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Author(s)	TANAKA, Y.
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FURTHER DATA ON THE REDUPLICATION IN SILKWORMS.

By

Y. Tanaka.

I. DISSIMILARITY OF MALE AND FEMALE GAMETIC SERIES IN THE STRIPED-YELLOW COUPLING.

As I have made out in the separate paper now under preparation for press¹, the reduplication in the normal-yellow repulsion and the moricaud-yellow coupling in the silkworm is not of the same intensity in male and female, but it follows quite distinct systems among the opposite sexes. In such cases the reduplication was complete in female, and it was partial in male. The similar sexual dimorphism of gametic series exists also in the striped-yellow coupling which is dealt with in the following pages.

In the previous paper² I have described two families in which coupling occurred between *striped* and *yellow*, the actual numbers being

Lot No.	H. 1'11	Lot No.	S. 5'11
Striped yellow (H. 1'12)	148	Striped yellow	134
Striped white (H. 2'12)	12	Striped white	10
Normal yellow (H. 3'12)	14	Plain yellow	7
Normal white (H. 4'12)	50	Plain white	43
Total	224		194

1. Occurrence of Different Systems of Gametic Reduplication in Male and Female Hybrids. Zeits. f. ind. Abst. u. Vererb. 1914.

2. Gametic Coupling and Repulsion in the Silkworm. This Journal, Vol. V, 1913. pp. 115-148.

Nine matings from H. 1'12 have been reared in 1913, which gave the following results :

	Striped yellow	Striped white	Normal yellow	Normal white	Total
* H. 1-1'12	194	—	80	100	374
H. 1-2'12	86	—	35	—	121
H. 1-3'12	210	—	80	—	290
* H. 1-4'12	192	—	91	81	364
H. 1-5'12	459	—	—	—	459
H. 1-6'12	204	23	12	54	293
H. 1-7'12	155	61	—	—	216
H. 1-8'12	247	26	24	65	362
H. 1-9'12	60	3	10	18	91

Apart awhile from the asterisked families (concerning which see later pages) all of the above results are according to expectation. Totals of those families in which four zygotic forms occurred are

	Striped yellow	Striped white	Normal yellow	Normal white	Total
H. 1-6, 8, 9'12 all together	511	52	46	137	746

Thus existence of a partial coupling between two dominant characters **S** (striped marking) and **Y** (yellow colour) can not be doubted here, and moreover the system of the reduplication seems, at a glance, to be that of $7 : 1 : 1 : 7$.¹ But that this was actually not the case has been amply proved by other facts which will be given later.

F₁ striped yellows (H. 29'12) derived from the cross striped yellow ♀ × normal white (*Aojiku*) ♂ gave the following F₂ offspring in the spring 1913.

	Striped yellow	Striped white	Normal yellow	Normal white	Total
H. 29-1'12	240	22	35	63	360

1. Expectation on such basis is 515.7 : 43.7 : 43.7 : 142.9.

H. 29-2'12	140	15	23	48	226
H. 29-3'12	300	35	33	91	459
H. 29-4'12	239	38	40	55	372
H. 29-5'12	342	36	41	94	513
H. 29-6'12	242	50	24	54	370
H. 29-7'12	195	31	29	39	294
H. 29-8'12	275	37	36	63	411
Total	1973	264	261	507	3005

Though the results appear to tempt one to supposition that 4 : 1 : 1 : 4 coupling¹ occurs in this case, this assumption was proved inadequate, as it was the case with the supposition of 7 : 1 coupling in H. 1 families described in the preceding page. The actual feature of the gametic distribution was first revealed by the following data.

a) Results of the cross double recessives (plain or *Kasuri*² whites) ♀ × diheterozygous striped yellows ♂.

