

## **TIMOFEEFF-RESSOVSKY, NIKOLAI VLADIMIROVICH**

(b. Kaluga district, Russia, 7 September 1900; d. Obninsk, USSR, 28 March 1981)  
genetics.

Little of Timofeff's early life can be ascertained at present. According to Zhores medvedev, Timofeff was of the Kaluga nobility in origin and as a youth took part in the Civil War. Before he graduated from Moscow State University in 1925, he had already (in 1922) commenced work in genetics under S.S. Chetverikov at the Kol'tsov Institute of Experimental Biology. After Lenin's death in 1924, the Kaiser-Wilhelm Institut für Hirnforschung (KWI), Located at Berlin-Buch, helped to organize a laboratory in Moscow for the study of Lenin's brain. In exchange, Oscar Vogt, director of the KWI, requested that someone be sent to his institute to organize a department of genetics, which Vogt considered to be an important adjunct to an institute of neurobiology and psychiatry. Although he had not yet received his doctoral degree, Timofeff already had a good grounding in the genetics of *Drosophila*, including population genetics and systematics, so his superiors recommended him for this appointment. In 1925, with his young wife, Helena (Elena) Aleksandrovna, also a geneticist, he went to Berlin for a projected stay of possibly six years.

Timofeff-Ressovsky evidently had a gift for languages, for he quickly became a master of spoken and written German; and by 1932, when he attended the Sixth International Congress of Genetics, held in Ithaca, New York, he had mastered English sufficiently to converse readily and to deliver a major address in that language. His memorable, widely consulted reviews, "The Experimental Production of Mutations" (1934) and "Mutations and Geographical Variation" (1940), reveal a fluent control of the English language that enabled him to make difficult concepts and novel developments extremely clear. Timofeff's mastery of German style was also evident, and his addresses were delivered with enthusiasm and vigor.

By 1927 the new department at the KWI was well established, and Timofeff entered upon a period of amazing scientific productivity that lasted through the troublous 1930's until the outbreak of World War II. Essentially, all of his contributions to genetics were accomplished in the fifteen years from 1925 to 1940. Timofeff managed quite successfully to stay out of Nazi politics. Even when Oscar Vogt retired in 1937, and Timofeff succeeded him as director of the KWI, he managed to limit his relationships with the political authorities to perfunctory appearances on public occasions, when he summarized in sober tones the gravity of the genetic load borne by human populations. His statements, from 1935 to 1938, to that effect in no way altered his conclusions, based on his own work, that it is unsafe to consider the effects of a harmful gene apart from its total "genetic milieu," that is, the entire genotype with its many significant modifiers of the action of any gene. Timofeff also believed that it is unsafe to judge the effects of a harmful gene apart from the "environmental milieu," including both the internal physiological system of an organism and the external environment, either or both of which can totally change the relative detrimental status of the gene in question. Timofeff never endorsed the racial policies of the Nazi Party and its eugenicists, or any particular eugenic measures.

Nevertheless, the time was an unhappy one for Timofeff. As the terror and political pressure on science increased, he began to search for ways to leave Germany. Although he could have accepted certain tentative offers from the United States, he did not wish to leave Europe; and in 1937 he wrote to Kol'tsov about the possibility of returning to the Soviet Union. Not even the rise to power over

genetics and agriculture of T.D. Lysenko and I. I. Present, and their persecution of any geneticists who upheld the condemned Mendelian-Morganian theories accepted in the West, dissuaded him, nor did the arrests of two of his own brothers as well as many of their friends and many relatives of his wife. Nikolai I. Vavilov, president of the Academy of Agricultural Sciences, sent a message to Timofeeff by the American geneticist H.J. Muller, who at this time escaped from Moscow to Spain and thence to Edinburgh, to warn him that only disaster could await him were he to return to his native land; Kol'tsov smuggled a letter to Timofeeff through the Swedish embassy. He wrote, according to Medvedev, "Of all the methods of suicide, you have chosen the most agonizing and difficult. And this not only for yourself, but also for your family. . . If you do decide to come back, though, then book your ticket straight through to Siberia!" Timofeeff stayed on in Berlin.

