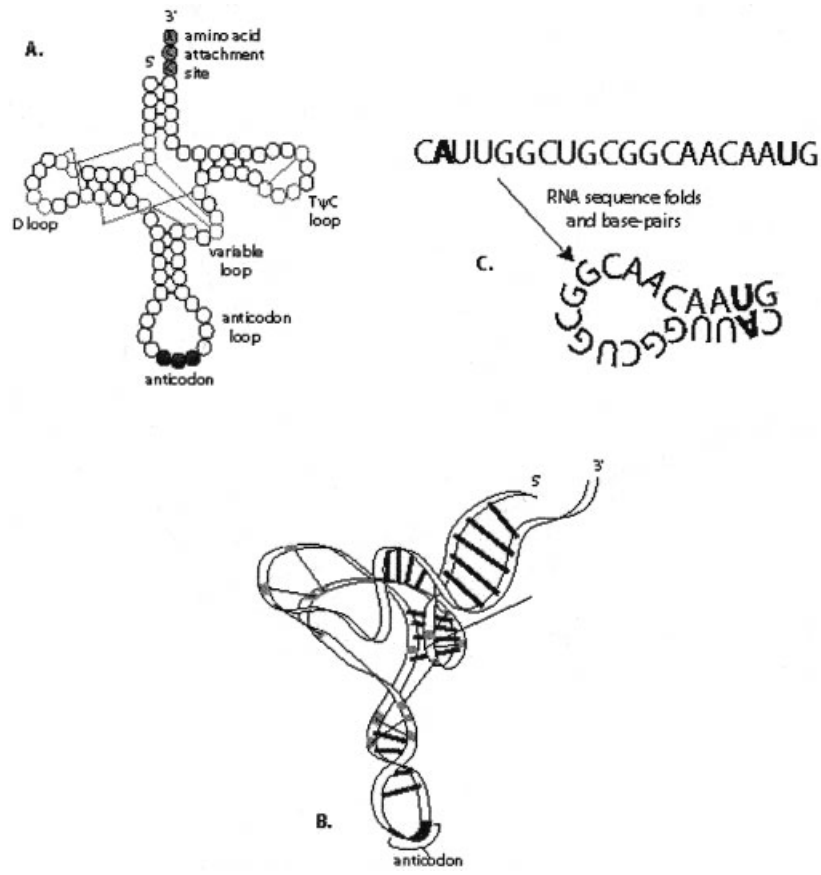

Figure 3. RNA molecule structure. **A.** Two-dimensional tRNA cloverleaf. **B.** Three-dimensional L structure. **C.** Schematic illustration of how a hypothetical stem-loop folded structure requires that the sequencing coding for the tRNA must have complementary nucleotides in appropriate places (the highlighted **U** and **A**). A and B reprinted from[2].

