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Ribosomal Ribonucleic Acid in Evolution

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Aspects of the structure of rRNA in eukaryotes that illustrate the extent to which different regions of the molecules have diverged in evolution will be reviewed; the independent evolution of parts of the precursors to rRNA will be discussed.

Lava-Sanchez *et al.* (1972) have shown that the base composition of rRNA, and especially the relationship of the compositions of the '18S' and '28S' components, can be correlated with the major plant and animal Phyla. Thus the changes do not seem to have been entirely random.

M. Grunstein & M. Birnstiel (unpublished work) have shown, by studying the kinetics of hybridization of heterologous rRNA to DNA, that regions of the rRNA molecules have evolved to an extent that varies with evolutionary separation of the species; however, a small region of the molecule has been conserved, even between widely different species such as *Drosophila* and mouse and *Xenopus*.

Despite the large changes in composition and in sequence, the overall structure of the ribosomal subunits seems to have been conserved: P. Cammarano, A. Felsani, M. Gentile, C. Gualerzi, A. Romeon & G. Wolf (unpublished work) have shown that hybrid 80S ribosomes, prepared from pea and mouse or rat subunits in either combination, are active in the synthesis of polyphenylalanine stimulated by poly(U).

The above results may be correlated with a previous finding (Loening, 1968) that the molecular weight of the '18S' rRNA has been conserved in all eukaryotes at 0.7×10^6 , whereas that of the '28S' rRNA increases above 1.3×10^6 only in the animals. We have since found a number of small deviations from this rule. The most striking exception, however, is that of the amoeba *Acanthamoeba* (Loening, 1968),

in which the molecular weights of the rRNA are 1.6×10^6 and 0.9×10^6 . We have now shown that the component of molecular weight 1.6×10^6 is cleaved less than 2h after synthesis into two components plus '7S' RNA, which can be detected only after unfolding the molecule in 50% formamide. The two components have molecular weights of about 0.9×10^6 and 0.7×10^6 ; thus one of them has the same molecular weight as the amoeba '18S' RNA and the other the same molecular weight as the '18S' RNA from other eukaryotes.

This may be a coincidence, but it does again raise the question whether the '28S' rRNA has evolved by duplication of the '18S' rRNA gene followed by some divergence. There are many species in which the '28S' RNA is cleaved in or near the middle. In most plants and in yeast, but not in *Xenopus*, there is considerable homology between the '18S' and '28S' rRNA species, as measured by competitive hybridization.

There is no such systematic evolution of the precursor to rRNA. The amount of excess of non-ribosomal RNA in the precursor is much greater in warm-blooded animals than in any other species, and among the latter certain parts of the precursor seem to have changed very rapidly in size. In the amoeba mentioned above the amount of excess of RNA in the precursor is also exceptionally large, so that the molecular weight of the precursor is about 3.5×10^6 , compared with about 2.5×10^6 in other plants and protozoa.

It is clear from all these results that different parts of the ribosomal genes have changed at very different rates in evolution.

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Regulation of Ribosome Synthesis

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Knowledge of the mechanisms that regulate ribosome production in eukaryotic cells is still very fragmentary and incomplete. However, a considerable number of phenomena concerned with the regulation of ribosome synthesis have been described. Although these phenomena are usually not well understood in terms of mechanism, they nevertheless provide some clues and insights into the general types of regulatory mechanisms that are operative. Moreover, it is becoming evident that some of the general principles involved in the control of ribosome biosynthesis are also applicable to the regulation of other macromolecular constituents of the cell. A brief review and analysis of some of the following phenomena will be presented.