GAMETIC COUPLING AND REPULSION IN THE SILKWORM, BOMBYX MORI.

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With Pl. IX.

I. Introduction.

In the gametogenesis of an individual heterozygous for a factor or factors, all possible kinds of gametes as regards the presence or absence of the factor or factors are formed in equal numbers. For instance, in the case of a zygote heterozygous for two factors, **A** and **B**, the gametes to be produced is represented thus:

1 **AB** : 1 **Ab** : 1 **aB** : 1 **ab**,

and by the combination of these gametes there will be formed four classes of the offspring, **AB, Ab, aB** and **ab,** in the ratio of 9 : 3 : 3 : 1.

But a number of cases are known in which certain deviations from the above general rule have been observed. BATESON obtained, for example, the following result in the cross of the Sweet Pea **BL** × **bl,** where **B** is purple (blue factor); **b,** red; **L,** long pollen; **l,** round pollen. The F_1 plants were all purples with long pollen, and F_2 consisted of 1528 **BL** : 106 **Bl** : 117 **bL** : 381 **bl**. Here the numerical ratio is remarkably different from the normal 9 : 3 : 3 : 1 series.

To account for such an anomalous case, BATESON and his collaborators put forth a suggestion that here the possible gametic forms are not produced in equal numbers, but that certain gametes occur more frequently than others, *i. e.* a partial coupling takes place between **B** and **L**. The gametic series in such a partial coupling is not 1 : 1 : 1 : 1, but it may be set out in a general formula as:

n **AB** : 1 **Ab** : 1 **aB** : n **ab**,

which gives rise to the following phenotypic ratio in F_2:

$\{3n^2-(2n-1)\}$ **AB**: $(2n-1)$ **Ab**: $(2n-1)$ **aB**: $\{n^2-(2n-1)\}$ **ab**.

If in the above formula certain terms such as **Ab** and **aB** were entirely inhibited to occur, *i. e.* complete coupling takes place, the F_2 forms will be reduced to the simplest Mendelian ratio 3 **AB**: 1 **ab**.

The *gametic repulsion* or *spurious allelomorphism* is a phenomenon closely related to the coupling. In partial repulsion the gametic and zygotic series may be represented in a general way as follows:

Gametic series. 1 **AB**: n **Ab**: n **aB**: 1 **ab**.

Zygotic " . $(2n^2+1)$ **AB**: (n^2-1) **Ab**: (n^2-1) **aB**: 1 **ab**.

When the repulsion is perfect, the series will become much simpler thus:

Gametic series. 1 **Ab**: 1 **aB**,

Zygotic " . 2 **AB**: 1 **Ab**: 1 **aB**.

The gametic coupling and repulsion, or the reduplicated systems to use BATESON'S term recently suggested, are the most interesting and complicated cases among Mendelian inheritance.

During the last few years, a considerable number of examples of reduplicated systems were found in plants by various authors. In animals, on the contrary, although several cases of repulsion and a few examples of complete coupling taking place between the *sex-factor* and some *somatic* characters were reported by several authors, no instance of the phenomenon in question has been observed, as far as I am aware, to occur between two *somatic* characters.

In the course of Mendelian researches with the Silkworm, I have met with several complex cases which are undoubtedly due to the gametic coupling or repulsion between two *somatic* characters. I have also ascertained some remarkable facts in regard to coupling.

Though my experiments are not ended, but are in full progress at present, the more important results just mentioned will be described in the following pages.

I wish to express my hearty thanks to Mr. Y. TAKAHASHI who has given me many valuable suggestions during the study, and has kindly looked through the manuscripts.

I am also indebted to Mr. K. SUZUKI who reared and crossed in 1911 with unusual skill and care various strains of my silkworms in the College silkworm-nursery.

II. Description of the Races.

The silkworms used in the present experiments are of two races:

1) Japanese tetra-moulters.[1]

2) Chinese tri-moulters.[1]

1) Japanese tetra-moulters (Japanese normal white).

Of numerous tetra-moulting races, only two, viz. *Aojiku* and the "*Brown ant*" were employed. The former is one of the commonest breeds in Japan, amd the latter was one which appeared as a sport of an another well-known breed, *Matamukashi*. The characteristic of the latter is that the newly hatched larva or "ant" is reddish brown in colour, but not black as in the normal strains. Both of the races which I made of use are univoltine, their larvae being normal-patterned and spinning pure-white cocoons. They have been pure-bred for generations in our nursery and proved to be homozygous for their larval marking and cocoon colour.

2) Chinese tri-moulters.

In 1910 we procured an egg-carton from our Chinese friend Mr. NŪ in *Shan-tung*. The population reared from this material proved to be a mixture of various strains, not only as to the larval markings but also in respect of the cocoon colours and moulting-frequency, and from this mixture I have isolated the following strains[2] in the same year.

1) The term "tetra-moulters" means those races which pass through four moults, while the "tri-moulters" those which undergo only three ecdyses before they spin cocoons.

2) As to the detailed statements of the larval markings and cocoon colours of these races readers are referred to pp. 95 — 98 of this Volume.

a) Common or normal yellow. The larva is normal or common-patterned and yellow-blooded, *i. e.* yellow cocooner.

b) Normal white. All characteristics are the same with those of the first named, except that this is white-(colourless) blooded.

c) Striped yellow. The full-grown larva is generally black, but with segmental white stripes; the blood is yellow.

d) Moricaud yellow. The whole body of the larva shows a moricaud or darky appearance. Yellow-blooded.

e) Plain yellow. The larva is destitute of distinct markings and is yellow-blooded.

III. Mendelian Factors Concerned in the Present Research.

The Mendelian characters which are dealt with in the present experiments are as follows:

S,	Striped black.	**s,**	Absence of S; plain coat.
Z,	Zebra-patterned.	**z,**	" " Z; plain.
M,	Moricaud.	**m,**	" " M; plain.
N,	Normal or common patterned.	**n,**	" " N; plain.
Y,	Yellow blooded, viz. yellow cocoon colour.	**y,**	" " Y; white blooded or white cocoon.

Of the above-mentioned, the "presence" characters are, of course, dominant to the "absence" characters. Of the dominant factors, **N** is always hypostatic to **S, Z** and **M.** The inter-relations of the factors, **S, Z** and **M** are not yet fully tested, but I am inclined to think that these characters are nearly equipotent in their dominancy.

All the characters given above are known to be inherited independently of one another in normal cases. For instance, the yellow-cocoon (yellow blood) character and each marking character being due to the totally different genes, the latter can be found connected with or separated from the former.

Some of the Chinese strains used in the present experiments having been heterozygous for the moultinism, I often met with a mixture of tri-moulting and tetra-moulting larvae derived from the same parents. But in the following account this character is not altogether touched upon, since as yet it has not been fully studied.

IV. Gametic Repulsion.

I shall first describe cases of repulsion or spurious allelomorphism.

1. Complete repulsion between the normal pattern (N) and the yellow colour (Y).

a) The Chinese normal yellows isolated from the above mentioned mixed population in 1910 were paired *inter se*, and two matings of them gave the following results in 1911:

Lot No.	Normal yellow	Normal white	Plain yellow	Total.
N. 1.'10	84	5	41	130
N. 2.'10	154	66	86	306
Total	238	71	127	436

From these results, it may be inferred that the parental normal yellows were heterozygous for marking characters (normal and plain) as well as for cocoon colors (yellow and white), their formula being **NnYy.** From such a zygotic constitution we should expect four phenotypes in the subsequent generation, *i. e.* normal yellow, normal white, plain yellow and plain white in the ratio of 9: 3: 3: 1. But actually only the first three of these expected foıms were obtained, no plain white larva having occurred. These results can be easily comprehended if we assume the occurrence of complete repulsion between normal and yellow. On this assumption we have only three forms, normal yellow (**NynY**), normal white (**NyNy**) and plain yellow (**nYnY**) in the ratio of 2: 1: 1. If this assumption is correct the hetero-zygous normal yellow ought to produce, when mated among themselves, three forms of offspring in the proportion 2: 1: 1 as in the preceding generation, and the other two forms, normal white and plain yellow, should remain true to their parents, because they are homozygous both for the marking and colour characters. This assumption proved correct as may be seen from what is described below.

