ALTERNATIVE EXPRESSIONS FOR PROBABILITY-GENERATING FUNCTIONS

CONCERNING AN INHERITED CHARACTER AFTER A PANMIXIA

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1. Introduction.

In a recent paper\textsuperscript{1} we have discussed from a stochastic view-point a problem of estimating the distributions concerning an inherited character which consists of \( m \) multiple alleles at one diploid locus denoted by \( A_i \) \((i = 1, \ldots, m)\) and of which the inheritance is subject to Mendelian law. In succession, we have also discussed a related problem on mother-child combinations.\textsuperscript{2,3} Main tasks of these papers have been to obtain the expressions for respective probability-generating functions in explicit manners.

In any case, the generating function must be, of course, uniquely determined in a definite manner. However, our results have concerned not directly the generating functions themselves but somewhat indirectly the related functions from which the generating functions can be obtained as the constant terms of respective Laurent expansions with respect to parameters involved. Under such circumstances, it will be possible to find alternative sources of generating functions. In the present paper we shall illustrate the circumstances by deriving some alternative expressions for probability-generating functions.

As in the preceding papers, we consider a population of size \( 2N \) consisting of \( N \) females and \( N \) males. Let the given distributions of genotypes \( \{A_aA_b\} \) in females and in males be designated by

\[ \mathcal{F} = \{ \gamma_{ab} \} \quad \text{and} \quad \mathcal{M} = \{ M_{ab} \}, \]

respectively, so that

\[ \sum_{a \leq b} \gamma_{ab} = \sum_{a \leq b} M_{ab} = N. \]

The order of genes in a genotype being immaterial, any quantity accompanied by a pair of suffices indicating genes of a genotype should be supposed to be understood as symmetric with respect to the suffices; for instance, we suppose \( F_{ab} = F_{ba} \), etc.

2. Mother-child combinations with mothers of an assigned genotype.

We first consider the mother-child combinations with mothers of an assigned genotype, \( A_aA_b \) say. Introducing a set of \( m(m+1)/2 \) stochastic variables

\[ \mathcal{X} = \{ X_{fg} \} \quad (f, g = 1, \ldots, m, f \leq g), \]

we designate, in conformity with a notation used in a previous paper,\textsuperscript{3}

\[ \Psi(\alpha|\mathcal{X}) \equiv \Psi(\alpha|\mathcal{X} | \mathcal{F}; \mathcal{M}) \]

the probability that, after a panmixia, the mother-child combinations \( (A_\alpha A_\beta) \) \((f, g = 1, \ldots, m, f \leq g)\) amount to \( X_{fg} \), respectively. Here, and also in the subsequent discussions, each mating is supposed to produce one child so that in our present case there holds

\[ \sum_{f \leq g} X_{fg} = F_{\alpha\beta}. \]

Since a mother of any type \( A_\alpha A_\beta \) can produce, in general, merely a child of a type involving at least a gene in common with herself, the probability \( \Psi(\alpha|\mathcal{X}) \) must vanish out unless the \( X_i \)'s are equal to zero for all the impossible children' types \( A_\gamma A_\delta \), i.e., for \( f, g \neq \alpha, \beta \). The probability-generating function is now defined by
\[ \Phi(\alpha|z) = \sum_{X_f} \Psi(\alpha|X_f) \sum_{f \in g} Z_{fg}^f, \]

where \( g = \{Z_{fg}\} \) designates a set of \( m(m+1)/2 \) indeterminate variables and the summation in the last member extends over the whole range of \( X = \{X_{fg}\} \).

In a previous paper\(^1\) we have shown that the generating function now in consideration can be brought into a form

\[ \Phi(\alpha|z) = \frac{T_{ab}!}{N!} \sum_{\gamma_{ab}} (N - F_{\gamma_{ab}})! \prod_{a \leq b} M_{ab}! \prod_{a \leq b} Z_{ab}, \]

where the use is made of an abbreviation

\[ Z_{ab} = Z_{a+b} + Z_{a-b} + Z_{b-a} + Z_{ab}, \]

and the summation extends over all the possible sets of \( m(m+1)/2 \) integers \( \gamma_{ab} \) \((a, b=1, \ldots, m; a \leq b)\) satisfying the relations

\[ 0 \leq \gamma_{ab} \leq M_{ab} \quad (a, b=1, \ldots, m), \]

\[ \sum_{a \leq b} \gamma_{ab} = T_{ab}. \]

We thus have concluded that the generating function \( \Phi(\alpha|z) \) may be represented by the constant term, i.e., the coefficient of \( \prod_{a \leq b} t_{ab}^{\gamma_{ab}} \)
in the Laurent expansion around the origin of the expression

\[ \Phi(\alpha|z|t) = \Phi(\alpha|z|t|F; \Omega), \]

regarded as a rational function of \( m(m+1)/2 \) variables \( t = \{t_{ab}\} \) \((a, b=1, \ldots, m; a \leq b)\), an expression defined by

\[ \Phi(\alpha|z|t) = \frac{F_{ab}!(N - F_{\gamma_{ab}})!}{N!} \prod_{a \leq b} M_{ab}! \sum_{a \leq b} (tZ_{ab} + Z_{m-1,m}) \]

regarded as a rational function of \( 1 + m(m+1)/2 \) variables \( \gamma \) and \( t = \{t_{ab}\} \).

We now enter into a main discourse of the present paper. The generating function written above can be brought into the form

\[ \Phi(\alpha|z) = \frac{F_{ab}!(N - F_{\gamma_{ab}})!}{N!} \sum_{\gamma_{ab}} (M_{ab})! \gamma_{ab}, \]

In view of \( \sum_{a \leq b} \gamma_{ab} = F_{ab} \), the last expression implies that it is representable as the constant term in the Laurent expansion around the origin of the expression

\[ \Phi(\alpha|z|t) = \Phi(\alpha|z|t|F; \Omega) \]

regarded as a rational function of a variable \( t \), where the asterisk above the product symbol indicates that the factor corresponding to \((a,b) = (m-1,m)\) must be omitted.

