ON "MATERNAL INHERITANCE"

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INTRODUCTION

There is a type of heredity known as "maternal inheritance" because the characters are influenced more by the egg than by the spermatozoon; but they are proved, nevertheless, to have their own allelomorphs and to be subject to Mendel's law of segregation.

Since the late Prof. Toyama (1913) used the term "maternal inheritance" for the first time in his study on the egg color of the silk-worm, Bombyx mori L., much interest has been centered on the problem and it came to be believed by some that there is really such a special type of heredity. But it seems that the study has been limited chiefly to the egg color (Toyama 1912, 1913, Tanaka 1919) and voltinism (Toyama, 1912, 1913, McCracken 1909, Castle 1910, Cleghorn 1918, Watanabe 1918, 1919) in the silk-worm. Besides these, there are some characters which have been erroneously treated as maternal inheritance. Indeed, cases of maternal inheritance are apt to be confused, not only with plastid inheritance,¹ but also with the phenomena of Bateson's "mono-

¹If there are self-perpetuating materials in the cytoplasm, they must be inherited chiefly through the egg cell; and, in fact, there is excellent genetic evidence that a peculiar kind of inheritance in certain chlorophyll characters is due to the transmission of self-perpetuating bodies called plastids in the cytoplasm. Therefore I recognize the plastid inheritance as one type of heredity, and cannot agree with Emerson (1914) who ascribes its cause to the variability of unit factors, nor with Plate (1913) who calls it "falsche Vererbung."
lepesis," or with cases of inheritance in which all or some of the paternal chromosomes fail to function, leaving the embryo with its maternal set alone.

Consequently, all the definitions of maternal inheritance are very ambiguous and no one has established clearly its *raison d'être* as a type of heredity. Recently Morgan (1919) has given a definition as follows:

"'True' maternal inheritance relates to peculiarities of the egg or larva that are due to materials already present in the egg-cytoplasm when the egg is laid."

I cannot agree with him when he establishes, without tracing its causes, a special type of heredity based upon a peculiar phenomenon concerning only the characters of the egg or larva,—that is, the characters of earlier stages of development. Tanaka (1919) studied the inheritance of the egg color of the silk-worm and stated the characteristics of maternal inheritance as follows:

"Segregation is found among the batches,—that is, there are two kinds of mother moths, one of which lays only the dominant-colored eggs and the other lays only the recessive-colored ones. In other words, dominant- and recessive-colored eggs do not mix in a batch."

But the author of the present paper has been able by the following experiments to show this proposition to be false.

Now the most typical instance of maternal inheritance heretofore known is the brown or reddish-brown color of the silk-worm eggs which was first studied by Toyama. But his study consisted chiefly in the selection of the brown-colored race and was lacking in the detailed crossing experiments. Tanaka (1919), basing his conclusions on Toyama's study of his crossing experiments, came to the wrong conclusion, as quoted above.

I could not help doubting the existence of maternal inheritance as a type of heredity; and to clear up this question I have studied, since 1918, crossing experiments on the brown-colored eggs of the silk-worm. I have been able to show that, if we suppose a time is needed for every unit factor to manifest its own action, i.e., "time of action," we can clearly understand the so-called maternal inheritance without any peculiar assumption. I am firmly convinced that it is not irrational to suppose that "time of action" is required for everything, and that such assumption does not conflict with physical nor chemical principles. The following series of experiments will throw some light upon this matter.

Before giving details of my investigations, I wish to express my heartfelt thanks to Prof. Dr. Chiyomatsu Ishikawa, Prof. Dr. E. G. Conklin.
and Prof. Dr. G. H. Shull, for their valuable advice and their kindness in revising the manuscript.

MATERIALS, METHODS AND REMARKS

The brown-colored race here used was first selected by Toyama from a Japanese divoltine white race and since 1916 has bred true for 12 generations to its brown-colored character of the eggs laid.

