BIORESOURCE COLLECTIONS

Genetic Collections of St. Petersburg University*

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Abstract

Bioresource collections represent a unique source of biological diversity for research in genetics and related disciplines. The Department of Genetics and Biotechnology of St. Petersburg State University is the oldest department of genetics in Russia, founded in 1919. Throughout the entire period of development, the geneticists of St. Petersburg University have collected unique forms of plants, animals and microorganisms, on which their research was based. Many of these studies including regulation of translation termination in yeast, amyloids and prions of different organisms, genetic mapping of valuable morphological and biochemical traits to create first rye chromosome maps, and several aspects of transcription regulation in plants, had a significant novelty. The most active accumulation of collections of genetic resources at St. Petersburg State University started in the 1950–1970s when important scientific directions in the genetics of microorganisms, plants and animals, many of which continue today, were established at the department. Genetic collections are actively used in educational work for teaching dozens of educational courses. Currently, the interdisciplinary genetic collections of St. Petersburg State University consist of seven sections including genetic collections of rye, radish, garden pea, *Chlamydomonas* algae, *Saccharomyces* yeast and plasmids, *Komagataella* yeast, *Drosophila* fly. This review describes in detail the collections of the Department of Genetics and Biotechnology of St. Petersburg State University and discusses their current state, application and development prospects.

Keywords: Bioresource collections, genetic collections, yeast, rye, plasmid, *Saccharomyces cerevisiae, Drosophila melanogaster, Komagataella phaffii, Secale cereale, Chlamydomonas reinhardtii, Raphanus sativus, Pisum sativum.*

Introduction

The Department of Genetics and Biotechnology (former Department of Genetics and Breeding) of St. Petersburg (Leningrad) State University was established in 1919 as the Department of Genetics and Experimental Zoology of Petrograd University by Prof. Yuri A. Filipchenko (Goroschenko, 1994). It was the first department of genetics in Russia. Since the beginning of its existence, the department has accumulated the created varieties and forms in the form of genetic collections, but most of them were lost during the period of so-called Lysenkoism. The active formation of the department's genetic collections, which have survived to this day, began in the late 1950s when genetics was restored in the USSR (Inge-Vechtomov, Zhouravleva, and Golubkova, 2019).

* This article is dedicated to the 300th anniversary of St. Petersburg State University.

In fact, the collections accumulated to date reflect the long history of studying the genetics of plants, animals and microorganisms at the Department of Genetics and Biotechnology of St. Petersburg State University and key milestones in its development. Thus, the formation of genetic collections of Drosophila began in the late 1950s after the return of Prof. Mikhail E. Lobashev to the department as its head in 1957 (Inge-Vechtomov, 2007). At the end of the 1950s, the formation of a radish genetic collection began, a key contribution to which was made by Dr. Stanislava Narbut (Narbut, 1966). Later, in the 1960s, the formation of the Peterhof collection of rye lines was started by Dr. Vasily S. Fedorov (Fedorov, 1961, 1964), Dr. Viktor G. Smirnov, Dr. Svetlana P. Sosnikhina (Fedorov and Smirnov, 1967; Fedorov, Smirnov, and Sosnikhina, 1971; Sosnikhina et al., 2005) and, later joined by Dr. Anatoly V. Voilokov (Voylokov, Fuong, and Smirnov, 1993).

The Peterhof Genetic Collection of *Chlamydomonas reinhardtii* green algae strains was created at the Department of Genetics and Biotechnology of St. Petersburg State University in the 1964 by Dr. K. V. Kvitko and Dr. A. V. Stolbova (Kvitko, Borshchevskaya, Chunaev, and Tugarinov, 1983). Until now, it is the only genetic collection of photosynthetic eukaryotic microorganisms in Russia. The Peterhof Genetic Collection of Yeast has been founded in 1963 in the laboratory of Physiological Genetics of the Biological Institute and at the Department of Genetics and Biotechnology of St. Petersburg University (Inge-Vechtomov, 1963; Andrianova, Samsonova, Sopova, and Inge-Vechtomov, 2003) and currently consists of two parts located in Peterhof and at the main building of the Department of Genetics and Biotechnology on Vasilevskiy Island. Later, a genetic collection of *Komagataella phaffii* (syn *Pichia pastoris*) methylotrophic yeast was started by Dr. Mikhail N. Smirnov, Dr. Marina V. Padkina and Dr. Elena V. Sambuk (Karabelsky, Zinovieva, Smirnov, and Padkina, 2009).

Currently, Genetic Collections of St. Petersburg University comprise seven sections including collections of rye, radish, garden pea, *Chlamydomonas* algae, *Saccharomyces* yeast and plasmids, *Komagataella* yeast, and *Drosophila* fly. The total number of stocks including plant lines and strains of microorganisms and flies exceeds 2000. Much attention that has recently been paid to the systematization and revision of bioresource collections (Tikhonovich et al., 2022; Khlestkina et al., 2022) reflects their paramount importance for basic and applied research in genetics and other fields of natural sciences as well as in the educational process. In this review, we describe the current state of Genetic Collections of SPbSU, and discuss several recent works performed using the samples of the genetic collections.

The Peterhof Genetic Collection of Rye

Rye (*Secale cereale* L.) is a traditional agricultural plant of eastern and northern Europe. In Russia and Belarus, rye is mainly used for baking bread, as a forage and cover crop. For geneticists rye is a very interesting object because a high level of heterogeneity in the genomes is still preserved in comparison with many other agricultural plants. The reason for this is a complicated system of self-incompatibility in rye plants which leads to an obligate cross-pollination and intricate process of relatively recent domestication of rye. Both of these factors lead to the preservation of a high level of heterozygosity for many genes controlling morphological, biochemical and other traits. Also, rye is resistant to many biotic and abiotic factors, is able to grow on barren soil and gives good yield even in northern parts of Russia. Winter rye is more common for cultivation except for northern regions of Russia like Siberia and the Urals, where summer rye is preferable because of hard winters with extremely low temperatures which winter rye cannot tolerate (Sherstnev, 1980).

The collection of rye genetic lines is a valuable source to study the inheritance of qualitative and quantitative morphological traits, genetic control of autofertility, genetic aspects of meiosis, and genetics of interspecies incompatibility. High level of heterozygosity in natural populations of weedy rye as well as rye varieties like Vyatka allowed it to isolate homozygous forms that differ in morphological characteristics in comparison to initial plants.

Two main approaches were chosen for the selection of forms with interesting morphological traits. The first one was an isolation of plants with morphological deviations directly in the samples of weedy rye and Vyatka variety and their collective reproduction. This led to the production of self-incompatible rye lines with different colors of vegetative and generative parts of plants. The second approach was focused on the production of autofertile lines. Mutations of autofertility make self-pollination of single plants possible and allow the selection of homozygous inbred lines, which facilitates the study of the genetic control of interesting traits. Three different rye populations were the source of autofertility, the trait was transferred via hybridization with plants of variety populations. The initial autofertile lines of the collection, with which crosses were carried out, are the following: the line M (*monstrosum* mutation), originating from the population of Vetvistokolosaya; BBV line lacking a wax coat isolated from the population Belozernaya; Kr line selected from a weedy rye sample with a red ear color. Autofertile lines are propagated by the method of group and individual isolation.

Moreover, some autofertile inbred lines of the collection were isolated as the progeny from plants with mutations of the gametophyte incompatibility system, found *de novo* in populations of varieties. The Peterhof genetic collection contains 90 inbred rye lines with mutations of autofertility propagated by the individual isolation method.

