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## Algebraic Methods in Evolutionary Genetics

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### Abstract

This paper is a survey of some results obtained in evolutionary genetics by algebraical methods. The main topics: 1. Some special classes of algebras which arising in population genetics (stochastic, baric, BERNSTEINIAN, genetic etc.). 2. The BERNSTEIN's problem and the stationary genetic structure. 3. The convergence to an equilibrium, the rate of convergence. 4. The exact linearization of evolutionary equation. 5. The exact formulae for evolutionary spectrum and for solution of the evolutionary equation.

Key words: *Population genetics, BERNSTEIN, BERNSTEIN's problem, evolutionary equation.*

### 1. Introduction

The algebraical character of heredity was discovered by MENDEL [1]. Later SEREBROVSKY [2] and GLIVENKO [3] described "MENDELian algebra" in detail. The systematic study of algebra arising in evolutionary genetics was initiated by ETHERINGTON [4–9]. He singled out the nilpotent property essential to these algebras and formalized it in his definition of special train algebra (STA). The theory and application of these algebra were successfully further advanced by SHAFER [10], GONSHOR [11–13], HOLGATE [14–20], HEUCH [21] and various other scientists. However this approach has proved to be somewhat inadequate [22], [23]. On the contrary, an adequate description of genetic situations demands the refusal of constructing too general algebraical theory and it is REIERSÖL in his remarkable paper [24] who points the way to getting at the problem. The development of REIERSÖL's method led to the exact solution of evolutionary equations first for "free" populations [22] and later in other situations [25].

As is well known, the MENDELian one-locus population is balanced on the level of gametas (genes) and comes to equilibrium on the level of zygotas in one generation. In the early 1920-s BERNSTEIN posed [26] the problem of an explicit description of all evolutionary operators which satisfy the "principle of stationarity", that is reaching equilibrium in the first generation of offsprings. BERNSTEIN solved [27–29] this problem in the lowest dimension and also in some other particular cases of arbitrary dimension. Subsequent analysis [22] has shown that BERNSTEIN's problem on the whole went beyond the framework of genetics. With restrictions imposed by this framework it has been solved by the author in

[22], [30], [31]. An alternative class of solutions is given in [32] but the general solution is not yet known. In any case BERNSTEIN's problem has proved to be to a large extent an algebraical one [31], [33]. The "BERNSTEINIAN" algebras which arise in the problem mentioned are connected with STA though they are not STA themselves [20].

This paper is a short survey of some results obtained in evolutionary genetics by algebraical method. For the sake of simplicity we are restricting ourselves to free populations though such phenomena as sex differentiation, polyploidy, mutations and migrations may be studied by the same methods. But evolutionary equations which embrace selection demand the application of analytical methods ([34] for example). For this reason the dynamics of selection are outside this survey.

## 2. Evolutionary operators and stochastic algebras

The formal free population of dimension  $n$  is the object given by the finite set  $\{e_1, \dots, e_n\}$  and by the set of numbers  $\pi_{ik,j}$  ( $i, k, j = 1, \dots, n$ ) which satisfy conditions

$$\pi_{ik,j} = \pi_{ki,j} \geq 0, \quad \sum_{j=1}^n \pi_{ik,j} = 1.$$

The elements  $e_i$  are said to be the hereditary types,  $\pi_{ik,j}$  — the coefficients of heredity (one can interpret  $\pi_{ik,j}$  as probabilities of appearing of offspring  $e_j$  from parents  $e_i, e_k$ ).

Let us consider  $n$ -dimensional real space  $\mathfrak{R}^n$  with basis  $\{e_1, \dots, e_n\}$ . The algebra which has the structure constants  $\pi_{ik,j}$  in this basis is said to be the algebra of population. Thus

$$e_i e_k = \sum_{j=1}^n \pi_{ik,j} e_j \quad (i, k = 1, \dots, n).$$

It is evident that the algebra of population is commutative but, in general, nonassociative one. The algebra in  $\mathfrak{R}^n$  with structure constants satisfying above condition is said to be the stochastic algebra (cf. [35]).

The quadratic transformation

$$V: x'_j = \sum_{i,k=1}^n \pi_{ik,j} x_i x_k \quad (j = 1, \dots, n)$$

in the simplex

$$\Delta: x_i \geq 0 \quad (i = 1, \dots, n), \quad \sum_{i=1}^n x_i = 1$$

is called the evolutionary operator of population.

The points  $x \in \Delta$  are said to be the states of population. The set of those  $e_i$ , for which  $x_i > 0$  is said to be the support of  $x$  (supp  $x$ ). The state  $x$  is said to be the inner state if supp  $x = \{e_1, \dots, e_n\}$ , i.e.  $x_i > 0$  for all  $i$ .

Speaking in the terms of algebra:  $Vx = x^2$  ( $x \in \Delta$ ).

The fixed points of operators  $V$  (i.e. idempotents of algebra) in the simplex are said to be the equilibrium states. By BROWER's fixed-point theorem there exists at least one equilibrium state.

The subalgebra of the stochastic algebra is said to be coordinate subalgebra if it is the linear hull of some nonvoid subset  $\{e_{i_1}, \dots, e_{i_r}\}$  of basis. The coordinate subalgebras correspond (by definition) to the subpopulations of given population or to the invariant facet of simplex  $\Delta$ . The stochastic algebra (population) is said to be the nondivisible one if it has not coordinate subalgebras (subpopulations) which are different from it.

**Theorem 1.** *If for some state  $x$*

$$\text{supp } Vx \subset \text{supp } x$$

*then linear hull  $\text{Lin}(\text{supp } x)$  is the coordinate subalgebra.*

**Corollary 1.** *For every equilibrium state  $x$  the linear hull  $\text{Lin}(\text{supp } x)$  is the coordinate subalgebra.*

**Corollary 2.** *For nondivisibility of stochastic algebra it is necessary and sufficient that all equilibrium states were the inner states.*

### 3. Baric algebras. BERNSTEINIAN algebras

Let  $\mathfrak{A}$  be  $n$ -dimensional commutative algebra,  $s \neq 0$  the linear multiplicative functional (i.e. the homomorphism in the principal field<sup>1</sup>). The pair  $(\mathfrak{A}, s)$  is said to be baric algebra, the functional  $S$  is said to be the weight [5]. For example, the functional

$$s(x) = \sum_{i=1}^n x_i$$

may be the weight in any stochastic algebra.

Another example: Let  $A$  be the linear operator in vector space,  $s$  such linear functional that  $A^*s = s$  (i. e.  $s(Ax) = s(x)$ ). Let us determine multiplication:

$$xy = \frac{1}{2} \{s(x) Ay + s(y) Ax\}.$$

Then the functional  $S$  becomes the multiplicative one and it may be considered as weight. When  $A = 1$  one obtains the "unit algebra" which describes the multiplication of gametas in one-locus MENDELIAN population: if  $a_1, \dots, a_m$  are gametas then

$$a_i a_k = \frac{1}{2} a_i + \frac{1}{2} a_k \quad (1 \leq i, k \leq m)$$

in correspondence with partition of zigota  $a_i a_k$  in meiosis.