As the material of the normal race, which has slate-colored eggs, I adopted a Japanese divoltine white race called "Yamatonishiki" which bred true to its normal-colored character of the eggs for 16 generations.

As Toyama mentioned, the color of the shell and yolk of both variants are the same and we must attribute the chief cause of those characteristics to the pigments in the serosa, a product of the combination of both parental gametes.

The artificial method of hatching and method of breeding I adopted are quite the same as those mentioned in my previous paper (Uda 1919), so there will be no need of repeating them. But I must mention here the reason why I have adopted the divoltine races as material for the investigation, in spite of the disadvantage that the color of their non-hibernating eggs is yellowish white, since no pigments are produced in the serosa, and it is thus impossible to detect the zygotic constitution with respect to the egg color. Notwithstanding this difficulty, the divoltine races are satisfactory for such studies, because, as has recently been made known from Watanabe’s (1918, 1919) experiments, even the divoltine races may be made univoltine by raising the incubating temperature to 30°C. It is quite advantageous therefore to use them for the experiment, since we can on the one hand study the egg color in each generation, and on the other hand, we can raise two generations in a year without any artificial method of hatching.

For the sake of convenience I use the following abbreviations:

“Brown” refers to brown-colored eggs, and in some cases also to the moth which lays brown-colored eggs.

“Normal” refers to normal or slate-colored eggs, and in some cases also to the moth which lays normal-colored eggs.

“Mixed” refers to the mixed batch of brown and normal eggs.

CROSSES BETWEEN BROWN ♀ AND NORMAL ♂

F1 generation

All were brown throughout all the batches, and I was unable to detect any difference between the pure brown parent and F1 hybrids, in the intensity of the brown color of the eggs.
The F₂ generation produced by the F₁ hybrids above described were found to contain normal and brown in the ratio shown in line 1 of table 1; but these brown are a little different from those of the F₁ hybrids, i.e., they are darker than the pure brown. In other words, they apparently assume an intermediate color between slate and brown. On the contrary, we cannot detect any difference between the pure normal and the F₂ hybrids in the intensity of the normal color of their eggs.

Thus, contrary to TANAKA (1919), it will be seen that in F₂ there are found both normal and brown in all the batches exactly in the ratio