	Striped yellow	Striped white	Normal yellow	Normal white	Total
H. 45-2'12 (plain wh. ♀ × H. 29'12 ♂)	88	45	55	97	285
Expect. on 2 : 1 : 1 : 2	95.0	47.5	47.5	95.0	285.0
S. 1'13 (<i>Kasuri</i> wh. ♀ × H. 1-5'12, str. yel. (12'13) ♂)	171	67	67	190	495
Expect. on 3 : 1 : 1 : 3	185.6	61.9	61.9	185.6	495.0
S. 2'13 (ditto)	186	92	101	198	577
Expect. on 2 : 1 : 1 : 2	192.3	96.2	96.2	192.3	577.0
S. 3'13 (ditto)	204	61	80	181	526
Expect. on 3 : 1 : 1 : 3	197.25	65.75	65.75	197.25	526.00
S. 8'13 (<i>Arayahime</i> ♀ × H. 37-1'12, str. yel. (292'13) ♂)	113	39	33	148	333
Expect. on 3 : 1 : 1 : 3	124.9	41.6	41.6	124.9	333.0

1. Expectation on such assumption will be 1983.30 : 270.45 : 270.45 : 480.80.

2. This is recessive to the normal.

S. 9'13 (ditto)	94	35	39	94	262
Expect. on 3 : 1 : 1 : 3	98.25	32.75	32.75	98.25	262.00
S. 11'13 (<i>Kasuri</i> wh. ♀ × H. 29-8'12, str. yel. (160'13) ♂)	143	73	78	135	429
Expect. on 2 : 1 : 1 : 2	143.0	71.5	71.5	143.0	429.0
Total (S. 1, 3, 8, 9'13)	582	202	219	613	1616
Expect. on 3 : 1 : 1 : 3	606	202	202	606	1616
Total (H. 45-2'12 and S. 2, 11'13)	417	210	234	430	1291
Expect. on 2 : 1 : 1 : 2	430.3	215.2	215.2	430.3	1291.0

From these results we know that the **S-Y** coupling in the male gametic series was neither on 7 : 1 : 1 : 7 nor on 4 : 1 : 1 : 4, but it follows either 3 : 1 : 1 : 3 or 2 : 1 : 1 : 2 system.

b) Results from the cross diheterozygous striped yellows ♀ × double recessives (normal whites) ♂.

	Striped yellow	Normal white	Total
H. 58-1'12 (H. 29'12 ♀ × <i>Chohakuryu</i> ♂)	208	215	423
H. 58-2'12 (ditto)	208	233	441
H. 58-3'12 (ditto)	167	152	319
Total	583	600	1183
Expect. on 1 : 1	591.5	591.5	1183.0

Thus it is evident that a complete repulsion occurs in the female gametic series.

The results above described brought to light the gametic series in **SsYy** animal (into which **S** and **Y** were introduced by the same parent). They do not follow the same system of the reduplication in male and female, but they distinctly differ from each other, namely:

	SY	Sy	sY	sy
Spermatozoa	{ 3	: 1	: 1	: 3
	{ 2	: 1	: 1	: 2
Eggs	1	:		1

The union of such gametic series will give rise to the following zygotic series:

Gametic series						Zygotic series			
♀			♂			Str.	Str.	Non-str.	Non-str.
SY	sy	SY	Sy	sY	sy	yel.	wh.	yel.	wh.
1	1	3	1	1	3	11	1	1	3
1	1	2	1	1	2	8	1	1	2

The ratios 11 : 1 : 1 : 3 and 8 : 1 : 1 : 2 show an approximation to the systems 11.80 : 1 : 1 : 3.27 (=177 : 15 : 15 : 49 which results from the 7 : 1 coupling on both sexes) and 7.33 : 1 : 1 : 1.78 (=66 : 9 : 9 : 16 that is the outcome of the 4 : 1 series on both sexes) respectively. So they seem liable to be mistaken for ordinary 7 : 1 or 4 : 1 coupling. The actual figures are compared with the numbers expected on the above ratios.

