# MATERNAL INHERITANCE AND MENDELISM.

## (FIRST CONTRIBUTION.)

BY K. TOYAMA.

*(Zoological Institute, College of Agriculture,
Tokyo Imperial University.)*

(With Plate XX.)

## CONTENTS.

In my first contribution to the study of hybridology of insects published in 1906 (10), it was shown that certain colour-characteristics of the egg of the Siamese silk-worm follow Mendel's law of heredity. Thanks to the kind suggestion of Prof. Bateson of London, we again undertook a similar series of experiments with various breeds of the silk-worm. Some of the results obtained during the last five years which seem to us to be not without interest to students of heredity will be described in the following pages.

## I. Certain Egg-characteristics of the Silk-worm.

Before going further, we shall first enumerate certain egg-characteristics which are the subject of the present paper.

*Colour.* The ordinary colour of the Japanese silk-worm eggs is a light greenish white when newly laid. With the formation of the blastoderm, the egg gradually assumes a brownish tint which at last turns into brownish slate shaded with some light pink or purple (Figs. 1, 3, 11). There may be found, however, many variants, some rather deeper, some lighter, and some with different shades. Now and again it happens that some eggs characterized by extraordinary variations of colour are found among normal ones, such as reddish brown (Fig. 2), whitish grey (Fig. 4), blue (Fig. 5), greenish slate (Figs. 6, 10, 12), crimson (Fig. 7), orange, greenish white and many others. Most of the eggs deposited by Japanese green breeds are more or less shaded with green. When newly laid, they are yellowish green and are much deeper in colour than those deposited by ordinary white breeds. Most of the Chinese or European breeds come in a similar category.

*Shape.* The normal shape of the silk-worm eggs is oval, slightly pointed at one end, where a micropyle is situated (see Figs. 1—7). It is a little flattened and its surface is convex when newly laid but after a few days it becomes depressed in the middle, thus producing the characteristic form which is familiar to us. In this characteristic, as in the case of the colour, we observed many variants, some of them being quite extraordinary, for instance such as spindle-shaped eggs (Fig. 13) or other irregularly shaped ones, etc. which will be discussed minutely afterwards.

## II. ORIGIN OF THE CHARACTERISTICS ABOVE ENUMERATED.

The egg consists of the shell, vitelline membrane, serosa and yolk, and each of them is coloured or shaded with certain tints or pigments, except the vitelline membrane which mostly remains colourless in nearly all breeds.

The shell is usually translucent and is slightly tinted with certain colours. In Japanese breeds it is usually white or slightly shaded with brown, flesh-colour, green, or dirty-white or some other tint. That of some Japanese green, Chinese or European breeds is coloured yellowish green or pale green. The colour of the eggs is consequently more or less influenced by the colour of the shell. As to the shape, it is chiefly determined by the characteristics of the shell, which is derived from the epithelium of the oviduct.

The cause of the egg-colour is, however, mostly due to the pigments deposited in the serosa which are seen through the shell.

The colour of the yolk plays a certain part in the production of the egg-colour only in the case where the formation of the dark pigments in the serosa does not take place, i.e. in newly laid eggs or those oviposited by the spring brood of di-, tetra-, or multivoltine breeds.

The object of the present series of experiments is to know what influence, if any, these variants have upon the trend of heredity in their offspring. As to the origin of these variants we are quite ignorant whether they are produced by mutation or by hybrid mutation or some other causes which are yet unknown to us. We only know that they are seldom found among eggs laid by the normal-egged breeds generally reared in Japan.

## III. RESULTS OF LINE BREEDING OF CERTAIN VARIANTS.

### SERIES 1. *The Reddish-Brown Eggs* (Figs. 1, 2).

In the winter of 1907, Mr K. Ishivata, one of the famous silk-worm breeders in the district of Fukushima in Japan, kindly offered me some normal (Fig. 1) and brown (Fig. 2) egg batches[1] laid by a divoltine white breed called "Shinkawachi," and said that both of them, even when inbred, gave the antagonistic characteristics in the offspring and thus it was very difficult to establish them as constant forms.

---

[1] All through this paper, the word "batch" represents the total eggs laid by a moth.

As the colour of the shell and yolk of both variants was the same, we must attribute the chief cause of those characteristics to the pigment of the serosa, a product of the combination of both parental gametes. We started our breeding experiments in the spring of 1908.

### *The First Generation.* 1908. *Spring.*

We reared two batches of eggs from each variant. The normal series gave 72 matings or batches and the brown series 87, all of which were divoltine white in colour and we were unable to distinguish which were normal and which were brown. This characteristic, producing uncoloured eggs, is one of the normal characteristics of di-, tetra- or multivoltine breeds in Japan. In these breeds, the egg laid by the spring brood generally produces no dark pigments in the serosa and consequently it remains whitish until the embryo is completely developed. Tropical multivoltine breeds, such as Siamese white or yellow which produce 8 or 9 broods in a year, never produce any dark pigment in the serosa, the colour of the egg therefore being determined by that of the yolk and the shell. Sometimes it happens that certain eggs of the spring brood of di- or multivoltine breeds turn into the ordinary dark slate-colour, in which case most or all of them become univoltine in character and do not hatch until next spring comes. On the contrary, all the eggs laid by the summer or autumn broods of divoltine or other multivoltine breeds deposit normal dark pigments in the serosa, thus giving various colours characteristic to the respective breeds.

### *The Second Generation.* 1908. *Summer.*

Summer broods derived from the whitish eggs of the spring broods from normal and brown series yielded the antagonistic characteristics as shewn below.

1. *Eggs laid by the Summer Broods of the Brown Series.*

| Number of Matings | Normal Batches | Brown Batches | Mixed Batches | Totals |
|---|---|---|---|---|
| No. 15. 11 | 0 | 11 | 7 | 18 |
| No. 19. 12 | 10 | 19 | 29 | 58 |
| Totals ... | 10 | 30 | 36 | 76 |

2. *Eggs laid by the Summer Broods of the Normal Series*

| Number of Matings | Normal Batches | Brown Batches | Mixed Batches | Totals |
|---|---|---|---|---|
| No. 18. 12 | 4 | 4 | 4 | 12 |
| ,, 14 | 2 | 5 | 12 | 19 |
| ,, 9 | 1 | 1 | 2 | 4 |
| No. 4. 1 | 3 | 0 | 0 | 3 |
| Totals ... | 10 | 10 | 18 | 38 |

In the former or brown series, 10 were normal, 30 brown and 7 a mixture of both normal and brown eggs in the same batch, and therefore in this series the normal colour-characteristics remained as recessive. The reverse is the case in the normal series, which produced 10 normals, 10 browns and 18 mixtures, that is to say, the brown is recessive in this series.

### *The Third Generation of Normal Series.*

In the autumn of 1908, three normal-coloured batches derived from summer broods of the normal series were reared. They gave 58 batches, among which there were 28 normals, 14 browns and 16 mixed batches, that is to say, they again produced the antagonistic character.

The third generation of the brown series or brown batches laid by the summer brood in 1908 were reared in the spring of 1909. They gave, as is usual, all divoltine whitish eggs.

### *The Fourth and Further Generations.*

The fourth generation of the normal series derived from normal eggs laid by the normal series in the autumn of 1908 gave divoltine white eggs, a few being univoltine normals and browns. The same is the case in the fifth generation which was reared in the spring of 1910. In the spring of 1911, i.e. in the sixth generation, we noticed for the first time that this series of normal characteristic inbreeding gave all normal batches with a few divoltine white batches, which may be considered to be normal coloured in character, that is to say, they breed true to parents.

On the contrary, the fourth generation of the brown series or summer brood of 1909 yielded, without exception, brown eggs. Since then we have reared them through two generations without producing any antagonistic characteristic. Hence it may be said that this brown form is established as a constant form.

Respective figures obtained by this series of experiments are given in Table I.

## TABLE I.

*Brown-egged Series.*

| Number of Matings | Number of Univoltine batches produced | | | Divoltine batches | Total batches |
|---|---|---|---|---|---|
| | Normal | Brown | Mixture | White | |
| 1908 (Spring brood). First generation. | | | | | |
| 15* | 0 | 0 | 0 | 26 | 26 |
| 19* | 0 | 0 | 0 | 61 | 61 |
| Totals ... | 0 | 0 | 0 | 87 | 87 |
| 1908 (Summer brood). Second generation. | | | | | |
| 19. 12* | 10 | 19 | 29 | 0 | 58 |
| 15. 11 | 0 | 11 | 7 | 0 | 18 |
| Totals ... | 10 | 30 | 36 | 0 | 76 |
| 1909 (Spring brood). Third generation. | | | | | |
| 19. 12. 9 | 0 | 0 | 0 | 32 | 32 |
| ,, 12* | 0 | 0 | 0 | 35 | 35 |
| ,, 25 | 0 | 0 | 0 | all white | all white |
| Totals ... | 0 | 0 | 0 | 67 | 67 |
| 1909 (Summer brood). Fourth generation. | | | | | |
| 19. 12. 12. 1* | 0 | 3 | 0 | 0 | 3 |
| ,, 2 | 0 | 2 | 0 | 0 | 2 |
| ,, 3 | 0 | 18 | 0 | 0 | 18 |
| ,, 4 | 0 | 8 | 0 | 0 | 8 |
| ,, 5* | 0 | 33 | 0 | 0 | 33 |
| Totals ... | 0 | 64 | 0 | 0 | 64 |
| 1910 (Spring brood). Fifth generation. | | | | | |
| 19. 12. 12. 1. 2* | 0 | 0 | 0 | 26 | 26 |
| ,, 5. 8 | 0 | 0 | 0 | 18 | 18 |
| Totals ... | 0 | 0 | 0 | 44 | 44 |
| 1910 (Summer brood). Sixth generation. | | | | | |
| 19. 12. 12. 1. 2. 1 | 0 | 107 | 0 | 0 | 107 |
| ,, ,, 2 | 0 | 116 | 0 | 0 | 116 |
| ,, ,, 3 | 0 | 86 | 0 | 0 | 86 |
| ,, ,, 4 | 0 | 108 | 0 | 0 | 108 |
| ,, ,, 5 | 0 | 105 | 0 | 0 | 105 |
| ,, ,, 6 | 0 | 50 | 0 | 0 | 50 |
| Totals ... | 0 | 572 | 0 | 0 | 572 |

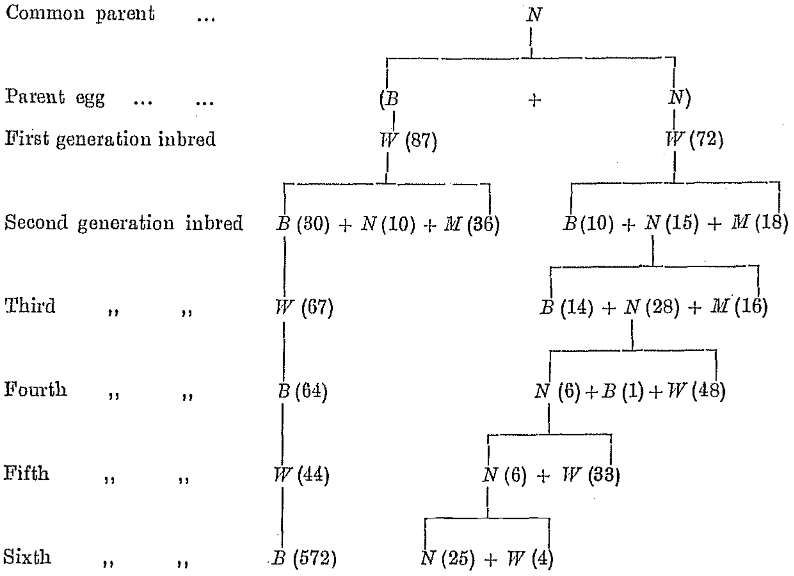
*Normal-egged Series.*

| Number of Matings | Number of Univoltine batches produced | | | Divoltine batches | Total batches |
|---|---|---|---|---|---|
| | Normal | Brown | Mixture | White | |
| 4* | 0 | 0 | 0 | 30 | 30 |
| 18* | 0 | 0 | 0 | 42 | 42 |
| Totals ... | 0 | 0 | 0 | 72 | 72 |
| 1908 (Summer brood). Second generation. | | | | | |
| 4. 1 | 3 | 0 | 0 | 0 | 3 |
| 18. 9 | 1 | 1 | 2 | 0 | 4 |
| 18. 12* | 6 | 4 | 4 | 0 | 14 |
| 18. 14 | 5 | 5 | 12 | 0 | 22 |
| Totals ... | 15 | 10 | 18 | 0 | 43 |
| 1908 (Autumn brood). Third generation. | | | | | |
| 18. 12. 5* | 0 | 9 | 4 | 0 | 13 |
| ,, 9* | 0 | 5 | 8 | 0 | 13 |
| ,, 20* | 28 | 0 | 4 | 0 | 32 |
| Totals ... | 28 | 14 | 16 | 0 | 58 |
| 1909 (Spring brood). Fourth generation. | | | | | |
| 18. 12. 5. 17 | 4 | 0 | 0 | 18 | 22 |
| ,, 9. 25 | 0 | 1 | 0 | 10 | 11 |
| ,, 20. 18* | 2 | 0 | 0 | 20 | 22 |
| Totals ... | 6 | 1 | 0 | 48 | 55 |
| 1910 (Spring brood). Fifth generation. | | | | | |
| 18. 12. 20. 18. 19* | 6 | 0 | 0 | 20 | 26 |
| 18. 12. 20. 18. 26 | 0 | 0 | 0 | 13 | 13 |
| Totals ... | 6 | 0 | 0 | 33 | 39 |
| 1911 (Spring brood). Sixth generation. | | | | | |
| 18. 12. 20. 18. 19 (5 matings) | 25 | 0 | 0 | 4 | 29 |

* Eggs laid by the mating marked with an asterisk are used as the parents of the next generation.

To avoid complication, we give below a graphical summary:

$B$ = brown egg batch; $N$ = normal-coloured; $W$ = divoltine white; $M$ = mixture of brown and normal-coloured eggs in a batch.



From the results above obtained, we observe that complete segregation between the two characteristics, the brown and the normal-coloured, took place and that each may be established as a constant form from their common stock. It is much easier, however, to establish the brown as a constant form than the normal.

Moreover, we learn that during two or three generations both characteristics even when inbred produce antagonistic characteristics in their offspring, a fact which apparently seems to run counter to Mendelian principles, but which in reality is in perfect accordance with the principles, as will be seen in "General considerations."

### SERIES 2. *The Blue-egged Variant* (Fig. 5).

The phenomena of inheritance, similar to those above described, were observed in the inbreeding of the blue variant. This form is a sport from a divoltine normal-egged breed called "Kuni-nishiki," and is characterized by the special blue colour of the egg.

In the spring of 1910, only one batch (No. 20) was obtained, through the kindness of Mr S. Saito in Ghifu-Ken. The worms, cocoons, and moths derived from them were all normal in character. They, inbred, gave 30 batches of eggs, of which, 12 batches were divoltine white, and the remaining 18 all normal-coloured, which suggest to us that all the batches in this generation would be all normal-coloured ones.

Three divoltine white batches (Nos. 1*, 3 and 4) which were reared in the summer gave three kinds of eggs, some batches being blue, as in the parental blue, others blue shaded with a brown, which we called "intermediate colour" and the rest normal-coloured batches. There were no batches in which both blue and normal or intermediate forms were found mixed. Respective figures obtained are given below:

| Number of Matings | Number of blue batches produced | Number of intermediate batches | Normal-coloured | Totals |
|---|---|---|---|---|
| 20. 1* | 21 | 54 | 68 | 143 |
| 20. 3 | 12 | 65 | 76 | 153 |
| 20. 4 | 14 | 46 | 60 | 120 |
| Totals | 47 | 165 | 204 | 416 |

Of 416 batches derived from three parent batches, 47 were blue, 204 normal-coloured and the remainder intermediate. In the blue-coloured eggs, we distinguished both light and dark-shaded ones. The former we called "light blue" and the latter "dark blue."

Five blue batches (Nos. 6, 14*, 24*, 25 and 28) laid by the mating No. 20. 1 were reared in the spring of 1911. They oviposited, without any exception, 251 batches of eggs, all of them being divoltine white.