Consequently, by introducing, with a set of further \( m(m+1)/2 \) variables \( \gamma^1 = \{\gamma_{ab}\} \) \((a, b=1, \ldots, m; a \leq b)\), an expression defined by

\[ \Phi(\alpha|\gamma|t) \equiv \Phi(\alpha|\gamma|t|F; \Omega) \]

regarded as a rational function of \( m(m+1)/2 \) variables \( t = \{t_{ab}\} \) \((a, b=1, \ldots, m; a \leq b)\). Or, our generating function may be given also by the constant term in the Laurent expansion around the origin of the expression

\[ \Phi(\alpha|\gamma|t) = \Phi(\alpha|\gamma|t|F; \Omega) \]

regarded as a rational function of \( 1 + m(m+1)/2 \) variables \( \gamma \) and \( t = \{t_{ab}\} \).
our generating function is then also given by the constant term in the Laurent expansion around the origin of the last expression regarded as a rational function of \( m(m+1)/2+1 \) variables \( s' = \{ \alpha_{ab} \} \) and \( t \).

In case where \( A_i A_b \) is homozygous, \( A_i A_i \) say, we have

\[
Z_{ab} = \frac{Z_{ia} + Z_{ib}}{2} \quad (a, b = 1, \ldots, m),
\]

while in case where \( A_i A_b \) is heterozygous, \( A_i A_j \quad (i \neq j) \) say, we have

\[
Z_{ab} = \frac{Z_{ia} + Z_{ib} + Z_{ja} + Z_{jb}}{4} \quad (a, b = 1, \ldots, m).
\]

Hence, by distinguishing the cases according to whether \( A_i A_b \) is homozygous or heterozygous, the final expression derived above for \( \Phi(\alpha|\beta|\gamma; t) \) can be brought into more precise forms, namely

\[
\Phi(\alpha|\beta|\gamma; t) = \frac{F_i! (N-F_i)!}{N!^t} \prod_{a \leq b} M_{ab} \left( \frac{Z_{ia} - t Z_{ib}}{2} \right)^{N} \Phi(\alpha|\beta|\gamma;i, t).
\]

\[
\Phi(\alpha|\beta|\gamma; t) = \frac{F_i! (N-F_i)!}{N!^t} \prod_{a \leq b} M_{ab} \left( \frac{Z_{ia} + Z_{ib} + Z_{ja} + Z_{jb}}{4} \right)^{N} \Phi(\alpha|\beta|\gamma;i, t).
\]

It would be noted, by the way, that the generating function \( \Phi(\alpha|\beta|\gamma) \) itself is expressible, for instance, by means of a contour integral. In fact, if we consider for a while the indeterminate quantities \( t \) and \( \Delta_{ab} \quad (a, b = 1, \ldots, m ; \ a \leq b) \) as complex variables, we may write

\[
\Phi(\alpha|\beta|\gamma) = \frac{1}{2\pi i} \int_{|t|=1} \Phi(\alpha|\beta|\gamma|t) \frac{dt}{t}
\]

or

\[
\Phi(\alpha|\beta|\gamma) = \frac{1}{(2\pi \sqrt{-1})^{m(m+1)/2+1}} \int_{|t|=1} \Phi(\alpha|\beta|\gamma|t) \frac{dt}{t} \prod_{a \leq b} \frac{d\alpha_{ab}}{\Delta_{ab}}.
\]

where the integration is taken around the unit circumference on respective complex planes in the positive sense.

Here we restrict ourselves to this brief account, since such integral representations will not be availed in the subsequent discussions. However, analogous remarks apply, of course, also to the generating functions which will appear later, though they will not be repeated explicitly.

The generating function having been thus established in an explicit manner, it is now ready to compute the means or variances and other statistics for the stochastic variables.

For instance, logarithmic differentiation of the expression

\[
\Phi(\alpha|\beta|\gamma; t) = \frac{F_i! (N-F_i)!}{N!^t} \prod_{a \leq b} M_{ab} \left( \frac{Z_{ia} + Z_{ib}}{2} \right)^{N} \Phi(\alpha|\beta|\gamma;i, t)
\]

with respect to \( Z_{ii} \) yields

\[
\frac{\partial}{\partial Z_{ii}} \log \Phi(\alpha|\beta|\gamma; t) = \frac{M_{ii}}{t Z_{ii}} + \frac{1}{2} \sum_{b \neq i} \frac{M_{ib}}{t Z_{ii} + Z_{ib} + \frac{1}{2} M_{ib}}.
\]

whence follows, after putting \( \gamma = \{ 1 \} \), i.e., \( Z_{ab} = 1 \quad (a, b = 1, \ldots, m; \ a \leq b) \),

\[
\frac{\partial}{\partial Z_{ii}} \Phi(\alpha|\beta|\gamma; t) = \frac{F_i! (N-F_i)!}{N!^t} \prod_{a \leq b} M_{ab} \left( \frac{M_{ii} + \sum_{b \neq i} M_{ib}}{2} \right).
\]