	Striped yellow	Striped white	Normal yellow	Normal white	Total
H. 1-6, 8, 9'12 (3 families)	511	52	46	137	746
Expect. on 11 : 1 : 1 : 3 zyg. ser.	512.9	46.6	46.6	139.9	746.0
H. 29-1-8'12 (8 families)	1973	264	261	507	3005
Expect. on 8 : 1 : 1 : 2 zyg. ser.	2003.3	250.4	250.4	500.9	3005.0

The expectation is, as it is shown, fairly realised.

2. TWO NEW INSTANCES OF THE REDUPLICATION IN SILKWORMS.

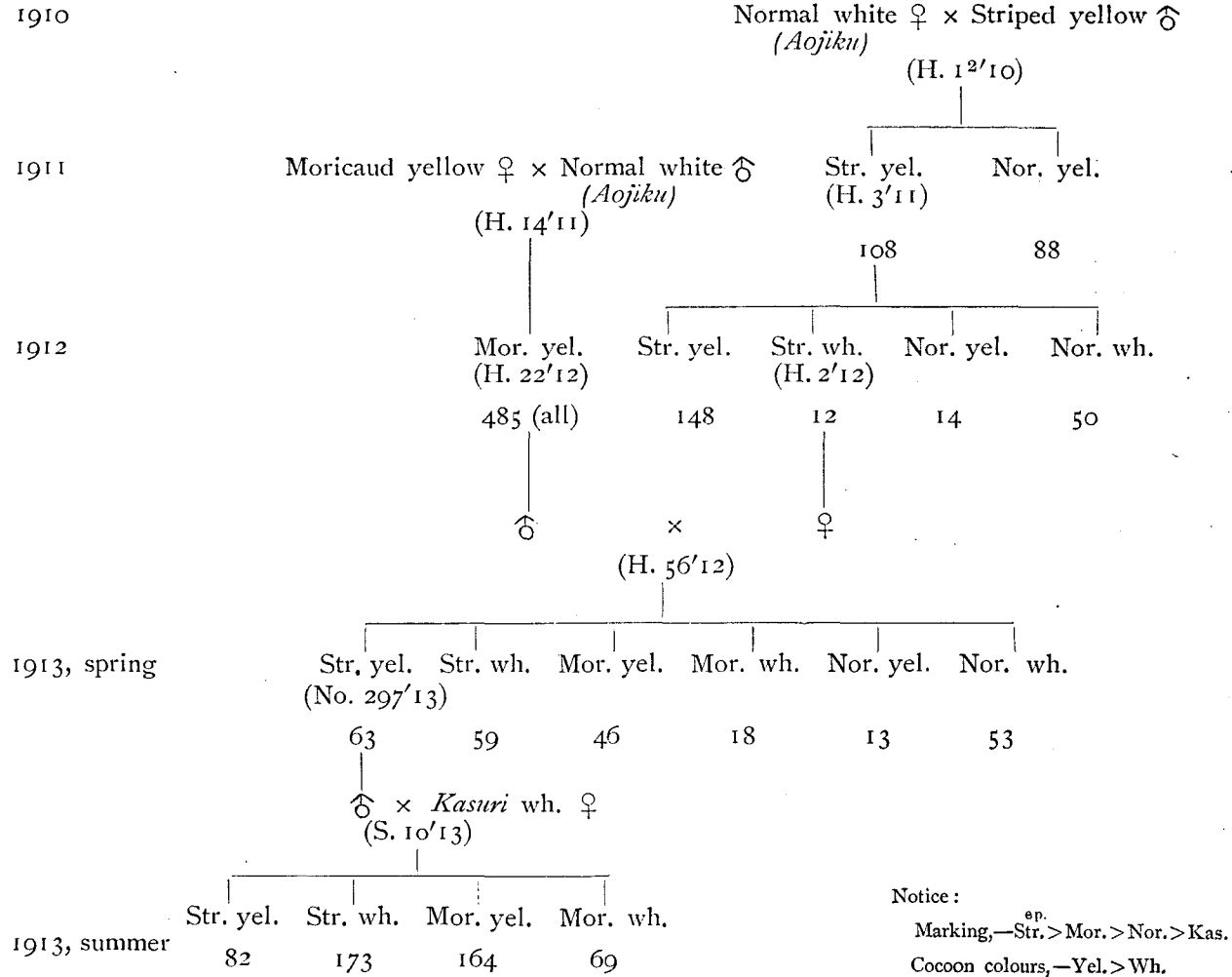
Besides those cases of gametic reduplication hitherto described by the writer¹ two new examples were found in the silkworm. One was the repulsion between **S** and **Y**, while the other was the coupling between **N** (normal marking) and **Y**.