\[
\begin{array}{|c|c|c|c|c|c|c|c|}
\hline
\text{NUMBER OF TABLE} & \text{NUMBER OF HATCHES} & \text{NORMAL} & \text{BROWN} & \text{TOTALS} & \text{RATIOS} & \text{PROBABLE ERROR (P.E.)} & \text{DEVIATION} \\
\hline
1 & 166 & 73,358 & 24,431 & 97,789 & 3.0007:0.9993 & ±0.0007 & ±0.0037 \\
2 & 63 & 24,963 & 8,554 & 33,517 & 2.9791:1.0209 & ±0.0209 & ±0.0064 \\
3 & 11 & 3,969 & 1,354 & 5,323 & 2.9825:1.0175 & ±0.0175 & ±0.0160 \\
4 & 22 & 6,545 & 6,734 & 13,579 & 2.9624:1.0076 & ±0.0163 & ±0.0116 \\
5 & 267 & 114,070 & 38,409 & 152,479 & 2.9924:1.0076 & ±0.0076 & ±0.0030 \\
6 & 43 & 14,828 & 5,111 & 19,939 & 2.9747:1.0253 & ±0.0253 & ±0.0083 \\
7 & 3 & 757 & 249 & 1,006 & 3.0100:0.9900 & ±0.0100 & ±0.0368 \\
8 & 9 & 3,593 & 1,194 & 4,787 & 3.0023:0.9977 & ±0.0023 & ±0.0169 \\
9 & 24 & 6,610 & 6,853 & 13,463 & 3.0032:0.9968 & ±0.0031 & ±0.0116 \\
10 & 24 & 8,950 & 3,090 & 12,040 & 2.9734:1.0266 & ±0.0266 & ±0.0106 \\
11 & 23 & 5,658 & 5,633 & 11,291 & 2.9044:1.9956 & ±0.0044 & ±0.0127 \\
12 & 11 & 4,766 & 1,614 & 6,380 & 2.9881:1.0119 & ±0.0119 & ±0.0146 \\
13 & 12 & 3,328 & 3,376 & 6,704 & 1.9587:2.0143 & ±0.0143 & ±0.0165 \\
14 & 2 & 556 & 531 & 1,087 & 2.8460:1.9540 & ±0.0460 & ±0.0409 \\
15 & 73 & 18,362 & 18,908 & 37,270 & 1.9707:2.0293 & ±0.0293 & ±0.0070 \\
16 & 4 & 1,602 & 553 & 2,155 & 2.9735:1.0265 & ±0.0265 & ±0.0252 \\
17 & 16 & 4,329 & 4,551 & 8,881 & 1.9498:2.0502 & ±0.0502 & ±0.0143 \\
18 & 96 & 37,915 & 12,881 & 50,796 & 2.9857:1.0143 & ±0.0413 & ±0.0052 \\
19 & 36 & 13,155 & 4,449 & 17,604 & 2.9891:1.0109 & ±0.0109 & ±0.0038 \\
20 & 57 & 24,642 & 8,222 & 32,864 & 2.9933:1.0007 & ±0.0007 & ±0.0064 \\
21 & 7 & 1,829 & 1,813 & 3,642 & 2.0088:1.9912 & ±0.0088 & ±0.0224 \\
22 & 21 & 8,468 & 2,972 & 11,435 & 2.9725:1.0275 & ±0.0275 & ±0.0109 \\
23 & 19 & 5,202 & 5,351 & 10,553 & 1.9718:2.0282 & ±0.0282 & ±0.0131 \\
24 & 4 & 1,420 & 488 & 1,908 & 2.9769:1.0231 & ±0.0231 & ±0.0267 \\
25 & 5 & 1,388 & 1,427 & 2,816 & 1.9723:2.0277 & ±0.0277 & ±0.0254 \\
26 & 3 & 943 & 320 & 1,263 & 2.9865:1.0135 & ±0.0135 & ±0.0329 \\
27 & 6 & 1,999 & 682 & 2,681 & 2.9825:1.0175 & ±0.0175 & ±0.0226 \\
28 & 2 & 562 & 509 & 1,071 & 2.0990:1.9010 & ±0.0990 & ±0.0412 \\
\hline
\end{array}
\]
3 : 1. Consequently, it is shown to be a mistake that in F₂ we have only the dominant type,—which has hitherto been regarded as the characteristic of maternal inheritance.

It is seen throughout all of my experiments that one moth lays only normal eggs, another lays only brown eggs, a third lays normal and brown eggs mixed. The normal eggs of the first and the third cases are quite the same as the pure normal, and the brown eggs of the second case are quite the same as the pure brown. But the brown eggs of the third case are always darker than the pure brown and appear intermediate between the normal and the brown as above mentioned. For the sake of convenience I have named them brown in the tables.

\( F₃ \) generation

It was found that brown in the previous generation (F₂) produced brown offspring without a single exception.

Some of the normal in F₂ produced exclusively normal offspring and the others were found to segregate in the ratio, 3 normal : 1 brown, as summarized in line 2 of table 1.

\( F₄ \) generation

It was found that brown in the previous generation (F₃),—even those in the mixed batches,—produced brown offspring without a single exception.

Normal from pure-bred in the previous generation produced only normal offspring, i.e., they bred true to normal. But normal from the mixed batches were found to behave as those of F₃; namely, some of them produced exclusively normal offspring while the others segregated in the ratio 3 normal : 1 brown. (See line 3 of table 1.)

Back-crosses

I back-crossed the cross-bred form with both of the pure parent breeds, and found F₁ × normal and its reciprocal produced normal only. In the case of F₁ × brown a segregation occurred in the ratio 1 normal : 1 brown as line 4 of table 1 shows, but its reciprocal, i.e., brown \( φ \times F₁ \sigma \), produced exclusively brown offspring.

