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GENETIC STUDIES ON THE SILKWORM

BY

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With Pl. I–VI

I. INTRODUCTORY.

All works in genetics done during the past fifteen years have increased the interest attaching to the silkworm moth, *Bombyx mori* L., which would appear to represent one of the series of animals occupying a truly central position among the forms drawing attention from both theoretical and economic points of view. In particular, the silkworm affords the material, perhaps, most appropriate for the genetic study, not only because there are a considerable number of races which freely mate together, but because the moth is polygamous and the feeding period lasts only 25–35 days.[1]

In spite of their effort previous observers have directed little attention to the genetic interrelations of unit characters or factors. The present experiments were undertaken in 1910 and are still in progress. The results, so far as obtained, were preliminarily published at occasions. In the following pages I will give a full account of my experiments down to the year 1915, including the formerly reported facts which will be found especially in Chapter **IV**.

It is, perhaps, worth while to note that the present experiments concern in the main not the adult characters, but the larval which are, therefore, to

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[1] Besides these, we can see more than two generations a year in bivoltine and polyvoltine races; even in univoltines, the eggs may be forced to hatch repeatedly in the same year through the artificial methods first discovered by VERSON (with electricity) and DUCLAUX and BOLLE (with acids), which have recently been improved by Japanese sericulturists.

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be regarded as the parental characters recapitulated in the course of ontogenetic development. A given character is not only transmissible, but so precisely transmissible as to reappear in a stage or stages proper to it.

The figures put as the suffix to each lot number indicate in the present paper, the year of *rearing*, in contrast to those in my papers published until 1914, which refer to the year of *egg-deposition*.

The formulae **ABab, AbaB, AaBb** and **A-B-** are used in different senses; **ABab** and **AbaB** stand for the hybrids derived from the gametes **AB** × **ab** and **Ab** × **aB** respectively, while **AaBb** represents either sort of these hybrids. **A-B-** indicates any zygote that involves at least one dose of both **A** and **B.**

The symbols of hereditary factors concerned in the present work are as follows:

S, striped marking,[1]	**s,** absence of S;
M, moricaud marking,	**m,** absence of M;
P, plain or non-marked,	**p,** absence of P;
Q, quail marking,[2]	**q,** absence of Q;
PQ, normal marking,	**pq,** pale-quail marking;
Z, zebra marking,	**z,** absence of Z;
L, multilunar marking,	**l,** absence of L;
K, knobbed skin,	**k,** smooth;
O, opaque skin,	**o,** transparent or "oily";
B, melanic,	**b,** chocolate;
T, 3-moulting,	**t,** 4-moulting;
Y, yellow cocoon,	**y,** absence of Y;
G, green cocoon,	**yg,** white cocoon.

The silkworms in my experiments were reared entirely in the College nursery up to 1913; in the summer of 1913 and the spring of 1914 they were partly reared in the Sericultural Institute of Hokkaido, while the culture in

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[1] This "striped" must be distinguished from the "striped" of TOYAMA, which I prefer to designate as "zebra", the term first adopted by COUTAGNE and later often employed by TOYAMA himself.

[2] This name is substituted for the "Kasuri" of my 1914a paper.

1915 was almost exclusively done in the Imperial Institute of Sericulture at Fukushima.

I wish to take this opportunity to express my heartiest thanks to Prof. Hatta and Prof. Goto for their kindness in looking through the manuscript, and giving many valuable advices. My obligations are also due to Prof. Suda and Prof. Toyama for the warmest courtesy shown by them in the course of the study.

II. THE GENETIC CONSTITUTION OF THE LARVAL PATTERNS: COMPLETE COUPLING OF **Q** WITH **S** AND **M**.

1) Pale-quail, Quail, Plain, Normal, Moricaud and Striped.

The most common types of the larval pattern in the silkworm are eight, viz.

Striped (striped black),
Moricaud,
Normal,
Quail,
Plain,
Pale-quail,
Zebra,
Multilunar.

The characteristics of these marking types are very distinct in usual cases. Of the elementary spots which enter into the markings, the most striking are the "eye-spots" or "eyebrows" on the mesothorax (II segment), and the anterior semilunar spots on the V segment; these spots are invariably present in common in the striped, moricaud, normal and quail. Pale-quail has faint "semilunules" but no "eyebrows"; plain is devoid of both; multilunar is provided with "eyebrows" aud "semilunules" only when it is combined with the quail factor, while in zebrine type, the spots under consideration are, even in the absence of the quail factor, developed to a certain extent, though the spots are made markedly distinct by that factor.

