103. *Probaility-theoretic Investigations on Inheritance.* *III$_2$. Further Discussions on Cross-Breeding.*

(Continuation.)

By Yûsaku KOMATU.

Department of Mathematics, Tokyo Institute of Technology and Department of Legal Medicine, Tokyo University.

(Comm. by T. FURUHATA, M.J.A., Oct. 12, 1951.)

3. Proof of main result.

In order to prove the main result stated in (2.30), (2.31) by induction, we must first generalize the table inserted in the preceding section to the case of passage from the $(n-1)$th to the nth generation, stating as follows. In the table, the notation $\mu_{uv}^{(l)}$ is used in slightly exteded meaning such that a convention is made:

$$\mu_{uv}^{(l)} = \mu_{vu}^{(l)}, \quad \mu_{uu}^{(l)} = 0 \quad (u, v = 0, 1, 2, \ldots, 2^{l-1}). \tag{3.1}$$

Further, the notation $d(\alpha)$ for any natural number α means the highest power of 2 which appears in the decomposition of 2α into prime numbers; i.e., $d(\alpha)$ is defined in such a manner that α is divisible by $2^{d(\alpha)-1}$ but not by $2^{d(\alpha)}$. In particular, if α is an odd number, $d(\alpha)$ is always equal to unity.

class in the nth generation	mating-class in the $(n-1)$th generation	frequency of each mating-class
X'^{2^n}	$X'^{2^{n-1}} \times X'^{2^{n-1}}$	$\lambda' - \sum_{l=1}^{n} \sum_{k=1}^{2^{l-1}} \mu_{0k}$
$X'^{2^n-(2\alpha-1)} X''^{2\alpha-1}$ $(1 \leqq \alpha \leqq 2^{n-2})$	$X'^{2^{n-1}-h} X''^{h} \times X'^{2^{n-1}-(2\alpha-1)+h} X''^{2\alpha-1-h}$ $(0 \leqq h < \alpha)$	$2\mu^{(n)}_{h,\,2\alpha-1-h}$
		$2\mu^{(n)}_{h,\,2\alpha-h}$
$X'^{2^n-2\alpha} X''^{2\alpha}$ $(1 \leqq \alpha \leqq 2^{n-2})$	$\begin{cases} X'^{2^{n-1}-h} X''^{h} \times X'^{2^{n-1}-2\alpha+h} \\ X''^{2\alpha-h} \ (0 \leqq h < \alpha) \\ X'^{2^{n-1}-\alpha} X''^{\alpha} \times X'^{2^{n-1}-\alpha} X''^{\alpha} \end{cases}$	$\sum_{l=n+1-d(\alpha)}^{n} \Big(2 \sum_{0 \leqq h < 2^{l-n-1}\alpha} \mu^{(l-1)}_{h,\,2^{l-n}\alpha-h} - \sum_{k=0}^{2^{l-1}} \mu^{(l)}_{2^{l-n}\alpha,\,k}\Big)\, 2\mu^{(n)}_{h,\,2\alpha-h}$
$X'^{2^n-2\alpha} X''^{2\alpha}$ $(2^{n-2} < \alpha < 2^{n-1})$	$\begin{cases} X'^{2^{n-1}-h} X''^{h} \times X'^{2^{n-1}-2\alpha+h} \\ X''^{2\alpha-h} \ (\alpha < h \leqq 2^{n-1}) \\ X'^{2^{n-1}-\alpha} X''^{\alpha} \times X'^{2^{n-1}-\alpha} X''^{\alpha} \end{cases}$	$\sum_{l=n+1-d(\alpha)}^{n} \Big(2 \sum_{2^{l-2} \geqq h > 2^{l-n-1}\alpha} \mu^{(l-1)}_{h,\,2^{l-n}\alpha-h} - \sum_{k=0}^{2^{l-1}} \mu^{(l)}_{2^{l-n}\alpha,\,k}\Big)\, 2\mu^{(n)}_{h,\,2\alpha-1-h}$
$X'^{2^n-(2\alpha-1)} X''^{2\alpha-1}$ $(2^{n-2} < \alpha \leqq 2^{n-1})$	$X'^{2^{n-1}-h} X''^{h} \times X'^{2^{n-1}-(2\alpha-1)+h} X''^{2\alpha-1-h}$ $(\alpha \leqq h \leqq 2^{n-1})$	
X''^{2^n}	$X''^{2^{n-1}} \times X''^{2^{n-1}}$	$\lambda'' - \sum_{l=1}^{n} \sum_{k=0}^{2^{l-1}-1} \mu^{(l)}_{2^{l-1},\,k}$
		$\lambda' + \lambda'' = 1$

