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Historical Article

The role of the *Drosophila* genetic collection in the formation of modern scientific research directions and in the educational process at the Department of Genetics and Biotechnology of Saint Petersburg State University

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ABSTRACT

Genetic analysis, as a fundamental method of genetics, is possible under the obligatory condition of presence of hereditarily different variants of the same features. Success of the analysis depends on the breadth of diversity of hereditary forms available to the researcher. In this regard, creation and maintenance of genetic collections is the first stage of genetic analysis. At present, genetic collections, including *Drosophila*, have not lost their primary importance even despite the obvious superiority of molecular methods in genetics and shift of research to the level of features characterizing the peculiarities of individual molecules. In many ways, it is the collection material that serves as a starting point in the development of new research directions in modern genetics. In addition, it should be noted that the task of the educational process at the university is to develop the student's ability to analyze, critically evaluate the results of the experiment, and understand the logic of the experiment. In this regard, the use of genetic collections is an integral part of the educational process, allowing to stimulate the development of the required qualities.

Keywords: genetic collections; *Drosophila melanogaster*; educational process; scientific school.

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Историческая статья

Роль генетической коллекции дрозофилы в формировании направлений исследований и в образовательном процессе на кафедре генетики и биотехнологии Санкт-Петербургского государственного университета

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АННОТАЦИЯ

Генетический анализ как основополагающий метод генетики возможен при обязательном выполнении условия — наличие наследственно различающихся вариантов одних и тех же признаков. Успешность проведения анализа зависит от широты разнообразия наследственных форм, имеющихся у исследователя. В этой связи создание и поддержание генетических коллекций представляет собой первый этап осуществления генетического анализа. В настоящее время генетические коллекции, в том числе дрозофилы, не потеряли своей первостепенной значимости даже несмотря на очевидное превосходство молекулярных методов в генетике и смещение исследований на уровень признаков, характеризующих особенности отдельных молекул. Во многом именно коллекционный материал служит отправной точкой в становлении новых направлений исследований в современной генетике. Кроме того, нельзя не отметить, что задача образовательного процесса в университете — это формирование у учащегося способности к анализу, критическому оцениванию результатов эксперимента, понимание студентом логики постановки эксперимента. В этой связи использование генетических коллекций — неотъемлемая часть образовательного процесса, позволяющая стимулировать развитие требуемых качеств.

Ключевые слова: генетические коллекции; *Drosophila melanogaster*; образовательный процесс; научная школа.

Как цитировать

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The largest genetic collections are available for *Drosophila melanogaster*, one of the leading model organisms in genetics. Initially, the creation of Drosophila collections was linked to several universities in the United States, where special centers for genetic material preservation were established, housing hundreds of Drosophila strains. Subsequently, similar centers appeared in Europe, particularly in Sweden, as well as in Russia. The Department of Genetics and Biotechnology at Saint Petersburg State University has been building its current *Drosophila melanogaster* genetic collection since the late 1950s, when the Lysenkoist era ended and genetics could be revived in Russia. The first strains were brought to the Department of Genetics and Breeding at Leningrad State University in April 1957 by Ilya Zakharov, with the support of Mark Belgovsky of the Institute of Biophysics of the USSR Academy of Sciences in Moscow. The new collection of Drosophila strains was primarily used as educational material for practical classes within the department's general genetics course. It also served as scientific material for coursework and graduation theses. Moreover, Drosophila strains were used in numerous studies, largely related to one of the department's research topics, mutation mechanisms. In these studies, initiated by Mikhail Lobashev, Head of the Department of Genetics and Breeding, Drosophila served as a model organism to demonstrate the role of the organism's physiological status in mutations. Lobashev's students Kira Vatti and Margarita Tikhomirova contributed greatly to these studies. These researchers and their students demonstrated how sex, development stage, and germ cell differentiation stage affect the frequency of various types of mutations. One of the most significant findings of these Drosophila studies was the confirmation of the presence of premutational damage, which could be identified using an original approach: the combined effect of a mutagenic factor and a non-mutagenic factor that modifies its result. These studies were made possible by the availability of Drosophila strains that allowed identifying and assessing the frequency of mutations such as nondisjunction and sex chromosome loss, sex-linked recessive lethal mutations, translocations, and other types of mutations, as well as Drosophila strains with defects in various repair systems [1, 2].

Notably, Drosophila genetic collections are not static, but are constantly replenished with newly identified mutations, synthetic genetic lines, and material derived from long-term breeding. Breeding goals are extremely diverse and are determined by research trends that are considered most relevant at a given time. Let us look at two examples that clearly demonstrate the significance of the Drosophila genetic collection in shaping new research areas at the Department of Genetics and Breeding, now the Department of Genetics and Biotechnology at Saint Petersburg State University.