To the fundamental types just enumerated, a number of new larval forms can be added by combination of factors. For instance, striped-quail and moricaud-quail are extracted respectively from the offspring of the crosses striped × quail and moricaud × quail; likewise zebra-quail and multilunar-quail are produced. Striped-zebra, multilunar-zebra, moricaud-zebra, multilunar-striped, multilunar-moricaud, and any combination of zebra and multilunar with other types may be obtained by due crossing. The chocolate series differs from the ordinary or melanic series in lacking the black factor **B**, but runs, in other points, exactly parallel with the latter. When **B** is absent, the just hatched larva ("ant") is, whatever its ultimate marking may be, reddish brown in distinct contrast to the ordinary black. Through the whole larval life the chocolate character usually comes out distinctly in all marking of **b**-series with the only exception of plain which is entirely devoid of marking.

It has been shown in my previous works (1913 a,b), that striping is epistatic to moricaud, and moricaud to normal, and normal to plain. Let us now turn to examine the behaviour of pale-quail and quail towards other marking types.

As is described in future pages, there exists a great variation in regard the pigment intensity of normal as well as quail, ranging from the forms with lightest eye-spots to those with darkest. It is not a rare occurrence that lightest normal or quails (with faintest "eye-brows") appear in the offspring of crossing plain or pale-quail (the types with no "eyebrows") with one of the distinctly "eyebrowed" types (normal, quail, striped and moricaud). This phenomenon probably depends upon the existence of multiple factors concerning the marking in question; the point will be dealt with later in more detail (Chapter **VI**). For the moment, there is no great inconvenience for theoretical analysis, if we count the lightest normal with the plain, and the lightest quails with the pale-quails. Such heterogeneous classes are marked with an asterisk * in this and the following chapters.

When pale-quail is paired to plain, F_1 generation consists of only plain which split, in the next generation, into 3 plain and 1 pale-quail.

	Plain		Pale-quail	Total
A 391'15	308		82	390
Ratio	3	:	1	

F_1 hybrids back-crossed to the recessives gave plain and pale-quail in about equal numbers.

	Plain	Pale-quail	Totals
A 431'15	55 *	78 *	133
A 432'15	107 *	96 *	203
Totals	162	174	336
Ratio	1 :	1	

Thus plain (**P**) is evidently a simple dominant to pale-quail (**p**). Pale-quail also behaves as a simple recessive to quail, as the following data show:

	Quail	Pale-quail	Totals
A 424'15 (pale-quail ♀ × F_1[1] ♂)	153	134	287
A 425'15 (F_1[1] ♀ × pale-quail ♂)	264	244	508
Totals	417	378	795
Ratio	1 :	1	

Consequently I represent quail by **Q**, and pale-quail by **q**.

Now we come to the consideration of the behaviour of plain (**Pq**) to quail (**pQ**). When these two dominants were brought together by crossing, the resulting pattern was neither plain nor quail, but the normal, which split, in F_2, into four forms, i. e. normal, plain, quail and pale-quail in the ratio 9 : 3 : 3 : 1.[2] F_2 families from such crosses are given below:

	Normal	Plain	Quail	Pale-quail	Totals
C 16'14	119	49	34	20	222
C 29–1'14	281	127	102	35	545
C 29–2'14	260	103	95	25	483
C 29–3'14	305	114	94	35	548
C 29–4'14	231	71	83	37	422
Totals	1196	464	408	152	2220
Expected	1249	416	416	139	2220
Ratio	9 :	3 :	3 :	1	

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[1] Ex quail × pale-quail.

[2] TOYAMA (1912 b) gave a brief account of this phenomenon, but the relations between plain or quail factor and striped or moricaud were not noted by him.

If the heterozygosis is brought about by crossing the homozygous normal with the pale-quail, F_2 results are practically the same with those given above:

F_2 ex normal × pale-quail.