Further, by separating the constant term in the Laurent expansion of the last expression, we obtain

\[
\frac{\partial}{\partial Z_{ii}} \Phi(\alpha|\beta|\gamma; t) = \frac{F_i! (N-F_i)!}{N!^t} \prod_{a \leq b} M_{ab} \left( \frac{M_{ii} + \sum_{b \neq i} M_{ib}}{2} \right).
\]
Thus, the mean of the variable $X_{ij}$ in case of mothers of the genotype $A_iA_i$ is given by the formula

$$\overline{X}(ii; ii) = F_{ii} p_k^{(M)}$$

in conformity with a result previously derived, where $p_k^{(M)}$ is defined by

$$p_k^{(M)} = \frac{1}{N} (M_{ii} + \sum_{b \neq i} M_{ib} \cdot \frac{1}{2})$$

In quite a similar manner, we can again derive the corresponding formulas for remaining mother-child combinations. They are set out as follows:

$$\overline{X}(ii; ik) = F_{ii} p_k^{(M)}$$

$$\overline{X}(ij; ik) = F_{ij} \cdot \frac{1}{2} \cdot p_k^{(M)}$$

$$\overline{X}(ij; ij) = F_{ij} \cdot \frac{1}{2} \cdot (p_k^{(M)} + p_j^{(M)})$$

$$\overline{X}(ij; ik) = F_{ij} \cdot \frac{1}{2} \cdot p_k^{(M)}$$

Here the different letters $i$, $j$, and $k$ are supposed to indicate different genes.

The same result can also be obtained in a similar manner by means of the expression for $\Phi(x; y; z; t)$.

In fact, we get

$$\frac{\partial}{\partial z_{ij}} \Phi(x; y; z; t) = \frac{F_{ij}! (N-F_{ij}!) \prod_{a \neq b} M_{ab}!}{N! \cdot t^{F_{ii}}} \left[ t^{2} + \frac{1}{2} \right] \sum_{m=0}^{N-t} \left( \sum_{a \neq b} \left( t_{ab} + t_{ba} \right) \right) \left( \sum_{a \neq b} \left( \frac{1}{2} \right)^{m} \right),$$

whence follows

$$\frac{\partial}{\partial z_{ij}} \Phi(x; y; z; t) = \frac{F_{ij}! (N-F_{ij}!) \prod_{a \neq b} M_{ab}!}{N! \cdot t^{F_{ii}}} \left[ t^{2} + \frac{1}{2} \right] \sum_{m=0}^{N-t} \left( \sum_{a \neq b} \left( t_{ab} + t_{ba} \right) \right) \left( \sum_{a \neq b} \left( \frac{1}{2} \right)^{m} \right).$$

Consequently, separation of the constant term in the Laurent expansion of the last expression leads to

$$\overline{X}(ii; ii) = \frac{3}{\partial z_{ij}} \Phi(x; y; z; t)$$

Similarly for the remaining types of mother-child combination.

The variances of the stochastic variables as well as the covariances between them can also be derived in a similar manner by means of either expression obtained above. However, since actual procedure of computation based on the present formulas is, compared with that explained in a previous paper, rather troublesome and hence not preferable, it will here be passed over.

3. Mother-child combination with both members of assigned genotypes.

We now observe a mother-child combination in which both constituents are of assigned genotypes, $(A_\alpha \, A_\alpha; A_\beta \, A_\beta)$, i.e., a mother of $A_\alpha \, A_\alpha$ and her child of $A_\beta \, A_\beta$, say. Introducing a single stochastic variable $X$ extending over all integers contained in an interval $0 \leq X \leq F_{\alpha\beta}$, we now designate by

$$\Psi(x; \beta; \gamma | X) = \Psi(x; \beta; \gamma | f; \beta\gamma)$$

the probability that after a panmixia the mother-child combination $(A_\alpha \, A_\alpha; A_\beta \, A_\beta)$ amounts to $X$, in conformity with a notation availed in a previous paper. The probability-generating function is then defined by

$$\Phi(x; \beta; \gamma | f; \beta\gamma) = \sum_{X=0}^{F_{\alpha\beta}} \Psi(x; \beta; \gamma | X) X^X,$$

$z$ designating an indeterminate variable.

Before entering into the main discourse, we make here previously an agreement. Similarly as in the previous section, we shall concern in the following lines, instead of the generating functions themselves, related functions from which the formers are obtained as the constant terms in the Laurent expansions. Our agreement now states that every Laurent expansion of a related function under consideration which is rational with respect to respective
parameters is supposed to concern exclusively the origin of the set of parameters, as the centre of expansion where the function possesses eventually a pole.

Now, the possible mother-child combination may be classified essentially into five types: \((A; A; A; A; A); (A; A; A; A; A; A); (A; A; A; A; A; A; A); (A; A; A; A; A; A; A; A); (A; A; A; A; A; A; A; A)\), here the suffixes \(i, j, k\) indicating different genes. For these types of combination, possible genotypes of a male who can be the spouse of mother \(i\), e., the father of child are restricted to those involving at least one gene \(A_i, A_j, A_k\) or \(A_{ik}\), respectively. Further, in every type of combination, since the distinction among the genes other than those respectively enumerated above is a matter of indifference, they may be gathered to a single aggregate which plays a role of an ideal imaginary gene, \(A_{\omega}\) say.

In the following, we shall deal with the first type of combination, \((A; A; A; A; A)\), especially in detail. Since the remaining types are treatable almost similarly, we shall later write down only their final results.

