SOLUTION OF A MATHEMATICAL PROBLEM CONNECTED WITH THE THEORY OF HEREDITY[1]

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Translator's Note: Although a French resumé of the article here translated appeared in *Comptes Rendus*,[2] it is so condensed due to space restrictions that in reporting on Bernstein's work for the Statistical Seminar at the University of California, it became necessary to refer to the original Russian paper. Because of the obvious language difficulty together with the extreme rareness[3] of the Ukrainian publication in this country, and because of the current interest in the application of statistical theories to genetics, it seemed advisable to make this important article available to a much larger class of readers.

It is regretted that, due to the present conditions, it was impracticable to obtain the author's comments on this translation, and it is hoped that the slight changes and additions inserted, to clarify some of the more difficult passages, would have met with his approval.

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1. Let us consider N classes of individuals which possess the property that the cross of any two of these individuals produces an individual belonging to one of the above N classes. We will call such a set of classes a "closed biotype." We will suppose only that the probability of obtaining an individual of class j as a result of crossing two individuals of classes i and k has some definite value $A_{ik}^{j} = A_{ki}^{j}$, and we will call these probabilities[4] "heredity coefficients of a given biotype." It follows from the definition of a closed biotype that

$$\sum_{j=1}^{N} A_{ik}^{j} = 1. \tag{1}$$

Let α_j be the probability that an individual belongs to class j, then under panmixia[5] the probability of belonging to class j in the next generation is given by

$$\alpha_j' = \sum_{i,k} A_{ik}^{j} \alpha_i \alpha_k. \tag{2}$$

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[1] The original was published in the *Annales Scientifiques de l'Ukraine*, Vol. 1 (1924), p. 83–114.

[2] *C. R. Ac. Sc.*, Vol. 177, pp. 528–531, 581–584.

[3] Thanks are due to the Brown University Mathematical Library for their loan of this rare periodical.

[4] A_{ik}^{j} is, of course, the relative probability that an offspring belong to class j, given that the parents belong to classes i and k.

[5] That is, complete absence of selection.

Similarly we have for the next generation

$$\alpha_j'' = \sum_{i,k} A_{ik}^j \alpha_i' \alpha_k' \tag{3}$$

and so on.

The problem which we now propose is as follows:

For what heredity coefficients under panmixia will the distribution of probabilities achieved in the second generation remain unaltered in all subsequent generations?

If the heredity coefficients satisfy this condition, then the law of heredity which corresponds to them is called "stable."

2. We prove first of all that *the Mendelian law is stable*. The Mendelian law has to do with three classes of individuals, the first two of which are pure races, while the third is a hybrid race such that the cross of an individual of the first class with an individual of the second class *always* produces an individual of the third class. It follows therefore that

$$A_{11}^1 = A_{22}^2 = A_{12}^3 = 1, \quad \text{while}$$

$$A_{11}^2 = A_{22}^1 = A_{11}^3 = A_{22}^3 = A_{12}^1 = A_{12}^2 = 0.$$

The remaining 9 coefficients are defined as follows:

$$A_{13}^1 = A_{23}^2 = A_{13}^3 = A_{23}^3 = A_{33}^3 = 1/2$$

$$A_{33}^1 = A_{33}^2 = 1/4, \quad \text{while} \quad A_{13}^2 = A_{23}^1 = 0.$$

If, for simplicity, we denote the probabilities of belonging to the first, second or third class by α, β, γ, then (2) becomes

$$\alpha' = (\alpha + \tfrac{1}{2}\gamma)^2 \qquad \beta' = (\beta + \tfrac{1}{2}\gamma)^2 \qquad \gamma' = 2(\alpha + \tfrac{1}{2}\gamma)(\beta + \tfrac{1}{2}\gamma), \tag{4}$$