<sup>1</sup> Only case where the principal field is  $\mathfrak{R}$ -field of reals is interesting for applications to genetics.

The linear functional  $f$  on the baric algebra  $(\mathfrak{A}, s)$  is said to be invariant linear form [22] if  $f(x^2) = s(x) f(x)$  (i.e.  $f(x^2) = f(x)$  for  $s(x) = 1$ ), or equivalently

$$f(xy) = \frac{1}{2} \{s(x) f(y) + s(y) f(x)\}.$$

The invariant linear forms constitute the subspace  $I$  of dual space  $\mathfrak{A}^*$ . It is evident that  $s \in I$  hence  $\dim I \geq 1$ . The annihilator  $I^l \subset \mathfrak{A}$  is the ideal, factor-algebra is the unit algebra (with the weight  $S$ ). The annihilator of whole algebra  $\text{Ann } \mathfrak{A} = \{x \mid xy = 0 (\forall y)\}$  is also the ideal and  $\text{Ann } \mathfrak{A} \subset I^l$ . Both these ideals are contained in the "barideal"  $\mathfrak{R} = \text{Ker } S$ .

The baric algebra is said to be two-level (or correct) [22], [31] if  $x^2$  depends on the values of invariant linear forms on the element  $x$  only, i.e. if  $x_1 \equiv x_2 \pmod{I^l} \Rightarrow x_1^2 = x_2^2$ . The genetic meaning of this definition will be explained later. For algebra to be two-level it is necessary and sufficient that  $\text{Ann } \mathfrak{A} = I^l$ .

The baric algebra  $(\mathfrak{A}, s)$  is said to be BERNSTEINIAN algebra (cf. [20], [22]) if the identity

$$(x^2)^2 = s^2(x) x^2$$

is true.

All two-level algebras are BERNSTEINIAN, but there are noncorrect algebras between BERNSTEINIAN ones [22] beginning with dimension  $n = 3$ . The correct algebras are characterized by the identity.

Let us consider the structure of BERNSTEINIAN algebra. All those elements of BERNSTEINIAN algebra  $(\mathfrak{A}, s)$  which have the form  $e = x^2$  ( $s(x) = 1$ ) are idempotents and on the contrary every nonzero idempotent has such a form.

Lemma ([22], [36]). *If  $e \neq 0$  the idempotent in the BERNSTEINIAN algebra then the linear operator  $L_e y = 2ey$  in the barideal  $\mathfrak{R}$  is the projector. The numbers  $m = \text{rg } L_e + 1$ ,  $\delta = \text{def } L_e$  do not depend on  $e$ .*

The pair of numbers  $(m, \delta)$  is said to be the type of the BERNSTEINIAN algebra. It is evident that  $m \geq 1$ ,  $m + \delta = n$ . An algebra of the type  $(n, 0)$  is unit one. An algebra of the type  $(1, n - 1)$  is "constant" one:  $xy = s(x) s(y) e$  (thus  $x^2 = e$  when  $s(x) = 1$ ).

**Theorem 2.** *Let  $U = \text{Im } L_e$ ,  $W = \text{Ker } L_e$ . If*

$$x = se + u + w \quad (s = s(x), u \in U, w \in W)$$

*then*

$$x^2 = s^2e + (su + 2uw + w^2) + u^2$$

(the bracketed expression belongs to  $U$ ,  $u^2 \in W$ ).

This is the algebraical formulation of the theorem which describes the BERNSTEIN's quadratic mapping given in [22].

For the algebra to be two-level one it is necessary and sufficient that the following identities were true:  $uw = 0$ ,  $w^2 = 0$ , i.e.

$$x^2 = s^2e + su + u^2.$$

**Corollary.**  $\dim I \cong m$ . *The equality is reached if and only if the algebra is the two-level one.*

The linear functional  $g$  on the algebra  $\mathfrak{A}$  is said to be the vanishing linear form if  $g(x^2) = 0$ . The subspace  $N$  of all vanishing forms is the annihilator of the ideal  $\mathfrak{Q}^2$ . It follows from theorem 2 that  $\dim N \cong \delta$  for BERNSTEINIAN algebra.

The BERNSTEINIAN algebra is said to be the exceptional algebra if  $\dim N = \delta$  (this is equivalent to the identity  $u^2 = 0$ ).

**Theorem 3.** *There exists nontrivial (i.e. nonproportional to  $s$ ) invariant form in the unexceptional BERNSTEINIAN algebra.*

This result is obtainable by the methods of [37] where the following theorem is proved.

**Theorem 4.** *If the inequality*

$$\dim N < \delta - \frac{(m-1)(m-2)}{2}$$

*is valid in the BERNSTEINIAN algebra of the type  $(m, \delta)$  or if  $\delta = 1, N = 0$ , or if  $\delta = 0$ , then the algebra is the two-level one. If the integers  $m, \delta, d$  ( $m \cong 1, \delta \cong 2, 0 \cong d \cong \delta - 2$ ) satisfy the inequality*

$$d \cong \delta - \frac{(m-1)(m-2)}{2}$$

*then there exists noncorrect BERNSTEINIAN algebra of the type  $(m, \delta)$  with  $\dim N = d$ .*

Let us note in connection with this the following fact.

**Theorem 5.** *All BERNSTEINIAN algebras of the type  $(m, \delta)$  with  $\delta = \frac{m(m-1)}{2}$ ,  $\dim N = 0$ , are isomorphic.*

The representative of this class of the isomorphic algebras is the one-locus MENDELIAN algebra of zygotas

$$a_i a_k \cdot a_j a_l = \frac{1}{4} \{a_i a_j + a_i a_l + a_k a_j + a_k a_l\}.$$

The type number  $m$  coincides here with the number of alleles  $a_1, \dots, a_m$  (and hence with the number of homozygotas) and  $\delta = \frac{m(m-1)}{2}$  is equal to the number of heterozygotas.

#### 4. The BERNSTEIN's problem

This problem consists in the explicit description of all evolutionary operators  $V$  satisfying the condition  $V^2 = V$ , i.e. the law of stationarity discovered by PEARSON [38] for the simplest case. Using the algebraical language it is necessary to describe all stochastic BERNSTEINIAN algebras ("BERNSTEINIAN populations").

The first result in this direction is the following theorem of BERNSTEIN on the "necessity of MENDEL's law" [27] [29], [22], [33].

**Theorem 6.** *If evolutionary operator  $V$  for  $n=3$  is stationary one ( $V^2=V$ ) and  $\pi_{12,3}=1$  (i.e. all offsprings of  $e_1$  and  $e_2$  are of the type  $e_3$ ), then  $V$  is HARDY-WEINBERG [39], [40] operator*

$$x'_1 = p^2, \quad x'_2 = q^2, \quad x'_3 = 2pq$$

where

$$p = x_1 + \frac{1}{2} x_3, \quad q = x_2 + \frac{1}{2} x_3$$

(with exclusion of the cases of complete disappearance of  $e_1$  or  $e_2$  between offsprings).