In order to assert the validity of the table by induction, we go back by one generation and assume now the validity of the corresponding table for $(n-1)$th generation.

First, there exist $2^{n-1}+1$ possible types of matings concerned by the class $X'^{2^{n-1}}$ in the $(n-1)$th generation; they are expressed by $X'^{2^{n-1}}\times X'^{2^{n-1}}$ and $X'^{2^{n-1}}\times X'^{2^{n-1}-k}$ $(1\leqq k\leqq 2^{n-1})$. Among them, the frequencies of the latter 2^{n-1} types are, by definition, equal to $2\mu^{(n)}_{0k}$ $(1\leqq k\leqq 2^{n-1})$, respectively. Since the class X'^{2^n} in the nth generation results from the former type alone, its freqnency is obtained by subtracting the half sum of the last 2^{n-1} quantities from the frequency of the class $X'^{2^{n-1}}$ in the $(n-1)$th generation and hence given by

$$(3.2)\qquad \lambda'-\sum_{l=1}^{n-1}\sum_{k=1}^{2^{l-1}}\mu^{(l)}_{0k}-\frac{1}{2}\sum_{k=1}^{2^{l-1}}2\mu^{(n)}_{0k}=\lambda'-\sum_{l=1}^{n}\sum_{k=1}^{2^{l-1}}\mu^{(l)}_{0k}.$$

Next, there exist α possible types of matings in the $(n-1)$th generation which can produce the class $X'^{2^n-(2\alpha-1)}\,X''^{2\alpha-1}$ $(1\leqq\alpha\leqq 2^{n-2})$ in the nth generation; they are expressed by $X'^{2^{n-1}-h}\,X''^{h}\times X'^{2^{n-1}-(2\alpha-1)+h}\,X''^{2\alpha-1-h}$ $(0\leqq h<\alpha)$, whose frequencies are, by definition, equal to

$$(3.3)\qquad 2\mu^{(n)}_{h,\,2\alpha-1-h}\qquad (0\leqq h<\alpha),$$

respectively.

Now, there exist $\alpha+1$ possible types of matings in the $(n-1)$th generation which can produce the class $X'^{2^n-2\alpha}\,X''^{2\alpha}$ $(1\leqq\alpha<2^{n-2})$ in the nth generation; they are expressed by $X'^{2^{n-1}-h}\,X''^{h}\times X'^{2^{n-1}-2\alpha+h}\,X''^{2\alpha-h}$ $(0\leqq h<\alpha)$ and $X'^{2^{n-1}-\alpha}\,X''^{\alpha}\times X'^{2^{n-1}-\alpha}\,X''^{\alpha}$. Among them, the frequencies of the former α types are, by definition, equal to

$$(3.4)\qquad 2\mu^{(n)}_{h,\,2\alpha-h}\qquad (0\leqq h<\alpha),$$

respectively. To determine the frequency of the latter type, we consider all the types of matings concerned by $X'^{2^{n-1}-\alpha}\,X''^{\alpha}$ except only the latter type itself; they are expressed by $X'^{2^{n-1}-\alpha}\,X''^{\alpha}\times X'^{2^{n-1}-k}\,X''^{k}$ $(k\neq\alpha)$. Contribution of the class $X'^{2^{n-1}-\alpha}\,X''^{\alpha}$ to these 2α types is altogether $\sum_{k=0}^{2^{n-1}}\mu^{(n)}_{\alpha k}$, the convention (3.1) being here taken into account. Hence, in view of the identities $d(\alpha/2)=d(\alpha)-1$ $(2\mid\alpha)$ and $d(\alpha)=1$ $(2\nmid\alpha)$, we see that the frequency of $X'^{2^{n-1}-\alpha}\,X''^{\alpha}\times X'^{2^{n-1}-\alpha}\,X''^{\alpha}$ is given by

