The Founding of Population Genetics: Contributions of the Chetverikov School 1924-1934

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Of the eighteen founders of the synthetic theory of evolution listed by G. G. Simpson in his book, *The Meaning of Evolution*,[1] four are Russian in origin and training: S. S. Chetverikov, N. V. Timofeev-Resovsky, N. P. Dubinin, and Th. Dobzhansky. All are significant primarily for the same type of studies: analyses of the genetic variability of wild populations, and the development of sophisticated notions of the role of the genetic and environmental backgrounds in determining the expression and fitness of genes. Furthermore, Dobzhansky's work comes later than that of the first three, and he himself was among the first to credit their work with originating many of the concepts and experimental approaches which he has applied so fruitfully.

Thus it is especially lamentable that an informed student of evolution today in the West, though he would probably be familiar with the work of the Western founders of the synthetic theory, might well have only a vague notion of the contributions of Chetverikov, Timofeev-Resovsky, and Dubinin. This lack is perhaps natural enough: it reflects the scant treatment given them in the biological literature, which generally has only brief mentions of their early works. And this lack in turn is to be largely explained by the unavailability of many important articles published in the 1920's and 1930's in Russian, and often unavailable in most Western libraries in any language.

In order to put this study in the proper perspective, it is perhaps advisable to delineate what will not be discussed. First, the Russian School made important contributions to genetics which, however significant, do not bear directly on population genetics. Hence I will not discuss the contemporaneous work on position

1. George Gaylord Simpson, *The Meaning of Evolution* (New Haven: Yale University Press, 1949), p. 278. In later editions, Simpson adds I. I. Schmalhausen.

effect (by Dobzhansky, I. B. Panshin, and others), on chemical mutagenesis (I. A. Rapoport and colleagues), or on the substructure of the gene, termed "step-allelomorphism" by Russian workers (I. I. Agol, A. S. Serebrovsky, and Dubinin.) Second, I wish to concentrate only on work completed and published before 1935, since our concern is with the founding of population genetics and not its later development. Finally, I wish to restrict myself to studies of the genus *Drosophila*. This is a natural enough restriction, since *Drosophila* was by far the best understood genus genetically, thanks to the Morgan School, whose work together with that of the Russian School has made *Drosophila* the mainstay of most experimental population genetics since then.

I wish to focus on the work of Sergei S. Chetverikov and of the students who worked with him in the decade after the Bolshevik Revolution. Their scientific contributions are threefold. First, the experimental work under Chetverikov's direction by Timofeev-Resovsky on a naturally occurring *Drosophila* population led to the development of clear ideas concerning the influence of genetic and environmental backgrounds on the fitnesses and effects of genes. Second, it was Chetverikov's 1926 theoretical paper, "On Certain Features of the Evolutionary Process from the Viewpoint of Modern Genetics,"[2] which initially bridged the gap between Mendelism and Darwinism, or, to be more precise, between the genetics of the Morgan School; biometrics and mathematical studies as developed by Karl Pearson, G. H. Hardy, H. T. J. Norton, and others; and studies of natural variation from natural history. Finally, in order to test experimentally certain theoretical conclusions, Chetverikov and his students undertook the first genetic analysis of free-living *Drosophila* species and founded experimental population genetics. This led almost immediately to a series of studies by Dubinin, of which the first is of special interest.

Accordingly, we will consider in order; the formation of the Russian School, its scientific contributions, and its historical significance.

The impact of the Morgan School on Russian genetics was

2. Sergei S. Chetverikov, "O nekotorykh momentakh evoliutsionnogo protsessa s tochki zreniia sovremennoi genetiki," *Zhur. Eksper. Biologii*, 2 (1926), pp. 3-54. The Russian original is reprinted in *Biulleten' Moskovskogo Obshchestva Ispytatelei Prirody, Otdel Biologii*, *LXX* (1965), 4:33-74. For an English translation, see that done by Malina Barker, edited by I. M. Lerner, which appeared under the title in the text, *Proc. Amer. Phil. Soc.*, *105* (1961), pp. 167-95. In general, quotations in the text are taken from the Lerner translation.

post-revolutionary, and this impact was heightened by efforts of the new Soviet regime to stimulate the development of genetics. L. C. Dunn relates the following episode which illustrates the light in which the development of biology was regarded by the new Soviet regime: "Koltsov . . . walked with Lenin in the 1920 Leningrad famine. Lenin said, 'The famine to prevent is the next one, and the time to begin is now!' "[3] As a result of this conversation, emergency funds were partly spent to build the Institute of Applied Botany, and biological work received priority support.

The presence of a promising number of experienced biologists, coupled with government interest in the development of biology for practical reasons, no doubt contributed to the rapid development of the three major genetics schools which arose in Russia in the early twenties.[4] One group developed around I. A. Philipchenko in Leningrad; also in Leningrad was a second group, headed by N. I. Vavilov, who had moved from Saratov to establish a department of applied botany and plant breeding that later developed into the USSR Institute of Plant Breeding. While Leningrad had been developing as a center for research in plant genetics, Moscow was developing as a center for animal genetics, due largely to the efforts of N. K. Koltsov, S. S. Chetverikov, and A. S. Serebrovsky.