In [33] this theorem was proved algebraically using the abovementioned Theorem 2.

For  $n=3$  the problem was solved by BERNSTEIN himself [28], [29] but genetic explanation of these results was given essentially later [22]. Besides BERNSTEIN obtained certain results for arbitrary  $n$ . We shall formulate them using the convenient but not present in BERNSTEIN's works algebraical language.

**Theorem 7.** *If the stochastic BERNSTEINIAN algebra has  $r$  "pure types", i.e. idempotents:  $e_i^2 = e_i$  ( $i=1, \dots, r$ ) and the remaining types are their "hybrids", i.e. paired products  $e_i e_k$  ( $1 \leq i, k \leq r$ ), then the algebra is the onelocus MENDELIAN algebra of zygotas.*

**Theorem 8.** *If all heredity coefficients in the stochastic BERNSTEINIAN algebra are positive ( $\pi_{i,k,j} > 0$ ), then algebra is the constant one, i.e. the distribution of offsprings does not depend on the distribution of parents.*

At last, BERNSTEIN described all stochastic BERNSTEINIAN algebra with two pure types:  $e_1^2 = e_1$ ,  $e_2^2 = e_2$  and  $\pi_{12,j} > 0$  ( $3 \leq j \leq n$ ). He discovered between them essentially new, compared with HARDY-WEINBERG operator, law of heredity for  $n=4$ :

$$\begin{aligned} x'_1 &= (x_1 + x_3)(x_1 + x_4) & x'_3 &= (x_3 + x_1)(x_3 + x_2) \\ x'_2 &= (x_2 + x_3)(x_2 + x_4) & x'_4 &= (x_4 + x_1)(x_4 + x_2) \end{aligned}$$

and named it as the "quadril" law. The genetic explanation of this law was proposed in [22] and will be given later in the present paper.

The BERNSTEIN's proof is rather untransparent and the proof of the Theorem 8 is apparently not quite correct. Now we have the proofs of all BERNSTEIN's results which use the theory stated in § 2. In particular, rather short proof of Theorem 8 was given in [52]. It appeared that the condition  $\pi_{ii,j} > 0$  is sufficient but really it is even sufficient that the algebra is indecomposable.

The further results concerning BERNSTEIN's problem were obtained in the series of our papers. In [41], [42] BERNSTEINIAN populations of the types  $(n-1, 1)$  and  $(2, n-2)$  respectively were described. In particular, this gives the solution of BERNSTEIN's problem for  $n=4$ . In [32] all exceptional BERNSTEINIAN populations

were described. But all these formal laws of heredity are outside genetics. This is explained in the next paragraph which is devoted to the genetic restriction of BERNSTEIN's problem.

### 5. The stationary genic structure

HARDY-WEINBERG operator is parametrized by the intermediate variables  $p, q$ . It is possible to consider them as the probabilities of the allele genes  $A$  in the genetic population which is in the state  $(x_1, x_2, x_3)$  (they are the probabilities of genotypes  $AA, aa, Aa$  respectively). The stationarity of HARDY-WEINBERG operator (PEARSON's law) is a consequence of the law of conservation of genes' probabilities: in the next generation

$$p' = x'_1 + \frac{1}{2} x'_3 = p^2 + pq = p$$

$$q' = x'_2 + \frac{1}{2} x'_3 = q^2 + pq = q$$

from which

$$x''_1 = p'^2 = p^2 = x'_1, \quad x''_2 = q'^2 = q^2 = x'_2, \quad x''_3 = 2p'q' = 2pq = x'_3.$$

Hence the variables  $p, q$  are the invariant linear forms parametrizing the evolutionary operator. They are the generators of cone  $C$  of all nonnegative forms in the space  $I$  of the invariant linear forms. They are distinguished from other generators by the following norming: the maximal coefficients in  $p$  and  $q$  of  $x_1, x_2, x_3$  are equal to one.

It is more natural from genetic point of view do not postulate the stationarity but to draw it from the genetic structure of zygotas. The corresponding definitions were introduced by author in [22], [30] and are following.

Be  $C$  the cone of the nonnegative invariant linear forms. It is the finitely generated cone in the space  $I$  of all invariant linear forms,  $\text{Int } C \neq \emptyset$ .

Be

$$(1) \quad \mu_i = \sum_{k=1}^n \mu_{ik} x_k \quad (i = 1, \dots, \nu)$$

are the generators of cone  $C$  normed in such a way that  $\max_k \mu_{ik} = 1$ . The evolutionary operator  $V$  (of the population) has by definition the stationary genic structure (s.g.s) if it may be represented in a form

$$x'_j = \sum_{i,k=1}^{\nu} c_{ik,j} \mu_i \mu_k$$

where

$$c_{ik,j} \geq 0.$$

Because  $\mu'_i = \mu_i$ , it is  $x'_j = x_j$ , i.e.  $V^2 = V$ , and s.g.s. gives the stationarity of evolutionary operator. The correspondent algebra is the two-level BERNSTEINIAN algebra.

**Theorem 9.** *The two-level BERNSTEINIAN operator has s.g.s.*

We note that the linear operator (1) corresponds to meiosis and the quadratic operator (2) – to fertilization. We call them the operators of meiosis and fertilization respectively. If  $\mu$  is the operator of meiosis,  $\varphi$  is the operator of fertilization then the evolutionary operator  $V = \varphi\mu$  and  $\mu V = \mu$ .

If the linear forms  $\mu_i$  are linearly independent (i.e.  $C$  is the minihedral cone) then we shall say that  $V$  has the elementary genetic structure (e.g.s.).

The explicit form of e.g.s. was formed in [22] and the explicit form of s.g.s. was given in [30], [31]. Some situations anomalous from genetic point of view were omitted and their separate analysis was given in the last paragraph of [31]. The "normal" population is defined by the following conditions: 1)  $x'_j \neq 0$  ( $1 \leq j \leq n$ );

$$2) x'_i \neq \text{const. } x'_j \quad (1 \leq i, j \leq n); \quad 3) \frac{\partial(Vx)}{\partial x_i} \neq \frac{\partial(Vx)}{\partial x_k} \quad (1 \leq i, k \leq n).$$

**Theorem 10.** *The evolutionary operator possessing the normal e.g.s. of  $(m, \delta)$  type has a form<sup>1</sup>*

$$(3) \quad \begin{cases} x'_i = \mu_i^2 + 2\mu_i \sum_{k \neq i} a_{ik} \mu_k & (1 \leq i \leq m) \\ x'_{m+j} = 2b_j \mu_j \mu_k & (1 \leq j \leq \delta) \end{cases}$$

where

$$(4) \quad \mu_i = x_i + \sum_{j=1}^{\delta} c_{ij} x_{m+j}$$

and 1) pairs of indexes  $(i_1, k_1), \dots, (i_\delta, k_\delta)$  are different,  $i_1 < k_1, \dots, i_\delta < k_\delta$ ; 2)  $C_{i_\delta j} > 0$ ,  $C_{k_j j} > 0$ ,  $C_{i_\delta j} + C_{k_j j} = 1$ , the remaining  $C_{ij} = 0$ ; 3)  $0 < b_j \leq 1$ ; 4)  $a_{ik} \geq 0$  and  $a_{ik} = a_{ki} = \frac{1}{2}$  for all pairs not mentioned in 1); 5) the "equations of genetic balance"

$$a_{i_\delta j} + c_{i_\delta j} b_j = \frac{1}{2}, \quad a_{k_j j} + c_{k_j j} b_j = \frac{1}{2}$$

are satisfied.

