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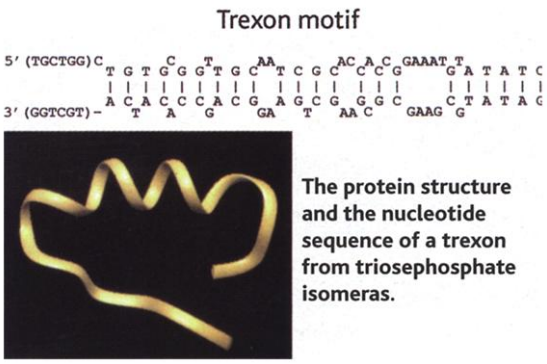
Selfish DNA and the Origin of Genes

A PALINDROMIC REPEAT OF ABOUT 150 BASE pairs was found by H. Ogata and colleagues to be inserted into many protein-coding genes of *Rickettsia conorii*, the bacterium that causes Mediterranean spotted fever (Reports, 13 Oct., p. 347). The corresponding amino acids encoded by these repeats are thought to be expressed in the mature proteins. The authors suggest that the amino acid segments in the DNA conform to a general motif—an α helix flanked by turns or loops. Finally, Ogata *et al.* propose that these *Rickettsia* palindromic elements (RPEs) represent an example of selfish DNA (DNA that has no apparent cellular function) participating directly in the creation of new protein sequences.

The findings confirm my earlier work in which I arrived at many of the same conclusions, but starting from a different perspective. Instead of examining DNA sequences, I analyzed protein sequences, specifically the amino acid sequences of proteins from multi-gene families (such as thionin and transforming growth factor–β) (*1*). These proteins appear to have evolved from smaller modules that I called duplication units, which have a characteristic structure: an α helix and a short turn or loop. There were also amino acid sequence similarities among these various segments from diverse proteins. Two of these segments, GBP-4 from galactose/glucose binding protein and neurophysin-3 (*1*), show striking similarity (nearly 50% homology) to the central conserved region described by Ogata *et al.*

I also found that the duplication unit was encoded by a short inverted repeat segment of DNA that resembled transposable genetic elements (see the figure). I termed these segments "trexons," for transposable exons. The RPEs described by Ogata *et al.* appear to be very similar to trexons. I proposed that the trexons arose from the initial building blocks of RNA and suggested that these segments represented "selfish DNA" acting at the level of the exon rather than the intron (*1*). It is rewarding to see that this work has been confirmed in convincing fashion by another group. In view of the different research approaches that led to such similar conclusions, it may be time to reconsider the idea that exons were static gene elements that gained mobility only by association with introns.

I would submit that trexons and RPEs are modern-day vestiges of the earliest phase of sequence creation in a highly mobile RNA world. Certain features of *Rickettsia* (for example, their close similarity to mitochondria and their slow-paced growth) may have helped these segments survive through evolution more or less intact. I have suggested that these mobile genetic elements encoded protein segments that were specialized for participating in protein-protein and protein-polynucleotide interactions (*1*). The RPEs from *Rickettsia* may serve similar roles and define either a protein interaction domain or a polynucleotide-binding motif.



The protein structure and the nucleotide sequence of a trexon from triosephosphate isomeras.

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Response

STRUCTURAL AND FUNCTIONAL MODULARITY of proteins is well established. Occurrences of homologous domains in otherwise different proteins suggest the recurrent use of modular units in evolution. The combinatorial advantage of modular units to design diverse proteins is obvious, but the precise relation between evolutionarily successful modules and mobile sequence units is not yet clear. The "trexon" hypothesis proposed by Dwyer (*1*) and the palindromic element (RPE) that we discovered in several *Rickettsia* species (*2*) provide an interesting al-

ternative to the "exon shuffling theory," in which the mobile element precisely coincides with the limits of existing coding exons, thus restricting the evolutionary game to some sort of "card shuffling." The finding of the RPEs suggests a greater flexibility in the evolution of genes.

First, the insertions of RPEs realize a flow of genetic material across the boundary between noncoding and protein-coding sequences. In addition, we recently noticed that one of the RPEs (rpe22 of *R. conorii*) previously annotated as "intergenic" is located within the gene coding for tmRNA (the transfer/messenger RNA molecule used to rescue stalled ribosomes and to clear the cell of incomplete polypeptides) (*3*). Thus, the RPE appears capable of parasitizing both protein and RNA structures. The generality of such an influx of genetic material from noncoding to coding sequences deserves further study.

Second, the host proteins targeted by the RPE are different among the species in the same genus. This indicates that RPE insertions occurred after the divergence of those *Rickettsia* species and that the RPE proliferation might be continuing.

Third, the insertion of the RPE at sites that code for a part of the protein that is on the surface, but not necessarily in between domains or within the constraints of exon boundaries, argues for the possibility of a significant evolution of preexisting protein domains and/or coding exons. For example, the RPE found in the DNA polymerase I of *R. helvetica* and *R. felis* is located on the surface of the exonuclease domain (*4*). Domain insertions within other domains have been described for other proteins, for example, the cat muscle pyruvate kinase, which consists of four different domains. One of the domains forming a β barrel is located within one of the loops of the other α/β barrel domain (1PKM of Protein Data Bank). The structural and functional consequences of such iterative insertions of domains within domains (a "Russian doll" evolutionary model) remain to be analyzed to better understand the flexibility of genes and genome, as well as the evolutionary modularity of genetic material.

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4. See the supplemental figure associated with our report (*2*) available at *Science* Online at www.sciencemag.org/feature/data/1051142.shl

Scientific Whaling

THE INFORMATION ABOUT THE HISTORY OF scientific whaling that R. L. Brownell Jr. and coauthors provide in their Letter is incomplete (1 Dec., p. 1696). Their comparison of the numbers of whales killed during the last decade under scientific permits to those taken under such permits in earlier times (thousands compared with hundreds, respectively) does not take into consideration that the tens of thousands of whales taken during the days of commercial whaling generally provided adequate material for whale scientists. Brownell *et al.* also mention the reported take of almost 5000 minke whales during a decade; however, this take is biologically insignificant when measured against a total population estimate of more than 700,000 minke whales for the Southern Hemisphere. The Japanese have provided the data from these scientific whaling operations on a regular and timely basis to the International Whaling Commission (IWC) and its Scientific Committee.

> "Like it or not, the Japanese scientific whaling program is operating legally."

Like it or not, the Japanese scientific whaling program is operating legally. On the other hand, it is doubtful that the Southern Ocean Sanctuary, established by the IWC in 1994, would pass scrutiny if tested in international courts (*1*). As Brownell *et al.* note, Japan voted against establishment of the sanctuary and takes its annual catch of Antarctic minke from within sanctuary boundaries. The issue of scientific whaling is neither scientific or legal. It is a cultural repugnance of some to the operations of others and has been described by an Irish delegate to the IWC as "cultural imperialism" (*2*).

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