	Normal	Plain	Quail	Pale-quail	Totals
A 413′15	212	52 *	64	25 *	353
A 452′15	152	49 *	59	15 *	275
A 453′15	183	59 *	44	20 *	306
A 354′15	168	60	68	18 *	314
A 456′15	168	48	46	17	279
Totals	883	268	281	95	1527
Expected	859	286	286	96	1527
Ratio	9 :	3 :	3 :	1	

The results of back-crossing follow:

F_1 normal ♀♀ (ex normal × pale-quail) mated to double recessive ♂♂.

	Normal	Plain	Quail	Pale-quail	Totals
A 375′15	126	116	117	95	454
A 459′15	95	82 *	73	75 *	325
A 460′15	85	86	99	85 *	355
Totals	306	284	289	255	1134
Expected	283.5	283.5	283.5	283.5	1134.0

F_1 normal ♂♂ (ex normal × pale-quail) mated to double recessive ♀♀.

	Normal	Plain	Quail	Pale-quail	Totals
A 461′15	90	62 *	81	71 *	304
A 462′15	58	49 *	60	58 *	225
A 463′15	72	74	61	70 *	277
A 464′15	49	65 *	74	46 *	234
Totals	269	250	276	245	1040
Expected	260	260	260	260	1040

The results mentioned above can be put into a diagram as follows:

Plain (Pq) × Quail (pQ) or
Normal (PQ) × Pale-quail (pq)

Normal (PpQq) × Pale-quil (ppqq)

Norm.	Pl.	Qu.	Pal. qu.	Norm.	Pl.	Qu.	Pal. qu.
(PQ)	(Pq)	(pQ)	(pq)	(PQ)	(Pq)	(pQ)	(pq)
9 :	3 :	3 :	1	1 :	1 :	1 :	1

This is exactly parallel to the classical case of fowl-comb inheritance investigated by BATESON and PUNNETT (1905). The most important point brought out by the above experiments is that the normal pattern is really not a simple character as formerly imagined, but a compound character depending upon two allelomorphs **P** and **Q**; this holds true with the normal of any strain or of any colour intensity.

Now we are able to arrange the marking factors in the order of their epistasis as follows:

$$\mathbf{S} > \mathbf{M} \begin{array}{l} > \mathbf{P} > \mathbf{p} \\ > \mathbf{Q} > \mathbf{q} \end{array}$$

In one of my previous papers (1914 a), I put forth a question on the genetic constitution of the striped and moricaud markings, i. e. which of the formulae **SN** and **MN** on one hand, and **Sn** and **Mn** on the other were correct. Substituting **N** by **PQ**, and **n** by **pq** according to the just mentioned results, the question is no other than the comparison of the formulae **SPQ** and **Spq**, and **MPQ** and **Mpq**. Further experiments done since in this direction solved the question; the formulae **SPQ** and **MPQ** proved to be right, in which **Q** was completely coupled with **S** and **M.**

When striped is crossed with quail, F_1s are alike to homozygous striped, except somewhat reduced development of the melanin in hybrids. F_2 families consisted of four forms, striped, striped-quail, normal and quail in the ratio 9 : 3 : 3 : 1.

	Striped	Striped-quail	Normal	Quail	Totals
C 5–1′14	118	32	34	12	196
C 9–1′14	140	44	67	12	263
C 9–2′14	141	46	63	18	268
C 9–3′14	186	41	54	15	296
C 12–1′14	143	37	57	18	255
C 12–2′14	112	49	51	14	226
C 14–1′14	117	52	60	10	239
C 14–2′14	100	51	56	20	227
A 624′15	94	72	42	22	230
A 625′15	131	50	52	20	253
A 626′15	103	38	26	11	178
A 628′15	230	67	89	25	411
Totals	1615	579	651	197	3042
Expected	1711	570	570	190	3041
Ratio	9 :	3 :	3 :	1	

In the striped-quail, a new marking which first appeared in my experiments in 1914, the patterns characteristic to striped (**S**) and quail (**pq**) are apparently combined in contrast to the ordinary striped marking which is an apparent combination of striped and normal (**PQ**) (TANAKA, 1914a, p. 15). It is evident that the genetic constitution of the ordinary striped is **SPQ**, and that of the striped-quail is **SpQ**. The following data can only be explained by the assumption just given.

F_2 striped-quails inbred.

	Striped-quail	Quail	Total
A 100′15	228	56	284

Striped-quail ♀ × pale-quail ♂.

	Striped-quail	Quail	Total
A 107′15	166	180	346

F_2 striped-quail ♂♂ paired to pale-quail ♀♀.