According to genetic interpretation [22], [43] the population which follows the hereditary law (3), (4) is one-locus one and is determined by alleles  $A_1, \dots, A_m$  with the presence (besides homozygotas) the heterozygotas  $A_{i_1} A_{k_1}, \dots, A_{i_\delta} A_{k_\delta}$  and no others. There exists the meiotic drive:  $A_{i_j} A_{k_j} \rightarrow c_{i_j j} A_{i_j} + c_{k_j j} A_{k_j}$ . As the result of junction of two different alleles  $A_i A_k$  homozygotas  $A_i A_i$ ,  $A_k A_k$  are arising with respective probabilities  $a_{ik}$  and  $a_{ki}$ , and for the mentioned pair  $i = i_j$ ,  $k = k_j$  the heterozygotic genotype is formed with probability  $b_j$ .

<sup>1</sup> with possible change of numeration of hereditary types.



When  $m = 2, \delta = 1$  the family of stationary hereditary laws is two-parametric one and constrains HARDY-WEINBERG law.

Theorem 11. *Every normal nonelementary s.g.s. corresponds to some decomposition of the types number  $n$  to two factor,  $n = m_1 m_2$  and with suitable double indexation of the types  $x_{ik}$  ( $1 \leq i \leq m_1, 1 \leq k \leq m_2$ ) the evolutionary operator has a form*

$$(5) \quad x'_{ik} = \mu_i \lambda_k$$

where

$$(6) \quad \mu_i = \sum_{k=1}^{m_2} x_{ik}, \quad \lambda_k = \sum_{i=1}^{m_1} x_{ik}.$$

When  $m_1 = m_2 = 2$  the BERNSTEIN's quadril is arising. According to the genetic interpretation [22], [43] the population which follows the hereditary laws (5), (6) is one-locus one, determined by male alleles  $A_1, \dots, A_m$  and female alleles  $B_1, \dots, B_m$ , and as a result every zygota is of a form  $A_i B_k$ . The fertilization is taking place by the mixture of genes of different sexes (by the junction of "pollen cell" and "ovule").

Thus nonelementary s.g.s. differs from e.g.s. by the presence of sexual differentiation of genes.

Once more let us underline that in accordance with Theorems 10, 11 no other stationary hereditary law based on gene's structure does not exist.

### 5. The language of the differential operators. The convergence to an equilibrium

The essentially unbalanced picture arises if more than one locus in genetic is taking into consideration. A lot of research work was carried out to investigate this case (note [44-48], [25]) and it was REIERSÖL who had proposed the most transparent approach [24].

Let there exists the set of genes  $\{a_{ik}\}$  where  $i$  ( $1 \leq i \leq l$ ) is the number of locus,  $k$  ( $1 \leq k \leq m_i$ ) is the number of allele. Then the following genotypes of gametas are possible:  $g = a_{1k_1} \dots a_{lk_l}$  ( $1 \leq k_1 \leq m_1, \dots, 1 \leq k_l \leq m_l$ ). The possible crossing overs (simple and multiple) are described in one-to-one correspondence by partition  $U|V$  of the set of loci  $L = \{1, \dots, l\}$  in two classes ( $U \subset L, V = L \setminus U$ , the pair  $U, V$  being unordered). The distribution of probabilities  $p = p(U|V)$  is given in the set of all partitions ("of linkage distribution" [45]). The population algebra is constructed on the level of gametas in the following way.

For given gamete  $g = \prod_{i=1}^l a_{ik_i}$  and given partition  $U|V$  let

$$g_U = \prod_{i \in U} a_{ik_i}, \quad g_V = \prod_{i \in V} a_{ik_i}.$$

Then

$$g \times h = \frac{1}{2} \sum_{U|V} p(U|V) (g_U h_V + g_V h_U).$$

It is possible to write this "table of multiplication" as

$$(7) \quad g \times h = \frac{1}{2} \sum_{U|V} p(U|V) (D_U g \cdot D_V h + D_V g \cdot D_U h)$$

where for example,

$$D_U = \prod_{i \in U} D_i \quad \left( D_i = \sum_{k=1}^{m_i} \frac{\partial}{\partial a_{ik}} \right)$$

are the formal differential operators. In the linear space generated by all gametes the algebra has the form, analogously to (7):

$$G \times H = \frac{1}{2} \sum_{U|V} p(U|V) (D_U G \cdot D_V H + D_V G \cdot D_U H).$$

In particular, the evolutionary operator is

$$(8) \quad G' = G \times G = \sum_{U|V} p(U|V) D_U G \cdot D_V G.$$

We shall denote the algebra described as  $\mathfrak{A}(L; p)$ .

For every subset  $A \subset L$  the induced distribution of linkage is defined as

$$p_A(u|v) = \sum_{U \supset u, V \supset v} p(U|V)$$

and the corresponding algebra as  $\mathfrak{A}(A; p_A)$ . The direct check proves

Lemma [24]. Let  $\bar{A} = L \setminus A$ . The operator  $\hat{D}_A = D_{\bar{A}}$  is homomorphism of algebra  $\mathfrak{A}(L; p)$  into  $\mathfrak{A}(A; p_A)$ , i.e. it is linear one and

$$D_{\bar{A}}(G \times H) = D_{\bar{A}}G \times D_{\bar{A}}H.$$

This lemma is the principle one for the systematic application of mathematical induction to the investigation of evolution of  $l$ -locus population (induction being carried by  $l$ ). Its genetic essence is that the evolution in any subset of loci (with the induced distribution of linkage) coincides with the restriction of evolution of full system.

In a very simple way one can obtain from lemma the following theorem.

Theorem 12. For any given number of loci  $l \geq 1$  every trajectory  $\{G_k\}_0^{\infty}$ .

$$G_{k+1} = G_k \times G_k \quad (k=0, 1, 2, \dots)$$

converges to equilibrium state  $G_{\infty}$  (which depends on the initial state  $G_0$ ).

From now on let us suppose that the induced linkage distribution for every pair of loci is such that  $p(i|j) \neq 0$  (loci are not "rigidly linked"). It does not belittle the generality as it is possible to unite the rigidly linked loci. But the appearance of the following formulae depends on the presence or absence of such loci.

