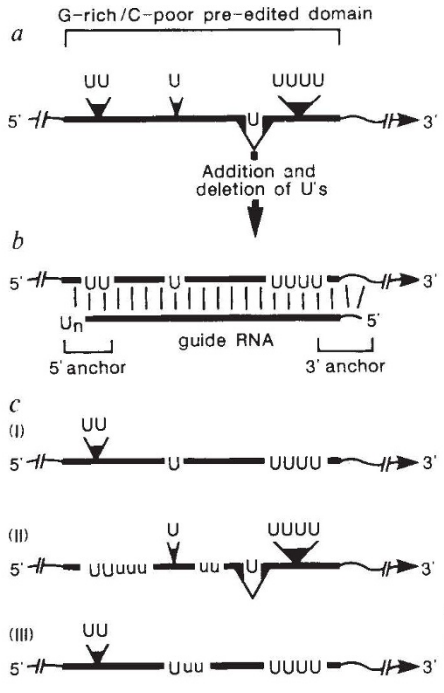
for their role in RNA editing. But the stage in the process at which they act is still not clear. Although the sequences of some partially edited transcripts suggested that the entire editing process proceeded along the mRNA in a 3′ to 5′ direction[2] (*c* in the figure), others[4,7] are hard to reconcile with such a model (*ii* and *iii* in the figure). Strikingly, these partially edited RNAs have U residues indiscriminately added to or deleted from both correct and incorrect positions only within a precisely defined editing domain[7]. These observations suggest a revised model[7] including first, recognition of the domain to be edited; second, cycles of indiscriminate additions and deletions of U residues within this domain; and third, 'zipping-up' of the guide RNA(s) with the partially edited mRNA in a 3′ to 5′ direction, with the cessation of addition and deletions of U residues only when the guide RNA is fully base-paired with the mRNA.

Whether they extend over the entire mRNA or are confined to highly localized segments, nearly all pre-edited mRNA domains have a striking strand bias of G over C nucleotides[6], although they share




RNA editing of kinetoplast mRNAs. *a*, A pre-edited transcript of a cryptogene. RNA editing adds (Us above) or deletes (U below) uridylyl residues at the positions indicated. *b*, The final correctly edited mRNA (above) whose sequence is specified by a guide RNA (below), whose 5′ sequence is complementary to a stretch of up to 16 nucleotides 3′ to the pre-edited domain (3′ anchor). A non-encoded tail of U residues on the 3′ end of the guide RNA forms a base-paired 5′ anchor with the 5′ end of the pre-edited domain. *c*, *i*, Partially edited intermediates indicating that editing progresses 3′ to 5′; *ii* and *iii*, Other partially edited RNAs containing U residues incorporated in wrong positions and numbers within the editing domain.

no other sequence similarities. Could G-richness be a basis for recognition? There may be a precedent in telomerase, the enzyme involved in nuclear chromosomal telomere synthesis. The telomeric DNA strand that serves as a primer substrate for telomerase also has a composition bias of G over C residues, and this G-rich strand is apparently recognized by telomerase on the basis of G-richness, as opposed to sequence specificity[9]. G-rich, C-poor DNA can assume folded structures stabilized by non-Watson–Crick $G_{anti}$-$G_{syn}$ base pairs, and RNA can also form such pairs[10]. Conceivably, such a folded structure could be recognized by the editing machinery.

How did cryptogenes arise? The similarity between the amino-acid sequence encoded by the final edited mRNA in a kinetoplast and the counterpart protein in other species argues for a common ancestor gene. Thus, the cryptogene seems more likely to be a derived form of the gene. In one possible scheme, the single ancestor gene, or a segment of it, was duplicated either as DNA or RNA, and one copy was transposed onto either maxicircles or minicircles to form short guide RNA genes (the inverted repeats at the ends of the guide RNA-encoding segments[6] could be relics of such transposition). An RNA form of the other gene copy became the cryptogene through the same type of deletions and additions of U residues as in modern RNA editing, except that the equilibrium was heavily weighted toward deletions rather than additions of U residues.

RNA editing remains enigmatic, evoking the impression that it is a clue to something we may somehow have missed. When the mechanism is elucidated by the use of *in vitro* systems, it will perhaps provide insights into the evolutionary origin and role of this unconventional use of the genetic material. □

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# Boris N. Veprintsev (1928–1990)

THE death, on April 11 of Boris N. Veprintsev robbed Russia of one of its true intellectuals. Professionally a zoologist and biophysicist, he was also much engaged in political activity. His life reflected much of the tragedy of modern Russia. His father Nikolay was a professional revolutionary who joined the Russian Social-Democratic Party (the Bolsheviks) in 1903. He suffered twice from repressions after the Great October Revolution and died in exile in 1941. From Nikolay, Veprintsev inherited both a hot temper and courage.

Arrested in 1951, Veprintsev suffered the devastating conditions of prison and exile together with such outstanding people as L. N. Gumilev, M. I. Kazanin and L. A Voznesensky. He was freed in 1954, and returned to Moscow University, where he had been an undergraduate, to study the biophysics of membranes, specifically those of axons of ventral nerve cords from rainworms. Later, with the biologist D. A. Sakharov, he extended his studies to the giant neurons of brain ganglia of nudibranchiates. And, at the laboratory of biophysics of the nerve cell at the Institute of Biophysics in Puschino, near Moscow — which he founded in 1963 — he initiated experiments on *in vitro* cultivation of nerve cells, studies on choline receptors, and on correlation between biochemical processes and electrical activity, function and plasticity of nerve cells.

But zoology and conservation had always ranked equal with biophysics for Veprintsev — his recordings of birdsong from Russia are well known to ornithologists. For many years, he promoted the idea of genome conservation, which originally seemed quite fantastic to many people. The idea was to maintain the frozen gametes and embryos of endangered species so that it would be possible to restore them in the future.

Presented by Veprintsev and N. N. Rott at the International Congress of the All-World Organization of Nature Conservation in Ashkhabad in 1975, the idea was supported by many scientists, Sir Peter Scott among them. Veprintsev was elected Chairman of the International Committee on the Conservation of Genetic Resources, in which position he stimulated collaboration between Soviet and foreign specialists. But it was only in 1989 that he was able to meet colleagues abroad. The new plans, hopes, energy and enthusiasm developed on these trips were broken by the severe disease that soon led to his untimely death.

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