$$(3.5)\qquad 2\sum_{0\leqq h<\alpha/2}\mu^{(n-1)}_{h,\alpha-h}+\sum_{l=n-d(\alpha)+1}^{n-1}\Bigl(2\sum_{0\leqq h<2^{l-n}\alpha/2}\mu^{(l-1)}_{h,2^{l-n+1}\alpha/2-h}-\sum_{k=0}^{2^{l-1}}\mu^{(l)}_{2^{l-n+1}\alpha/2,k}\Bigr)$$
$$-\sum_{k=0}^{2^{n-1}}\mu^{(n)}_{\alpha k}=\sum_{l=n+1-d(\alpha)}^{n}\Bigl(2\sum_{0\leqq h<2^{l-n-1}\alpha}\mu^{(l-1)}_{h,2^{l-n}\alpha-h}-\sum_{k=0}^{2^{l-1}}\mu^{(l)}_{2^{l-n}\alpha,k}\Bigr);$$

the empty sum being supposed, as usual, to denote zero.

The above arguments remain to apply also to the case $\alpha=2^{n-2}$. Hence, among $2^{n-1}+1$ possible types of matings, denoted by $X'^{2^{n-1}-h}X''^{h}\times X'^{h}\,X''^{2^{n-1}-h}$ $(0\leqq h<2^{n-2})$ and $X'^{2^{n-2}}\,X''^{2^{n-2}}\times X'^{2^{n-2}}\,X''^{2^{n-2}}$ in the $(n-1)$th generation, which can produce the class $X'^{2^{n-1}}\,X''^{2^{n-1}}$ in the

nth generation, the frequencies of the former 2^{n-2} types and the latter type are equal to

$$(3.6) \qquad 2\mu^{(n)}_{h,2^{n-1}-h} \qquad (0 \leqq h < 2^{n-2})$$

and

$$(3.7) \qquad \sum_{l=2}^{n}\Big(2\sum_{0\leqq h<2^{l-3}} \mu^{(l)}_{h,2^{l-2}-h} - \sum_{k=0}^{2^{l-1}} \mu^{(l)}_{2^{l-2},k}\Big),$$

respectively.

Thus, we conclude that the upper half part of the preceding table is surely valid. The remaining lower half part of the table can be deduced in quite a similar manner. But, we may rather make use of the symmetry character of the table with respect to the interchange of X' and X'', whence the desired result will immediately follow.

Now, the frequency of A_i in each of the classes $X'^{2^{n-1}-u}X''^{u}$ $(0 \leqq u \leqq 2^{n-1})$ is evidently given by

$$(3.8) \qquad 2^{-(n-1)}((2^{n-1}-u)p'_i + up''_i).$$

Hence, the frequencies of genotypes A_{ii}, A_{ij} $(i \neq j)$ in the nth generation, which are produced by matings of the type $X'^{2^{n-1}-u}X''^{u} \times X'^{2^{n-1}-v}X''^{v}$ $(0 \leqq u, v \leqq 2^{n-1})$ in the $(n-1)$th generation, are in view of (1.5) given by

$$(3.9) \qquad \begin{aligned} &2^{-(2n-2)}((2^{n-1}-u)\,p'_i+up''_i)((2^{n-1}-v)\,p'_i+vp''_i), \\ &2^{-(2n-2)}\{((2^{n-1}-u)\,p'_i+up''_i)((2^{n-1}-v)\,p'_j+vp''_j) \\ &\quad +((2^{n-1}-v)\,p'_i+vp''_i)((2^{n-1}-u)\,p'_j+up''_j)\}. \end{aligned}$$

The frequency of the gene A_i in each of the classes $X'^{2^n-u}X''^{u}$ $(0 \leqq u \leqq 2^n)$ is, corresponding to (3.8), evidently given by

$$(3.10) \qquad 2^{-n}((2^n-u)\,p'_i+up''_i),$$

but the individual description of these values is omitted in the table, since they will not be used for the present, till we arrive at the end of the present paper.

