Title	A STUDY OF MENDELIAN FACTORS IN THE SILKWORM, BOMBYX MORI
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Citation	The journal of the College of Agriculture, Tohoku Imperial University, Sapporo, Japan, 5(4), 91-113
Issue Date	1913-03-30
Doc URL	https://hdl.handle.net/2115/12514
Type	departmental bulletin paper
File Information	5(4)_p91-113.pdf

A STUDY OF MENDELIAN FACTORS
IN THE
SILKWORM, BOMBYX MORI.

By

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With Pl. VIII.

It can not be too much emphasized that in the study of herdedity experimentation is of the highest importance, but at the same time it goes without saying that its results must be subjected into an analysis, so to speak, from a theoretical point of view, for mere accumulation of data does not afford us a clue as to the nature of phenomena with which we are concerned.

Through the investigations of COUTAGNE, TOYAMA, KELLOGG, QUAJAT, MC CRACKEN and ISHIWATA, many interesting facts have been brought to light regarding the phenomena of inheritance in silkworms, the characters, studied being larval markings, cocoon colours, wing colours in the moth[1], colour and other properties of eggs[2], "ant" colours[3], and furthermore, some physiological peculiarities, namely voltinism[4] and .moultinism[5]. But it is worth noting that by those authors much attention was not paid to the theoretical

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[1] Melanic and whitish wing patterns.

[2] Adhesiveness and non-adhesiveness.

[3] Black and brown "ants." ("Ant" means newly hatched larva.)

[4] Univoltinism and bivoltinism. By univoltinism we mean that the worm completes only one generation in a year, while by bivoltinism it is meant that two generations are completed in a year.

[5] Tri-moultinism and tetra-moultinism. For the sake of convenience, I use the term voltinism with a numerical prefix to designate number of moulting, e. g. tri-moultnism and tetra-moultinism denote three and four moultings respectively.

side of the question, Prof. TOYAMA being, as far as I am aware, the only author who explained his results by Mendelian factors. Generally speaking, however, his system of analysis seems to have been based on the original view of MENDEL, who considered that "there was a factor corresponding to the dominant character and another factor corresponding to the recessive character of each alternative pair of unit-characters, and the characters were alternative because no gamete could carry more than one of the two factors belonging to the alternative pair". (PUNNET, 1911, p. 28.)

In the following page I shall quote the experimental results of Prof. TOYAMA and other authors and try to show that they can be interpreted with no difficulty on a more recent hypothesis, the presence and absence hypothesis, now generally accepted by students of genetics.

By the way it may be noted here that I have been also engaging upon a series of hybridization experiments with the silkworm during the last few years and that the results so far obtained, differing greatly at some points from what has been reported by the above-named investigators, will be described in another paper in this journal.

Toyama's Results and His Factors.

In a paper published in 1906* dealing with the inheritance of larval markings, cocoon colours, and other characters in the silkworm, Prof. TOYAMA uses in the case of monohybridism symbols **D** and **R** to denote a dominant and a recessive character respectively, while in the case of dihybridism he assumes a factor for each character. On this assumption all the cases were explained without difficulty. But he met with two complex cases which he describes as "modified dihybrids".

1. First example of the "modified dihybrids".

In a cross, Japanese white ♀ × Siamese yellow ♂, he obtained uniform yellow-cocooners in F_1, which consisted of the following four classes behaving differently in production of F_2 offspring.

F_1	F_2
Class 1.	Yellow only.
" 2.	3 yellow : 1 white.
" 3.	3 yellow : 1 salmon[1].
" 4.	9 yellow : 3 salmon : 4 greenish white to pure white.

The yellows of the fourth class consisted again of four categories, a certain of which splitting in F_3 into three forms, yellow, salmon and greenish to pure white in the ratio given above. But as regards how such a remarkable case of Mendelian inheritance is brought about, Prof. TOYAMA offers no interpretation.

2. Second example of the "modified dihybrids".

The cross between Japanese common white females and Siamese zebra[2] white males produced in F_1 in some cases (1) only zebra-patterned, in other cases (2) zebra and common in equal numbers, and in still other cases (3) zebra, common and plain[3] in the ratio 2 : 1 : 1. Zebras of the first class, when inbred, yielded three F_2 forms in the proportion of 12 zebra : 3 common : 1 plain.