while on iteration we get the equivalent of (3), namely

$$\begin{aligned} \alpha'' &= [(\alpha + \tfrac{1}{2}\gamma)^2 + (\alpha + \tfrac{1}{2}\gamma)(\beta + \tfrac{1}{2}\gamma)]^2 = (\alpha + \tfrac{1}{2}\gamma)^2(\alpha + \beta + \gamma)^2 \\ \beta'' &= [(\beta + \tfrac{1}{2}\gamma)^2 + (\alpha + \tfrac{1}{2}\gamma)(\beta + \tfrac{1}{2}\gamma)]^2 = (\beta + \tfrac{1}{2}\gamma)^2(\alpha + \beta + \gamma)^2 \\ \gamma'' &= 2[(\alpha + \tfrac{1}{2}\gamma)^2 + (\alpha + \tfrac{1}{2}\gamma)(\beta + \tfrac{1}{2}\gamma)][(\beta + \tfrac{1}{2}\gamma)^2 + (\alpha + \tfrac{1}{2}\gamma)(\beta + \tfrac{1}{2}\gamma)] \\ &= 2(\alpha + \tfrac{1}{2}\gamma)(\beta + \tfrac{1}{2}\gamma)(\alpha + \beta + \gamma)^2. \end{aligned} \tag{5}$$

Since $\alpha + \beta + \gamma = 1$, it follows that $\alpha'' = \alpha'$, $\beta'' = \beta'$, $\gamma'' = \gamma'$, and hence the Mendelian law is stable.

3. The first rather important result can be stated as follows:

THEOREM: *If three classes form a closed biotype under a stable heredity law, which is such that the cross of an individual of the first class with an individual of the second class always produces an individual of the third class, then the first two classes represent pure races and the law of heredity is the Mendelian law.*

If the original probabilities are α, β, γ, then the corresponding probabilities for the next generation can be written as follows:

$$
\begin{aligned}
\alpha_1 &= A_{11}\alpha^2 + 2A_{12}\alpha\beta + A_{22}\beta^2 + 2A_{13}\alpha\gamma + 2A_{23}\beta\gamma + A_{33}\gamma^2 = f(\alpha, \beta, \gamma),\\
(6)\quad \beta_1 &= B_{11}\alpha^2 + 2B_{12}\alpha\beta + B_{22}\beta^2 + 2B_{13}\alpha\gamma + 2B_{23}\beta\gamma + B_{33}\gamma^2 = \varphi(\alpha, \beta, \gamma),\\
\gamma_1 &= C_{11}\alpha^2 + 2C_{12}\alpha\beta + C_{22}\beta^2 + 2C_{13}\alpha\gamma + 2C_{23}\beta\gamma + C_{33}\gamma^2 = \psi(\alpha, \beta, \gamma),
\end{aligned}
$$

where $A_{ik} + B_{ik} + C_{ik} = 1$. Since $C_{12} = 1$, by assumption, it follows that

$$B_{12} = A_{12} = 0,$$

since all the coefficients must be positive, or zero.

The mathematical problem before us consists in determining three homogenous quadratic forms f, φ, and ψ in α, β, γ with non-negative coefficients such that

$$f + \varphi + \psi = 1 = (\alpha + \beta + \gamma)^2$$

and satisfying the conditions of stability, namely

$$
(7)\qquad
\begin{aligned}
f(\alpha_1, \beta_1, \gamma_1) &= f(\alpha, \beta, \gamma) = \alpha_1,\\
\varphi(\alpha_1, \beta_1, \gamma_1) &= \varphi(\alpha, \beta, \gamma) = \beta_1,\\
\psi(\alpha_1, \beta_1, \gamma_1) &= \psi(\alpha, \beta, \gamma) = \gamma_1,
\end{aligned}
$$

for all α, β, γ such that[6] $\alpha + \beta + \gamma = 1$. The third equation is, of course, a consequence of the first two.

The functions f, φ and ψ, being continuous, assume infinitely many values, unless they are constants, in which case they may be expressed as quadratic forms by

$$f = p(\alpha + \beta + \gamma)^2, \qquad \varphi = q(\alpha + \beta + \gamma)^2, \qquad \psi = r(\alpha + \beta + \gamma)^2$$

where p, q, r are constants. But, since the coefficient of $\alpha\beta$ is zero in f and φ, and 1 in ψ, this reduces to the trivial case $f = 0$, $\varphi = 0$ and $\psi = 1$, which we can neglect.