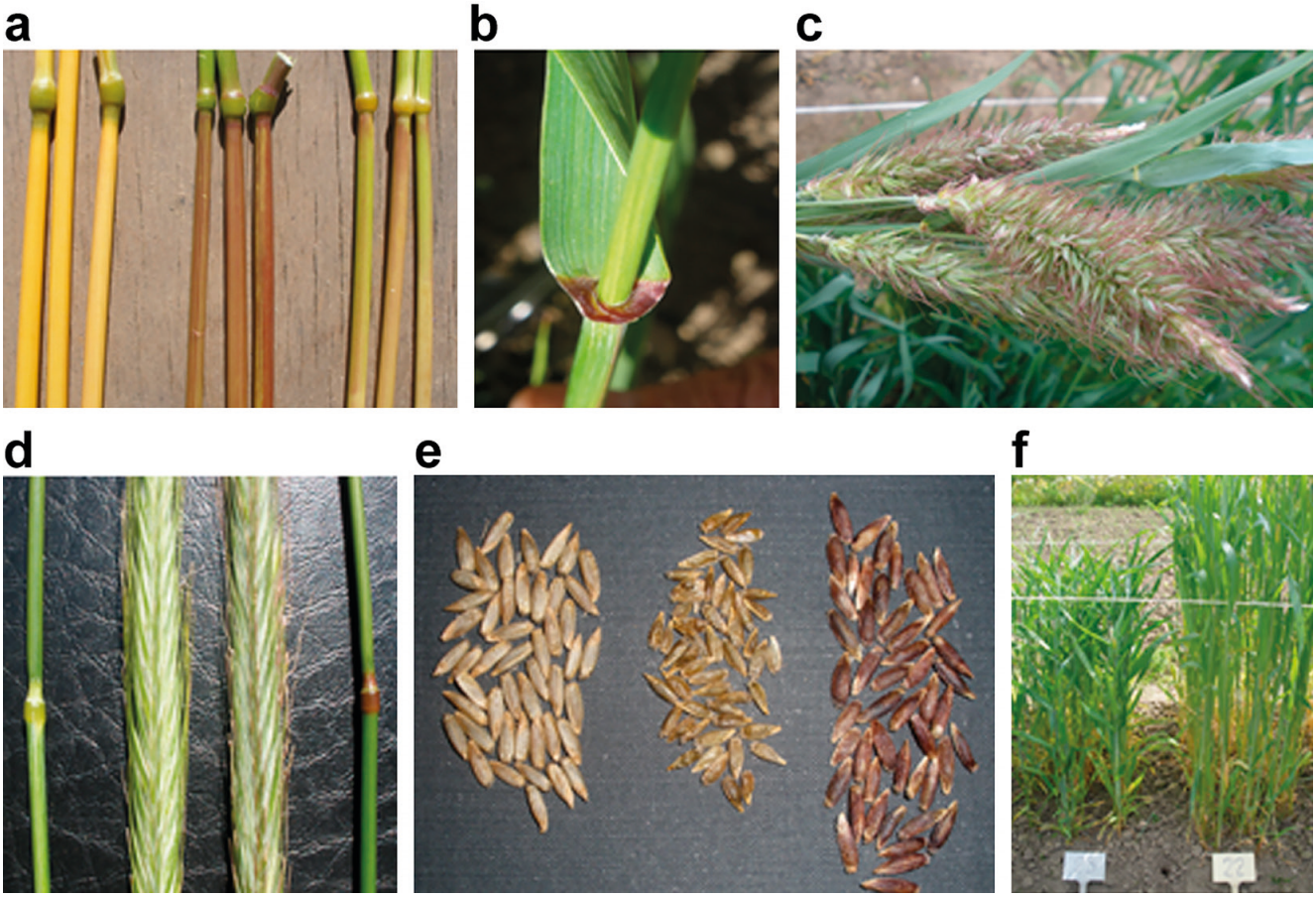

Fig. 1. Morphological traits of rye lines: *a* — variation of stem colors (yellow, brown, green); *b* — red ear phenotype; *c* — branched spikes (mutation *monstrosum*); *d* — stems and spikes of anthocyaninless (left) and (right) of wild type plant (accumulation of anthocyanins in nodules and spikes); *e* — variation of grain color, left to right: yellow, brown and violet grains; *f* — variation of stem height: left — dwarf mutation (short stems), right — wild type plants (long stems).

At present, the Peterhof's genetic collection of rye contains 120 self-incompatible lines and autofertile inbred lines carrying morphological mutations. Rye lines and their F1 and F2 hybrids are used in education as living illustrations of Mendel's law of heredity during the summer practice and for undergraduate and PhD students' work. Lines with different colors of grains are used for studying anthocyanin biosynthesis (Zykin et al., 2018), genetic control of post-zygotic interspecies incompatibility (Tsvetkova, Tikhenko, Hackauf, and Voylokov, 2018; Tikhenko et al., 2018), and economically valuable traits of rye and triticale (Braun et al., 2019).

The Genetic Collection of Radish

Radish (*Raphanus sativus* L.) is an economically and ecologically significant agricultural plant belonging to the Brassicaceae family and close to the model object *Arabidopsis thaliana.* Currently, radish genome has been sequenced and annotated (Kitashiba et al., 2014; Xu et al., 2023). In terms of classification, radish is a group of varieties of the species *R. sativus* L., including "small radish" or "cherry radish" — *R. sativus* var. *radicula* Pers., an annual plant with a short life cycle. By origin, there are European, Japanese and Chinese groups of varieties.

Unlike other plant species with a storage root, radish is an annual plant which is easy to cultivate indoors. This fact, as well as its relationship with Arabidopsis, makes radish a convenient object for studying the genetic mechanisms that regulate the development of a storage root.

The work on the creation of the genetic collection of radish was started at the Department of Genetics and Biotechnology of St. Petersburg State University in the 1950s from the inbreeding of individual plants of five radish varieties (Narbut, 1966). Radish is a species with a sporophyte system of self-incompatibility, so the seed obtained by inbreeding occurred only in plants carrying autofertility mutations.

Currently the genetic collection of radish includes 33 lines of approximately the 40th generation of inbreeding, that differ in autofertility, flowering time, morphological characteristics (stem length, leaf shape, shape and color of the storage root, type of anthocyanin, the presence of anthocyanin in stem and petiole, shape and color of the corolla), biochemical characteristics (spec-

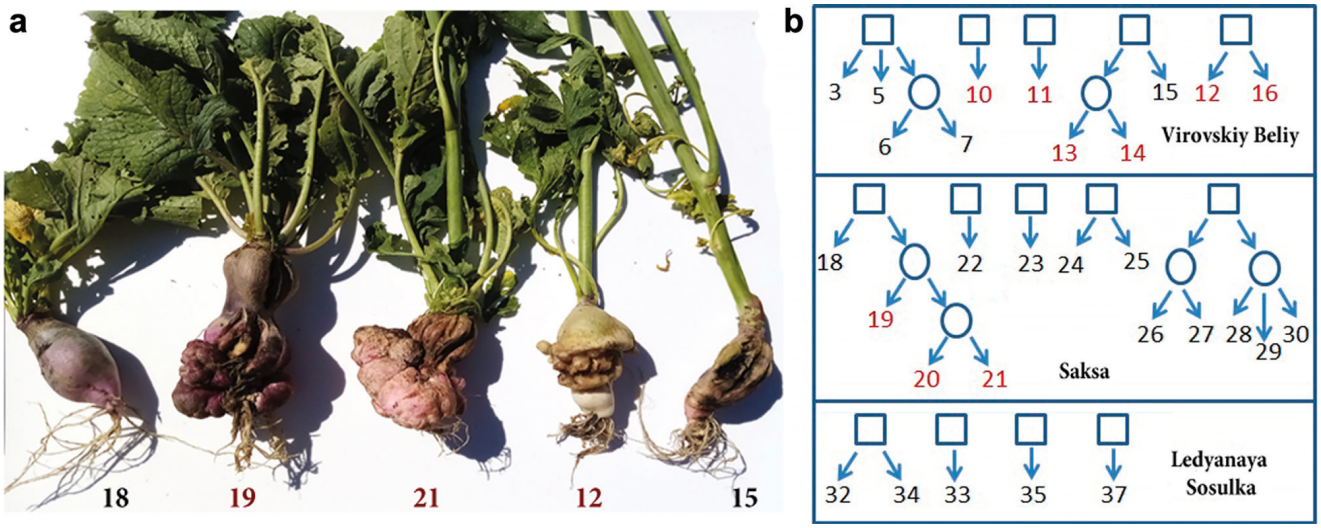

Fig. 2. Spontaneous tumors of radish inbred lines: *a* — morphology of radish roots of some inbred lines; *b* — genealogy of the radish genetic collection. Tumorous line numbers are marked in red.

tra of isoenzymes), and also the reaction to phytohormones in the *in vitro* culture (Lutova and Dodueva, 2019). A number of radish lines also have developmental anomalies: dwarfism (the line "nana" is a gibberellin-deficient dwarf) and vice versa very long stem, chlorophyll deficiency, shoot waves due to violation of gravitropism (dominant mutations *Wsh1* and *Wsh2*), ovary overgrowth, etc. (Buzovkina and Lutova, 2007).