Eight white divoltine batches were reared in the same summer. Both the light and dark blue series yielded again the antagonistic characteristics as shewn below:

| Number of Matings | | Light Blue | Dark Blue | Normal | Totals |
|---|---|---|---|---|---|
| 20. 1 light blue | 14. 3 | 13 | 0 | 8 | 21 |
| | 14. 15 | 21 | 12 | 15 | 48 |
| | 14. 20* | 4 | 4 | 0 | 8 |
| Totals ... | | 38 | 16 | 23 | 77 |
| 20. 1 dark blue | 24. 4 | 0 | 0 | 3 | 3 |
| | 24. 9 | 1 | 0 | 0 | 1 |
| | 24. 14 | 2 | 0 | 2 | 4 |
| | 24. 25 | 0 | 1 | 2 | 3 |
| | 24. 27 | 0 | 0 | 3 | 3 |
| Totals ... ... | | 3 | 1 | 10 | 14 |
| Grand totals ... | | 41 | 17 | 33 | 91 |

Of the eight parent batches, four gave both blue and normal-coloured batches, two all blue batches and the rest only normal-coloured ones, the total number of batches produced by them being 91.

In the spring of 1912, six blue batches (three light and three dark blue) derived from the lineage which produced only blue batches were reared separately as in the former generations. They gave the following egg-batches:

| Number of Matings | Number of Univoltine blue batches | Number of Divoltine white batches | Mixed batches | Total number of batches |
|---|---|---|---|---|
| Dark blue series | | | | |
| No. 20. 1. 14. 20. 2 | 0 | 63 | 0 | 63 |
| ,, ,, 3 | 1 | 18 | 0 | 19 |
| ,, ,, 4* | 22 | 64 | 1 | 87 |
| Light blue series | | | | |
| No. 20. 1. 14. 20. 1* | 5 | 91 | 0 | 96 |
| ,, ,, 8 | 0 | 52 | 0 | 52 |
| ,, ,, 10 | 0 | 18 | 0 | 18 |
| Totals ... | 28 | 306 | 1 | 335 |

Of 335 batches derived from the six blue parent batches, 306 were divoltine white as is usual in the divoltine breed, and 28 were univoltine blue coloured and only one was a mixed batch consisting of both divoltine white and univoltine blue-coloured eggs.

The summer brood derived from four batches of light blue series and four batches of dark blue series gave the following batches:—

*Light Blue Series.*

| Number of parent batch | Number of dark blue batches laid | Number of light blue batches laid | Normal | Totals |
|---|---|---|---|---|
| No. 20. 1. 14. 20. 4. 4 | 29 | 42 | — | 71 |
| ,, ,, 5 | 22 | 36 | — | 58 |
| ,, ,, 19 | 14 | 16 | — | 30 |
| ,, ,, 22 | 6 | 2 | 1 (?) | 9 |
| Totals ... ... | 71 | 96 | 1 (?) | 168 |

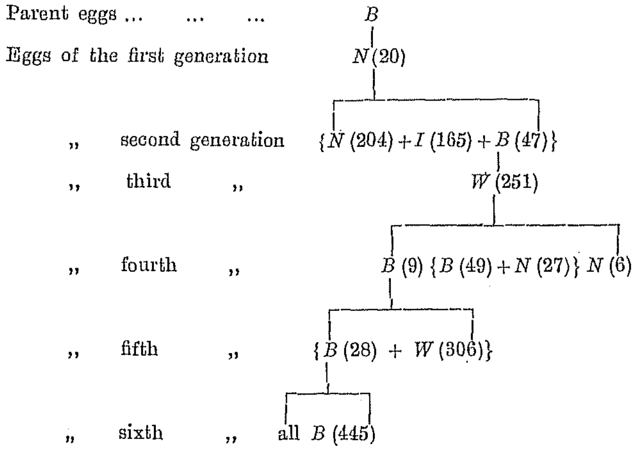
*Dark Blue Series.*

| Number of parent batch | Number of dark blue batches laid | Number of light blue batches laid | Normal | Totals |
|---|---|---|---|---|
| No. 20. 1. 14. 20. 1. 1 | 6 | 33 | — | 39 |
| ,, ,, 12 | 20 | 45 | — | 65 |
| ,, ,, 15 | 25 | 46 | — | 71 |
| ,, ,, 16 | 19 | 49 | — | 68 |
| ,, ,, 25 | 13 | 31 | 2 (?) | 46 |
| Totals ... ... | 83 | 204 | 2 (?) | 289 |

Now we are able to extract the blue-egged characteristic as a constant form. As to the light and dark forms, they seemed to be fluctuations of the same character, blue.

*Résumé:*

$B$ = light and dark blue batches; $I$ = intermediate; $N$ = normal; $W$ = divoltine white; $M$ = mixed batch consisting of divoltine white and univoltine blue-coloured eggs.



### SERIES 3. *The Whitish-Grey egged Variant* (Fig. 4).

This variant from the normal egged breed is characterized by the peculiar structure of the shell. As is well known, the shell of normal breeds is elastic and translucent, its surface being smooth. That of the variant, on the contrary, is rather brittle and opaque, and is milky white in colour, in consequence of which the colour of the serosa can barely be seen through the shell and thus a peculiar whitish grey colour is produced. The surface of the shell is not smooth as in the normal shell, but begins to become irregularly corrugated as soon as the ventral plate is formed. There is no depression in the middle, which is a common characteristic of the egg laid by normal breeds.

In the spring of 1909, we obtained two batches of grey eggs, one being derived from the univoltine white reared in the district of Hyōgŏken, and the other which came from Fŭkŭshimanken is derived from the normal divoltine white, "Aobiki." They were reared separately and each of them gave both normal and grey batches, that is to say, the former deposited one grey and one normal batch (Table III) and the latter 15 normals and 20 greys (Table II); no mixed batches were produced in these cases. (See Tables II and III.)

In the second generation (summer brood of 1909), moths derived from both normal and grey eggs paired *inter se*, yielded again, with no

## TABLE II.

*Pedigree of the Whitish-Grey Variant*, No. 24.

Parent egg ... ... ... All whitish-grey

First generation (Spring of 1909) 15 normals + 20 grey batches

*Normal-egged Series.*

| | Number of Matings | Number of normal batches | Number of grey batches | Total batches |
|---|---|---|---|---|
| Second generation (Summer of 1909) | No. 24. 3 | 4 | 4 | 8 |
| | ,, 6 | 4 | 1 | 5 |
| | ,, 21 | 2 | 0 | 2 |
| | ,, 22 | 3 | 1 | 4 |
| | ,, 24* | 7 | 0 | 7 |
| Totals | ... ... | 20 | 6 | 26 |
| Third generation (Spring of 1910) | 24. *N* 24. 1 | 34 | 0 | 34 |
| | ,, 2* | 41 | 0 | 41 |
| | ,, 2 × 1 | 2 | 0 | 2 |
| | ,, 3 | 21 | 0 | 21 |
| | ,, 3 × 1 | 5 | 0 | 5 |
| | ,, 4 | 22 | 0 | 22 |
| | ,, 4 × 1 | 10 | 0 | 10 |
| | ,, 5 | 23 | 0 | 23 |
| Totals | ... ... | 158 | 0 | 158 |
| Fourth generation (Summer of 1910) | 24. *N* 24. 2. *N* 1* | 142 | 0 | 142 |
| | ,, 2 | 24 | 2 (?) | 26 |
| | ,, 5 | 5 | 0 | 5 |
| | ,, 7 | 71 | 0 | 71 |
| | ,, 8 | 87 | 0 | 87 |
| | ,, 22 | 66 | 0 | 66 |
| | ,, 23 | 3 | 0 | 3 |
| Totals | ... ... | 398 | 2 | 400 |
| Fifth generation | 24. *N* 24. 2. No. 1. (*N* 10, 14, 18, 22, 25) | | | |
| | Mixture of 5 batches | 38 | 0 | 38 |
| | do. No. 12 | 47 | 0 | 47 |
| Totals | ... ... | 85 | 0 | 85 |

*Grey-egged Series.*

| | Number of Matings | Number of normal batches | Number of grey batches | Number of B-grey batches | Mixture of *G* and *BG* ‡ | Total batches |
|---|---|---|---|---|---|---|
| Second generation (Summer of 1909) | 24. *G* 1 | 2 | 1 | 0 | — | 3 |
| | ,, 3 | 2 | 5 | 0 | — | 7 |
| | ,, 4* | 10 | 15 | 0 | — | 25 |
| | ,, 16 | 1 | 2 | 0 | — | 3 |
| | ,, 20 | 10 | 10 | 0 | — | 20 |
| | ,, 16 × 1 | 0 | 1 | 0 | — | 1 |
| | Totals | 25 | 34 | 0 | — | 59 |
| Third generation (Spring of 1910) | 24. *G* 4. 1* | 7 | 13 | 1 | — | 21 |
| | ,, 4 | 18 | 22 | 4 | — | 44 |
| | ,, 25 | 15 | 9 | 0 | — | 24 |
| | ,, 26 | 9 | 5 | 3 | — | 17 |
| | ,, 28 | 18 | 8 | 1 | — | 27 |
| | Totals | 67 | 57 | 9 | — | 133 |
| Fourth generation (Summer of 1910) | 24. *G* 4. *G* 1. *G* 1* | 0 | 7 | 36 | — | 43 |
| | ,, 7 | 11 | 38 | 7 | — | 56 |
| | ,, 8 | 32 | 41 | 24 | — | 97 |
| | ,, 11 | 22 | 47 | 27 | — | 96 |
| | ,, 21 | 9 | 31 | 11 | — | 51 |
| | ,, 28 | 26 | 16 | 0 | — | 42 |
| | Totals | 100 | 173 | 69 | — | 342 |
| Fifth generation | 24. *G* 4. *G* 1. *G* 1. *G* 6 | 0 | 18 | 14 | 1 | 33 |
| | ,, 7 | 0 | 19 | 17 | 0 | 36 |
| | ,, 16 | 0 | 4 | 9 | 0 | 13 |
| | ,, 22 | 0 | 18 | 18 | 0 | 36 |
| | ,, 24 | 2† | 5 | 8 | 6 | 21 |
| | Mixture of 5 batches | 2† | 56 | 40 | 8 | 106 |
| | Totals | 4 | 120 | 106 | 15 | 245 |

* Those matings marked with an asterisk are the parent of next generation.

† Normal eggs found in these matings are not true normal form, the shell being rather thin when compared with that of normals.

‡ *BG* = B-greys.

exception, normal and grey batches. Thus five matings of the normal series from the divoltine breed yielded 20 normals and 6 greys; six matings of the grey series from the same breed similarly gave 25 normals and 35 greys. (See Table II.)

The third generation of the normal series which were reared in the spring of 1910 yielded all normal egged batches which when inbred remained true to parents in subsequent generations: i.e. they became homozygous. This was not the case in the grey series. Five matings of the grey series in the spring of 1910 (third generation) gave 67 normals and 67 greys, in addition nine batches of a new variant which we have as yet never observed in our breeds.

This new variant is characterized by the thin translucent shell which has fine wrinkles over it and by a shape a little longer than normal eggs. There is no depression in the middle. We shall call this kind of variant "B-grey," since it more resembles the grey form than the normal ones. In the case of moths laying B-grey eggs the actual number of eggs laid is always much smaller than the number laid by moths laying eggs of normal colour, even though the parents belong to the same batch. The worms which came out from the *BG* are so weak that we can hardly get any moth and consequently we are unable to trace the order of its inheritance.

Of six grey matings of the grey series which were reared in the summer of the same year (fourth generation), five again yielded 100 normals, 173 greys and 69 B-grey batches. One mating, on the contrary, gave no normal eggs except the grey and B-grey, the respective figures obtained being 7 and 36.

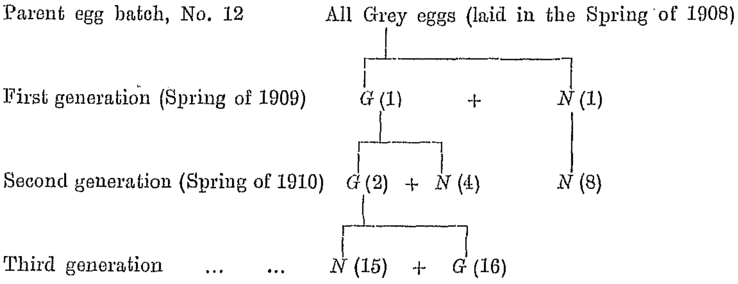
The fifth generation derived from the grey mating, which in the last generation yielded no normal batches, gave 245 batches in which 120 were grey, 106 B-greys, 5 mixture of grey and B-grey, and 4 which look like an intermediate form between normals and B-greys.

Details of figures obtained in each mating of each generation will be seen in Tables II and III.

From the results above quoted, we are able to say that, as in the case of first and second series, both normal and grey characteristics segregate from one another, and it is easier to get rid of the antagonistic characters in the normal than in the grey. The appearance of the new form which may probably be due to the new combination of allelomorphs renders the phenomena of inheritance rather complicated. Hence if we consider the *G* and *BG* forms as a single form, the results come in the same category, which was mentioned in the former series of experiments.

### TABLE III.

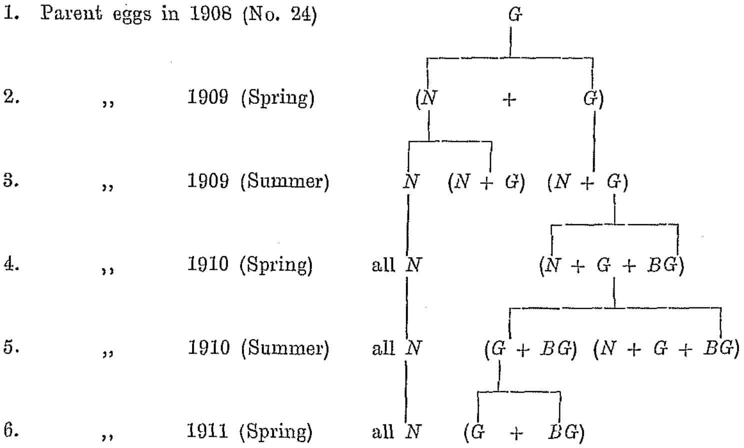
*Pedigree of Whitish-grey Eggs derived from the Normal Univoltine White.*



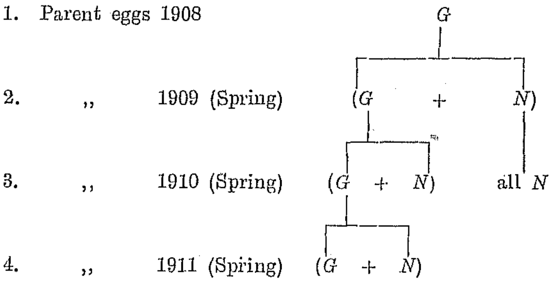
These figures will be again summarized graphically as below:

A.

*G* = Grey egg batch, *N* = Normal, *BG* = B-Grey.



B.



### SERIES 4. *The Spindle-shaped Eggs* (Fig. 13).

In the early spring of 1909, we obtained half a batch of the eggs laid by a Japanese normal univoltine white. The egg is long and spindle-shaped, and is slightly pointed at both ends. There is no depression in the middle which is a characteristic common to normal silk-worm eggs.

The first generation which was reared in the spring of 1909 gave eggs which were quite normal in shape and other characteristics. The egg-batches obtained were only six in number.

The second generation derived from the normal eggs yielded moths which paired *inter se* deposited 46 batches of eggs in which we found both normal and spindle-shaped ones, the number found in each mating being as follows:

| Number of Matings | Number of normal batches | Number of spindle-shaped batches | Totals |
|---|---|---|---|
| 1 | 18 | 5 | 23 |
| 6 | 15 | 8 | 23 |
| Totals | 33 | 13 | 46 |

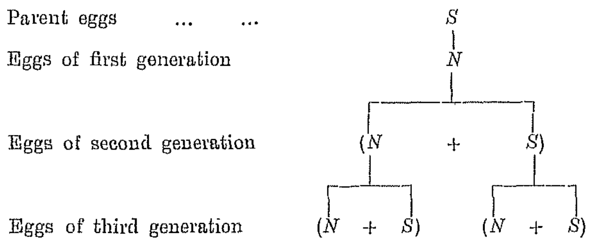
Of 46 batches derived from two normal matings, 13 were spindle-shaped and 33 normal-shaped batches, no mixed ones.

In the third generation which was reared in the spring of 1911, both normal and spindle-shaped eggs gave moths which, when inbred, laid two kinds of eggs, normal and spindle-shaped; the respective figures obtained in each mating are shewn below:

| | Eggs laid | | | |
|---|---|---|---|---|
| Number of Matings | Normal batches | Spindle-shaped batches | Mixture | Totals |
| Spindle-shaped egg, No. 1. 10 | 25 | 2 | — | 27 |
| ,, ,, 12 | | | | |
| ,, ,, 24 | | | | |
| Normal eggs, No. 6 (8 batches) | 24 | 3 | 1 | 28 |

Owing to the great havoc made by "flacherie," the mortality of worms was so great that we only obtained a small number of moths, yet we are able to prove that both characteristics even when inbred again produce the antagonistic characteristic. Thus the order of inheritance of these characteristics may be represented as below:

$S$ = spindle-shaped eggs; $N$ = normal-shaped.



