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TWO CRUCIAL APPROACHES IN CONTEMPORARY DEVELOPMENTAL AND EVOLUTIONARY GENETICS

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ABSTRACT

Relationships among genes, not individual alleles, are basic units of developmental information, targets of inheritance and selection. The smallest functional combination of an allele is the ratio with other alleles in a polygenic system, and amount of homo- and heterozygous relationships could determine especially the development of quantitative characters, as well as their adaptive response to natural selection, without changing the basic structure of a population.

During last century biologists, and especially population geneticists, paid their full attention to the studies of individual *variability* in natural and laboratory conditions, answering the questions about its amounts, causes and significance. The explanations why and how individuals within a species are so much alike to each other, i.e. what are the origins of these *adaptive similarities*, had been in a good part neglected.

INTRODUCTION

When describing the reduction of huge numbers of individuals of many species of animals (e.g. insects and rodents) after exposure to sharp conditions of 'winters' (so called "bottle neck effects"), we still have an unsatisfactory explanation how these survived populations, with ostensibly reduced sizes, are capable, already in early months of the 'spring', to demonstrate a re-constitution and repeatable increase of their genetic polymorphism, giving rise to the basis for a further flourishing of their structures in coming optimal conditions. Since the frequency of alleles is being used as the basis of population- genetic variability, sharp selection during 'winters' may produce, e.g. in a two-locus system, only a survival of extreme *aabb* or *AABB* genotypes. Without new mutations, they may hardly constitute and re-new the variability of 'spring' populations, especially not in one or two generations.. This, however, happens, with observed ratios of corresponding genotypes reminding to theoretical expectation for 'two loci traits', and with further population balances established already in following generations.

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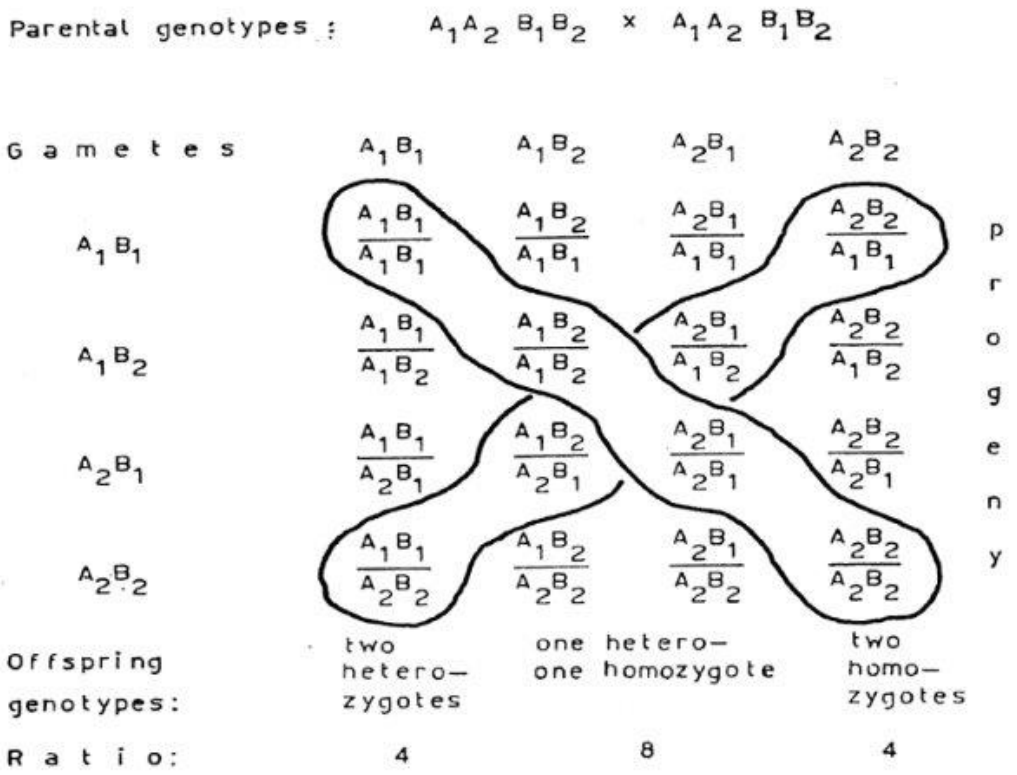
- The crucial difference is that the basic target of natural selection mustn't be a determined allelogene, but *its smallest functional combination,* which on the basis of homo- or heterozygous relationships could be the ratio with other alleles at corresponding loci from an adequate polygenic system. Variable classes with different degrees of homo- and heterozygosity (that may determine different phenotypic expressivities) contain an equal number of used alleles with 'additive effects' (*aaBBcC = a ABbCc*, etc), so that any class that survive under specific pressures of natural selection may have approximately equal 'allelic' variation, that generates further quick establishment of population polymorphisms and adaptation (see, also, Marinkovic 1977; Petanovic and Marinkovic 1978; Zivotovski 1984; Cluster et al. 1988; Phillips 1998).As shown in Figure 1, the survival based on additive effects of the numbers of homo- and heterozygous *combinations (from aaBBcc or AAbbcc to AaBbcC or aAbBCc)* gives equally good distribution as predicted in Nilson-Ehle theory for quantitative traits controlled by alleles with cumulative effects (1:2:1; 1:4:6:4:1; etc).. However, additive effect of no's of homo- or heterozygous *combinations* provides a similar

