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## MULTILEVEL SYSTEM OF HEREDITY AND ITS ONTOGENETIC AND PHYLOGENETIC CONSEQUENCES

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*Based on the analysis of the history of the gene notion, hidden assumptions and weakness of one of the main prerequisites of neo-Darwinian concept of evolution -- the heredity concept -- are demonstrated. On the basis of the criticism of the atomistic gene concept the mendelian paradox is formulated. Systemic gene concept and its complement, the multilevel concept of heredity, yield the solution of this paradox on the contemporary level of knowledge. These concepts are outlined in the present paper, and their explanatory and heuristic potentials are indicated.*

Key words: atomistic gene concept, epigenetics, systemic gene notion, extended heredity notion, genetic assimilation

### INTRODUCTION

Darwinian theory of the origin of species by means of natural selection which laid the foundations to the theory of evolution (and has often been identified with it) belongs to the most vividly discussed theories in the whole science. One of the hidden assumptions underlying most of the evolutionary discussions is the question of the completeness of the explanatory basis of evolutionary phenomena, or that of the level of generality of their explanation, respectively. The point is (taking into

account only development of the theory of evolution since 1930s, i.e. since the origin of the synthetic theory of evolution or neo-Darwinism), whether it is possible to explain all phenomena related to the evolution of the organic world by means of neo-Darwinistic mechanisms, and, if so, at which level of description and generalized interpretation.

Unfortunately, most attempts to define the area of validity of the neo-Darwinistic postulates and the criticisms of the correctness of their generalization for the general theory of evolution used to be up to recent times rejected as anti-Darwinistic (often for not purely scientific reasons as, e.g., by Čižek 1981). Nevertheless, recent advances in biology show still more convincingly that the "classical" theory of evolution is able to explain only some evolutionary phenomena, especially those at the population level, i.e. in principle the so-called microevolutionary phenomena.

Already soon after the origin of the synthetic theory of evolution first problems appeared which could not be satisfactorily explained in the frame of that theory and disturbed the inner consistency and purity of its basic postulates. But it was, above all, the development of molecular biology which enabled the study of proper mechanisms of heredity, especially to those of the storage, expression and transmission of information coded in the DNA, i.e. the study of mechanisms which were till that time the subject of speculation only.

During the last years, a number of concepts have been suggested helping to surpass some narrow limits of the neo-Darwinian paradigm, e.g. that of *developmental constraints* (see, e.g., Alberch 1982, Wagner 1985), those of co-called *non-hereditary phylogenetic characters* and *phylogenetic action of environment* (Novák 1982a,b). These concepts as well as many others (see, e.g., Ho and Saunders 1984) deal with long forgotten evolutionary problems. They liberate thus the theory of evolution from the neo-Darwinian genetic determinism and enable us to shift from the study of stochastic evolutionary regularities to the search for real regularities and mechanisms underlying the stochastic ones and to enter the "black-box" of population genetics with the phenotype of parental generation as an input and phenotypes of filial generation as output.

We believe, nevertheless, that the most perspective way out from the neo-Darwinian paradigm as well as for evaluation of the significance of neo-Darwinism (i.e. definition of the level of its validity) is a revision of the heredity and gene notions.

### HEREDITY AND THE GENE CONCEPT

In a previous paper (Zemek 1983) it was shown how the originally broad but non-structured Darwin's notion of heredity as a general a priori feature of an organism as a whole was reduced to a function of a set of genes, and how were later the Mendel's concept of the hereditary determinant and Johannsen's (1909) concept of gene subsequently substantiated. Genes, originally understood as rather abstract units of characters (determinants), were later identified with certain chromosome sites and, finally, after the discovery of the role of nucleic acids with certain sequences of DNA nucleotides.

It has been clear already since the discovery of the transcription and translation mechanisms, that sequences of the DNA bases can directly determine the sequences of aminoacids in proteins only and, moreover, that they can do it only under several limited conditions or constrains (given, e.g., by ribosome structure): The old scheme *one gene - one character* still survives in generalizing theoretical papers. In cases when this scheme evidently does not agree with data genetic determinism still has a possibility to escape to the concept of polygenic determination of characters, or to that of pleiotropic gene effects. In a more cultivated form, genetic determinism uses to be substantiated by the regulative function of proteins from which it follows, that the development of certain phenotypic characters is guided by enzymes. Because these enzymes are determined by an information coded in the DNA, the questions of heredity of even complex character was believed to be solved. With some restrictions the scheme *one gene - one enzyme* is applicable to unicellular organisms in which identification of enzyme with character has some biological sense.