Here TOYAMA assumes that there exist three definite factors, namely:

Zebra-ness (**S**), Commonness (**C**), Plainness (**N**),

the parental cross being:

$$(\mathbf{C} + \mathbf{N}) \times (\mathbf{S} + \mathbf{N}).$$

He remarks: "In this combination, we take for granted that both the characters in the parenthesis sometimes act as a whole character, sometimes as separate characters". Thus in cases the gametic combination takes place in the following fashion:

$$(\mathbf{C} + \mathbf{N}) \times (\mathbf{S} + \mathbf{N}) = \mathbf{SC} + \mathbf{SN} + \mathbf{CN} + \mathbf{N},$$

F_1 individuals produced will consist of zebra, common and plain, representing the third of the above-mentioned three classes. If, on the other hand, (**C** + **N**) and (**S** + **N**) simply combine together as such, then F_1 offspring will consist of zebras only and represent the first class. These zebras, when

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1) "Pale-pinkish-yellow" as he calls.

2) "Striped" according to his expression.

3) "Pale" as he designates.

mated *inter se*, will give rise to three forms, zebra, common and plain, in the ratio 12 : 3 : 1, as may be seen from the expression given below:

$$(\mathbf{C}+2\,\mathbf{CN}+\mathbf{N})\times(\mathbf{S}+2\,\mathbf{SN}+\mathbf{N})=\underbrace{8\,\mathbf{SCN}+3\,\mathbf{SN}+1\,\mathbf{SC}}_{12\text{ zebra}}+\underset{:\ 3\text{ common}}{3\,\mathbf{CN}}+\underset{:\ 1\text{ plain}}{1\,\mathbf{N}.}$$

But such a varying inter-relation supposed by TOYAMA to exist between $(\mathbf{S}+\mathbf{N})$ and $(\mathbf{C}+\mathbf{N})$ appears somewhat complicated and hardly comprehensible.

3. In a later paper TOYAMA (1910, a) denotes the common pattern by **C**, the plain by **c**, and the brown spotted or poly-lunar 1) by **P**, assuming that the poly-lunar is fully developed only in presence of **C**. Thus the offspring from the cross between poly-lunar and plain will be as follows:

$$\mathrm{P}\qquad \underset{\text{Poly-lunar}}{\mathbf{PC}}\ \times\ \underset{\text{Plain}}{\mathbf{cc}.}$$

$$\mathrm{F}_1\qquad \underset{\text{Poly-lunar}}{\mathbf{PCcc}}$$

$$\mathrm{F}_1\text{ gametes}\qquad \mathbf{PC},\ \mathbf{cc},\ \mathbf{Pc},\ \mathbf{Cc}.$$

$$\mathrm{F}_2\ \underbrace{1\,\mathbf{PPCC}+4\,\mathbf{PCcc}+2\,\mathbf{PCPc}+2\,\mathbf{PCCc}}_{9\text{ poly-lunar}\quad :}+\underbrace{2\,\mathbf{Cccc}+1\,\mathbf{CCcc}}_{3\text{ common}\quad :}+$$

$$\underbrace{2\,\mathbf{Pccc}+1\,\mathbf{PPcc}}_{3\text{ faintly spotted}:}+\underset{1\text{ plain}}{1\,\mathbf{cccc}.}$$

The above assumption is quite peculiar in as much as it admits the formation of such a gametic combination as **cc** in which *two doses* of a character occur in one and the same gamete.

4. In his recent work (TOYAMA, 1912) on the varying dominance of certain white breeds, TOYAMA again touches upon the question of factorial constitution of the silkworm. The fact that some European white races behave sometimes as dominant and sometimes as recessive to the yellow colour was first found and discussed by COUTAGNE, and later by KELLOGG, neither of them coming to a clear conception of the case. This paradoxical phenomenon found its solution in TOYAMA'S demonstration that the white races used by COUTAGNE and KELLOGG were not absolutely pure, but a mixt-

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1) A larval form provided with a pair of round or lunar patterns on the dorsum of each segment.

ure of dominant and recessive whites. In this paper TOYAMA represents the characters in question as follows:

Dominant white (**W**), Recessive white (**w**),
Yellow (**Y**),

and assumes that an allelomorphic relation exists not only between **W** and **w**, but also between **Y** and **W** or **w**. Adequacy of this assumption, however, may perhaps be doubted from the standpoint of the presence and absence hypothesis.

The following discussion on the Mendelian genes in the silkworm is based upon my experimental results as well as those obtained by previous observers. As my experiments, however have been concernd chiefly with the inheritance of larval markings and cocoon colours, a stress in the present paper is naturally laid on these characteristics.

The Author's Factors.[1]

I) Factors For Larval Markings.

1) **N.** Common or normal pattern.

The full-grown larva which contain this factor is provided with three pairs of distinct markings, its ground coat-colour being white or faintly shaded. The first pair of the markings, "ocular" pattern or "eye-spot" as it is often called, occurs on the second segment, the second pair, "horse-shoe" or anterior "lunule", on the fifth segment. The last pair which is found on the eighth segment is smaller and less conspicuous than the preceding two. The normal pattern is most common in the Japanese races, hence the name, but it is also found in other Asiatic and European races.