Making use of the above table, we obtain the frequencies of homozygote A_{ii} and of heterozygote A_{ij} $(i \neq j)$ in the nth generation. Thus, we get

$$\begin{aligned} \bar{A}_{ii}(n) = &\Big(\lambda' - \sum_{l=1}^{n}\sum_{k=1}^{2^{l-1}} \mu^{(l)}_{0k}\Big)p'^2_i \\ &+ \frac{1}{2^{2n-2}}\sum_{\alpha=1}^{2^{n-2}}\sum_{h=0}^{\alpha-1} 2\mu^{(n)}_{h,2\alpha-1-h}((2^{n-1}-h)\,p'_i+hp''_i)((2^{n-1}-2\alpha+1+h)\,p'_i \\ &+ (2\alpha-1-h)\,p''_i) + \frac{1}{2^{2n-2}}\sum_{\alpha=1}^{2^{n-2}}\Big\{\sum_{h=0}^{\alpha-1} 2\mu^{(n)}_{h,2\alpha-h}((2^{n-1}-h)\,p'_i+hp''_i) \end{aligned}$$

$$\times\left(\left(2^{n-1}-2\alpha+h\right)p_i'+(2\alpha-h)\,p_i''\right)+\sum_{l=n+1-d(\alpha)}^{n}\left(2\sum_{0\leq h<2^{l-n-1}\alpha}\mu^{(l-1)}_{h,2^{l-1-n}\alpha-h}\right.$$

$$\left.-\sum_{k=0}^{2^{l}-1}\mu^{(l)}_{2^{l-n}\alpha,k}\right)\left(\left(2^{n-1}-\alpha\right)p_i'+\alpha p_i''\right)^2\Bigg\}$$

$$+\frac{1}{2^{2n-2}}\sum_{\alpha=2^{n-2}+1}^{2^{n-1}-1}\Bigg\{\sum_{h=\alpha+1}^{2^{n-1}}2\mu^{(n)}_{h,2\alpha-h}\left(\left(2^{n-1}-h\right)p_i'+hp_i''\right)\left(\left(2^{n-1}-2\alpha+h\right)p_i'+(2\alpha-h)p_i''\right)$$

$$+\sum_{l=n+1-d(\alpha)}^{n}\left(2\sum_{2^{l-2}\geq h>2^{l-n-1}\alpha}\mu^{(l-1)}_{h,2^{l-1-n}\alpha-h}-\sum_{k=0}^{2^{l}-1}\mu^{(l)}_{2^{l-n}\alpha,h}\right)\left(\left(2^{n-1}-\alpha\right)p_i'+\alpha p_i''\right)^2\Bigg\}$$

$$+\frac{1}{2^{2n-2}}\sum_{\alpha=2^{n-2}+1}^{2^{n-1}}\sum_{h=\alpha}^{2^{n-1}}\mu^{(n)}_{h,2\alpha-1-h}\left(\left(2^{n-1}-h\right)p_i'+hp_i''\right)$$

$$\times\left(\left(2^{n-1}-2\alpha+1+h\right)p_i'+(2\alpha-1-h)\,p_i''\right)$$

$$+\left(\lambda''-\sum_{l=1}^{n}\sum_{k=0}^{2^{l-1}-1}\mu^{(l)}_{2^{l}-1,k}\right)p_i''^2$$

$$\text{(3.11)}\qquad=\left(\lambda'-\sum_{l=1}^{n}\sum_{k=1}^{2^{l}-1}\mu^{(l)}_{0k}\right)p_i'^2$$

$$+\frac{1}{2^{2n-3}}\sum_{\alpha=1}^{2^{n-1}}\sum_{0\leq h<\alpha/2}\mu^{(n)}_{h,\alpha-h}\left(\left(2^{n-1}-h\right)p_i'+hp_i''\right)\left(\left(2^{n-1}-\alpha+h\right)p_i'+(\alpha-h)\,p_i''\right)$$