The three classes of offspring just mentioned being mated *inter se* gave the following result in 1912.

The plain yellow and normal white bred true to their own type, four matings of the former having produced 1116 individuals which were all plain yellow, while three matings of the latter produced 998 worms which were all normal white without excepetion. The normal yellows, on the contrary, splitted into three forms as in the preceding generation.

Lot No.	Normal yellow	Normal white	Plain yellow	Total
N. 4.[1] '11	168	77	81	326
N. 4.[2] '11	154	72	62	288
N. 4.[3] '11	136	86	68	290
Total	**458**	**235**	**211**	**904**
Expectation	452	226	226	904

We may express the above result diagramatically as follows:

1910 Normal yellow × Normal yellow
(NynY) **(NynY)**
Gametes **Ny, nY** **Ny, nY**

1911 238 Normal yellow 71 Normal white 127 Plain yellow
Gametes **Ny** | **nY** **Ny** **nY**

1912 458 Normal yellow 235 Normal white 211 Plain yellow Constant Constant

b) Japanese normal white *(Aojiku)* females were mated with Chinese striped yellow males in 1910. Two matings from this cross gave in 1911 the striped and normal yellows nearly in the proportion of 1 : 1, the actual result being 269 striped yellow: 203 normal yellow. This result, together with others to be described later, indicates that the striped parent was homozygous for yellowness, but heterozygous for striped character. As the normal parent is of course homozygous both for the marking and colour, the case may be graphically represented as follows:

P (1910)	Normal white **ssNNyy**	×	Striped yellow **SsnnYY**
F_1 (1911)	Striped yellow **SnYsNy**		Normal yellow **snYsNy**

F_1 normal yellow mated *inter se* gave the following offspring.[1]

Lot No.	Normal yellow	Normal white	Plain yellow	Total
H. 2.' 11	80	30	28	138
Expectation	69.0	34.5	34.5	138.0

Here again normal and yellow characters are brought into the cross by the different parents, and therefore a perfect repulsion occurs between them.

c) A Japanese normal white *(Aojiku)* female was crossed with a homozygous plain yellow of Chinese origin. The F_1 larvae which were all normal yellow yielded three forms of F_2 offspring.

Lot No.	Normal yellow	Normal white	Plain yellow	Total
H. 5.' 11	123	88	61	272

I had only one mating of this cross reared in 1912, nevertheless it was the most important mating for the confirmation of the assumption that a perfect repulsion takes place between the normal and yellow characters, when these are brought into one individual by the different parents. Here the cross had been made between two homozygous strains, the zygotic constitutions of which were exactly known, and the hereditary behaviour

1) As to the behaviour of the F_1 striped yellow, see the later pages.

of the cross may be represented thus:

P (1910)	Normal white **NyNy**	×	Plain yellow **nYnY**
F_1 (1911)		Normal yellow **NynY**	
Gametes		**Ny** | **nY**	
F_2 (1912)	123 normal yellow **NynY**	88 normal white **NyNy**	61 plain yellow **nYnY**
	2	: 1 :	1

The experimental results set forth above seem sufficient to support the assumption that there occurs a complete repulsion between two dominant characters, normal marking (**N**) and yellow colour (**Y**), in the heterozygotes derived from a cross, normal white (**NyNy**) × plain yellow (**nYnY**).

Below is given a summary of the results produced by these heterozygous normal yellows mated *inter se* in 1911.

Lot No.	Normal yellow	Normal white	Plain yellow	Total
N. 4^1. '11	168	77	81	326
N. 4^2. '11	154	72	62	288
N. 4^3. '11	136	86	68	290
N. 2. '11	80	30	28	138
N. 5. '11	123	88	61	272
Total	**661**	**353**	**300**	**1314**
Expectation	657.0	328.5	328.5	1314.0

Thus the actual figures closely accord with the theoretical numbers calculated on the assumption which we have stated above.

II. Complete repulsion between stripedness (S) and yellowness (Y).

A batch of the cross homozygous Japanese normal white *(Aojiku)* ♀ × heterozygous striped yellow (S. 5.' 11) ♂ produced in 1912 the following offspring:

Lot No.	Striped white	Normal yellow	Total
H. 17. '11	63	65	128

Here we have encountered a curious phenomenon. Two pairs of the characters by which the parents differed from each other appeared in an exactly-reversed combination in their offspring, that is to say, the striped larvae were all white-blooded instead of being yellow-blooded, and the normal-patterned were all provided with yellow blood instead of being white-blooded. As the parental formulae are known to be **ssNNyy** *(Aojiku)* and **SsnnYy** (S. 5. '11 striped yellow) respectively, we should expect, if the inheritance was normal, the offspring to be as follows:

1 **SnYsNy** ....Striped yellow
1 **SnysNy** ....Striped white
1 **snYsNy** ....Normal yellow
1 **snysNy** ....Normal white

But as already stated such was not the case. Therefore we are forced to suppose that there occurs a perfect repulsion between the striped marking and the yellow colour. The case may be diagramatically expressed thus:

1911	Normal white **ssNNyy**	×	Striped yellow **SsnnYy**
Gametes	**sNy**		**Sny, snY**
1912	Striped white **SnysNy**		Normal yellow **snYsNy**
Ratio	1	:	1
Observed	63		65
Expected	64		64

I have had only one mating of this cross. But there seems to be no way of explanation other than that there takes place an absolute repulsion between stripedness and yellowness. Moreover, it is highly probable that the striped yellow parent used in the present cross is produced by combination of **Sny** and **snY** gametes, but not by that of **SnY** and **sny** gametes. (Table III, S. 3.'10, Table V, H. 17.'11).

III. Complete repulsion between stripedness (S) and normal pattern (N).

While the two preceding cases of repulsion were observed between marking character and cocoon colour, the one now to be described below occurred between two marking characters.

The cross (H. 1. '10), homozygous Japanese normal white *(Aojiku)* ♀ × heterozygous Chinese striped yellow ♂, provided the most interesting materials for the present research. As I have already stated, (Repulsion, Case 1, b), this cross produced striped and normal yellows in nearly equal numbers, and since the zygotic formula of these F_1 striped yellows (H. 1. '11) is **SnYsNy** (see Repulsion, Case 1, b and also Table V), it was but natural to expect that *six* F_2 forms would be produced in the following ratio:

27	**SNY**	36	striped yellow
9	**SnY**		
9	**SNy**	12	striped white
3	**Sny**		
9	**sNY**	9	normal yellow
3	**sNy**	3	normal white
3	**snY**	3	plain yellow
1	**sny**	1	plain white

Quite contrary to the above expectation only *four* phenotypes appeared in the experiment as shown below:

Striped yellow	148
Striped white	12
Normal yellow	14
Normal white	50
Total	224

It is evident from the above result that a complete repulsion took place between stripedness (**S**) and normalness (**N**). The gametes produced by these F_1 striped yellows (**SnYsNy**) must have been, therefore, of only *four* kinds as follows:

SnY, sNY, Sny, sNy.

By random combination of these gametes there must arise *four* F_2 forms—as observed in the experiment— striped yellow, striped white, normal yellow and normal white, in the ratio of 9 : 3 : 3 : 1. This normal ratio is, however, disturbed in the present case by virtue of partial coupling taking place between the striped and yellow factors, the detailed statement of which is given in the following pages.