We now write (7) in the form

$$
(8)\qquad
\begin{aligned}
\alpha_1 &= f(\alpha, \beta, \gamma) = \alpha(\alpha + \beta + \gamma) + F_1(\alpha, \beta, \gamma)\\
\beta_1 &= \varphi(\alpha, \beta, \gamma) = \beta(\alpha + \beta + \gamma) + F_2(\alpha, \beta, \gamma)\\
\gamma_1 &= \psi(\alpha, \beta, \gamma) = \gamma(\alpha + \beta + \gamma) - F_1(\alpha, \beta, \gamma) - F_2(\alpha, \beta, \gamma).
\end{aligned}
$$

Since

$$
(9)\qquad f(\alpha, \beta, \gamma) = \alpha(\alpha + \beta + \gamma), \qquad \varphi(\alpha, \beta, \gamma) = \beta(\alpha + \beta + \gamma),
$$
$$\psi(\alpha, \beta, \gamma) = \gamma(\alpha + \beta + \gamma),$$

[6] The fact that the variables α, β, γ are not independent does not preclude the validity of identifying their coefficients in the equations that follow, since all these equations are homogeneous.

are obviously solutions of (7), it follows that $F_1(f, \varphi, \psi) = 0$ and $F_2(f, \varphi, \psi) = 0$. But, as we have just seen, f, φ and ψ assume infinitely many values. Therefore F_1 and F_2 either have a linear factor in common, or else are proportional and irreducible.[7]

We first show that F_1 and F_2 do not have only a linear factor, $l\alpha + m\beta + n\gamma$, in common, for if they did this factor would vanish for $\alpha = f$, $\beta = \varphi$, $\gamma = \psi$ so that

$$(10) \qquad lf(\alpha, \beta, \gamma) + m\varphi(\alpha, \beta, \gamma) + n\psi(\alpha, \beta, \gamma) = 0.$$

But since neither f nor φ have a term in $\alpha\beta$, while ψ has, $n = 0$. Also, since f and φ have no negative coefficients, l and m are of opposite signs. Let $l \geqq 0$, while $m = -p$, where $p \geqq 0$. Then the third equation (8) can be written

$$(11) \qquad \psi(\alpha, \beta, \gamma) = \gamma(\alpha + \beta + \gamma) + (A\alpha + B\beta + C\gamma)(l\alpha - p\beta).$$

The coefficients of α^2 and β^2 in ψ must be non-negative. Therefore it follows that $A \geq 0$, while $B \leq 0$. But the coefficient of $\alpha\beta$ in ψ is 2, while $Bl - Ap$ cannot be positive. Therefore F_1 and F_2 have no linear factor in common, and must be proportional. But since the coefficient of $\alpha\beta$ in f and φ is zero, the coefficient of $\alpha\beta$ in both F_1 and F_2 must be -1, and therefore F_1 and F_2 are equal and we can write $F_1 = F_2 = F$, and (8) becomes:

$$(12) \qquad \begin{aligned} f(\alpha, \beta, \gamma) &= \alpha(\alpha + \beta + \gamma) + F(\alpha, \beta, \gamma) \\ \varphi(\alpha, \beta, \gamma) &= \beta(\alpha + \beta + \gamma) + F(\alpha, \beta, \gamma) \\ \psi(\alpha, \beta, \gamma) &= \gamma(\alpha + \beta + \gamma) - 2F(\alpha, \beta, \gamma), \end{aligned}$$

where F is an irreducible, homogeneous, quadratic form in α, β, γ. Furthermore, the coefficient of α^2 in F must be zero, since were it positive, the coefficient of α^2 in f would exceed 1, and were it negative, the coefficient of α^2 in φ would also be negative, which is impossible. Similarly, the coefficient of β^2 in F is also zero. We can therefore write F in the form

$$(13) \qquad F(\alpha, \beta, \gamma) = -\alpha\beta + c\alpha\gamma + d\beta\gamma + e\gamma^2.$$

Moreover, we know that

$$(14) \qquad F(\alpha', \beta', \gamma') = F(\alpha S + F, \beta S + F, \gamma S - 2F) = 0,$$

for all values of α, β, γ, such that $\alpha + \beta + \gamma = S = 1$. Expanding (14) in Taylor series about the point $(\alpha S, \beta S, \gamma S)$ in three space we get only three terms in the expansion, since all the derivatives of order greater than the second are identically zero, and the constant term can be obtained very simply by putting $\alpha = \beta = \gamma = 0$ in $F(\alpha S + F, \beta S + F, \gamma S - 2F)$. In this way we have

[7] See Bôcher, *Introduction to Higher Algebra*, p. 210, Theorem 3.