The common pattern is epistatic to the plain, but hypostatic to the striped, zebra and moricaud. (Experiments: TOYAMA, KELLOGG, The Author.)

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[1] Probably there may be a considerable number of genetic factors in regard to the inheritance of larval markings and cocoon-colours, but I take into consideration only those characters which hereditary behaviours are exactly known. The inter-relations of these factors have been confirmed, as is stated elsewhere, by numerous experimental data furnished by various observers including those of the author himself.

2) **S.** Striped black.

The larva is generally black, except the inter-segmental regions of abdominal segments where we find transverse white bands. "Eye spot" and two pairs of "lunules" are always present there, but they can not be distinctly observed in consequence of the general darkness of the body. The characteristic stripes become more conspicuous towards the later stage of larval life, while the young worms are hardly distinguishable from those of other strains. This type is often found in the Chinese races.

The striped black is epistatic to the common and to the plain. (Experiments: TOYAMA, The Author.)

3) **Z.** Zebra-pattern or tiger-banded.

The larva of this strain is white, but provided with inter-segmental bands of black to dark brown colour, so that it shows an appearance characteristic to the coat of zebra or tiger. Such a strain is met with in Siamese, Chinese, Korean and some European (*Italian salmon*, *Papillons noirs*, etc.) races.

The zebra-pattern is dominant to the common and plain types. (Experiments: COUTAGNE, KELLOGG, TOYAMA.)

4) **M.** Moricaud [1] or darky.

Besides the body is provided with the distinct marking pairs, "eye-spots" and "lunules", it is covered by numerous irregular dark striations and dots which give the larva a peculiar appearance somewhat resembling to the wild mulberry-silkworm, *B. mori var. mandarina*. This type is often encountered in Chinese, Korean and some European (*Bagdad*, etc.) races.

The moricaud is dominant to the normal and plain characters. (Expriments: COUTAGNE, TOYAMA, KELLOGG, The Author.)

5) **sszzmmnn.** Plain; absence of all marking characters.[2]

When very young this form is provided with some distinct markings, so that it is scarcely distinguishable from the larvae of normal type. Later, these markings become less conspicuous and at last are reduced to mere faint

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[1] A French name used by COUTAGNE and later also by KELLOGG.

[2] Apparently the plain contains a factor or factors on which the markings of young larvae depend. But as we are dealing with marking in the full-grown larvae in the present discussion, such factors are not taken into consideration.

shades or totally disappear sfrom the full-grown larvae. The plain silkworms being one of the most common strains, it is found in almost all European and Asiatic races.

The plain is of course recessive to all marked characters. (Experiments: TOYAMA, KELLOGG.)

Equipotency and Incomplete Dominance of Marking Characters.

In the crosses moricaud × zebra, COUTAGNE obtained a new type of marking, i. e. moricaud-zebra, in which the moricaud and the zebra-pattern simultaneously appeared with equal strength. According to TOYAMA an apparent combination of two distinct markings also takes place between polylunar pattern and the striped, moricaud or zebra. These curious phenomena are perhaps due to equivalency of the dominating power of two characters for which an individual is heterozygous.

On the other hand incomplete dominancy of marking characters is also remarkable in heterozygous striped or moricaud. The heterozygous forms of these marked strains are always lighter-coloured than the homozygous individuals. Thus we can distinguish, without great difficulty, the **SSzzmmnn** larvae from the **Sszzmmnn**, and the **sszzMMnn** individuals from the **sszzMmnn** form.

II) Factors for Cocoon Colours.

1) **Y.** Yellow cocoon.

By the term "yellow" we mean all coloured cocoons, except green ones, varying from creamy to golden yellow. A constant colour-correlation between cocoon and blood color is a well known fact; the yellow-cocoon spinners are always yellow-blooded, while the white cocooners are white-(colourless) blooded. The blood colour is visible through the cuticular coat of the larva, especially on the ventral side of the body and on the abdominal legs. When we speak of "yellow silkworms", therefore, we mean yellow-legged larvae, and at the same time yellow-cocoon spinners. It must be noted, however, that the intensity of the yellow leg-colour is by no means proportional to that of the cocoon colour. In my experiments it was found that some larvae with so faintly yellowish legs that they were mistaken for white-legged ones spun intensely yellow-coloured cocoons, while some of the worms which had deep-yellow legs produced merely creamy or salmon-yellow cocoons.

2) **I.** Inhibitor.

This factor totally suppresses the development of yellow colour. The inhibitor is contained by the so-called dominant whites in the European races, for instance *Bagdad, Blanc pays, Blanc des Alpes,* etc., the constitution of the homozygous forms of them being **IIYY** or **IIyy.** The larva which involves this factor is always white-blooded, but the cocoon is often shaded with light greenish colour. (Experiments: COUTAGNE, KELLOGG.)