Explicitly or implicitly, all of Timofeeff's genetic studies addressed the major questions of the time concerning the relation of genes and mutations to the processes of evolution. The first were experiments begun before Timofeeff left Moscow and extended through 1933. These were studies of the reversibility of gene mutations; for if, he reasoned, mutations were the basis of evolutionary change, they must not always be completely destructive. If a mutant gene could mutate back to a state restoring the original wild phenotype, the original mutation must not have been a total loss of substance, as many eminent scientists skeptical about the role of gene mutations in evolution supposed. Timofeeff's investigations of reverse mutation were concerned principally with the white eye-color locus of *Drosophila melanogaster*. His first reverse mutations were spontaneous occurrences; but after Muller's discovery of the induction of mutations at vastly increased frequencies by exposure of the flies to X rays, Timofeeff quickly made use of the new technique.

Although subsequent investigations have revealed that this locus is not really a simple single gene but a compound of several pseudoalleles, Timofeeff established several generalizations that have not yet been challenged. First, he confirmed the earlier reports relating to other genetic loci that, by means of exposure to X rays, reverse mutations, as well as forward mutations, can be obtained. That is, not only could the gene at the selected locus, which is necessary for the production of red eye color in the flies, be made to mutate to an allele that resulted in white eye color or an intermediate shade, but the less effective or important alleles could be made to mutate back to the red eye color allele.

Next Timofeeff demonstrated that the mutation rates in opposed directions are different and depend upon what particular allele is mutating. He showed that some reverse mutations cannot be secured in a single step but may be obtained in two or more successive steps. He also discovered isoalleles (WA and WR) that are distinguishable only on the basis of their mutation rates. He proved that the recurrence of the original alleles was demonstrable on a pleiotropic basis, that is, of several types of phenotypic effects, not only the eye color but also the form of the spermatheca, color of testes, viability of males, and fertility of females.

Timofeeff was probably the first geneticist to realize that in studies of reverse mutation it is essential to exclude the possibility that the reversion is actually not at the site of the original forward mutation but that a mutation at a suppressor locus elsewhere might be involved. His techniques for excluding that possibility in interpreting his own results were inadequate but represented a significant development of technique at the time.

Significant studies in the analysis of the relationships between X-ray dose and mutation rate formed a second major part of Timofeeff's contributions. He was among the early workers to conform the linear dose relationship for sex-linked lethals. He demonstrated that the proportions between sex-linked lethals and visibles did not change with dose; that neither the fractionation of the dose nor the dose rate affected the mutation frequency; that the mutation frequency for a given dose was independent of the hardness of the rays; and that within the limits of 10° and 35°C the temperature during radiation has no effect. Some of these generalizations are now considered to be more limited because they were applicable only to mutations induced in mature spermatozoa; but in general

Timofeeff's studies in this area were among the most important and fundamental in early mutation work, second in importance only to those of H. J. Muller and L. J. Stadler.

An entirely different type of study, and one of classic value to this day, was Timofeeff's investigation of the influence of the residual genotype and of selected environmental conditions on the expression of particular mutant genes. This work utilized especially the mutant *venae transversae incompletae* (*vti*) of *Drosophila funebris*. It led Timofeeff to a distinction between the penetrance, expressivity, and specificity of the mutant gene. Of particular importance was the discovery that each of these parameters of gene expression can to a certain degree vary independently. The modifying genes in the rest of the genotype provide a "genotypic milieu" that, together with the "external milieu" of environmental variables and the "internal milieu" (the physiological variables), determines the expression in the organism of the primary gene alleles. It was demonstrated that the genotypic milieu present in different geographic strains of a species varies in respect to its effect upon the expression of *vti*.