V. Gametic Coupling.

Two cases of partial and one example of complete coupling were observed in my experiments.

A. Partial coupling.

I. Partial coupling between stripedness (S) and yellowness (Y).

a) The hereditary behaviour of the F_1 striped yellow **SnYsNy** just referred to above (H. 1. '11) clearly points to the conclusion that there occurs a partial coupling between striped marking and yellow colour, as may be seen from the following consideration.

If we take for granted that a perfect repulsion occurs between striped and normal character in the F_1 striped yellows, we should obtain four F_2 forms in the ratio

9 striped yellow
3 striped white
3 normal yellow
1 normal white.

But actually such was not the case as shown in the following table.

	Actual figures	Expectation on the normal gametic distribution
Striped yellow	148	126
Striped white	12	42
Normal yellow	14	42
Normal white	50	14
Total	224	224

As the experimental result shows a great excess of the normal white, we are naturally led to think that a partial coupling occurs between stripedness and normalness.

To determine the system on which the partial coupling now under consideration occurs the actual numbers observed are not of course sufficiently large. But it seems to be quite probable that here the 7 : 1 : 1 : 7 system is followed. From the gametic series 7 **SnY** : 1 **Sny** : 1 **sNY** : 7 **sNy**, we may expect F_2 forms as follows:

	Actual figures	Expectation on 7 : 1 basis	Ratio on 7 : 1 basis
Striped yellow	148	154.9	177
Striped white	12	13.1	15
Normal yellow	14	13.1	15
Normal white	50	42.9	49
Total	224	224.0	256

However it must be noted here that there are two another modes of explanation for the present case, which are described below.

i) Suppose that there occur *a*) a complete repulsion between **N** and **Y**, and *b*) a partial coupling between **S** and **Y** on the 7 : 1 system, thus producing the gametic series, 7 **SnY** : 1 **SNy** : 1 **snY** : 7 **sNy**. Then we should get five F_2 forms in the following ratio:

Striped yellow	177
Striped white	15
Normal yellow	14
Normal white	49
Plain yellow	1
Total	256

The theoretical numbers calculated on the above ratio are given below together with the actual figures obtained:

	Expectation	Actual figures
Striped yellow	154.9	148
Striped white	13.1	12
Normal yellow	12.3	14
Normal white	42.9	50
Plain yellow	0.8	0
Total	224.0	224

We see that the theoretical expectation on this supposition shows a less accordance with the observed figures than that given in the foregoing lines.

ii) The case can also be explained by assuming *a*) a complete repulsion between **S** and **N**, and *b*) a partial repulsion between **N** and **Y**. On such an assumption we may expect the similar gametic series as that given above *i. e.* 1 **sNY**, 7 **SnY**, 7 **sNy**, 1 **Sny**.

In fact, we have at present no positive reason to preclude a partial coupling between **S** and **Y** against a *partial repulsion* between **N** and **Y**. The fact, that a *complete repulsion* does occur between **N** and **Y** in certain cases (Repulsion, Case 1), is not sufficient in itself to disprove the occurrence of a partial repulsion between them, in as much as I have found, as will be described later, that in one case a *partial coupling* takes place between **S** and **Y** factors, while in other case a *perfect coupling* occurs between them.

Nevertheless it seems more probable that the case mentioned above is due to a partial attraction of **S** and **Y**. The following case positively speaks for the correctness of that view.

b) The striped yellows of the Lot S. 5. '11, which were heterozygous as regards both the marking (striped and plain) and the colour characters (yellow and white), were mated among themselves. One of the batches in this lot was reared, which gave the following result:

Lot No.	S. 5. '11
Striped yellow	134
Striped white	10
Plain yellow	7
Plain white	43
Total	194

The above figures widely differ from those calculated on the normal ratio 9: 3: 3: 1 which is shown below:

Striped yellow	109.1
Striped white	36.4
Plain yellow	36.4
Plain white	12.1

If we assume, on the contrary, the occurrence of a partial coupling of striped marking with yellow colour on the 7: 1 system, the result can be at once accounted for thus:

	Actual figures	Expectation on 7 : 1 basis
Striped yellow	134	134.1
Striped white	10	11.4
Plain yellow	7	11.4
Plain white	43	37.1
Total	194	194.0

As the above table shows, the observed numbers are very close to the calculated.

Since there exists no "presence" factor other than those given above, *i. e.* stripedness and yellowness, there is least possibility of occurrence of other reduplicated systems in this case.

II. Partial coupling between the moricaud marking (M) and the yellow colour (Y).

In 1910 some of the Chinese moricaud yellow larvae were selected by their outer characteristics, and five matings were made among themselves. Of these matings, progeny of four were reared in 1911, each of which consisted of two different forms, moricaud yellow and plain yellow. The actual numbers of the larvae produced by these four matings taken together are 680 moricaud yellow and 232 plain yellow, which almost exactly represent the 3 : 1 ratio.

A single mating (M. 7. '10) shows, however, a little complication, giving the following offspring:

Lot No.	M. 7. '10
Moricaud yellow	104
Moricaud white	12
Plain yellow	5
Plain white	38
Total	159

Apparently the result is accounted for by the assumption of a partial coupling between moricaud and yellow. The expectation on the 7 : 1 : 1 : 7 series is as follows:

	Actual figures	Expectation
Moricaud yellow	104	109.9
Moricaud white	12	9.3
Plain yellow	5	9.3
Plain white	38	30.5
Total	159	159.0

If the above assumption is correct, the Lot M. 7. '10 must have been **MmYy** × **MmYy**, and produced the following gametes:

7 **MY**, 1 **My**, 1 **mY**, 7 **my**.

By recombination of these gametic forms, we should obtain:

49 **MYMY** + 14 **MYMy** + 14 **MYmY** } 98 **MYmy** + 2 **MymY** }	....177 moricaud yellow
1 **MyMy** + 14 **Mymy**	15 moricaud white
1 **mYmY** + 14 **mYmy**	15 plain yellow
49 **mymy**	49 plain white

Our assumption is supported by the results obtained by inbreeding the F_1 phenotypes.

Four matings of the F_1 plain white gave 774 F_2 individuals altogether, which were all plain white, *i. e.* remained true to their parents. One mating of the plain yellow yielded 136 plain yellow and 54 plain white, or approximately the ratio 3 : 1. One of the matings of moricaud white gave 152 moricaud white and 39 plain white, or nearly the ratio 3 : 1. Three batches of the moricaud yellow lot produced in all 483 larvae which were entirely moricaud yellow. Two matings in the same lot, on the other hand, gave four F_2 phenotypes as follows:

Lot No.	M. 9.[1] '11	M. 9.[2] '11	Total
Moricaud yellow	61	131	192
Moricaud white	8	21	29
Plain yellow	5	17	22
Plain white	10	47	57
Total	84	216	300

All these results are explicable by the supposed factorial constitution of the F_1 forms and by the assumption that a partial coupling takes place between moricaud marking and yellow colour in the heterozygous moricaud yellow (**MYmy**). The experimental figures fairly agree with the numbers calculated on the 7 : 1 : 1 : 7 basis as shown in the following table.

	Actual figures (two matings)	Expectation
Moricaud yellow	192	207.4
Moricaud white	29	17.6
Plain yellow	22	17.6
Plain white	57	57.4
Total	300	300.0

B. Complete coupling.

A case of complete coupling between the striped and yellow characters was observed in my experiments. These characters showed, as stated above, the phenomenon of partial coupling (presumably on 7 : 1 system) on certain occasions, while in the present case a complete coupling took place between them. Such an inconstancy as regards the intensity of coupling is difficult to explain at present.