The set of states of equilibrium is described by the formula

$$G = \prod_{i=1}^l H_i$$

where  $H_i$  is an arbitrary state of the  $i$ -th locus (i.e. the element of algebra  $\mathfrak{A}(i; 1)$ ). In particular,

$$G_{\infty} = \prod_{i=1}^l \hat{D}_i G_0.$$

6. The exact linearization of evolutionary equation. Evolutionary spectrum

The nonlinear evolution equation (8) gives possibility for exact linearization in the following meaning (cf. [45], [46], [24], [15], [22], [25]).

**Theorem 13.** *For any given distribution of linkage there exists such real polynomial*

$$\varphi(\tau) = \tau^d + a_1 \tau^{d-1} + \dots + a_d$$

that all trajectories  $\{G_k\}_0^{\infty}$  ( $G_{k+1} = G_k \times G_k$ ) are satisfying the linear equation

$$G_{k+d} + a_1 G_{k+d-1} + \dots + a_d G_k = 0 \quad (k = 0, 1, 2, \dots).$$

Thus the expansion of "hereditary memory" of population permits to describe linearly the influence of the past states on the present ones. "The depth of memory"  $d$  depends on the number of loci only and grows rapidly with the growth of  $l$ :

$l$	1	2	3	4	5	$\dots \rightarrow \infty$
$d_l$	1	2	4	7	19	$\dots \ln d_l \sim \frac{l^2}{\ln l}$

The polynomial  $\Phi(\tau)$  is constructed by the recurrence for algebra  $\mathfrak{A}(L; p)$  using the analogous polynomials of subalgebras  $\mathfrak{A}(A; p_A)$  ( $A \subset L, A \neq L$ ). It is called the evolutionary polynomial (of given algebra or population), its roots are called the evolutionary roots and the set of roots is called the evolutionary spectrum. The evolutionary spectrum was described in [21] (cf. [17]) recursively. The following explicit formula for evolutionary roots was obtained in [22].

Let  $p(K)$  ( $K \subset L$ ) be the probability of subset  $K$  to be not parted,

$$p(K) = \sum_{K \subset U} p(U | V).$$

**Theorem 14.** *The evolutionary spectrum is the set of values*

$$(9) \quad \lambda_{K_1 | \dots | K_r} = \prod_{i=1}^r p(K_i)$$

which correspond to all such possible systems  $K_1 | \dots | K_r$  of not intersecting subsets  $K_i \subset L$  ( $r \geq 1, i = 1, \dots, r$ ) that  $|K_i| \geq 2$ .

Such systems  $K_1 | \dots | K_r$  are said to be the permissible partitions. The evolutionary roots appear to be the polynomials from  $p(U | V)$ . The formula (9) gives

**Theorem 15.** *The evolutionary roots considered as polynomials from  $p(U | V)$  are distinct.*

This does not rule out the presence of the multiple roots for the given distribution of linkage (it is the case, for example, for independent loci).

7. The genetic algebra

It is possible to connect with any algebra  $\mathfrak{A}$  the associative algebra  $\widetilde{\mathfrak{A}}$  generated by the multiplication operators  $L_x y = xy$  ( $x, y \in \mathfrak{A}$ ). Let  $\dim \mathfrak{A} = n < \infty$ . Let us consider the characteristic polynomial of operator  $L_x$  :

$$D_x(\lambda) = \det(\lambda I - L_x) = \sum_{k=0}^n (-1)^k \sigma_k(x) \lambda^{n-k}.$$

Here  $\sigma_k(x)$  are the homogeneous polynomial in respect to  $x$  of degree  $k$  ( $k = 0, 1, \dots, n$ ),  $\sigma_0(x) = 1$ .

Following ETHERINGTON [5] the baric algebra  $(\mathfrak{A}, s)$  is said to be the train-algebra (TA) if the forms  $\sigma_k(x)$  are depending on  $s(x)$  only, i.e.  $\sigma_k(x) = c_k s^k(x)$  ( $k = 1, \dots, n$ ;  $c_k = \text{const.}$ ). In this case the roots of polynomial

$$D(\lambda) = \sum_{k=0}^n (-1)^k c_k \lambda^{n-k}$$

is said to be the train-roots.

By the classic HAMILTON-CAYLEY theorem we obtain:

Lemma. *The identity*

$$x^{m+n} - c_1 x^{m+n-1} + \dots + (-1)^n c_n x^m = 0 \quad (m = 1, 2, \dots)$$

is true in TA for all  $x$  with  $s(x) = 1$ . Here the powers of elements are determined as the "principle" ones:

$$x^{m+1} = x^m x \quad (m = 1, 2, \dots; x^1 = x).$$

Corollary. *Barideal  $\mathfrak{R} = \text{Ker } s$  coincides in TA with the set of nilpotents.*

Remember now that an element of algebra is said to be the nilpotent one if some its power is equal to 0. For any baric algebra the nilpotents are contained in barideal but do not fill it up. In general the set of nilpotents is not ideal (even subspace) due to nonassociativity. But if it is the ideal then it is called the nilideal. Thus, the barideal in TA is the nilideal. The barideal in BERNSTEINIAN algebra is the nilideal too though this algebra is not necessarily TA.

Example. Let us decompose the space  $\mathfrak{R}^n$  in the direct sum  $E \dot{+} U \dot{+} W$  where  $\dim E = 1, \dim W = 1$ . Let  $e, w$  be the vectors, generating  $E, W$  respectively. Let

$$x^2 = s^2 e + (s + \omega) u$$

for  $x = se + u + \omega w$  ( $s, \omega \in \mathfrak{R}; u \in U$ ). This is BERNSTEINIAN algebra with the weight  $s(x) = s$ . If  $x = e + \omega w, y = u$  ( $u \in U$ ) then

$$L_x y = \frac{1 + \omega}{2} y$$

i.e.  $\frac{1 + \omega}{2}$  is the eigenvalue of operator  $L_x$  which depends on parameter  $\omega$  while  $s(x) = 1$ .

If  $\mathfrak{A}$  is the BERNSTEINIAN algebra of the type  $(m, \delta)$ ,  $x \in \mathfrak{A}$ ,  $x^2 = x$ ,  $s(x) = 1$ , then  $D_x(\lambda) = (\lambda - 1) \left( \lambda - \frac{1}{2} \right)^{m-1} \lambda^\delta$ . Therefore if it is TA then the train-roots are  $1, \frac{1}{2}, 0$  with multiplicities  $1, m - 1, \delta$ .

**Theorem 16.** *If the BERNSTEINIAN algebra  $\mathfrak{A}$  has no vanishing linear form different from zero (otherwise speaking  $\mathfrak{A}^2 = \mathfrak{A}$ ) then it is TA.*

The baric algebra  $(\mathfrak{A}, s)$  is said to be the special train-algebra (STA) [7] if the powers of its barideal are ideals themselves and some power is equal to zero.