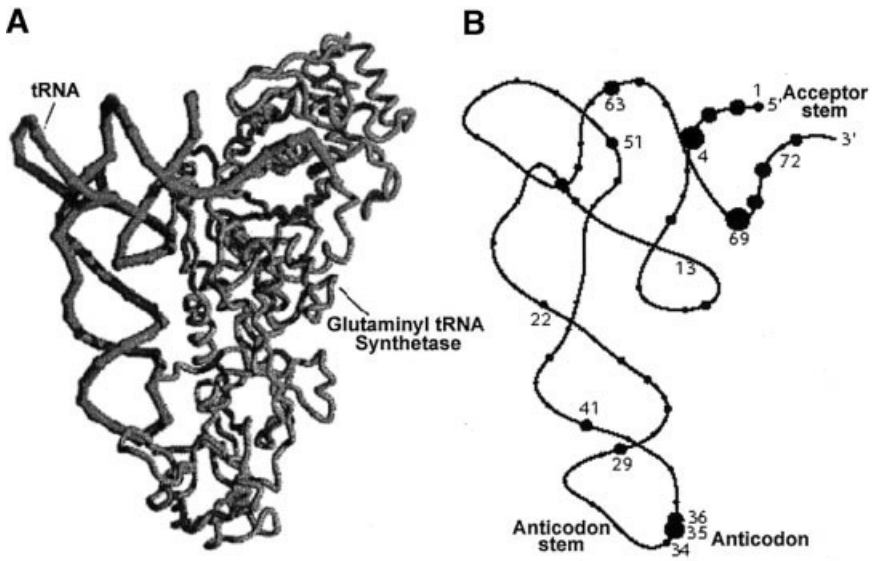

Figure 4. The mutual combinations that are the basis of the supercode. **A.** The binding of an aaRS (thinner ribbon to the right) to its corresponding tRNA (thicker ribbon, left) involves recognition of parts across the structures of both molecules (this shows Gln-tRNA^{Gln}, glutaminyl-tRNA synthetase, bound to tRNA-Gln). **B.** tRNA with nucleotide positions represented by circles; the size of a circle indicates the frequency with which that position is involved in recognition and hence binding with its aaRS (from[4]).

nome) specific to that aa. It does this by a combined chemical interaction among protein, RNA, and aa in which the aaRS recognizes a flexible variety of "identity elements" in the tRNA's 3-dimensional structure, involving the acceptor arm, the anticodon loop itself and other sites (as well as negative identifiers that preclude binding non-cognate tRNA's), there are also proofreading enzymes that check the proper charging of tRNA's.[4] The different tRNA's to which the same aa binds share unique identity elements, and the bonds formed involve around 20% of the tRNA's surface area (Figure 4), in an embrace of many touches.[5]

AaRS's charge tRNA's with their aa's in two different ways: directly and indirectly. The direct pathway relies on 20 aaRS's that discriminate between all 20 aa's, while the indirect route uses some non-discriminating aaRS's.[7] The indirect pathway, requires an additional step. A non-discriminating aaRS charges its cognate tRNA with the appropriate aa, but also charges some non-cognate tRNA's with the same aa. The non-cognate aa then undergoes chemical modification that converts it to the proper aa for that tRNA. For example, if we denote the tRNA type by tRNA^{aa}, a non-discriminating GluRS charges both tRNA^{Glu} and tRNA^{Gln} with Glu (glutamic acid) to produce Glu-tRNA^{Glu} and Glu-tRNA^{Gln}, but the Glu attached to the latter complex is then modified to become Gln (glutamine) to make everybody happy. It is all of this that makes the supercode a "code."

The aaRS's comprise two largely unrelated classes each with ten genes (Table 2). The genes coding for aaRS's in each class share short sequence motifs and the resultant folding shape for the aaRS protein. Each class attaches the aa to a different side of the tRNA molecule. Different major branches of life have different subsets of these systems: we and other mammals basically use a simple, direct system,[6,8] and sequence phylogenies of the aaRS genes do not completely fit the standard phylogenetic tree of archaeae, bacteria and eukaryotes (including us). This suggests that these enzymes or even the translation mechanism, arose twice in evolution, either because of dual origins of translation itself or a deep evolutionary history of *horizontal* transfer of these vital genes, that is, between taxa.[9]

tRNA and the Origins of Complex Life

Complex life—like ourselves—arose after the protein coding system made possible arbitrarily long strings of aa's (proteins) whose sequence could be reliably specified, so they did not have to arise spontaneously by self-assembly based on the chemical properties of free-floating aa's in a primordial soup. But there are inklings that the RNA supercode may have arisen originally from just such chemical properties, and not have been code-like at all.

