GENETICS

The 100th Anniversary of the Department of Genetics and Biotechnology, St. Petersburg State University

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Abstract

At least twice in its history, the Department of Genetics of the St. Petersburg University played a key role in the development of the field of genetics in Russia: first, at the outset of the origins of genetics in the country; and then once again during its comeback after Lysenkoism. At the beginning of the 20th century, the study of genetics in Russia was lagging significantly behind Europe and the United States. The first Russian paper on genetics, "Mendelism or the Theory of Breeding," was published by Professor Yelly Bogdanov only in 1914 (Bogdanov, 1914), years after Thomas Hunt Morgan and his students had laid the foundation for the chromosome theory of inheritance. This publication is a summary of key achievements and events in science and education that have taken place at the Department of Genetics of the St. Petersburg University over the course of the past 100 years.

Keywords: history of the Department of Genetics of the St. Petersburg University.

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The First Department of Genetics in the Country

The first department of genetics in Russia, the Department of Genetics and Experimental Zoology, was founded in 1919 at the Petrograd University by Yuri Alexandrovich Filipchenko (Goroschenko, 1994) [Fig. 1a]. In 1911, right after graduating from the University, he traveled to Germany, to the laboratory of Oscar Hertwig, to work on his master's thesis. It was in Germany that he met the famous geneticist Richard Goldschmidt. In the spring of 1912, Filipchenko visited the Stazione Zoologica in Naples, Italy. In September 1913, soon after presenting his master's thesis, he began teaching a new course, "The Study of Heredity and Evolution," at the Natural Sciences Division of the Department of Physics and Mathematics. This was one of the first courses in genetics in the country. The very first course was started by Andrey Afanasievich Sapegin in Odessa in 1912 (Ursu, 2012).

On November 15, 1917, Filipchenko successfully defended the first doctor's dissertation in genetics in Russia, "The Variability and Inheritance of the Skull in Mammals," and received a doctorate in zoology and comparative anatomy.

In 1920, Filipchenko founded the Laboratory of Genetics at the recently opened Peterhoff Institute for Natural Sciences (PINS) of the Petrograd University. Filipchenko's scientific interests focused on the problems of inheritance and variation of quantitative traits in animals and plants. Subsequently, Filipchenko and his colleagues studied quantitative genetics in wheat in the experimental



Fig. 1. Heads of the Department of Genetics in different years. a) Yury Alexandrovich Filipchenko (1882–1930); b) Alexandr Petrovich Vladimirsky (1886–1939); c) Yury Ivanovich Polyansky (1904–1993); d) Pavel Grigoryevich Svetlov (1892–1976); e) Georgy Dmitrievich Karpechenko (1899–1941); f) Mikhail Sergeevich Navashin (1896–1973); g) Nikolai Vasilyevich Turbin (1912–1998); h) Mikhail Efimovich Lobashev (1907–1971).

field in PINS. Filipchenko was highly proficient at applying the methods of variational statistics, and later became a specialist in what would later be termed genetic analysis. The development of these interests throughout Filipchenko's scientific career is clearly evident. His outstanding qualifications in general biology and fluency in three European languages — German, English, and French — helped him in his career as a scientist and educator (Kaidanov, 1994).

Yuri Filipchenko played a crucial role in organizing the Institute of Genetics at the Academy of Sciences of the USSR. It began on February 14, 1921, when he delivered a paper at the session of the Council for the Committee for the Natural Production Forces of Russia (CNPF). In his report, Filipchenko argued the necessity to form a scientific division for studying eugenics in Petrograd. The Council decreed "to organize within the CNPF a bureau for eugenics and to charge the executive committee with the task of estimating the associated expenses" (Konashev, 1994). After going through a number of name changes, the Bureau for Eugenics was reorganized into the Laboratory of Genetics in 1930, and later, in 1933, into the Institute of Genetics at the Academy of Sciences of the USSR, headed by Nikolai Vavilov.

Filipchenko arranged several animal-breeding expeditions to Central Asia and the Caucasus. Among his students and young fellow scientists who took part in these expeditions were Ya. Ya. Lus (Lusis), T. K. Lepin, A. I. Zuitin, N. N. Medvedev, and Theodosius Dobzhansky. In 1927, Dobzhansky [Fig. 2], on a scholarship from the Rockefeller Foundation, moved to work in T. H. Morgan's laboratory in the USA, where he later became the founder of the Synthetic Theory of Evolution (Dobzhansky, 1937), "inherited" Morgan's laboratory, and became widely regarded as the world's foremost geneticist.