a) The Repulsion between **S** and **Y**.

This occurred in one (S. 10'13) of the families reared during the summer 1913. The origin of the family in question is as follows.

¹ 1913 l. c. and 1914 l. c.

Table I.



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As above pedigree shows the heterozygous striped yellows (No. 297/13) in the spring 1913¹ have received the stripedness from the mother, and the yellowness from the father. Occurrence of gametic repulsion between these dominant characters may naturally be anticipated² as the result of such crossing, and practically the figures obtained in the succeeding season represent the reduplicated series of the male parent as such, the *Kasuri* white being absolute recessive to the striped yellow.

	Striped yellow	Striped white	Moricaud yellow	Moricaud white	Total
Observed	82	173	164	69	488
Expected on 1 : 2 : 2 : 1 basis	81.3	162.7	162.7	81.3	488.0

Thus it is evident that a partial repulsion of lowest intensity takes place in the *male* gametes of **SsYy**, when the factors **S** and **Y** have been introduced by the different parents. We cannot tell with confidence at present what happens in the *female* heterozygote, though there are some reasons in imagining occurrence of a complete repulsion in it.

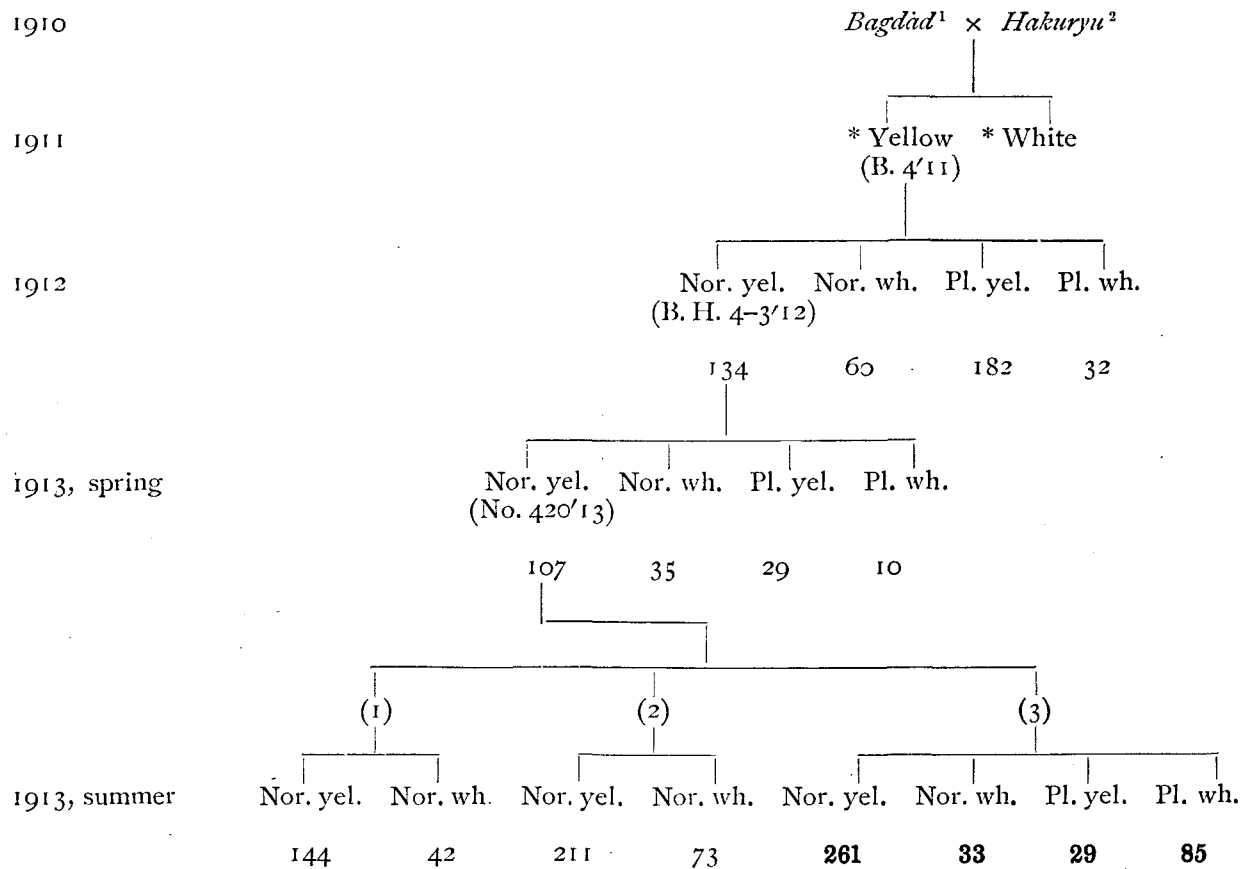
b) The Coupling between **N** and **Y**.