The above-mentioned series of experiments are shown briefly and clearly in the diagram on the opposite page. The Arabic numeral in parenthesis at the right of the “Mixed” in these diagrams denotes the number of table which shows the segregating ratio in that mixed batch. To save space and expense the tables of original data have been merely summarized in table 1 accompanying this paper.
CROSSES BETWEEN NORMAL $\varnothing$ AND BROWN $\sigma$

The reciprocal crosses yielded results practically the same as those above-mentioned, excepting that in the $F_1$ generation I obtained exclusively normal-colored eggs in all batches, and that some of the normal

<table>
<thead>
<tr>
<th>Brown $\varnothing \times$ Normal $\sigma$</th>
<th>$F_1$</th>
</tr>
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<tbody>
<tr>
<td>Brown</td>
<td>$F_1$</td>
</tr>
<tr>
<td>Mixed (1)</td>
<td></td>
</tr>
</tbody>
</table>

$F_2$

<table>
<thead>
<tr>
<th>Normal 3 : 1</th>
<th>Brown 1 : 1</th>
</tr>
</thead>
<tbody>
<tr>
<td>Normal</td>
<td>Mixed (2)</td>
</tr>
<tr>
<td>Normal</td>
<td>Brown</td>
</tr>
</tbody>
</table>

$F_3$

<table>
<thead>
<tr>
<th>Normal 3 : 1</th>
<th>Brown 1 : 1</th>
</tr>
</thead>
<tbody>
<tr>
<td>Normal</td>
<td>Mixed (3)</td>
</tr>
<tr>
<td>Normal</td>
<td>Brown</td>
</tr>
<tr>
<td>Brown</td>
<td>$F_4$</td>
</tr>
</tbody>
</table>

Back-crosses

<table>
<thead>
<tr>
<th>Brown $\varnothing \times F_1\sigma$</th>
<th>Normal $\varnothing \times F_1\sigma$</th>
<th>$F_1\varnothing \times$ Brown $\sigma$</th>
<th>$F_1\varnothing \times$ Normal $\sigma$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brown</td>
<td>Normal</td>
<td>Normal</td>
<td>Normal</td>
</tr>
<tr>
<td>Normal</td>
<td>Mixed (4)</td>
<td>Mixed (4)</td>
<td>Mixed (4)</td>
</tr>
<tr>
<td>Normal</td>
<td>Brown</td>
<td>Normal</td>
<td>Brown</td>
</tr>
</tbody>
</table>

from pure-bred in $F_3$ segregated in the ratio 3 normal : 1 brown; the whole of which results are better shown briefly in tabular form on page 328.

DISCUSSION AND CONCLUSIONS

We can consider from the series of experiments above-mentioned that normal and brown are alleomorphic with each other, the former being dominant over the latter. But the following two points are peculiar to these experiments and conflict with the Mendelian expectation:

1. In the $F_1$ generation the eggs manifest in color entirely the maternal character, whether it was dominant or recessive.

2. The back-cross of brown $\varnothing \times F_1\sigma$ produced brown only, and did not segregate in the usual ratio, i.e., 1 : 1.

In order to make this point clearer I investigated the color of eggs produced by crossing $F_1$, $F_2$, $F_3$ and back-cross, in succession, with the
pure recessive breed, brown. Besides these, I studied the next generation of the back-crosses which revealed their zygotic constitution. These results will be clear from the diagram on page 330. The arrow indicates the direction of the cross, in each case pointing from the male to the female of the given cross.

\[
\begin{align*}
\text{Normal } \varnothing \times \text{Brown } \sigma^p & \rightarrow \text{F}_1 \\
\text{Normal} & \rightarrow \text{F}_1 \\
\text{Mixed (5)} & \rightarrow \text{F}_4 \\
\end{align*}
\]

The general hereditary phenomena here which apparently conflict with Mendelism may be summarized as follows:

1. When we use a female of one of the pure breeds, brown or normal, as the mother moth, the eggs laid are always the same in color as those of the pure breed to which the mother belongs, no matter whether the egg characters of the paternal breed be dominant or recessive, and also whether his zygotic constitution with respect to egg color be homozygous or heterozygous. In other words, the condition of the blood with reference to the character in question is due to the condition of the mother regardless of the condition of her mate.