From the very beginning, Filipchenko maintained close contacts with the most prominent geneticists both in Russia and abroad: Nikolai Vavilov, Nikolai Koltzov, Thomas Hunt Morgan, William Bateson, and others [Fig. 3]. After Filipchenko's death, these contacts brought leading representatives of Morgan's school — Hermann Joseph Muller and Calvin Blackman Bridges — to do research and teach at the Institute of Genetics, upon Vavilov's invitation.

After Filipchenko's death in 1930, the Department of Animal Genetics was headed by Alexander Vladimirsky [Fig. 1b]. In 1932 two departments of genetics coexisted at the University: the Department of Animal

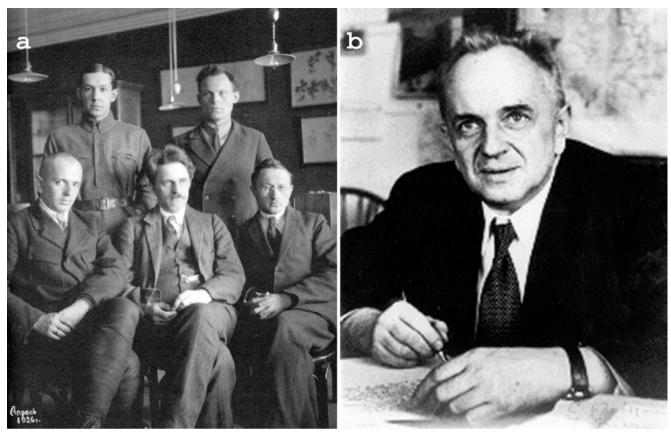


Fig. 2. Th. G. Dobzhansky (1900–1975). a) Dept. of Genetics and Experimental Zoology (1926), from left to right: seated — Th. G. Dobzhansky, Yu. A. Filipchenko, Ya. Ya. Lus; standing — V. I. Saveliev, N. N. Medvedev; b) Th. G. Dobzhansky in 1960s, USA.

Genetics and the Department of Plant Genetics. The latter was organized upon the initiative of Vavilov himself, who had recommended Georgy Karpechenko [Fig. 1e] as the head of the department.

The breadth of Yuri Filipchenko's interests is reflected in his numerous published scientific papers, textbooks, and popular science articles, which have been reissued several times. His *Popular Biology* alone has been reissued sixteen times. Filipchenko spearheaded an enormous body of a new field of science; many of its representatives became famous geneticists: M. L. Belgovsky, A. A. Prokofieva-Belgovskaya, N. S. Baturin, F. G. Dobzhansky, A. I. Zuytin, I. I. Kanaev, Yu. Ya. Kerkis, N. N. Kolesnik, T. K. Lepin, Ya. Ya. Lus, N. N. Medvedev, Yu. M. Olenov, E. P. Radjably, N. Ya. Fedorova, R. A. Mazing, Yu. L. Goroschenko, and others.

In the beginning of the 1920s, many scientific discussions on the problems of genetics, particularly focusing on the problem of inheritance of acquired traits, took place in Russia. Yuri Filipchenko took active part in these discussions. Unfortunately, underlying these discussions were unmistakably ideological tendencies. These tendencies deepened in the 1930s. During that period, the situation at the first department of genetics

in the Leningrad University gradually became more and more threatening. Already on January 14, 1929, an open letter against Yuri Filipchenko was published in *The Student Life* newspaper. Similarly, difficult times arrived for Nikolai Koltsov and his Institute for Experimental Biology. In 1939, the Institute was reformed and a new director was appointed. Also in 1939, the magazine *Under the Banner of Marxism* organized an academic discussion with Trofim Lysenko presiding over the panel and acting as a leading researcher, following in the steps of the newly developed teachings of Ivan Michurin.

In 1940, during a trip to Western Ukraine, Nikolai Vavilov was arrested. He died in 1943 in a Saratov prison from malnourishment (Pringle, 2009). In connection with Vavilov's case, Georgy Karpechenko was arrested and executed in 1941. Grigory Levitsky, the first cytogeneticist in Russia, also perished in prison. Georgy Nadson, who together with Gennady Filipov discovered the effect of ionizing radiation on genetic variation (1925) ahead of Hermann Muller, was arrested in 1937 and executed in 1939. This tragic fact became public only in 1990 (Zakharov and Surikov, 1989). The list goes on (see *Science Persecuted*, 1991, 1994, Yaroshevsky, ed.). The "academic discourse" of the 1930s, WWII, and the Au-



Fig. 3. From left to right: upper row — W. Bateson, O. Vogt, H. Federlei; lower row — N. I. Vavilov, Yu. A. Filipchenko, V. A. Dogel, I. I. Sokolov, Peterhoff Natural-Scientific Institute, Leningrad State University, 1925.

gust 1948 Session of the All-Union Academy of Agricultural Sciences, which outlawed the study of genetics in the USSR, threw the science at least a generation back. Teaching genetics was banned in the country, and thousands of geneticists and those who publicly supported them and shared their scientific views were fired from universities and research facilities throughout the Soviet Union (Soyfer, 1994; Borinskaya et al., 2019).