Sergei S. Chetverikov (1880–1959) was a butterfly taxonomist by training, but his concern with entomology and evolutionary problems was complemented by an interest in genetics and biometrics.[5] By the time he had graduated from Moscow University in 1906 he had already published an article[6] in which he called attention to the evolutionary significance of what he termed "population waves": periodic and radical decimation of insect populations which in his view allowed the role of natural

3. L. C. Dunn, "Science in the USSR: Soviet Biology," *Science, 99* (1944), pp. 65-67.

4. These three schools are discussed briefly by Theodosius Dobzhansky, "The Crisis in Soviet Biology," *Continuity and Change in Russian and Soviet Thought*, E. J. Simmons, ed. (Cambridge: Harvard University Press, 1955) and also by Sos I. Alikhanian, "Soviet Genetics," *Soviet Life*, January 1966.

5. For material on Chetverikov's life and work, see Sergei S. Chetverikov, "Autobiographical Note," written in 1956, *Nova Acta Leopoldina*, N. S., *143* (1960), pp. 308-310. Some additional information is also available in I. M. Lerner's introduction to the Malina Barker translation of Chetverikov's "On Certain Features . . . ," *Proc. Amer. Phil. Soc., 105* (1961), pp. 167-69; also B. L. Astaurov, "Two Landmarks in the Development of Genetical Concepts," *Biulleten' Moskovskogo Obshchestva Ispytatelei Prirody, 70* (1965), pp. 25-32.

6. Chetverikov, "Volny zhizni" (Waves of Life), *Dnevnik Zootd.*, Moscow Society of Naturalists, 3.

selection to be periodically "swamped" by chance phenomena. It was thus one of the earliest papers to call attention to what Sewall Wright would twenty-five years later term "genetic drift," and according to Chetverikov's own evaluation, the paper "produced a sensation in Russian readership circles."[7]

In the decade preceding the Revolution, Chetverikov taught entomology at the Moscow University for Women and published papers on entomology. After the October Revolution, the University for Women was merged with Moscow University; Chetverikov remained on the faculty where he taught entomology and "theoretical systematics." By 1924 he had developed two entirely new courses in biometry and genetics which he taught until 1929.

Aleksandr Serebrovsky had established a department of genetics at Moscow University, and it was to Professors Chetverikov and Serebrovsky that H. J. Muller in August 1922 brought laboratory *Drosophila melanogaster* strains from the United States.[8] Theodosius Dobzhansky, then an instructor at the University of Kiev and subsequently of Leningrad, borrowed from these strains, and their introduction was a major stimulus to laboratory work on *Drosophila* in Russia. Investigations had begun as early as 1920 on free-living *Drosophila* from suburban Moscow, but the Muller strains were the first available with a known genetic history.[9] According to the testimony of N. K. Koltsov, Muller's impact was also a personal one, in that he

7. Chetverikov, "Autobiographical Note." Translated by the author from German. Chetverikov borrowed certain features of the theory proposed by Rev. John T. Gulick which suggested that non-adaptive evolution could occur as a result of inbreeding of a few isolated individuals. This notion Chetverikov applied to the case of radically fluctuating insect population sizes. The author is presently engaged in a study of the intellectual currents of thought which led to the almost simultaneous exposition of a theory of "genetic drift" by Sewall Wright, and of a strikingly similar theory of "genetico-automatical processes," by D. D. Romashov and N. P. Dubinin—both in 1931, and apparently independently.

8. The significance of Muller's 1922 visit is repeatedly emphasized in Russian genetics literature of the period. For example, Th. Dobzhansky, "Kleinere Mitteilungen," Z. *Induktive Abstammungs-Vererbungslehre*, *34* (1924), p. 245, refers to a culture brought by Muller in August, 1922. (Dobzhansky's fuller communication [43, 1927, p. 330] mistakenly gives the date as August 1923 due to a misprint.) See also N. K. Koltsov, "On the Work of the Institute of Experimental Biology in Moscow," *Uspekhi Eksperimental'noi Biologii*, *8* (1929), p. 23; and A. S. Serebrovsky and V. V. Sakharov, "New Mutations in *Drosophila melanogaster*," *Zhur. Eksper. Biologii*, *1* (1925). All these sources may be referred to for brief descriptions of Muller's visit.