Another classic series of investigations performed by Timofeeff related to "viability mutations". From the standpoint of interest in the evolutionary process and especially of the action of natural selection, it was of critical importance in the 1930's to show whether recessive lethal mutations—which most studies of mutation rates had been based—were indeed the commonest kind of mutations, or whether in fact there were many more mutations with less drastic effects upon viability, defined as the ability of the organism to survive to the age of reproduction. In a program involving a stupendous amount of work, Timofeeff succeeded in showing that X rays induce about twice as many mutations without visible effects but detrimental in some measure to viability as they induce lethal and sublethal mutations combined, from the same dose of X rays. He also detected a single radiation-induced mutation with increased viability. For this mutant and the others, the measured viability was different at different temperatures.

A further important contribution to an understanding of the evolutionary significance of mutations was derived from the analysis of the viability of different mutations in *Drosophila funebris* when placed in different combinations with other mutants. Timofeeff demonstrated that the standard viability of a particular mutant at a given temperature offered a scant basis for predicting what the viability would be under the same conditions when it was combined with other mutants. Thus a combination of *ev* and *sn*, rated individually at viabilities of 104 percent and 79-88 percent of normal (wildtype), proved to be 103 percent, whereas *ev* with *Va* (rated at 89 percent) turned out to be 84 percent. In other words, the viability of the compound was sometimes as good as the higher of the component mutants taken singly, sometimes as poor as the poorer of the component mutants. Sometimes it was intermediate. It could even exceed the better, or fall below the poorer, of the component mutants taken alone. From the standpoint of clarifying the selective process upon the raw material of evolution, the mutations, this investigation is one of the most important ever made by anyone.

Timofeeff's later work on the nature of mutation and deductions regarding the nature of the gene itself was highly stimulating to geneticists the world over. The primary contribution was one made jointly with K. G. Zimmer and Max Delbrück (published in 1935). It represented the debut in genetics of the young physicist Delbrück, whose conversion to biology would alone have constituted a major achievement by Timofeeff, for after leaving Germany for America, Delbrück pioneered with Salvador Luria in the study of mutations in bacteria and virtually founded bacterial genetics; then went on to play an equally significant role in establishing bacteriophage genetics; and became a Nobel laureate and a father of molecular genetics of vast influence. He warmly attributed his early training in genetics and his insight into the problems of mutation of Timofeeff-Ressovsky.

In the paper with Zimmer and Delbrück, Timofeeff led off with a masterly summation of all the existent data on mutation, both radiation-induced and spontaneous. He deduced that the dependence

of the latter on temperature (corrected for the altered length of the generations at different temperatures (revealed a Q<sub>10</sub> of about 5, which throws it far outside the range of ordinary chemical reactions. He analyzed the spectrum of mutability of different loci, and the relation of mutation rate to dose of radiation, and with Zimmer and Delbrück concluded that a mutation is a molecular rearrangement within a particular molecule, and the gene a union of atoms within which a mutation, in the sense of molecular rearrangement or dissociation of bonds, can occur. The actual calculations of the size of the gene, deduced from calculations on the assumption of a spherical target, were not cogent, as Delbrück wryly admitted in his Nobel Prize lecture, but the entire approach to the problem of mutation and the gene adopted by the three collaborators was highly stimulating to other investigations.

Later, Timofeeff wrote a book, *Das Trefferprinzip in der Biologie*, with K. G. Zimmer as coauthor. Its publication was delayed, however, until after World War II (1947), at which time it was principally of historical interest. It continued a full, masterly summary of the data on radiation-induced mutation up to 1940, and, in spite of the fact that later work by other investigators showed that mutation may be induced indirectly through the production of free radicals in the medium or inner milieu surrounding the chromosomes, Timofeeff's deductions are still valid for the considerable proportion of mutations that are induced by direct hits rather than indirect effects.