The most interesting morphological abnormality in the radish genetic collection is the spontaneous tumor formation. For the first time this trait was seen in individual plants already in the second generation of inbreeding (Narbut, 1967). The large tumors with practically absent signs of differentiation appear on the roots of certain radish lines during the transition of plants to flowering. These tumors result from the proliferation of pericycle and cambium cells and represent a mass of small undifferentiated cells with a large number of spirally arranged vessels (Il'ina, Dodueva, Ivanova, and Lutova, 2006; Lebedeva (Osipova) et al., 2015). Tumors are a model for studying the systemic control of cell proliferation and differentiation, which is organized differently in plants and in animals (Doonan and Sablowski, 2010). However, most examples of tumor formation in higher plants are formed under the influence of various pathogens: bacteria, fungi, protozoa, nematodes, and arthropods. At the same time, spontaneous tumors in plants are relatively rare and are formed in plants with a certain genotype — mutants, interspecific hybrids or inbred lines (Dodueva et al., 2020). Thus, tumors in the radish inbred lines are of great interest for studying the genetic control of this phenomenon (Fig. 2).

In some cross combination between radish lines from Saksa cultivar, the ability to form tumors was shown to be inherited as a monogenic trait which depends on recessive *tur* mutation (Matveeva et al., 2004). The most probable cause of root tumor formation in the radish lines is elevated cytokinin (CK) levels. Indeed, the free CK content of tumorous radish line roots is several times higher than that of roots from related but non-tumorous lines (Matveeva et al., 2004). The analysis of cell proliferation patterns in the tumors of the radish inbred lines revealed meristematic foci that were located in the tumor periphery and that resemble RAMs, including the presence of IAA-response maxima and *RsWOX5* expression (Lebedeva (Osipova) et al., 2015). Finally, the analysis of transcriptome of spontaneous radish tumors compared to lateral roots of the same lines at the same stage of development revealed a sharp increase in the expression levels of a large number of cell cycle genes acting at different stages of its regulation, from the G1-S transition to cytokinesis, and also a decrease in the expression of genes that regulate tissue differentiation — for example, regulators of cell wall lignification and regulators of the biosynthesis of secondary metabolites, such as glucosinolates (Tkachenko et al., 2021).

By now, the genetic collection of radish is used for studying the role of meristem regulators in the development of storage root and spontaneous tumors (Lebedeva (Osipova) et al., 2015; Kuznetsova, Dodueva, Gancheva, and Lutova, 2022; Tkachenko et al., 2021). The genomes of two related Saksa lines contrasting in the ability to spontaneously form tumors were sequenced and are currently in work.

The Educational Collection of Garden Pea Lines

The garden pea (*Pisum sativum* L.) is historically the first experimental object of genetics used by Gregor Johann Mendel in his experiments. These are annual herbs with weak climbing stems. Their leaves are compound, pinnate and end in branched tendrils, with which they cling

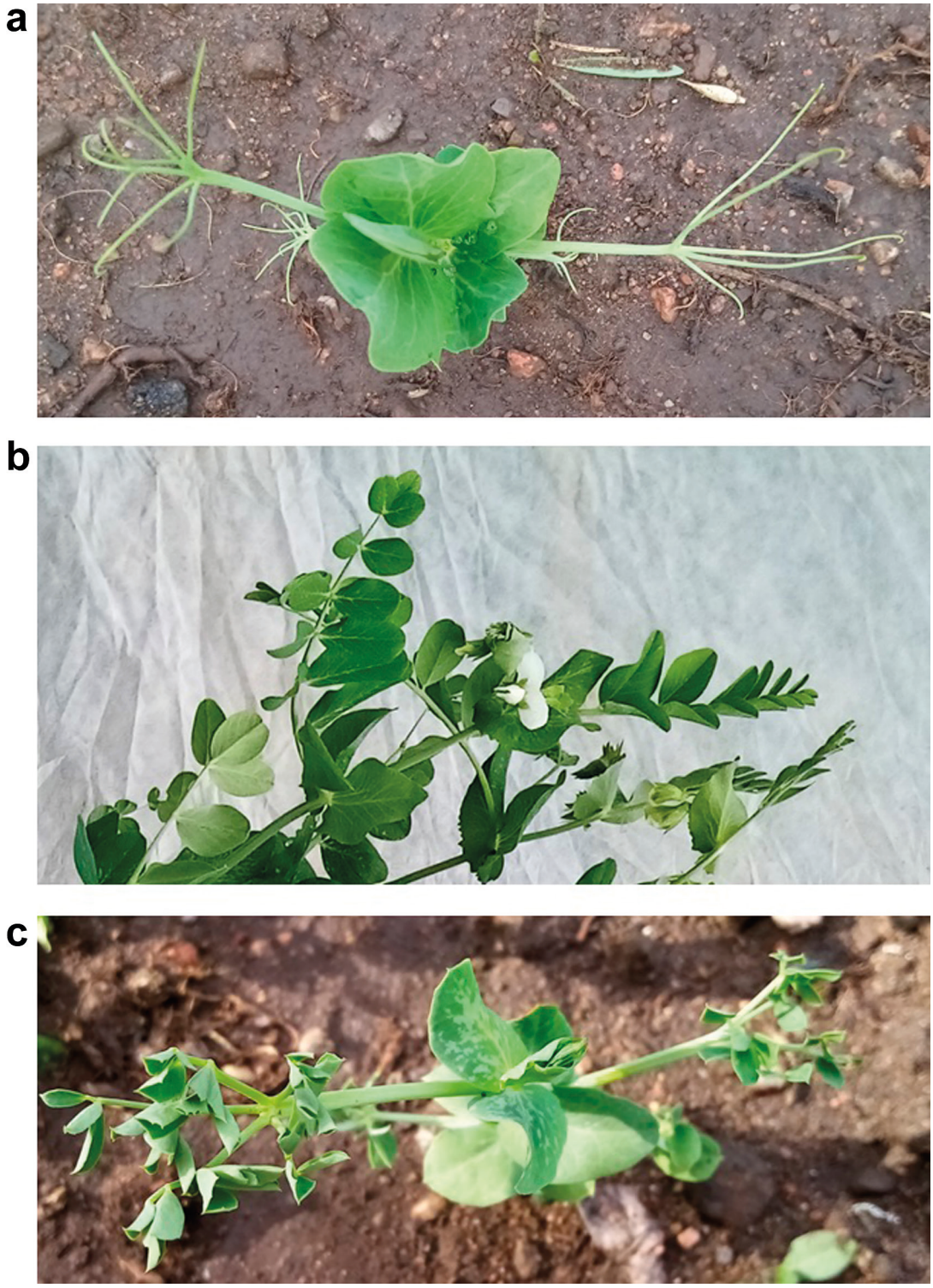

Fig. 3. Various types of *Pisum sativum* L. leafs: *a* — the *af* (afila) mutation, which converts leaflets to tendrils; *b* — the *tl* mutation, which converts tendrils to leaflets; *c* — the double mutant *af tl*.

to other plants. Large stipules are located at the bottom of the leaf. Pea flowers have a moth-type corolla. Pea is a self-pollinator (cross-pollination is possible under unfavorable conditions, such as drought), does not suffer from inbreeding depression, which simplifies the maintenance of genetic collections. In addition, it has a high economic value, and many studies are aimed at increasing its productivity.

At the Department of Genetics and Biotechnology of St. Petersburg State University, a genetic collection of garden pea has been assembled for use in the educational process. The basis of the collection began to form in the 1980s, some varieties were provided by N. I. Vavilov All-Russian Institute of Plant Genetic Resources (VIR) and All-Russia Research Institute for Agricultural Microbi-

ology (ARRIAM). Currently, it consists of 35 lines that differ in morphological features. The collection includes a number of dwarf forms. Thus, the *le* (length, mutation in gibberellin 3-β-oxidase gene) mutation leads to the appearance of a dwarf plant with reduced internodes (Bilova, Ryabova, and Anisimova, 2016). Considerable attention is paid to anomalies in the leaf structure. The complex legume leaf normally includes stipules, rachis, leaflets, and tendrils. In the *af* mutants (afila, "whiskered leaf"), additional tendrils are located in place of the leaves; such plants cling to each other so actively that they do not need external support. Photosynthesis is carried out by stipules. The *tl* mutation, on the contrary, causes the tendrils to turn into leaflets (Kosterin, 2015) (Fig. 3). Other mutants differ in the shape and color of the seeds, the presence and distribution of anthocyanins in the stem.