9. Koltsov, "On the Work . . . ," p. 23.

"infected" young Russian workers with a sense of "enthusiasm for the study of *Drosophila* genetics."[10]

Koltsov, who earlier had operated an experimental station in animal genetics near Moscow, had been chosen to direct the recently established Institute of Experimental Biology which had been established in 1916 and reorganized after the Revolution. In 1922 Koltsov entrusted to Chetverikov the organization and direction of the genetics section of the Institute, a post which he held until 1929 when, according to B. L. Astaurov, one of his students, he was "forced to break off his work on *Drosophila* population genetics";[11] he left Moscow, for reasons which remain obscure.[12] He never returned to his earlier *Drosophila* studies. For the next three years he worked as a zoo consultant in Sverdlovsk, and from 1932 to 1935 he taught mathematics at a *tekhnikum* in Vladimir, just east of Moscow. In 1935 he went to Gorkii University to teach genetics, and he soon became head of the biology faculty. He worked there until 1948 and lived in the city of Gorkii until his death on July 2, 1959.[13]

The period of Chetverikov's tenure at Moscow University (1919–1929), and especially at the Institute of Experimental Biology (1924–1929), was the formative period of the Russian School of population genetics. According to his own recollection, Chetverikov "collected a narrow circle of students and co-workers" about him, and over a number of years gave a seminar in "the relationships between evolutionary theory and the newest results in genetics."[14] This group included a num-

10. *Ibid.* (Translated by the author from Russian.)

11. B. L. Astaurov, "Two Landmarks . . . ," p. 27. (Translated by the author from Russian.)

12. The only published suggestion as to the reason for Chetverikov's departure comes from Th. Dobzhansky: "In 1929 [Chetverikov] was banished from Moscow, as were some of his collaborators. In their enthusiasm they forgot caution. They organized a closed genetics and evolution discussion group, the acceptance into which of new members was by unanimous secret ballot of the old members. This was too much for Stalin's secret police." Whether this was the sole reason, who was responsible for the banishment, how it was engineered, and how and by whom resisted (if at all): these and other matters remain unclear. Dobzhansky's article, "Sergei Sergeevich Tshetverikov: 1880-1959," (*Genetics*, 55 [1967], pp. 1-3) from which the above quotation is taken, contains useful biographical information on Chetverikov not previously published in English.

13. Chetverikov writes in his autobiographical note: "In 1948 I resigned from all positions." There can be little doubt that the official victory of Lysenko over his geneticist rivals in that year was the major cause of Chetverikov's resignation; health became a contributing factor, since in the following year Chetverikov had a series of heart attacks and became blind.

14. Chetverikov, "Autobiographical note."

ber who were later to become prominent in world science, among them N. V. Timofeev-Resovsky, N. P. Dubinin, B. L. Astaurov, and D. D. Romashov, all of whom Chetverikov had initiated into research.

Dobzhansky has acknowledged his debt to the work of members of this group—indeed his earliest work on *Drosophila* (1923–1927) was done on flies obtained from the Chetverikov Laboratory. Hence, in terms of training and intellectual influence, we are justified in speaking of Dobzhansky as an offshoot of the Russian School, though he left for America in 1927; likewise, Timofeev-Resovsky, who studied with Chetverikov for several years, is clearly part of the Russian School, even though after 1925 he did most of his work in Germany, based at Buch, just north of Berlin.

In the twenties Chetverikov's group developed and clarified a number of concepts which were to lead to important work in later decades, and initiated the wide-scale genetic analyses of natural populations of *Drosophila* on which much modern population genetics is based. It is to one of the most important of these concepts—his idea of the "genotypic milieu"—that we shall now turn.

As Chetverikov readily admitted,[15] his school did not originate the notions of pleiotropic and epistatic gene action. It was William Bateson who first demonstrated the role of gene interaction in producing a phenotypic character in 1907.[16] At roughly the same time, the studies of Nilsson-Ehle on the genetics of cereals were showing that many cases of continuous variation could be explained if it was assumed that certain major genes were interacting with other genes so as to increase, decrease, or alter their effects.[17] Thus, Nilsson-Ehle wrote that an inherited difference between individuals or strains may be due to "the joint actions of many genes,

15. Chetverikov, "On Certain features . . . ," (Lerner trans., p. 189).

16. William Bateson and R. C. Punnett, "Experimental Studies in the Physiology of Heredity" (1905-1909), in J. A. Peters, *Classic Papers in Genetics* (Prentice-Hall, 1959). One of these investigations concerned the genetic basis of the shape of poultry combs. Bateson showed that when a gene 'R' (which by itself produced a comb shape termed "rose") was present with another gene 'P' (which yields by itself a shape termed "pea,") the resulting combination 'RP' produced a comb of an entirely different shape, which he called "walnut." The two genes had thus interacted to produce a phenotypic character, the new comb shape.

17. H. Nilsson-Ehle, "Kreuzungsuntersuchungen an Hafer und Weizen," *Lunds Univ. Aarsk. N.E. Afd.* 2, 5, 2: 122. Cited in Th. Dobzhansky, *Genetics and the Origin of the Species*, 3rd ed., rev. (New York: Columbia University Press, 1951), p. 71.

each having a small effect in relation to the total nonheritable fluctuation of the character in question."[18]

Effects that would now be termed pleiotropic and epistatic were also discovered in *Drosophila.* In work reported 1912–1914, J. S. Dexter did experiments on *Drosophila* involving "beaded" wing, a highly variable character which is often nearly normal in appearance. Dexter showed that "the degree of abnormality and the proportion of abnormal offspring are both capable of being altered, within limits, by selection or by crossing to a normal stock."[19] After 1914, Morgan, Muller, Altenburg, and Dexter showed that many modifier genes existed in *Drosophila,* and that they were inherited in Mendelian fashion.