In 1966, a unique large-scale genetic selection experiment was initiated on Lobashev's recommendation. It aimed at assessing the consequences of selection by adaptively important traits in Drosophila. The work was led by Leonid Kaidanov. For more than five decades, students, postgraduates, and researchers worked under his guidance to select Drosophila by the trait of low sexual activity in males [3]. This meticulous work produced over 1.5 thousand generations of Drosophila strains with low sexual activity in males and related inbred strains. Thus, numerous strains differing by the same non-adaptive trait were obtained. This material was then used to draw very important conclusions regarding the consequences of selection by this trait.

Among the most significant findings of this study is the persistence of hereditary heterogeneity in the low-activity strain, despite dozens of inbred generations. Artificial selection by a decrease in an adaptively important trait leads to an increase in strain mutability, as indicated by the accumulation of recessive mutations that reduce viability, primarily in Drosophila's chromosome 2 [4]. Inverse selection aimed at increasing sexual activity (high-activity strain) reduced the burden of harmful mutations while increasing the accumulation of supervital mutations.

To determine the source of the increased mutation rate in the selected strains, the content of mobile genetic elements in the genomes of the low-activity strain and related strains was analyzed [5]. The genomes of these strains carry a variety of retrotransposons, the distribution of which within individual chromosomes remains constant during hundreds of generations of strains maintained in the collection. The subsequent analysis of a collection of strains related to the low-activity strain and differing in adaptability revealed certain patterns in the movement of mobile genetic elements across the genome, which were associated with the results of selection in different directions. To clarify the role of mobile genetic elements in selection by an adaptive trait, the hobo mobile genetic element was analyzed. High- and low-activity Drosophila strains differed in the qualitative and quantitative composition of hobo element copies [6].

Thus, Kaidanov's collection of highly inbred related Drosophila strains differing in reproductive function at the Department of Genetics and Biotechnology served as the foundation for a new research area not only within the department, but also in genetics as a whole, focusing on the genetic consequences of close inbreeding and selection. Drosophila, in turn, serves as a unique breeding model due to the universal organization and functioning of the genetic material of all living organisms.

Tikhomirova's work on Drosophila selection for heat tolerance is the second unique example of creating a collection of Drosophila strains, which served as the

foundation for another research area in the department. In continuation of previous research on mutagenesis, the role of adaptation to high temperatures in mutations was studied. For this purpose, a heat-resistant T strain was developed in 1980. The strain could live and reproduce at 32°C, which is above the threshold temperature for *Drosophila melanogaster*. The T strain enabled assessing the effect of genotypic and ontogenetic adaptation to elevated temperature in mutagenesis. Genotypic and ontogenetic adaptations were modeled by exposing the T strain and wild-type strain that developed at different temperature conditions to heat stress at 37°C. The temperature of 37°C resulted in heat shock in Drosophila that developed at both 25°C and 32°C. Lower temperatures (33 or 35°C) did not cause stress in heat-tolerant Drosophila [7]. Stress responses in heat-tolerant Drosophila determined further research on the role of heat shock proteins in protecting against high temperatures. For this purpose, another Drosophila strain was selected, with the temperature-sensitive mutation *l(1)ts403* and impaired heat shock protein synthesis [8]. It was previously shown that the synthesis of heat shock proteins in this mutant is inhibited at the post-transcriptional level. The temperature-sensitive mutation *l(1)ts403* was an allele of the *sbr* (*small bristles*) gene. The gene *sbr*, in turn, is an ortholog of the evolutionarily conserved gene *Nxf1*, which is responsible for the nuclear export of mRNA. Thus, it became clear that impaired heat shock protein synthesis is associated with a defect in the export of mRNA of heat shock genes [9]. Currently, the collection of the Department of Genetics and Biotechnology includes eight strains carrying mutations of different molecular origin in the *sbr* gene of Drosophila (*DmNxf1*). The mutant allele sbr^{12} is a 30-bp deletion [10], which is lethal in homozygotes and is maintained on the FM6 balancer chromosome. The allele sbr^{5} is a 494-bp deletion that removes the end of exon 8, the beginning of exon 9, and the intron between them [11]. Similar to the allele sbr^{12}, it is lethal in homozygotes and is maintained on the FM6 balancer chromosome. The deletion $Df(1)v^{L4}$ removes the gene *sbr* and is lethal in homozygotes. The allele sbr^{10} is the temperature-sensitive mutation *l(1)ts403* and is characterized by a series of point substitutions. In particular, the substitution of C with T at position 416 of the nucleotide sequence leads to the replacement of proline with leucine at position 139 of the amino acid sequence in the RNA-binding domain [12]. This mutation can be characterized as a conditional temperature-sensitive lethal mutation. Sequencing of the sbr^{1} allele revealed no changes in the coding region of the gene; its phenotypic effect is expressed by the disruption of the structure of scutellar bristles, up to their absence. The analysis of mutant alleles of the *sbr* gene in Drosophila (*DmNxf1*) demonstrated a wide pleiotropic effect characterized by nondisjunction in meiosis in females [13], spindle defects in meiosis [11], cytokinesis, induction of male sterility [14], and behavioral anomalies [15]. The observed effects indicate the multifunctionality of this gene products and their involvement in fundamental cellular processes. It was later discovered that the export of mRNA from the nucleus to the cytoplasm is not the only function of the DmNxf1 protein. Modern molecular cytogenetic methods enabled the use of strains with the *sbr* (*DmNxf1*) gene mutation as a model for assessing the role of the DmNxf1 protein in nuclear-cytoplasmic mRNA export, embryogenesis, neurogenesis, and chromosome disjunction regulation.