$$+\frac{1}{2^{2n-3}}\sum_{\alpha=1}^{2^{n-2}}\sum_{l=n+1-d(\alpha)}^{n}\left(\sum_{0\leq h<2^{l-n-1}\alpha}\mu^{(l-1)}_{h,2^{l-1-n}\alpha-h}-\frac{1}{2}\sum_{k=0}^{2^{l}-1}\mu^{(l)}_{2^{l-n}\alpha,k}\right)\left(\left(2^{n-1}-\alpha\right)p_i'+\alpha p_i''\right)^2$$

$$+\frac{1}{2^{2n-3}}\sum_{\alpha=2^{n-2}+1}^{2^{n-1}-1}\sum_{l=n+1-d(\alpha)}^{n}\left(\sum_{2^{l-2}\geq h>2^{l-n-1}\alpha}\mu^{(l-1)}_{h,2^{l-1-n}\alpha-h}\right.$$

$$\left.-\frac{1}{2}\sum_{k=0}^{2^{l}-1}\mu^{(l)}_{2^{l-n}\alpha,k}\right)\left(\left(2^{n-1}-\alpha\right)p_i'+\alpha p_i''\right)^2$$

$$+\frac{1}{2^{2n-3}}\sum_{\alpha=2^{n-1}+1}^{2^{n}-1}\sum_{2^{n-1}\geq h>\alpha/2}\mu^{(n)}_{h,\alpha-h}\left(\left(2^{n-1}-h\right)p_i'+hp_i''\right)\left(\left(2^{n-1}-\alpha+h\right)p_i'\right.$$

$$\left.+(\alpha-h)p_i''\right)+\left(\lambda''-\sum_{l=1}^{n}\sum_{k=0}^{2^{l-1}-1}\mu^{(l)}_{2^{l}-1,k}\right)p_i''^2$$

and similarly, for $i\neq j$,

$$\bar{A}_{ij}(n)=2\left(\lambda'-\sum_{l=1}^{n}\sum_{k=1}^{2^{l}-1}\mu^{(l)}_{0k}\right)p_i'p_j'$$

$$+\frac{2}{2^{2n-3}}\sum_{\alpha=1}^{2^{n-1}}\sum_{0\leq h<\alpha/2}\mu^{(n)}_{h,\alpha-h}\left\{\left(\left(2^{n-1}-h\right)p_i'+hp_i''\right)\left(\left(2^{n-1}-\alpha+h\right)p_j'\right.\right.$$

$$\left.\left.+(\alpha-h)p_j''\right)+\left(\left(2^{n-1}-\alpha+h\right)p_i'+(\alpha-h)\,p_i''\right)\left(\left(2^{n-1}-h\right)p_j'+hp_j''\right)\right\}$$

$$\text{(3.12)}\qquad+\frac{1}{2^{2n-4}}\sum_{\alpha=1}^{2^{n-2}}\sum_{l=n+1-d(\alpha)}^{n}\left(\sum_{0\leq h<2^{l-n-1}\alpha}\mu^{(l-1)}_{h,2^{l-1-n}\alpha-h}\right.$$

$$\left.-\frac{1}{2}\sum_{k=0}^{2^{l}-1}\mu^{(l)}_{2^{l-n}\alpha,k}\right)\left(\left(2^{n-1}-\alpha\right)p_i'+\alpha p_i''\right)\left(\left(2^{n-1}-\alpha\right)p_j'+\alpha p_j''\right)$$

$$
+\frac{1}{2^{2n-4}}\sum_{\alpha=2^{n-2}+1}^{2^{n-1}-1}\ \sum_{l=n+1-d(\alpha)}^{n}\left(\sum_{2^{l-2}\geq h>2^{l-n-1}\alpha}\mu^{(l-1)}_{h,2^{l}-n_{\alpha}-h}-\frac{1}{2}\sum_{k=0}^{2^{l-1}}\mu^{(l)}_{2^{l}-n_{\alpha},k}\right)
$$
$$
\times((2^{n-1}-\alpha)p'_i+\alpha p''_i)\,((2^{n-1}-\alpha)p'_j+\alpha p''_j)
$$
$$
+\frac{1}{2^{2n-3}}\sum_{\alpha=1}^{2^{n-1}-1}\ \sum_{2^{n-1}\geq h>\alpha/2}\mu^{(n)}_{h,\alpha-h}\{((2^{n-1}-h)p'_i+hp''_i)\,((2^{n-1}-\alpha+h)p'_j
$$
$$
+(\alpha-h)p''_j)+((2^{n-1}-\alpha+h)p'_i+(\alpha-h)p''_i)\,((2^{n-1}-h)p'_j+hp''_j)\}
$$
$$
+2\left(\lambda''-\sum_{l=1}^{n}\sum_{k=0}^{2^{l-1}-1}\mu^{(l)}_{2^{l-1},k}\right)p''_ip''_j\,.
$$