3) **i.** Absence of inhibitor.

The inhibitor is always absent from yellow-cocooners and the so-called recessive whites.

4) **y.** Absence of yellow; white cocoon.

A recessive white results from the absence of both the factors for yellow and its inhibitor; it may be expressed as **iiyy.** The larva of recessive white is white-blooded, and spins pure white cocoon. All oriental whites, as yet known fall into this category. (Experiments: TOYAMA, The Author.)

Experimental Results of Previous Authors in the Light of the Presence and Absence Hypothesis.

1) The results of the author.

The experimental results of the author are all interpretable on the basis of his postulated factors described above. The more important of these results are described in detail in a separate paper.

2) The results of KELLOGG and QUAJAT.

In their works, we find no complex cases of Mendelian inheritance, except the varying behaviours, i. e. individual idiosyncrasies of KELLOGG, of the white-cocooners. These irregularities were, as already mentioned, worked out by TOYAMA. A few other deviations seem to be merely accidental.

3) TOYAMA's results.

I shall take here only the more complicated of his experimental results which I have referred to in the preceding pages.

A. First example of the "modified dihybrids"

We denote the factors[1] concerned as:

C, the colour factor; **c,** absence of colour;
Y, the yellow factor; **y,** absence of yellow;

and the gametic compositions[1] as:

CY, yellow; **cY,** salmon;
Cy, greenish white; **cy,** pure white.

In the cross **CY** × **cy**, F_1 will be all yellow, which will segregate to four forms in F_2.

F_1 gametes F_2

$$(\mathbf{CY}+\mathbf{cY}+\mathbf{Cy}+\mathbf{cy})=\begin{cases} 1\,\mathbf{CYCY}+2\,\mathbf{CYcY}+2\,\mathbf{CYCy}+4\,\mathbf{CYcy} & 9 \text{ yellow.} \\ 1\,\mathbf{cYcY}+2\,\mathbf{cYcy}\dots\dots\dots\dots & 3 \text{ salmon.} \\ 1\,\mathbf{CyCy}+2\,\mathbf{Cycy}\dots\dots\dots\dots & 3 \text{ greenish white.} \\ 1\,\mathbf{cycy}\dots\dots\dots\dots\dots\dots & 1 \text{ white.} \end{cases}$$

Analysis of the third generation of this series is given in Table I.

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[1] These genetic factors and gametic compositions are merely temporarily assumed here. Whether these assumptions are applicable to any other similar cases is to be tested by future experiments.

Table I.

F₂			F₃			
				Apparent character		
Apparent character	Genetic constitution	Gametes	Zygotes	Ratio	Actual figures	Expectation
Yellow	CYCY	CY	CYCY	all yellow	all yellow	all yellow
	CYcY	CY cY	1 CYCY 2 CYcY	3 yellow	444 yellow	448.5
			1 cYcY	1 salmon	154 salmon	149.5
	CYCy	CY Cy	1 CYCY 2 CYCy	3 yellow	771 yellow	754.5
			1 CyCy	1 greenish white	235 greenish white	251.5
	CYcy	CY cY Cy cy	1 CYCY 2 CYcY 2 CYCy 4 CYcy	9 yellow	320 yellow	318.9
			1 cYcY 2 cYcy	3 salmon	111 salmon	106.3
			1 CyCy 2 Cycy	3 greenish white	136 greenish white to white	141.8
			1 cycy	1 white		
Salmon	cYcY	cY	cYcY	all salmon	not reared	—
	cYcy	cY cy	1 cYcY 2 cYcy	3 salmon	164 salmon	163.5
			1 cycy	1 white	55 white	54.5
Greenish White	CyCy	Cy	CyCy	all greenish white	greenish white to white	greenish white to white
	Cycy	Cy cy	1 CyCy 2 Cycy	3 greenish white		
			1 cycy	1 white		
White	cycy	cy	cycy	all white	all white	all white

As the above Table shows, our theoretical expectation fairly agrees with the actual figures.

The fourth generation is also interpretable in the same way.

B. Second example of the "modified dihybrids".

The parental population among which the crossing was made evidently consisted of individuals of various compositions. These different zygotic forms are designated as Class 1, 2 and 3.

Table II.1)

P_1			F_1			
Class No.	Japanese common white	Siamese zebra white	Zygotes	Apparent character		
				Ratio	Actual figures	Expectation
1	ZNZN	ZnZn	zNZn	all zebra	all zebra	all zebra
2	zNzN	Znzn	1 zNZn	1 zebra	291	315
			1 zNzn	1 common	339	315
3	zNzn	Znzn	1 zNZn 1 znZn	2 zebra	352	365.0
			1 zNzn	1 common	196	182.5
			1 znzn	1 plain	182	182.5

F_1 (zNZn) individuals of the first class in the above Table will give, when mated *inter se*, the following F_2 offspring:

Table III.