Now, as shown in a previous paper\(^2\), we first have

\[
\Phi(\zeta; \zeta | z) = \frac{M_{\omega}! M_{\omega}! M_{\omega}!}{N!} \sum \frac{F_{z\omega}! (M_{\omega} - y_{\omega})!}{N!} \cdot \left( \frac{z+1}{2} \right)^{y_{\omega}},
\]

where \(M_{\omega}\) and \(M_{\omega}\) designate the frequencies of ideal genotypes \(A_i A_{\omega}\) and \(A_{\omega} A_{\omega}\), respectively, in the male-population, namely they are defined by

\[
M_{\omega} = \sum_{b \neq A} M_{b}, \quad M_{\omega} = \sum_{a \neq A} M_{a},
\]

and the summation affixed below by \(y\) extends over all the partitions of \(F_{z\omega}\) into three integers \(y_{i}, y_{j}\), and \(y_{k}\), satisfying

\[
y_{i}, y_{j}, y_{k} \geq 0; \quad y_{i} + y_{j} + y_{k} = F_{z\omega}.
\]

Introducing a parameter \(u\), the generating function \(\Phi(\zeta; \zeta | z)\) is given by the constant term in the Laurent expansion of an expression

\[
\Phi_{u}(\xi; \xi | z) = \frac{M_{\omega}! M_{\omega}! M_{\omega}!}{N!} \sum_{u} \frac{F_{\xi}!}{u_{\xi}} \cdot \left( \frac{z+1}{2} \right)^{y_{\omega}} \\
\cdot \left( u + 1 \right)^{N-F_{\xi}} M_{\omega}! M_{\omega}! M_{\omega}!.
\]

Introducing a further parameter \(v\), the latter is given by the constant term in the Laurent expansion of an expression

\[
\Phi_{v}(\xi; \xi | z, v) = \frac{M_{\omega}! M_{\omega}! M_{\omega}!}{N!} \sum_{v} \frac{F_{\xi}}{(u+1+v)^{N-F_{\xi}}}
\cdot \left( \frac{z+1}{2} \right)^{y_{\omega}} \\
\cdot \left( u + 1 \right)^{N-F_{\xi}} M_{\omega}! M_{\omega}! M_{\omega}!.
\]

By putting \(u = t_i / t_{\omega}\) and \(v = 1 / t_{\omega}\) in the last expression, it is brought into the form

\[
\Phi(\zeta; \zeta | t_i, t_{\omega}) = \frac{M_{i}! M_{\omega}! M_{\omega}!}{N!} \sum_{t_i} \frac{F_{i}! (t_i + 1 + v)}{t_i^{N-F_{\xi}}}
\cdot \left( \frac{z+1}{2} \right)^{y_{\omega}} \\
\cdot \left( t_i + t_{\omega} + 1 \right)^{N-F_{\xi}}.
\]

Consequently, our generating function is thus represented by the constant term in the Laurent expansion around the origin of the last expression regarded as a rational function of two arguments \(t_i\) and \(t_{\omega}\). The final result just concluded is nothing but the one arrived at in a previous paper\(^2\). As remarked there and indeed as readily shown, the generating function is also expressible by the constant term in the Laurent expansion of an expression

\[
\Phi(\zeta; \zeta | z, t_i, t_{\omega}) = \frac{F_{i}! (N-F_{\xi})! M_{\omega}! M_{\omega}! M_{\omega}!}{N!} \sum_{t_i} \frac{F_{i}!}{t_i^{N-F_{\xi}}}
\cdot \left( \frac{z+1}{2} \right)^{y_{\omega}} \\
\cdot \left( t_i + t_{\omega} + 1 \right)^{N-F_{\xi}}.
\]

We shall now proceed to construct an alternative expression for determining the generating function.
A glance at its own expression shows that our generating function $\Phi(i; i | z)$ is given by the constant term in the Laurent expansion, besides of $\Phi(i; i | z | w)$, also of an expression

$$\Phi(i; i | z | w) = \frac{M_{i w} F_{i w} (N - F_{i w})!}{N! z^{M_{i w}}}.$$

regarded as a rational function of an argument $u$. Introducing a further parameter $v$, the latter is given by the constant term in the Laurent expansion of an expression

$$\Phi_0(i; i | z, v) = \frac{M_{i w} F_{i w} (N - F_{i w})!}{N! z^{M_{i w}}} (u z + \frac{z + 1}{2})^{M_{i w}} (u + 1)^{N - M_{i w}}.$$

By putting again $u = t / t_w$ and $v = 1 / t_w$, it is brought into the form

$$\Phi(i; i | z | t, t_w) = \frac{M_{i w} F_{i w} (N - F_{i w})!}{N! (N - M_{i w})! t^{M_{i w}} t_w^{N - M_{i w}}}.$$

Consequently, our generating function is represented by the constant term in the Laurent expansion around the origin of the last expression regarded as a rational function of two arguments $t_i$ and $t_w$.

On the other hand, we can derive, besides the one just obtained, another form of an alternative expression producing the generating function. In fact, we can define, instead of $\Phi(i; i | z | u)$, another function

$$\Phi_1(i; i | z | u) = \frac{M_{i w} F_{i w} (N - F_{i w})!}{N! (z + 1)^{M_{i w}} (u + 1)^{N - M_{i w}}}.$$

regarded as a rational function of arguments $u$ and $v$. As readily seen, it is also expressible by the constant term in the Laurent expansion of an expression

$$\Phi_1(i; i | z | t) = \frac{M_{i w} F_{i w} (N - F_{i w})!}{N! t^{M_{i w}} (t + 1)^{N - M_{i w}}}.$$

Consequently, our generating function is represented by the constant term in the Laurent expansion around the origin of the last expression regarded as a rational function of a single argument $t$. We have thus derived, for a type of mother-child combination $(A_i A_i | A_j A_j)$, several analytical expressions, of which everyone yields the generating function as the constant term of its Laurent expansion around the origin with respect to a set of respective relevant parameters. For every remaining type of mother-child combination, a similar procedure will leads to a corresponding result.

We set out in the following lines the results which are derived in such a manner. In every expression, the generating function is obtained as the constant term of its Laurent expansion around the origin of the respective set of parameters.

