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Nikolai Vladimirovich Timofeeff-Ressovsky: A Biologist's Outlook

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The world outlook of a scientist who greatly contributed to the development of a certain scientific field during his long life is an extremely complex phenomenon. There is no doubt that it is based on the scientist's character, primarily his mental capacity (largely determined genetically) for comprehensive understanding and profound analysis. Against this background, an important role is obviously played by the "environment" of the scientist's childhood and youth, his education, research experience, milieu, and the diversity and significance of personalities surrounding him, including not only specialists in related fields and scientists in general (Dobzhansky, 1976; Lewontin, 1982).

Thirty years ago, Vorontsov and Yablokov (1970) commemorated N.V. Timofeeff-Ressovsky's 70th anniversary by publishing an article devoted to his life and work. This was the first such article in Soviet scientific literature, and Timofeeff-Ressovsky's students and colleagues argued about it, accepting or rejevting certain conclusions. They also asked Timofeeff-Ressovsky's opinion about his career as a biologist. He noted that his work in science developed "remarkably logically," emphasizing that his interest in certain problems was determined by the natural hierarchy of the levels of life organization and life studies. Note that Timofeeff-Ressovsky actively discussed the levels at which life is *studied*; the fact that the discussion actually concerned the objectively existing levels of life *organization* logically followed from his words. According to A.N. Tyuryukanov, Timofeeff-Ressovsky mentioned that he had "passed through the levels." Indications that the concept of these levels played an important role in Timofeeff-Ressovsky's work are also found in his memoirs (Timofeeff-Ressovsky, 1995).

Let us consider Timofeeff-Ressovsky's scientific work from this standpoint. Historically, Russian biologists, who had recently learned Mendelian genetics after the rediscovery of Mendel's laws in the early 20th century (for example, see the fundamental book by Bogdanov, 1914), became isolated from the international scientific community because of World War I and the October Revolution, followed by the civil war in Russia. Meanwhile, genetic research in foreign centers progressed rapidly. By the beginning of World War I, T.H. Morgan and his talented coworkers, C.B. Bridges, A.H. Sturtevant, and H.J. Müller, had formulated the chromosome theory of heredity, including the concept of crossing over (its key component). In the early 1920s, this was a well-substantiated and generally accepted theory, and *Drosophila* became a classical object of genetic research. Although Russian biologists had some information about these developments, they were astonished when H.J. Müller visited Soviet Russia in 1922 and brought *Drosophila* cultures. Biologists who worked in Moscow together with N.K. Kol'tsov and S.S. Chetverikov realized how greatly foreign geneticists had progressed in their research. Timofeeff-Ressovsky and other scientists of this team (B.L. Astaurov, S.M. Gershenzon, P.F. Rokitskii, and others) recalled that they all faced the problem of what to do in this situation. The results obtained abroad obviously required detailed analysis, but the scientists had to decide on the approach to their own studies, as catching up with foreign specialists by following the same route was apparently inexpedient. Discussions resulted in choosing an original approach based on traditions of the Russian natural science of the 19th century. The main directions of Timofeeff-Ressovsky's studies (in both genetics and biology in general) corresponded to this program and reflected his adherence to the concept of the levels of life organization and analysis.

(1) *Cell level.* Once it became clear that the discrete units of heredity (genes) actually exist and are located in the cell nucleus, in chromosomes, the question arose as to what the gene is. A possible way to answer this was to expose genes to the effects of various external factors inducing mutations. In the early 1920s, D.D. Romashov and Timofeeff-Ressovsky made such an attempt using ionizing radiation (Timofeeff-Ressovsky *et al.*, 1966). However, these experiments failed, because the scientists used *Drosophila funebris* flies from natural populations with a very high background mutation level and had no precise methods for reliably detecting new mutations, such as that proposed by Müller for *D. melanogaster* in 1927 (Müller, 1927). They decided to suspend this research, as some essential component was lacking. In this context, the methodological aspect is important. Timofeeff-Ressovsky had never been interested in studying "the effect of something upon something," regarding such an approach as unscientific. He thought and acted in a different way, using various factors as tools for revealing the structure of the object studied.