Experiments have shown that what

TABLE 2. TABLE OF AMINOACYL-tRNA SYNTHETASE CLASSES AND THE AMINO ACIDS THEY ATTACH (FOR TERMS AND DETAILS SEE[6] AND HTTP://WWW.CS.STEDWARDS.EDU/CHEM/CHEMISTRY/CHEM43/CHEM43/TRNA/TMP-1112108482.HTM)

	Class I	Class II
Members	ArgRS, CysRS, GlnRS, GluRS, IleRS, LeuRS, MetRS, TrpRS TyrRS, ValRS	AlaRS, AsnRS, AspRS, GlyRS, HisRS, LysRS II, PheRS, ProRS, ThrRS, SerRS
Sequence motifs	HIGH, KMSKS	Motifs 1, 2 and 3
Active site typology	Rossmann fold, ~170 amino acids	Anti-parallel β fold, ~250 amino acids
tRNA binding site	Minor groove side of acceptor arm	Major groove side of acceptor arm
Aminoacylation site	3′-OH of tRNA	2′-OH of tRNA (except PheRS)
Amino acids charged	Bulkier amino acids	Smaller amino acids

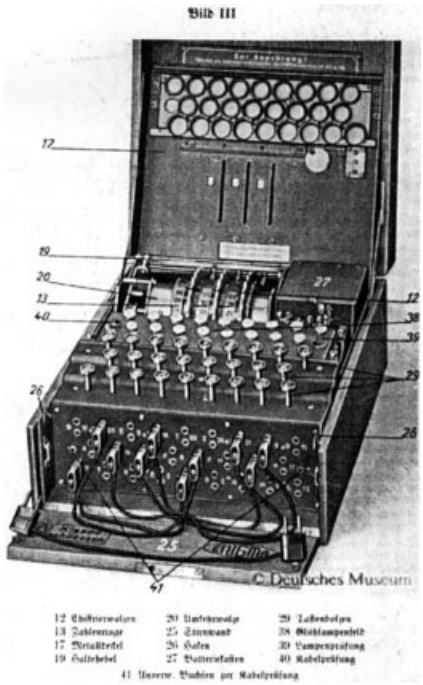

Figure 5. The Enigma machine.

has been frozen in life is not entirely by accident relative to the chemical properties of the components. For example, **AGA** codes for arginine and arginine may be attracted to the chemical "smell" of **AGA.** The coding system may have arisen by such primeval attractions that may then have been the *functional* units of life. Only later did these RNA triplets become part of tRNA intermediaries between DNA and mRNA.[10–16]

However, experiments show that the same aa is attracted by RNA sequences other than the triplets of today's system. So Francis Crick may have been at least partly right to refer to the current codon system as a "frozen accident" in evolution—whatever coding pattern was established first, stuck. Regardless of its origins, any such connections are today unrelated to the use of the coding system to specify the structure of proteins: the use of arginine in millions of places in millions of proteins has nothing to do with any affinities between arginine and **AGA.** That's what makes the system a code.[1,2] The main plot of the story of evolution may have been the turning of an original *operational* supercode into a flexible *informational* protein code that became the basis for the diversity of life we know today.

EVOLUTION OF THE SUPERCODE: MULTIPLE PARTNERS WALTZING THROUGH TIME

The supercode is interesting in its own right and may bear lessons for our own evolution. It exemplifies how the many parts of a complex information-based system must be constrained and evolve simultaneously. This is an elegant example of epistasis (interaction between games) or *coevolution.* A newly arising mutation that affects one component of such a system must be matched by a compatible change elsewhere in the system (the **U** with the **A** highlighted in Figure 3C) if it is not to destroy the in-place organization. There must be extensive epistasis in the supercode—the interaction among parts of the same gene, a tRNA sequence, or different genes such as different copies of the cognate tRNAs or those and the corresponding aaRS. The supercode shows how complex coevolution was already inherent in the earliest, simplest aspects of life.