Complete coupling between the striped marking (S) and the yellow colour (Y).

A striped yellow female of the Lot S. 5. '11 was mated with a "*Brown ant*" male (Japanese normal white), and its offspring was reared in 1912. The result follows:

Lot No.	H. 19. '11
Striped yellow	215
Normal white	188
Total	403

Thus all of the striped larvae were yellow, while the normal individuals were all white with no exception.

As the maternal striped yellow (S. 5. '11) is heterozygous in the marking and colour, as stated before, and the paternal homozygous in both of these characters, we have no way of interpretation of the above result except by supposing that there occurred a complete coupling between striped and yellow characters. On this assumption we may expect two forms of the offspring, striped yellow and normal white, in equal numbers. The pedigree may be given diagramatically as follows:

1911	**SnYsny** Striped yellow	×	**sNysNy** Normal white
Gametes	**SnY, sny**		**sNy**
1912	**SnYsNy**		**snysNy**
Ratio	1 striped yellow	:	1 normal white
Observed	215		188
Calculated	201.5		201.5

VI. Tables.

In the following Tables will be given the genealogical relations, genetic constitutions, theoretical expectations and actual figures of the various lots of silkworms used in the present research. It is hoped that these Tables will serve to give a clearer understanding of the foregoing descriptions.

Table I.

Plain Series.

Lot No.	Apparent characters and Genetic formulae	Segregation	Gametes	Lot No.	Zygotic formulae	Apparent characters	Ratio	Actual figures	Expectation
P. 1. '10	Plain yellow szmnYszmnY	normal	szmnY	P. 1. '11	szmnYszmnY	plain yellow	all	all	all
P. 1. '11	Plain yellow szmnYszmnY	"	szmnY	P. 1. '12	szmnYszmnY	plain yellow	all	229	229

Table II.

Normal Series.

Lot No.	Apparent characters and Genetic formulae	Segregation	Gametes	Lot No.	Zygotic formulae	Apparent characters	Ratio	Actual figures	Expectation
N. 1. '10	Normal yellow NynY	complete repulsion	Ny nY	N. 1. '11	2 NynY	normal yellow	2	84	65.0
				N. 2. '11	1 NyNy	normal white	1	5	32.5
				N. 3. '11	1 nYnY	plain yellow	1	41	32.5
						Total		130	130.0
N. 2. '10	Normal yellow NynY	complete repulsion	Ny nY	N. 4. '11	2 NynY	normal yellow	2	154	153.0
				N. 5. '11	1 NyNy	normal white	1	66	76.5
				N. 6. '11	1 nYnY	plain yellow	1	86	76.5
						Total		306	306.0
N. 4.¹ '11	Normal yellow NynY	complete repulsion	Ny nY	N. 1. '12	2 NynY	normal yellow	2	168	163.0
				N. 2. '12	1 NyNy	normal white	1	77	81.5
				N. 3. '12	1 nYnY	plain yellow	1	81	81.5
						Total		326	326.0
N. 4.² '11	Normal yellow NynY	complete repulsion	Ny nY	N. 4. '12	2 NynY	normal yellow	2	154	144
				N. 5. '12	1 NyNy	normal white	1	72	72
				N. 6. '12	1 nYnY	plain yellow	1	62	72
						Total		288	288
N. 4.³ '11	Normal yellow NynY	complete repulsion	Ny nY	N. 7. '12	2 NynY	normal yellow	2	136	145.0
				N. 8. '12	1 NyNy	normal white	1	86	72.5
				N. 9. '12	1 nYnY	plain yellow	1	68	72.5
						Total		290	290.0
N. 5.¹ '11	Normal white NyNy	normal	Ny	N. 10. '12	NyNy	normal white	all	251	251
N. 5.² '11	" "	"	"	N. 11. '12	"	" "	"	412	412
N. 5.³ '11	" "	"	"	N. 12. '12	"	" "	"	335	335
N. 6.¹ '11	Plain yellow nYnY	"	nY	N. 13. '12	nYnY	plain yellow	"	253	253
N. 6.² '11	" "	"	"	N. 14. '12	"	" "	"	416	416
N. 6.³ '11	" "	"	"	N. 15. '12	"	" "	"	208	208
N. 6.⁴ '11	" "	"	"	N. 16. '12	"	" "	"	239	239

Table III.

Striped Series.

Lot No.	Apparent characters and Genetic formulae	Segregation	Gametes	Lot No.	Zygotic formulae	Apparent characters	Ratio	Actual figures	Expectation
S. 1. '10	Striped yellow SnYsnY	normal	SnY snY	S. 1. '11	1 SnYSnY 2 SnYsnY	striped yellow	3	265	257
				S. 2, '11	1 snYsnY	plain yellow	1	78	86
						Total		343	343
S. 2. '10	Striped yellow SnYsnY	"	SnY snY	S. 3. '11	1 SnYSnY 2 SuYsnY	striped yellow	3	152	148.5
				S. 4. '11	1 snYsnY	plain yellow	1	46	49.5
						Total		198	198.0
S. 3. '10	Striped yellow SnYsny × Striped yellow SnYsnY	partial coupling normal	7 SnY 1 Sny 1 snY 7 sny 1 SnY 1 snY	S. 5. '11	7 SnYSnY 1 SnySnY 8 snYSnY 7 snySnY 1 SnysnY	24 striped yellow	3	129	142
				S. 6. '11	1 snYsnY 7 snysnY	8 plain yellow	1	60	47
						Total		189	189
S. 1.[1] '11	Strtped yellow SnYSnY	normal	SnY	S. 1. '12	SnYSnY	striped yellow	all	230	230
S. 1.[2] '11	Striped yellow SnYsnY	"	SnY snY	S. 2. '12	1 SnYSnY 2 SnYsnY	striped yellow	3	232	246
				S. 3. '12	1 snYsnY	plain yellow	1	96	82
						Total		328	328
S. 2. '11	Plain yellow snYsnY	"	snY	S. 4. '12	snYsnY	plain yellow	all	409	409
S. 5. '11	Striped yellow SnYsny	partial coupling	7 SnY 1 Sny 1 snY 7 sny	S. 5. '12	49 SnYSnY 14 SnYSny 14 SnYsnY 98 SnYsny 2 SnysnY	striped yellow	177	134	134.1
				S. 6. '12	1 SnySny 14 Snysny	striped white	15	10	11.4
				S. 7. '12	1. snYsnY 14 snYsny	plain yellow	15	7	11.4
				S. 8. '12	49 snysny	plain white	49	43	37.1
						Total	256	194	194.0

Table IV.

Moricaud Series.