	Striped-quail	Quail	Totals
A 105′15	155	146	301
A 106′15	153	129	282
A 108′15	175	172	347
Totals	483	447	930

When quail is crossed with the striped-quail heterozygous for **S**, the results are exactly similar to those given above, no ordinary striped being produced. It is, therefore, evident that pale-quail and quail are equally destitute of the factor necessary for turning the striped-quail into the ordinary striped.

Striped-quail ♀ × quail ♂.

	Striped-quail	Quail	Total
A 113′15	137	109	246

Quail ♀♀ × Striped-quail ♂♂.

	Striped-quail	Quail	Totals
A 114′15	211	231	442
A 115′15	184	180	364
A 122′15	201	217	418
Totals (4 families)	733	737	1470

On the other hand, crosses of plain with heterozygous striped-quail produced the ordinary striped and normal instead of striped-quail and quails. Similar results are obtained by crossing normal and striped-quail. It is obvious that plain and normal have a common factor, the introduction of which turns striped-quail into ordinary striped; this factor is undoubtedly **P**.

Striped-quail ♀ × Plain ♂.

	Striped-quail	Normal	Total
A 116′15	171	174	345

Plain ♀♀ × striped-quail ♂♂.

	Striped	Normal	Totals
A 117′15	176	182	358

A 119′15	198	187	385
Totals (3 families)	545	543	1088
Expected	544	544	1088
A 118′15	343	0	343

The results of the above experiments, are explicable only on the assumption that the factorial constitution of striped-quail and striped is respectively **SpQ** and **SPQ.**

Quite similar results were obtained with regard to the moricaud and moricaud-quail markings. F_1 animals produced by the cross of moricaud and quail show no significant difference from the homozygous moricaud; they were inbred as well as cross-bred with recessives with the following results.

F_1 moricauds inbred.

	Moricaud	Moricaud-quail	Normal	Quail	Totals
C 13–1′14	97	21	25	15	158
C 13–2′14	132	34	44	17	227
C 13–3′14	63	24	44	2	133
A 80′15	252	89	82	28	451
Totals	544	168	195	62	969
Expect.	545	182	182	60	969

F_2 moricaud-quails inbred.

	Moricaud-quail	Quail	Totals
A 101′15	530	0	530
A 102′15	120	45	165

Pale-quail ♀ × moricaud-quail ♂.

	Moricaud-quail
A 103′15	367

Moricaud-quail ♀♀ × quail ♂♂.

	Moricaud-quail	Quail	Total
A 104′15	458		
A 109′15	82		
A 110′15	203	219	422

Quail ♀♀ × moricaud-quail ♂♂.

	Moricaud-quail	Quail	Total
A 111′15	193	152	345
A 112′15	103		

Moricaud-quail ♀ × plain ♂.

	Moricaud	Normal	Total
A 120′15	164	161	325

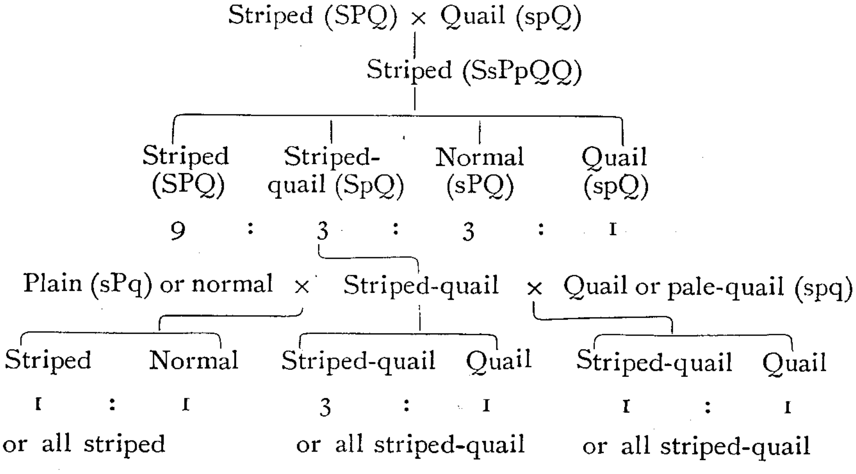
Plain ♀ × moricaud-quail ♂.

	Moricaud
A 121′15	444

Moricaud-quail ♀ × normal ♂.