2. Even from crosses between moths developed only from the brown—the recessive—eggs, we sometimes obtain the mixed batches. And the ratio of normal to brown is 3 : 1 or 1 : 1.
These conditions cannot, indeed, be found in the common types of inheritance, but it would be hasty to conclude immediately from these facts that a new type of heredity is involved. The segregating ratio of 3:1 in F₂, F₃, and F₄, and the ratio of 1:1 in the back-crosses can be explained only by Mendel's law of segregation, assuming that normal and brown are allelomorphic to each other. And the fact that the brown eggs in the mixed batches were found, by crossing inter se, to breed true to their type, is also an indication that brown is a recessive allelomorph, in accord with Mendelism. Then, what leads to the peculiarities noted above? The following in my opinion will solve the riddle of such peculiarities and will perhaps be acknowledged to be a general phenomenon of heredity.

It will be clear from the above experiments that, while the eggs homozygous for the normal factor always give rise to slate-colored eggs, the eggs heterozygous for the same factor sometimes manifest the recessive color, brown. Such an anomalous heterozygous type is limited to the cross-bred form between the pure brown ♀ and the pure normal ♂, the reciprocals, on the contrary, being always of normal color. But, as both of these crosses are quite the same in the segregating phenomena in the subsequent generations and in the back-crosses, the zygotic constitution is clearly the same in both. In other words, while the eggs differ in color, the moths developed from them lay quite the same-colored eggs.

Next, while the F₁ brown eggs are similar in color to those of the pure brown, the F₁ female moth arising from the brown eggs gives, when fertilized by a pure normal male, the ratio of 3 normal-colored to 1 brown egg; the female from the pure brown eggs, on the contrary, gives only brown eggs with the male moth of the pure normal. Consequently we can see that the pure brown and the heterozygous brown are similar to each other in the phenotypic color of eggs from which they develop, but differ from each other genotypically, as shown by the color of the eggs they lay.

Thus, we know that the character of the moth, with respect to the color of the eggs it lays, coincides with the expectation from its zygotic constitution and thus falls in perfectly with Mendelism, but it is not always so with the color of eggs from which the moth developed. In other words, the factors for the brown and the normal manifest their own effects only in the later stages of development. And the cause of the anomaly in the early stages of development, i.e., in the egg stage, is owing to the fact that the factor for the egg color in the male gamete, being
UDA, Hajime, "On Maternal Inheritance"

Genetics 8: 330 Jl 1923
LEGENDS FOR PLATE 1

- Pure brown
- Pure normal
- Brown
- Normal
- Mixed

Produced by crossing. (Ratios in the mixed are given in the circles and the summary of the data will be easily found in table 1 by the Arabic numeral above)

- Brown eggs
- Normal eggs

In the mixed batches

The arrows indicate the direction of the crosses, in each case pointing from the male to the female of the given cross.
introduced into the egg at the moment of the fertilization, has not time enough to manifest its own effect even if it be dominant.

In almost all the hereditary phenomena hitherto known, both in animals and plants, the characters which are repeated generation after generation according to the Mendelian formula relate to the later stages of development. And the cases which appear to show no male effect, relate to the characters in the early stages of development, i.e., chiefly the characters of the egg or the larva in animals and those of the seed or the cotyledon in plants.

Such being the case, I am firmly convinced that we can generalize the above interpretation; that is, a certain time is generally required for every unit factor to manifest its own action, i.e., "the time of action."

Although such an assumption has never been clearly stated, it has been sometimes vaguely considered by a number of previous authors.