Timofeeff was well aware of the dimensions of the problem, and one of his last papers before the war (published in 1937) was an investigation of the direct versus indirect influence of irradiation on the mutation process. In this study he compared the effects of direct irradiation of the chromosomes in the spermatozoa of *Drosophila* with the effects of irradiating the plasma of the eggs and then introducing unirradiated chromosomes from the sperm into it. Finding no increase in mutation in the latter case, in contrast with the former, he concluded that there is no indirect effect of radiation on mutation. This was a valid conclusion for the circumstances, for the indirect effects later demonstrated by other geneticists do not ensure for the length of time required for the fertilization of eggs by untreated spermatozoa. Indirect effect produced by the formation in the medium of chemical mutagens of a semipermanent character are of course a different phenomenon, the ignorance of which Timofeeff could not avoid, since chemical mutagenicity was discovered only during and after World War II, and Germany was shut off from knowledge of these developments until the 1950's.

When it became evident in the spring of 1945 that Germany would soon fall to the combined pressure of the Western and the Russian armies, Timofeeff's friends urged him to escape from Berlin to the West before he was captured by the Soviet troops. I was personally informed by his good friend Boris Rashevsky, director of the Max-Planck Institut für Biophysik in Frankfurt, that at considerable personal risk Rashevsky made a special trip to Berlin in the winter or spring of 1945 to urge Timofeeff to make his way to the West while there was still a possibility of getting out of Berlin. Timofeeff, however, refused to leave the institute in Berlin-Buch, for which he had by then assumed principal responsibility. Although his oldest son had been captured by the Nazis in underground activity and sent to a concentration camp, where he subsequently died, Timofeeff did not fear personal reprisals from the German government; and he spoke with conviction of his belief that no one else could talk to the Russian commanders when they arrived and save the institute and its personnel from damage and disruption except himself.

From this point on, we must rely on the writings of Zhores Medvedev to tell us the sequel. When the Russian forces did arrive in Berlin-buch, Timofeeff was confirmed in the post of director of the Hirnforschungs-Institut and indeed temporarily saved both the equipment and the personal from destruction. Soon, however, a new high command replaced the original field commanders. Most of the equipment was taken away and sent to Russia, and Timofeeff was arrested and sent to Moscow. After a period of imprisonment and investigation in the Lubianka prison, on a charge of being a German spy, Timofeeff was transferred to the Butyrka prison. He stayed there for some months, with

his characteristic energy organizing a Scientific and Technical society, with lectures by members who included physicists, electronic engineers, and a chemist in addition to the geneticist. Here Timofeeff made the acquaintance of Aleksandr Solzhenitsyn, who has described life in this prison so graphically.

Next Timofeeff was sent to a special labor camp in northern Kazakhstan and condemned to "general labor only." Again he organized a scientific society to save himself and his fellow scientists from intellectual death. He was not so fortunate physically and began to suffer badly from malnutrition and avitaminosis. The lack of vitamin A in the prison diet was responsible for a swift decline in his vision, verging on blindness. Fortunately, he was saved by the need in the Soviet Union for scientists knowledgeable in radiobiology and radiation genetics, as the Soviet program to develop first a nuclear bomb and then a hydrogen bomb got under way. He was shipped back to Moscow in a crowded prison wagon, forced to stand crushed together with others most of the time, and arrived unconscious. In the Central Prison Hospital strenuous efforts saved his life, but his vision, although improving, remained permanently impaired. According to Medvedev, he was never again able to use a microscope and could read only with a large magnifying glass and a brightly lighted page.

After his recovery, Timofeeff was transferred to a laboratory in the ural atomic establishment. For the first time in two years, he was able to write to his wife in Germany, who thereupon hastened to be reunited with him, together with their younger son, who had remained with his mother in Berlin. They were of course all virtually imprisoned and closely guarded. There was also trouble from the archenemies of genetics in Russia, the Lysenkoists. I. E. Glushchenko, a follower of Lysenko, singled him out as a "sworn enemy" of the people, and orders went out from Moscow to ban genetic research in all institutes; the classic subject of genetic research, the laboratory stocks of *Drosophila* flies, were to be destroyed. At this juncture, Timofeeff virtually created a new science for himself. He called it "radiation biogeocenology," defined as the science of the radiation aspects of total ecology, the complete living community of organisms, earth, air, and waters in their fullest interdependence.