	Moricaud	Normal	Total
A 364′15	220	231	451

The above results may be summed up in the following diagram :— 1)



2) Complete Coupling of **Q** with **S** and **M.**

As the data given in my previous papers (1913 b, 1914 a) and those in Chapter **IV** of the present work show, the striped animal, when crossed with the normal, gives no plain in F_2 but only striped and normal; when crossed with the plain, on the contrary, the striped produces F_2 zygotic series consisting of striped and plain and no distinct normal. The mating of light

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1) The reciprocal of each cross gives identical result. For moricaud inheritance, turn "striped" and "**S**" to "moricaud" and "**M**" respectively.

normal and striped gives F_2 normal which are lightly marked; if dark normal are used as the recessive parents, F_2 normal are intensely marked: in other words, the marking types of normal parents reappears in F_2 with nearly equal intensity. So long as the genetic constitution of the striped is not explained, the above results might seem to suggest multiple allelomorphic relation of the striping, normal and plain factors (STURTEVANT, 1915). But this was not, as shown below, actually the case.

Striped-quails (**SpQ**) were crossed with pale-quails (**spq**), and the individuals which are heterozygous for only **SQ** were obtained. The hybrids were mated *inter se*, as well as cross-bred with double recessive.

Heterozygous striped-quails (**SsppQq**) inbred.

	Striped-quail	Pale-quail	Totals
A 501′15	228	55 *	283
A 502′15	294	105 *	399
A 511′15	246	62 *	308
A 512′15	162	65 *	227
Totals	930	287	1217
Expect.	913	304	1217

The hybrid (**SsppQq**) ♀♀ × pale-quail (**ssppqq**) ♂♂.

	Striped-quail	Pale-quail	Totals
A 515′15	209	220 *	429
A 516′15	225	207 *	432
Totals	434	427	861
Expect.	430.5	430.5	861.0

Pale-quail (**ssppqq**) ♀♀ × the hybrid (**SsppQq**) ♂♂.

	Striped-quail	Pale-quail	Totals
A 513′15	125	117 *	242
A 514′15	47	40 *	87
A 517′15	141	155 *	296
Totals	313	312	625
Expect.	312.5	312.5	625.0

The fact that deserves notice in the above results, is the total absence of distinct quails which were to be expected if the **Q** factor is independently transmissible. On the other hand, the **Spq** form, if present, ought to be an apparent combination of **S** and **pq** patterns, namely a very light form of **SpQ**; but no individuals which could be regarded as "striped-pale-quail" appeared at all. Hence it follows that **Q** is completely coupled with **S** in both sexes. Moreover, the linkage is somewhat peculiar in that **S** can never exist without **Q**, while **Q** can be present regardless of the **S** factor. A similar relation is advocated by PUNNETT (1915) for **D** and **E** factors in the coat colour of the rabbit.

The following data are explicable on the same assumption.—

Triple hybrids were produced by crossing the striped (**SPQ**) with the pale-quail (**spq**); the hybrids were either inbred or back-crossed with the recessives.

Trihcterozygous striped (**SsPpQq**) inbred.

	Striped (SPQ)	Striped-quail (SpQ)	Plain (sPq)	Pale-quail (spq)	Totals
A 521′15	119	53	42	18	232
A 524′15	122	64	46	18	250
A 531′15	76	51	38	21	186
A 532′15	113	40	41 *	10 *	204
A 539′15	224	85	72 *	28 *	409
A 540′15	120	46	40	24	230
Totals	774	339	279	119	1511
Expect.	850	283	283	95	1511
Ratio	9 :	3 :	3 :	1	

Triheterozygous striped (**SsPpQq**) ♀♀ × pale-quail (**sspppq**) ♂♂.

	Striped	Striped-quail	Plain	Pale-quail	Totals
A 536′15	58	74	65	95 *	292
A 537′15	80	85	78 *	84 *	327
Totals	138	159	143	179	619
Expect.	154.75	154.75	154.75	154.75	619.00

Pale-quail ♀♀ × trihetorozygous striped ♂♂.

	Striped	Striped-quail	Plain	Pale-quail	Totals
A 534'15	67	54	63 *	64 *	248
A 535'15	58	63	64	47	232
Totals	125	117	127	111	480
Expect.	120	120	120	120	480

If **S** and **Q** were not completely coupled together, one should expect such combinations as **SPq**, **Spq**, **sPQ** (normal) and **spQ** (quail) to appear in addition to those actually produced. The absence of these forms can not be accounted for unless **S-Q** coupling is assumed.