Lot No.	Apparent characters and Genetic formulae	Segregation	Gametes	Lot No.	Zygotic formulae	Apparent characters	Ratio	Actual figures	Expectation
M. 1. '10	Moricaud yellow MYMY × Moricaud yellow MYmY	normal "	MY MY mY	M. 13. '11	1 MYMY 1 MYmY	moricaud yellow	all	all	all
M. 2. '10	Moricaud yellow MYMY	"	MY	M. 14. '11	MYMY	moricaud yellow	"	"	"
M. 3. '10	Moricaud yellow MYmY	"	MY mY	M. 1. '11	1 MYMY 2 MYmY	moricaud yellow	3	158	158
				M. 2. '11	1 mYmY	plain yellow	1	53	53
						Total		211	211
M. 4. '10	Moricaud yellow MYmy	partial coupling	7 MY 1 My 1 mY 7 my	M. 3. '11	7 MYMY 1 MyMY 8 mYMY 7 myMY 1 MymY	24 moricaud yellow	3	172	183
	× Moricaud yellow MYmY	normal	1 mY 1 MY	M. 4. '11	1 mYmY 7 mymY	8 plain yellow	1	72	61
						Total		244	244
M. 5. '10	Moricaud yellow MYmy	partial caupling	7 MY 1 My 1 mY 7 my	M. 5. '11	7 MYMY 1 MyMY 8 mYMY 7 myMY 1 MymY	24 moricaud yellow	3	169	161
	× Moricaud yellow MYmY	normal	1 MY 1 mY	M. 6. '11	1 mYmY 7 mymY	8 plain yellow	1	46	54
						Total		215	215
M. 6. '10	Moricaud yellow MYmY	normal	MY mY	M. 7. '11	1 MYMY 2 MYmY	moricaud yellow	3	181	181.5
				M. 8. '11	1 mYmY	plain yellow	1	61	60.5
						Total		242	242.0
M. 7. '10	Moricaud yellow MYmy	partial coupling	7 MY 1 My 1 mY 7 my	M. 9. '11	49 MYMY 14 MYMy 14 MYmY 98 MYmy 2 MymY	moricaud yellow	177	104	109.9
				M. 10. '11	1 MyMy 14 Mymy	moricaud white	15	12	9.3
				M. 11. '11	1 mYmY 14 mYmy	plain yellow	15	5	9.3
				M. 12. '11	49 mymy	plain white	49	38	30.5
						Total	256	159	159.0
M. 1.[1] '11	Moricaud yellow MYMY	normal	MY	M. 1. '12	MYMY	moricaud yellow	all	275	275
M. 1.[2] '11	Moricaud yellow MYmY	"	MY mY	M. 2. '12	1 MYMY 2 MYmY	moricaud yellow	3	180	175
				M. 3. '12	1 mYmY	plain yellow	1	53	58
						Total		233	233
M. 2. '11	Plain yellow mYmY	"	mY	M. 4. '12	mYmY	plain yellow	all	176	176
M. 3.[1] '11	Moricaud yellow MYmY	"	MY mY	M. 5. '12	1 MYMY 2 MYmY	moricaud yellow	3	343	343.5
				M. 6. '12	1 mYmY	plain yellow	1	115	114.5
						Total		458	458.0
M. 3.[2] '11	Moricaud yellow MYMY	"	MY	M. 7. '12	MYMY	moricaud yellow	all	267	267
M. 4.[1] '11	Plain yellow mYmY	"	mY my	M. 8. '12	1 mYmY 2 mYmy	plain yellow	3	242	241.5
				M. 9. '12	1 mymy	plain white	1	80	80.5
						Total		322	322.0
M, 4.[2] '11	Plain yellow mYmy	"	mY my	M. 10. '12	1 mYmY 2 mYmy	plain yellow	3	345	343.5
				M. 11. '12	1 mymy	plain white	1	113	114.5
						Total		458	458.0
M. 4.[3] '11	Plain yellow mYmy	"	mY my	M. 12. '12	1 mYmY 2 mYmy	plain yellow	3	215	207
				M. 13. '12	1 mymy	plain white	1	61	69
						Total		276	276
M. 5. '11	Moricaud yellow MYMY	"	MY	M. 14. '12	MYMY	moricaud yellow	all	306	306
M. 6.[1] '11	Plain yellow mYmy	"	mY my	M. 15. '12	1 mYmY 2 mYmy	plain yellow	3	17	18.75
				M. 16. '12	1 mymy	plain white	1	8	6.25
						Total		25	25.00
M. 6.[2] '11	Plain yellow mYmy	"	mY my	M. 17. '12	1 mYmY 2 mYmy	plain yellow	3	26	35.25
				M. 18. '12	1 mymy	plain white	1	21	11.75
						Total		47	47·00
M. 7. '11	Moricaud yellow MYMY	"	MY	M. 19. '12	MYMY	moricaud yellow	all	229	229
M. 8. '11	Plain yellow mYmY	"	mY	M. 20. '12	mYmY	plain yellow	"	200	200
M. 9.[1] '11	Moricaud yellow MYMY	"	MY	M. 21. '12	MYMY	moricaud yellow	"	115	115
						plain yellow ?	—	2	—
M. 9.[2] '11	" "	"	"	M. 22. '12	"	moricaud yellow	all	239	239
M. 9.[3] '11	" "	"	"	M. 23. '12	"	" "	"	129	129
						normal white ?	—	4	—
M. 9.[4] '11	Moricaud yellow MYmy	partial coupling	7 MY 1 My 1 mY 7 my	M. 24. '12	49 MYMY 14 MYMy 14 MYmY 98 MYmy 2 MymY	moricaud yellow	177	61	58
				M. 25. '12	1 MyMy 14 Mymy	moricaud white	15	8	5
				M. 26. '12	1 mYmY 14 mYmy	plain yellow	15	5	5
				M. 27. '12	49 mymy	plain white	49	10	16
						Total	256	84	84
M. 9.[5] '11	Moricaud yellow MYmy	partial coupling	7 MY 1 My 1 mY 7 my	M. 28. '12	49 MYMY 14 MYMy 14 MYmY 98 MYmy 2 MymY	moricaud yellow	177	131	149.3
				M. 29. '12	1 MyMy 14 Mymy	moricaud white	15	21	12.7
				M. 30. '12	1 mYmY 14 mYmy	plain yellow	15	17	12.7
				M. 31. '12	49 mymy	plain white	49	47	41.3
						Total	256	216	216.0
M. 10. '11	Moricaud white Mymy	normal	My my	M. 32. '12	1 MyMy 2 Mymy	moricaud white	3	152	143
				M. 33. '12	1 mymy	plain white	1	39	48
						Total		191	191
M. 11. '11	plain yellow mYmy	"	mY my	M. 34. '12	1 mYmY 2 mYmy	plain yellow	3	136	142.5
				M. 35. '12	1 mymy	plain white	1	54	47.5
						Total		190	190.0
M. 12.[1] '11	Plain white mymy	"	my	M. 36. '12	mymy	plain white	all	201	201
						plain yellow ?	—	1	—
						moricaud white?	—	1	—
M. 12.[2] '11	" "	"	"	M. 37. '12	"	plain white	all	124	124
M. 12.[3] '11	" "	"	"	M. 38. '12	"	" "	"	193	193
M. 12.[4] '11	" "	"	"	M. 39. '12	"	" "	"	226	226

?. Exceptional irreguralities, perhaps accidental.

Table V.

Hybrid Series.