**Theorem 17** [7]. *There exists the basis  $e_0, e_1, \dots, e_{n-1}$  ( $s(e_0) = 1, s(e_i) = 0 (i > 1)$ ) in any  $n$ -dimensional STA for which the multiplication table is of the following triangular form:*

$$e_0^2 = e_0, \quad e_0 e_i = \sum_{k=i}^{n-1} c_{0i,k} e_k \quad (i = 1, \dots, n - 1),$$

$$e_i e_j = \sum_{k=\max(i,j)+1}^{n-1} c_{ij,k} e_k \quad (i, j = 1, \dots, n - 1).$$

This basis is said to be the special train-basis.

**Corollary.** *Every STA is TA. Its train-roots are*

$$\lambda_0 = 1, \quad \lambda_i = c_{0i,i} \quad (i = 1, \dots, n - 1).$$

Following SHAFER [10] the baric algebra is said to be the genetic algebra (GA), if for any noncommutative polynomial  $f(\xi_1, \dots, \xi_r)$  the characteristic polynomial of operator  $f(L_{x_1}, \dots, L_{x_r})$  depends on the weights  $s(x_1), \dots, s(x_r)$  only. If it is evident that every GA is TA.

**Theorem 18.** *For the baric algebra to be GA it is necessary and sufficient that it contains the special train-basis.*

Thus every STA is GA (inverse is not true [10]).

The sufficiency in Theorem 18 is proved immediately [10]. In a proof of necessity the characterization of GA in terms of nilpotence of barideal and solvability of Lie algebra generated by operators  $L_x$  [20] is used (the proof in [20] is incomplete but it is corrigible).

The overwhelming majority of algebras arising in the specific genetic situations in connection with evolutionary operators belongs to the class of GA [7], [10–12], [14], [17–19]. Every two-level BERNSTEINIAN algebra is GA (inverse is not true).

It is possible to investigate an evolution in context of genetic algebra considering the sequence of “plenary” powers  $x^{[k+1]} = (x^{[k]})^2$  ( $k = 0, 1, 2, \dots$ ),  $x^{[0]} = x$ . The exact linearization of evolutionary equation in some particular cases was carried out by ETHERINGTON [6] and in full generality by HOLGATE [15], HEUCH [21].

**Theorem 19** [15]. *The linear equation of form*

$$x^{[m+k]} + b_1 x^{[m+k-1]} + \dots + b_m x^{[k]} = 0 \quad (k = 0, 1, 2, \dots)$$

with constant (for  $s(x)=1$ ) coefficients is satisfied in any GA. The roots of the polynomial  $\lambda^m + b_1 \lambda^{m-1} + \dots + b_m$  have a form

$$(2\lambda_0)^{k_0} (2\lambda_1)^{k_1} \dots (2\lambda_{n-1})^{k_{n-1}}$$

where  $\lambda_i$  are the train-roots,  $(k_0, k_1, \dots, k_{n-1})$  vary in some set of the integer lattice.

The minimal set  $Q$  which is fitted for the whole manifold of  $n$ -dimensional GA was discovered by KURINNOY [23]. But even it is redundant compared with individual genetic situations. For example, the evolutionary spectrum for one-locus haploid population is described by our formula (9). But, as HOLGATE showed [17], the correspondent algebra is GA and its train-roots are  $1, \frac{1}{2}p(K)$  ( $K \subset L, |K| \geq 2$ ).

Hence in this case the exponents  $k_0, k_1, \dots, k_{n-1}$  are taking values 1, 0 only and this gives a small part of the set  $Q$ , found in [23].

The convergence of the trajectories is in essence the result of the exact linearization, as the following lemma is valid.

**Lemma.** *If the sequence  $\{x_k\}_0^\infty$  of points of simplex satisfies the linear equation*

$$x_{m+k} + a_1 x_{m+k-1} + \dots + a_m x_k = 0 \quad (K=0, 1, 2, \dots)$$

with constant coefficients then there exists

$$\bar{x} = \lim_{k \rightarrow \infty} \frac{x_0 + \dots + x_k}{k+1}$$

and if no root  $\lambda \neq 1$  of the characteristic equation

$$\lambda^m + a_1 \lambda^{m-1} + \dots + a_m = 0$$

is located on the circumference  $|\lambda|=1$ , then the sequence  $\{x_k\}_0^\infty$  has the limit.

### 8. The exact solution of the evolutionary equation

Taking as a starting point the Theorem 13, 14 one can write an arbitrary solution of evolutionary equation in a form

$$G_t = \sum_{K_1 | \dots | K_r} C_{K_1 | \dots | K_r}(G_0) \left( \prod_{i=1}^r p(K_i) \right)^t$$

where coefficients are depending on the initial state  $G_0$  only. To obtain the exact form of solution  $G_t$  it is sufficient now to calculate coefficients  $C_{K_1 | \dots | K_r}$  explicitly. For  $r=0$  (i.e. for the void partition  $K_1 | \dots | K_r$ ) it is simple procedure:

$$C_{\emptyset}(G_0) = \prod_{j=1}^l \hat{D}_j G_0.$$

For  $r>0$  it is necessary to introduce [22] the measures of unbalance of an arbitrary state  $G$ . If  $K \subset L, |k| \geq 2$ , then the measure of unbalance of the state  $G$  in

respect to subset  $K$  is

$$E_K(G) = \hat{D}_K G - \prod_{j \in K} \hat{D}_j G$$

where  $\hat{D}_k$  are the differential operators, described in § 5. Evidently the state  $G$  is balanced in respect to loci entering  $K$  if and only if  $E_K(G) = 0$ .

Let

$$E_{K_1 | \dots | K_r}(G) = \prod_{i=1}^r E_{K_i}(G)$$

be the measure of unbalance of the state  $G$  in respect to partition  $K_1 | \dots | K_r$ . We shall "complete" it to

$$\overline{E_{K_1 | \dots | K_r}(G)} = E_{K_1 | \dots | K_r}(G) \prod_{j \in \cup K_i} \hat{D}_j G.$$

Theorem 20 [22]. For  $r > 0$  the formula

$$C_{K_1 | \dots | K_r}(G_0) = \sum_{Q_1 | \dots | Q_\rho} A_{K_1 | \dots | K_r}^{Q_1 | \dots | Q_\rho} \overline{E_{Q_1 | \dots | Q_\rho}(G_0)}$$

is true where

- 1)  $Q_1 | \dots | Q_\rho$  ( $|Q_j| \geq 2$  ( $j = 1, \dots, \rho$ ),  $\rho \geq r$ ) vary all partitions which satisfy conditions: a)  $\forall Q_j \exists K_i: Q_j \subset K_i$ ; b)  $\forall K_i \exists Q_j: Q_j \subset K_i$ ;
- 2) coefficients  $A_{K_1 | \dots | K_r}^{Q_1 | \dots | Q_\rho}$  are dependent on the distribution of linkage only.