To Chetverikov, however, belongs the credit for clarifying the importance of gene interaction for evolution. In his lengthy theoretical article (1926) which will be discussed later, his treatment of the evolutionary importance of gene interactions and of the genetic background, which he terms the "genotypic milieu," stands out for its clarity and insight.

Chetverikov develops the earlier notion of pleiotropy, which was previously applied to one gene affecting a limited number of characters, into a more generalized concept of the "genotypic milieu":

> Each gene does not act isolately from the whole genotype, is not independent of it, but acts, manifests itself, *within it,* in relation to it. *The very same gene will manifest itself differently, depending on the complex of the other genes in which it finds itself.* For it, this complex, this genotype, will be the *genotypic milieu,* within the surroundings of which it will be externally manifested. And as *phenotypically* every character depends for its expression on the surrounding external environment, and is the reaction of the organism to the given external influences, so *genotypically* each character depends for its expression on the structure of the whole genotype, and is a reaction to definite internal influences.[20]

From here he moves to a discussion of the evolutionary implications of the "genotypic milieu." True, Chetverikov agrees, selection cannot alter the gene itself—a point made

18. *Ibid.*
19. T. H. Morgan, A. H. Sturtevant, H. J. Muller, and C. B. Bridges, *The Mechanism of Mendelian Heredity* (New York: Henry Holt, 1915), p. 195.
20. Chetverikov, "On Certain Features . . ." (Lerner trans., p. 190; Russian reprint, p. 66).

by Morgan repeatedly—but it can and will alter the expression of the gene in subtle ways and hence is a "creative process" in evolution.

> *Any* newly arising mutation may appear in connection with the selected feature either as an "enhancer" or a "weakener." In the case of an "enhancer," selection will pick it up and spread this gene in subsequent generations through the whole population, enhancing the selected trait. In this way selection does not cease with the passage of the selected character into the homozygous condition, but is extended further for an indefinitely long time, acting on the whole genotype.
>
> Exactly this process occurs also in nature under the influence of natural selection. It no longer merely selects a given mutation, nor only selects genes favored by it; its influence extends a great deal further over the total complex of genes, over the whole "genotypic milieu," on the background of which a given gene will manifest itself in various ways. In selecting one trait, one gene, selection indirectly also selects a definite genotype milieu, a genotype most favorable for the manifestation of the given character.
>
> By removing thus unfavorable combinations of genes, selection aids the realization of a more advantageous genotypic milieu. *Selection results in the enhancement of the trait,* and in this sense *it actively participates in the evolutionary process.*[21]

Hence Chetverikov put forth the first clear statement of the importance of the "genotypic milieu." Its experimental demonstration and further clarification, however, was the work of N. V. Timofeev-Resovsky. It was he who, in the words of Fothergill,[22] "stabilized" the concept of the interaction of genetic factors in a series of papers published 1925-1934, reporting work begun under Chetverikov's direction, 1923-1925.

In the first of these papers, "On the Phenotypic Expression of the Genotype,"[23] Timofeev-Resovsky used stocks of a

21. *Ibid.*

22. P. G. Fothergill, *Historical Aspects of Organic Evolution* (London, 1952), p. 237.

23. N. V. Timofeev-Resovsky, "O fenotipicheskom proiavlenii genotipa: 1. Genovariatsiia radius incompletus u Drosophila funebris," *Zhur. Eksper. Biologii, 1* (1925), pp. 93-142. An English article covering much of the same material appeared under the title, "Studies of the Phenotypic Manifestation of Hereditary Factors: I. On the Phenotypic Manifestation of

mutant in *Drosophila funebris* called "radius incompletus" (*ri*) in order to demonstrate that the phenotypic expression of *ri* varies according to the genetic environment in which it occurred. This work led him to distinguish three phenomena in the phenotypic manifestation of the gene which were shown to vary independently:

> In the intensity of the gene manifestation, the frequency of appearance, or *penetrance*, must be distinguished from the degree of expression of the character, or *expressivity;* the third phenomenon is *specificity*, or localization, extent, array of variants, and morphophysiological nature of the character.[24]

The *ri* character, however, proved unsuitable for the analysis of the third phenomenon, specificity, and hence work was done on another recessive autosomal gene of *Drosophila funebris* whose expression depends on the presence of *ri*: this mutation is called *vti* (*venae transversae incompletae*) and breaks or abolishes the crossveins of the wings. Although this work was briefly reported earlier and was "essentially completed by 1928,"[25] it was most completely described in an article published in 1934-5, "On the Influence of the Genotypic Milieu and of the Environment on the Expression of the Genotype."[26]

Timofeev-Resovsky employed the following strategy: in order to evaluate the effect of the genotypic milieu on the expression of the trait *vti*, he created a series of uniform but different genotypic backgrounds into which he introduced *vti* and *ri* in the homozygous condition; whereupon he tested the penetrance, expressivity, and specificity of the *vti* trait. To get the most diverse array of genetic backgrounds possible, he crossed flies homozygous for the *vti* and *ri* traits with various laboratory cultures and with wild flies from geographically diverse populations (from Moscow, Leningrad, Kiev, Central Russia, Saratov,

the Genovariation *Radius incompletus* in *Drosophila funebris*," *Genetics*, *12* (1927), pp. 128-165.