As I have described in the separate paper (1914, l. c.) the repulsion between **N** and **Y** that occurs in the heterozygote ex **NNyy** × **nnYY** is partial in the male, but it is complete in the female. If **N** and **Y** were brought into the hybrid by the same parent, on the other hand, what there will be happened? The following result, though insufficient, points to occurrence of at least some couplings, possibly 2 : 1 : 1 : 2 in ♂— and complete in ♀, in such a cross. The pedigree and the actual numbers are diagrammatically given below.

1. The entire result in this generation is easily accounted for as follows. As the gametic series would have been 1 **SY** : 1 **sy** in the mother, and 3 **MY** : 1 **My** : 1 **mY** : 3 **my** in the father (**N**-factor being understood), the offspring should be in the ratio 4 str. yel. : 4 str. wh. : 3 mor. yel. : 1 mor. wh. : 1 nor. yel. : 3 nor. wh. This has been precisely realised, the expectation being 63 : 63 : 47 : 16 : 16 : 47.

2. Couplings arise, as stated elsewhere, in F₂ ex str. yel. × non-str. wh.

Table II.



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1. European dominant white, univoltine.

2. Japanese normal white, bivoltine.

* Marking characters, as well as the actual numbers were not recorded.

Though the preceding pedigree begins with the cross of dominant and recessive whites, we may put the inhibitor, to which the *Bagdad white* owes its dominancy, out of consideration in the present investigation, because the descendants given above all belong to the yellow series in which the factor in question is necessarily absent.

The result in 1912 is what may be accounted for on the basis that the parents were $nnYy \text{ ♀} \times NnYy \text{ ♂}$, and 1 : 2 : 2 : 1 repulsion occurred in male side. On such assumption we may expect the following zygotic series, which is very close to the actual figures.

	Normal yellow	Normal white	Plain yellow	Plain white	Total
Observed	134	60	182	32	408
Expected	136 (4)	68 (2)	170 (5)	34 (1)	408

The numbers in the spring 1913 precisely accord to 9 : 3 : 3 : 1 series, the expectation being as follows :

	Normal yellow	Normal white	Plain yellow	Plain white	Total
Observed	107	35	29	10	181
Expected	102	34	34	11	181

The result seems suggestive to normal distribution of gametic forms in both sexes. Nevertheless I am inclined, from the following reasons, to believe existence of the underlying reduplication even in this case. In the first place, some of the normal yellows in 1912 (No. 420'13) were possibly produced by union of the gametes Ny and nY , while others were derived from combination of NY and ny ; thus the reduplication in the former was repulsion, and that in the latter was coupling. In the second, the sexual dimorphism of gametic series in the reduplication hitherto described, must be assumed to exist also in the present case. If therefore it chanced a repulsion to occur in one parent, the *father*, and a coupling to take place in another, the *mother*, the gametic series would be

	NY		Ny		nY		ny
♂	1	:	3	:	3	:	1
♀	1			:			1

whence the apparently normal zygotic series, 9 : 3 : 3 : 1, may result.