The latter dependence is complicated one but nevertheless it may be described explicitly [22]. In particular, we shall mention the formula

$$A_K^Q = (-1)^{|K \setminus Q|}$$

and the approximation formula

$$(10) \quad G_l \approx \prod_{j=1}^l \hat{D}_j G_0 + \sum_K [p(K)]^l \sum_{Q \subset K} (-1)^{|K \setminus Q|} \overline{E_Q}(G_0)$$

which follows from the former and previous formulae. This is an approximation with error  $\epsilon^2$ ,  $\epsilon$  being the maximum of norm of the measure of unbalance.

If  $l \leq 3$  the formula (10) is sharp one (cf. [24], where it has another form for  $l \leq 3$ ). For  $l = 4$  the measure of unbalance of the "second order"  $E_{Q_1 | Q_2}(G_0)$  ( $|Q_1| = 2$ ,  $|Q_2| = 2$ ) are appearing for the first time and by Theorem 20 one has

$$C_{K_1 | K_2}(G_0) = A_{K_1 | K_2}^{K_1 | K_2} E_{K_1 | K_2}(G_0)$$

where

$$A_{K_1 | K_2}^{K_1 | K_2} = \frac{p(K_1 | K_2)}{p(K_1) p(K_2) - p(L)}$$

Simultaneously

$$C_K(G_0) = \sum_{Q \subset K} (-1)^{|K \setminus Q|} \overline{E_Q(G_0)} - \sum_{K_1 | K_2} A_{K_1 | K_2}^{K_1 | K_2} E_{K_1 | K_2}(G_0).$$

The exact solution for four loci has a form

$$G_t = \prod_{j=1}^4 D_j G_0 + \sum_K C_K(G_0) [p(K)]^t + \sum_{K_1 | K_2} C_{K_1 | K_2} [p(K_1) p(K_2)]^t$$

with abovementioned values of coefficients.

The explicit formula of evolution has the same character as asymptotic development in nonlinear mechanics, but here development contains the finite (though great) number of summands. In accordance with Theorem 20 the coefficient of  $\lambda'_{K_1 | \dots | K_r}$  has the order of  $\epsilon^r$ . The value  $\epsilon$  is measuring the "distance" to the equilibrium. Besides, some (usually many) probabilities  $p(K)$  may stay as small parameters. The members containing  $\lambda'_{K_1 | \dots | K_r}$  for  $r > 1$  are small not only due to  $\epsilon^r$  but due to  $\lambda_{K_1 | \dots | K_r} = p(K_1) \dots p(K_r)$  too.

### 9. The rate of stabilization

The rate of stabilization (of convergence to equilibrium) is measured by the value

$$\alpha = \max_{G_0} \lim_{t \rightarrow \infty} \sqrt[t]{\|G_t - G_0\|}.$$

Theorem 21 ([22], cf. [47]). *The formula*

$$\alpha = \max_{|K|=2} p(K)$$

is valid.

This is already following from the representation ( ) of evolutionary spectrum and from the nonpossibility of the equality

$$\sum_{p(K)=\alpha} C_K(G_0) = 0$$

to be true identically in respect to  $G_0$ .

The latter is proved using formulae [22] for coefficients  $A_K^{Q_1 | \dots | Q_e}$ .

Thus, it is always  $\alpha \cong p(L)$ .

Theorem 22 [22]. *For  $l \geq 3$  loci*

$$\alpha \cong \frac{\left\lfloor \frac{l-1}{2} \right\rfloor}{2 \left\lfloor \frac{l-1}{2} \right\rfloor + 1} \cong \frac{1}{3}$$

(is the entire part). *The equality holds in these estimates for some distribution of linkage.*<sup>1</sup>

<sup>1</sup> Rather unrealistic one.



Thus, the evolution, depending on three or four loci, can not approach the equilibrium with the rate exceeding  $\left(\frac{1}{3}\right)^t$ ; depending on five or six loci – with the rate exceeding  $\left(\frac{2}{5}\right)^t$  etc. In the absence of the negative interference [49] the inequality  $\kappa \cong \frac{1}{2}$  is true. In particular, it is true when the simple crossing overs are independent and also when more than one group of linkage is present in the set of loci considered. If the simple crossovers are independent and have the same probability  $p$ , then

$$\kappa = \begin{cases} q = 1 - p & \left( p \cong \frac{1}{2} \right) \\ 1 - 2pq & \left( p \cong \frac{1}{2} \right). \end{cases}$$

In conclusion we note that the many results of §§ 5, 6, 8, 9 were carried [25], [50], [51] to other genetic situations (sex linkage, polyploidy, mutation).

#### Zusammenfassung

Es wird ein Überblick über einige Resultate der Evolution(sgenetik) mittels algebraischer Methoden gegeben und folgendes behandelt:

1. Spezielle Klassen von Algebren (stochastische, barische, BERNSTEINSche, genetische), 2. das BERNSTEINSche Problem und die stationäre genetische Struktur, 3. Konvergenzprobleme, 4. exakte Linearisierung der Evolutionsgleichung sowie die exakte Formel für das Evolutionsspektrum und für die Lösung von Evolutionsgleichungen.

#### References

- [1] MENDEL, G., 1866: Versuche über Pflanzen-Hybriden. Verhandl. d. Naturforsch. Vereins in Brünn, IV, 3–47.
- [2] А. С. СЕРЕБРОВСКИЙ, 1934: О свойствах менделистических равенств. Доклады АН СССР **2**, 33–36.
- [3] В. И. ГЛИВЕНКО, 1936: Менделевская алгебра. Доклады АН СССР **13**, 371–372.
- [4] ETHERINGTON, I. M. H., 1939: On non-associative combinations. Proc. Roy. Soc. Edinb. **59**, 153–162.
- [5] ETHERINGTON, I. M. H., 1939: Genetic algebras. Proc. Roy. Soc. Edinb. A **59**, 242–258.
- [6] ETHERINGTON, I. M. H., 1940, 1945: Commutative train algebras of ranks 2 and 3. J. Lond. Math. Soc. **15**, 136–148 (Corrigendum: *ibid* **20**, 238).
- [7] ETHERINGTON, I. M. H., 1941: Special train algebras. Quart. J. Math. (Oxford) (2) **12**, 1–8.
- [8] ETHERINGTON, I. M. H., 1941: Dublication of linear algebras. Proc. Edinb. Math. Soc. (2) **6**, 222–230.
- [9] ETHERINGTON, I. M. H., 1941: Non-associative algebra and the symbolism of genetics. Proc. Roy. Soc. Edinb. B. **61**, 24–42.
- [10] SHAFER, R. D., 1949: Structure of genetic algebras, Amer. J. Math. **71**, 121–135.
- [11] GONSHOR, H., 1960: Special train algebras arising in genetics. Proc. Edinb. Math. Soc. (2) **12**, 41–53.
- [12] GONSHOR, H., 1965: Special train algebras arising in genetics, II Proc. Edinb. Math. Soc. (2) **14**, 333–338.
- [13] GONSHOR, H., 1971: Contributions to genetic algebras. Proc. Edinb. Math. Soc. **17**, 289–298.
- [14] HOLGATE, P., 1966: Genetic algebras with polyploidy, Proc. Edinb. Math. Soc. (2) **15**, 1–9.