24. N. W. Timofeef-Ressovsky, "Uber den Einfluss des genotypischen Milieus und Aussenbedingungen auf die Realisation des Genotyps," *Nachr. (Biologie) Ges. Wiss. Goettingen. Math.-Physik. Kl. N.F. Fachgruppe IV* vol. I (1934-5). Dr. Roger Milkman kindly made available to me his unpublished translation of this article into English, under the title "On the influence of the genetic background and of the environment on the expression of the genotype: the mutation *vti (venae transversae incompletae)* in *Drosophila funebris*." Quotations used in the text are taken from his translation.

25. *Ibid.* (Milkman trans., p. 1).

26. *Ibid.*

the Crimea, the Caucasus, and so on). Homozygous *vti ri* flies which appeared in the F_2's were inbred and selected for various expressions of the trait. These populations were inbred for 25–35 generations (until selection had no further effect on the expression of the trait), resulting in populations essentially homozygous for *vti* modifiers. The penetrance was then measured as the percentage of individuals from such lines showing the trait; expressivity was measured as the percentage of offspring exhibiting the trait which totally lacked the posterior crossvein; and specificity was tabulated using a simple classification system based on the amount and location of crossvein deletion.

When data on penetrance in the thirty cultures were collected, a variation in penetrance was found ranging between 41% and 100%. Since these data were gathered simultaneously and under identical environmental conditions, and since all cultures are homozygous for *vti ri,* these differences are inherited, and are caused by the different array of modifying genes present in each culture. Expressivity also varied, ranging from 12% to 100%. In general, high penetrance was accompanied by high expressivity; but when we consider only those cultures with 100% penetrance, expressivity ranged between 29.3% and 100%, and hence expressivity was shown to be in large part independent of penetrance. The cultures also varied in the fields of influence or specificity, and this variation failed to correlate with either penetrance or expressivity. When Timofeev-Resovsky went on to test how environmental factors can influence penetrance, expressivity, and specificity, he found that while changes in food and humidity did not noticeably affect the *vti* phenotype, temperature affected penetrance and expressivity at two key points in development: the first larval stage and the pupal stage. The specificity, however, was not affected by temperature, but only by the "genotypic milieu."

The influence of Timofeev-Resovsky's conceptual innovation did not await the 1934 publication of his most complete treatment of the subject. Rather the impact of his 1925 article was immediate among Russian workers: as early as 1926, Russian work on *Drosophila* mutants began distinguishing between penetrance, expressivity, and specificity.[27] Later in 1925, Timo-

27. E.g., E. I. Balkashina, "Vliianie genotipa na mnozhestvennoe vyrazhenie genovariatsii *Alae curvatae* u *Drosophila funebris Meig.,*" (The influence of the genotype on the multiple expression of the genovariation [mutation] *Alae curvatae* in *Drosophila funebris Meig.*) *Zhur. Eksper. Biologii,* 2 (1926), no. 2-3.

feev-Resovsky left Moscow and moved to Buch, just north of Berlin, where he continued his work, keeping in close contact with his Russian colleagues.

Within a year of Timofeev-Resovsky's departure for Germany, his teacher, Chetverikov, had incorporated his work on the genetic background into a general statement of the evolutionary process which is considered by Th. Dobzhansky[28] to be the first that put to rest Jenkin's objections to the theory of evolution by natural selection, and the first of the founding papers of population genetics, preceding those of Wright, Fisher, and Haldane. Chetverikov's reasoning in this paper led to experimental work which has been justifiably termed "trail-blazing" by I. M. Lerner,[29] and hence it will be worth our while to explore this reasoning.

The purpose of Chetverikov's major theoretical work, "On Certain Features of the Evolutionary Process from the Viewpoint of Modern Genetics,"[30] is clearly formulated at the outset:

> Genetics is in similar contradiction with conventional views of general evolutionary concepts and in this, undoubtedly, lies the reason that Mendelism was greeted with such hostility by many outstanding evolutionists, both here and abroad. The present article sets itself the goal of clarifying certain aspects of evolution in the light of current genetic concepts.[31]

Chetverikov begins his discussion by treating the "origin of mutations in nature." He argues that the process of mutation observed in the laboratory is also going on under natural conditions, but that the occurrence of such mutations is not evident, primarily because recessive mutants would arise in the heterozygous condition and would "remain hidden from the eye."[32]

28. Th. Dobzhansky, *Mankind Evolving: The Evolution of the Human Species* (New Haven and London; Yale University Press, 1962), p. 136.