Lastly we come to the discussion of a family, No. 420-3'13, reared during the summer 1913. The figures in this family seem to tempt one to the supposition that the 4 : 1 : 1 : 4 coupling exists in both parents. Presumably, however, this supposition is not correct, but here the male and female gametic series would have been distinct as it was the case with the striped-yellow and moricaud-yellow couplings. Thus if we assume the gametic series as

	NY		Ny		nY		ny
♂	2	:	1	:	1	:	2
♀	1			:			1

we may expect the following numbers:

	Normal yellow	Normal white	Plain yellow	Plain white	Total
Observed	261	33	29	85	408
Expected	272	34	34	68	408
	(8)	(1)	(1)	(2)	

Conclusive results are to be obtained, however, only from the crosses **NnYy** ♀ × **nnyy** ♂ and the reciprocal, where **NnYy** has been produced by union of **NY** and **ny**.

P. S. In my previous paper (1913, l. c., p. 122 and Table V), I have described a family (H. 17'11) in which apparently complete repulsion occurred between **S** and **Y** in spite of the family has been derived from the cross *Aojiku* (normal white) ♀ × striped yellow ♂. Whether there may exist, in certain occasion, a complete reduplication in *male*, or whether the above result is due to any mistake by which sex-signs have been reversed, is at present uncertain. No similar case has as yet been found in other families.

3. COMPLEX PHENOMENA RELATING TO THE STRIPEDNESS.

Some irregularities observed in the heredity of the striped character are described in the following lines.

a) Occurrence of a Rare Zygotic Series $2 \mathbf{AB} : 1 \mathbf{aB} : 1 \mathbf{ab}$.

In a partial reduplication all possible F_2 zygotic combinations (i. e. four) are produced, while in a complete repulsion three, and in a complete coupling only two phenotypes can occur. Whenever there are only three phenotypes present the zygotic series should be, on an ordinary occasion, $2 \mathbf{AB} : 1 \mathbf{Ab} : 1 \mathbf{aB}$, the last term (\mathbf{ab}) being absent.

In my experiments with the silkworm, however, I have met with two families giving an evidence for possibility of $2 \mathbf{AB} : 1 \mathbf{aB} : 1 \mathbf{ab}$ zygotic series when inbred where no \mathbf{Ab} individual occurred. An account of these families is given here.

The striped yellows of the family H. 1'12 (Table III), the generation preceding that under consideration, would, as may be inferred from their pedigree, have consisted of four different forms with regards the zygotic constitution, namely \mathbf{SSYY} , \mathbf{SSYy} , \mathbf{SsYY} and \mathbf{SsYy} . The offspring of two matings amongst nine matings of these striped yellows showed a peculiar feature as given below¹.

	Striped yellow (\mathbf{SY})	Normal yellow (\mathbf{sY})	Normal white (\mathbf{sy})
H. 1-1'12	194	80	100
H. 1-4'12	192	91	81
Total	386	171	181
Calculated on $2 : 1 : 1$	369.0	184.5	184.5

The Complete pedigree is put forth in the following table.