distribution of available alleles enabling that survival of anyone of the classes prevents the loss of allelic and genetic variability, and guaranties the perspective of a recovery of population-genetic variation in following generations. This is a necessary and additional alternative to the classical explanation of genetic control of developments of quantitative traits (based on additive effects of individual alleles), applied so far for more than a century in population and quantitative genetics (Nilson-Ehle 1909; Emerson and East 1913, etc.).

- With all respects to Johan Gregor Mendel and his followers classical geneticists, the offspring in any species of organisms is not produced on the basis of random (i. e. free) meiotic combinations of parental chromosomes and their alleles.

There is a very restricted number of developmental programs, determined by specific combinations of chromosomal allelogenes, that are realized and exposed to gametic- and ontogenesis selection, giving rise to highly adaptive individuals, and not to a great majority of other programs that did not pass the life-cycle selections. Such basic and positively selected in meiotic divisions *functional combinations of allelogenes* are becoming the real units of inheritance, as well as later the basic targets of Darwinian selection, with GAMETES, and their highly selected genomes, as INITIALS OF NEW GENERATIONS. To understand better developmental processes and gene-enzyme relationships we used *Drosophila model,* studying for decades the variation of some of crucial metabolic pathways (e.g., Cluster et al. 1988; Kovac and Marinkovic 1999), with a tendency to achieve individual variation of ca. 1 mg weight semi-wild flies, using starch-gel electrophoresis.

Figure 1 The progeny of the cross $A_1A_2B_1B_2 \times A_1A_2B_1B_2$, grouped according to the number of homozygous and heterozygous combinations at two loci in different chromosomes.



2 pairs of alleles		*3 pairs of alleles*	
2 homo at both loci	1/4	3 homo : 0 hetero	1/8
1 homo : 1 hetero	2/4	2 „ : 1 „	3/8
2 hetero at both loci	1/4	1 „ : 2 „	3/8
		0 „ : 3 „	1/8

4 pairs of alleles		*5 pairs of alleles*		*6 pairs of alleles*	
4 homo : 0 hetero	1/16	5 homo : 0 hetero	1/32	6 homo : 0 hetero	1/64
3 „ : 1 „	4/16	4 „ : 1 „	5/32	5 „ : 1 „	6/64
2 „ : 2 „	6/16	3 „ : 2 „	10/32	4 „ : 2 „	15/64
1 „ : 3 „	4/16	2 „ : 3 „	10/32	3 „ : 3 „	20/64
0 „ : 4 „	1/16	1 „ : 4 „	5/32	2 „ : 4 „	15/64
		0 „ : 5 „	1/32	1 „ : 5 „	6/64
				0 „ : 6 „	1/64

Table 1. Twenty four out of 72 possible 3rd-chromosomal types for five allozyme markers, in gametes giving 400 Drosophila melanogaster individuals, with a probable order of their evolutionary origin (1=100; 96=mut.allele,etc.)