I. Case of a homozygous mother $A_i A_i$.
By means of the formulas just obtained, several statistics for the stochastic variables are readily computed. For instance, logarithmic differentiation of the expression

\[ \Phi_1(\xi, \eta; z| t, \omega) = \frac{M_{s1}! M_{s2}! F_{s1}! (N - F_{s2})!}{N! (N - M_{sw})!} \left( \frac{z - 1}{z} \right)^{M_{sw} + (1 + t + t_z) M_{sw}} \]

\[ \Phi_2(\xi, \eta; z| t) = \frac{F_{s1}! (N - F_{s1})!}{N! t F_{s2}^s} \left( \frac{z - 1}{z} \right)^{M_{sw} + (1 + t + t_z) M_{sw}} \]

\[ \Phi_3(\xi, \eta; z| A, A; a, b) = \frac{F_{s1}! (N - F_{s1})!}{N! a^s b^s} \left( \frac{z - 1}{z} \right)^{M_{sw} + (1 + t + t_z) M_{sw}} \]

and so on.

(ii) \( (A_1; A_1; A_1; A_1) \)

\[ \xi = i, \quad M_{kxo} = \sum_{b \neq k} M_{kb}, \quad M_{sw} = \sum_{a \neq b} M_{ab}. \]

By separating the constant term in the Laurent expansion, we again obtain the mean of \( \mathbf{X} \) in the form

\[ \mathbf{X} = \sum_{b \neq k} M_{kb}, \quad \mathbf{X}_{sw} = \sum_{a \neq b} M_{ab}, \]

\[ \mathbf{M}_{sw} = \sum_{b \neq k} M_{kb}, \quad \mathbf{M}_{sw} = \sum_{a \neq b} M_{ab}. \]

\( \mathbf{v} = (A_1; A_1; A_1; A_1), \quad \xi = 1. \]

\( \mathbf{s} = k, \quad \mathbf{m}_{sw} = \sum_{b \neq k} M_{kb}, \quad \mathbf{m}_{sw} = \sum_{a \neq b} M_{ab}. \]

By means of the formulas just obtained, several statistics for the stochastic variables are readily computed. For instance, logarithmic differentiation of the expression

\[ \Phi_2(\xi; \xi; z| t) = \frac{F_{s1}! (N - F_{s1})!}{N! t F_{s2}^s} \left( \frac{z - 1}{z} \right)^{M_{sw} + (1 + t + t_z) M_{sw}} \]

with respect to \( z \) yields

\[ \frac{\partial}{\partial z} \log \Phi_2(\xi; \xi; z| t) = M_{sw} - \frac{t}{1 + t z} + M_{sw} \frac{z - 1}{1 + t z + \frac{1}{2}}, \]

whence follows, after putting \( z = 1 \),

\[ \frac{\partial}{\partial z} \Phi_2(\xi; \xi; 1| t) = \frac{F_{s1}! (N - F_{s1})! (1 + t)^N}{N! t F_{s2}^s} \left( \frac{z - 1}{z} \right)^{M_{sw} + (1 + t)^M_{sw}} \]

By separating the constant term in the Laurent expansion, we again obtain the mean of \( \mathbf{X} \) in the form

\[ \mathbf{X}(\xi; \xi) = \frac{\partial}{\partial z} \Phi(\xi; \xi; z) \]

Similarly for the remaining types of combination.

4. Distributions of genotypes.
In a previous paper\(^1\), the problem of estimating the distributions of genotypes after a panmixia has been dealt with in full detail for general case of any number of alleles. As remarked there, the problem can be reduced to one in which there concern a fewer number of alleles, though the argument has concerned there with the general case for the sake of completeness.

We shall now explain a possibility of obtaining an alternative expression from which the generating function also follows. However, since the result previously established is considerably satisfactory, the present rather primitive procedure will look to disadvantage compared with the previous one.

For the sake of brevity, we illustrate here the simplest case \(m=2\) somewhat minutely. Let accordingly two alleles be denoted by

\[
A \quad \text{and} \quad B
\]

and the given distributions of three genotypes \(AA, AB, BB\) in females and in males be denoted by

\[
F_1, F_2, F_3 \quad \text{and} \quad M_1, M_2, M_3,
\]

respectively, so that

\[
F_1 + F_2 + F_3 = M_1 + M_2 + M_3 = N;
\]

\(N\) being fixed, \(F_1\) and \(M_3\) are dependent.

Introducing a set of three stochastic variables \(X, Y\) and \(Z\) of which the range is given by

\[
H: \quad X, Y, Z \geq 0; X + Y + Z = N,
\]

we designate by

\[
\Psi(X, Z) = \Psi(X, Z | F_1, F_3; M_1, M_3)
\]

the probability that the distribution of \(AA, AB\) and \(BB\) in the next generation after a panmixia becomes \(X, Y\) and \(Z\), respectively; \(Y\) being dependent. Our present purpose is then to derive the probability-generating function defined by

\[
\Phi(u, w) = \sum_{X, Y, Z} \Psi(X, Z) u^X w^Z.
\]

We first consider a partition of the whole of males into three classes according to three genotypes of females to be married. Namely, let each of \(M_\tau (\tau = 1, 2, 3)\) individuals be divided into three classes, empty classes being admitted, in such a manner

\[
M_\tau = \sum_{\tau = 1}^{3} x_{\tau \tau}, \quad F_\tau = \sum_{\sigma = 1}^{3} x_{\tau \sigma}.
\]

Let the matings take place such that the \(x_{\tau \sigma}\)'s \((\tau = 1, 2, 3, \sigma = 1, 2, 3)\) males are combined with \(F_\tau\) females for \(\tau = 1, 2, 3\). Here, the suffix \(\tau\) indicates a genotype of a male, while the suffix \(\sigma\) indicates a genotype of a female concerned; the suffixes 1, 2 and 3 correspond to \(AA, AB\) and \(BB\), respectively.