Despite the fact that the Genetic Collection of Garden Pea Lines is mainly used in the educational process, there are several recent important studies performed by the staff of the Department of Genetics and Biotechnology of St. Petersburg State University together with the colleagues from ARRIAM and other institutions using garden pea as the main object of research. Recently, functional plant amyloid proteins were first discovered in the seeds of garden pea (Antonets et al., 2020). Different studies are focused on the research of symbiotic relationships between pea and rhizobia, the nitrogen-fixing bacteria: an analysis of diversity of nucleotide sequences of pea symbiotic-related genes *PsSym29* and *PsNRLK1* (Zhukov et al., 2022), transcriptomic analysis of the expression patterns of pea *C-TERMINALLY ENCODED PEPTIDES* (*PsCEP*) genes involved in plant growth and response to environmental factors, including symbiotic nodule development (Lebedeva et al., 2022a), analyzing of *CLE* (*CLAVATA3/Embryo Surrounding Region*) genes which supposedly play a role in an inhibition of nodulation (Lebedeva et al., 2022b), investigating the structure and functions of rhizobial amyloid proteins (Kosolapova et al., 2019, 2022). All the results complement a complicated picture of legume plants and nodulating bacteria interplay.

The Peterhof Genetic Collection of *Chlamydomonas reinhardtii* (PGC)

The Peterhof Genetic Collection of *Chlamydomonas reinhardtii* green algae strains (PGC) was actually created at the Department of Genetics and Biotechnology of St. Petersburg State University in the 1964 by Prof. K. V. Kvitko and Dr. A. V. Stolbova (Stolbova et al., 1971, Kvitko, Borshchevskaya, Chunaev, and Tugarinov, 1983). Until now, it is the only genetic collection of photosynthetic eukaryotic microorganisms in Russia.

The goal of the collection creation was to study the genetic control of fundamental biological processes in a plant cell — photosynthesis, biogenesis and functioning of chloroplasts, the structure and functions of the flagellum apparatus, the molecular organization of membranes and the metabolism of chloroplast pigments — chlorophylls and carotenoids. The collection is based on wild-type strains of single-celled green alga *Chlamydomonas reinhardtii* (*C. reinhardtii*) — a model object of genetics of photosynthesis.

Green flagellates from the genus *Chlamydomonas* are unicellular haploid organisms that have a complex life cycle (involving sexual and asexual reproduction) and are capable of differentiation. These green algae sharing a common ancestor with land plants have fundamental features related not only to plants but also to animals. The collections of protozoa and algae in Europe and Russia support more than 50 species of algae including marine, freshwater and soil forms, but the natural and induced variety is obtained for only two species representing two ecological types — the facultative heterotroph *C. reinhardtii* and obligate phototroph *C. moewusii*. The most studied strains of *C. reihardtii* — cultures of 137C (+) and 137C (–) descendants of one zygote were first isolated by J. Smith in 1945 from the soil of a potato field in Massachusetts (USA). These cultures were transferred to Leningrad University from the Levin Collection (USA) as wild-type strains in 1975 (Kvitko, Borshchevskaya, Chunaev, and Tugarinov, 1983).

The unicellular and genetically tractable green alga *C. reinhardtii* was first developed as a model organism to elucidate fundamental cellular processes such as photosynthesis, light perception and the structure, function and biogenesis of cilia. Various studies of *C. reinhardtii* have profoundly advanced plant and cell biology, and have also impacted algal biotechnology and human disease (Harris, 2001).

The Peterhof Genetic Collection contains 70 *Chlamydomonas* mutants with impaired photosynthesis, chlorophyll biosynthesis mutants, auxotrophic and light-sensitive mutants and mutants with an impaired cell wall (Fig. 4).

The main types of mutants include the following groups: morphological (shape, size, coloring of colonies); biochemical (auxotrophy, resistance to antibiotics, inhibitors, antimetabolites); nutrition: (photo-, auto-, hetero, mix-, auxotrophy); breathing (aerobic, respiratory failure); mobility (violation of flagella functions, photo- and chemotaxis); photosynthesis (loss of phototrophy — acetate dependence); pigmentation (with defects in chlorophyll and carotenoid biosynthesis). *Chlamydomonas* strains from the collection are used in scientific experimental studies of the genetic regulation of the photosynthesis processes and biosynthesis of chloroplast pigments, as well as the genetic control of adaptation mechanisms in photosynthesizing cells to various environmental factors (light, temperature, etc.)

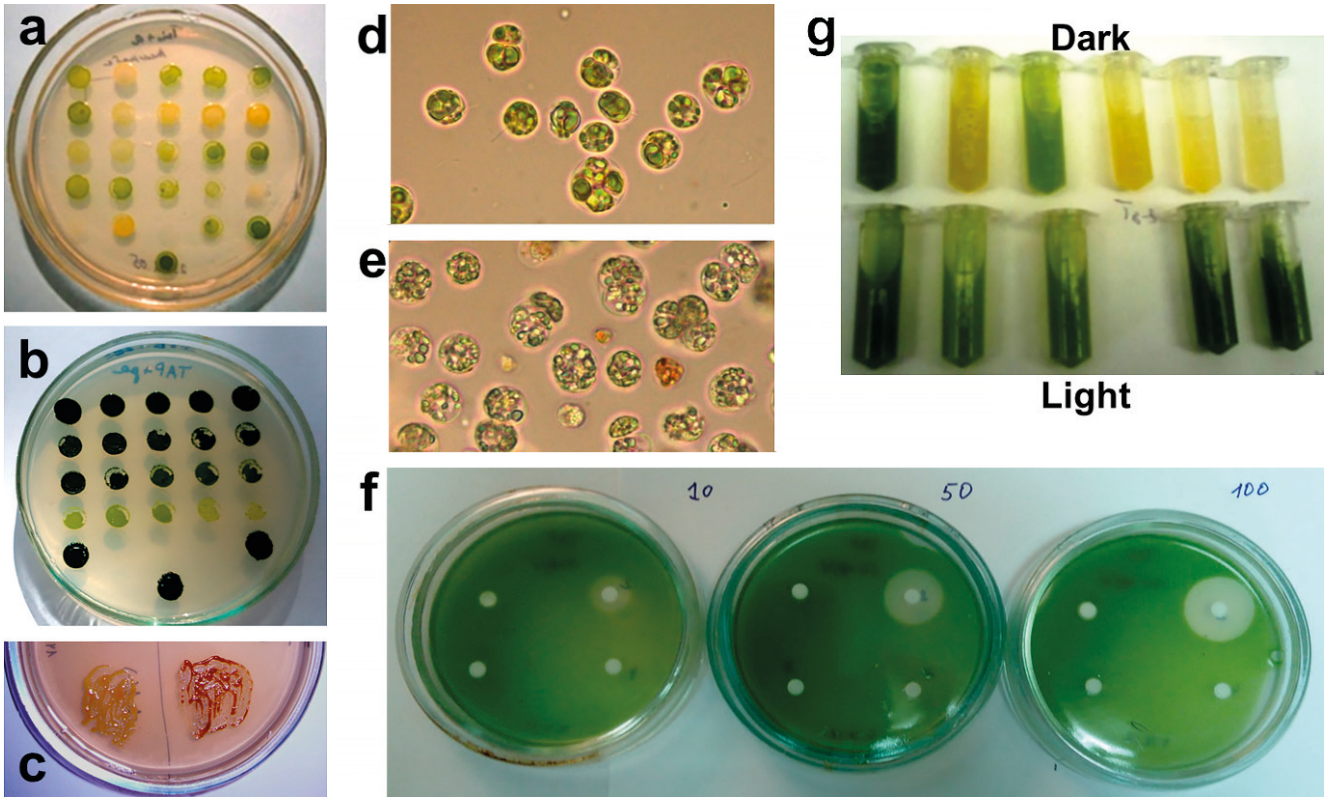

Fig. 4. *Chlamydomonas reinhardtii* strains from PGC: *a* — pigment mutants of *C. reinhardtii* from PGC, growing in the dark on Petry plates; *b* — *C. reinhardtii* strains from PGC, growing in the light on Petry plates; *c* — *Chlamydomonas* mutant cultures, accumulating protoporphyrin IX; *d* — the wild type (137C) cells of unicellular green alga *C. reinhardtii*; *e* — mutant cells, accumulating protoporphyrin IX; *f* — *C. reinhardtii* cell culture can be used in bioassay detection of a variety of toxic compounds such as pesticides. Presence of herbicide activities was indicated by clearing zones around the paper disks on the lawn 2–3 days after application; *g* — cell suspensions of the pigment mutants of *C. reinhardtii* from PGC, growing in light and dark conditions.