Quite a similar relation is observed between **Q** and **M**.

F_2 offspring ex the cross moricaud-quail (**MpQ**) × pale-quail (**mpq**).

	Moricaud-quail	Pale-quail	Totals
A 481'15	253	85 *	338
A 482'15	324	96 *	420
A 483-1'15	261	86 *	347
A 483-2'15	210	76 *	286
Totals	1048	343	1391
Expect.	1043	348	1391

Diheterozygous moricaud-quail (**MmppQq**) ♀ × pale-quail (**mmppqq**) ♂.

	Moricaud-quail	Pale-quail	Total
A 486'15	170	145	315

Pale-quail (**mmppqq**) ♀♀ × diheterozygous moricaud-quail (**MmppQq**) ♂♂.

	Moricaud-quail	Pale-quail	Totals
A 484'15	131	131 *	262
A 485'15	112	114	226
Totals	243	245	488

Triple heterozygotes (**MmPpQq**) paired *inter sc.*

	Moricaud (MPQ)	Moricaud-quail (MpQ)	Plain (mPq)	Pale-quail (mpq)	Totals
A 476'125	296	68	53 *	21 *	438

A 477'15	195	67	55	22 *	339
A 480–1'15	208	75	65	32 *	380
A 480–2'15	191	76	82	31	380
Totals	890	286	255	106	1537
Expect.	865	288	288	96	1537
Ratio	9 :	3 :	3 :	1	

Triheterozygous moricaud (**MmPpQq**) ♀♀ × pale-quail (**mmppqq**) ♂♂.

	Moricaud	Moricaud-quail	Plain	Pale-quail	Totals
A 472–1'15	89	66	81	78 *	314
A 472–2'15	73	81	72	66	292
A 475'15	76	66	67	63	272
A 479'15	115	116	101	109 *	441
Totals	353	329	321	316	1319
Expect.	329.75	329.75	329.75	329.75	1319.00

Pale-quail (**mmppqq**) ♀♀ × triheterozygous moricaud (**MmPpQq**) ♂♂.

	Moricaud	Moricaud-quail	Plain	Pale-quail	Totals
A 471'15	50	56	59	68	233
A 473'15	56	71	67	63	257
A 474'15	60	48	67	61 *	236
A 478'15	86	78	64	84 *	312
Totals	252	253	257	276	1038
Expect.	259.5	259.5	259.5	259.5	1038.0

The above results show beyond doubt that **M** is completely coupled with **Q** in both sexes.

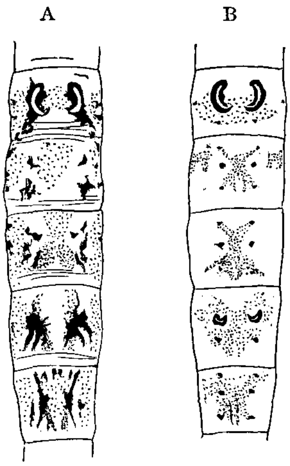
3) Zebra and Multilunar; on the Physiological Functions of Factors **P** and **Q**.

Zebra and multilunar are peculiar patterns, never standing in epi– or hypostatic relation to any other marking, that is, **Z** and **L** characters develop in combination with any marking with which they may be brought together, so that any apparent combination such as **SZ** (striped-zebra), **PZ** (plain-zebra), **LZ** (multilunar-zebra), **LQ** (multilunar-quail) etc. is possible. **Z** and **L** are inherited independently of each other, and of other markings as well.

The pale-quail (**pq**) is in general a quail of very dilute tone, but is totally destitute of "eye-spots" which are present in the quail. The **Q** factor may therefore be regarded as the saturator, the presence of which transforms the pale-quail into a fully pigmented quail pattern. When **P** gene is introduced into the pale-quail strain, the faintly marked pale-quail type is turned into an absolutely markingless or plain form. In case of its co-existence with **P**, the **Q** factor develops the "eyebrows" and two pairs of the "similunules" in nearly equal (sometimes slightly reduced) intensity, as where **Q** alone is present; but all irregular lines and spots characteristic to the quail disappear through the presence of **P**— the resulting form is namely the normal marking. In other words, **P** is partially recessive and partially dominant to **Q**.