The research of the *sbr* (*DmNxf1*) gene functions involves an assessment of its impact on imago lifespan. One phase of the study used females with different genotypes: $sbr^{12}/FM6$, $sbr^{5}/FM6$, $sbr^{del}/FM6$ (with *sbr* gene deletion), sbr^{1}, standard laboratory wild-type strains *Oregon-R* and *Canton-S*, as well as hybrid females *C-S/FM6* (+/*FM6*) and sbr^{del}/*C-S* (sbr^{del}/+) (Fig. 1).

Females with the *sbr5/FM6* genotype showed a decrease in maximum lifespan. There were differences in the maximum lifespan of females with the $sbr^{5}/FM6$ and $sbr^{12}/FM6$ genotypes. These mutations are known to influence protein structure (SBR^{5}: deletion of 57 amino acids, SBR^{12}: deletion of 10 amino acids), damaging the NTF2-binding domain and affecting interactions with partner proteins. The effect of the sbr^{5} mutation is most likely due to an extensive deletion that significantly alters protein structure and functions. Notably, the presence of the *sbr1* allele in homozygotes causes a twofold reduction in lifespan in females. This mutation apparently affects the regulatory regions of the *sbr* (*DmNxf1*) gene, which may cause changes in gene expression and disrupt mRNA transport. Impaired mRNA transport obviously affects all cellular processes and can result in reduced viability.

Thus, the use of strains carrying mutations of different molecular origin in the *sbr* gene of Drosophila (*DmNxf1*) allows assessing specialized cytoplasmic functions of the DmNxf1 protein, which appear to be related to the transport and maintenance of specific mRNAs in an untranslated state or their degradation. Our research priorities in this area include assessing the impact of *DmNxf1* gene mutations on ribonucleoprotein complex formation, as well as identifying partner proteins and RNA targets required for normal neurogenesis.

The active participation of students in faculty research is an essential component of university education. This approach is aimed at preparing future scientists, which requires students to develop skills in experimental design, data analysis, and critical assessment of research findings. For a long time, the genetic analysis course was the basic course in genetics at the department, with practical training in addition to lectures as a prerequisite. The most notable accomplishment of the genetic analysis

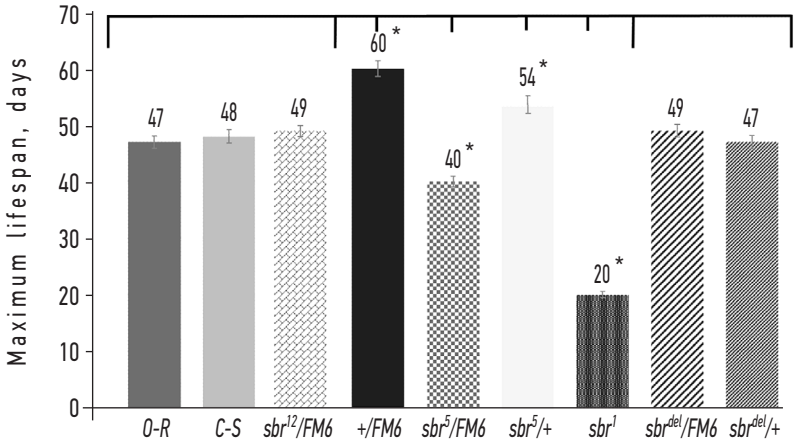

Fig. 1. Maximum lifespan of *Drosophila melanogaster* females of different genotypes. *p <0.05, statistically significant differences between the maximum lifespan indices of flies of the compared genotypes.
Рис. 1. Максимальная продолжительность жизни самок *Drosophila melanogaster* разных генотипов. *p <0,05 — статистически значимые различия между показателями максимальной продолжительности жизни мух сравниваемых генотипов.

course at the Department of Genetics and Breeding is the invaluable contribution of Associate Professor Vasily Fedorov to Russia's genetic education system. He created this course and was the first to teach it Leningrad State University's Department of Genetics and Breeding during Russia's tough period of genetics persecution. His legacy was later carried on by talented faculty members like Vatti, Tikhomirova, Mikheev, and Mamon.