All the possible permutations of \(N\) genotypes of males amount to

\[
N! / M_1! M_2! M_3!,
\]

while the permutations of \(F_\tau\) genotypes of females to be married with males of \(\tau\) th class amount to

\[
F_\tau! / x_{1 \tau}! x_{2 \tau}! x_{3 \tau}! (\tau = 1, 2, 3).
\]

On the other hand, the matings \(AA \times AA, AA \times AB, AA \times BB, AB \times AA, AB \times AB, AB \times BB, BB \times AA, BB \times AB, BB \times BB\) produce a child of \(AA\) with probability 1, 1/2, 0, 1/2, 1, 1/2, 0, 1/2, 1, respectively. Consequently, we get

\[
\Psi(X, Z) = M_1! M_2! M_3! \sum_{\tau = 1}^{3} \frac{F_\tau!}{x_{1 \tau}! x_{2 \tau}! x_{3 \tau}!}
\]

\[
. \sum_{\omega_1, \omega_2, \omega_3} \frac{x_{1 \tau}! x_{2 \tau}! x_{3 \tau}!}{x_{1 \omega_1}! x_{2 \omega_2}! x_{3 \omega_3}!} \left( \frac{1}{2} \right)^{x_{1 \omega_1}} \left( \frac{1}{2} \right)^{x_{2 \omega_2}} \left( \frac{1}{2} \right)^{x_{3 \omega_3}}
\]

\[
. \frac{x_{1 \tau}! x_{2 \tau}! x_{3 \tau}!}{x_{1 \omega_1}! x_{2 \omega_2}! x_{3 \omega_3}!} \left( \frac{1}{2} \right)^{x_{1 \omega_1}} \left( \frac{1}{2} \right)^{x_{2 \omega_2}} \left( \frac{1}{2} \right)^{x_{3 \omega_3}}.
\]


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The range \( \mathcal{K} \) of the first sum extends over all the possible partitions of \( N \) males, while the range \( \mathcal{L} \) of the second sum is given by

\[
\left\{ \begin{array}{l}
\chi_{11}^{(1)} + \chi_{12}^{(2)} = \chi_{11},
\chi_{12}^{(1)} + \chi_{12}^{(2)} = \chi_{12},
\chi_{22}^{(1)} + \chi_{22}^{(2)} + \chi_{22}^{(3)} = \chi_{22},
\chi_{22}^{(1)} + \chi_{22}^{(2)} + \chi_{22}^{(3)} = \chi_{22},
\chi_{12}^{(1)} + \chi_{12}^{(2)} + \chi_{12}^{(3)} = \chi_{12},
\chi_{22}^{(1)} + \chi_{22}^{(2)} + \chi_{22}^{(3)} + \chi_{32} = \chi_{32}.
\end{array} \right.
\]

the letters indicating exclusively non-negative integers.

Among nine quantities \( x_{\sigma \tau} (\sigma, \tau = 1, 2, 3) \), only four are independent. We may take, for instance, \( x_{11}, x_{12}, x_{22}, x_{23} \) as independent variables. The remaining five are then determined uniquely, i.e., there hold the identities

\[
\left\{ \begin{array}{l}
\chi_{11} = M_1 - x_{11} - x_{12},
\chi_{12} = x_{12},
\chi_{22} = M_2 - x_{22} - x_{32},
\chi_{23} = x_{23},
\chi_{32} = M_3 - x_{32} - x_{33},
\end{array} \right.
\]

the duality concerning interchange of suffices 1 and 3 being here noted.

On the other hand, among eleven quantities indicating the numbers of children produced, again only four are independent for a fixed pair of \( X \) and \( Z \). We may take, for instance, \( x_{11}, x_{12}, x_{22}, x_{23}, x_{32} \) as independent variables. The remaining seven are then determined uniquely, i.e., there hold the identities

\[
\left\{ \begin{array}{l}
\chi_{11}^{(1)} = M_1 - x_{11} - x_{12},
\chi_{11}^{(2)} = x_{11},
\chi_{12}^{(3)} = x_{12},
\chi_{12}^{(4)} = x_{12},
\chi_{22}^{(5)} = x_{22} - x_{32},
\chi_{22}^{(6)} = x_{22},
\chi_{32}^{(7)} = x_{32} - x_{33},
\chi_{32}^{(8)} = x_{32}.
\end{array} \right.
\]

we thus obtain

\[
\Phi(u, w) = \frac{M_1! M_2! M_3! F_1! F_2! F_3!}{N! Z! M_1 + F_2}
\]

the independent variables in \( \mathcal{L} \); \( \mathcal{K} \), \( \mathcal{L} \) being, as stated above, \( X, Z, \chi_{11}, \chi_{12}, \chi_{22}, \chi_{23}, \chi_{32} \), respectively.

By making use of multinomial identities

\[
\sum_{X, Z} \frac{u^X w^Z}{X_{11}^{(1)} X_{12}^{(2)} X_{22}^{(3)} X_{23}^{(4)} X_{32}^{(5)} X_{11}^{(6)} X_{12}^{(7)} X_{22}^{(8)} X_{23}^{(9)} X_{32}^{(10)} X_{32}^{(11)} X_{32}^{(12)}}{1 X_{11}^{(1)} X_{12}^{(2)} X_{22}^{(3)} X_{23}^{(4)} X_{32}^{(5)} X_{11}^{(6)} X_{12}^{(7)} X_{22}^{(8)} X_{23}^{(9)} X_{32}^{(10)} X_{32}^{(11)} X_{32}^{(12)}} = \frac{1}{X_{11}^{(1)} X_{22}^{(3)}} (1 + u) X_{32}^{(5)}
\]