In 1955, two years after the death of Stalin, Timofeeff was released from imprisonment. He had already become scientific director of the laboratory in the Urals where he worked. He now began to form a biophysics section within the Ural branch of the U.S.S.R. Academy of Sciences, and it soon "became the most productive biological establishment in the Urals and Siberia" (Medvedev, p. 99). At Miassovo, near Sverdlovsk, Timofeeff also founded a summer seminar on genetics and theoretical biology, the first such center in existence in the Soviet Union since 1948. It was very popular with scientists and, like the dozens of papers and monographs he issued through the Ural branch of the U.S.S.R. Academy of Sciences, it exerted a profound effect on the renaissance of biology after the demise of Lysenkoism.

On the occasion of the centenary of Charles Darwin's publication of the *Origin of Species*, the Deutsche Akademie der Naturforscher Leopoldina (East Germany) decided to confer four Darwin Prizes on Russian geneticists and evolutionists. Of these persons, S. S. Chetverikov, Timofeeff's first teacher of genetics and a founder of population genetics, was one, and N. V. Timofeeff-Ressovsky was another. The other two were I. I. Schmalhausen and N. P. Dubinin. The four distinguished scientists were invited to Berlin to receive the honors to be conferred upon them, but in 1959 none of the four was permitted to go. Instead, the medals and diplomas were forwarded to them by mail. Chetverikov died before receiving his medal. Schmalhausen had been dismissed from his posts in 1948, and his books destroyed. Timofeeff was in the Urals, and received his medal while at the summer institute of genetics he had founded at Miassovo. Even Dubinin, who was already a corresponding member of the U.S.S.R. Academy of Sciences, was disgraced and dismissed from his post as director of the Institute of Genetics and Cytology in Novosibirsk, at the special direction of Nikita Khrushchev. The Soviet Union was clearly not yet ready for a renaissance of genetics and evolution.

By 1962 Timofeeff had been convinced by his friends that he should defend a thesis and acquire a doctoral degree, for in the Soviet Union every administrator in science must possess such a degree,

regardless of the eminence of his scientific contributions and the distinction with which he is regarded outside the country. Timofeeff did so, and was awarded the degree of doctor of biological sciences by the Ural branch of the U.S.S.R. Academy of Sciences. This academic standing had to be confirmed by a commission in Moscow, which was still controlled by Lysenko, and the commission balked. Not until October 1964, after Timofeeff had moved to Obninsk to become head of a section of genetics and radiobiology, and after Khrushchev had resigned, was Lysenko's power curbed. Timofeeff was finally confirmed in the possession of his doctorate, became the recognized leader of research in radiation biology and genetics at the Obninsk Institute of Medical Radiology of the Academy of Medical Sciences, and began to give many lectures and courses, write popular books in the fields in which he was an authority, and, as in Miassovo, it organize a summer institute.

Even so, Timofeeff's difficulties were not at an end. In 1965, on the occasion of the centennial of Mendel's discovery of the laws of heredity, the Czechoslovak Academy of Sciences planned an international celebration to be held in Brno. Timofeeff was invited to be one of twenty noted geneticists to receive the newly established Mendel Medal and to present a paper at the memorial symposium. He was, however, not permitted to go. The necessary exit dossiers required to go abroad were blocked by deliberate delays, first in the Academy of Medical Sciences and later in the Kaluga Provincial Committee of the Communist Party of the Soviet Union. Timofeeff's medal was eventually delivered to him in Moscow by a Czechoslovak embassy official in December 1965.

