

HEREDITY OF BEHAVIOR IN THE CONTEXT OF THE CURRENT EVOLUTIONARY SYNTHESIS:

1. GENERAL PREREQUISITES

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ABSTRACT - A brief review of the development of the heredity notion is presented and the impossibility of reduction of heredity to the genetic channel of information transmission only is indicated. A behavioral channel of information transmission is discussed in this respect, and its relative autonomy and interactions with other channels of heredity are evaluated.

KEY WORDS: Neo-Darwinism, Mendelian Paradox, Multilevel Heredity, Heredity of Behavior

INTRODUCTION

Analyzing the history of evolutionary biology we can see that it beared, since 1930s up to late 1970s, all characters of the normal science sensu Kuhn (1972). This period of its development, known as the paradigm of neo-Darwinism, or the synthetic theory of evolution, began to be disturbed during late 1970s, when not only its critics, but also some of the more sophisticated neo-Darwinists started to point out the necessity to surpass the relatively very narrow limits of this evolutionary paradigm (see, e.g., Mayr 1982a,b).

GENERAL FOUNDATIONS

The intellectual background of every paradigm seems always to be originally broader than the proper paradigm which develops on its basis. Why is this so? Every hypothesis or theory which builds a basis of a paradigm needs to be proved, may it be by philosophical, logical, experimental, or other means. The respective efforts of founders of every theory are thus necessarily oriented towards proving those key points of the given theory which could

be approached by means of current sciences. In the framework of the respective research program these means turn soon to goals, and only the approached key points and their methodological basis start to be considered as the basis for the developing paradigm, while other aspects and problems of the broader background of the respective theory go rapidly forgotten (Kedrov 1978). In the following period of normal science it is then largely abstracted from these forgotten aspects and problems and those of them which are not explainable in the frame of the given paradigm are often declared to be non-scientific.

In view of the general analysis presented above, it appears that the neo-Darwinian "new synthesis" of 1930s has not been a synthesis in full sense of this word, but more likely a "synthesis" between an abridged concept of heredity and abridged Darwin's concept of speciation by means of natural selection.

FROM DARWINIAN EVOLUTION TO MENDELIAN GENETICS

Due to the paradigm ruling in the then biology, the three basic questions for Darwin and his contemporaries were whether a final number of species exists or not, whether species are God-created and whether these species are immutable, or not. In response to this situation, Darwin (1859) named his fundamental book "On the origin of species", although he later repeatedly pointed out that the species problem is of minor or even of no importance for him, and although he had a rather confused conception of species (Kottler 1978, Sulloway 1979). The success of the Darwinian evolutionism consisted, however, in that Darwin proposed the first known mechanism of evolution -- the natural selection (see Limoges 1970, Mayr 1972, Eldredge 1977, Ruse 1979, Brower 1984).

As indicated by Jenkin's (1867) comments on the Darwin's concept of accumulation of favourable deviations by means of natural selection, the weakest point in Darwin's theory was his broad and confused concept of heredity. Darwin's (1868) theory of pangenesis aimed at explaining heredity failed to do so, especially due to Darwin's too diffuse and quantitativistic (though not Lamarckian, as often suggested) concept of the relation between somatic mutations and changes in reproductive organs. In short, Darwin was not able to solve the question why certain deviations are accumulated by natural selection and not dissolved in the process of reproduction.

A possible solution of this problem was suggested by the Mendelian genetics. Mendel (1866) deduced from his experiments with plant cultivars that an atomic determinant for each character should exist in the zygote. Johannsen (1909) formalized and elaborated this concept and designed Mendel's character determinants as genes. Parallely, "characters" were ontologized (cf. Mlíkovský et al. 1985), and so were the genes (as discrete atomic units placed on chromosomes), too. On the other hand, before Mendel's ideas were rediscovered in 1900, Weissmann (1885) developed his concept of germ lines. Mendel's and Weissmann's ideas were later combined in the classical (Mendelian) genetics, without taking into account that the relative isolation of germ lines is more likely a product of evolution than its genetic prerequisite (Socha and Zemek 1982).

FROM MENDELIAN GENETICS TO NEO-DARWINISM

After the constitution and rapid acceptance of genetics, the situation of evolutionary biology in 1910s/1920s was as follows: the problem of heredity seemed to be solved, but the then genetics seemed to be contradictive to the Darwinian theory of natural selection. Hence, a problem arose: if Darwinism is correct, genetics has to be adjusted with the theory of natural selection.

This problem and, thus, Jenkin's paradox too, were for the first time solved in the genetic theory of natural selection developed in 1920s/1930s by R.A. Fisher, S.S. Četverikov and others (see, e.g., Provine 1971). This theory showed at a phenomenological level how an accumulation (not dissolution) of mutations is possible in natural populations. Nevertheless, it encompassed two fundamental shortcomings:

(1) it reduced the heredity problem to genetics and, followingly, the whole evolution process to genetic level, and

(2) accepted only the one-way information flow from the genotype to the phenotype, not vice versa.

By this, the genetic theory of evolution degraded the role of environment to an unstructured modificatory agent of hereditary (i.e. genetic) information. Hence, neo-Darwinism reduced heredity to only one, undifferentiated, level (the genetic one), and the environment to a rather abstract medium of evolution.