Lot No.	Apparent characters and Genetic formulae	Segregation	Gametes	Lot No.	Zygotic formulae	Apparent characters	Ratio	Actual figures	Expectation
H. 1.[1] '10	*Aojiku* (sNysNy) ♀ × Striped yellow ♂ (SnYsnY)	normal	sNy	H. 1. '11	1 SnYsNy	striped yellow	1	161	138
			SnY snY	H. 2. '11	1 snYsNy	normal yellow	1	115	138
						Total		276	276
H. 1.[2] '10	*Aojiku* (sNysNy) ♀ × Striped yellow ♂ (SnYsnY)	"	sNy	H. 3. '11	1 SnYsNy	striped yellow	1	108	98
			SnY snY	H. 4. '11	1 snYsNy	normal yellow	1	88	98
						Total		196	196
H. 1. '11	Striped yellow (SnYsNy)	complete repulsion between S and N, partial coupling between S and Y	7 SnY 1 Sny 1 sNY 7 sNy	H. 1. '12	49 SnYSnY 14 SnYSny 14 SnYsNY 98 SnYsNy 2 SnysNY	striped yellow	177	148	154.9
				H. 2. '12	1 SnySny 14 SnysNy	striped white	15	12	13.1
				H. 3. '12	1 sNYsNY 14 sNYsNy	normal yellow	15	14	13.1
				H. 4. '12	49 sNysNy	normal white	49	50	42.9
						Total	256	224	224.0
H. 2. '11	Normal yellow (snYsNy)	complete repulsion	snY sNy	H. 6. '12	2 sNysnY	normal yellow	2	80	69.0
				H. 7. '12	1 sNysNy	normal white	1	30	34.5
				H. 8. '12	1 snYsnY	plain yellow	1	28	34.5
						Total		138	138.0
H. 2. '10	*Aojiku* (NyNy) ♀ × Plain yellow (nYnY) ♂	normal	Ny / nY	H. 5. '11	NynY	normal yellow	all	372	372
H. 5. '11	Normal yellow (NynY)	complete repulsion	Ny nY	H. 9. '12	2 NynY	normal yellow	2	123	136
				H. 10. '12	1 NyNy	normal white	1	88	68
				H. 11. '12	1 nYnY	plain yellow	1	61	68
						Total		272	272
H. 6. '11	*Aojiku* (NyNy) ♀ × N. 3. '11 plain yellow (nYnY) ♂	normal	Ny / nY	H. 12. '12	NynY	normal yellow	all	343	343
						normal white ?	—	1	—
H. 7. '11	N. 3. '11 plain yellow (nYnY) ♀	"	nY	H. 13. '12	NynY	normal yellow	"	333	333
	× *Aojiku* (NyNy) ♂		Ny			normal white ?	—	1	—
H. 8. '11	*Aojiku* (NyNy) ♀ × N. 2. '11 normal white (NyNy) ♂	"	Ny / Ny	H. 14. '12	NyNy	normal white	"	315	315
H. 9. '11	*Aojiku* (NyNy) ♀	"	Ny	H. 15. '12	1 nYNy	normal yellow	1	142	129
	× N. 4. '11 normal yellow (nYNy) ♂	complete repulsion	Ny nY	H. 16. '12	1 NyNy	normal white	1	116	129
						Total		258	258
H. 10. '11	N. 4. '11 normal yellow (nYNy) ♀	complete repulsion	Ny nY	H. 17. '12	1 NynY	normal yellow	1	151	158
	× *Aojiku* (NyNy) ♂	normal	Ny	H. 18. '12	1 NyNy	normal white	1	165	158
						Total		316	316
H. 11. '11	*Aojiku* (mNymNy) ♀ × M. 14. '11 moricaud yellow (MnYMnY) ♂	normal	mNy / MnY	H. 19. '12	mNyMnY	moricaud yellow	all	453	453
H. 12. '11	M. 14. '11 moricaud yellow (MnYMnY) ♀ × *Aojiku* (mNymNy) ♂	"	MnY / mNy	H. 20. '12	mNyMnY	moricaud yellow	all	293	293
H. 13. '11	*Aojiku* (mNymNy) ♀ × M. 1. '11 moricaud yellow (MnYMnY) ♂	"	mNy / MnY	H. 21. '12	MnYmNy	moricaud yellow	all	354	354
H. 14. '11	M. 1. '11 moricaud yellow (MnYMnY) ♀ × *Aojiku* (mNymNy) ♂	"	MnY / mNy	H. 22. '12	MnYmNy	moricaud yellow	all	485	485
H. 15. '11	*Aojiku* (NyNy) ♀	"	Ny	H. 23. '12	1 NynY	normal yellow	1	135	134
	× N. 1. '11 normal yellow (NynY) ♂	complete repulsion	Ny nY	H. 24. '12	1 NyNy	normal white	1	133	134
						Total		268	268
H. 16. '11	M. 3. '11 moricaud yellow (MnYmnY) ♀ × *Brown ant* (mNymNy) ♂	normal	MnY mnY	H. 25. '12	1. MnYmNy	moricaud yellow	1	198	210
			mNy	H. 26. '12	1 mnYmNy	normal yellow	1	222	210
						Total		420	420
H. 17. '11	*Aojiku* (sNysNy) ♀	normal	sNy	H. 27. '12	1 SnysNy	striped white	1	63	64
	× S. 5. '11 striped yellow (SnysnY) ♂	complete repulsion	Sny snY	H. 28. '12	1 snYsNy	normal yellow	1	65	64
						Total		128	128
H. 18. '11	S. 5. '11 striped yellow (SnYsnY) ♀ × *Aojiku* (sNysNy) ♂	normal	SnY snY	H. 29. '12	1 SnYsNy	striped yellow	1	211	211
			sNy	H. 30. '12	1 snYsNy	normal yellow	1	211	211
						Total		422	422
H. 19. '11	S. 5. '11 striped yellow (SnYsny) ♀	complete coupling	SnY sny	H. 31. '12	1 SnYsNy	striped yellow	1	215	201.5
	× *Brown ant* (sNysNy) ♂	normal	sNy	H. 32. '12	1 snysNy	normal white	1	188	201.5
						Total		403	403.0

VII. Historical Review.

Since the phenomenon of gametic coupling was first adequately studied in the Sweet Pea by BATESON and his collaborators in 1906, a number of similar cases have been observed by these and many other authors. The experimental results hitherto known in this field are summarized in the following pages.

A List of the Known Cases of Gametic Coupling and Repulsion.

I. Gametic Coupling.

A. Plants.

Plant name	Characters	System	Authors	Year
Sweet Pea	A)[1] Blue factor[2] and B) long pollen. *a) Red colour and b) round pollen.*	7 : 1 : 1 : 7	Bateson, Saunders, and Punnett.	1906
Sweet Pea	A) Blue factor and B) long pollen. *a) Red colour and b) round pollen.*	15 : 1 : 1 : 15[3]	Bateson, Saunders, and Punnett.	1908
Sweet Pea	A) Dark axil and B) fertility. *a) Light axil and b) sterility.*	15 : 1 : 1 : 15	Bateson, Saunders, and Punnett.	1908
Pea *(Pisum)*	A) Tendril and B) round seed. *a) No-tendril or 'acacia' type and b) wrinkled seed.*	63 : 1 : 1 : 63	de Vilmorin and Bateson.	1911

1) A and B express the dominant characters, while *a* and *b* denote the corresponding recessive factors.

2) When the blue factor exists the flower is purple.

3) The 7 : 1 series was observed in the F_2 families of the cross *Blanche Burpee* × *Emily Henderson*, while in F_3 of the same cross the gametic system followed was of 15 : 1 : 1 : 15 type. The latter was also the case with the F_2 offspring of *Bush* × *Cupid* crosses.

Primula sinensis	A) Magenta colour and B) short styled. *a) Red colour and b) long styled.*	7 : 1 : 1 : 7	Gregory	1911
Sweet Pea	A) Blue factor and B) erect standard. *a) Red colour and b) hooded standard.*	127 : 1 : 1 : 127	Bateson and Punnett.	1911
Maize	A) Red cob, B) red pericarp and C) dark silks. *a) White cob, b) colourless pericarp, and c) light silks.*	complete	Emerson.	1911
Maize	A) Dark purple husks, B) purplish pericarp and C) purple cob. *a) White husks, b) colourless pericarp, and c) white cob.*	complete	Emerson.	1911
Antirrhinum	A) Fundamental factor for red colour and B) non-homogeneousness or 'picturatum' type. *a) No-red and b) homogeneousness.*[1]	7 : 1 : 1 : 7[2]	Baur.	1911 1912
Maize	A) Coloured aleurone and B) horny endosperm. *a) White aleurone and b) waxy endosperm.*	3 : 1 : 1 : 3	Collins.	1912

1) When red-factor and non-homogeneousness are brought in by different parents, the gametic distribution is normal, no gametic repulsion occurring between them.

2) The actual figures, when the various families in the same group are taken as a whole, closely accord with the expectation on the 7 : 1 : 1 : 7 basis. If, on the other hand, each family is considered separately considerable deviations from expectation are shown.