Although we are not yet able to establish this variant as a constant form, we may infer from the above facts that it comes in the same category as the variants just referred to.

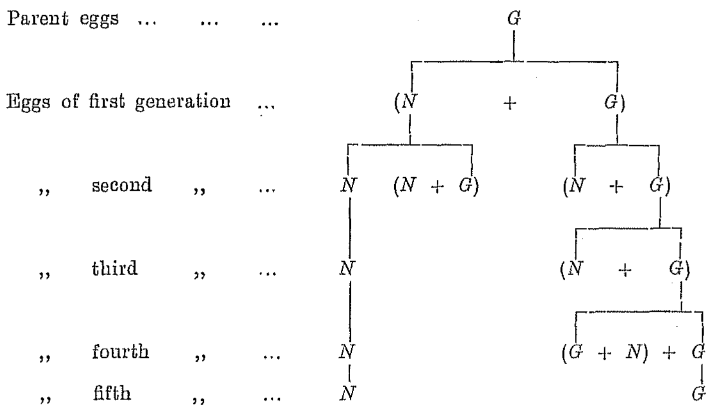
Of the various egg-characteristics discussed in the series of experiments above referred to, we know that those in the first and second series are derived from the colour of the serosa, those in the third and fourth series from the shell, whose special structure gave the egg some characteristics different from normal-shelled eggs.

Notwithstanding their origin being different, their order of inheritance is nearly the same.

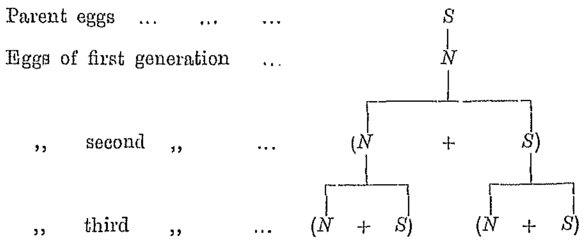
Let us now compare the results obtained in the third and fourth series, which are represented as below:

### 1. *The Results of the Third Series.*

($G$ and $BG$ are considered to be a single character $G$.)

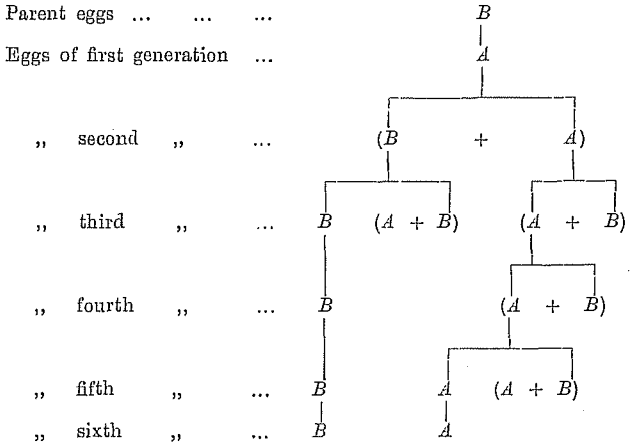


### 2. *The Results of the Fourth Series.*



In this case, if we consider the parent egg, *G* in the third series, as the *N* of the first generation of the fourth series, both results come in a single form which may be represented as below:

$A = G$ in the third and $N$ in the fourth series;
$B = N$ in the third and $S$ in the fourth series.



If we compare the results obtained by the first and the second series of experiments, we can easily see that they behaved in inheritance in a similar manner to those above described, certain inconsistent results being due perhaps to the appearance of divoltine white eggs which prevented the elimination of the antagonistic characteristics during one generation.

## IV. CROSSING OF VARIOUS BREEDS OR VARIANTS POSSESSING DIFFERENT EGG-CHARACTERISTICS.

### SERIES 1. *Crosses between the wild (Theophila mandarina, M.) and the domesticated (Bombyx mori, L.) mulberry silk-worms.*

The egg of the wild mulberry silk-worm (Fig. 10, *a*, *b*) is deposited in a small group on stems or twigs of the mulberry tree. When newly laid, it is a straw yellow (Fig. 10, *b*) which with the formation of the blastoderm gradually assumes a brownish tint and at last turns greenish grey (Fig. 10, *a*). The shape is nearly the same as those of cultivated ones, while the size is little smaller than the latter. The shell is straw yellow and translucent.

The egg of the domesticated silk-worm used in this series of experiments is light greenish white when newly oviposited. It gradually assumes, as in the wild form, a brownish tint and turns brownish slate with some shade of purple or pink, i.e. it assumes the normal colour of Japanese silk-worm eggs (Figs. 1, 3, 11). The shell is nearly white, rarely faintly shaded with a greenish, brownish, or other tint.

In the spring of 1905, five wild female moths were mated with domesticated males (tetravoltine Tōbuhime). They deposited, with no exception, eggs whose characteristics are the same as those of pure wild ones in every respect, such as colour, shape, size and brood character (voltinism). On comparing them with those laid by pure wild parents, we were not able to find any difference at all.

Eleven reversed matings (uni-, di-, and tetravoltine females with wild males) gave, on the contrary, eggs which are similar in shape, colour and voltinism to those of pure domesticated ones (Fig. 11). Even the eye of experienced breeders is not able to distinguish the cross-bred eggs from those laid by maternal pure breeds.

Other five batches derived from divoltine females in the spring brood mated with wild males are all divoltine white in colour, and thus the order of inheritance is entirely maternal, no paternal influence being observed in those reciprocal matings.

The worms which emerged from the reciprocal $F_1$ eggs were reared in the summer of the same year. Moths derived from the eggs laid by the wild female matings (five matings) gave 56 batches of eggs, all of them being uniform in their characteristics. When oviposited, they were light greenish yellow and much lighter in colour than the $F_1$ and gradually assumed a brownish colour which finally turned a greenish slate. Although they resemble the $F_1$ eggs very much in colour, they are darker and the colours are more decided than the latter, and have no dirty or dull shade which is common in the eggs of *Theophila*. The shell is of clear greenish yellow and deeper than that of the $F_1$ or pure wild forms. Therefore, we may easily distinguish $F_1$ eggs from $F_2$ eggs. There are, however, certain variations of colour in the same batch or between different batches, but no trace of the colour-characteristics of the domesticated parents, and consequently we may say that the colour-characteristic derived from the wild parent dominates over that from the domesticated parent.

In the spring of 1906, we reared worms derived from the $F_2$ eggs. Owing to the prevalence of grasserie and diarrhoea, all of them died without attaining their mature stage. It will be noted here that, as far as our experiments went, the hybrid form is much more easily injured by those diseases than the pure domesticated form, especially in the case where the male parents were of the wild form. It is, therefore, very difficult to rear a good supply of the hybrid form for experiments. We were therefore compelled to continue our experiments with back-crossed form paired with domesticated one which is healthier than the first cross.

### *Back-crosses.*

In the summer of 1905, cross-bred moths from the $F_1$ eggs were mated with pure domesticated ones. Reciprocal matings gave, as in the case of $F_1$, diametrically opposite results. Four $F_1$ females mated with pure domesticated males gave all greenish slate eggs whose colour is quite the same as that of the $F_2$ eggs before mentioned, while those laid by 12 domesticated females (tetravoltine white) mated with the cross-bred $F_1$ males produced, without exception, eggs with characteristics quite maternal.

The worms derived from the former matings all died in consequence of the two diseases above mentioned, while those from the latter, being much more able to resist those diseases, gave some moths in the end of the autumn of 1905, that is to say, the third brood of 1905. 36 batches of eggs resulted from the *inter se* breeding, in which we found many different coloured batches as is shewn below:

| Number of Matings | Greenish-slate batches | Japanese normal colour-batches | Mixture of various shaded eggs | Totals |
|---|---|---|---|---|
| I | 0 | 2 | 3 | 5 |
| I *b* | 1 | 0 | 0 | 1 |
| II *a* | 9 | 8 | 5 | 22 |
| II *c* | 0 | 2 | 1 | 3 |
| II *e* | 3 | 0 | 2 | 5 |
| Totals | 13 | 12 | 11 | 36 |

Of 36 batches or matings obtained, 13 were greenish slate as in their parents, 12 Japanese normal colour, the rest being a mixture of both kinds of eggs and some intermediate ones in various proportions.

Owing to certain variations found in a batch, or between various batches, and the scanty number of matings obtained from each parent, we are unable to give the exact numerical proportions of these various coloured batches, but we certainly see that the uniform coloured $F_2$ characteristic disintegrated into various coloured forms.

In the spring of 1906, we reared worms derived from normal-coloured eggs. Moths paired *inter se* gave all divoltine white eggs. The fourth generation from these divoltine white eggs were reared in the summer of 1906. Three matings gave three kinds of egg batches, as in the former generations, namely:

| Number of Matings | Greenish-slate | Japanese normals | Mixture | Totals |
|---|---|---|---|---|
| II*a*, 3 | 5 | 7 | 3 | 15 |
| ,, 4 | 4 | 10 | 5 | 19 |
| ,, 5 | 2 | 4 | 10 | 16 |

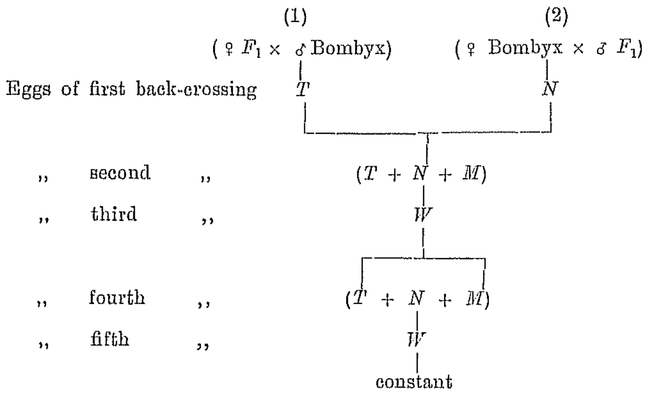
In 1907, we made similar experiments. The worms which came out from normal-coloured batches gave all divoltine white eggs in the spring. The summer broods gave 30 batches of eggs, all of them being of the normal Japanese colour. Since then they have bred true to parents, never giving any greenish coloured ones.

*Résumé:*

*T* = greenish-slate coloured batches like those laid by pure *Theophila*.
*N* = brownish-slate coloured egg batches, common to normal Japanese breeds.
*M* = mixture of those two kinds of eggs above-mentioned and some intermediate coloured eggs.
*W* = divoltine white.

| | (1) | (2) |
|---|---|---|
| | (♀ Theophila × ♂ Bombyx) | (♀ Bombyx × ♂ Theophila) |
| $F_1$ eggs | *T* | *N* |
| $F_2$ eggs | *T* | *T* |

*Back-Crossing.*



We see that the phenomena of inheritance observed in $F_1$ eggs and in back-crosses are exactly maternal, no trace of paternal influence, and that both *Theophila* and *Bombyx* coloured characteristics segregate from each other, and may be extracted again in their original form.

## SERIES 2. *Crosses between the Whitish grey-egged and Normal-egged forms.*

In the spring of 1909, we made crosses between the whitish grey-egged and the normal-egged breeds. The grey-egged breed used in this series of experiments was the very same breed used in the second series of experiments before mentioned, that is to say, Grey No. 24. Normal-egged breeds were: (1) tetravoltine white (Onodahime), (2) divoltine albino extracted from a cross between divoltine "Chiyodzuru" and "Chūsū" albino, (3) divoltine "Shinkawachi," and (4) "$H_4$ albino" extracted from a cross between Japanese tetravoltine white and the wild mulberry silk-worm.

(*a*) Tetravoltine normal-egged females (Onodahime) mated with males of Grey No. 24.

Three matings were made in the spring of 1909 which gave all normal divoltine white $F_1$ eggs. Of the summer broods derived from the $F_1$ eggs, those from two batches yielded both normal and grey (34 normals and 15 greys) $F_2$ batches and the remainder only normal batches.

Some of the $F_2$ batches hatched in August, which were the third brood of 1909. Seven batches were reared separately and when matured gave, without any exception, normal $F_3$ batches, the number being 461. Their posterity only gave one batch of grey eggs in four successive generations during which they produced 1042 batches. Thus we may safely say that some of the normal-egged form which appeared in the $F_2$ are homozygous from their first appearance.

Descendants of the $F_2$ grey batches derived from the same summer brood, on the contrary, produced the antagonistic normal-coloured batches in $F_3$ (the spring of 1910). Of five matings reared, four yielded grey, normal, and B-grey $F_3$ batches, while one gave grey and B-grey, no normal batches. In the former, we found 20 normal, 34 grey, and 5 B-grey batches, and in the latter 6 greys and 3 B-greys.

In the summer of 1910 we again reared nine grey batches, one of which was derived from a mating which did not produce any normal eggs in the last generation. Each of them yielded three kinds of $F_4$ batches, normal, grey, and B-grey, except three matings (Nos. 2. 4. 1; 2. 8. 6; 2. 8. 4) which gave only grey and B-grey batches. The total number of $F_4$ batches obtained in the former matings was 78 (26·5 %) normals, 126 greys, and 90 B-greys, and in the latter 51 greys and 30 B-greys. Two B-grey $F_3$ batches which were reared in the same season gave only four $F_4$ batches, one being grey and three B-greys, no normal batches.

The autumn (1910) brood derived from the summer grey brood, which laid only grey and B-grey batches, gave $F_5$ batches, in which we again found normal batches, but their proportion became gradually lessened as the figures show, namely, of five matings derived from the grey mating No. 6 which did not produce any normal batches in the summer, two gave 28 normals, 71 greys, 39 B-greys, $F_5$ batches, the remainder 68 greys and 55 B-greys. Of seven derived from No. 1 mating, which as in the former gave no normals in the summer, five gave three kinds of $F_5$ batches (15 normals, 52 greys and 27 B-greys) and two no normal batches (12 greys, 18 B-greys). In the former lineage, therefore, the proportion of normal batches is 20 % and in the latter 14·4 %.

In the spring of 1911, we again reared nine grey batches derived from the brood which produced no normal batches in the last generation. They gave 103 $F_6$ batches of eggs of which 49 were grey, 49 B-greys and five a mixture of both kinds of batches.

Ten batches of B-grey eggs derived from the same parents as above matings were reared, but all of them died before attaining maturity.

## TABLE IV.

*Crossing between Tetravoltine Normal-egged and Heterozygous Grey-egged Variant No. 24.*

(♀ Normal-egged × ♂ Grey-egged variant)

$F_1$ eggs (Spring, 1909) ... All normals (Nos. 1, 2, 3)

| | No. of Matings | No. of normals | No. of greys | Totals |
|---|---|---|---|---|
| $F_2$ eggs (Summer, 1909) ... | 1* | 6 | 0 | 6 |
| | 2* | 16 | 14 | 30 |
| | 3* | 18 | 1 | 19 |
| Totals ... ... | | 40 | 15 | 55 |

*Normal-egged Series.*

| | Year | Number of Matings | Normal | Grey | B-grey | Totals |
|---|---|---|---|---|---|---|
| $F_3$ | 1909 | 1. 1* | 71 | 0 | 0 | 71 |
| | (August) | 1. 2 | 61 | 0 | 0 | 61 |
| | | 2. 2* | 42 | 0 | 0 | 42 |
| | | 3. 1 | 87 | 0 | 0 | 87 |
| | | 3. 2 | 7 | 0 | 0 | 7 |
| | | 3. 3 | 49 | 0 | 0 | 49 |
| | | 3. 6 | 49 | 0 | 0 | 49 |
| | | Totals ... | 366 | 0 | 0 | 366 |
| $F_4$ | 1910 | 1. 1. 7 | 39 | 0 | 0 | 39 |
| | (Spring) | ,, 10 | 28 | 0 | 0 | 28 |
| | | ,, 16 | 27 | 0 | 0 | 27 |
| | | ,, 23 | 28 | 0 | 1(?) | 29 |
| | | ,, 26 | 50 | 0 | 0 | 50 |
| | | 2. 2. 2 | 32 | 0 | 0 | 32 |
| | | ,, 4 | 30 | 0 | 0 | 30 |
| | | ,, 11 | 28 | 0 | 0 | 28 |
| | | ,, 7* | 39 | 0 | 0 | 39 |
| | | ,, 18 | 22 | 0 | 0 | 22 |
| | | Totals ... | 323 | 0 | 1 | 324 |
| $F_5$ | 1910 | 2. 2. 7. 4 | 96 | 0 | 0 | 96 |
| | (Summer) | ,, 5* | 76 | 0 | 0 | 76 |
| | | ,, 7 | 24 | 0 | 0 | 24 |
| | | ,, 11 | 27 | 0 | 0 | 27 |
| | | ,, 12 | 4 | 0 | 0 | 4 |
| | | Totals ... | 227 | 0 | 0 | 227 |

*Grey-egged Series.*

| | Number of Matings | Normal | Grey | B-grey | Mixed | Totals |
|---|---|---|---|---|---|---|
| $F_3$ | 2. 1* | 0 | 6 | 3 | — | 9 |
| | ,, 4* | 7 | 10 | 1 | — | 18 |
| | ,, 5* | 11 | 13 | 0 | — | 24 |
| | ,, 8* | 1 | 7 | 0 | — | 8 |
| | ,, 16* | 1 | 4 | 4 | — | 9 |
| | Totals ... | 20 | 34 | 5 | — | 59 |
| $F_4$ | 2. 1. 5 | 5 | 8 | 4 | — | 17 |
| | 2. 4. 1* | 0 | 27 | 9 | — | 36 |
| | 2. 16. 8 | 16 | 27 | 13 | — | 56 |
| | 2. 16. 3 | 29 | 30 | 29 | — | 88 |
| | 2. 5. 2 | 9 | 34 | 20 | — | 63 |
| | 2. 5. 6 | 11 | 20 | 12 | — | 43 |
| | 2. 8. 4 | 0 | 1 | 1 | — | 2 |
| | 2. 8. 3 | 8 | 7 | 12 | — | 27 |
| | 2. 8. 6* | 0 | 23 | 20 | — | 43 |
| | Totals 3 matings | 0 | 51 | 30 | — | 81 |
| | 6 ,, | 78 | 126 | 90 | — | 294 |
| | No. 2. 1 *BG* 1 | 0 | 1 | 0 | — | 1 |
| | 4. 7 | 0 | 0 | 3 | — | 3 |

* Those marked with an asterisk are the parents of next generation.