FROM NEO-DARWINISM TO THE FORMULATION OF THE MENDELIAN PARADOX

The success of neo-Darwinism in solving many evolutionary problems posed to biologists in the first half of the 20th century had an unhappy side-effect: it caused that many fruitful ideas of evolutionists produced before neo-Darwinism was constituted were forgotten and had to be later re-discovered. In the context of the present paper, the most important of them was the idea on assimilation of acquired characters developed by Waddington (1957) and anticipated already by Darwin (1868) in his theory of pangenesis and later by Baldwin (1896).

This idea includes two important implicate assumptions:

- (1) that more levels of hereditary information transmission exist than the sole one assumed to exist by classical neo-Darwinists, and
- (2) that these levels are interconnected in some way.

These ideas of Waddington and his predecessors could not be, despite of all the efforts by epigenetists, fully understood until recent achievements in molecular genetics disturbed the classical gene notion (see Zemek 1983) and enabled the formulation of the so-called Mendelian paradox (Zemek et al. 1985). The essence of this paradox lays in two contradictory findings: On the one hand, we know that heredity (in the sense of Mendelian genetics) does exist at a phenomenological level, as is well evidenced by hybridization experiments, while, on the other hand, at the DNA level, which should contain the units of heredity, no such units ("genes") were found which could be identified with character determinants expected to be present there by classical neo-Darwinists (see Zemek 1983, Zemek et al. 1985).

Possible solutions of this paradox are indicated on the one hand especially in the Dubinin's concept of the systemic gene (see Berdyšev et al. 1980) and, on the other hand, in Beljaev's (1981) concept of vertical and horizontal channels of heredity. We regard both these concepts as complementary to one another and included them into the concept of multilevel heredity developed by us (Zemek et al. 1985). For a schematic representation see Figure 1. Also several other authors came in last years to similar conclusions (e.g., Plotkin and Odling-Smee 1981, Odling-Smee 1983, Nečas 1985). This approach makes it possible to bring into context and explain various older and modern concepts in evolutionary biology, such as the relation between genetics and epigenetics, concepts of selfassembly and of developmental constraints (see, e.g., Bonner 1982, Mlíkovský and Novák 1985), and especially the above mentioned Waddington's (1957) concept of

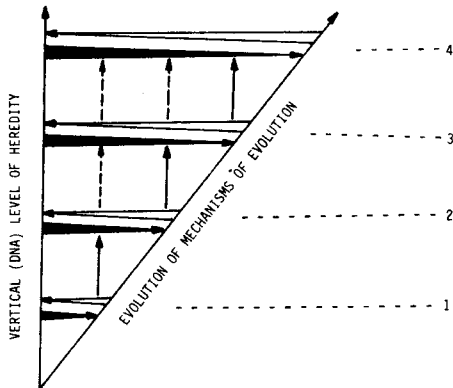


Fig. 1. Scheme of the main levels of heredity and their interrelations. 1 = cellular level of heredity at which the vertical (DNA) heredity directly interacts with this first horizontal one (by means of cell epigenetics); 2 = somatic heredity level (epigenetics of multicellular organisms); 3 = heredity of behavioral patterns; 4 = social heredity (after Zemek et al. 1985).

genetic assimilation. Moreover, it makes possible to come back at a new level to a broad heredity notion (see Zemek et al. 1985).

MENDELIAN PARADOX, THE EXTENDED HEREDITY NOTION, AND THE HEREDITY OF BEHAVIOR

Since the cell organization originated, not only information for the polypeptide synthesis beared by DNA (which constitutes one channel of heredity), but also starting systemic (epigenetic) conditions for the control of the DNA reading (which constitute another channel of heredity) were transmitted between generations. Both these channels for information transmission enter into the evolution (and ontogeny) of multicellular organisms as a complex unit. In the course of evolution the information importance of the whole parental organism for the control of gametogenesis and, in the case of viviparity, also for embryogenesis, or even for the morphogenesis as such, continually increases.

One of the prerequisites most important for the development of the information function of cell structures is the substitution of morphogenetic factors (signals) of the external environment by internal factors (Zemek

and Socha 1982). A new channel of information transmission between generations -- the channel of behavioral heredity develops in organisms which are capable of learning at the CNS level. In organisms with developed social life habits also social channel (*sensu stricto*) of information transmission develops.

At each higher level of heredity, not only mutations occurring at lower level can express themselves, but each heredity level can, since the moment of its constitution, produce also its own types of mutations. In addition, each higher heredity level limits the variability of processes running at lower heredity levels, what leads to their canalization and regulates thus also the mutation process at those lower levels.

Behavior seems evidently to be not only a metastructure above and independent of morphology and physiology (see, e.g., Severcov 1922, Leonovič 1982, 1985b), but appears also to act morphogenetically during ontogeny (cf., e.g., Leonovič 1985a). Behavior can thus contribute to the integration of the animal body (cf. Šmal'gauzen 1938, Medawar 1957, and others).

In addition, just like at other levels of heredity, changes (mutations) can appear also at behavioral level, where they are usually called discoveries. They may, but need not, influence changes at other heredity levels (see Mlíkovský and Zemek 1986). Moreover, behavioral mutations can spread through populations (cf. Mlíkovský 1986) and behave thus quite analogously to mutations at other levels of heredity.

It seems then to be evident that the problem of behavior determination cannot be studied on the basis of a dichotomous distinction between hereditary and non-hereditary behavior, or behavior components, respectively. Some aspects of this problem are treated in more detail elsewhere (Mlíkovský and Zemek 1986).

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