The Revival of Genetics in Russia

After the death of Alexander Vladimirsky, the Department of Animal Genetics was headed by Yury Polyansky [Fig. 1c] from 1939 to 1941. In 1941, when Polyansky was drafted to fight in WWII, he was replaced by Pavel Svetlov [Fig. 1d], who held this position until 1948. After Karpechenko's arrest in 1941, the Department of Plant Genetics was headed by B. G. Potashnikova, the wife of I.I. Present. In 1945–1948, the Department was headed by N. V. Turbin [Fig. 1f]. In 1948, he became head of the unified Department of Genetics and Breeding. In 1954–1956, this position was occupied by M. S. Navashin [Fig. 1g].

In 1957, Mikhail Lobashev (1907-1971) became the head of the Department of Genetics and Breeding [Fig. 1h]. His name is closely associated with the revival of the field of genetics at the Leningrad University. His early years became broadly known from the novel The Two Captains by Soviet author Veniamin Kaverin. The protagonist of the novel, Sasha Grigoriev, was based on Lobashev himself. Already at a young age, while studying in a commune school where he was sent as a homeless orphan, Lobashev demonstrated proclivity for art and took art classes. In Leningrad, Lobashev briefly deliberated whether to enter the University or the Academy of Arts. Based on his drawings and the photographs of his sculptures, the latter was eager to accept him without entrance exams. To paraphrase Hugo Iltis, the biographer of Gregor Mendel (Iltis, 1924), "It could have very well been that Leningrad would have had one representative of Socialist Realism more and one outstanding scientist less."

Lobashev made his final choice after reading Charles Darwin's *On the Origin of Species* and Ernst Haeckel's *The Art Forms of Nature*. In August 1929, he passed the entrance exams and was accepted into the Division of Biology of the Department of Physics and Mathemat-

ics at Leningrad University. The following year — the year of Filipchenko's death — Lobashev transferred to the Department of Genetics. Unlike Vladimirsky, he did not become a supporter of the theory of inheritance of acquired characteristics, yet kept his interest in the problem of variability throughout his life. By the 1930s, several excellent schools of biological thought flourished at the Department of Biology, which had diverged from the Department of Physics and Mathematics and become a separate entity, led by the likes of A. A. Uhtomsky, V. L. Komarov, S. P. Kostichev, V. N. Sukachev, D. I. Deyneka, K. M. Deryugin, V. A. Dogel, and Yu. Filipchenko. They were representatives of the old, pre-revolutionary intelligentsia, who actively passed their knowledge and scientific traditions down to the new generation of researchers, predominantly of proletariat origin.

As a future scientist, Mikhail Lobashev fell under the strong influence of the physiological disciplines, which he studied relentlessly. He sat through the course of cytophysiology by Professor D. N. Nasonov, which stimulated Lobashev to formulate his physiological hypothesis of the mutation process.

After graduating in 1932, and even before going to postgraduate school, Lobashev was hired to work at the Institute of Genetics of the Academy of Sciences of the USSR, created by Vavilov on the basis of the Laboratory of Genetics, which in turn was organized by Yuri Filipchenko. At the Institute, Lobashev met Vavilov and became impressed by the strength of his personality and his talent as a scientist. He met and became friends with Ya.Ya. Lus, one of Filipchenko's first collaborators, as well as American geneticists Calvin Bridges and Hermann Muller, whom he considered to be "the world's best specialists in *Drosophila*".

In 1935, Lobashev defended his dissertation entitled "On the Nature of Action of Chemical Factors on the Mutation Process". His official opponents during the defense were Hermann Muller (the future Nobel Prize laureate), Georgy Karpechenko (who was later executed during the period of repression of genetics), and E. Bauer (executed in 1938). On April 11, 1936, Lobashev published the article "Artificial Induction of Mutations" in Izvestiya newspaper. The closing remarks for the article were written by Muller, who highly praised Lobashev's work. These studies became the foundation for the physiological hypothesis of mutation, which became Lobashev's doctoral thesis, which he defended in 1946, soon after returning home from war. In it, Lobashev was the first scientist in the world to place the concepts of "mutation" and "repair" together (Lobashev, 1946, 1947). Since then, the dependence of mutagenesis on DNA repair systems has been widely accepted. Unfortunately, soon after his work was published, the author of the physiological hypothesis was deprived of any possibility to develop it any further.