TABLE IV.—(*continued*).

*Crossing between Tetravoltine Normal-egged and Heterozygous Grey-egged Variant No. 24.*

*Normal-egged Series.*

| | Year | Number of Matings | Normal | Grey | B-grey | Totals |
|---|---|---|---|---|---|---|
| $F_6$ | 1910 | 2. 2. 7. 5. 4 | 22 | 0 | 0 | 22 |
| | (Autumn) | ,, 13* | 80 | 0 | 0 | 80 |
| | | ,, 11 | 39 | 0 | 0 | 39 |
| | | ,, 17 | 37 | 0 | 0 | 37 |
| | | ,, 20 | 41 | 0 | 0 | 41 |
| | | ,, 77 | 29 | 0 | 0 | 29 |
| | Totals | ... | 248 | 0 | 0 | 248 |
| $F_7$ | 1911 | 2. 2. 7. 5. 13. 3 | 243 | 0 | 0 | 243 |
| | (Spring) | ,, 6 | | | | |
| | | ,, 17 | | | | |
| | | ,, 18 | | | | |
| | | ,, 19 | | | | |

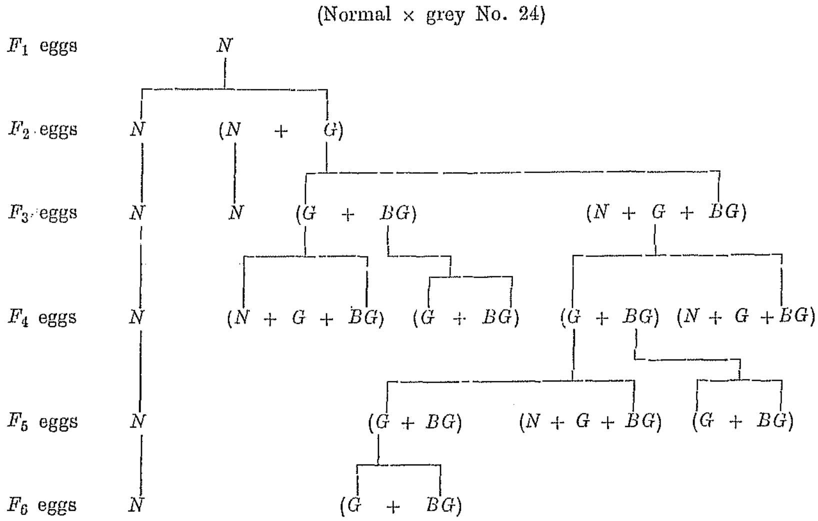
*Grey-egged Series.*

| | Number of Matings | Normal | Grey | B-grey | Mixed | Totals |
|---|---|---|---|---|---|---|
| $F_5$ | 2. 8. 6. 1 | 12 | 39 | 21 | — | 72 |
| | ,, 4 | 0 | 2 | 2 | — | 4 |
| | ,, 6 | 16 | 32 | 18 | — | 66 |
| | ,, 11 | 0 | 14 | 18 | — | 32 |
| | ,, 44* | 0 | 42 | 35 | — | 77 |
| | Totals 2 matings | 28 | 71 | 39 | — | 138 |
| | 3 ,, | 0 | 58 | 55 | — | 113 |
| | 2. 8. 6. *BG* 3 | 0 | 11 | 11 | — | 22 |
| | ,, *BG* 9 | 0 | 1 | 3 | — | 4 |
| | ,, *BG* 12 | 0 | 0 | 1 | — | 1 |
| | Totals ... ... | 0 | 12 | 15 | — | 27 |
| | 2. 4. 1. 8 | 6 | 15 | 8 | — | 29 |
| | ,, 9 | 0 | 8 | 12 | — | 20 |
| | ,, 12 | 11 | 14 | 7 | — | 32 |
| | ,, 17 | 2 | 13 | 6 | — | 21 |
| | ,, 20 | 3 | 6 | 3 | — | 12 |
| | ,, 27 | 0 | 4 | 6 | — | 10 |
| | ,, 19 | 3 | 4 | 3 | — | 10 |
| | Totals 5 matings | 25 | 52 | 27 | — | 104 |
| | 2 ,, | 0 | 12 | 18 | — | 30 |
| $F_6$ | 2. 8. 6. 44. 3 | 0 | 5 | 8 | — | 13 |
| | ,, 6 | 0 | 4 | 1 | — | 5 |
| | ,, 21 | 0 | 2 | 5 | — | 7 |
| | ,, 6*b* | 0 | 3 | 5 | — | 8 |
| | ,, 9*b* | 0 | 15 | 9 | 3 | 27 |
| | ,, 12*b* | 0 | 1 | 2 | 1 | 4 |
| | ,, 12*c* | 0 | 7 | 12 | 0 | 19 |
| | ,, 16*c* | 0 | 6 | 6 | 1 | 13 |
| | ,, 19*c* | 0 | 6 | 1 | 0 | 7 |
| | Totals ... | 0 | 49 | 49 | 5 | 103 |

---

* Those marked with an asterisk are the parents of next generation.

The respective figures obtained in each mating in every generation are represented in Table IV which will be summarized as below:



The results are nearly the same as those obtained in the original grey variant which is inbred, except the appearance of the constant $N$ form in $F_1$.

(*b*) Exactly the same results were obtained when we crossed a normal-egged breed extracted from a cross between divoltine "Chiyodzuru" and the univoltine albino before referred to with the grey-egged variant No. 24. The results of experiments are tabulated below (Table V).

(*c*) In this series we made again similar matings as in the previous two series of experiments. Three females from the divoltine normal-egged white called "Shinkawachi" and two from the normal-egged extracted form called *E* III were mated with males derived from the very same grey variant used in the preceding experiments. They gave as in former cases, all $F_1$ normal egg-batches, no grey ones.

Two batches from the former and one from the latter were reared in the next season. The former gave 93 $F_2$ batches and the latter 13 $F_2$ batches, all of them being normal batches. Five batches of the former and one batch of the latter were again reared in the next season. The former gave 968 $F_3$ batches of normal eggs and the latter 10 $F_3$ normal batches.

## TABLE V.

(♀ *Normal* × ♂ *Grey*).

| | | | |
|---|---|---|---|
| $F_1$ eggs (Spring, 1909) | Normal divoltine white (one batch) | | |

| | | Egg-batches produced | | |
|---|---|---|---|---|
| | Number of matings | Normal batches | Grey batches | Total |
| $F_2$ eggs (Summer, 1909) | 6* | 13 | 11 | 24 |

| | Number of Parent | Normal | Grey | Totals | Number of Parent | Normal | Grey | B-grey | Totals |
|---|---|---|---|---|---|---|---|---|---|
| $F_3$ eggs (Spring, 1910) | 6. 3 | 5 | 0 | 5 | 6. 16* | 14 | 28 | 5 | 47 |
| | 6. 7* | 10 | 12 | 22 | 6. 18* | 7 | 11 | 8 | 26 |
| | 6. 21 | 9 | 12 | 21 | 6. 19* | 7 | 6 | 6 | 19 |
| | Totals | 24 | 24 | 48 | Totals | 28 | 45 | 19 | 92 |
| | | | Grey series | | | | Grey series | | |

| | Number of Parent | Normal | Grey | B-grey | Totals | Number of Parent | Normal | Grey | B-grey | Totals |
|---|---|---|---|---|---|---|---|---|---|---|
| $F_4$ eggs (Summer, 1910) | 6. 7. 3* | 0 | 33 | 22 | 55 | 6. 16. 12* | 44 | 49 | 0 | 93 |
| | ,, 14 | 18 | 12 | 0 | 30 | ,, 13 | 6 | 4 | 0 | 10 |
| | ,, 8 | 8 | 14 | 0 | 22 | | | (B-grey series) | | |
| | ,, 9 | 17 | 41 | 28 | 86 | 6. 16. 7 | 0 | 1 | 30 | 31 |
| | | | | | | ,, 8 | 0 | 11 | 10 | 21 |
| | | | | | | ,, 18 | 0 | 0 | 4 | 4 |
| | | | | | | 6. 18. 1 | 0 | 0 | 6 | 6 |
| | | | | | | 6. 19. 1 | 0 | 2 | 0 | 2 |
| | | | | | | ,, 8 | 0 | 14 | 3 | 17 |
| | | | Grey series | | | | | Grey series | | |

| | Number of Parent | Normal | Grey | B-grey | Total | Number of Parent | Normal | Grey | B-grey | Total |
|---|---|---|---|---|---|---|---|---|---|---|
| $F_5$ eggs (Spring, 1911) | 6. 7. 3 (4 and 5) | 2 | 3 | 6 | 11 | 6. 16. 12 (5 and 16) | 8 | 16 | 0 | 24 |

Parents of next generation.

In the next generation paired *inter se*, both series again yielded only normal-egged $F_4$ batches, the number of batches produced in the former series being 66 and in the latter 123. Now it is quite certain that in these matings there is no grey factor which has lain dormant as in the former matings.

The facts obtained in these three series of experiments and those from the second series of the line breeding suggest to us, *firstly* that among the eggs of grey-batch No. 24, there are two kinds of grey eggs, one having the grey factor in its zygotic composition, while another has no grey factor, in spite of its being grey in colour; that is to say, some grey eggs are heterozygous for the normal factor, some homozygous normals; *secondly* that the normal and the grey segregate from each other in their succeeding generation as other Mendelian characters do; *thirdly* that it is much easier to free the normal form from the antagonistic character than the grey; and, lastly, that the normal form does not produce any other form when it becomes free from the grey form, while the grey form segregates into another form even after being freed from the normal form. From this fact we may safely infer that the grey is more complicated in its constitution than the normal.

### SERIES 3. *Crosses between Yellow and White forms of Japanese Tetravoltine Breed, "Onodahime."* (Fig. 9, *a* and *b*.)

Normal Japanese tetravoltine breeds are generally white cocoon-spinners, as far as we are aware. In the year 1905, we obtained a mixed breed consisting of white and yellow cocoon-spinners, the latter being a yellow-blooded form. Each form was reared separately and was established as a constant form. In the spring of 1907 reciprocal crossings between these forms were made.

Yellow females mated with white males gave $F_1$ eggs which are all yellow when newly laid[1] (Fig. 9, *b*). This is the characteristic egg-colour of the yellow form. The reversed mating gave, on the contrary, all pale white $F_1$ eggs (Fig. 9, *a*) which is also the characteristic colour of the white form. It will be necessary to note here that the colour of newly laid eggs is determined by that of the shell and the yolk, both of them being maternal in their origin.

The worms which came out from the reciprocal $F_1$ eggs were reared in the late autumn of the same year. All the worms were yellow-blooded and spun yellow cocoons without any exception. The moths paired *inter se* gave all yellow $F_2$ eggs which are quite the same as those laid by the pure yellow forms.

In the spring of 1908, the $F_2$ yellow eggs gave two kinds of worms, the one being yellow-blooded, the other white-blooded; the total figures found in those matings are shown below:—

| Number of Group | Number of yellow-blooded worms | Number of white-blooded worms | Totals |
|---|---|---|---|
| I | 485 | 169 | 654 |
| II | 567 | 160 | 727 |
| Totals ... ... | 1,052 | 329 | 1,381 |
| Mendelian expectation | 1,035 | 345 | 1,380 |

---

[1] In this series of experiments, we only refer to the colour of the egg when newly laid, i.e. the colour of eggs before the formation of the blastoderm takes place.

The moths derived from these yellow- and white-blooded worms were paired in the following ways:

I ♀ White-blooded moths × ♂ White-blooded
II ♀ White ,, ,, × ♂ Yellow ,,
III ♀ Yellow ,, ,, × ♂ Yellow ,,
IV ♀ Yellow ,, ,, × ♂ White ,,

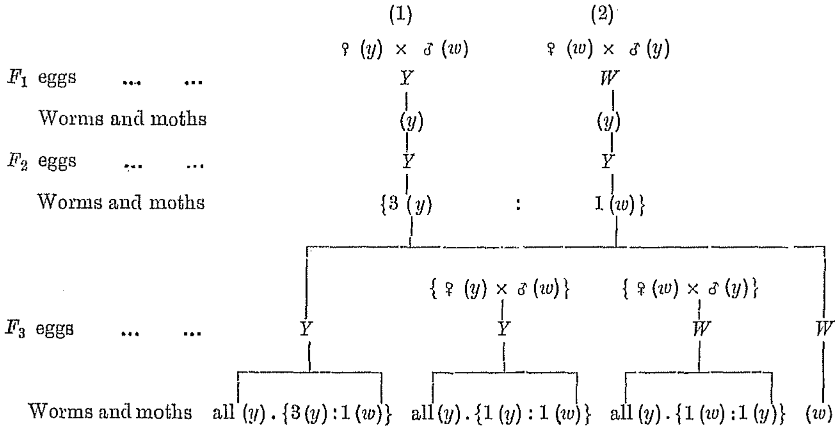
They gave the results which are tabulated below:—

| | | Parents | | | Worms which emerged from the egg | | |
|---|---|---|---|---|---|---|---|
| Group | Number of Matings | Female | Male | Colour of the eggs laid | Yellow | White | Totals |
| I | I No. 9 | white | white | pale white | 0 | all white | all white |
| | II ,, 1*a* | ,, | ,, | ,, | ,, | ,, | ,, |
| | ,, ,, 10 | ,, | ,, | ,, | ,, | ,, | ,, |
| | ,, ,, 13 | ,, | ,, | ,, | ,, | ,, | ,, |
| | ,, ,, 21 | ,, | ,, | ,, | ,, | ,, | ,, |
| II | II No. 6 | white | yellow | pale white | 59 | 51 | 110 |
| | ,, ,, 13 | ,, | ,, | ,, | 17 | 0 | 17 |
| | ,, ,, 14 | ,, | ,, | ,, | 242 | 0 | 242 |
| | ,, ,, 23 | ,, | ,, | ,, | 27 | 19 | 46 |
| III | II No. 9 | yellow | yellow | brownish yellow | 0 | 0 | 0 |
| | ,, ,, 3 | ,, | ,, | ,, ,, | 109 | 30 | 139 |
| | ,, ,, 4 | ,, | ,, | ,, ,, | 39 | 14 | 53 |
| | ,, ,, 5 | ,, | ,, | greenish yellow | 0 | 0 | 0 |
| | ,, ,, 11 | ,, | ,, | brownish yellow | 71 | 17 | 88 |
| | ,, ,, 16 | ,, | ,, | ,, ,, | 0 | 0 | 0 |
| | ,, ,, 24 | ,, | ,, | greenish yellow | 54 | 13 | 67 |
| Totals | ... | ... | ... | ... ... | 273 | 74 | 347 |
| IV | I No. 6 | yellow | white | yellow | 65 | 55 | 120 |

As the Table shews, if yellow-blooded females (both homozygous and heterozygous) are used, whether they are mated with their own males or other white males, the results are always the production of brownish or greenish yellow eggs which is a characteristic of the yellow-blooded form. In like manner, white-blooded females mated with yellows (homo- and heterozygous) or whites gave all whitish eggs, characteristic of the white form. Thus we may say in this case as in the other cases before cited, the colour characteristics of the egg are not influenced by the zygotic composition of the egg after fertilization, but by their maternal zygotic constitution before fertilization, and therefore there is no sign of male characteristics to be seen in the egg, but in the larval stage their relation is quite Mendelian.