(Chekunova et al., 2001). Strains from the collection can also be used for the development of test systems for assessing the environmental safety of water resources, cyto- and genotoxicity of drugs used in agriculture for plant protection. A number of photosensitive and pigment mutants from PGC were transferred to the Chlamydomonas Resource Center (https://www.chlamycollection.org/) in the 1990s–2000s.

The Peterhof Genetic Collection of Yeast Lines (PGL)

The Peterhof Genetic Collection of Yeast Lines (PGL) has been founded in 1963 in the Laboratory of Physiological Genetics of the Biological Institute and at the Department of Genetics and Biotechnology of St. Petersburg University (Inge-Vechtomov, 1963; Andrianova, Samsonova, Sopova, and Inge-Vechtomov, 2003) and currently consists of two parts located in Peterhof and at the main building of the Department of Genetics and Biotechnology on Vasilevskiy Island.

Currently, the Peterhof part of the collection contains 276 yeast strains, most of them are the strains of baker's yeast *Saccharomyces cerevisiae*, marked with various mutations and used in various lines of genetic experiments. Most of the strains in the collection are multiply marked and carry both one or more mutations in the genes encoding markers for yeast transformation, and mutations in specific genes affecting various genetic processes. In particular, the yeast strains with mutations marking the translation machinery, tester strains for mutagenesis studies and for α-test used in genetic toxicology, donors and recipients for cytoduction, are presented in the collection. A large set of the strains with different nonsense alleles and mutations in the genes coding for the components of translation apparatus allows the study of regulation of the translation. The strains carrying different variants of the [*PSI*$^+$] prion (Fig. 5) are also included in the collection. Of particular interest is a set of strains that allows mapping recessive mutations due to the directed loss of any of the 16 chromosomes. The collection also contains *S. cerevisiae* strains and the strains of some other yeast species which may be used in industry and biotechnology.

All the yeast strains are stored in polypropylene tubes at –70 °C in the presence of 20 % glycerol (Sherman, Fink, and Hicks, 1983). Stored cultures are checked periodically for viability and matching the specified strain genotype which allows to maintain the purity and authenticity of the collection.

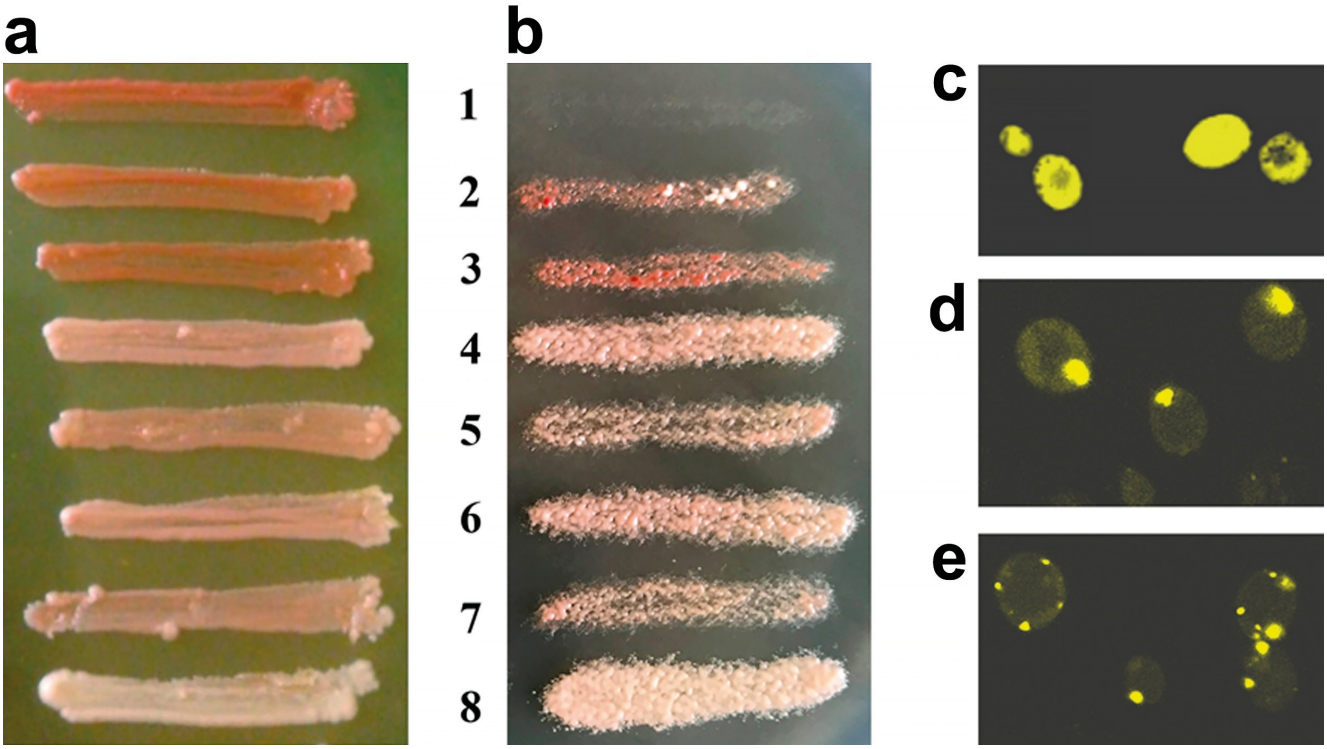

Fig. 5. Phenotypes of isogenic derivatives of the k5–35V-D924 strain carrying different variants of the [*PSI*$^+$] prion: *a* — colouring of the derivatives of initial k5–35V-D924 [*psi*$^-$] strain (1) and its isogenic [*PSI*$^+$] derivatives (2–9) on the YEPD medium; *b* — growth of the initial k5–35V-D924 [*psi*$^-$] strain (1) and its isogenic [*PSI*$^+$] derivatives (2–9) on the 4th day of incubation on the medium without adenine. Variants of the [*PSI*$^+$] prion are characterized by different efficiency of suppression of the *ade1–14* nonsense mutation, which can be seen as differences in colony color on the complete YEPD medium (*a*) and in efficiency of the growth on the medium without adenine (*b*). The strains with strong [*PSI*$^+$] variants (8) are characterized by white color of colonies on YEPD and high growth rate on the medium without adenine, the strains with weak [*PSI*$^+$] (2,3) have a dark pink color on YEPD and weak growth on the medium without adenine, the strains with moderate [*PSI*$^+$] variants (4–7) have an intermediate manifestation. The initial [*psi*$^-$] strain (1) is red on YEPD and does not grow on medium without adenine; *c*, *d*, *e* — the distribution of the Sup35NM-YFP protein in the k5–35V-D924 [*psi*$^-$] cells (*c*) and the cells of k5–35V-D924 derivatives carrying weak [*PSI*$^+$] (*d*) and strong [*PSI*$^+$] (*e*). The Sup35 protein forms the aggregates in the cytoplasm of [*PSI*$^+$] cells (*d*, *e*) and is evenly distributed in the cytoplasm of [*psi*$^-$] cells (*c*), which can be seen by fluorescence microscopy using chimeric fluorescent proteins such as Sup35NM-YFP (*c*, *d*, *e*). Typically, strong [*PSI*$^+$] strains (*e*) have a higher number of aggregates per cell than weak ones (*d*).