Leaving out of consideration original requirements on genes, i.e. that they should be units of recombination, mutation and function at

the same time (what was rejected already by Benzer 1957, 1962, and Demerec 1961), and considering genes as units of function only, we come to Ingram's (1957) scheme *one gene - one polypeptide chain*. This renews the question whether gene (defined now as a sequence of DNA bases which codes a sequence of aminoacids of one polypeptide chain) has some direct and unequivocal relation to character determination. (Note, that to consider a polypeptide chain as a character has no biological meaning). We know that many proteins which participate in ontogenetic regulations are constructed from polypeptide chains and formed into their final structural and functional form in various cell parts (frequently fairly distant from the place of their origin) or even in intercellular space (see, e.g., Berdyšev and Krivoručenko 1979).

This happens not only on the basis of their self-assembly (which is after all determined by the orderliness and physical peculiarities of individual aminoacids the place of which in primary structure of polypeptides is given by the sequence of DNA bases), but, also by certain physical and chemical properties of the given cell part, or, more generally, by a *complex of systems conditions* of the place of the finalization of functional structures of a higher order than are polypeptides, or by systems conditions of the cell, or organism as a whole, respectively. These systems conditions fulfill at the same time a role of certain constraints which determine what, when and in which amount shall be produced and thus play also certain informational role. They can play both the inductive and restrictive role and are able to change themselves (to develop) within a certain range which is given by both the conditions of their external environment and by the degree of *canalization* of epigenetic (developmental) processes or their plasticity.

Already at this stage it was clear: (1) *that DNA itself can hardly contain all the necessary information for development of characters*, (2) *that the information value of a certain sequence of DNA bases depends on the informational background of the whole cytoplasmic cell content and its external environment*, and (3) *that DNA does not bear any a priori information, but requires an information value only in a certain context given by evolution of the function of mechanisms of the DNA rep-*

*lication, transcription and translation and informational content of cytoplasm, cell structure or organism as a whole, respectively.*

However, the final smash to the proponents of strict genetic determinism and classical neo-Darwinism brought only further discoveries of the gene ultrastructure (in molecular sense). Then, in connection with the discovery of RNA processing and splicing in archebacteria and eucaryotes, the question "why genes in pieces" (Gilbert 1978, 1979) arose.

Moreover, transcription units (genes) are overlapping (see, e.g., Kolata 1977), i.e. certain sections of DNA transcript (exons) can be build into various mRNAs. All these data as well as those indicating the possibility of different modes of "reading of the same codon (cf., e.g., Barrell et al. 1980), and data indicating the evolutionary antiquity of splicing mechanisms (Fox 1981, Mahler et al. 1981, etc.) justify and specify the conclusions made above.

### THE MENDELIAN PARADOX

Recognizing on the grounds discussed above that we are not able to detect at the level of basic substrate of the transmission of hereditary information, any continuous sequence of DNA bases which in the full sense of the word could serve as a code for an elementary functional unit, i.e. any gene, the following questions arise:

- (1) How is it possible to explain the Darwinian "power of heredity"?
- (2) Which structures carry hereditary information and are organized in such a way that the phenomenological description (and what else is the statistical processing of hybridization experiments) induces ideas about atomic heredity units?
- (3) How the stochastic variability is generated?

One of the possible solutions of this problem is to return to the original, broad and general Johannsen's (1909) gene concept, in which the term gene is used only as designation of any material substrate responsible for the transmission and development of (phenotypic) characters (cf. Zemek 1983). Concretization of this abstract concept is the

Dubin'in's *systemic gene concept* (see Berdyšev et al. 1980). Here, the gene includes all structures and processes which are responsible for the reproduction of characters in filial generations, i.e. from the DNA level to the environmental determinants. This concept assumes a priori the canalization of epigenetic pathways shaping the character. The Mendelian paradox can be solved only by such a gene concept. However, the characters are not determined by some atomic genes laying on chromosomes, and splitting or combination of characters is not adjusted by any such gene, but by the stability of the epigenetic (developmental) pathways selected and perfected during the course of all the previous evolution of given organism. On this basis most of the phenomenological and descriptive rules of the Mendelian and population genetics require a new and more precise meaning. It is, however, necessary to note, that the Dubin'in's gene concept confuses developmental constraints, which are the basic condition for self-organization, and the inner information coded in DNA or in other informational structures of the organism actually necessary for character transmission.