- [15] HOLGATE, P., 1967: Sequences of powers in genetic algebras, *J. Lond. Math. Soc.* **42**, 489–496.
- [16] HOLGATE, P., 1967: Jordan algebras arising in population genetics. *Proc. Edinb. Math. Soc.* **15**, 291–294.
- [17] HOLGATE, P., 1968: The genetic algebra of  $K$  linked loci. *Proc. Lond. Math. Soc.* (3) **18**, 315–327.
- [18] HOLGATE, P., 1968: Interaction between migration and breeding studied by means of genetic algebras. *J. Appl. Prob.* **5**, 1–8.
- [19] HOLGATE, P., 1970: Genetic algebras associated with sex linkage. *Proc. Edinb. Math. Soc.* (2) **17**, 113–120.
- [20] HOLGATE, P., 1972: Characterizations of genetic algebras. *J. Lond. Math. Soc.* **6**, 169–174.
- [21] HUGH, I., 1972: Sequences in genetic algebras for overlapping generations. *Proc. Edinb. Math. Soc.* **18**, 19–29.
- [22] Ю. И. Любич, 1971: Основные понятия и теоремы эволюционной генетики свободных популяций, *Успехи матем. наук XXVI*, № 5, **161**, 51–116. = *Russian Math. Surveys* **26**, № 5, 51–123.
- [23] Г. Ч. Куринной, 1976: Замечание об эволюционном спектре генетических алгебр. *Вестник Харьковского унив.* № 134, вып. **41**, 89–95.
- [24] REIERSÖL, O., 1962: Genetic algebras studied recursively and by means of differential operators. *Math. Scand.* **10**, 25–44.
- [25] В. М. Киржнер, 1973: О поведении траекторий некоторого класса генетических систем. *Доклады АН СССР* **209**, № 2, 287–290.
- [26] С. Н. Бернштейн, 1922: О приложении математики к биологии «Наука на Украине» вып. **1**, 14–19.
- [27] BERNSTEIN, S. N., 1923: Demonstration mathématique de la loi d'hérédité de Mendel, *C. R. Acad. Sci. (Paris)* **177**, 528–531.
- [28] BERNSTEIN, S. N., 1923: Principe de stationarité et generalisation de la loi de Mendel, *C. R. Acad. Sci. (Paris)* **177**, 581–584.
- [29] С. Н. Бернштейн, 1924: Решение одной математической проблемы, связанной с теорией наследственности, *Ученые записки научно-исследов. кафедр Украины, отд. матем.* вып. № 1, 83–115.
- [30] Ю. И. Любич, 1973: К математической теории наследственности. *Доклады АН СССР* **209**, № 5, 1028–1030 (*Soviet Math. Dokl.* **14**, 579–581).
- [31] Ю. И. Любич, 1974: Двухуровневые бернштейновские популяции. *Матем. сб.* **95** (137) № 4, 606–628. (*Math. USSR Sb.* **24**, N. 4, 593–615).
- [32] Ю. И. Любич, 1976: Квазилинейные бернштейновские популяции *Теория функций, функцион. анализ и их приложения (Харьков)* вып. **26**, 79–84.
- [33] Ю. И. Любич, 1976: Алгебраическое доказательство теоремы С. Н. Бернштейна о необходимости закона Менделя. *Вестник Харьковского унив.* № 134, вып. **41**, 85–88.
- [34] Ю. И. Любич, Г. Д. Майстровский, Ю. Г. Ольховский, 1976: Сходимость к равновесию под действием отбора в однолокусной популяции, *Доклады АН СССР* **226**, № 1, 58–60 (*Soviet Math. Dokl.* **17** N. 1, 55–58).
- [35] RAFFIN, R., 1951: Axiomatisation des algebras genetiques. *Acad. Roy. Belg. Bull. Cl. Sci.* (5) **37**, 359–366.
- [36] Ю. И. Любич, 1972: В редакцию УМН, *Успехи матем. наук XXVII*, № 6, 265.
- [37] Ю. И. Любич, 1974: Об одном классе квадратичных отображений *Теория функций, функцион. анализ и их приложения (Харьков)* вып. **21**, 36–42.
- [38] PEARSON, K., 1904: On the generalized theory of alternative inheritance with special reference to Mendel's laws. *Phil. Trans. Roy. Soc. A* **203**, 53–86.
- [39] HARDY, G. H., 1908: Mendelian proportions in a mixed population. *Science* **28**, 49–50.
- [40] WEINBERG, W., 1908: Über den Nachweis der Vererbung beim Menschen. *Jahreshefte Verein f. Vaterl. Naturk. in Württemberg* **64**, 368–383.
- [41] Ю. И. Любич, 1973: Строение бернштейновских популяций типа  $(n-1, 1)$ . *Успехи матем. наук XXVIII*, № 5, 247–248.
- [42] Ю. И. Любич, 1975: Строение бернштейновских популяций типа  $(2, n-2)$ . *Успехи матем. наук*, **XXX** № 1, 247–248.
- [43] Ю. И. Любич, 1973: Об аналогах закона Харди-Вайнберга, *Генетика IX* № 10, 139–144 (*Soviet Genetics* **9**, 1321–1325).

- [44] ROBBINS, R. B., 1918: Application of mathematics to breeding problem. *Genetics* **3**, 73–92.
- [45] GEIZINGER, H., 1944: On the probability theory of linkage in Mendelian heredity. *Ann. Math. Statist.* **15**, 25–57.
- [46] BENNET, J. H., 1954: On the theory of random mating. *Ann. Eugenics* **18**, 311–317.
- [47] ELLISON, B. E., 1966: Limit theorems for random mating in infinite populations. *J. Appl. Prob.* **3**, 94–114.
- [48] KESTEN, H., Quadratic transformations: a model for population growth I. *Adv. Appl. Prob.* **2**, 1–82.
- [49] BAILEY, N. T., 1961: *The mathematical theory of genetic linkage*. Oxf., Clarendon.
- [50] В. М. КИРЖНЕР, 1972: О поведении траекторий полиплоидных генетических систем с миграциями, «Вычисл. матем. и вычисл. техника» (Харьков, ФТИНТ АН УССР) вып. **3**, 141–143.
- [51] В. М. КИРЖНЕР, Ю. И. ЛЮБИЧ, 1974: Общее эволюционное уравнение и предельная теорема для генетических систем без отбора. *Доклады АН СССР* **215**, № 4, 776–779.
- [52] Ю. И. ЛЮБИЧ, 1973: Об одной теореме С. Н. Бернштейна. *Сиб. мат. журн.* **XIV**, № 3, 678–679.

Received: VI/30/1977

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