Probable evolut. origin	Sod 3-24.6	3rd-chromos. gametic types Pgm 3-43.4	Est-C 3-47.7	Odh 3-49.2	Acph 3-101.1	Estimated freq.in 400 ind.
I.	1	1	1	1	1	447
II.	1	1	103mut	1	1	163
III.	1	96mut	1	1	1	64
IV.	1	1	1	98mut	1	28
V.	90mut	1	1	1	1	16
VI.	1	96rec	103	1	1	12
VII.	90rec	1	103	1	1	10
VIII.	1	1	103rec	98	1	9
IX.	1	103mut	1	1	1	6
X.	1	103rec	103	1	1	2.5
XI.	1	96rec	1	98	1	3
XII.	90rec	96	1	1	1	1
XIII.	90	1	1rec	98	1	0.5
XIV.	90rec	96rec	103	1	1	0.5
XV.	1	1	1	1	97mut	9
XVI.	1	1	103	1rec	97	5
XVII.	1	96rec	103	1rec	97	8
XVIII.	1	96	1	1rec	97	0.5
XIX.	90	1	1	1rec	97	0.25
XX.	90	1rec	103	1rec	97	0.25
XXI.	1	1	1	1	94mut	9
XXII.	1	1	103	1rec	94	4.5
XXIII.	90	1	1	1rec	94	0.5
XXIV.	1	1	103rec	98rec	94	0.5

In a detailed analysis of gene-enzyme variation in nine polymorphic loci at three chromosomes of 400 *Drosophila melanogaster* individuals, which control phosphor-sugar metabolic cycle , Marinkovic (1999, 2002) found that the proportion of realized combinations of available alleles in 800 3rd and 2nd chromosomes was smaller than 0.2% when entering their gametes! Namely, out of 78.000 possible combinations of observed alleles, only 160 variants have been detected. Despite of a minor theoretical chance that two individuals may have the same genotype at 9 loci (< 1/30.000!), we found such genotypes repeated 2-22 times in 78 variants, 82 being unique in that many out of 400 ind/s. This means that no more than 1 pro mile of possible combinations of observed chromosomal markers could be present in spermatozoa of adult males of Drosophila, before these gametes enter a competition to produce viable zygotes. During gamete competition a further reduction of variability occurs (to <1%), which is relatively modest at the levels of egg-to-adult survivals.

Final reduction to adaptive geno- and phenotypes gives rise to individuals that are impressively similar to each other within a species, which diversity is based mostly on *combinative traits* as basic targets of environmental selection. Table 1 presents 24 out of 72 possible third-chromosomal types of five allozyme markers in 800 gametes giving 400 *D. melanogaster* individuals, with the probable order of their evolutionary origin (Marinkovic 2002). It can be seen that there is a gradual increase of rare alleles in genotypes which are less repeated, or unique, in contrast to those with higher fitness, showing that optimal homozygosity in frequent genotypes is balanced in natural populations by the greater heterogeneity of rare variants.

Both of these qualities must be treated together as important components of fitness, establishing a balanced relationship between the frequency of their representatives and the amount of their polymorphism. The higher their frequency, the lower is their allelic polymorphism (and vice versa), which is the main adaptive strategy for maintaining co-adaptive gene-enzyme systems. Evolutionary auto-synthesis of structural and functional living systems determines the direction and the destiny of existing developmental programs for an organism species (see, also, Crkvenjakov and Drmanac 2007), with a parallel activity of natural selection that contributes to a survival of programs with the highest adaptive properties. From our Table 1 it can be seen that the basic ancestral structures are stable and conservative, with a prevalence of monomorphic loci in great majority of their genes, contributing to a narrow variability of individuals as the carriers of these structures, and similarities (e.g.) of their metabolic systems. The new mutations and variants of allelic combinations are gradually incorporated, but only if they in the same time contribute to an increase of adaptive complexity, and maintain the harmony of an observed system. As a result, these systems should become a bit more versatile, efficient, and more stable than before, which increases their chance for survival in their adaptive environments. The fact that the biggest part of ontogenetic and polymorphic adaptive variation is *based on combined properties* of a relatively restricted numbers of allelic variants, gives us an information that a scope of such differences in populations with a few hundreds and with a few thousands individuals is not ostensibly different, enabling a fast recovery of the structures seemingly lost after bottle-neck situations. Understanding the origins of *biological variation* together with the nature of

fascinating similarities of individuals and populations of a species, becomes now a necessity, within the scopes of the studies of contemporary developmental and evolutionary genetics.

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Experimental part of this study, including starch-gel electrophoresis analysis of 9 polymorphic gene-enzyme systems in fruit-fly males weighted less than 1 mg, has been proceeded in Laboratory of Prof. F. J. Ayala at the Californian University in Davis. Figure 1 Possible differential selection affecting allelic combinations in a two-locus model of determination of a quantitative trait. Table 1 Twenty four out of 72 possible third-chromosomal types for five allozyme markers, in gametes giving 400 *D. melanogaster* individuals, with a probable order of their evolutionary origin.

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