*Résumé*:

$Y$=yellow eggs; $W$=white eggs; $(y)$=yellow-blooded worms and moths; $(w)$=white-blooded worms and moths.



### SERIES 4. *Crosses between various Breeds which lay different coloured Eggs.*

This series of experiments was undertaken with the intention of observing the influence of egg-characteristics belonging to the breed used as male parents towards the characteristics of $F_1$ eggs.

(1) Reciprocal matings between Chinese whites from the Joken and Kainei districts and Japanese univoltine breeds, "Aojiku" and "Chūsū."

Egg-colour of the Chinese breeds: dark-slate, more or less shaded with green in various degrees, sometimes without any green shade. We call this colour Chinese normal colour.

Egg-colour of the Japanese breeds (Figs. 1, 3, and 11): brownish slate, more or less shaded with pink or purple. This is the ordinary egg-colour of Japanese breeds.

| Matings | Number of Matings | Colour of $F_1$ eggs |
|---|---|---|
| ♀ Chinese Joken × ♂ Japanese Aojiku | 10 | all Chinese colour |
| ♀ ,, Kainei × ♂ ,, Chūsū | 13 | ,, ,, |
| ♀ Japanese Aojiku × ♂ Chinese Joken | 10 | Japanese ordinary colour |
| ♀ ,, Chūsū × ♂ ,, Kainei | 15 | ,, ,, |

(2) Reciprocal crosses between the Japanese green breed (Seihaku) and the extracted normal-egged breed (Ivg), or the univoltine white, "Sekai-ichi."

Egg-colour of the green breed: ordinary brownish slate with various shades of green (Fig. 6), some of them having no green shade. It resembles in colour the Chinese colour but the shades are different, so we are able to distinguish the Chinese colour from that of Japanese green.

| Matings | Number of Matings | Colour of $F_1$ eggs |
|---|---|---|
| ♀ Green × ♂ "Ivg" | 5 | one batch normal slate, the rest a mixture of various green shaded eggs, i.e. ordinary colour of green breed |
| ♀ Ivg × ♂ green | 6 | Japanese normal colour |
| ♀ Sekai-ichi × ♂ green | 5 | ,, ,, ,, |

(3) Reciprocal matings between the wild mulberry silk-worm (*Theophila mandarina*) and Japanese normal-egged breeds (Shinyahime), tetravoltine "Onodahime," tetravoltine "Tōbuhime," univoltine "Matamukashi").

Egg-colour of *Theophila*: grey, more or less shaded with green, as has already been described.

| Matings | Number of Matings | Colour of $F_1$ eggs |
|---|---|---|
| ♀ Shinyahime × ♂ *Theophila* | 8 | all Japanese normal colour |
| ♀ Onodahime × ♂ ,, | 2 | ,, ,, ,, |
| ♀ Univoltine Matamukashi × ♂ *Theophila* | 2 | ,, ,, ,, |
| ♀ Tōbuhime × ♂ *Theophila* | 3 | ,, ,, ,, |
| ♀ *Theophila* × ♂ Tōbuhime | 3 | all *Theophila* colour |
| ♀ ,, ♂ Matamukashi | 2 | ,, ,, |

(4) Reciprocal matings between the normal (Fig. 1) and the reddish brown egged (Fig. 2) forms found in the divoltine breed, "Shinkawachi."

| Matings | Number of Matings | Colour of $F_1$ eggs |
|---|---|---|
| ♀ normal × ♂ reddish-brown | 20 | all normal colour |
| ♀ reddish-brown × ♂ normal | 15 | all reddish-brown, few being a little darker shaded |

(5) Reciprocal crossings between the European yellow, "Papillons noirs" and the Japanese normal-egged breed, "Tatsutahime."

Egg colour of "Papillons noirs": slate grey, more or less shaded with green as in Japanese green; sometimes without any greenish shade; the general colouration, however, differs from that of the Chinese, Japanese or *Theophila* green, each of them having its own characteristics: egg-colour of "Tōbuhime," normal Japanese colour.

| Matings | Number of Matings | Colour of $F_1$ eggs |
|---|---|---|
| ♀ Papillons noirs × ♂ Tatsutahime | 2 | European greenish slate |
| ♀ Tatsutahime × ♂ Papillons noirs | 2 | all divoltine white |

(6) Reciprocal crosses between European breeds (Italian white and Sina blanc) and Japanese normal-coloured breeds (divoltine Shinkawachi, tetravoltine Tatsutahime, and divoltine Asakanishiki).

The egg-colour of these European breeds are practically the same as that of Papillons noirs, i.e. greenish-shaded slate.

| Matings | Number of Matings | Colour of $F_1$ eggs |
|---|---|---|
| ♀ Italian white × ♂ Shinkawachi | 3 | slate grey |
| ,, ,, ,, | 7 | mixture of various greenish-shaded greys and normal slates |
| ♀ Shinkawachi × ♂ Italian white | 3 | Japanese normal colour |
| ♀ Tatsutahime × ♂ Italian white | 25 | all divoltine white |
| ♀ Asakanishiki × ♂ Sina blanc | 7 | ,, ,, |
| ♀ Italian white × ♂ Tatsutahime | 4 | a mixture of various green-shaded greys and normal slates |
| ♀ Sina blanc × ♂ Asakanishiki | 6 | the same colour as the above |

(7) Reciprocal crossing between albino and colour-egged breeds.

The colour-egged breeds used in this series of experiments were:

1. European yellow, Papillons noirs.

2. Japanese white, "Sekai-ichi," "Tako," "Chūsū," and the extracted white "Ivg," univoltine green, "Seihaku."

3. Albino: univoltine Chūsū albino (the colour of the egg is a greenish white, sometimes faintly shaded with orange), another is the Chinese orange breed, its eggs being clear orange with certain variations in intensity.

| Matings | Number of Matings | Colour of $F_1$ eggs |
|---|---|---|
| ♀ Orange × ♂ Papillons noirs | 1 | light pinkish brown |
| ♀ Orange × ♂ Sekai-ichi | 5 | mixture of orange to dark-pinkish browns |
| ♀ Orange × ♂ Green | 5 | 4 light pinkish brown with various dark shades<br>1 dark pinkish grey |
| ♀ Orange × ♂ Ivg | 5 | 2 Orange, slightly shaded with a dark pink<br>3 a mixture of orange, dark pink, and a few normal eggs |
| ♀ Chūsū albino × ♂ Univoltine Chūsū | | some batches are all white, some white mixed with various shaded eggs |
| ♀ Chūsū albino × ♂ Chiyodzuru | | the same as the above |
| ♀ Papillons noirs × ♂ Orange | 3 | European green-shaded eggs, one being little lighter in colour than the others |
| ♀ Sekai-ichi × ♂ Orange | 5 | all normal brownish grey |
| ♀ Green × ♂ Orange | 5 | various green-shaded eggs, characteristic to the green breed |
| ♀ Ivg × ♂ Orange | 6 | all normal brownish grey |
| ♀ Tako × ♂ Orange | 4 | the same as the above |
| ♀ Chiyodzuru × ♂ Chūsū albino | 4 | the same as the above |

In the crossings above quoted, we compared the reciprocal $F_1$ eggs with those laid by pure maternal breeds in each case, and came to the conclusion that the colour-characteristics of the egg are governed by those of the female parent. As far as our experiments went, it is very difficult to distinguish between these $F_1$ eggs and those laid by pure maternal breeds, even to the eye of experienced breeders the line of demarcation was indistinguishable, except in the case of albinotic matings.

As to the albinotic matings, the case is rather different from that of the coloured matings, since the eggs laid by albino females mated with coloured males sometimes were more or less influenced by the male characteristics and sometimes shewed no male influence. In the Chūsū albino matings we often obtained pure white $F_1$ eggs, while in the orange albino these maternally characterized eggs were rarely found.

Now then, we may draw the conclusion that most of the egg-colours which are commonly met with in various breeds are maternal in inheritance, in spite of the origin of these different colours being due to the pigments which are deposited in the serosa. In Chinese, European and in some green breeds the green colour of the shell may help the production of these greenish shades, but it is not the chief cause of the green colour.

Concerning albino breeds which gave rise to more intricate series of results when crossed with other coloured breeds, we shall describe them in the second contribution of this subject.

From the series of experiments above mentioned, we know that all the colour-characteristics of the silk-worm egg are maternal in inheritance with the exception of the albino, in which the recessive uncoloured characteristic of the female parent is sometimes more or less influenced by the dominant coloured male. We must not forget, however, that there are breeds whose egg-characteristics behave exactly as other normal Mendelian characteristics do. We shall now describe a case of this kind studied by us.

### SERIES 5. *Inheritance of the "Crimson-egged" Breed.*

In the spring of 1909 we obtained, through the kindness of Mr J. Ariga of the Nagano district, two batches of eggs laid by a divoltine breed. This breed is characterized by the special colour of the egg which is a clear crimson-red. It is one of the most strikingly coloured eggs we have ever had. In one batch (No. 5) we found 30 normal coloured eggs and in another (No. 20) only two normal eggs, all the remainder were crimson-red.

### *Characteristics of this Breed.*

From the results given by rearing through consecutive generations, it was ascertained that all the worms were normal patterned and there was no considerable difference from normal breeds, except in the colour of the head and eyes. In the fourth and fifth stages, we clearly observed that the head of the worm was of a light reddish brown as contrasted with the normal brownish grey of normal-egged breeds. The eyes, both simple and compound, were tinged with crimson. The eggs when newly laid are white as is the case in normal breeds. With the formation of the blastoderm, they gradually changed into a light orange, then into brownish orange and at last into clear crimson. They do not remain the same in colour throughout the year; when the development of the embryo is in its earlier stages they take on some shade of brown which gradually merges into a clear crimson. After the hibernation, when the development of the embryo again takes place in spring, they assume a dark shade of crimson and the pigments are not uniformly distributed in the serosa. The shell is white. The shape is quite normal. The cocoons are white, and their form is cylindrical with the constriction in the middle like that of the normal Japanese breed. The moths are white, with faint markings as in normal light moths. We shall call this breed the "Crimson-egged" breed.

### *Crossing experiments with Normal Breeds.*

Reciprocal matings between the crimson-egged and many normal breeds were made. Female moths derived from the spring brood of the crimson breed were mated with males from tetravoltine white (Onodahime), the extracted normal-egged breed derived from a cross between Japanese white and the Chinese dark-wormed breed, and the divoltine white (Renzoku). These three breeds were all true in their normal egg-colour characteristic. The results of the reciprocal matings are shewn below:

#### A. $F_1$ *Eggs.*

1. (♀ normal breed × ♂ crimson breed.)

| Female parent | Male parent | Number of Mating | Eggs laid ($F_1$) |
|---|---|---|---|
| Tetravoltine white (Onodahime) | Crimson | 6 | divoltine white |
| ,, ,, ,, | ,, | 7 | ,, ,, |
| The extracted normal breed | ,, | 11 | ,, ,, |
| ,, ,, ,, | ,, | 12 | normal dark colour |
| ,, ,, ,, | ,, | 13 | ,, ,, |
| ,, ,, ,, | ,, | 14 | ,, ,, |
| Divoltine white (Renzoku) | ,, | 15 | ,, ,, |
| ,, ,, | ,, | 16 | ,, ,, |

Of eight matings, five gave all normal dark eggs, while three gave all divoltine white eggs, which is the maternal characteristic of tetra- or divoltine females in their spring brood.

2. (♀ crimson breed × ♂ normal breed.)

The reversed matings gave results identical with those represented.

|  | Female parent | Male parent | Number of Matings | Eggs laid ($F_1$) |
|---|---|---|---|---|
| 1 | Crimson | Tetravoltine Onodahime | 4 | normal dark |
|  | ,, | ,, ,, | 5 | ,, ,, |
| 2 | ,, | The extracted normal-egged form from the cross between *Bombyx mori* and *Theophila mandarina* | 2 and 3 | divoltine white |
| 3 | ,, | Chinese "Dragon horn" | 1 | greenish slate |

The results of the reciprocal matings shew us that in the $F_1$ eggs normal coloured or greenish coloured characteristics dominate over the crimson, while the voltine characteristics are, as in other egg-characteristics before enumerated, maternal in inheritance.

### B. $F_2$ *Eggs.*

The worms and moths derived from the reciprocal normal-coloured $F_1$ eggs in the summer of 1910 were all dark-eyed, and the moths paired *inter se* gave the following $F_2$ eggs:

| Matings | Number of Matings | Eggs laid by each moth |  | Totals |
|---|---|---|---|---|
|  |  | Normal | Crimson |  |
| ♀ Tetravoltine "Onodahime"<br>♂ Crimson | 6. 1 | 342 | 136 | 478 |
|  | 6. 2 | 294 | 103 | 397 |
|  | 6. 8 | 369 | 103 | 472 |
|  | 6. 9 | 374 | 103 | 477 |
|  | 6. 10 | 314 | 124 | 438 |
|  | 6. 11 | 192 | 77 | 269 |
|  | 6. 12 | 334 | 109 | 443 |
|  | 7. 6 | 300 | 97 | 397 |
|  | 7. 13 | 272 | 107 | 379 |
|  | 7 × 6. 28 | 214 | 88 | 302 |
|  | Totals | 3001 | 1047 | 4048 |
| ♀ Extracted normal-egged breed from the cross, Japanese white × Chinese black-wormed breed<br>♂ Crimson | 11. 1 | 278 | 96 |  |
|  | 11. 2 | 176 | 68 |  |
|  | 11. 4 | 319 | 115 |  |
|  | 11. 6 | 351 | 123 |  |
|  | 11. 7 | 330 | 119 |  |
|  | Totals | 1454 | 521 |  |

| Matings | Number of Matings | Eggs laid by each moth: Normal | Eggs laid by each moth: Crimson | Totals |
|---|---|---|---|---|
| ♀ Crimson<br>♂ Tetravoltine "Onodahime" | 4. 3 | 293 | 93 | |
| | 4. 5 | 301 | 126 | |
| | 9 | 347 | 128 | |
| | 10 | 359 | 96 | |
| | 11 | 332 | 83 | |
| | 13 | 355 | 112 | |
| | 14 | 275 | 89 | |
| | Nos. 1, 2, 4, 8, 15—18 all divoltine whites | | | |
| | Totals | 2262 | 727 | 2989 |
| ( ♀ Crimson No. 20 | 2. 1 | 230 | 80 | 310 |
| ♂ E III. 11. 1. 3) | 3. 3 | 82 | 24 | 106 |
| ( ♀ Crimson × ♂ "Dragon-horn") | 1. 15 | 319 | 124 | 443 |
| | 1. 16 | 290 | 105 | 395 |
| | 1. 17 | 389 | 110 | 499 |
| Totals | | 1,310 | 443 | 1,753 |
| Grand totals | | 8,027 | 2,738 | 10,765 |
| Expectation | | 8,073$\frac{3}{4}$ | 2,691$\frac{1}{4}$ | 10,765 |

Every mating, except those which gave divoltine white eggs, yielded both crimson and normal-coloured eggs in an approximate proportion of $3N : 1R$ respectively; the total number of crimson and normal-coloured eggs obtained from 17 $F_1$ dark-eyed moth matings being 5026 and 1691 respectively, that is to say, 3 normals : 1 crimson.