F_1		F_2			
Zebra	Gametes	Zygotes	Apparant character		
			Ratio	Actual figures	Expectation

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1) In the present analysis we shall give, for the sake of simplicity only those factors necessary for the interpretation of the case.

zNZn	ZN, Zn, zN, zn	1 ZNZN 2 ZNZn 2 ZNzN 4 ZNzn 1 ZnZn 2 Znzn	12 zebra	2366	2377.5
		1 zNzN	3 common	597	594.4
		1 znzn	1 plain	202	198.1

Since all succeeding generations can be similarly explained as above, any further analysis is not needed.

C. The case of poly-lunar pattern.

Here we may express the characters as:

P, Poly-lunar pattern; **p,** Absence af **P**;
N, Common pattern; **n,** Absence of **N.**

If we assume the poly-lunar pattern to be fully developed only in presence of **N,** we shall obtain the following diagram:

P **PN** × **pn**
Poly-lunar Plain

F_1 **PNpn**
Poly-lunar

F_1 gametes **PN, Pn,** | **pN, pn.**

F_2 9 **PN** 3 **pN** 3 **Pn** 1 **pn**
Poly-lunar Common Faint poly-lunar Plain

D. The case of dominant and recessive whites.

Since dominant white, either in animals or in plants, is now generally regarded as due to the presence of a factor that prevents the production of colour in individuals which would otherwise be coloured, the formula constructed in conformity with this view are perhaps to be preferred to TOYAMA's formulae based apparantly on Mendel's original view. These two series of formulae are given below:

	(I)	(II)
Dominant (European) white	**W**	**IY** or **Iy**
Recessive (Asiatic) white	**w**	**iy**
Yellow	**Y**	**iY**

In terms of TOYAMA's factors the possible schemes of inheritance in crosses between dominant and recessive whites are as follows:

	P	F_1	F_2
1)	**WW** × **ww**	= all white (**Ww**)	= all white
2)	**Ww** × **ww**	= " " (**Ww+ww**)	= " "
3)	**WY** × **ww**	= yellow (**wY**)	= 3 yellow 1 white
		white (**Ww**)	= all white

On the other hand, in terms of my factors the possible pedigrees of the cyosses under review will be as follows:

	P	F_1	F_2
1)	**IyIy** × **iyiy**	= all white (**Iyiy**)	= all white
2)	**Iyiy** × **iyiy**	= all white (**Iyiy+iyiy**)	= all white
3)	**IYIY** × **iyiy**	= all white (**IYiy**)	= 13 white 3 yellow
4)	**IYiY** × **iyiy**	= 1 white (**IYiy**)	= 13 white 3 yellow
		1 yellow (**iYiy**)	= 1 white 3 yellow
5)	**IYIy** × **iyiy**	= 1 white (**IYiy**)	= 13 white 3 yellow
		1 white (**Iyiy**)	= all white

Thus it is clear that by thorough experimental study of the hereditary behaviours of crosses between dominant and recessive whites we may determine which of the two views here touched upon is more adequate. It is hoped later to take up a detailed study on this subject.

4) COUTAGNE'S results.

In COUTAGNE'S experiments several examples of complicated Mendelian inheritance were observed. These are tabulated and analysed below in the light of the presence and absence hypothesis. As was the case in the foregoing discussion I shall mention here only those factors in which either or both of the parents are heterozygous, or only those factors by which the two parents differ from each other.

Table IV.

Series 1.

Year	Lot No.	Apparent character	Genetic canstitution	Gametes		Zygotes	Apparent character		
							Ratio	Actual figures	Expectation
1895	O	Zebra yellow (*Papillons noirs*) ♂	ZziiYy	ZiY Ziy ziY ziy	F_1	1 ZiYziY 1 ZiyziY	2 zebra yellow	116	114.7
						1 ZiYzIY 1 ZiyzIY	2 zebra white	108	114.7
		Plain white (*Blanc des Alpes*) ♀	zzIiYY	zIY ziY		1 ziYziY 1 ziYziy	2 plain yellow	124	114.7
						1 ziYzIY 1 ziyzIY	2 plain white	111	114.7
							Total	459	458.8
1896	AR	F_1 zebra yellow ♀, ♂	ZiyziY	ziY ZiY Ziy ziy	F_2	1 ZiYZiY 2 ZiYziY 2 ZiYZiy 4 ZiYziy	9 zebra yellow	236	247.0
						1 ZiyZiy 2 Ziyziy	3 zebra white	80	82.3
						1 ziYziY 2 ziYziy	3 plain yellow	89	82.3
						1 ziyziy	1 plain white	34	27.4
							Total	439	439.0