Similarly **S** is in general decidedly epistatic to **M**, but in certain parts of the body the **M** character comes to view in **SM** zygotes (Text-figs. 2–4), i. e. **S** partially dominates over the **M**, but is partially recessive to it.

These facts evidently show that the relation of dominance and recessiveness of Mendelian factors is by no means so simple as is generally assumed.



Text-fig. 1.
A, quail marking; B, normal marking

Several subclasses which are distinguished by difference in the colour intensity of the quail (**pQ**) and normal (**PQ**), must be supposed to bring forth their differential intensity owing to the existence of different subtypes of **Q** gene, the other component (**P**) of the normal marking serving simply as a negative or suppressing factor.

P also influences the multilunar pattern. When **L** is combined with no other marking but **P** (**PqL**), multilunar spots become so faintly yellowish that one might overlook them unless special attention is given, whereas in multilunar-normal (**PQL**), multilunar-quail (**pQL**), and even in multilnnar-pale-quail (**pqL**), the spots under consideration are much more distinct. Consequently there are cases apparently peculiar, in which **PqL** animals heterozygous for **P** give more deeply pigmented multilunar offspring (**pqL**), when inbred or cross-bred with recessive. On the other hand, **Z** develops the characteristic black bands which are nearly equally intense without regard to the presence or absence of **P** or of other marking factors.

III. MULTIPLE ALLELOMORPHISM AND COMPLETE REPULSION.

The inheritance of markings, which was looked upon by STURTEVANT (1915) as being due to multiple allelomorphism, has been proved in the majority of cases to be owing to complete coupling, as explained in the preceding chapter. There is, however, a single case which must be explained on the basis of complete repulsion. This is the subject of this section.

It was mentioned in a paper of mine (1914a, p. 6) that a striped[1] (ex striped × moricaud) yielded, by crossing with the quail *(Kasuri)*, no other recessives but striped and moricaud. This was the only case which suggested a hereditary relation between **S** and **M**; but further data have since been obtained, so that we are justified in drawing the following conclusion.

F_1 individuals (**SsMm**) ex the cross striped (**Sm**) × moricaud (**sM**) appeared at first sight just the same as the striped parent. On careful examination it was found that the **SM** individuals distinctly differed from the ordinary striped ones (**Sm**); the former being provided, in addition to the **S** pattern, with the characteristic spots on the head-case, on the ventral side of the thorax, and on the inter-segmental bands, so that we are able to distinguish externally the **Sm** individuals from the **SM**, which will be designated as the "striped-moricaud."

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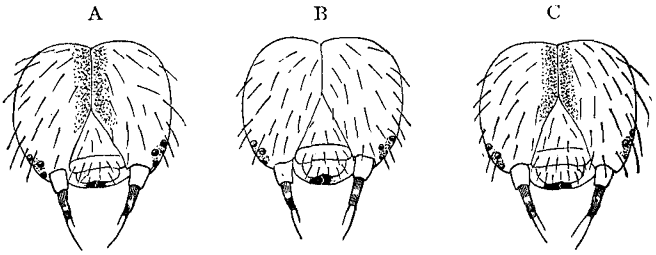
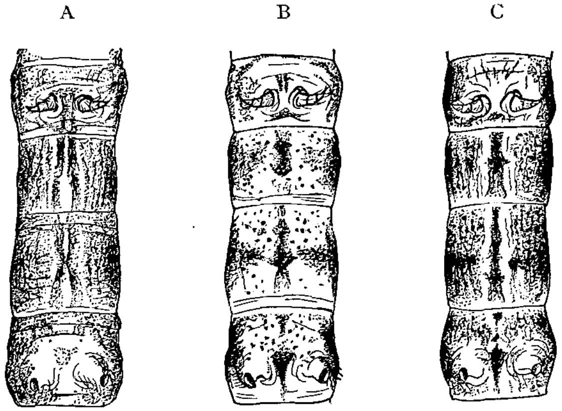
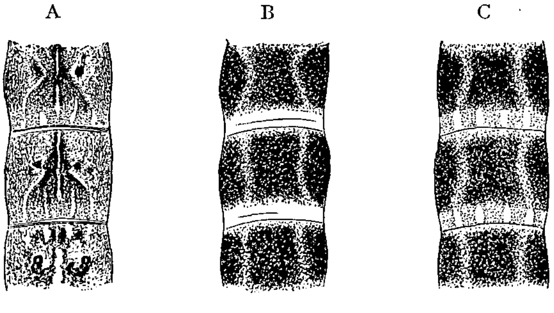
[1] In reality striped-moricaud.