For these reasons we believe that the only way how to answer these questions is to recognize more than one level of heredity. Such a concept was anticipated by Beljaev (1981) and is complementary to the Dubin'in's systemic gene concept. Beljaev distinguishes *vertical heredity* and *horizontal heredity*. As the vertical heredity he considers the information transmission by means of the DNA replication, while as the horizontal heredity he considers all other means of information transmission, i.e. cytoplasmic heredity (or, more precisely, cell epigenetics), epigenetics of multicellular organisms, and social heredity.

#### THE EXTENDED HEREDITY NOTION: AN OUTLINE

From the general point of view it is possible to say that there are many substrates which, due to the properties of their material structure, can be used for modulation of informational signals, for informational storage and transmission. General logic of the development of many informational structures (organs which take part in informational processes) of living organisms shows that *their evolution starts*

from the structures with originally quite different functions. The usual potential polyfunctionality of most structures makes their use possible, besides their structural and physiological function, also for informational functions. We demonstrated (Socha and Zemek 1978) that *selection acts not only in the sense of perfection of the original vital function but also of a new informational one* - in many cases without disturbing the original function. From the macroscopic point of view the informational function is often masked by the original one. This is also the reason why only structures specialized for information processing (e.g. DNA, or, in some cases, the egg structure) were taken into consideration and studied in connection with the heredity problem.

#### *Molecular level of heredity*

Starting from this presumption and conclusions achieved in the paragraph on the heredity and gene concept in this paper, we may conclude that, generally speaking, there is no need to transcribe all the information (program) necessary for morphogenesis on the DNA, but only that which is necessary for the synthesis of polypeptide chains, which are the basic building elements of the living matter. Only from the point of view of the ensurance of the identical reproduction of these elements it is possible to consider the DNA as the basic carrier of hereditary information, or as a fundamental channel of heredity.

#### *Cellular level of heredity*

Recognizing that the DNA is the basic channel of heredity, we may come to the next higher one, which is that based on the cell epigenetics. It is surprizing that none of the proponents of the genetic determinism recognized the fact that not only DNA, but also a certain part of cytoplasm is transferred from the parental to the filial generation. The whole structure of this cytoplasm (not only certain cytoplasmic elements as, e.g., plastids) fulfils informational function. The main function of this cell channel of heredity is the *reproduction of starting conditions* for the DNA reading and of signals for the cell morphogenesis. This channel functions not only in unicellular organisms, but enters, in a

modified form as a block also in the morphogenesis and reproduction of multicellular organisms, because the starting point of the development of most multicellular organisms is one cell - zygote - respectively.

### *Somatic level of heredity*

We may observe, that in the course of evolution, the information content of gametes increases. In the case of anisogamy especially the egg cell structure acquires in addition to its nutritional function, due usually to ordering of egg substances into gradients, informational importance for morphogenesis. Finally also egg structure evolved which had mainly the informational function - cortex. The formation of the egg structure is importantly influenced by the properties of the egg-producing tissue so that changes of these properties during the life of an organism can manifest themselves in the changes of properties of the egg cell structure. By this a possibility for the existence another channel of hereditary transmission originates (see also Socha and Zemek 1982). In such a way the *whole structure of the multicellular organisms requires the general informational function*. During the evolution the changes in the soma of these organisms can reflect themselves into material composition and orderliness of the egg structure. Such changes of cytoplasm become also the subject of the selection if the results of their action modify the course of morphogenesis in direction of higher adaptation of the organism as a whole. In such a way also morphogenetic signals, such as external environment can be substituted by new inner ones. This idea of a *substitution* of one morphogenetic signal by another one (Zemek and Socha 1982), the basis of which may be different material substrates with analogical morphogenetic effect, is based on the Waddington's (1953, 1957) concept of genetic *assimilation*. During evolution of viviparity the informational importance of the whole maternal organism increases.

### *Behavioral level of heredity*

If we take into account, that behavior is not only an independent meta-structure above morphology and physiology (see, e.g., Leonovič 1982, Zemek and Mlíkovský in press), but acts also morphogenetically during



ontogeny (cf., e.g., Leonovič 1985), a new channel of heredity appears. In addition to the information for the modification of epigenetic pathways and for maintenance of those which were selected during evolution as more convenient for realization of behavioral adaptation, this channel bears also information on behavioral patterns as such. In this way behavior becomes the ruling factor of adaptation and, at the same time, a channel of hereditary transmission with more grades of freedom than have the lower ones (cf. Mlíkovský 1982, in press).

A special type of behavior is the *social behavior*, on the basis of which so far the last level of heredity, the *social heredity* (sensu Dubinin 1972) originated. Discerning behavior as a specific level of heredity has been indicated in another context also by Plotkin and Odling-Smee (1981), Strzałko and Henneberg (1982), and Odling-Smee (1983).