$$(15)\quad \begin{aligned} F(\alpha S + F, \beta S + F, \gamma S - 2F) &= F(\alpha S, \beta S, \gamma S) \\ &+ F[F'_\alpha(\alpha S, \beta S, \gamma S) + F'_\beta(\alpha S, \beta S, \gamma S) - 2F'_\gamma(\alpha S, \beta S, \gamma S)] \\ &+ F(F, F, -2F) = 0. \end{aligned}$$

Since F is a homogeneous form of the second degree

$$(16)\quad F(\alpha S, \beta S, \gamma S) = S^2 F(\alpha, \beta, \gamma); \quad F(F, F, -2F) = F^2 F(1, 1, -2),$$

while its derivatives with respect to α, β, γ are homogeneous linear forms so that

$$(17)\quad F'_\alpha(\alpha S, \beta S, \gamma S) = SF'_\alpha(\alpha, \beta, \gamma).$$

Substituting these in (15) and dividing out an $F(\alpha, \beta, \gamma)$, which is not identically zero, we get

$$(18)\quad S^2 + S[F'_\alpha(\alpha, \beta, \gamma) + F'_\beta(\alpha, \beta, \gamma) - 2F'_\gamma(\alpha, \beta, \gamma)] = -F(\alpha, \beta, \gamma)F(1, 1, -2).$$

But since $F(\alpha, \beta, \gamma)$ is irreducible, $F(1, 1, -2)$ must be zero. Dividing by S we finally get

$$(19)\quad S = 2F'_\gamma - F'_\alpha - F'_\beta$$

or $(\alpha + \beta + \gamma) = 2(c\alpha + d\beta + 2e\gamma) - (-\beta + c\gamma) - (-\alpha + d\gamma)$ from which it follows that

$$c = d = 0, \qquad e = 1/4,$$

and hence

$$(20)\quad F(\alpha, \beta, \gamma) = \gamma^2/4 - \alpha\beta.$$

Therefore we have found that

$$(21)\quad \begin{aligned} f(\alpha, \beta, \gamma) &= \alpha(\alpha + \beta + \gamma) + \gamma^2/4 - \alpha\beta = \alpha^2 + \alpha\gamma + \gamma^2/4 = (\alpha + \tfrac{1}{2}\gamma)^2, \\ \varphi(\alpha, \beta, \gamma) &= \beta(\alpha + \beta + \gamma) + \gamma^2/4 - \alpha\beta = \beta^2 + \beta\gamma + \gamma^2/4 = (\beta + \tfrac{1}{2}\gamma)^2, \\ \psi(\alpha, \beta, \gamma) &= \gamma(\alpha + \beta + \gamma) - \tfrac{1}{2}\gamma^2 + 2\alpha\beta = 2(\alpha + \tfrac{1}{2}\gamma)(\beta + \tfrac{1}{2}\gamma), \end{aligned}$$

which is the Mendelian law.

4. We have therefore shown that the Mendelian law is a necessary consequence of any stable law, which is such that the cross of the first two classes produces the third hybrid class. We have not even assumed *a priori* that the first two classes are pure races. From a theoretical point of view it is interesting to investigate the possibility of crossing two pure races under different laws of heredity, which are nevertheless stable.

We will therefore suppose to start with that the coefficients of α^2 in $f(\alpha, \beta, \gamma)$

and of β^2 in $\varphi(\alpha, \beta, \gamma)$ are equal to unity. Beginning with equations (8) of the previous section, which merely express the condition that the heredity law under consideration be stable we can write

$$F_1 = F = -a\alpha\beta + c\alpha\gamma + d\beta\gamma + e\gamma^2. \tag{22}$$

As before, F_1 and F_2 cannot have a linear factor in common, hence they are proportional, and we can write $F_2 = \lambda F$, $F_1 = F$. We therefore have five coefficients to determine: a, c, d, e, and λ. Since

$$F(\alpha S + F, \beta S + \lambda F, \gamma S - (\lambda + 1)F) = 0 \tag{23}$$

we have an analogue of (19)

$$S = (1 + \lambda)F'_\gamma - F'_\alpha - \lambda F'_\beta \tag{24}$$

or

$$\alpha + \beta + \gamma = (1 + \lambda)(c\alpha + d\beta + 2e\gamma) + a\beta - c\gamma + \lambda a\alpha - \lambda d\gamma.$$