1. Cf. p. 2.

Striped yellow males (No. 8'13) in one of the families under consideration were crossed with bivoltine *Kasuri* white females, and the offspring were reared during the summer of the same year. The results follow:

	Striped yellow	Striped white	Normal yellow	Normal white	Total
S. 6'13 (<i>Kasuri</i> white ♀ × 8'13 ♂)	162	84	74	178	498
S. 7'13 (ditto)	222	—	188	—	410
S. 12'13 (ditto)	231	—	221	—	452

The matter which became clear to us from these results is nothing but that some of the striped yellow parents were **SsYy**, in which 2 : 1 : 1 : 2 coupling occurred, and some others were **SsYY** in their zygotic constitutions. This gives us, as far as it goes, apparently no clue to solution of the question how such a peculiar system as 2 **AB** : 1 **aB** : 1 **ab** (where **A** stands for **S**, **B** for **Y**) has been brought forth in the preceding generation. Thorough analysis of the case may be expected only after sufficient data have been accumulated.

If we assume a spontaneous elimination of **S**-factor in **SsYy** ♂ the foregoing case may easily be accounted for. But this assumption is evidently premature at present.

b) A Peculiar Type of Gametic Coupling between **S** and **Y**.

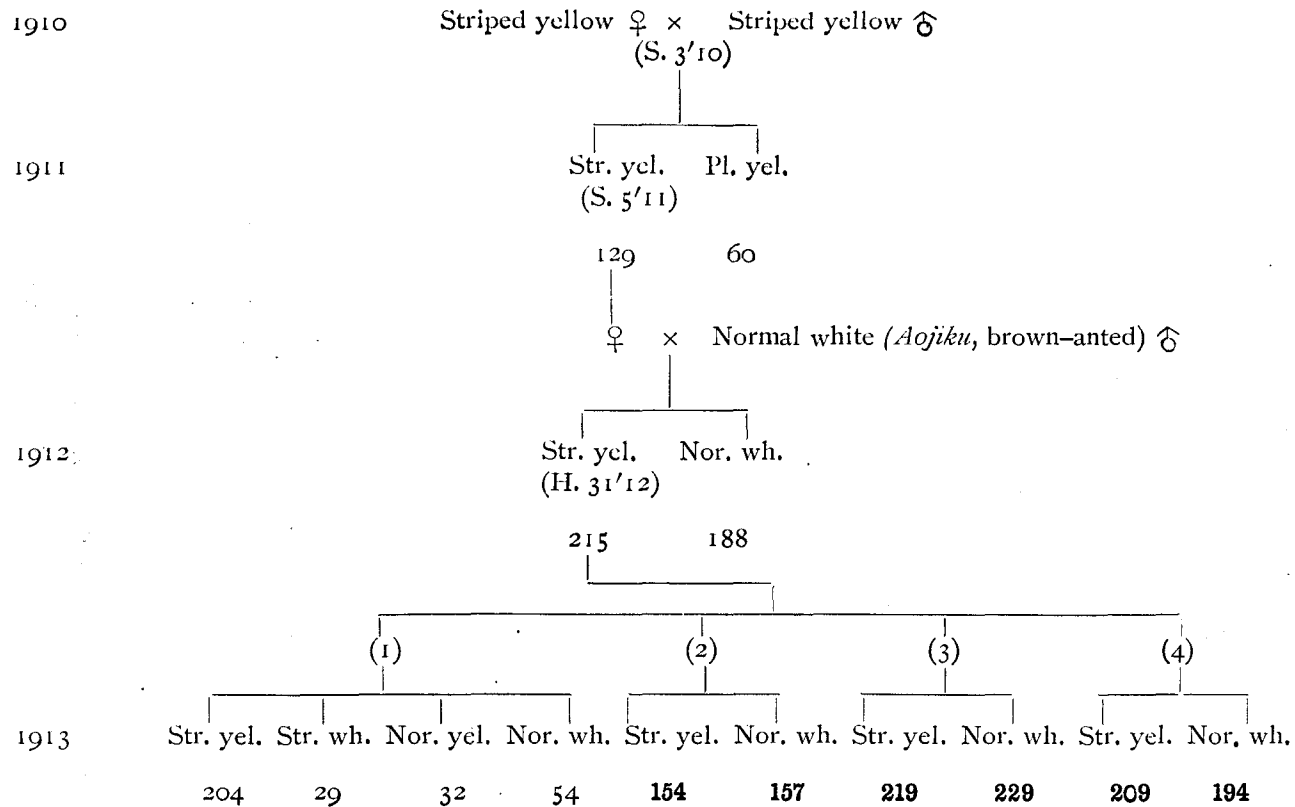
As mentioned in the foregoing pages the zygotic series in striped-yellow coupling are, in usual case, as follows:

	Str. yel.	Str. wh.	Nor. yel.	Nor. wh.
	11	1	1	3
or	8	1	1	2

These are effected from the male gametic series 3 : 1 : 1 : 3 and 2 : 1 : 1 : 2 respectively, the female gametes being 1 **SY** : 1 **sy** in both cases. An aberrant phenomenon from this general rule, however, was observed in the families H. 31-2, 3, 4'12 in which only two zygotic forms, double dominant and double recessive, occurred in *equal* numbers.

The actual figures and the origin of the families are given below.

Table IV.



FURTHER DATA ON THE REDUPLICATION IN SILKWORMS.

Among the four families derived from H. 31'12, the result in (1) is explained on the basis of the usual system of reduplication of **S-Y** coupling¹, the results in the rest show, on the contrary, quite a distinct feature. In these latter families we find only two zygotic forms in nearly equal ratio, the actual numbers in total being

	Str. yel.	Nor. wh.
Nos. 2, 3, 4 all together	582	580

We cannot consider above results as due to a complete coupling of an ordinary nature, because we should expect, if such were the case, double dominant and double recessive forms in the ratio 3 : 1 instead of 1 : 1 ratio which was attained by the present families.

If the simultaneous dropping out of the factors **S** and **Y** in the male parent has been assumed, above results may be simply explained. But we have at present no positive evidence in support of this assumption.

4. ON THE GENETIC CONSTITUTIONS OF THE STRIPED AND MORICAUD MARKINGS.

The question dealt with here concerns whether the genetic constitutions of the striped and moricaud markings (in homozygous condition) are **SSnn** and **MMnn** respectively, or are actually **SSNN** and **MMNN**.

As experimental results described elsewhere show, F_2 families ex striped \times normal involved only striped and normal individuals, but no other marking, plain for instance. On the basis of **SSnn** view, on the other hand, we are to expect three forms of marking in F_2 , i. e. striped, normal and **ssnn** markings. As this did not actually happen, however, we must, for explanation of the phenomenon, assume a complete replusion between **S** and **N**.

If the formula **SSNN** was accepted, on the contrary, above result is simply analysed without need of assuming any reduplication, but another difficulty occurs here. In F_2 ex **SSNN** \times **ssnn** (plain) we should expect

1. (2 : 1 : 1 : 2) ♂ \times (1 : 1) ♀. Cf. p. 5.

the normal-marked ones besides the striped and plain-marked specimens. This is contrary to the actual results, F_2 generation practically involving striped and plains but no individuals normally marked. Thus we are forced again to assume a reduplication, namely, complete coupling between **S** and **N**.

The same thing may be said as regards the relation of the formulae **MMnn** and **MMNN** i. e. we must assume complete repulsion between **M** and **N** for **MMnn** system, and complete coupling between them for **MMNN** view.

On the striped and moricaud larvae the normal marking ("eye-spots" and "lunules") co-exists with that marking which is characteristic of the striped or the moricaud. This fact seemingly points to the **SSNN** and **MMNN** formulae. But it is, at the same time, not unreasonable to suppose that the normalness actually partakes of the striped or the moricaud marking, the characteristic being freely developed by **S**- or **M**-factor in absence of **N** as well as in presence of it.

We are, as these comparisons show, unable to determine, at present, which of the formulae above stated are more adequate. Therefore I will prefer, until more positive evidence to the contrary is obtained, the expressions **SSnn** and **MMnn** which were adopted in my previous papers.

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Agricultural College,

Tohoku Imperial University,

Sapporo.

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