Yeast strains of the collection have different origins. A number of strains belong to Peterhof genetic lines (PGL). The distinguishing feature of these lines is that they are descended from inbred variants of the XII industrial race of the yeast *S. cerevisiae*, and thus originate from a single diploid cell of a particular yeast species (Inge-Vechtomov, 1963). In this respect, the PGL strains differ from the strains of the YGSC collection (Berkeley, USA) widely used in genetic studies, originating from the Carbondale genetic lines. These lines were constructed by repeated crosses between different strains of *S. cerevisiae* and other *Saccharomyces* species and, thus, are heterogeneous according to the content of genome regions of various yeast species, although the predominant part of the genome in these strains belongs to *S. cerevisiae* (Mortimer and Johnston, 1986). Along with the strains of Peterhof genetic lines, the collection contains yeast strains of Carbondale and other genetic lines, kindly provided by different laboratories. A significant part of the strains in the collection is of hybrid origin, representing the segregants from crossing PGL strains with strains of other genetic lines.

A wide variety of genotypes of strains included in the Peterhof Genetic Collection of Yeast, the presence of specific mutant alleles of various genes in them, determine their extensive use in scientific experiments. As indicative, but by no means the only, examples of such studies, we can mention works on the identification and study of the mechanisms of the inheritance and interactions of yeast prions including [*PSI*$^+$], [*PIN*$^+$] and [*NSI*$^+$] (Chernoff et al., 1995; Derkatch et al., 1996, 1997; Saifitdinova et al., 2010; Nizhnikov et al., 2012, 2016; etc.) and amyloids (Ryzhova et al., 2018; Sergeeva et al., 2019), studying the structure and function of the genes of omnipotent nonsense suppressors *SUP35* and *SUP45* (Inge-Vechtomov and Andrianova, 1970; Chernoff et al., 1992; Ter-Avanesyan et al., 1993; Moskalenko et al., 2003; Tributsina, Zemlyanko, Bondarev, and Zhouravleva, 2020; Zhouravleva, Bondarev, Zemlyanko, and Moskalenko, 2022; etc.), creation and improvement of a sensitive yeast system for genotoxicology — alpha test (Inge-Vechtomov and Repnevskaya, 1989; Stepchenkova et al., 2011; Zhuk, Stepchenkova, and Inge-Vechtomov, 2020).

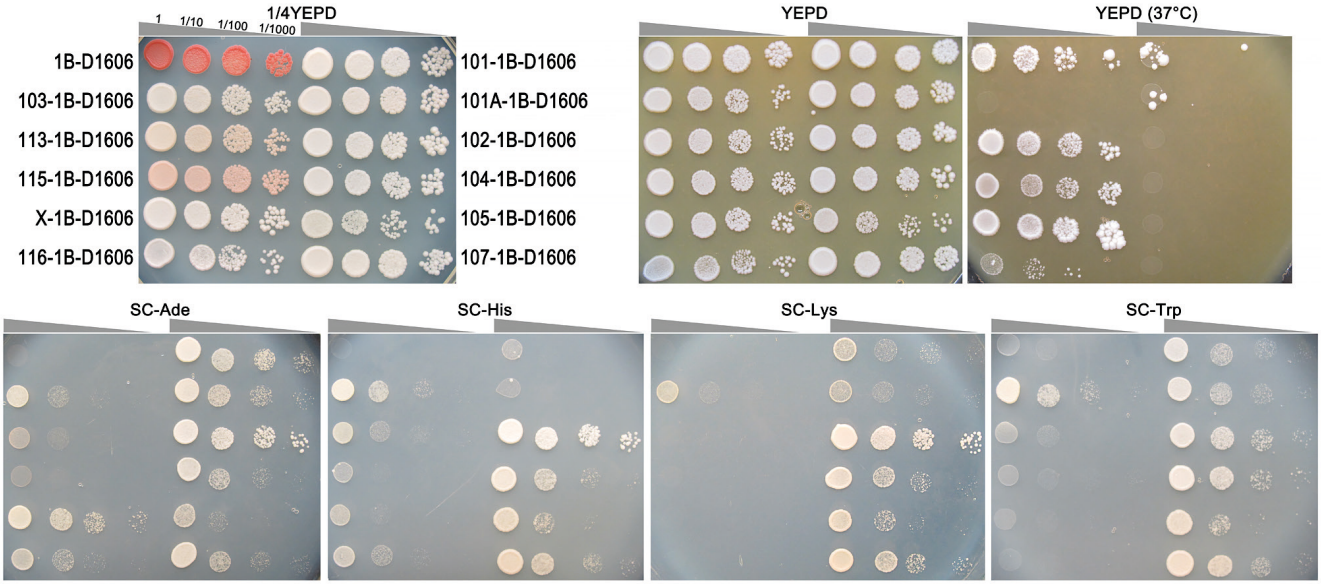

Fig. 6. Phenotypes of the *sup45* mutant strains preserved in the Peterhof Genetic Collection of Yeast. Tenfold serial dilutions of the liquid yeast cultures were spotted onto the full or selective media plates. Plates were incubated for six days at 26 °C unless indicated otherwise. YEPD is a full medium, containing yeast extract, peptone, and glucose. 1/4YEPD medium contains less yeast extract and peptone (Eaglestone, Ruddock, Cox, and Tuite, 2000); it is used for the color (red-white) selection of the *ade1* and *ade2* mutants and for assessment of suppression of the *ade1–14* nonsense mutation. Other selective plates are SC media (synthetic complete) lacking one of the essential compounds (e. g., SC-Ade contains all the necessary components, except for the adenine). Strains are the derivatives of 1B-D1606 (*MAT*α *ade1–14 his7–1 lys9-A21 trp1–289 ura3–52 leu2–3,112 gal10–1B*) with mutations in the *SUP45* gene. Numbers designate mutation names (e. g., 101–1B-D1606 contains *sup45–101* mutation) according to Moskalenko et al., 2003. Growth of strains on a selective media indicates suppression of nonsense mutation in the gene responsible for the synthesis of the missing compound (e. g., growth on the SC-Ade is caused by suppression of the *ade1–14* mutation).

The second part of the collection of yeast strains located in the main building of the Department of Genetics and Biotechnology was systematized by Dr. Polina B. Drozdova and Dr. Andrew G. Matveenko. In its core are the strains preserved by laboratory staff from 2000 to 2014, however some of the strains have been obtained since the 1980s. Currently, 184 strains obtained in the laboratory are preserved, however, new strains are deposited on occasion. The collection contains strains originating from the Peterhof genetic collection (Andrianova, Samsonova, Sopova, and Inge-Vechtomov, 2003), but mainly those of hybrid origin, i. e., having both Peterhof and Berkeley yeast strains as ancestral (Drozdova et al., 2016a). The collection strains have been used in most laboratory works. Several strains of the collection were characterized using whole genome sequencing and subsequent bioinformatic analysis (Drozdova et al., 2016a; Drozdova, Mironova, and Zhouravleva, 2016b; Matveenko et al., 2019; Barbitoff et al., 2021; Maksiutenko et al., 2021).

The study of the suppression of nonsense mutations in yeast has been one of the main fields of research in the Laboratory of Physiological Genetics since its establishment (Inge-Vechtomov, 1963; Inge-Vechtomov and Andrianova, 1970). Investigation of the recessive nonsense-suppressors led to the discovery of the *SUP1* (*SUP45*) and *SUP2* (*SUP35*) genes, coding for the release factors eRF1 and eRF3, respectively (Zhouravleva et al., 1995; Stansfield et al., 1995). A number of *sup35* and *sup45* mutants was obtained (Moskalenko et al., 2003; Chabelskaya et al., 2004). The strains selected during that work and their derivatives are in the core of the yeast collection of the St. Petersburg part of the laboratory of physiological genetics. Not only yeast strains, but also plasmids containing the same mutant alleles cloned into yeast expression vectors are stored in the collection.