\[
\sum_{X, Z} \frac{u^X w^Z}{X_{11}^{(1)} X_{12}^{(2)} X_{22}^{(3)} X_{23}^{(4)} X_{32}^{(5)} X_{11}^{(6)} X_{12}^{(7)} X_{22}^{(8)} X_{23}^{(9)} X_{32}^{(10)} X_{32}^{(11)} X_{32}^{(12)}}{1 X_{11}^{(1)} X_{12}^{(2)} X_{22}^{(3)} X_{23}^{(4)} X_{32}^{(5)} X_{11}^{(6)} X_{12}^{(7)} X_{22}^{(8)} X_{23}^{(9)} X_{32}^{(10)} X_{32}^{(11)} X_{32}^{(12)}} = \frac{1}{X_{11}^{(1)} X_{12}^{(2)} X_{22}^{(3)} X_{23}^{(4)} X_{32}^{(5)} X_{11}^{(6)} X_{12}^{(7)} X_{22}^{(8)} X_{23}^{(9)} X_{32}^{(10)} X_{32}^{(11)} X_{32}^{(12)}} (1 + u) X_{32}^{(5)}
\]

\[
\sum_{X, Z} \frac{u^X w^Z}{X_{11}^{(1)} X_{12}^{(2)} X_{22}^{(3)} X_{23}^{(4)} X_{32}^{(5)} X_{11}^{(6)} X_{12}^{(7)} X_{22}^{(8)} X_{23}^{(9)} X_{32}^{(10)} X_{32}^{(11)} X_{32}^{(12)}}{1 X_{11}^{(1)} X_{12}^{(2)} X_{22}^{(3)} X_{23}^{(4)} X_{32}^{(5)} X_{11}^{(6)} X_{12}^{(7)} X_{22}^{(8)} X_{23}^{(9)} X_{32}^{(10)} X_{32}^{(11)} X_{32}^{(12)}} = \frac{1}{X_{11}^{(1)} X_{12}^{(2)} X_{22}^{(3)} X_{23}^{(4)} X_{32}^{(5)} X_{11}^{(6)} X_{12}^{(7)} X_{22}^{(8)} X_{23}^{(9)} X_{32}^{(10)} X_{32}^{(11)} X_{32}^{(12)}} (1 + u) X_{32}^{(5)}
\]
the generating function can be brought into the form
\[ \Phi(u, w) = \frac{M_1! M_2! M_3! F_1! F_2! F_3!}{N! 2^{M_2 + F_2}} \]
\[ \cdot \sum_{x_{11}, x_{12}, x_{13}} \frac{\binom{N}{x_{11}, x_{12}, x_{13}}}{w^{x_{11}} (1 + w)^{x_{12}} (1 + w)^{x_{13}}} \cdot \frac{x_{11}! x_{12}! x_{13}!}{x_{11}! x_{12}! x_{13}!} \cdot \frac{1}{x_{11}! x_{12}! x_{13}!} \]
\[ \cdot \left( \frac{u + 2 + w}{(1 + \lambda)(1 + u)} \right)^{x_{11}} \left( \frac{w}{1 + w} \right)^{x_{12}} \left( \frac{1}{1 + u} \right)^{x_{13}} \]
\[ \cdot \left( \frac{w}{1 + w} \right)^{x_{11}} \left( \frac{1}{1 + u} \right)^{x_{12}} \left( \frac{w}{1 + w} \right)^{x_{13}} \]

Next, we get a relation
\[ \Phi(V_L, W) \]

\[ \text{in which the sum of the right-hand member is equal to the constant term in the Laurent expansion around the origin of an expression} \]
\[ \text{regarded as a rational function of \( X \).} \]

On the other hand, we have
\[ \text{Hence,} \]
\[ \Phi(u, w) \]

\[ \text{is given by the constant term in the Laurent expansion around the origin of an expression} \]
\[ \left( \frac{1 + w}{1 + w} \right)^{M_2 - x_{12}} \left( \frac{M_2 - F_2 + x_{12}}{1 + \lambda} \right)^{M_2 - x_{13} + x_{12}} \]
\[ \left( \frac{1 + w}{1 + w} \right)^{x_{11}} \left( \frac{1 + w}{1 + w} \right)^{x_{12}} \left( \frac{1 + w}{1 + w} \right)^{x_{13}} \]

\[ \text{regarded as a rational function of \( \lambda \).} \]

Further, the last sum is equal to the constant term in the Laurent expansion around the origin of an expression
\[ \left[ \left( \frac{u + 2 + w}{(1 + \lambda)(1 + u)} \right)^{x_{11}} \left( \frac{w}{1 + w} \right)^{x_{12}} \left( \frac{1}{1 + u} \right)^{x_{13}} \right] \]
\[ \cdot \left( \frac{w}{1 + w} \right)^{x_{11}} \left( \frac{1}{1 + u} \right)^{x_{12}} \left( \frac{w}{1 + w} \right)^{x_{13}} \]

regarded as a rational function of \( \xi \) and \( \zeta \).

Thus, we finally obtain the desired result: The probability-generating function \( \Phi(u, w) \) is representable as the constant term in the Laurent expansion around the origin of the expression
\[ \Phi(u, w|\lambda, \xi, \zeta) = \frac{M_1! M_2! M_3! F_1! F_2! F_3!}{N! (N - F_2)!} \]
\[ \cdot \left( \frac{u + \lambda}{1 + u} \right)^{M_1} \left( \frac{1 + \lambda}{1 + w} \right)^{M_2} \left( \frac{w}{1 + w} \right)^{M_2} \left( \frac{1}{1 + u} \right)^{M_2} \]
\[ \cdot \left( \frac{1 + w}{1 + w} \right)^{x_{11}} \left( \frac{1 + w}{1 + w} \right)^{x_{12}} \left( \frac{1 + w}{1 + w} \right)^{x_{13}} \]

regarded as a rational function of three arguments \( \lambda, \xi \) and \( \zeta \).