Driesch (1903), Boveri (1903) and Conklin (1915) have found that in the crosses of the sea urchins the male effect is first noticed when the larval skeleton is formed. In the crossing experiments with White and Black Leghorns, Davenport (1906) states that white becomes perfectly dominant over black in the grown-up fowls, while the young heterozygous chicks show some dark pigment. Lynch's (1919) study has clearly shown that the effect of a lethal factor in Drosophila is manifested after the larval stages.

Morgan (1914) used the term "deferred nuclear influence," explaining the results of Conklin's experiments on Cynthia and those of Miss Pinney's (1918) observations on the many crosses between different species of fishes, both of which are cases where no paternal influence is manifested during the early embryonal stages. Would it not be more reasonable in these cases to think that these are rather the natural results of a certain "time of action" required for the manifestation of the paternal factors than to vaguely ascribe them as the results of the "delay" of the nuclear influence?

Now, the results of all our experiments will be clearly accounted for upon such an assumption; and the two points mentioned which apparently conflict with Mendelism will also be cleared up, for it will be at the later stage of development, i.e., the imago stage; that the factors for normal and brown will manifest their effects upon the egg cytoplasm.

2 The full development of the capacity to produce brown or slate-colored eggs may be attained at some other stage between the egg and the imago, but there is no way to determine this exactly, because the factors in question both relate only to the color of the eggs.
Furthermore, the fact that the brown eggs in the mixed batches are
darker than the pure brown and apparently assume an intermediate color
between normal and brown may be easily understood if we consider that
the cytoplasm of the egg was already affected by the action of the egg
nucleus of the normal.

On the whole, we are, I believe, justified in denying the existence of
"maternal inheritance" as a special type of heredity. And I cannot help
admiring the keen observation of Bateson (1913, p. 264) who stated
that:

"Seeds are in botany what larvae are in zoölogy, and no example is yet
known in which the maternal impress extends beyond the seed stage."

Next we shall briefly touch on the hereditary phenomena of voltinism
in the silk-worm, which has hitherto been known as the other striking
case of so-called maternal inheritance.

As known for a long time the voltinism is very easily changed by the
environment, especially by the incubating temperature. My extensive
observations prove that there are often found two types differing in their
voltinism in a single batch. So it is very doubtful, I think, that differing
voltinism may be due to different allelomorphic factors and that it is
transmitted according to maternal inheritance. But, even if it be a fact
that each type of voltinism has its own factor, the crossing experiments
hitherto made on voltinism may be easily understood by the assumption
of "time of action." And in this case we can also see that the "time of
action" may be varied by the environment. This explanation will surely
be more defensible than the establishment of a peculiar type of inheri-
tance.

In connection with my hypothesis, I shall add a few words in conclu-
sion on the theory Löeb (1916, 1917) has recently published, which may
be summarized as follows (Löeb 1916, p. iv):

"The egg (or rather its cytoplasm) is the future embryo upon which
the Mendelian factors in the chromosomes can impress only individual
characteristics."

Though such an idea was also maintained by Boveri (1903) and Conk-
lin (1915), it must be admitted that the cytoplasm is in many cases not
able to manifest its action without the presence of a nucleus. A number
of facts which show the action of the nucleus in regeneration, assimilation
and in many other physiological phenomena of cells, clearly reveal the
importance of the nucleus. Is it not then more reasonable to think that
the cytoplasmic differentiation observed in many eggs before the entrance
of a spermatozoön is, after all, produced by the action of the egg-nucleus?
Can we not also consider that the phylogenetic stages characteristic of the phylum, class, order, family, genus and species, which appear at the earlier stages of development, are determined by the egg-nucleus, while the characters which become manifested at the later stages are the result of the action of both the paternal and maternal nuclei?

Thus I think that the essential substance which brings about differentiation of the cells in development, either at the earlier or later stages, is derived only from the nucleus, and manifests itself in the phenotype after a suitable "time of action."

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