## CONCLUSIONS

To escape difficulties of description and explanation of many evolutionary phenomena, which arose in the frame of the neo-Darwinian paradigm, the necessity originated to liberate the abstract atomistic gene concept and to leave out the strict genetic determinism with its so-called "central genetic dogma". Systemic gene concept and its complement, the concept of multilevel heredity, give us the possibility to escape the consequences of the neo-Darwinian concept of evolution without destroying the "heredity power", which is necessary for the Darwinian concept of heredity.

This concept of multilevel heredity gives a more real basis for explanation of the laws of heredity and of the relations between the heredity and variability. Systemic gene concept maintains the general features of classical atomistic gene, but its own properties are not given by the properties of only one material substrate (carrier), but by the stability of epigenetic processes. Thus, systemic gene is a projection through a whole canalized epigenetic pathway, i.e. through all the levels of heredity. The multilevel system of heredity explains the origin and changes (mutations) of such genes.

Each structure, which can store information, can produce (in connection with the properties of its material composition) its own variability. This is true from the DNA level to the levels of behavioral and social heredity. These modifications are the subject of natural selection. The perfection of the given character by means of natural selection can proceed on the basis of modifications at one level only, or it can be correlated with modifications at other levels. Variability at the first three levels of heredity can serve also as a material for substitution of morphogenetic signals of the higher level by morphogenetic factors of the lower ones (e.g., external temperature → inner pH → new order of egg gradients → enzyme or hormone). It is the basis for the so-called genetic assimilation.

Regardless of the level of heredity at which a new modification originates, its fixation can proceed from either higher levels to the lower ones, or vice versa. Mutations at the DNA level can reflect themselves at one or more higher levels and, on the other hand, the changes at the behavioral level can reflect themselves at the lower ones, e.g., through the fixation of one epigenetic pathway from the set of possible ones on the basis of various expression of information stored at the DNA level. In such a way, changes at lower levels build the basis for changes of characters (or origin of new ones) at higher levels, and vice versa. The interrelations between the basic heredity levels are summarized in figure 1.

The origin of new levels of organization of organisms and of new levels of information processing gives always rise to a new set of evolutionary mechanisms. Thus, the concept of multilevel heredity is also in concordance with the modern approach to evolution, which may be characterized as an *evolution of the mechanisms of evolution* (Šmal'gauzen 1968), or as *evolution of evolution* (Zavadskij and Kolčinskij 1973). These concepts show the narrow limits of the uniformitarianistic doctrine.

Admittably, the concept of multilevel heredity outlined in the present paper is based rather on logical and heuristic consequences of

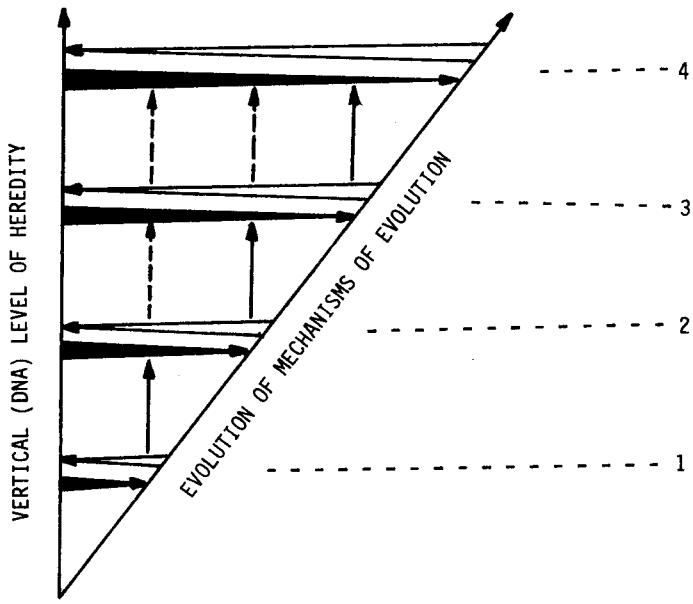


Fig. 1. Scheme of the main levels of heredity and their interrelations. 1 = cellular level of heredity at which the vertical (DNA) directly interacts with this first horizontal one (by means of cell epigenetics); 2 = somatic heredity level (epigenetics of multicellular organism); 3 = heredity of behavioral patterns; 4 = social heredity.

both neo-Darwinian paradigm and of molecular biology than on detailed investigations of empiric material. We believe that future investigations will confirm the general validity of our approach and facilitate further detailization of the main levels of heredity.

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