Applying these fromulae to case $n-1$ instead of n and subtracting the so obtained expressions from the above ones, we get, by remembering the fact that $d(\alpha)$ is equal to 1 for any odd integer α, after some calculations,

$$
\begin{aligned}
(3.13)\quad &\bar{A}_{ii}(n)-\bar{A}_{ii}(n-1)\\
&=\left\{\frac{1}{2^{2n-3}}\sum_{k=1}^{2^{n-2}}k^2\sum_{h=0}^{2^{n-2}-k}\mu^{(n-1)}_{h,h+k}-\frac{1}{2^{2n-2}}\sum_{k=1}^{2^{n-1}}k^2\sum_{h=0}^{2^{n-1}-k}\mu^{(n)}_{h,h+k}\right\}(p'_i-p''_i{}^2)
\end{aligned}
$$

and, for $i\neq j$,

$$
\begin{aligned}
(3.14)\quad &\bar{A}_{ij}(n)-\bar{A}_{ij}(n-1)\\
&=2\left\{\frac{1}{2^{2n-3}}\sum_{k=1}^{2^{n-2}}k^2\sum_{h=0}^{2^{n-2}-k}\mu^{(n-1)}_{h,h+k}-\frac{1}{2^{2n-2}}\sum_{k=1}^{2^{n-1}}k^2\sum_{h=0}^{2^{n-1}-k}\mu^{(n)}_{h,h+k}\right\}\\
&\qquad\times(p'_i-p''_i)(p'_j-p''_j)\,.
\end{aligned}
$$

We have assumed that the desired result is valid for $n-1$ instead of n; i.e., made the assumption of induction stating that

$$
(3.15)\quad
\begin{aligned}
&\bar{A}_{ii}(n-1)-\bar{A}_{ii}(0)=-\Gamma^{(n-1)}(p'_i-p''_i)^2\,,\\
&\qquad\qquad\qquad\qquad(i,j=1,\ldots,m;\ i<j).\\
&\bar{A}_{ij}(n-1)-\bar{A}_{ij}(0)=-2\Gamma^{(n-1)}(p'_i-p''_i)(p'_j-p''_j)
\end{aligned}
$$

Comparing the above obtained expressions for $\bar{A}_{ii}(n)-\bar{A}_{ii}(n-1)$ and $\bar{A}_{ij}(n)-\bar{A}_{ij}(n-1)$ with the last relations and remembering that the relation

$$
(3.16)\quad \Gamma^{(n-1)}-\frac{1}{2^{2n-3}}\sum_{k=1}^{2^{n-2}}k^2\sum_{h=0}^{2^{n-1}-k}\mu^{(n-1)}_{h,h+k}+\frac{1}{2^{2n-2}}\sum_{k=1}^{2^{n-1}}k^2\sum_{h=0}^{2^{n-1}-k}\mu^{(n)}_{h,h+k}=\Gamma^{(n)}
$$

is valid, we conclude that the desired result (2.30), (2.31) is really true. Thus, we complete the proof of our main result.

We notice finally, by the way, that the sum of the frequencies of all the possible mating-classes, listed in the last table, is equal to $\lambda' + \lambda'' = 1$, the fact which has already been inserted in the table and which can also immediately be verified. On the other hand, suppose that these frequencies are weighted by the corresponding frequencies of genes given in (3.10), then the weighted sum is equal to the frequency $\lambda' p_i' + \lambda'' p_i'' = p_i$ of the respective gene in the limit distribution.

—To be Concluded—