In January of 1948, Lobashev was elected dean of the Department of Biology of Leningrad University. In August 1948, the infamous session of the Academy of Agricultural Sciences was held, after which all geneticists and their sympathizers were expelled from universities throughout the country. Fortunately for Lobashev, he was invited by Leon Orbeli to work at the Pavlov Institute of Physiology in Koltushi — a small town near Leningrad — where Lobashev was able to continue his work, and eventually became professor of physiology. After returning to the Department of Genetics in 1957 as its dean, Lobashev actively developed a new scientific concept — the systemic regulation of genetic and cytogenetic processes — in which he yet again demonstrated his prowess of a visionary researcher.

Yet another idea developed by Lobashev upon his return to the Leningrad University — the concept of signal (cultural) inheritance — served him as both a scientific and ethical principle. He stood by the credo: "Cadres for cadres!" His first order of business was the revival of teaching genetics at the University. In 1957, he began teaching general genetics, which became the basis of his textbook *Genetics* (Lobashev 1963, 1967). The history behind the publication of this book is full of drama and deserves its own chapter (see Inge-Vechtomov, 2015).

Another personality that played an important role in reviving genetic research at the Department of Plant Genetics, as well as teaching genetic analysis at the department, was Vasily Fedorov (1903-1976). Beginning in 1929, Fedorov [Fig. 4a] worked with Karpechenko in Detskoe Selo. In 1931-1935, he taught genetics at the postgraduate school at the All-Union Institute for Plant Breeding and the All-Union Courses for Skill Improvement organized by Vavilov. In 1939, he left the position of dean of the Department of Agronomy of the Leningrad Agricultural Institute. In 1948, he came to work at Leningrad University. He was assigned to the University "to improve" the Department of Genetics; the fact that he had at some point worked with Vavilov was somehow overlooked. During the Michurin era, Fedorov taught the course on the critique of the chromosome theory of inheritance. During lectures, he devoted a great deal of time to describing the chromosome theory in detail (because, according to him, "one must fully understand a theory in order to criticize it"), but usually had no time left for the actual criticism. Using this method, he taught several students who later became prominent scientists: the corresponding member of RAS I.A.Zakharov (a student at the Department of Microbiology at the time), Prof. K. V. Kvitko, Prof. I. B. Surikov, Prof. A. L. Yudin, Prof. Yu.B. Vakhtin, Prof. V.G. Smirnof, and others. When Lobashev returned to the University as head of the Department of Genetics, Fedorov further developed his course into an original course of Genetic Analysis (Zakharov, 2003; Zakharov-Gezekhus, 2016).





Fig. 4. a) Vasily Sergeevich Fedorov (1903–1976); b) N. V. Timofeev-Ressovsky and M. E. Lobashev, 1960s.

Of utmost importance to the new generation of budding geneticists were a series of lectures by "ideological Morganists" that Lobashev organized. Among the lecturers and presenters were: A. A. Prokofyeva-Belgovskaya, S. I. Alikhanyan, N. V. Timofeev-Ressovsky, P. M. Zhukovsky, and others. Also among lecturers were scientists from abroad who had just started visiting the USSR on a regular basis: Charlotte Auerbakh (UK), D. Boyce (Canada), D. Lewis, Clement Markert (USA), Boris Ephrussi, Nadine Plus, Piotr Slonimski (France), and others. Meeting one the greatest biologists of the 20th century, Nikolay Timofeev-Ressovsky, who was a good friend of Lobashev and regularly visited the Department with lectures, made a huge impression on us students at the Department of Genetics and Selection back then. The relationship between the two great scientists [Fig. 4b] were very strained at first, but eventually developed into a friendship that lasted a lifetime (see: Inge-Vechtomov, 2004).

At the first opportunity, Lobashev began sending his young fellow researchers to other laboratories abroad. The department organized and conducted numerous conferences, which were always an all-faculty effort.

By the 1960s, the Department had already offered three specializations: animal genetics (*Drosophila*, chickens, mice), plant genetics (rye, radishes, tomatoes, peas, etc.), and genetics of microorganisms (*Saccharomyces* yeast, algae). It also featured four research laboratories. Despite such diverse backgrounds, a single, overreaching research field was outlined for the department: Systemic Regulation of Genetic and Cytogenetic Processes. A present-day equivalent of this outline, which unites research from all the members of the department, is described as the Mechanisms of Integration of Genetic Processes.