B. Animals.

Animal name	Characters	System	Author	Year
Drosophila (Fruit-fly)	A) Sex-factor and B) pink eye-colour.[1] a) *'No sex-factor'*[2] *and b) orange eye.*	complete	Morgan.	1911
Drosophila	A) Sex-factor and B) eye-colour producer. a) *'No sex-factor' and b) white eye.*	complete	Morgan.	1911
Drosophila	A) Sex-factor and B) long wing. a) *'No sex-factor' and b) short wing.*	complete	Morgan.	1911

II. Gametic Repulsion.

A. Plants.

Plant name	Characters	System	Authors	Year
Sweet Pea	A) Erect standard and B) blue factor. a) *Hooded standard and b) red colour.*	complete or very high intensity.	Bateson, Saunders, and Punnett.	1908
Sweet Pea	A) Dark axil and B) fertility. a) *Light axil and b) sterility.*	complete	Bateson and Punnett.	1911
Sweet Pea	A) Normal flower-form and B) fertility. a) *'Cretin' type and b) sterility.*	1 : 3 : 3 : 1	Bateson and Punnett.	1911
Sweet Pea	A) Blue factor and B) long pollen. a) *Red colour and b) round pollen.*	1 : 7 : 7 : 1	Bateson and Punnett.	1911

1) The pink colour is always accompanied by the sex-factor, but the sex-factor may exist without pink eye.

2) Morgan assumes that the individuals which involve two sex-factors are female, and those which carry only one sex-factor are male.

Primula sinensis	A) Light stem[1] and B) green stigma.[2] *a) Dark stem and b) red stigma.*	complete	Gregory.	1911
Primula sinensis	A) Magenta colour and B) short style. *a) Red colour and b) long style.*	complete	Gregory.	1911
Maize	A) Red cob and B) half red pericarp. *a) White cob and b) colourless pericarp.*	complete	Emerson.	1911
Aquilegia	A) Variegated green leaf and B) homogeneously green leaf. *a) Absence of 'variegate' factor and b) absence of homogeneously green factor, i. e. 'chlorina' colour.*	complete	Baur.	1912
Silene Armeria	A) Rich pigment and B) saturator. *a) Less pigment and b) absence of saturator.*	complete	Correns.	1912

B. Animals.

Animal name	Characters	System	Authors	Year
Abraxas (Currant-moth)	A) Femaleness and B) 'grossulariata' factor. *a) Maleness and b) 'lacticolor' character.*	complete	Raynor and Doncaster.	1906
			Doncaster.	1908

1) This is due to the presence of the 'pallifying' factor which effects the partial suppression of colour in the stem being dominant over the dark colour of the latter.

2) This is also due to an inhibitor which completely suppresses the red colour, hence the dominant green stigma results.

Canary	A) Femaleness and B) black-eye factor. *a) Maleness and b) pink-eye character.*	complete	Durham and Marryat.	1908
Fowl	A) Femaleness and B) masking or suppressing factor. *a) Maleness and b) absence of masking factor.*	complete	Bateson and Punnett.	1908
Fowl	A) Femaleness and B) barring factor. *a) Maleness and non-barred character.*	complete	Spillman.	1908
			Pearl and Surface.	1910
			Morgan and Goodale.	1911
Fowl	A) Femaleness and B) dominant 'silver'. *a) Maleness and b) absence of dominant 'silver'.*	complete	Hagedoorn.	1909
			Bateson and Punnett.	1911

As the above list shows, there have been observed a great many cases of coupling and repulsion in plants. Several cases of complete repulsion and a few of complete coupling[1] in animals are also known.

But all of these interesting phenomena in animals were found in connection with the sex-character. There is no case of coupling or repulsion known to occur independently of that factor. Furthermore the phenomena of the *partial coupling* and *partial repulsion* have been found hitherto only in the vegetable world.

According to BATESON, a coupling or a repulsion results from an unequal occurrence of the various gametic forms in the gametogenesis of a heterozygote, as has been mentioned at the beginning of this paper. The coupling and

1) BATESON conceives the complete 'coupling' as a perfect union of the characters which are known to depend on separate allelomorphs. I also use the term in the same meaning.

repulsion are not fundamentally different phenomena, but they are dependent on the manner in which the 'presence' characters, A and B for instance, are brought into the cross. A coupling occurs when A and B are brought in by the same parent, but a repulsion takes place when they come from different parents.

As to the process which gives rise to the assumed partial gametic series, BATESON and PUNNETT put forth a suggestion (1911,b) that the case may be easily understood if we suppose as multiple reduplication of certain gametic forms (AB and ab in coupling, Ab and aB in repulsion) effected in the gametogenesis.

COLLINS maintains the possibility of the occurrence of intermediate gametic series such as 2 : 1, 4 : 1, 5 : 1, 6 : 1, etc., besides those assumed by BATESON and others, *i. e.*, 3 : 1, 7 : 1, 15 : 1, 63 : 1, and so forth.

BAUR suggests not only the occurrence of some intermediate systems, but also possible existence of n : 1 : 1 : x series, in which x is greater than n.

VIII. General Discussion and Conclusion.

In the foregoing pages, I have described six cases of repulsion and coupling observed in the Silkworm. All of them occurred between the yellow colour of the cocoon and the marking characters of the larva, except a single case of repulsion which took place between two marking factors. These cases may be summarized as follows:

1) *Complete repulsion* between *Normal marking* and *Yellow colour.*
2) *Complete repulsion* between *Striped marking* and *Yellow colour.*
3) *Complete repulsion* between *Striped marking* and *Normal marking.*
4) *Partial coupling* between *Moricaud marking* and *Yellow colour.*
5) *Partial coupling* between *Striped marking* and *Yellow colour.*
6) *Complete coupling* between *Striped marking* and *Yellow colour.*

The evidence for the occurrence of these reduplicated systems rests, in some of these cases, upon the result of a single mating, but in others it rests upon the results of several matings from the various lots. On the whole these experimental results set forth in the preceding pages are, as far as they go, almost exactly what we should expect to get if our assumption is correct.

Furthermore, though the numbers of the individuals reared were not sufficiently large to determine the gametic series, I am inclined to think that the partial coupling in my case was on the 7 : 1 : 1 : 7 system. The actual figures are in fair accordance with the theoretical expectation on that system.

As may be seen from what I have given in the historical review, partial repulsion is less common than partial coupling. In plants the examples of repulsion as yet known are for the most part perfect, while the majority of coupling phenomena is partial. The same rule probably also holds good with animals. At least with the Silkworm such seems to be the case, for I have encountered here two examples of partial and one of complete coupling, while the three cases of the repulsion were all complete.

A striking fact has been found with regard to the genetic interrelation of the striped marking and yellow colour. It is the occurrence of two different systems of gametic coupling between these characters, a partial coupling on the 7 : 1 : 1 : 7 system on the one hand, and a complete coupling on the other. BATESON met with a similar case in the sweet pea, where as a result of the partial coupling of the purple colour (*i. e.* the blue factor) with the long pollen, he obtained the 7 : 1 series in F_2 of the cross *Blanche Burpee* × *Emily Henderson*, while the F_3 offspring of the same cross showed a closer agreement with the expectation on the 15 : 1 basis. The latter system also appeared in F_2 of the *Bush* × *Cupid* cross. The question how such phenomena arise is not solved as yet.

As to the adoption of the terms 'coupling' and 'repulsion', though their appropriateness may be questioned, yet I prefer from the following reasons to preserve them in their original sense: 1) the terms are already widely accepted, 2) to keep the 'coupling' distinguished from 'repulsion' is at least convenient, because the F_2 phenotypic ratios resulting from them are fundamentally different. The term 'reduplicated system' may be conveniently used as a general name including both coupling and repulsion.

