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The Concept of Cellular Evolution

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Summary. A central evolutionary question is whether the eucaryotic cytoplasm represents a line of descent that is separate from the typical bacterial line. It is argued on the basis of differences between their respective translation mechanisms that the two lines do represent separate phylogenetic trees in the sense that each line of descent independently evolved to a level of organization that could be called procaryotic. The two lines of descent, nevertheless shared a common ancestor, that was far simpler than the procaryote. This primitive entity is called a progenote, to recognize the possibility that it had not yet completed evolving the link between genotype and phenotype. This concept changes considerably the view one takes toward cellular evolution.

Key words: Evolution – Ribosomes – Genotype-Phenotype – Cytoplasm – Endosymbiosis – Procaryote – Eucaryote – Progenote

Life on this planet began over three billion years ago (Schopf, 1972). While fossil evidence permits a reasonable reconstruction of its history over the past half billion years, it provides only the barest clues to the earlier events that led to the basic cell type (the "common ancestor") and its initial radiation into the major phylogenetic groups. However, the cell itself is an historical record, and , as the biologist is now beginning to learn, this is far more extensive than the fossil record. Through this "molecular paleontological record" it should be possible ultimately to reconstruct a good deal of early evolutionary detail (Zuckerkandl and Pauling, 1965).

While a lack of facts is certainly the major obstacle at present to an understanding of the evolution of the cell, it is clear that our present, crude understanding of this evolution is rooted in outmoded and ill-defined concepts, and so does not even cope adequately with the few facts that are available.

All speculation as to the evolution of cells starts with the assumption that procaroytes evolved first and then gave rise to eucaryotes, which in one sense must be true. The problem is that various writers do not state explicitly what *they* mean by the

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assumption. The crux of the matter seems to be a failure to define "procaryote" and "eucaroyte", terms whose meanings have changed considerably with time. Initially "procaryote-eucaryote" meant an organizational distinction. It conveyed the hierarchical nature of biological organization – i.e. metazoa comprise organs, which are formed from eucaryotic cells, which contain procaryote-like entities (e.g. chloroplasts, mitochondria), and so on. This is not basically a phylogenetic distinction. However, the extensive and detailed molecular descriptions of bacteria and of higher cells that are now given are necessarily phylogenetic. No precise formulation of the evolutionary issue is possible if the phylogenetic and organizational aspects of "procaryote" and "eucaryote" are confused.

From an organizational viewpoint it is evident not only that eucaryotic entities evolved from procaryotic ones, but also that the latter ultimately arose from a simpler, unnamed class of entities. However, this purely organizational picture of events need not lead to the conventionally accepted phylogenetic interpretation of the evolutionary sequence – in which an ancestral procaryote gives rise to a procaryotic tree, from whose branches arise certain species that symbiotically conjoin to produce the ancestral eucaryote, and so on (see Fig. 19.1 in Broda, 1975; Margulis, 1970). What this latter view takes for granted – that there existed but one ancestral procaryote and so a single procaryotic tree, but one ancestral eucaryote and so a single eucaryotic tree – is in fact a central and unanswered question.

We would here explore one of the more important facets of this question, the origin of the eucaryotic cytoplasm. The cytoplasm appears to represent the "engulfing" species in the endosymbiosis that is the eucaryotic cell. Its characteristics are sufficiently non-bacterial that some writers have expressed reservation concerning its relationship to bacteria (Stanier, 1970). Nevertheless, the free-living ancestor represented today by the cytoplasm must at some point (before the evolutionary additions of organelles and similar structures) have been a procaryote in the *organizational* sense, – i.e., it was a level simpler than an eucaryotic cell. The question is whether, this ancestor arose from the same phylogenetic tree as did typical, i.e. bacterial procaryotes. For the reasons to be given we feel the eucaryotic cytoplasm came from a line of descent that achieved procaryotic organizational status independently from the typical bacterial line. If this be true then we must revise those attitudes concerning eucaryote evolution that are based on the preconception that the cytoplasmic component arose relatively late in the evolutionary scheme from the bacterial tree, just as the organelles seem to have done.

Discussions of cellular evolution tend to take for granted the nature of the "gene". This is a serious mistake, for at least in its early evolutionary stages the nature of the cell is shaped by the nature of the linkage between genotype and phenotype. Indeed, to a large extent the evolution of the cell *is* the evolution of the genotype-phenotype relationship. Although we possess no direct knowledge as to its evolution, certain of the properties of the translation mechanism permit us reasonably to infer characteristics of its evolution. The translation apparatus is very large and complex by standards of molecular automata (Haselkorn and Rothman-Denes, 1973). There can be only one reason for this; its size is essential to the accuracy with which the mechanism functions. There exists a direct correlation between the "size" of an automaton – as measured roughly by number of components – and the accuracy of its function (Burks, 1970).