Lobashev devoted a great deal of energy to modernizing and broadening the research and educational facilities of the Department. For a more detailed account of his endeavors, please refer to our collective work entitled Genetics: Yesterday and Today. For the 100th Anniversary of the Department of Genetics and Biotechnology, St. Petersburg State University (Inge-Vechtomov, ed., 2019). In it, you will also find information about the research directions that the department is currently investigating.

The Department of Genetics and Breeding (since 2012: Genetics and Biotechnology). The Recent History

After Mikhail Lobashev's death in 1971, Assistant Professor Kira Vatti took over the responsibilities of heading the Department. In 1972, Professor Sergey Inge-Vechtomov [Fig. 5d] was elected as department head. Since 2015, Professor Galina Zhouravleva has been acting in this capacity [Fig. 6h].

Based on the research and teaching methods established by Lobashev, the Department further developed the concept of systemic regulation of genetic processes — that is, their dependence on the mechanisms responsible for the integration of cellular, organismic, and finally, ecosystemic levels of biological organization. Another direction that the Department pursued during that period was the study of gene structure and function, and the expression of genetic information, primarily at the level of translation, as well as research in the area of protein inheritance.

Further development of plant genetics in particular led to the creation of extensive genetic collections for radishes, strawberries, tomatoes, etc. Work on expand-

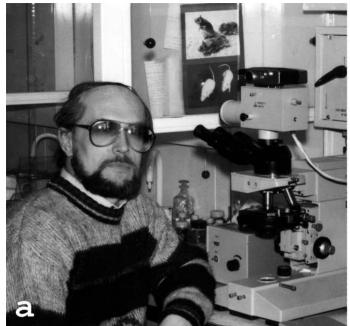








Fig. 5. a) E. V. Daev; b) L. A. Lutova; c) L. A. Mamon; d) S. G. Inge-Vechtomov.

ing the genetic collections and broadening the research of rye continued. After V.S. Fedorov, this research was headed by V.G. Smirnov [Fig. 6a], who also taught cytogenetics at the Department after his return from training at the Marcus M. Rhoades laboratory (Indiana University, USA) in 1964. Rye linkage maps were created using both traditional morphological and molecular markers: isozymic polymorphism of proteins and nucleotide polymorphism of DNA. The study of rye cytogenetics was enriched with methods of differential chromosome staining and the study of genetically determined anoma-

lies during meiosis. Considerable effort was also put into studying rye-wheat hybrids (Voilokov et al., 2019).

Molecular biology of plant genetics was further developed in the Laboratory of Genetic and Cellular Engineering of Plants (headed by Professor L. A. Lutova) established in 2000 [Fig. 5b]. The new laboratory conducts research in plant regeneration, genetics of plant tumorigenesis, and studying the role of transcription factors in these processes. The laboratory also studies horizontal gene transfer between agrobacteria and plants. In 2000, the laboratory began a new long-term project — breeding



Fig. 6. a) V. G. Smirnov; b) I. A. Zakharov-Gezekhus; c) L. Z. Kaidanov (1936–1998); d) A. P. Galkin; e) V. S. Baranov; f) A. V. Voilokov; g) Yu. O. Chernov; h) G. A. Zhouravleva; i) E. I. Stepchenkova; k) M. V. Padkina; l) M. N. Smirnov (1938–2012); m) I. A. Tikhonovich; n) K. V. Kvitko (1932–2014).

plants that produce pharmaceutical compounds (interferon in particular). This research is being conducted in close collaboration with the Biochemical Genetics Laboratory headed by M. V. Padkina [Fig. 6k]. In its research, the laboratory uses genetic collections of different plants preserved at the department — radish, pea, potato, and others — as well as different genetic forms of *Arabidopsis thaliana*. The laboratory also develops methods for improving the resistance to insect pests by genetically modifying the sterol metabolism of plants (Lutova et al., 2019).

The department also conducts research in ecological genetics. The impetus for this new direction was the previous work with two intensively studied model organism: *Drosophila* and the yeast *Saccharomyces*. These two organisms are tightly connected in a single ecosystem: the yeast serves as the source of sterols — precur-

sors of the hormone ecdysone — for *Drosophila*. Ecdysone is crucial for the development of the fruit fly. *Drosophila* cannot synthesize ergosterol but can convert it into ecdysone. This research served as the foundation for the development of a model of a yeast-*Drosophila* ecological-genetic system in which each member was connected by consecutive stages of sterol metabolism. Yeast mutants deficient in ergosterol biosynthesis were used in a culture medium for *Drosophila* and demonstrated the effect of these modified ecological relations on the development of organisms, and genetic processes (mutagenesis, recombination) in *Drosophila* (Luchnikova, Inge-Vechtomov, Ibragimov, and Levchenko, 1981; Kamilova, Luchnikova, and Inge-Vechtomov, 1982).