It would be noted that there holds a remarkable quasi-symmetry. Namely, if we replace \( u, w, \lambda, \xi, \zeta \) by \( \lambda, w, \alpha, \zeta, \xi \), it remains unaltered except the interchange of \( \xi \) and \( \zeta \) and of suffices 1 and 3.

Now, the generating function having been established in an explicit manner, several statistics on stochastic variables can be obtained merely by differentiation together with separation of the constant term from Laurent expansion, though actual procedure of computation will be considerably troublesome.

We give here a brief sketch. Logarithmic differentiation of \( \Phi(u, w|\lambda, \xi, \zeta) \) with respect to \( u \) leads to
\[ \frac{3}{3u} \log \Phi(u, w | \lambda; \xi, \zeta) \]
\[ = M_1 \frac{1}{(1+u)^2} + M_3 \frac{-1}{(1+u)^3} \]
\[ + \frac{1}{1+u+\lambda} + \frac{1}{1+w+\lambda} \]
\[ + \frac{1}{2u} + \frac{1}{2w} + \frac{1}{(1+u+\lambda)^2} + \frac{1}{(1+w+\lambda)^2} \]
\[ + \frac{1}{(1+u+\lambda) + \frac{1}{1+w+\lambda} + \frac{1}{1+w+1+u}} \]
\[ + \frac{1}{1+u+\lambda} + \frac{1}{1+w+\lambda} + \frac{1}{1+w+1+u} \]

whence follows
\[ \frac{3}{3u} \Phi(1, 1 | \lambda; \xi, \zeta) \]
\[ = \frac{M_1}{N!} \frac{1}{(N-F_1)!} \frac{1}{\lambda F_0} \frac{(1 + \lambda)^N - (1 + \lambda) + 1}{(1+\lambda)^2} \]
\[ + \frac{1}{1+\lambda} + \frac{1}{1+w} + \frac{1}{(1+\lambda)(1+w)} \]

Thus, by separating the constant term of Laurent expansion, we get, after a suitable rearrangement of terms, the mean of \( X \) in the form
\[ \widetilde{X} = \frac{3}{3u} \Phi(1, 1) \]
\[ = \frac{1}{N} \left( \frac{F_1 + F_2}{2} \right) (M_1 + M_3) \]

In view of symmetry, we have
\[ \widetilde{Z} = \frac{3}{3w} \Phi(1, 1) \]
\[ = \frac{1}{N} \left( \frac{F_1 + F_2}{2} \right) (M_3 + M_2) \]

and hence further
\[ \widetilde{Y} = N - \frac{3}{2} \widetilde{X} - \widetilde{Z} \]
\[ = \frac{1}{N} \left( \frac{(F_1 + F_2)(M_3 + M_2)}{2} + (F_1 + F_2)(M_1 + M_3) \right) \]
\[ = \frac{N}{2} - \frac{(F_1 - F_2)(M_1 - M_3)}{2N} \]

Hence, putting
\[ \frac{3}{3u} \Phi(1, 1) = \frac{1}{N(N-1)} \]
\[ \cdot \left( \frac{(F_1 + F_2)^2 - (F_1 + F_2)}{2} \right) \left( (M_1 + M_3) - (M_3 + M_2) \right) \]

we obtain
\[ \widetilde{X} = N_{F_0}^{(P)} I_A^{(M)} \]
\[ \widetilde{Z} = N_{F_1}^{(P)} I_B^{(M)} \]
\[ \widetilde{Y} = N_{F_0}^{(P)} I_A^{(M)} + N_{F_2}^{(P)} I_B^{(M)} \]

Next, in order to derive the variance of \( X \), we further differentiate \( \partial log \Phi(u, w | \lambda; \xi, \zeta) / \partial u \) with respect to \( u \). We then get, after putting \( u = w = 1 \), substituting the expressions derived above for \( \partial log \Phi(u, w | \lambda; \xi, \zeta) / \partial u \) and then separating the constant term of the Laurent expansion,
\[ \frac{3^2}{3u^2} \Phi(1, 1) = \frac{1}{N(N-1)} \]
\[ \cdot \left( \frac{(F_1 + F_2)^2 - (F_1 + F_2)}{2} \right) \left( (M_1 + M_3) - (M_3 + M_2) \right) \]

The variance of \( X \) is then given by
\[ \text{var } X = \frac{3^2}{3u^2} \Phi(1, 1) + \widetilde{X} - \widetilde{X}^2 \]

Similarly, we obtain
\[ \frac{3^2}{3w^2} \Phi(1, 1) = \frac{1}{N(N-1)} \]
\[ \cdot \left( \frac{(F_3 + F_4)^2 - (F_3 + F_4)}{2} \right) \left( (M_3 + M_2) - (M_3 + M_2) \right) \]

and the variance of \( Z \) is given by
\[ \text{var } Z = \frac{3^2}{3w^2} \Phi(1, 1) + \widetilde{Z} - \widetilde{Z}^2 \]

Finally, we get in a similar manner
\[ \frac{3^2}{3w^2} \Phi(1, 1) = \frac{1}{N(N-1)} \]
\[ \cdot \left( \frac{(F_1 + F_2)(F_3 + F_4) - F_3}{2} \right) \left( (M_1 + M_3)(M_3 + M_2) - M_2 \right) \]
and the variance of $\bar{Y}$ is given by

$$\text{var} \bar{Y} = \text{var} \bar{X} + \text{var} \bar{Z} + 2\left\{ \frac{\sigma^2}{\mu_1^2} \Phi(1,1) - \bar{X} \bar{Z} \right\},$$

in which the last term except the factor 2 is nothing but the covariance between $\bar{X}$ and $\bar{Z}$:

$$\text{cov}(\bar{X}, \bar{Z}) = \frac{\sigma^2}{\mu_1^2} \Phi(1,1) - \bar{X} \bar{Z}.$$