29. I. M. Lerner's introduction to Chetverikov, "On Certain Features . . ." (Lerner trans.).

30. A number of interesting aspects of Chetverikov's paper will not be discussed here, e.g. his use of a reproductive isolation criterion in his definition of the species; his use of calculation and genetic notions in his modified restatement of the theory of speciation by isolation; and a more detailed discussion of his debt to biometrics, genetics, and natural history. We will rather be concerned with those theoretical arguments which lead him to *predict* a condition of natural populations, which subsequently led to experimental confirmation.

31. Chetverikov, "On Certain Features . . ." (Lerner trans., p. 169; Russian reprint, 1965, p. 34).

32. *Ibid.* (Lerner trans., pp. 170-174; Russian reprint, pp. 35-42). In his

What happens to newly arisen natural mutations? Chetverikov draws on the work of Hardy and of Pearson to show that a "free-crossing" (*svobodno skreshchivanyi*) or panmictic (randomly mating) population, in the absence of selection, would maintain all genes, including the new mutants, at a constant frequency. Given frequent mutations, then, each would be kept and spread, which leads Chetverikov to conclude that

> *a species, like a sponge, soaks up heterozygous mutations while remaining from first to last externally (phenotypically) homogeneous.*[33]

What role does selection play? Chetverikov cites a table prepared by the English mathematician H. T. J. Norton showing how many generations are required for selection intensities of various magnitudes to alter the relative frequencies of alleles. He observes that

> the process of the *transformation of the species*, that is, of the *complete replacement* of a former, unadapted form by the more adapted one, always proceeds, practically speaking, *to an end.*[34]

But from Norton's table he also concludes that selection, as well as repeated mutation, causes the build-up of hidden recessive mutants in the population, since harmful recessives are selected again more slowly than harmful dominants, which are quickly eliminated.

Perhaps the most important feature of Chetverikov's ideas was that they led to the first genetic analysis of a natural population, begun in 1925 and first reported two years later. Notice that the three separate lines of thought outlined above led Chetverikov to conclude that natural populations should contain a large amount of cryptic variability. If, because of continual natural mutation, the maintenance of the resultant mutants, and the slower elimination of recessive (hence hidden) mutants by selection, species "soaked up" mutations "like a sponge" while remaining phenotypically uniform, Chetverikov reasoned that an inbreeding of samples from wild populations should allow these mutations which are masked in the heterozygous condition to become homozygous and thus to be expressed.

discussion, Chetverikov also treats other reasons why these mutations would not be noticed in natural populations, e.g. their frequently lower viabilities. The quotation is from Lerner, p. 177.

33. *Ibid.* (Lerner trans., p. 178; Russian reprint, p. 48). In this and all quotations used in the text, the italics are those of Chetverikov.

34. *Ibid.* (Lerner trans., p. 182; Russian reprint, p. 56.)

To test his reasoning, Chetverikov and his students[35] captured 239 wild female *Drosophila melanogaster* which had already been fertilized in nature, mated the F_1's brother × sister, and examined the F_2's. No less than 32 different hereditary characters which had been masked heterozygotically were found.[36] Chetverikov understood the evolutionary significance of his results:

> All these facts confirm the conclusion that the usual wild populations are extraordinarily heterozygous and so at any given time have a rich supply of inherited variations which, with changes in the environment, can be useful and so must play a decisive role for the evolutionary process.[37]

In a piece of parallel work Timofeev-Resovsky (1927) analyzed 78 females of *Drosophila melanogaster* from Berlin and found similar results.[38]

The experimental investigations of the Chetverikov group (1925-1929) had been much more extensive than Chetverikov's brief communication in 1927 before the Fifth International Congress of Genetics had indicated.[39] Studies had been made of a whole range of naturally occurring *Drosophila* species from around Moscow: *Drosophila phalerata* (by B. L. Astaurov and N. K. Beliaev), *Drosophila transversa* (B. L. Astaurov), *Drosophila vebrissina* (E. I. Balkashina), and *Drosophila obscura* (S. M. Gershenson), and a study had been made of *Drosophila melanogaster* from Gelendzhik, near the Causasian coast of the Black Sea. But as a result of the breakup of the Chetverikov group which followed his precipitous departure from Moscow,

35. Astaurov, "Two Landmarks . . ." lists the students who participated in "this first work in Moscow": B. L. Astaurov, E. I. Balkashina, N. K. Beliaev, S. M. Gershenson, I. F. Rokitskii, and D. D. Romashov (p. 26).