As soon as Müller proposed his ClB method, Timofeeff-Ressovsky formulated and implemented an original program of radiation-genetic research. Its main results are summarized in the famous "green notebook" (or "green pamphlet"), a large paper written together with the physicists K.G. Zimmer and M. Delbruck (Timofeeff-Ressovsky *et al.*, 1935),[1] and the monograph by Timofeeff-Ressovsky and Zimmer (1947). Thus, considerable progress in understanding the structure of a gene was made: it was found that the gene is a macromolecule, and its size was estimated. This is the reason why Timofeeff-Ressovsky is among the founders of modern molecular genetics. From the standpoint of present-day molecular genetics and genetic engineering, the results obtained by his research team may be regarded as an important event in the history of studies on gene structure. Moreover, there is another aspect, which has not yet been fully understood: this cycle of studies is a rare case when the approach typical of theoretical physics was used in biological research.

(2) *Ontogenetic level.* When Mendel's laws were rediscovered, specialists began to distinguish between genes themselves and the results of their action, i.e., specific traits. Hence, questions arose concerning the way from a gene to a trait at the organism level, i.e., the factors affecting the phenotypic manifestation of a gene. Today, the corresponding field of genetic research (apparently, the least explored) is known as developmental genetics. In the 1920s, it was referred to as phenogenetics. The results of Timofeeff-Ressovsky's studies in phenogenetics, which are of fundamental significance, were described in his first publications. He used the model of the gene *radius incompletus* in *D. funebris*, which is expressed depending on the genotype of a fly and the environmental conditions of its development. On the basis of these studies, he formulated the concept of specific genotypic environment distinguished within the environment in general (a fact specifically noted by Chetverikov, his teacher, in the paper published in 1926) and introduced the measures characterizing the frequency and degree of gene manifestation (penetrance and expressivity, respectively) (Timofeeff-Ressovsky, 1925, 1927). His general ideas concerning the pathways of phenotypic manifestation of the gene (Timofeeff-Ressovsky, 1934a) are still of considerable significance (Ivanov, 1966).

(3) *Population level.* In the 1920s, the research field dealing with the fate of genes in populations was as yet unexplored. The development of mathematical population genetics began when G.H. Hardy, a great master of mathematical analysis, published his classic work (Hardy, 1908). Although the corresponding principle is justly known as the Hardy–Weinberg law, the first author apparently has priority in formulating the problem and proposing the method for solving it. Experimental population genetics did not exist at that time. To a great extent, this science owes its origin to Chetverikov, who was among the first to understand that the data provided by rapidly developing genetics are inconsistent with the Darwinian theory of evolution (Chetverikov, 1926; see also Timofeeff-Ressovsky *et al.*, 1973). In fact, he deductively predicted that natural populations are genetically heterogeneous and indicated a method for predicting this heterogeneity (Glotov, 1981). A number of Chetverikov's students began to collect material confirming his ideas, but the paper by Timofeeff-Ressovsky and Timofeeff-Ressovsky (1927) on *D. melanogaster* populations from Berlin-Buch proved to be the first in this series. The authors emphasized that this work is experimental proof of Chetverikov's *theory.*

Kol'tsov, Chetverikov, and the next generation of scientists representing the Moscow zoological school, including Timofeeff-Ressovsky, regarded population genetics primarily as the genetics of natural populations that provided new approaches to the analysis of phenomenology and mechanisms of intraspecific variation within the species range; in fact, this was a new level in zoogeographic research. This is why Timofeeff-Ressovsky's comprehensive work "Genetics and Evolution" (1939) has the subtitle "From the Standpoint of a Zoologist." The same tendency is characteristic of the extensive studies on temperature races in *Drosophila* (Timofeeff-Ressovsky, 1935), geographic variation in the ladybird *Epilachna chrysomelina* (Timofeeff-Ressovsky and Zarapkin, 1932; Zarapkin and Timofeeff-Ressovsky, 1932), and speciation in gulls (Stresemann and Timofeeff-Ressovsky, 1947). His article in the fundamental book *The New Systematics*, which actually gave rise to the synthetic theory of evolution, is obviously the work of a zoologist specialized in genetics (Timofeeff-Ressovsky, 1940a).