AU	F_1 zebra white ♀, ♂	ZiYzIY	ZIY ZiY zIY ziY	F_2	1 ZIYZIY 2 ZIYZiY 2 ZIYzIY 4 ZIYziY	9 zebra white	180	231.75
					1 ZiYZiY 2 ZiYziY	3 zebra yellow	109	77.25
					1 zIYzIY 2 zIYziY	3 plain white	87	77.25
					1 ziYziY	1 plain yellow	36	25.75
						Total	412	412.00
AS	F_1 plain yellow ♀, ♂	ziYziy	ziY ziy	F_2	1 ziYziY 2 ziYziy	3 plain yellow	441	421
					2 ziyziy	1 plain white	120	140
						Total	561	561
AT	F_1 plain white ♀, ♂	ziYzIY	ziY zIY	F_2	1 ziYziY	1 plain yellow	140	135
					2 ziYzIY 1 zIYzIY	3 plain white	399	404
						Total	539	539
AH	F_1 plain white ♀	ziYzIY	ziY zIY	F_2	1 ziYziY	1 plain yellow	210	214.5
	F_1 plain yellow ♂	ziYziY	ziY		1 zIYziY	1 plain white	219	214.5.
						Total	429	429
AI	F_1 zebra yellow ♂	ZiyziY	ZiY Ziy ziY ziy	F_2	1 ZiYziY 1 ZiyziY	2 zebra yellow	95	97.75
					1 ZiYzIY 1 ZiyzIY	2 zebra white	84	97.75
	F_1 plain white ♀	ziYzIY	ziY zIY		1 ziYziY 1 ziyziY	2 plain yellow	103	97.75
					1 ziYzIY 1 ziyzIY	2 plain white	109	97.75

							Total	391	391.00
	AL	F_1 zebra yellow ♀	ZiYziY	ZiY ziY	F_2	1 ZiYZiY 2 ZiYziY	3 zebra yellow	168	169
						1 ZiYZIY 2 ZiYzIY	3 zebra white	151	169
		F_1 zebra white ♂	ZiYzIY	ZIY ZiY zIY ziY		1 ziYziY	1 plain yellow	69	56
						1 ziYzIY	1 plain white	62	56
							Total	450	450
1897	MK	AT, F_2 plain white ♀, ♂	ziYzIY	ziY zIY	F_3	1 ziYziY	1 plain yellow	102	102
						2 ziYzIY 1 zIYzIY	3 plain white	305	305
							Total	407	407
	ML	AU, F_2 zebra white ♀, ♂	ZIYZiY	ZIY ZiY	F_3	1 ZiYZiY	1 zebra yellow	74	99
						2 ZIYZiY 1 ZIYZIY	3 zebra white	323	298
							Total	397	397

Table V.

Series 2.

Year	Lot No.	Apparent character	Genetic constitution	Gametes		Zygotes	Apparent character		
							Ratio	Actual figures	Expectation
1896	AM	O, F_1(Series 1) plain white ♀	ziYzIY	ziY zIY	F_2	1 ZiYziY 1 ZiyziY	2 zebra yellow	151	141
						1 ZiYzIY 1 ZiyzIY	2 zebra white	129	141

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1) We can not distinguish the common and plain larvae in COUTAGNE's paper, because he expresses both of them by a symbol ⊂⊃. This symbol is transferred here, *for the* sake of convenience, as the plain type in all cases of his experiments. The assumption, however, does not much affect the results so far as the present dsscussion is concerned.

		zebra yellow *(Papillons noirs)* ♂	ZiYziy	ZiY Ziy ziY ziy		1 ziYziY 1 ziyziY	2 plain yellow	156	141
						1 ziYzIY 1 ziyzIY	2 plain white	128	141
							Total	564	564
1897	ME	F_2 zebra yellow ♀, ♂	ZiYziY	ZiY ziY	F_3	1 ZiYZiY 2 ZiYziY	3 zebra yellow	288	297
						1 ziYziY	1 plain yellow	108	99
							zebra white ?	1	0
							Tota	396 + 1	396
	MF	F zebra white ♀, ♂	ZiYzIY	ZIY ZiY zIY ziY	F_3	1 ZIYZIY 2 ZIYZiY 2 ZIYzIY 4 ZIYziY	9 zebra white	234	265.0
						1 ZiYZiY 2 ZiYziY	3 zebra yellow	96	88.3
						1 zIYzIY 2 zIYziY	3 plain white	141	88.3
						1 ziYziY	1 plain yellow	0 ?	29.4
							Total	471	471.0
	MG	F_2 plain yellow ♀, ♂	ziYziY	ziY	F_3	ziYziY	plain yellow	475	475
							plain white ?	5	0
	MH	F_2 plain white ♀, ♂	ziYzIY	ziY zIY	F_3	1 ziYziY	1 plain yellow	152	120.5
						2 ziYzIY 1 zIYzIY	3 plain white	330	361.5
							zebra white ?	5	0
							zebra yellow ?	1	0
							Total	442 + 6	442