The development of ecological genetics at the Department of Genetics is closely linked with the All-

Russia Research Institute for Agricultural Microbiology (AIAM) under the leadership of its director, Igor Tikhonovich [Fig. 6m]. An academician of RAS, Tikhonovich graduated from and worked at the Department until he left to work at the Institute. Together with his colleagues, he studied the interaction between genetic regulation of soil microbiota and higher plants in nitrogen fixation. The research led to the discovery of the principle of complimentary genetic processes in soil microorganisms and plants. Both the fundamental and applied significance of this work cannot be underestimated, since it has paved the way for the development and production of microbiological (as opposed to chemical) fertilizers used in agriculture (Tikhonovich, 2019). The Laboratory of Genetic and Cellular Engineering of Plants of the Department of Genetics took active part in this research, studying the development of plant nodules, which are responsible for nitrogen fixing. This collaboration between the Department and the Institute for Soil Microbiology was spurred by the organization in 2003 of the Molecular Biology for Human and Environmental Health of Northwest Russia Research and Education Center (REC) at the University. The laboratory of Tikhonovich (who became a professor at the Department of Genetics) from the Institute for Soil Microbiology became part of the REC together with the Department of Genetics.

Research in ecological genetics further developed Lobashev's concept of systemic regulation of genetic processes, which had originally led to the creation of the physiological hypothesis (now theory) of the mutation process. This work was initially based on studying animals, primarily *Drosophila*: Kira Vatti and Margarita Tikhomirova studied the effect of high temperatures (a non-mutagenic factor) following a mutagenic exposure to X-rays. Soon, younger researchers joined the experiments and took the study in a completely new direction. For example, the work by Ludmila Mamon [Fig. 5c] shifted the focus of the study from heat shock (stress) proteins to the investigation of the transport and metabolism of messenger RNAs in *Drosophila* (Mamon, Barabanova, and Golubkova, 2019).

Another prominent development of the idea of systemic regulation originated in the study of mutagenic effects of stress induced with pheromones in mice. Initially, the effect had been shown primarily for somatic cells, and later, for gonadal cells. Of particular interest was the fact that the effect was demonstrated using the smell of alpha-males as the stressor — a highly efficient agent affecting younger males (Daev, 2019). Mice use smell as a means of communication. These experiments are being successfully conducted by a group led by Professor E. V. Daev [Fig. 5a] at the Animal Genetics Laboratory.

Yet another direction of studying the concept of systemic regulation of genetic processes was initiated by Professor Leonid Kaidanov [Fig. 6c]. Selecting

for the lowest sexual activity in Drosophila males, and then again for the highest activity, Kaidanov and his colleagues, in collaboration with Gvozdev's laboratory at the Institute for Molecular Genetics of the Academy of Sciences of the USSR, demonstrated the changes in the spectrum of mutational variability as a result of the conducted selection and inbreeding. In addition, they discovered the causes of genetic differences in the inbred strains obtained by changing the direction of selection. The underlying causes appeared to be connected to the characteristic distribution of transposons (mobile dispersed genes) in Drosophila's genome. The pattern of distribution and the number of mobile elements were highly specific for the inbred strains and changed abruptly when the direction of selection was reversed (Gvozdev et al., 1981; Iovleva, 2019).

The organization of the Laboratory of Genetics of Microorganisms at the Biological Institute in Old Peterhoff in 1959 served as a strong stimulus for furthering molecular genetics studies at the Department of Genetics. The first head of the laboratory was Ilya Zakharov (now RSA corresponding member I.A.Zakharov-Gezekhus) [Fig. 6b]. He was a graduate of the Department of Microbiology at the University and was invited as a postgraduate student by Lobashev. The first research object of the laboratory was the yeast Saccharomyces cerevisiae. At the end of 1959, K. V. Kvitko [Fig. 6n] joined Zakharov. Kvitko was a 1956 graduate of the Department of Genetics with a specialization in plant genetics, and was hired as lecture assistant to the staff. Kvitko began researching the mutation process in the unicellular alga Chlorella. He later included another species of algae in his research — Chlamydomonas, which better suited the research due to the presence of sexual reproduction and offered a possibility to conduct tetrad analysis. Both organisms were used to study the genetics of photosynthesis and the biogenesis of photosynthetic pigments (Chekunova, 2019).