## C. $F_3$ *Eggs.*

The mixed $F_2$ eggs laid by the cross, Tetravoltine normal egged × Crimson egged breed, were reared in the spring of 1910. Both the normal and crimson-coloured eggs found in each batch were reared separately and gave the following worms and moths:

| Number of parent batches | Number of normal and crimson eggs in each batch | Kinds of worms hatched: Dark-eyed | Kinds of worms hatched: Crimson-eyed | Moths |
|---|---|---|---|---|
| ♀ Tetravoltine<br>♂ Crimson No. 6. 1 | N. 342 | 281 (82 %) | 0 | all dark-eyed |
| | R. 136 | 0 | 46 (33 %) | all crimson-eyed |
| ,, No. 6. 8 | N. 369 | 301 (82 %) | 0 | all dark-eyed |
| | R. 103 | 0 | 28 (27 %) | all crimson-eyed |
| ,, No. 6. 9 | N. 374 | 290 (77 %) | 0 | all dark-eyed |
| | R. 103 | 0 | 40 (38 %) | all crimson-eyed |
| Mixed rearing of Nos. 6. 2 and 7. 6 | N. 594 | 465 (78 %) | 0 | all dark-eyed |
| | R. 200 | 0 | 91 (45 %) | all crimson-eyed |
| Crimson eggs derived from five batches | | | 89 | all crimson-eyed |

As the figures show, crimson-coloured eggs always produced crimson-eyed worms and moths and the normal ones gave dark-eyed worms and moths. Both the crimson and normal-eyed moths paired *inter se* gave the following $F_3$ egg-batches:

(1) *Crimson-eyed moths paired inter se.*

| Number of Matings | Colour of the eggs laid |
|---|---|
| No. 6. 8. 15 | all crimson-coloured eggs |
| No. 6. 9. 14 | ,, ,, ,, |
| No. 6. 8. (× pure crimson) 16 | ,, ,, ,, |
| No. 6. 1. (× pure crimson) 27 | ,, ,, ,, |
| No. 6. 8. (× No. 6. 1) 11 | divoltine white |
| No. 6. 2. (× No. 7. 6) 13 | ,, ,, |
| No. 6. 9. 15 | ,, ,, |

Of seven crimson-eyed matings, four gave all crimson-coloured eggs, while the remainder gave all divoltine white eggs which in the next generation gave rise to crimson-eyed worms and moths and laid all crimson-coloured eggs. We may say, therefore, that the crimson-coloured characteristic is segregated from the normal-coloured ones. The lineage of this series gave all crimson-coloured eggs in the succeeding generations.

(2) *Normal-eyed moths inbred.*

| Parents | Number of Matings | Eggs laid | | Totals |
|---|---|---|---|---|
| | | Normal | Crimson | |
| No. 6. 1 | 11 | 236 | 79 | 315 |
| ,, | 12 | all normals | | all normals |
| ,, | 13 | ,, | | ,, |
| No. 6. 8 | 15 | all divoltine white batches | | |
| No. 6. 9 | 4 | all normals | | all normals |
| ,, | 5 | ,, | | ,, |
| ,, | 7 | 3 : | 1 | |
| ,, | 8 | all normals | | all normals |
| ,, | 9 | ,, | | ,, |
| No. 6. 2 × No. 7. 6 | 6 | 3 : | 1 | |
| ,, ,, | 8 | 263 | 81 | 344 |
| ,, ,, | 12 | 248 | 83 | 331 |
| ,, ,, | 8 | 312 | 117 | 429 |
| ,, ,, | 15 | 3 : | 1 | |

### *Back-crossing of $F_1$ Dark-eyed Moths with extracted Crimson-eyed Moths.*

$F_1$ dark-eyed moths derived from the mating, ♀ crimson × ♂ tetravoltine white, were mated with crimson-eyed males derived from the $F_2$ eggs of the mating, ♀ tetravoltine × ♂ crimson. Each mating, as the theory demands, gave both normal and crimson-coloured eggs in an approximate proportion of 1 : 1, as the figures quoted below shew:

| Number of Matings | Eggs laid | | Totals |
|---|---|---|---|
| | Normals | Crimsons | |
| 8 | all divoltine white | | |
| 9 | 183 | 202 | 385 |
| 11 | 187 | 188 | 375 |
| 12 | 211 | 207 | 418 |
| 13 | 236 | 220 | 456 |
| 19 | 198 | 187 | 385 |
| Totals | 1015 | 1004 | 2019 |
| Expectation | 1009½ | 1009½ | 2019½ |

There are certain normal breeds in vogue which often throw off such crimson-coloured eggs. By the kind help of Mr K. Saito in Ghifu, we obtained two breeds reared in the district of Ghifuken which sometimes gave mixed batches consisting of normal and crimson eggs. The number of normal and crimson eggs respectively found in the batches given by him to us are enumerated below:

| Names of breeds | Number of Batches | Number of normal and crimson eggs found in each batch laid by a parent | | Totals |
|---|---|---|---|---|
| | | Normals | Crimson | |
| Univoltine "Ghinpaku" | 1 | 248 | 84 | 332 |
| ,, ,, | 7 | 413 | 120 | 533 |
| ,, ,, | 8 | 247 | 89 | 336 |
| ,, ,, | 13 | 167 | 73 | 240 |
| Totals | | 1075 | 366 | 1441 |
| Divoltine "Tamanashi" | 1 | 404 | 112 | 516 |
| ,, ,, | 3 | 306 | 141 | 447 |
| ,, ,, | 14 | 367 | 104 | 471 |
| Totals | | 1077 | 357 | 1434 |
| Grand totals | | 2152 | 723 | 2875 |
| Expectation | | 2156¼ | 718¾ | 2875 |

These figures suggest to us at once that the crimson-coloured characteristic is a Mendelian one, recessive to the normal-coloured as is the former crimson breed. We reared these eggs separately in the spring of 1910. Crimson-coloured eggs from two batches of the second breed gave, without any exception, crimson-eyed worms and moths, while normal-coloured gave all normal-eyed worms and moths. Both crimson and normal-eyed moths derived from the mixed batches of the above breeds when paired *inter se* oviposited the following batches:

$N$=normal-eyed; $R$=crimson-eyed moths.

| | Parent Moths | Eggs laid | | |
|---|---|---|---|---|
| Names of breeds | ♀ ♂ | Normals | Crimsons | Totals |
| Univoltine "Ghinpaku" | | | | |
| No. 8. 8 | $N \times N$ | 114 | 45 | 159 |
| No. 8. 9 | $N \times N$ | 334 | 92 | 426 |
| No. 13. 8 | $N \times N$ | 459 | 105 | 564 |
| No. 13. 9 | $N \times N$ | 338 | 106 | 444 |
| No. 13. 10 | $N \times N$ | all normals | | |
| Divoltine "Tamanashi" | | | | |
| No. 1 | $R \times R$ | all divoltine white eggs | | |
| No. 3 | $R \times R$ | ,, ,, ,, | | |
| No. 14, Nos. 8—14 | $R \times R$ | ,, ,, ,, | | |

As the figures shew, certain normal-eyed matings gave all normal dark-coloured eggs while others gave mixed batches (3 normals : 1 crimson).

The lineage of the crimson-eyed matings which yielded all divoltine white eggs remained true to parents in their successive generations, and gave crimson-coloured eggs without exception in the summer brood.

The order of inheritance of these characteristics is in exact accordance with the $F_3$ of a monohybrid cross, and the parental mixed eggs given by Mr Saito were undoubtedly $F_2$ eggs between the crimson and normal-coloured forms. Now we may clearly see that those crimson-coloured characteristics found in the three different breeds are in the same nature and Mendelize in the normal order, the crimson being hypostatic to the normal-coloured one.

*Résumé:*

$R$=crimson; $N$=normal.

$(N \times R)$ (reciprocal)

$F_1$ eggs $N$
$F_2$ ,, $(3N : 1R)$
$F_3$ ,, $N$ $(3N : 1R)$ $R$

$(F_1 \times R)$

$F_2$ ,, $(1N : 1R)$

### *Greater Death-rate of the Crimson-coloured Egg.*

During our experiments with the crimson breeds, either with the original divoltine or other extracted forms from cross-bred or mixed breeds, it has struck us that the number of worms which came out in spring from these eggs was very small, sometimes over 90 °/o were found to be dead; even in the case where the crimson eggs were found mixed with normal ones in the same batch, the mortality is much greater than that of the normal-coloured eggs. We give here certain figures of the death-rate observed in the crimson-coloured eggs laid by some breeds.

Fifteen batches selected at random from 84 crimson-coloured batches laid by the summer brood of the extracted crimson form, from the cross between the divoltine crimson and tetravoltine normal-coloured "Onodahime," gave the following figures:

TABLE VI.

| Number of batches | Total number of eggs laid | Number of dead eggs | Death-rate |
|---|---|---|---|
| 1 | 377 | 341 | 90·4 °/o |
| 2 | 368 | 269 | 73 °/o |
| 3 | 348 | 342 | 98·2 °/o |
| 4 | 439 | 389 | 88·6 °/o |
| 5 | 413 | 405 | 97·1 °/o |
| 6 | 283 | 321 | 88·1 °/o |
| 7 | 379 | 364 | 96 °/o |
| 8 | 277 | 243 | 87·7 °/o |
| 9 | 438 | 318 | 72·6 °/o |
| 10 | 365 | 149 | 40·8 °/o |
| 11 | 254 | 136 | 53·5 °/o |
| 12 | 304 | 244 | 80·2 °/o |
| 13 | 319 | 284 | 89 °/o |
| 14 | 424 | 403 | 95·2 °/o |
| 15 | 446 | 360 | 80·7 °/o |
| Totals | 5434 | 4568 | 84 °/o |

The average death-rate was 84 °/o, ranging from 40·8 °/o to 98 °/o in each batch. In 42 batches of eggs derived from the same breed, we have counted 15,194 eggs, of which 12,796 eggs were found dead in the spring; i.e. a death-rate of 84 °/o.

In the eggs laid by a cross-bred crimson form (a cross between an extracted crimson from the cross, "Divoltine crimson × Divoltine Chiyodzuru," and the crimson derived from the divoltine "Tamanashi") a considerably smaller percentage of dead eggs was noted than in the cross between divoltine crimson and tetravoltine white.

TABLE VII.

| Number of batches | Total number of eggs laid | Number of dead eggs | Death-rate |
|---|---|---|---|
| 1 | 481 | 52 | 10·8 % |
| 2 | 487 | 45 | 9·2 % |
| 3 | 481 | 52 | 10·8 % |
| 4 | 466 | 3 | 0·6 % |
| 5 | 471 | 260 | 55·2 % |
| 6 | 476 | 241 | 50·6 % |
| 7 | 514 | 90 | 17·6 % |
| 8 | 543 | 169 | 31·1 % |
| 9 | 515 | 342 | 66·9 % |
| 10 | 490 | 16 | 3·2 % |
| 11 | 529 | 377 | 71·2 % |
| 12 | 471 | 45 | 9·5 % |
| 13 | 459 | 223 | 48·5 % |
| 14 | 554 | 3 | 0·5 % |
| 15 | 477 | 224 | 47·5 % |
| Totals | 7414 | 2142 | 28·8 % |

In this crimson form the average death-rate is only 28·8 %; in certain matings nearly all the eggs were hatched, while in some others the death-rate mounted as high as 71·2 %.

In other crimson batches laid by an extracted crimson form derived from a cross between the divoltine crimson and "*E* III" breed (an extracted breed from a cross between the wild mulberry silk-worm and tetravoltine "Tōbuhime"), the figures quoted below were given:

TABLE VIII.

| Number of batches | Total number of eggs laid | Number of dead eggs | Death-rate |
|---|---|---|---|
| 1 | 234 | 181 | 77·3 % |
| 2 | 383 | 348 | 90·8 % |
| 3 | 335 | 102 | 30·4 % |
| 4 | 467 | 329 | 70·4 % |
| 5 | 360 | 66 | 18·3 % |
| 6 | 248 | 192 | 79·0 % |
| 7 | 326 | 303 | 92·9 % |
| 8 | 261 | 233 | 89·2 % |
| 9 | 362 | 199 | 54·9 % |
| 10 | 277 | 153 | 55·2 % |
| 11 | 394 | 283 | 71·8 % |
| 12 | 313 | 279 | 89·1 % |
| 13 | 340 | 322 | 94·7 % |
| 14 | 391 | 341 | 87·2 % |
| 15 | 374 | 355 | 94·9 % |
| Totals | 5065 | 3686 | 72 % |

In this form the death-rate is 72 °/o, varying, in individual cases, from 18·3 °/o to 94·9 °/o.

We have observed moreover that the death of the embryo inside the egg took place in its earlier stage. So we often found some dead eggs in August or September when a white patch appeared in one side of the egg (Fig. 8) which gradually became enlarged in size and at last the clear crimson colour became paler, while others were found dead after the embryo had completely developed. The majority of the deaths seem to occur, however, in the earlier developmental stage of the embryo.

Even in the same breed, the death-rate differed greatly according to the colour of the egg, and the voltine characters. Hence the divoltine white eggs laid by the very same breed which laid the eggs recorded in Table VI yielded a much smaller number of dead eggs than in the univoltine coloured eggs. Ten batches of eggs selected at random from fifty divoltine white egg-batches gave the following figures:

TABLE IX.

| Number of batches | Total number of eggs laid | Number of dead eggs | Death-rate |
|---|---|---|---|
| 7 | 191 | 60 | 31·4 °/o |
| 8 | 361 | 18 | 4·9 °/o |
| 9 | 111 | 51 | 45·9 °/o |
| 10 | 329 | 168 | 51 °/o |
| 11 | 272 | 196 | 72 °/o |
| 12 | 309 | 12 | 3·8 °/o |
| 13 | 186 | 18 | 9·6 °/o |
| 13*a* | 272 | 164 | 61·4 °/o |
| 14 | 413 | 64 | 15·5 °/o |
| 15 | 381 | 78 | 20·8 °/o |
| Totals | 2825 | 829 | 29·3 °/o |

that is to say, the average death-rate is 29·3 °/o, which varies from 3·8 °/o to 72 °/o in individual batches. The average death-rate found in fifty batches of eggs laid by the same breed is 19 °/o, while in the case of univoltine eggs it is 84 °/o, as already recorded in Table VI. In certain cases it occurred that some crimson-coloured eggs hatched in the summer. The death-rate of such divoltine crimson-coloured eggs was nearly the same as that of the white divoltine eggs.

Even more striking facts were observed when we examined the number of dead eggs found in the batches in which three different coloured eggs, normal, crimson, and albino, were found. These are the $F_2$ eggs laid by the cross, "$H_4$" albino and the divoltine crimson breed.

TABLE X.

| Number of batches | Normal eggs | | | Crimson eggs | | | Albino eggs | | |
|---|---|---|---|---|---|---|---|---|---|
| | Total number of eggs | Dead eggs | Death-rate | Total | Dead | Death-rate | Total | Dead | Death-rate |
| 1 | 194 | 33 | 17 % | 95 | 77 | 81 % | 91 | 12 | 13·1 % |
| 2 | 209 | 64 | 30·5 % | 66 | 49 | 74·2 % | 86 | 7 | 8·1 % |
| 3 | 195 | 23 | 13·8 % | 99 | 76 | 76·7 % | 88 | 30 | 34 % |
| 4 | 213 | 23 | 10·7 % | 75 | 61 | 81·3 % | 99 | 22 | 22·2 % |
| 5 | 213 | 79 | 37 % | 94 | 62 | 64·8 % | 87 | 5 | 5·7 % |
| Totals | 1024 | 222 | 21·6 % | 429 | 325 | 75·7 % | 451 | 76 | 16·8 % |

In spite of their being laid by the same parents, the mortality in those eggs whose colour was crimson was much greater than the others. While in normal and white-coloured eggs, the percentage of deaths was only 21·6 % and 16·8 % respectively, that of the crimson eggs was 75·7 %. Other ten similar batches gave the following figures:

| | Normal eggs | Crimson eggs | Albino eggs |
|---|---|---|---|
| Total number | 2315 | 956 | 1076 |
| Number of dead eggs | 406 | 650 | 288 |
| Death-rate | 17·5 % | 67·9 % | 26·7 % |

The facts above enumerated taught us that in every case in every breed which we have studied, those eggs coloured crimson have a greater death-rate than normal-coloured eggs, while divoltine eggs which are crimson in colour did not shew so high a death-rate as univoltine crimson-coloured eggs. These facts led us to conclude that the embryo of crimson-coloured eggs is not so long-lived as that in the normal-coloured eggs.

As to the cause of the early death of the embryo of the crimson-coloured eggs, we are quite ignorant at present, but we are inclined to believe that it may be due to the lack of certain pigments in the serosa which in some way help the respiration of the embryo during its development.

## V. GENERAL CONSIDERATIONS.

From the results of these series of experiments in both line and cross breedings above quoted, it now becomes clear that (1) those egg-characteristics above enumerated, except in the crimson breed, are determined by the characteristics of the female parent, on account of which the paternal characteristics even when dominant are almost negligible in their influence upon the character of the egg, that is to say, phenomena of inheritance are maternal; (2) gametic segregation of parental characteristics takes place as in normal Mendelian allelomorphism; and (3) in certain generations, both parental characteristics even when inbred give rise to the antagonistic characteristics which at first suggests that there is a departure from the normal rules.

Suppose, now, there are certain Mendelian characteristics which behave as maternal in inheritance. If they were reciprocally mated, what would be the result as regards their offspring? Let $D$ represent a dominant and $R$ a recessive factor, the results of their reciprocal matings would be diametrically opposite. In the case of a $D$ female mated with an $R$ male, the resulting $F_1$ eggs would be all $D$, while an $R$ female mated with a $D$ male would give all $R$ $F_1$ eggs, in spite of their zygotic constitutions being the same in both matings, namely, $DR$. And therefore, all the worms and moths derived from the $F_1$ $D$ or $R$ eggs will have the constitution $DR$, in which the $D$ behaves as an active factor in determining their characteristics. In the same way the egg-cell which has the composition of $DR$ during its development in the parent body is influenced by the $D$ factor only, and consequently after segregation, when it lost the antagonistic factor and became pure $D$ or $R$, it retains the $D$ characteristic before acquired. Thus the results of fertilization will be the production of all normal-coloured $F_2$ batches.