36. The only report by Chetverikov of this work was given at the Fifth International Congress of Genetics and published in the form: Tschetwerikoff, S. S., "Uber die genetische Beschaffenheit wilder Populationen," Z. *Induktive Abstammungs-Vererbungslehre, 46* (1928), pp. 38-39. (The spellings given in the text for Russian authors are generally transliterated from the Russian. Hence "Chetverikov"—though in German sources the name is variously spelled "Tschetwerikoff," "Tschetwerikov," and "Tschetverikov;" likewise, "N. V. Timofeev-Resovsky," instead of the German "N. W. Timoféef-Ressovsky," under which most of his works published in Germany, 1925-1945, appear; also "Koltsov," instead of "Koltzoff," or other variants.)

37. *Ibid.*, p. 39.

38. H. A. Timofeeff-Ressovsky and N. W. Timofeeff-Ressovsky, "Genetische Analyse einer freilebender *Drosophila melanogaster* Population," *Roux Arch. Entz. Mech. Organ, 109* (1927), pp. 70-109.

39. Astaurov, "Two Landmarks . . ." gives a good description of the work of the Chetverikov group by one of its members.

these results were only published fragmentarily. Hence the results of the Moscow sampling were first published in 1934 (by Gershenson[40]) and in 1935 (Balkashina and Romashov[41]).

The analysis of the genetic variability of wild populations of *Drosophila,* guided by Chetverikov until his departure from Moscow, was taken up in 1930 by Dubinin. A student of Chetverikov's at Moscow University until 1928, Dubinin had worked with A. S. Serebrovsky on the genogeography of domesticated fowl in 1929. Dubinin's first paper on *Drosophila* population genetics was based on research undertaken with fourteen coworkers.[42] Published in 1934, it is especially significant because it yielded a number of surprising and interesting results which stimulated a great number of later studies.

Dubinin and his collaborators collected samples from wild populations of *Drosophila melanogaster* from nine localities in the Caucasus and one in Central Russia in 1931 and 1932. They found some 61 identifiable mutants, which ranged in frequency from 3.9% to 33.1%. The concentrations and nature of the mutants found varied with the geographical source and within one source from year to year. Some of the mutations appeared identical to those obtained in laboratory strains, others were new alleles; some were present in all localities, others only in one. Dubinin's paper is also apparently the first to analyze the chromosomal polymorphism of natural populations, work that was later to be developed by Dobzhansky (beginning some four years later in 1938.)[43]

Hence Dubinin's study demonstrated chromosomal and genomic variability, but perhaps the most surprising result came from studies of the frequency of lethal recessives. Chet-

40. S. M. Gershenson, "Mutant Genes in a Wild Population of *Drosophila obscura,*" *Amer. Naturalist 68* (1934), p. 569.

41. E. I. Balkashina and D. D. Romashov, "Geneticheskoe stroenie populiatsii: I. Geneticheskii analiz Zvenigorodskikh (Moskovskoi oblasti) populiatsii *Drosophila phalerata* Meig., *transversa* Fall. i *vibrissina* Duda." (The genetic structure of populations: 1. The genetic study of Zvenigorodskii (Moscow region) populations of . . .) *Biologicheskii Zhur. 4,* no. 1.

42. N. P. Dubinin, M. A. Heptner, S. Iu. Bessmertnaia, S. Iu. Goldat, K. A. Panina, E. Pogossian, S. W. Saprikina, B. N. Sidorov, L. W. Ferry, M. G. Tsubina, "Eksperimental'nyi Analiz Ekogenotipov *Drosophila melanogaster,*" 1 (Experimental study of the ecogenotypes of *D. melanogaster*), pt. 1, *Biologicheskii Zhur.* 3 (1934), pp. 166-205. N. P. Dubinin, M. A. Heptner, Z. S. Nikoro, S. Iu. Bessmertnaia, W. N. Beliaieva, Z. A. Demidova, A. P. Krotkova, E. D. Postnikova; *ibid.,* pt. 2, *Biologischeskii Zhur., 3* (1934), pp. 206-216.

43. Th. Dobzhansky and M. L. Queal, "Genetics of Natural Populations: 1. Chromosome Variation in Populations of *Drosophila pseudoobscura* Inhabiting Isolated Mountain Ranges, I and II," *Genetics,* 23 (1938), p. 239; p. 463.

verikov, it should be recalled, simply mated brothers and sisters, and analyzed the F_2's for mutant traits. Such analysis will tell nothing about the frequency of lethals, however, since flies carrying homozygous lethals will simply not appear in the progeny to be counted. When new techniques of genetic analysis were used (the ClB technique, for example), the frequency of lethal mutations in the 10 natural populations ranged between 0% and 21.4%. In particular, 10–20% of the total number of second chromosomes analyzed carried recessive lethals. This outcome had not been expected at the time—Dobzhansky called it a "novel result—and a very startling one."[44] However, follow-up experiments done by a number of investigators corroborated Dubinin's findings.[45]

Dubinin's paper, by demonstrating the great allelic and genomic variability present in natural populations, became the first of a long series of such studies, to which he substantially contributed until 1948.