It is true that there is no positive reason to deny the possibility of the occurrence of intermediate series besides those forwarded by BATESON. But we must admit, on the other hand, that a decisive proof for the existence of such intermediate systems is also not yet discovered.[1]

Concerning the phenomena of coupling and repulsion there are many questions to be answered by future investgations. The more important of those are: 1) At which stage of the ontogeny of an individual does the coupling or repulsion occur?; 2) Is there any selective mating of gametes? 3) What is the actual cause of the coupling and repulsion? At present I have no data which throws light on these points.

I trust that I have furnished at least some positive data regarding the question whether the phenomena of gametic coupling and spurious allelomorphism in animals occur independently of the sex-character. In their important paper BATESON and PUNNETT remark: "Hitherto no case of coupling has been found in animals. Among the phenomena of repulsion, however, of which many examples exist, certain suspicious cases have been observed which may mean that in animals reduplicated systems, exist like those of plants. Nevertheless at present it seems not impossible that the two forms of life are really distinguished from each other in these respects" (1911,b). However to-day we have no need to make such a distinction regarding animals as distinguished from plants.

1) Quite recently, TROW (1912) found the 2 : 1 : 1 : 2 coupling between the *hairness* and the *ray-character* in *Senecio vulgaris*.

POSTSCRIPT. (March 20, 1913.) Two following data recently described by HAGEDOORN (*The genetic factors in the development of the Housemouse. Zeits. f. ind. Abst. u. Vererb. Bd. VI, pp. 97–136, 1912*) and PUNNETT (*Inheritance of coat colour in Rabbits. Journ. Gen. Vol. 2, pp. 221–238, 1912*) should be added.

Animal name.	Characters	System	Author	Year
Housemouse.	A) Colour factor and B) 'agouti' factor. *a) Albino and b) black.*	complete repulsion	Hagedoorn	1912
Rabbit.	A) Deepening factor for melanic pigment and B) extending factor for melanic pigment. *a) Absence of deepening factor and b) absence of extending factor.*	complete coupling	Punnett	1912

These are, as I believe, only literature of gametic reduplication between two characters independent of the sex-factor in animals.

IX. Summary.

1) Few examples of gametic coupling and repulsion, other than those which occur in connectien with the **sex-factor**, have been found hitherto in animals.

2) I have ascertained however that the phenomena of coupling and repulsion of certain **somatic characters** occur in the Silkworm as they do in plants.

3) **Partial coupling** in the Silkworm occurred **a**) between the moricaud marking and yellow colour, and also **b**) between the striped marking and yellow colour. These are, so far as I am aware, **the first record of partial gametic coupling found in animals.**

4) The gametic system on which the partial coupling occurred in the Silkworm in my experiments was presumably of the **7 : 1 : 1 : 7** type in either of both cases stated above.

5) **Complete coupling** took place between the striped marking and yellow colour.

6) **Complete repulsion** was found to occur **a**) between the normal marking and the yellow colour, **b**) between the striped marking and the yellow colour, and **c**) between the striped and normal markings.

March, 1913.

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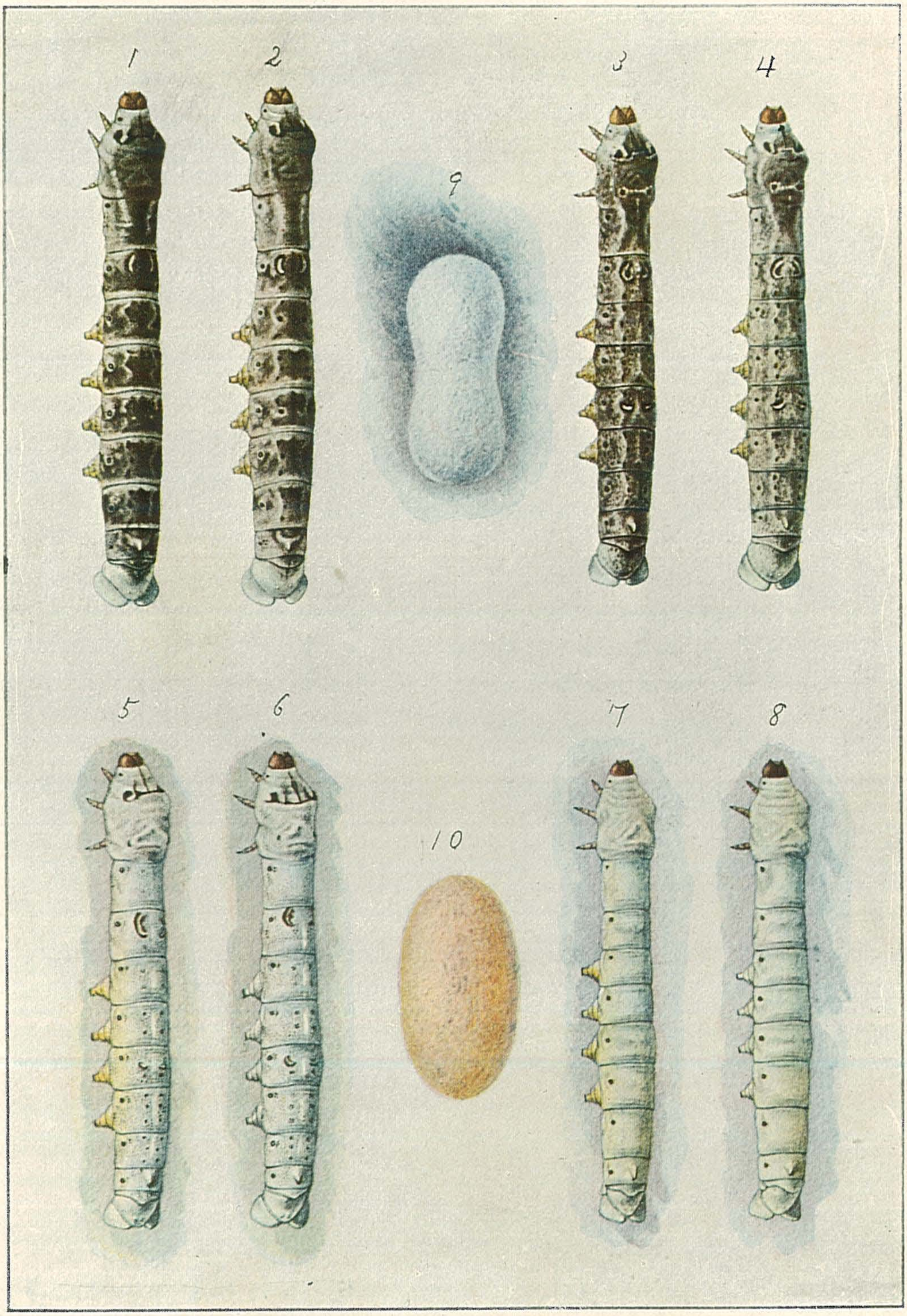
EXPLANATION OF PLATE IX.

Fig. 1-8. Silkworm larvae in a full-grown state.

Fig. 1. *Chinese striped yellow (homozygote).*
Fig. 2. *Chinese striped yellow (heterozygote).*
Fig. 3. *Chinese moricaud yellow (homozygote).*
Fig. 4. *Chinese moricaud yellow (heterozygote).*
Fig. 5. *Chinese normal yellow.*
Fig. 6. *Japanese normal yellow.*
Fig. 7. *Chinese plain yellow.*
Fig. 8. *Chinese plain white.*

Fig. 9-10. Cocoons.

Fig. 9. *Japanese, white cocoon.*
Fig. 10. *Chinese yellow cocoon.*



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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.'