In 1969, a new laboratory, the Physiological Genetics Laboratory, stemmed from the Laboratory of Genetics of Microorganisms headed by Kvitko in 1964-1975. The new laboratory continued the study of yeast genetics. It was headed by S. G. Inge-Vechtomov, who had just returned from the USA, having completed a scholarship program there. While studying at the Department of Genetics and Breeding, Inge-Vechtomov conducted standard experiments with Drosophila, but was persuaded by his supervisor, I. A. Zakharov, to switch his research to yeast genetics. I. A. Zakharov left the Department in 1964, and went on to work at the Leningrad Institute of Nuclear Physics. Before that, we had managed to successfully master tetrad analysis and designed a method for genetic analysis of yeast in random ascospore samples using the digestive juice of snails. By that time, the Peterhoff breeding stocks of yeast had already been developed as descendants of race XII of S. cerevisiae.

In the late 1950s to early 1960s, geneticists around the globe worked on developing numerous gene-enzyme systems or mutation systems. Delving deeper into the fine structure of the gene served as a precursor to the deciphering of the genetic code and the formation of a new paradigm in molecular genetics. During that period, we had just begun obtaining biochemical mutants in yeast of our Peterhoff breeding strains. Our interest was particularly drawn toward the red ade1 and ade2 adeninerequiring mutants. They were easily observed among many white (non-mutant) colonies. Thus, a real possibility to focus research on the gene problem arose, which signified a step in the "molecular direction". Eventually, a group of researchers focusing on the ade1-ade2 system formed. It included postgraduates of the Department of Genetics: S. A. Kozhin, B. V. Simarov, N. N. Khromov-Borisov, who had graduated from the Department of Chemistry, and T.R. Soidla, from the Tartu University. Soidla came to the Leningrad Department of Genetics with an already strongly developed interest in interallelic complementation. Later, E. P. Raipulis, the former student of Ya. Lus from Riga, who had studied Drosophila before, joined the group.

The team continued research for years in an amicable and productive atmosphere. Everybody was young and full of energy (Mironova, 2019). Lobashev himself encouraged the team's ardor, which could also be explained by the overall tendency toward the revival of genetics in general. Moreover, it was a period of self-education in science, and this is not always easy. The team was effectively looking for solutions to the problems that had already been solved; those were nevertheless invaluable steps to be taken on the way to "real" science. The young scientists had to confront their own paradoxes and resolve them in order to achieve true breakthroughs. And achieve breakthroughs they did.

Nikita Khromov-Borisov discovered a mutagenic effect of 6-N-hydroxilaminopurin, which was used for the induction of *ade1* and *ade2* mutants. While studying an extensive collection of these mutants, induced using a variety of chemical and physical mutagens, different suppressor mutations were found and nonsense mutations were identified. A highly detailed interallelic complementation map for the gene *ADE2* and recombination maps for *ADE1* and *ADE2* were devised. The phenomenon of allelic complementation induced by nonsense suppressors was discovered. Interallelic complementation in triploids was studied, which laid the groundwork for the genetic analysis of the quaternary structure of phosphorybosil-aminoimidazole carboxylase encoded by *ADE2*.

It was at that time that the study of mutations of two genes, *sup1* and *sup2* — now known as the omnipotent translational nonsense suppressors *SUP45* and *SUP35* — began. A broad range of characteristics of these mutants,

particularly their recessive nature, suggested in 1970 that they encoded the factors of translational termination (Inge-Vechtomov and Andrianova, 1970). A further collaboration with Moscow and French scientists, when G. A. Zhouravleva [Fig. 6h] worked at the University of Rennes in France (Zhouravleva et al., 1995), definitively proved that hypothesis. For more details of the history of this discovery, see the previously cited compendium (Inge-Vechtomov, 2019; Zhouravleva, 2019).

Paradoxically, the research of genetic regulation of translation termination was linked to the key work at the Department of Genetics carried out in the field of protein inheritance (Chernoff, 2019; Zhouravleva, 2019). In 1965, Brian Cox described a curious cytoplasmic [PSI]-factor — a nonsense suppressor — in yeast (Cox, 1965). Its physical nature was understood only in 1988, when Yu. O. Chernoff [Fig. 6g] and his group from the Laboratory of Physiological Genetics demonstrated that the amplification of SUP35 (SUP2) led to the induction of [PSI] in the cells of S. cerevisiae, which persisted even after the loss of the plasmid, bearing gene SUP35. The elimination of [PSI] occurs after the cultivation of cells in a growth medium enriched with guanidinium hydrochloride (Chernoff et al., 1988). Later, R. Wickner referred to these results when he offered his hypothesis of the prion nature of [PSI] and some other cytoplasmic determinants with similar characteristics in yeast (Wickner, 1994). Subsequently, Chernoff and his colleagues working at the Department of Genetics, and later at Georgia Tech University (USA), initiated a new direction of research: the study of the role of chaperone proteins in biogenesis and the persistence of prion (protein) hereditary determinants (Chernoff, 2019). This work is currently underway in the Laboratory of Amyloid Biology which Chernoff founded after he had won the International Mega Grant of the St. Petersburg University (Chernoff, 2019).