Only a few days had elapsed when a similar experience began. In the fall of 1965 the committee of the National Academy of Sciences of the United States, appointed to nominate recipients of the Kimber Gold Medal and Award in genetics, and of which the author of this article was a member, had chosen Timofeeff-Ressovsky to be the thirteenth recipient of the medal. I had personally prepared the nomination, and a good portion of the foregoing summation of Timofeeff's contributions to genetics is based on the unpublished memoir I circulated to the other members of the Kimber Award Committee. The medal itself and the monetary award of \$2,000 constitute, in the eyes of geneticists throughout the world, possibly the highest honor a geneticist could receive, outranking even the Nobel Prize in esteem. Only one other non-American had previously been awarded the medal (J. B. S. Haldane), and Timofeeff's own recruit for genetics, Max Delbrück, had been a previous recipient.

The unanimous nomination of Timofeeff by the committee was confirmed by the council of the academy, whose president wrote to Timofeeff in December 1965 to inform him of the honor. A special letter was also sent by President Seitz to the president of the U.S.S.R. Academy of Sciences, expressing the hope that Timofeeff would be permitted to attend the annual meeting of the U.S. Academy of Sciences in Washington in April 1966 to receive the medal and award.

Again the matter was referred to the Academy of Medical Sciences, within which Timofeeff's laboratory and section were located; and again the matter dropped out of sight. In the opinion of the authorities, the award to Timofeeff was simply a political provocation by the Americans. Eventually, as in the case of the Mendel Medal, the Kimber Gold Medal and Award had to be presented to Timofeeff in Moscow, on an occasion when the vice president of the U.S. Academy of Sciences was there for an official visit.

In 1969, while I was president of the American Association for the Advancement of Science, I made an official visit to the Soviet Union as a return courtesy for a visit to the AAAS by the officers of Znaniye, a very large, popular scientific association in Russia. When I spoke of my friendship with Timofeeff, in whose laboratory at Berlin-Buch I had worked in the spring and summer of 1933, I was shown with pride several popular books on genetics and evolution written for the organization by Timofeeff. Yet when I expressed the hope that I might meet with him, either at Obninsk or in Moscow, my suggestion met with a blank response. Upon inquiry, he was "away," or "not available." From Medvedev's book *The Medvedev Papers*, I later learned why (pp. 107–112).

Timofeeff was expectably excluded from attendance at the International Congress of Genetics held in Tokyo in 1967, where I had hoped to see him. He became a candidate for election to the U.S.S.R. Academy of Sciences in 1968, having in the previous five years published, according to Medvedev, more than fifty papers and a monograph. (These works still remain unknown in the West.) Nevertheless, Timofeeff's candidacy was turned down through the combined opposition of the Michurinists and of Lysenko himself. Favorable publicity in the press did not help Timofeeff's candidacy in the least. A dossier on his supposed political anti-Russian activities was compiled, and later it was used to put pressure on Timofeeff to resign a year before reaching the compulsory age of retirement for administrators (seventy years). For Timofeeff, this was a severe penalty, since his pension could not be based on any of the years he spent in Germany or while imprisoned. The denial of even one additional year was therefore serious.

The ultimate sequel is more pleasant to relate. Photographs are in the possession of the Library of the American Philosophical Society (Collection Caspari) sent by Timofeeff's friend, the plant geneticist Georg Melchers of Tübingen (West Germany). These photographs show participants at the meeting of the N. I. Vavilov All-Union Society of Geneticists and Selectionists at Lomonosov University in 1972. Especially revealing is a merry supper party at which Timofeeff and his wife are happily conversing with their old friends Georg Melchers and Hans Stubbe, the latter the leader of genetics in East Germany. In the meantime Timofeeff had been elected a member of the Leopoldina Academy and received its Mendel Medal in 1970. When the Thirteenth International Congress of Genetics met in Moscow in the summer of 1978, Timofeeff was a greatly honored senior member and at last met many of his friends and admirers from the Western countries. He died in Obninsk on 28 March 1981, in his eighty-second year, his wife having predeceased him. It seems possible that, like Vavilov, he will ultimately be posthumously rehabilitated and honored in his own country as its greatest geneticist, even though he was never elected to membership in the U.S.S.R. Academy of Sciences.

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**Bentley Glass**