A mutation in the coding region of most genes may be serious but at least only affect that one protein. But mutations in the supercode genes are different. A mutation that causes a tRNA to be charged with the wrong aa, or a mutation in an aaRS gene, would affect *all* proteins that use that particular aa or tRNA class. It may require a not-very-darwinian kind of selection to police such a system. The effects of a mis-specifying aaRS would not have to await a race with a predator, or a battle to defend a territory, for the effect to be manifest, and the animal (or plant) carrying the mutation to be eliminated. Instead, there is likely to be *developmental* or prezygotic selection that purifies cells *before* they become individuals, because any cell in the developmental lineage leading to the egg or sperm cells would be devastated by supercode mutations. There would never even be a chance for competitive selection of the usual darwinian kind *between* individuals. Similar statements probably apply to many gene regulation and cell housekeeping functions: human egg cells have to simmer for decades and sperm precursors have to divide repeatedly, and so on.

There is a general Darwinian prediction that evolution will drive selection to as early in life as possible, because it is cheaper in terms of biological investment to get rid of an offspring early rather than late. Prezygotic selection would be particularly cheap. Most species easily produce millions more gametes than they need; a woman begins life with 8 million eggs but even the most prolific uses only around 20 of them. Selection *within* organisms probably purges a lot of mutational variation that never shows up as Mendelian variation from parent to offspring, to compete via Malthusian population pressure for limited resources.

If this is right we should not expect many diseases caused by aaRS mutations, and that is the case. One possible exception are several mutations in the glycine-RS in affected by the neurological disease Charcot-Marie-Tooth syndrome.[17] These effects occur many years after birth, which is difficult to reconcile with the aspects of the tRNA system we have been describing. If aaRS mutations cause this disease, the likely mechanism is reduced efficiency, rather than major loss of function, of the aaRS gene. Close inspection should show widespread effects in the body, because tens of thousands of proteins include glycine. Still, it's curious.

CODES, CODES, AND MORE CODES: BUT SO WHAT?

It was a surprise in the last 50 years to learn that the intervening DNA between protein-coding genes, once called "junk," has a diversity of sequence-based coding functions. "The" genetic code has turned into a multiplicity of codes. DNA sequence specifying the classic genetic code, gene expression, chromosome packaging, and replication might be called linear or "horizontal" codes—sequences that, reading along the line, correspond to a sequence of aa's or are directly recognized by some kind of regulatory protein. Each such instance in the genome is independent. The supercode that charges tRNA with the right aa is a kind of "vertical" code, reading from tRNA

down to mRNA in ribosomes, and it isn't linear, because it's based on the 3-dimensional structure of tRNA and proteins that bind it, all of which must coevolve. It isn't independent either, because while the protein code provides open-ended aa strings for *any* gene, its supercode "staples" the individual elements together for *every* gene.

Prezygotic selection may explain how the supercode is maintained, but doesn't explain why such a mechanism evolved in the first place. To understand that we probably have to go back to when all life was simple and code *was* function. Today, 3–4 billion years later, the supercode protects the integrity of the protein code that makes biological diversity possible and preserves the unity of all life.

The problem of co-evolution is actually a general one. Most proteins fold up upon themselves in ways analogous to what happens to tRNA, and they interact with other substrates including proteins. Yet functions evolve. Explanations for this are not yet very satisfactory, but the general idea is that small mutational changes that do not make much difference to the system can accumulate within the various interacting components until eventually major differences have been achieved or at least could evolve rapidly (see a good discussion of this mechanism by Fontana[18]). However, there are so countlessly many possible mutations of varying levels of difference that it may require the low-cost, high-power ability of prezygotic or other very early selection to monitor. This may relate to more aspects of life than we have thought, and aspects of human evolution that we try to explain in terms of conventional selection may evolve for cellular rather than organismal reasons.

The subtlety and complexity of even the basic supercode exemplify the many other layers of codes, genetic and otherwise, by which life is lived and through which evolution works. But the supercode is different: if it were to break the way Turing broke the Enigma code, then we, like the U-boats, would be sunk (Fig. 5).

NOTES

We welcome comments on this column: kenweiss@psu.edu. There is a feedback *CrotchetyComments* page at http://www.anthro.psu.edu/weiss lab/index.html. We thank John Fleagle for critically reading the manuscript.

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