Initially, the practical part of the course included an introduction to genetic analysis using objects from various systematic groups. The goal was to demonstrate the universality of genetic patterns, taking into account the biological characteristics of experimental objects and special analysis methods. The biological objects included rye, tomato, Arabidopsis, and yeasts. This laid the groundwork for the subsequent successful work of graduates in various fields of genetics.

Given the rapid advancement of genetics in recent decades, particularly in molecular genetics and analysis techniques, the department's curriculum has been significantly restructured. Many topics covered in the theoretical and practical sections of the genetic analysis course have evolved into autonomous academic disciplines. The practical part of the course, which focused on Drosophila, remained unchanged.

This practical training, combined with a detailed description of *Drosophila melanogaster* biology, the characteristics of the diversity of its mutant forms, and various methodological aspects, assigns students the task of designing and conducting experiments illustrating specific sections of genetic analysis. The Department of Genetics and Biotechnology's extensive collection of mutant Drosophila strains provides a diverse range of materials for practical training in accordance with the changing tasks assigned to students. First and foremost, students master classical methods for identifying various types of mutations, such as lethal mutations in the X chromosome and large autosomes of Drosophila, nondisjunction and sex chromosome loss, and translocations between autosomes. Experimental tasks include mutual localization of several lethal mutations in the X chromosome, as well as determining the nature of inheritance of several mutations simultaneously when they interact and localize in the sex chromosome and autosome. Tasks are completed by generating reports, which prepares students for the subsequent presentation of graduate qualification work. Given the significance of Drosophila as an object in genetic training, a special manual titled "Genetic Analysis in Drosophila" was published in 2019 to aid students.

Another essential genetic education course at the department has been modified in recent years. The course in question is "Cytogenetics." Initially, this subject was viewed solely as a lecture course; however, it has since extended to incorporate a practical component. In this case, Drosophila also played a significant role, demonstrating its excellent properties as a cytogenetic object. Using Drosophila as an example, students can learn about different types of chromosomes (mitotic, meiotic, and polytene), independently prepare antemortem specimens, analyze them using modern microscopy equipment, and preserve the material for subsequent analysis.

The Drosophila collection plays a vital role in the department's educational process that goes beyond the genetic analysis and cytogenetics courses. The general genetics course is essential in the training of biologists, regardless of specialty. Thus, the course traditionally includes several practical sessions in classical genetics within the sections "Mendelism" and "Morganism." Students are particularly interested in classes on sex-linked inheritance and crossing-over, which use

Drosophila as an example. The genetic collection provides materials for these practical sessions, which may vary based on the demands of the time.

The reform of genetic education has mandated the development of new courses that demonstrate the practical aspects of genetics. The department's new disciplines include the genetic toxicology course, which is designed to familiarize students with approaches to identifying environmental factors with genetic activity. Similar to the courses mentioned above, practical training supplements and illustrates the theoretical component of this course. Drosophila is a mandatory test object for understanding the various test systems used in genetic toxicology. The department's genetic collection introduces students to a number of state-approved standardized tests for environmental factor testing. Students independently assess the genotoxic effects of proposed factors, which include widely used pharmaceuticals, cosmetic products, food components, and so on.

Drosophila research has traditionally involved students and postgraduates from the Department of Genetics. The findings of these studies were used in 5 doctorate theses, 22 candidate theses, 14 master theses, 17 bachelor graduate qualification works, and more than 30 specialist diplomas. The Drosophila genetic collection at the Department of Genetics and Biotechnology at Saint Petersburg State University continues to be an invaluable resource for both traditional and innovative research. The established scientific foundation enables the integration between training and research, which is an integral feature of the scientific school of Saint Petersburg State University's Department of Genetics. The material created and preserved by classical genetic methods opens up broad opportunities for applying modern molecular genetic techniques to clarify the intricate mechanics of genetic processes. The use of increasingly popular bioinformatics tools for comparing mutations in Drosophila to similar mutations in other organisms, including humans, allows investigating evolutionary transformations of genetic material, which has broad biological implications.

ADDITIONAL INFO

Authors' contribution. All authors made a substantial contribution to the conception of the study, acquisition, analysis, interpretation of data for the work, drafting and revising the article, final approval of the version to be published and agree to be accountable for all aspects of the study. Personal contribution of each author: L.V. Barabanova, writing and editing the main text of the article, discussing the results; D.M. Grudkova, collection and processing of materials, analysis of obtained data, discussion of results; E.V. Golubkova, general guidance, discussion of results, writing and editing the main text of the article.

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