The Russian School is important both because of what it ended and what it began. Many authors have alluded to the estrangement between two traditions in biology which characterized its history in the early decades of this century: the "experimentalist" and the "naturalist" traditions.[46] It is significant, then, that the Russian School is one of the earliest to draw from both traditions in order to clarify the evolutionary process. Its founder, Chetverikov, was an entomologist, a biometrician, and a geneticist. Indeed, his great theoretical paper set as its purpose the resolution of this split, and it drew heavily on natural history studies for species notions and the theory of isolation; on mathematical studies—for example, those of Hardy, Pearson, and Norton; and on the genetical studies of the Morgan School. And by turning the techniques of genetics onto the problems of evolution in a natural setting, he did much to heal the unfortunate gap between the naturalists and experimentalists in biology—in effect, by creating experi-

44. Th. Dobzhansky, "Concepts and Problems of Population Genetics," in *Cold Springs Harbor Symposia in Quantitative Biology*, vol. XX, p. 4.

45. For example, C. Gordon, "The Frequency of Heterozygosis in Free-living Populations of *Drosophila melanogaster* and *Drosophila subobscura*," *J. Genet.* 33 (1936), 25-60. Sturtevant also did a follow-up study, as he mentions in his *A History of Genetics* (New York, 1965), p. 110.

46. For example, N. W. Timofeef-Ressovsky, "Mutations and Geographic Variation," in Julian Huxley, *New Systematics* (Oxford, 1940). See also Julian Huxley, *Evolution: The Modern Synthesis* (New York: Harpers, 1942), pp. 24-25. Also, Th. Dobzhansky, *Genetics and the Origin of Species*, 1st ed. (New York: Columbia University Press, 1937).

mental population genetics and making evolutionary theory experimental.

The work of Chetverikov and the members of his school had shown the great possibilities in the genetic analyses of natural populations, in particular of *Drosophila*. The impact of these efforts was blunted by the breakup of the group in 1929 before the bulk of the material had been published, but it came nonetheless. Timofeev-Resovsky continued the work in Germany; Dubinin took up the studies: after the publication of their key works in 1934, together with the belated publication of the findings of the Chetverikov group, population genetics took on a dynamic of its own. In Russia the work proceeded apace: the work was continued by a whole team of investigators until 1948, including N. R. Beliaev, R. L. Berg, S. M. Gershenson, G. D. Muretov, I. M. Olenov, A. N. Promptov, D. D. Romashov, and G. G. Tiniakov, among others. Abroad, Dubinin's work led to confirming experiments in England by Gordon et al.,[47] and in the United States by Sturtevant,[48] and to the first in a momentous series by Dobzhansky and associates in which he credits Chetverikov, Dubinin, Timofeev-Resovsky, Gordon and Sturtevant with "opening new vistas" by investigations of the genetics of free-living populations—a subject "hitherto almost untouched."[49]

The ideas of the Russian School on the "genetic background," or the "genotypic milieu," did not have the same kind of immediate impact, at least on theoretical formulation. But their implications are profound. For example, if a gene's effect depends greatly on its genetic and environmental background, then alleles cannot be assigned fixed "fitness" values. It might also be noted that from this work follows the important idea that aberrant phenotypes are not necessarily due to the presence of single mutant genes, but may be rather the result of certain combinations of genes relatively frequent in a population. Thus, the aberrant *vti* phenotype, which occurs only very rarely in natural populations, is the result of a major gene, *vti*, which is relatively frequent in natural populations, interacting with a

47. C. Gordon, "The Frequency . . .," and also later Cecil Gordon, Helen Spurway and P. A. R. Street, *J. Genet*, *38* (1939). The references listed at the end of the 1939 piece, twenty-five in all, include most genetic analyses of wild populations done prior to that time—some eighteen in number. Significantly, some thirteen of these had been done by members of the Russian School: Chetverikov or his students, Timofeev-Resovsky, or Dubinin and colleagues.

48. A. H. Sturtevant, "Autosomal lethals in Wild Populations of *Drosophila pseudoobscura*," *Biol. Bull. Wood's Hole*, *73* (1937), 542-51.

49. Dobzhansky and Queal, "Genetics of Natural Populations, I," p. 463.

large number of modifying genes (including of course *ri*). I might add that the enormous implications of this conclusion for eugenics have only very recently been appreciated. To a considerable degree, then, recent investigations on "gene strategy," "genetic homeostasis," and other modern researches on the interrelation of genes in various systems are indebted to the notions of the genotypic milieu, developed by the Russian School.

Ernst Mayr has distinguished "classical population genetics" which presented evolutionary change as essentially an input or output of genes, from the "newer population genetics" in which a gene can have a constellation of selective values, depending on its genetic and environmental backgrounds.[50] If we accept this distinction, it is clear that conceptually and experimentally the Russian School had laid the basis for the "newer population genetics" even while the "classical" was being enunciated.

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50. Ernst Mayr, "Where are We?" *Cold Springs Harbor Symposia,* vol. XXIV (1959), p. 2.