The problem of intrapopulation genetic polymorphism was also regarded by Timofeeff-Ressovsky from the zoological–evolutionary standpoint, as follows from his studies on the polymorphism of heterozygotes at the mutation *ebony* in *D. melanogaster* (Svirezhev and Timofeeff-Ressovsky, 1966; Zurabyan and Timofeeff-Ressovsky, 1967) and adaptation polymorphism in the color of elytra in the ladybird *Adalia bipunctata* (Timofeeff-Ressovsky, 1940b; Svirezhev and Timofeeff-Ressovsky, 1966, 1967). The latter polymorphism is not yet fully understood as an ecological–genetic phenomenon, and this fact accounts for a failure to reproduce the "Timofeeff-Ressovsky effect" concerning seasonal fluctuations in the frequencies of black and red beetles (e.g., see Zakharov, 1992).

Timofeeff-Ressovsky experimentally demonstrated that combinations of mutations can result in improved viability even in cases when each of these mutations reduces the viability of its carriers (Timofeeff-Ressovsky, 1934b). As was specially noted by Schmalhausen (1968), this finding was principally important for the concept of adaptiveness (fitness).

[1] Here and below, only the main works are mentioned. For a complete list of references, see Timofeeff-Ressovsky, 1996.

(4) *Biogeocenotic level.* Apparently, Timofeeff-Ressovsky's interest in research at this level was associated with practical problems created by radioactive contamination. He is justly regarded as the founder of radiation biogeocenology (Timofeeff-Ressovsky, 1964). Research in this direction has been productive and is still regarded as promising. In particular, this is explained by the fact that Timofeeff-Ressovsky successfully developed the ideas of V.V. Dokuchaev, V.I. Vernadsky, and V.N. Sukachev concerning the biosphere of the Earth and its elementary units (biogeocenoses), applying them to studies in this specific field. Fundamental papers by Timofeeff-Ressovsky and Tyuryukanov (1966, 1967) provide ample evidence for such a conclusion.

Thus, Timofeeff-Ressovsky had every reason to say that he had passed through the levels. In addition to his research experience, however, other aspects of his life should be considered. One journalist wrote that Timofeeff-Ressovsky never spared his time and, hence, never lost it. This is quite correct. Throughout his life, Timofeeff-Ressovsky maintained close contact with dozens (if not hundreds) of people belonging to the intellectual community, including historians, writers, artists, and musicians as well as biologists, mathematicians, physicists, and chemists (see *Nikolai Vladimirovich Timofeeff-Ressovsky: Ocherki* ..., 1993; *N.V. Timofeeff-Ressovsky na Urale* ..., 1998). This factor, combined with "passing through the levels," apparently aided Timofeeff-Ressovsky in making large-scale generalizations of great methodological significance, such as the principle of covariant reduplication (Timofeeff-Ressovsky, 1960), the principle of amplifier in biology (Moglich *et al.*, 1944; Timofeeff-Ressovsky and Rompe, 1959), the concept of macro- and microevolution (Timofeeff-Ressovsky, 1958), and the concept concerning relationships between the biosphere and humankind (Timofeeff-Ressovsky, 1968). Toward the end of his life, he repeatedly discussed these generalizations in monographs written together with his students and colleagues (Timofeeff-Ressovsky *et al.*, 1968, 1973, 1978, 1981).

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