Equating coefficients of α, β, γ as before we have

$1 = c(1 + \lambda) + a\lambda$ or $c = (1 - \lambda a)/(1 + \lambda)$,

$1 = d(1 + \lambda) + a$ or $d = (1 - a)/(1 + \lambda)$,

$1 = 2e(1 + \lambda) - c - \lambda d = 2e(1 + \lambda) - (1 - \lambda a)/(1 + \lambda) - (1 - a)/(1 + \lambda)$,

or

$$e = (1 + \lambda - a\lambda)/(1 + \lambda)^2.$$

Therefore the most general quadratic form F satisfying our conditions can be written

$$F(\alpha, \beta, \gamma) = -a\alpha\beta + \frac{1 - \lambda a}{1 + \lambda}\alpha\gamma + \frac{1 - a}{1 + \lambda}\beta\gamma + \frac{1 + \lambda - a\lambda}{(1 + \lambda)^2}\gamma^2. \tag{26}$$

If we let $a\lambda = b$, this becomes

$$F(\alpha, \beta, \gamma) = -a\alpha\beta + \frac{1 - b}{a + b}a\alpha\gamma + \frac{1 - a}{a + b}a\beta\gamma + \frac{a + b - ab}{(a + b)^2}a\gamma^2. \tag{27}$$

Substituting this value of F into f, φ, ψ and simplifying, we get

$$f(\alpha, \beta, \gamma) = \left(\alpha + \frac{a}{a + b}\gamma\right)\left[\alpha + (1 - a)\beta + \left(1 - \frac{ab}{a + b}\right)\gamma\right], \tag{28}$$

$$\varphi(\alpha, \beta, \gamma) = \left(\beta + \frac{b}{a + b}\gamma\right)\left[(1 - b)\alpha + \beta + \left(1 - \frac{ab}{a + b}\right)\gamma\right],$$

$$\psi(\alpha, \beta, \gamma) = (a + b)\left(\alpha + \frac{a}{a + b}\gamma\right)\left(\beta + \frac{b}{a + b}\gamma\right),$$

where in order that all the coefficients be positive it is necessary and sufficient that $0 \leq a \leq 1$, and $0 \leq b \leq 1$. In case $a = b = 1$ formulas (28) coincide with (21) and we get the Mendelian law.

The question of whether there actually exist heredity laws which satisfy (28) with $a < 1$, and $b < 1$ can only be solved experimentally. Theoretically formulas (28) give the most general heredity law of a closed biotype consisting of three classes, with the condition that two of the three classes be pure races. It is easy to see that the only law of heredity in which all three classes are pure races is given by the particular solution of (8)

$$(29) \qquad f = \alpha(\alpha + \beta + \gamma), \quad \varphi = \beta(\alpha + \beta + \gamma), \quad \psi = \gamma(\alpha + \beta + \gamma),$$

in which $F_1 = F_2 = 0$.

5. Supposing as before that the heredity law is stable, it remains to prove the following theorem to exhaust all possible biotypes consisting of only three classes.

THEOREM: *If all classes are hybrid, then*

$$(30) \qquad f = p(\alpha + \beta + \gamma)^2, \quad \varphi = q(\alpha + \beta + \gamma)^2, \quad \psi = r(\alpha + \beta + \gamma)^2.$$

If only one of the classes represents a pure race, then either

$$(31) \qquad \begin{aligned} f &= (\alpha + \beta)[\tfrac{1}{2}(1 + b)(\alpha + \beta) + (1 - d)\gamma] \\ \varphi &= (\alpha + \beta)[\tfrac{1}{2}(1 - b)(\alpha + \beta) + d\gamma] \\ \psi &= \gamma(\alpha + \beta + \gamma) \end{aligned}$$

or

$$(32) \qquad f = \alpha S + a\alpha(\mu\beta + \gamma) \quad \text{and} \quad \mu\varphi + \psi = 0.$$