The studies of nonsense-suppression in yeast also led to a discovery of two non-Mendelian factors, [*PSI*$^+$] and *Isp*$^+$ (Cox, 1965; Volkov et al., 2002). The Sup35 protein was shown to form prion [*PSI*$^+$] which also became a subject for studies in the laboratory (Chernoff, Derkach, and Inge-Vechtomov, 1993; Chernoff et al., 1995; Wickner, 1994). As a result, [*PSI*$^+$] prion-containing strains are also a part of the collection and have been used for studies of prion propagation and amyloid-chaperone interactions (Matveenko et al., 2016, 2018; Barbitoff et al., 2017). Similarly to nonsense suppressor mutations, a number of mutations in the prion domain of the Sup35 protein was previously obtained (Bondarev, Shchepachev, Kajava, and Zhouravleva, 2013) and vectors for expression of these mutant alleles are now stored in the laboratory collection. The studies of the *Isp*$^+$ factor have also been an important field of research in the laboratory. The studies of *Isp*$^+$ uncovered aneuploidy as a factor affecting nonsense suppression efficiency (Drozdova, Mironova, and Zhouravleva, 2016b); all strains corresponding to the studies are also preserved in the collection.

The collection of strains is accompanied by the collection of 200 plasmids, which are preserved both as

DNA solutions and *E. coli* plasmid-containing strains. The majority of the preserved plasmids are yeast-bacterial shuttle vectors, however, vectors for protein production in *E. coli* are also present. Several dozens of the plasmids contain mutant alleles of the *SUP35* and *SUP45* genes. Particularly, suppressor *sup35* and *sup45* alleles with nonsense- and missense-mutations which can be used for plasmid shuffle experiments (Moskalenko et al., 2003; Chabelskaya et al., 2004; Tributsina, Zemlyanko, Bondarev, and Zhouravleva, 2020; Maksiutenko et al., 2021) are also a part of the collection. Vectors for the expression of *SUP35* with engineered mutations in the prion-forming domain of Sup35 are also present in the collection (Bondarev, Shchepachev, Kajava, and Zhouravleva, 2013; Danilov et al., 2019). Among the genes represented on the plasmids in the collection there are also genes encoding Q/N-rich proteins (e. g., *SFP1*, *SCH9*), translation factors (*TEF2–5*), and chaperones or chaperone-associated factors (*SIS1, CUR1*).

The Genetic Collection of *Komagataella phaffii* strains

The collection was initially formed to study the capabilities of *K. phaffii* cells to synthesize recombinant proteins in comparison with *S. cerevisiae*. For this purpose, strains producing different recombinant proteins were generated using widely known GS115 and X-33 *K. phaffii* strains (Karabelsky, Zinovieva, Smirnov, and Padkina, 2009). This part of the collection comprises 45 strains that produce immunomodulating proteins (e. g., interferons and interleukins) and different enzymes. These strains were used to optimize cultivation conditions, and to develop new techniques for *K. phaffii* transformation and generation of strains with multiple expression cassettes. Such experience stimulated further use of *K. phaffii* as a model organism for comparative studies on gene regulation in yeast cells.

Yeast *S. cerevisiae* is one of the most well-studied model organisms. It is hardly possible to overestimate the importance of discoveries that were made using this yeast and future perspectives of its applications in biology (Botstein and Fink, 2011). However, *S. cerevisiae* does not represent the whole variety of yeasts. The development of modern "omics" technologies (e. g., genomics, transcriptomics, proteomics, metabolomics) and gene editing methods now allows to conduct complex studies of other yeast species. Such studies are often stimulated by the practical importance of these "non-conventional" yeasts to the point when they may be considered as a prospective model organism (Bernauer, Radkohl, Lehmayer, and Emmerstorfer-Augustin, 2021).

Methylotrophic yeast *K. phaffii* is capable of utilizing methanol via metabolic pathway with a unique set of enzymes. Recent studies demonstrate that *K. phaffii* possesses a complex regulatory system that regulates methanol utilization genes. Some regulatory proteins are orthologous to proteins found in *S. cerevisiae*, which is not methylotrophic (Ata et al., 2021). *K. phaffii* is Crabtree negative and obligate aerobic in contrast to *S. cerevisiae*. Wherein main carbon metabolism gene sets in these yeasts are similar, different transcriptional control creates multitude. For example, overexpression of a single transcription factor is sufficient to convert *K. phaffii* into Crabtree positive yeast (Ata et al., 2018). Thus, comparative studies on gene regulation in *K. phaffii* and other yeast species are important for understanding the evolution of

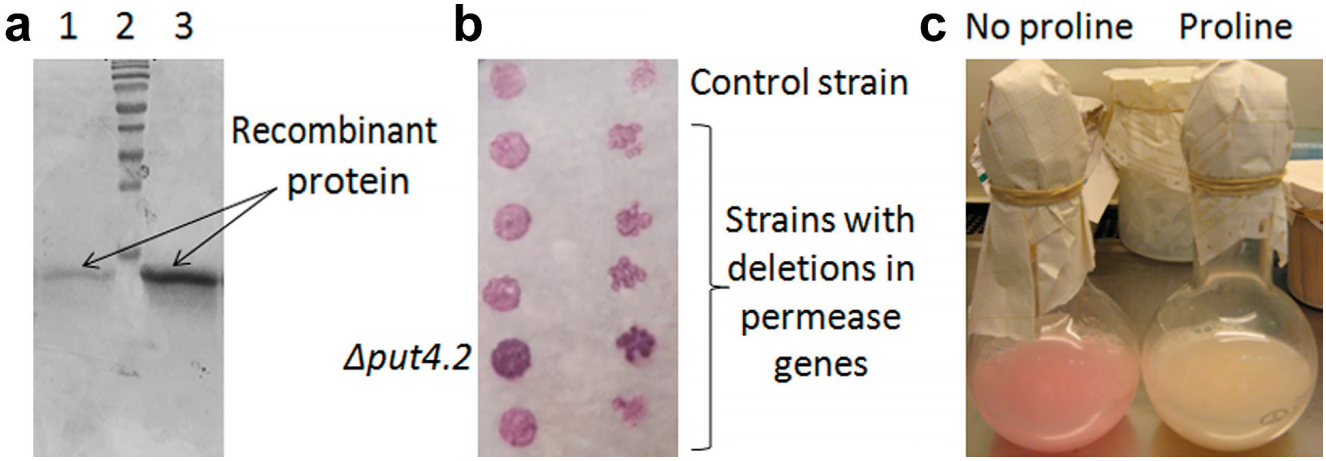

Fig. 7. Use of *K. phaffii* strains for synthesis of recombinant proteins and for studies on gene regulation in yeast cells: *a* — electropherogram of proteins secreted by *K. phaffii* strains producing modified recombinant interleukin 2/15. 1 — strain carries only one expression cassette, 2 — strain carries three expression cassettes, 3 — PageRuler prestained protein ladder (Thermo Fisher Scientific); *b* — activity of reporter acid phosphatase synthesized by *K. phaffii* strains grown on a medium with methanol and proline. All strains carry a reporter system with acid phosphatase coding sequence under control of the promoter of *AOX1* gene, which is crucial for methanol utilization. Strains also carry different deletions in permease genes. Proline in the media represses *AOX1* promoter activity. Deletion in *K. phaffii PUT4.2* permease gene results in derepression of this promoter and higher reporter acid phosphatase activity; *c* — cultures of *K. phaffii* strain carrying reporter system with red fluorescent protein (mRFP) coding sequence under control of the *AOX1* gene promoter. In media with methanol and without proline mRFP is synthesized in high amounts leading to the development of pink color of the culture. In media with methanol and proline mRFP is synthesized at lower quantities due to repression of *AOX1* gene promoter with proline.

regulatory systems. Such research is also of great practical importance due to the fact that *K. phaffii* is widely used as a production host in modern biotechnology.

In our studies we investigated the effect of different media components on gene expression in *K. phaffii* cells. For this purpose, a set of 69 strains carrying different reporter constructions and gene deletions was obtained. Using this part of the genetic collection we demonstrated that the presence of several amino acids (e. g., proline and methionine) in the media leads to drastic changes in gene expression in *K. phaffii* cells. Our studies also elucidated some molecular mechanisms of such regulation (Rumyantsev et al., 2021; Ianshina et al., 2023).

The Genetic Collection of *Drosophila melanogaster* Lines

The collection has been formed since the late 1950s, when it became possible to restore genetics in the USSR. In 1957, Prof. Mikhail E. Lobashev returned to the Department as its head. Since that time, the genetic collection of *Drosophila,* previously lost during the heyday of Lysenkoism, has been restored. Our collection contains 80 strains that are actively used in the educational process for setting genetic problems within the framework of the courses "General Genetics", "Genetic Analysis", "Cytogenetics", "Genetic Toxicology". In general, studies conducted using *Drosophila* not only arouse great interest among students, but are also of great importance in the theoretical and practical training of biologists. In the course of work, students acquire the skills of experimental research, master the methods of statistical processing of the obtained results, learn to analyze the results and draw competent conclusions.