?) These irregularities evidently are to be considered as accidental, as COUTAGNE himself recognizes it in the following words: "ces 4 lots ont été placés au début de l'élevage, sur des cartons trop rapprochés, et il a pu se faire quelque mélanges".

Table VI.

Series 3.

Year	Lot No.	Apparent character	Genetic constitution	Gametes		Zygotes	Apparent character		
							Ratio	Actual figures	Expectation
1896	AF	Moricaud white *(Bagdad vers noirs)* ♀	zMIYzMiY	zMIY zMiY	F_1	1 zMiYZmiY 1 zMiYZmiy	2 moricaud-zebra yellow	89	82.25
						1 zMIYZmiY 1 zMIYZmiy	2 moricaud-zebra white	86	82.25
		Zebra yellow *(Papillons noirs)* ♂	zmiYZmiy	ZmiY Zmiy zmiY zmiy		1 zMiYzmiY 1 zMiYzmiy	2 moricaud yellow	77	82.25
						1 zMIYzmiY 1 zMIYzmiy	2 moricaud white	77	82.25
							Total	329	329.00
1897	LX	F_1 moricaud zebra yellow ♀, ♂	zMiYZmiy	ZMiY ZMiy ZmiY zMiY Zmiy zMiy zmiY zmiy	F_2	1 ZMiYZMiY 2 ZMiYZMiy 2 ZMiYZmiY 2 ZMiYzMiY 4 ZMiYzMiy 4 ZMiYZmiy 4 ZMiYzmiY 8 ZMiYzmiy	27 moricaud-zebra yellow	90	136.3
						1 ZMiyZMiy 2 ZMiyZmiy 2 ZMiyzMiy 4 ZMiyzmiy	9 moricaud-zebra white	37	45.4
						1 zMiYzMiY 2 zMiYzMiy 2 zMiYzmiY 4 zMiYzmiy	9 moricaud yellow	29	45.4
						1 ZmiYZmiY			

					2 ZmiYZmiy 2 ZmiYzmiY 4 ZmiYzmiy	9 zebra yellow	66	45.4
					1 zMiyzMiy 2 zMiyzmiy	3 moricaud white	18	15.1
					1 ZmiyZmiy 2 Zmiyzmiy	3 zebra yellow	63[1]	15.1
					1 zmiYzmiY 2 zmiYzmiy	3 plain yellow	13	15.1
					1 zmiyzmiy	1 plain yellow	7	5.1
						Total	323	322.9
LY	F₁ moricaud-zebra white ♀, ♂	zMIYZmiY	ZMIY ZMiY ZmIY zMIY ZmiY zMiY zmIY zmiY	F₂	1 ZMiYZMiY 2 ZMiYZmiY 2 ZMiYzMiY 4 ZMiYzmiY	9 moricaud-zebra yellow	70	69.9
					1ZMIYZMIY 2 ZMIYZMiY 2ZMIYZmIY 2 ZMIYzMIY 4 ZMIYZmiY 4 ZMIYzMiY 4 ZMIYzmIY 8 ZMIYzmiY	27 moricaud-zebra white	189	209.7
					1 zMiYzMiY 2 zMiYzmiY	3 moricaud yellow	27	23.3
					1 ZmiYZmiY 2 ZmiYzmiY	3 zebra yellow	39	23.3
					1zMIYzMIY 2 zMIYzMiY 2 zMIYzmIY 4 zMIYzmiY	9 moricaud white	61	69.9

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[1] This is the only deviation from the expectation, and it is perhaps an accidental.

						1 ZmIYZmIY 2 ZmIYzmIY 2 ZmIYZmiY 4 ZmIYzmiY	9 zebra white	77	69.9
						1 zmiYzmiY	1 plain yellow	11	7.8
						1 zmIYzmIY 2 zmIYzmiY	3 plain white	23	23.3
							Total	497	497.1

In the foregoing Tables we see that the theoretical expectation on my assumed gametic and zygotic formulae in each series, is in close accordance with the experimental figures obtained by COUTAGNE. The most complicated cases, LX and LY, in his experiments are, as I believe, also clearly analysed. A few irregularities which we find in Tables V and VI are, as I already pointed out, evidently due to some accidental causes.