We have seen that if f, φ, and ψ are functions of $(\alpha + \beta + \gamma)$, then we arrive at (30), in the contrary case we arrive at (8). Here we distinguish two cases: 1) F_1 and F_2 are irreducible quadratic forms which are proportional: $F_1 = k_1F$, $F_2 = k_2F$, and 2) F_1 and F_2 have a common factor, which is a linear form. Suppose at first that F is a quadratic form. If none of the numbers k_1, k_2, and $k_1 + k_2$ is zero, then two of them may be taken as positive, say k_1 and k_2. But then the coefficients of α^2 and β^2 in F would have to vanish in order that ψ have no negative coefficients. But this case of two pure races has already been discussed, and leads to formulas (28). We must therefore suppose next that one of the numbers k_1, k_2, or $k_2 + k_1$ is zero. Suppose that $k_2 + k_1 = 0$, that is, that the third class is a pure race, and hence the coefficient of γ^2 in ψ is unity. Therefore, the coefficient of γ^2 in F must be zero. We can take $k = 1$, then $k_1 = -1$, and therefore the coefficient $\alpha\gamma$ in F is negative, say $-d$. We can now write

$$F = a\alpha^2 + b\alpha\beta + c\beta^2 - d\alpha\gamma + e\beta\gamma. \tag{33}$$

We have as before

$$F(\alpha S + F, \beta S - F, \gamma S) = 0, \tag{34}$$

from which we derive by Taylor's expansion

$$S = F'_\beta - F'_\alpha \tag{35}$$

or in other words

$$\alpha + \beta + \gamma = b\alpha + 2c\beta + e\gamma - b\beta + d\gamma - 2a\alpha,$$

which leads to

$$F = \tfrac{1}{2}(b - 1)\alpha^2 + b\alpha\beta + \tfrac{1}{2}(b + 1)\beta^2 - d\alpha\gamma + (1 - d)\beta\gamma \tag{36}$$

and hence to f and φ, which are as follows,

$$f = (\alpha + \beta)[\tfrac{1}{2}(1 + b)(\alpha + \beta) + (1 - d)\gamma], \tag{37}$$

$$\varphi = (\alpha + \beta)[\tfrac{1}{2}(1 - b)(\alpha + \beta) + d\gamma].$$

It now remains to suppose that F is a linear form. Let

$$F = \lambda\alpha + \mu\beta + \gamma. \tag{38}$$

Here the condition that the heredity law be stable leads as before to the equation

$$S = (k + k_1)F'_\gamma - kF'_\alpha - k_1F'_\beta = (k + k_1) - \lambda k - \mu k_1, \tag{39}$$

where k and k_1 are linear forms

$$k = a\alpha + b\beta + c\gamma, \qquad k_1 = a_1\alpha + b_1\beta + c_1\gamma. \tag{40}$$

Hence if we had no restrictions on signs and magnitudes we could select k arbitrarily, and then we would have $k_1 = [S + (\lambda - 1)k]/[1 - \mu]$, and the solution for f, φ, ψ would depend on five parameters, (λ, μ, a, b, c).

But since in $f = \alpha S + kF$, the coefficients of β^2, $\beta\gamma$ and γ^2 are non-negative $\mu b \geq 0$, and $b + \mu c \geq 0$, $c \geq 0$, and similarly from the same property of φ we have $\lambda a_1 \geq 0$, $c_1 \geq 0$, $a_1 + \lambda c_1 \geq 0$. But μ and λ cannot both be non-negative, for then $\lambda f + \mu\varphi + \psi = 0$ would be impossible.

Let $\mu < 0$, then $b = c = 0$, but then the coefficient of α^2 in f would be $1 + a\lambda$, which will be too big, unless $\lambda = 0$. Hence, $F = \mu\beta + \gamma$, $k = a\alpha$, and

$$f = \alpha S + a\alpha(\mu\beta + \gamma), \tag{41}$$

$$\psi = -\mu\varphi = \mu[S(\beta + \gamma) - a\alpha(\mu\beta + \gamma)]/[\mu - 1].$$

Hence we have exhausted all possible cases and have proved our theorem.

6. We can summarize our results as follows. The heredity laws of a closed biotype of three classes which are stable can be divided into the following types:

1. Two classes represent pure races. The heredity laws are given by (28), and in particular for the Mendelian case by (21).
2. There are no pure races, and every race can be obtained by crossing the other races. The heredity law is given by (30).
3. All three classes are pure races. The heredity law is given by (29). Any two classes of this biotype, also form a closed biotype.
4. One of the classes is a pure race. The heredity laws are given by (31) and (32).