In 1975, the Laboratory of Biochemical Genetics was opened at the Department of Genetics and Breeding. Its head, M. N. Smirnov [Fig. 6l], was a graduate of the Department of Biochemistry of the St. Petersburg University. He transferred to the Laboratory of Physiological Genetics from Timofeev-Ressovsky's laboratory at the Institute of Medical Radiology (Obninsk) upon invitation from Lobashev. After Smirnov's death in 2012, the Laboratory of Biochemical Genetics was headed by Professor M. V. Padkina [Fig. 6k]. The group's, and later the laboratory's, research focused on AIR-carboxylase, coded for by the ADE2 gene. Later, the research expanded to the study of genetic regulation of the biosynthesis of acid phosphatases in yeast. A detailed study of this model, and the many mutants for the regulation of acid phosphatase which resulted from it, allowed for their further use in studying the development of the producers of biologically active compounds: cytokines, the surface antigene of the hepatitis B virus, interferons, human interleukin-2, etc. The number of yeast species for cloning and production of biologically active compounds gradually expanded. This research laid the groundwork for a fruitful cooperation with the Laboratory of Genetic and Cellular Engineering of Plants headed by L. A. Lutova on the development of plant producers of the bovine γ -interferon (Padkina, Rumyanzev, and Sambuk, 2019).

Another example of fruitful collaboration outside the University in the aforementioned Molecular Biology for Human and Environmental Health of Northwest Russia Research and Education Center (REC) is the cooperation between the Laboratory of Prenatal Diagnostics (headed by the corresponding member of RAS, V.S. Baranov [Fig. 6e]) at the Dmitry Ott Institute for Obstetrics and Gynecology and the Department of Genetics of the St. Petersburg University in the area of education and research. We had united our efforts more than a decade prior to the three Academies (Agricultural, Medical and the so-called Big Academy) being merged in 2013. Firstly, this allowed the REC to prepare specialists for itself. Additionally, it helped create a practice and educational basis for the students. This also stimulated joint research of genetic polymorphism in human populations, the participation in the development of the Human Genetic Passport, human molecular genetics and cytogenetics, chromosome methylation, etc. Hundreds of students have attended lectures on human genetics and become acquainted with the ever-broadening horizons of application of genetics in medicine, diagnosis, prevention, and possibly cure for inherent diseases in humans (Baranov and Kusnetsova, 2019).

The organization of the St. Petersburg Branch of the Vavilov Institute of General Genetics RAS marked another remarkable highlight in the recent history of the Department. In 2005, the director of the Institute, RAS Academician Yu. P. Altukhov, and the rector of the University, APS Academician L. A. Verbitskaya, approved the initiative of the Department. The St. Petersburg Branch accepted graduates of the Department and worked in close cooperation with it. Sergey Inge-Vechtomov [Fig. 5d] was appointed director of the St. Petersburg Branch. The Branch currently comprises three laboratories. The Laboratory of Plant Genetics and Biotechnology (head: A. V. Voilokov [Fig. 6f]) conducts research on the rye genetic collection and rye-wheat hybrids (triticale). The Laboratory of Genetic Modeling of Human Diseases (head: A. P. Galkin [Fig. 6d]) specializes in the genetics and molecular biology of prions and amyloids, studying both pathological and adaptive functions of these aggregates in yeast and multicellular organisms, such as birds and mammals. The Laboratory of Mutagenesis and Genetic Toxicology (head: E. I. Stepchenkova [Fig. 6i]) studies genetic regulation and enzymology of mutagenesis. In addition, it conducts research on phenotypic

expression of primary lesions of genetic material, which Lobashev termed pre-mutational changes. The test system (alpha-test) designed on the basis of illegitimate mating ($\alpha \times \alpha$) in the heterothallic yeast *S. cerevisiae* demonstrated that up to 90% of primary lesions may be eliminated by repair systems, and only a small minority of them are converted into mutations.

In conclusion, it is necessary to stress that the hundred years of history of the Department of Genetics and Biotechnology at the St. Petersburg State University definitively illustrate how the development of scientific traditions based on adherence to the evolution of the application of scientific rigor to various fields of genetics, and attention to all, even most paradoxical results, spur creativity and open new horizons in scientific research. The same principles were used as the basis for the creation of the system of education in the field of genetics, but that is a topic for a future publication.

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