Summary.

1. Hitherto no theoretical studies except those of TOYAMA, have been made public on inheritance in the silkworm.

2. TOYAMA'S factors which appear to have been assumed after Mendel's original view are sometimes difficult to be applied to the interpretation of the more complicated cases of Mendelian inheritance.

3. The conception of the Mendelian genes assumed on the basis of the presence and absence hypothesis enables us to explain more simply and adequately all the experimental results obtained by previous investigators as well as those of the present author.

4. Our postulated factors or genes for the larval markings and cocoon colours, as far as yet experimentally confirmed are as follows:

For larval markings.

S, Striped black.	**s,** Absence of stripedness; plain.
Z, Zebra-pattern.	**z,** ” ” zebra-pattern; plain.
M, Moricaud.	**m,** ” ” moricaudness; plain.
N, Normal or common pattern.	**n,** ” ” normalness; plain.

For cocoon colours.

Y, Yellow.	**y,** Absence of yellowness; white.
I, Inhibitor, which prevents the development of yellow color.	**i,** ” ” inhibitor.

5. Normal marking is hypostatic to the striped, zebra and moricaud.

6. In my experiments I had no such matings as would have been suggestive for the determination of inter-relations of the genes **S, Z** and **M.** But the results obtained by previous observers appear to indicate, as far as they go, that these characters are almost equipotent with each other in their dominancy.

March 1913.

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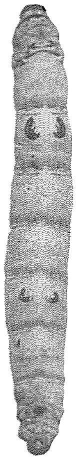
Explanation of Plate VIII.

Fig. 1. Normal pattern.
Fig. 2. Striped black. (Homozygous form.)
Fig. 3. Striped black. (Heterozygous form.)
Fig. 4. Moricaud. (Homozygous form.)
Fig. 5. Moricaud. (Heterozygous form.)
Fig. 6. Plain type.
Fig. 7. Zebra-pattern.

1



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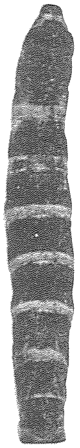

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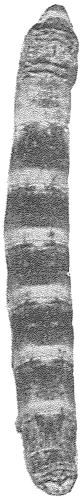

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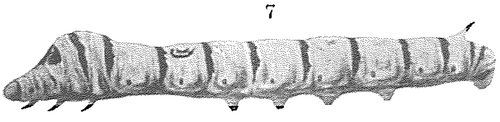

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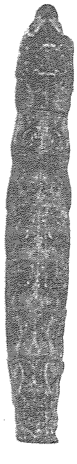

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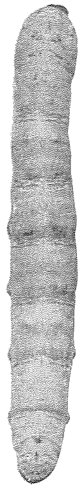

I–6, Suzuki photo. 7, Tanaka del.

Corrigenda.

Page.	
91.	Foot-note 5. For **voltinism** read **moultinism.**
95.	Line 11. For **however have** read **however, have.**
97.	Line. 1. For **disappear sfrom** read **disappears from.**
98.	Line 20. For **inhibitor** read **inhibition.**
101.	Table II, "Japanese common" coloumn. For **ZNZN** read **zNzN.**
101.	Table III, left-hand column. For **zebra** read **zygote.**
102.	Table. Add **2 zNzn** under **1 zNzN.**
103.	Line 14. For **cyosses** read **crosses.**
104.	Table IV, line 1. For **canstitution** read **constitution.**
105.	Lot No. AS. For **2 ziyziy** read **1 ziyziy.**
105.	Lot No. AH. right-hand column. For **429** read **429.0.**
107.	Lot No. ME. For **Tota** read **Total.**
107.	Lot No. MF. For **F zebra** read **F_2 zebra.**
110.	Undermost line. For **confirmed are** read **confirmed, are.**
113.	Heading. For **TEE** read **THE**

CORRIGENDA.

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Page.

92. Lowest but one line. Between ‘which’ and ‘consisted’ insert ‘produced four F_2 phenotypes—yellow, salmon, greenish white and white — in the ratio 9 : 3 : 3 : 1. Above F_2 yellows.’

92. Lowest line. For ‘F_2’ read ‘F_3.’

93. Line 1. For ‘F_1’ and ‘F_2’ read ‘F_2’ and ‘F_3’ respectively.

93. Line 8. For ‘F_3’ read ‘F_4.’

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Page.

122. Lot No. For ‘N. 2. ’11’ read ‘H. 2. ’11.’

122. Lot No. For ‘N. 5. ’11’ read ‘H. 5. ’11.’

130. Lot No. For ‘M. 9^1 ’11’ read ‘M. 9^4 ’11.’

130. Lot No. For ‘M. 9^2 ’11’ read ‘M. 9^5 ’11.’