Zygotically considered, however, the $F_2$ $D$ eggs are not the same in their constitution. As the result of the fertilization, some of them will be $DD$, some $DR$ and the rest $RR$. Consequently, the constitution of the $F_2$ moths derived from the $F_2$ $D$ eggs will be a mixture of $DD$, $DR$ and $RR$. Thus all the $F_2$ eggs, whether fertilized with $D$ or $R$ spermatozoon, will be all $D$ characterized.

As there is no means in this case of distinguishing a $DD$ worm or moth from a $DR$ or an $RR$, random matings between them are expected to occur. The result will be as below:

| | | | Colour of the $F_3$ eggs laid | Zygotic composition of the egg |
|---|---|---|---|---|
| 1. | *a.* | ♀ $DD$ × ♂ $DD$ = | $D$ | $DD$ |
| | *b.* | ♀ $DD$ × ♂ $DR$ = | $D$ | $(DD+DR)$ |
| | *c.* | ♀ $DD$ × ♂ $RR$ = | $D$ | $DR$ |
| 2. | *a.* | ♀ $DR$ × ♂ $DD$ = | $D$ | $(DD+DR)$ |
| | *b.* | ♀ $DR$ × ♂ $DR$ = | $D$ | $(DD+DR+RR)$ |
| | *c.* | ♀ $DR$ × ♂ $RR$ = | $D$ | $(DR+RR)$ |
| 3. | *a.* | ♀ $RR$ × ♂ $DD$ = | $R$ | $DR$ |
| | *b.* | ♀ $RR$ × ♂ $DR$ = | $R$ | $(DR+RR)$ |
| | *c.* | ♀ $RR$ × ♂ $RR$ = | $R$ | $RR$ |

In some cases female $DD$ moths will mate with $DD$, $DR$ or $RR$ males (series 1), in some others $DR$ females will mate with the same three kinds of males (series 2). The same holds good in the case of $RR$

females (series 3). The $F_3$ eggs laid by the first and the second series of matings will be all $D$ batches, since all females are $DR$ or $DD$. For the same reason, the third series of matings will give all $R$ batches. *The* $F_3$ *eggs* derived from the $F_2$ moths paired *inter se* will be, therefore, a *mixture of* $D$ *and* $R$ batches in certain proportions. If we assume that the number of males and females found in each batch is nearly the same, the proportion of $D$ and $R$ batches laid by *inter se* moths derived from an $F_2$ $D$ batch would be $6D : 3R$ or $2D : 1R$.

As in the case of the $F_2$, the zygotic constitution of $F_3$ $D$ and $R$ batches is not simple $D$ or $R$. As the formulae quoted just above shew, the constitution of certain $F_3$ $D$ batches is $DD$ (series 1 *a*), some batches $DR$ (series 1 *c*), some a mixture of $DD$ and $DR$ (series 1 *b* and series 2 *a*), or $DR$ and $RR$ (series 2 *c*), and the rest $DD$, $DR$ and $RR$ (series 2 *b*). We get similar results in the case of the $F_3$ $R$ eggs, some batches being $DR$ (series 3 *a*), some (series 3 *c*) $RR$, and the rest (series 3 *b*) a mixture of $DR$ and $RR$.

If moths derived from $F_3$ $D$ or $R$ batches were inbred, what will be the result in the dominant series?

In $F_3$ $D$ batches, as we have already observed, there are five different kinds of batches whose zygotic compositions are respectively: (1) $DD$, (2) $(DR+DD)$, (3) $DR$, (4) $(DD+DR+RR)$, (5) $(DR+RR)$. The moths derived from each kind paired *inter se* will produce the following $F_4$ batches:

| Mating | | Zygotic composition | Outward appearance of $F_4$ eggs |
|---|---|---|---|
| 1. $DD$ *inter se* $= DD \times DD =$ | | $DD$ | $D$ |
| 2. $(DR+DD)$ *inter se* $=$ | 1. | ♀ $DR \times$ ♂ $DR=(DD+DR+RR)$ | $D$ |
| | 2. | ♀ $DR \times$ ♂ $DD=(DD+DR)$ | $D$ |
| | 3. | ♀ $DD \times$ ♂ $DD=DD$ | $D$ |
| | 4. | ♀ $DD \times$ ♂ $DR=(DD+DR)$ | $D$ |
| 3. $DR$ *inter se* $=$ | | ♀ $DR \times$ ♂ $DR=(DD+DR+RR)$ | $D$ |
| 4. $(DD+DR+RR)$ *inter se* $=$ | 1. | ♀ $DD \times$ ♂ $DD=DD$ | $D$ |
| | 2. | ♀ $DD \times$ ♂ $DR=(DD+DR)$ | $D$ |
| | 3. | ♀ $DD \times$ ♂ $RR=DR$ | $D$ |
| | 4. | ♀ $DR \times$ ♂ $DD=(DD+DR)$ | $D$ |
| | 5. | ♀ $DR \times$ ♂ $DR=(DD+DR+RR)$ | $D$ |
| | 6. | ♀ $DR \times$ ♂ $RR=(DR+RR)$ | $D$ |
| | 7. | ♀ $RR \times$ ♂ $DD=DR$ | $R$ |
| | 8. | ♀ $RR \times$ ♂ $DR=(DR+RR)$ | $R$ |
| | 9. | ♀ $RR \times$ ♂ $RR=RR$ | $R$ |
| 5. $(DR+RR)$ *inter se* $=$ | 1. | ♀ $DR \times$ ♂ $DR=(DD+DR+RR)$ | $D$ |
| | 2. | ♀ $DR \times$ ♂ $RR=(DR+RR)$ | $D$ |
| | 3. | ♀ $RR \times$ ♂ $DR=(RR+DR)$ | $R$ |
| | 4. | ♀ $RR \times$ ♂ $RR=RR$ | $R$ |

Thus the $F_4$ eggs laid by the moths of the dominant series will be all $D$ in certain lineages while in others they will be a mixture of both $D$ and $R$ batches in different proportions.

In like manner, $F_3$ moths derived from the $F_3$ $R$ batches which consist of (1) $DR$, (2) $(DR+RR)$, and (3) $RR$ batches, when inbred will produce the following $F_4$ eggs:

| Mating | | Zygotic composition of egg-batches | Outward appearance of egg-batch |
|---|---|---|---|
| 1. *DR inter se* | | $♀ DR \times ♂ DR = (DD + 2DR + RR)$ | $D$ |
| 2. *(DR + RR) inter se* | 1. | $♀ DR \times ♂ DR = (DD + DR + RR)$ | $D$ |
| | 2. | $♀ DR \times ♂ RR = (DR + RR)$ | $D$ |
| | 3. | $♀ RR \times ♂ DR = (DR + RR)$ | $R$ |
| | 4. | $♀ RR \times ♂ RR = RR$ | $R$ |
| 3. *RR inter se* | | $♀ R \times ♂ R = RR$ | $R$ |

The $F_4$ eggs laid by the moths derived from $F_3$ $R$ eggs will be all $D$ batches in certain lineages, while there will be a mixture of $D$ and $R$ batches in some other lineages, and all $R$ batches in the remainder.

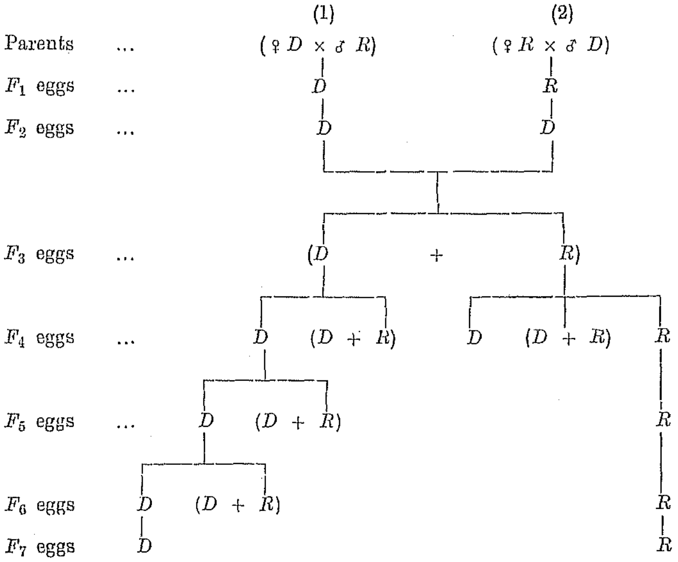
If we continually eliminate the lineage which produced the antagonistic characterized batches in this way in both series, each of them may be established as a constant or homozygous form. In the dominant series, the lineages which give all $F_4$ $D$ batches are three, namely: No. 1 or $DD$ series, No. 2 or $(DD+DR)$ and No. 3 or $DR$. If they are inbred, Series No. 3 would give mixed $F_5$ batches which are to be discarded from the dominant series, while the other two would give all $F_5$ $D$ batches. In $F_6$, those from No. 2 will disintegrate into their components, $D$ and $R$, and those which produced all $F_6$ $D$ batches will be the descendants of Series No. 1, or a lineage $DD$, which is a homozygous dominant from their first appearance.

To extract a homozygous dominant form from these series of crosses the elimination of six consecutive generations will be required, except when we luckily happen to pick out the lineage of $DD$ series, in which case we are able to get it in a constant form in a much less number of generations.

In the recessive series, however, if we select the lineage which produced all $R$ batches in $F_4$, the $R$ form is easily established as a constant form, since the zygotic composition of this series is $RR$.

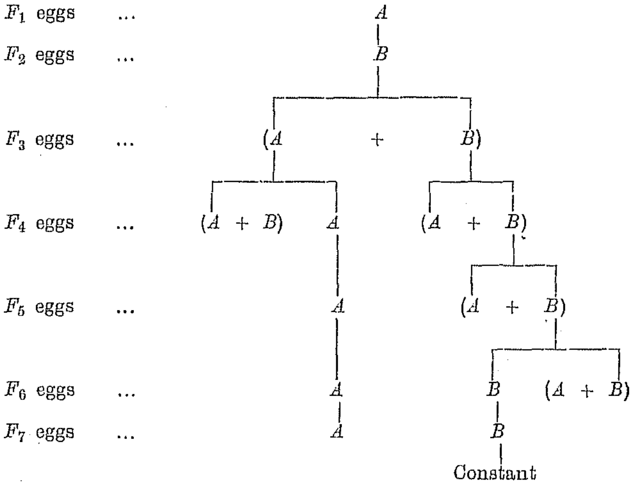
This is what we might expect to find according to Mendelian principles if the characteristic behaved as maternal in inheritance. If the $D$ form consists of two or more factors, disintegration of factors will

*Graphical résumé of the phenomena of inheritance above described.*



take place even after it is freed from the antagonistic recessive factor. We shall now try to compare the results obtained by us with those demanded by the theory.

First we shall quote here the results of inbreedings mentioned in the first part of this paper which are represented in the following scheme:



In this scheme, if we replace $A$ by $R$ and $B$ by $D$ we shall see that the results actually obtained and those calculated come in the same category, the whitish grey being dominant to the normal, and the brown and the spindle-shaped characteristics being recessive to normals. As to the yellow and white colours of newly laid eggs, the former is dominant to the latter.

Crosses between *Bombyx mori*, L. and *Theophila mandarina*, M., which gave the result mentioned below:

| | | (1)<br>(Theophila × Bombyx) | (2)<br>(Bombyx × Theophila) |
|---|---|---|---|
| $F_1$ eggs | ... | all *Theophila* colour | all *Bombyx* colour |
| $F_2$ eggs | ... | *Theophila* type | *Theophila* type |

may come in the same category, the *Theophila* colour being dominant towards that of the *Bombyx*.

### *Back-crossing.*

If females derived from the $F_1$ $D$ eggs were mated with the parental recessive form, we should expect to have the combination $♀\ DR \times ♂\ RR$, which gives all $D$ eggs, while in the reversed mating we should expect all $R$ eggs, in spite of the zygotic composition being a mixture of $DR$ and $RR$ in an equal proportion in both cases, since the maternal characteristic predetermines the egg-character. Of moths derived from the $D$ eggs, some will be, therefore, $DR$ in their constitution and the others $RR$. As we have however no means of distinguishing $DR$ males or females from $RR$ males or females, we must expect to have random matings between these two forms which will result in the following combination:

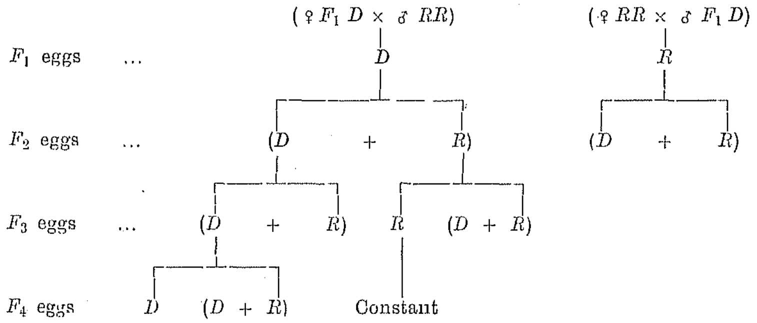
| | | Zygotic composition of egg-batches | Outward appearance of egg-batches |
|---|---|---|---|
| 1. | *a.* | $♀\ DR \times ♂\ DR=(DD+DR+RR)$ | $D$ |
| | *b.* | $♀\ DR \times ♂\ RR=(DR+RR)$ | $D$ |
| 2. | *a.* | $♀\ RR \times ♂\ DR=(DR+RR)$ | $R$ |
| | *b.* | $♀\ RR \times ♂\ RR=RR$ | $R$ |

Hence in this generation, certain matings will give all $D$ batches, others will give all $R$ batches.

As the formulae above mentioned shew, the $D$ and $R$ eggs are heterozygous except No. 2 *b* which is homozygous, and therefore the moths which came out from them even when paired *inter se* among those from the same batch would produce antagonistic eggs again.

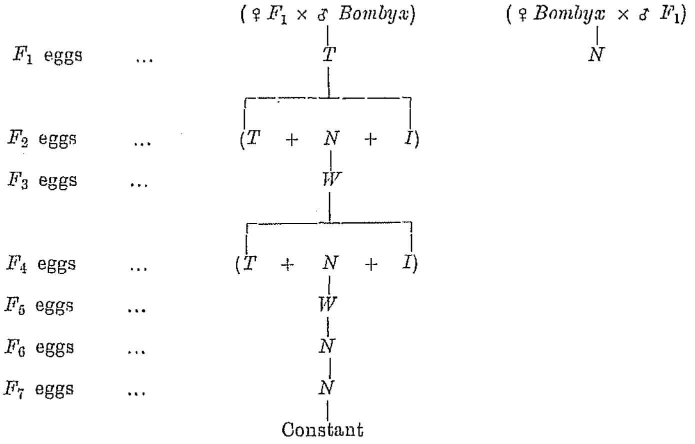
The further posterity of the lineages above mentioned will follow exactly the same course mentioned in the case of matings Nos. 4 and 5 (see page 393).

Thus the result of back-crossing may be summarized in the following scheme:



This expectation was realized by the results of back-crosses between the *Theophila-Bombyx* $F_1$ moths and pure *Bombyx* ones which are quoted below:

$T$=green-shaded eggs like those laid by *Theophila-Bombyx* $F_1$ moths.
$W$=divoltine white eggs; $N$=normal *Bombyx* eggs.
$I$=intermediate forms between *Theophila* and *Bombyx* or mixture.

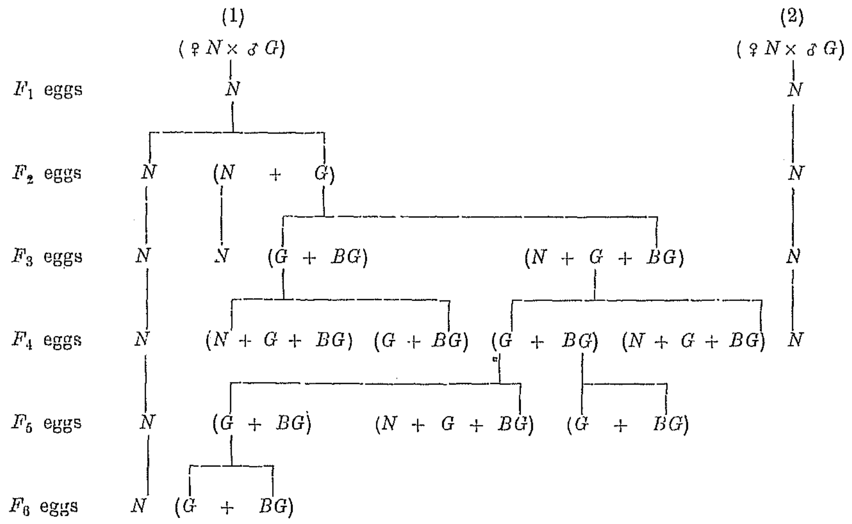


As the figures shew the result actually obtained by experiments is in perfect accordance with that demanded by the theory except for the appearance of the antagonistic characteristics in the $F_4$ of *Bombyx* typed or recessive series. This is due, I think, to the presence of divoltine white character which prevents the elimination of the antagonistic character in $F_3$ eggs.