Our collection provides an opportunity to conduct scientific work in a variety of areas. There are unique inbred strains which were obtained at our department and are not found anywhere else in the world. Two contrast strains — LA (low-activity), HA (high-activity), and its derivatives, were obtained by selection for decreased sexual activity of males followed by reverse selection for the same trait. These strains differ in a set of important adaptive characteristics — fertility, motor activity, sex ratio, lifespan, thermostability, etc. (Kaĭdanov et al., 1997; Iovleva and Mylnikov, 2007; Iovleva, 2016).

One of the areas of our research is the study of the mechanisms of systemic control of genetic processes and the evolution of gene families. A variety of mechanisms providing for the complexity of the transcriptome ensures a precise and coordinated regulation of organ-specific functions through a combination of cis-acting elements and trans-acting factors. The *D. melanogaster sbr* (*Dm nxf1)* gene has proven to be an excellent model for investigating these mechanisms. We have mutations in a gene *sbr* (*Dm nxf1)* in our collection that have pleiotropic effects. The pleiotropic effect of mutant alleles of the *sbr* gene affects such stages of *Drosophila* development as early embryogenesis, neurogenesis, spermatogenesis, and oogenesis, for which the synthesis and further fate of so-called long-lived mRNAs in the cytoplasm is of great importance. Thus, in addition to the universal function (providing nuclear mRNA export), the *sbr* gene in *D. melanogaster* can perform specialized functions, retaining its association with certain mRNAs after leaving the nucleus, influencing their biogenesis in the cytoplasm (Mamon et al., 2017, 2019; Mamon, Yakimova, Kopytova, and Golubkova, 2021; Yakimova, Golubkova, Saratseva, and Mamon, 2018; Surkova, Golubkova, Mamon, and Samsonova, 2018; Golubkova, Atsapkina, K'ergaard, and Mamon, 2020; Kozlov et al., 2022). Defects in one part of the SBR (DmNXF1) molecule may affect functions of some complexes without having significant effects on the functions of others. The propensity of SBR (DmNXF1) to multimerization imparts a wide range of variability in heterozygous individuals. RNP complexes can contain different ratios of normal to mutant protein subunits, and this variability can affect structural and functional features of the complex and explain variations in dominant negative effects due to the presence of mutant subunits (Fig. 8).

Drosophila, as an object of genetic research, plays an outstanding role in the development of the most important problems in modern genetics. This role does not decrease over time, but increases, along with the growth of the integral role of genetics in the system of biological sciences. The *Drosophila* collection of the Department of Genetics and Biotechnology of St. Petersburg State University allows to conduct research and educational work in this field at the modern level.

Conclusion

Taken together, the collections of the Department of Genetics and Biotechnology of St. Petersburg State University represent a significant source of unique genetic lines and strains of plants, microorganisms and animals, illustrating the development of genetic research at St. Petersburg State University over the past 70 years. The Genetic Collections of St. Petersburg State University are currently actively used in the educational process for practical classes in the "General Genetics" course and a number of other educational courses as well as in interdisciplinary research aimed primarily at studying transcription, translation, and replication in various groups of organisms, which creates the basis for their further replenishment and development.

It is necessary to pay attention to the fact that these are collections of living organisms, they are constantly changing, being updated and supplemented with new samples. It is especially important to note the inseparable connection between the educational process and scientific research conducted at the Department of Genetics and Biotechnology using the Genetic Collections of St. Petersburg State University.

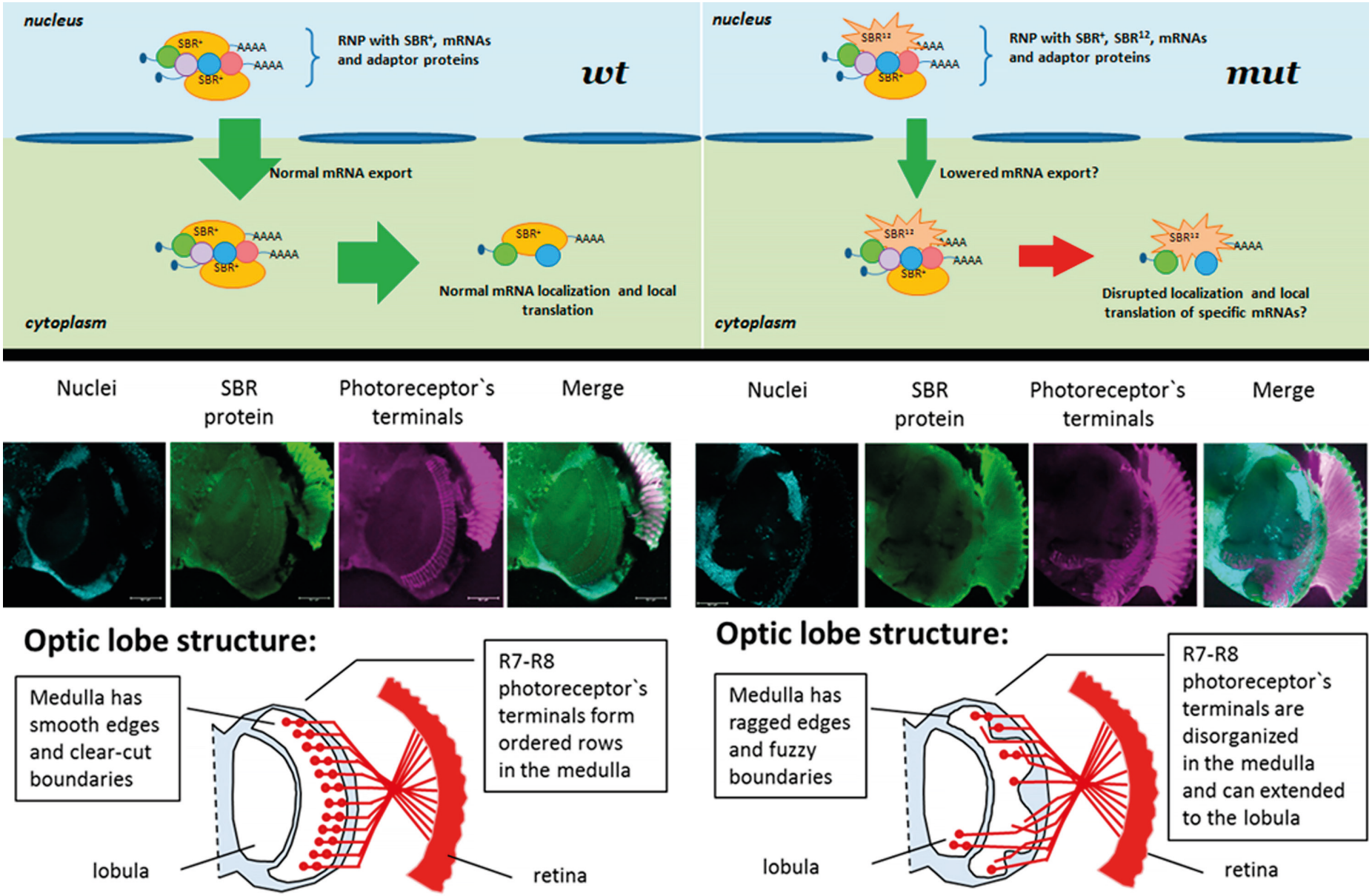

Fig. 8. Scheme illustrating the occurrence of pleiotropic effects of *sbr* (*DmNxf1*) gene mutations. Defects in photoreceptor axon pathfinding and developmental neurodegeneration are responsible for defects in the formation of medulla borders in males with *sbr12* mutation. The middle inset shows the structure of the *Drosophila* brain optic lobes in the normal and in the mutant flies. The presence of the mutant protein in transported RNPs can disrupt the localized translation of specific RNAs, which is necessary for proper axonal targeting or/and cytoskeletal rearrangement during axonal growth.

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Data availability:

The Catalogues of Genetic Collections of St. Petersburg University are available upon request by e-mail.

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