By similar reasoning, we can explain the results obtained by crosses between males of the grey variant No. 24 and females of the normal-egged breed.

In these crosses, as we have already seen, certain matings gave no grey eggs, while some gave both normal and grey batches in the order mentioned below:

$N$ = normal-egged batch; $G$ = grey-egged batch; $BG$ = $B$-grey.

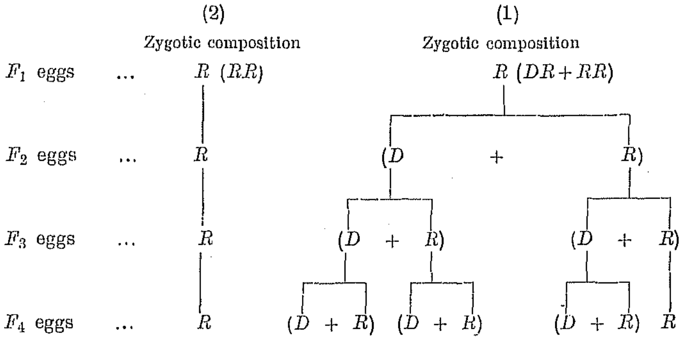


Before attempting to explain this result it will be necessary to note here that the grey variant No. 24 was picked out from certain normal-egged breeds in which a few batches of this variant sometimes appear, and consequently it is proper to consider it to be a heterozygous form. Let us suppose that the grey No. 24 batch is derived from such matings as (♀ $DR$ × ♂ $RR$), which give all $D$ eggs. In this case the constitution of the egg batch $D$ will be $(DR + RR)$. If normal-egged females which are recessive to the grey were mated with males derived from this $D$ batch, the following gametic combinations will be expected:—

1. ♀ $RR$ × ♂ $DR = F_1$ $R$ eggs $= (DR + RR)$.
2. ♀ $RR$ × ♂ $RR = F_1$ $R$ eggs $= (RR)$.

$F_1$ eggs laid by those matings are all $R$, but their zygotic constitutions are different from each other, as we easily see from the formulae above shewn. The resulting $F_2$ eggs will, therefore, be in some matings (No. 1) a mixture of $D$ and $R$ batches and in others (No. 2) all $R$. The lineage which gave all $F_2$ $R$ batches will remain true to parents in the succeeding generations, while another lineage which gave $D$ and $R$ batches in $F_2$ will again disintegrate into its components in the same way as we have already described in previous pages. The order of their inheritance will be as follows:

(♀ $N$ × ♂ grey variant No. 24.)



Here both actual and theoretical results, as in the former cases, agree perfectly in every respect.

Similar phenomena of maternal inheritance had already been observed in certain seed-characteristics of wheat by Biffen, of peas and maize by Bateson, Correns, Lock, Tschermak, etc. For instance, certain indented peas reciprocally crossed with the round gave the following results:

| | | (♀Indent × ♂ Round) | (♀ Round × ♂ Indent) |
|---|---|---|---|
| $F_1$ seeds | ... | Indent | Round |
| $F_2$ seeds | ... | Indent | Indent |
| $F_3$ seeds | ... | (Indent + Round) | (Indent + Round) |

In certain cases, however, strict segregation took place or an intermediate form was produced in $F_2$. It was, moreover, mentioned that in certain varieties those characteristics behaved quite normally in inheritance, namely, $F_1$ seeds are all indents which in $F_2$ segregate into three indents to one round.

Hence we are led to say that certain characteristics of the eggs of animals and of the seeds of plants behave in inheritance in a similar way.

We shall discuss in our next paper the appearance of intermediate or mixed batches in certain line- or cross-breedings, a fact which seems to be inconsistent with maternal inheritance. We are at present collating the facts gathered from certain experiments which we have just concluded, and from the trend of our results up to the present, we will, we think, be able to put forward a satisfactory explanation of this phenomenon. We merely, at present, say that this appearance is not really contradictory to the maternal inheritance.

### *Causes of Maternal Inheritance.*

Concerning certain characteristics such as the whitish grey, spindle-shaped, or yellow and white colour of newly laid eggs whose origin is due to the shell or yolk which are entirely derived from the maternal body, the maternal inheritance is the natural consequence, and may be compared with the inheritance of certain characteristics of the seed-coat of plants which are of purely maternal origin.

Concerning the colour of the egg, whose origin is due to the special pigments deposited in the serosa, the case is quite different. As the serosa is formed of cells derived from the conjugation of paternal and maternal nuclei, the egg-colour ought to be influenced by the paternal characteristics if they are dominant, but, as we see, it is entirely maternal in certain colours, such as the reddish brown, blue, normal colour, etc.

Nothing is as yet known as to why these serosa characteristics behaved as maternal in inheritance. We are now waiting the results of the further series of experiments which we have been engaged upon concerning this question.

There are other characteristics of the silk-worm which behave maternally in inheritance. They are the brood characters such as uni-, di-, or multivoltine, or "voltinism" of the silk-worm. The fact of maternal inheritance of these characteristics was first observed by me (1906) and was proved by McCracken (1909), who was led to the conclusion that the order of inheritance was non-Mendelian, while Castle (1910), upholding the fact that they are maternal in inheritance, says that univoltinism is a Mendelian dominant to divoltinism.

### *Voltinism.*

McCracken's results may be compared with those obtained by us in the series of experiments above referred to, but in the case of voltinism, as there are many causes disturbing the proper elimination of parental characteristics which are entirely neglected by her, it is rather premature to consider the phenomena of inheritance displayed by the character "voltinism" as non-Mendelian. We enumerate here those disturbing causes: (1) divoltine character may easily be changed by the influence of temperature during the incubation of the egg, more strictly, during the embryonal stage after sexual cells are liberated from the mesodermal tissue. If we expose eggs at this stage to a temperature of about 60—65° F. or lower until hatching, all the moths derived from them will lay divoltine whitish eggs; on the contrary, if we subject them to a temperature of 80° F. or more, all the eggs will become univoltine coloured ones. This is a well-known fact among Japanese breeders and has been made use of for industrial purposes for the last twenty years. (2) The eggs laid by the second brood of the divoltine breed are identical in appearance with the univoltine eggs and hibernate without hatching. In the case of crossing, we are, therefore, unable to eliminate divoltine characterized eggs from the univoltine in every alternate generation. (3) The maternal inheritance referred to above, which also prevents the proper elimination of antagonistic characters.

These are the causes why, I think, the character " voltinism " behaved so irregularly that McCracken considered it to be non-Mendelian. Generally speaking, I believe, the order of inheritance of the " voltinism " of the silk-worm will follow the course before mentioned in our scheme.

In a later paper I propose to give a fuller account of the phenomena connected with voltinism.

Before concluding this paper, I wish to express my sincere thanks to Prof. W. Bateson who has kindly assisted me in many ways when preparing this paper for press. Thanks are also due to Mr S. Hashimoto, assistant in our laboratory, who has helped me in rearing the worms used in our experiments since 1906.

## VI. SUMMARY.

1. In the egg of the silk-worm there are certain special characteristics of shape, colour, etc. which differ in different breeds or even in the same breed. Japanese green breeds generally lay green-shaded eggs varying in depth of colour, often mixed with normal coloured ones. Most of the Chinese and European breeds lay similar green-shaded eggs, both of them, however, being distinguishable from each other by special lustres and shades. Eggs of the Japanese normal breeds are, however, brownish slate shaded with some light pink or purple.

Among the eggs laid by Japanese normal-egged breeds we often find many variants in shape and colour, a smaller number of the variant being sometimes found in a batch, frequently in Mendelian proportions,

while in other cases the whole of a batch will be found to consist of a variant.

2. Breeding experiments were made on the following egg-characteristics:

1. Greenish-shaded *Theophila* colour (Fig. 10).
2. Various green colours of Japanese green and some Chinese or European breeds (Fig. 6).
3. The reddish brown variant derived from the normal-egged breed (Fig. 2).
4. The blue variant from the normal breed (Fig. 5).
5. The whitish grey variant from the normal breed (Fig. 4).
6. The spindle-shaped variant from the normal breed (Fig. 13).
7. The crimson variant from the normal breed (Figs. 7 and 8).
8. Yellow, brownish-shaded yellow and white colours of newly laid eggs of the yellow and white cocoon breeds (Fig. 9).
9. The brownish slate colour of Japanese normal breeds (Figs. 1, 3, and 11).

3. Some of these characteristics such as the normal brownish-slate, reddish brown, blue, crimson, etc., arose from the special pigments deposited in the serosa, which is produced by the conjugation of parental nuclei, while others, such as whitish grey, spindle-shaped or the colour of newly laid eggs are due to the shell or yolk which are of purely maternal origin. The colour of greenish-shaded eggs, such as are found in Japanese green breeds, and some Chinese or European breeds, is mostly derived from the serosa, but it is more or less influenced by the colour of the shell which is slightly tinted with green, or some other colours.

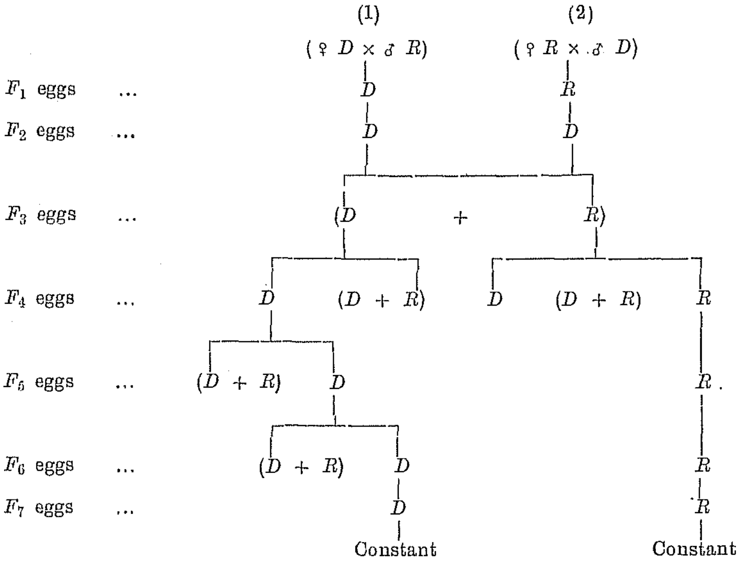
4. Those characteristics, in spite of the fact that their origin is different, behave in the same way as regards inheritance, except the crimson-coloured variant, which Mendelize in the normal order. The order of inheritance is represented in the following schemes (page 403).

The order of inheritance represented by the first scheme seems to be non-Mendelian, but really it is Mendelian, the cause of the disturbance of the proper order being due to the fact of maternal inheritance, in which paternal characteristics remain dormant, even dominant ones, in the egg stage.

## (1)

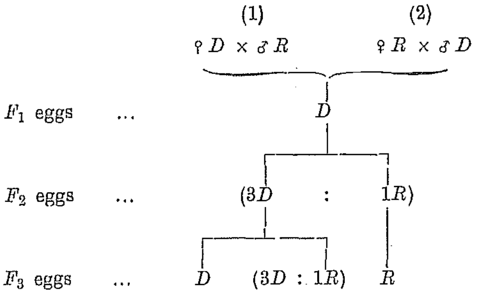
The case where characteristics behaved maternally in inheritance, such as normal, reddish brown, grey, etc.

$D$ = dominant ; $R$ = recessive characteristics.



## (2)

The case where characteristics behaved in normal Mendelian order, such as the crimson colour.



In the former scheme, the $D$ represents dominant coloured batches, the $R$ recessive and $(D+R)$ a mixture of both $D$ and $R$ batches, while in the latter the $D$ and $R$ represent a single batch of $D$ and $R$ eggs and the $(3D : 1R)$ a mixed batch consisting of $D$ and $R$ in the proportion of 3 : 1.

5. The hereditary relations of those characteristics above enumerated: as to the shape, the whitish grey is dominant towards the Japanese normal which is in turn dominant to the spindle-shaped characteristic. As regards the colour, the greenish slate stands first in dominancy, next comes the Japanese normal brownish slate; hypostatic to it comes perhaps the blue and then reddish brown and lastly the crimson. In the colours of newly laid eggs, the white is hypostatic to yellow or brownish yellow. The relation between the normal and the crimson is the ordinary Mendelian one, the former being epistatic to the latter.

6. In the crimson-coloured eggs extracted from various breeds or crosses, the death-rate is always much greater than that of eggs from the normal, or albino breeds. Even when those three kinds of eggs are laid by the same parent, the same is the case. In divoltine crimson breeds, the divoltine white eggs laid by the spring or first brood are much healthier than those crimson-coloured eggs laid by the summer or second brood.

7. The phenomena of inheritance observed in the eggs of the silkworm may be well compared with those observed in certain seed-characteristics of plants, such as maize, peas, wheat, etc.

## EXPLANATION OF PLATE XX.

Fig. 1. Normal-coloured egg of divoltine "Shinkawachi."
Fig. 2. Reddish-brown variant from divoltine "Shinkawachi."
Fig. 3. Normal-coloured egg of the original breed of the whitish-grey variant.
Fig. 4. Whitish-grey variant.
Fig. 5. Blue variant derived from divoltine "Kuni-nishiki."
Fig. 6. Green-shaded egg from the Japanese green breed.
Fig. 7. Crimson-coloured variant.
Fig. 8. Dead egg of the crimson variant.
Fig. 9*a*. Newly laid egg of tetravoltine white.
Fig. 9*b*. Newly laid egg of tetravoltine yellow.
Fig. 10. Egg of *Theophila mandarina*.
Fig. 10*a*. Matured egg.
Fig. 10*b*. Newly laid egg.
Fig. 11. $F_1$ eggs between female divoltine "Shinkawachi" and male *Theophila mandarina*.
Fig. 12. $F_2$ eggs of the above mating.
Fig. 13. Batch of spindle-shaped eggs laid by a moth.

Every figure except No. 13 is very much magnified, actual size being about 1·15 mm. in length and 0·95 mm. in breadth.

## LITERATURE CITED.

1. BATESON, W. *Mendel's Principles of Heredity*, 1909.
2. BAUR, E. *Einführung in die experimentelle Vererbungslehre*, 1911.
3. BIFFEN, R. H. "Mendel's Law of Inheritance and the Wheat Breeding." *Journ. Agric. Sci.* Vol. I. No. 1, 1905.
4. CASTLE, W. E. "The Effect of Selection upon Mendelian Characters manifested in one Sex only." *Journ. of Exp. Zool.* Vol. VIII. No. 2, 1910.
5. CORRENS, C. "Bastarde zwischen Maisrassen." *Bibliotheca Botanica*, 1901.
6. LOCK, H. "Studies in Plant Breeding in the Tropics." II and III. *Ann. Roy. Bot. Gard., Peradeniya*, Vol. III. 1906.
7. M^cCRACKEN, J. "Heredity of the Race-characters Univoltinism and Bivol tinism in the Silk-Worm. A case of non-Mendelian Inheritance." *Journ. of Exp. Zoology*, Vol. II. No. 4, 1909.
8. TOYAMA, K. "The Hybridology of Insects. I. On some Silk-Worm Crosses, with special reference to Mendel's Law of Heredity." *Bulletin of the College of Agriculture, Tokyo Imperial University*, Vol. VII. 1906.
9. ——. "On the Polygamous Habit of the Silk-Worm." *Ibid.* 1906.
10. ——. "A Sport of the Silk-Worm, and its Heredity Behaviour." *Ibid.* 1909.
11. ——. "On Varying Dominance of certain White Breeds of the Silk-Worm." *Zt. f. indukt. Abst.- und Vererbungslehre*, Bd. VII. Nr. 3, 4, 1912.
12. TSCHERMAK, E. "Über die gesetzmässige Gestaltungsweise der Mischlinge." *Zt. f. d. landw. Versuchw. in Osterr.* 1902.

---

CAMBRIDGE: PRINTED BY JOHN CLAY, M.A. AT THE UNIVERSITY PRESS