Text-fig. 2. Frontal view of the head-case.
A, moricaud; B, striped; C, striped-moricaud.



Text-fig. 3. Ventral view of III–VI segments of moricaud (A), striped (B), and striped-moricaud (C).



Text-fig. 4. Dorsal view of VI–VIII segments of moricaud (A), striped (B), and striped-moricaud (C).

It has been stated in my previous papers and elsewhere in the present, that the factors **S** and **M** are alternative to their recessives **s** and **m** respectively. Now, in inbreeding **SmsM** individuals, four possible combinations,— **SM**, **Sm**, **sM** and **sm** in the ratio 9 : 3 : 3 : 1 are expected, provided that **S** and **M** be independently transmitted. But this was, in reality, not the case.

H 27–1′13 striped white × H 56′13 moricaud white
(SSmmyy) (ssMmyy)

	Striped-moricaud white (SmysMy)	Striped white (Smysmy)
N 7′14	246	124

	Striped-moricaud white (SMy)	Striped white (Smy)	Moricaud white (sMy)
A 37′15	73	59	31

Parents doubtful (perhaps SsmmYY × ssMmYY)

	Striped-moricaud yellow (SMY)	Striped yellow (SmY)	Moricaud yellow (sMY)	Normal yellow (smY)
O 1–4′14	64	77	73	59

	Str. mor. yel. (SMY)	Str. yel. (SmY)	Mor. yel. (sMY)
A 43′15	144	59	67

F_2 forms **SM**, **Sm** and **sM** came forth nearly in the ratio 2 : 1 : 1 (actual numbers 217 : 118 : 98), and no individual of **sm** constitution was produced at all. Such a zygotic series is possible only when a complete **S-M** repulsion occurs in one or both sexes. In order to test the male and female gametic series separately, the heterozygous striped-moricaud were crossed with double recessives reciprocally; the resulting generation involved only the two phenotypes, striped and moricaud, but no other forms.

Striped white ♀ × P 86′14 moricaud yellow ♂
(Ssmmyy) (ssMmYy)

	Str. mor. yel. (SMY)	Str. mor. wh. (SMy)	Str. yel. (SmY)	Str. wh. (Smy)	Mor. yel. (sMY)	Mor. wh. (sMy)	Norm. yel. (smY)	Norm. wh. (smy)
A 247′15	66	22	25	55	65	12	16	66 [1]

♀ (Str. mor. yel.) × A 99′15 pale-quail white ♂

	Str. wh. (Smy)	Mor. yel. (sMY)
A 548′15	287	212

A 252′15 quail white ♀ × A 43′15 striped-moricaud yellow ♂
(smy) (SMY)

	Str. yel. (SmY)	Mor. yel. (sMY)
A 541′15	121	127

A 183′15 plain white ♀ × A 43′15 striped-moricaud yellow ♂
(smy) (SMY)

	Str. yel. (SmY)	Mor. yel. (sMY)
A 542′15	211	180

A 255′15 plain white ♀ × A 43′15 striped-moricaud yellow ♂

	Str. yel.	Mor. yel.
A 545′15	190	213

P 86′14 moricaud yellow [2] × P 77′14 striped white
(ssMmYy) (Ssmmyy)

	Str. mor. yel. (SsMmYy)	Str. wh. (Ssmmyy)	Mor. yel. (ssMmYy)	Nor. wh. (ssmmyy)
A 246′15	113	126	102	117

A 99′15 pale-quail white (ssmmyy) ♀♀ × ♂♂ (Str. mor. yel., 113)

Str. yel. (SsmmYy) — Str. wh. (Ssmmyy) — Mor. yel. (ssMmYy) — Mor. wh. (ssMmyy)

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[1] The phenotypic proportion of this family is explicable on the basis of **M**-**Y** coupling (3 : 1 : 1 : 3).

[2] As to the complete coupling of **M** and **Y** in the female hybrid, see the next chapter.

A 543′15	38	89	98	45
A 546′15	18	61	44	16
Totals[1]	56	150	142	61
	206		203	
Ratio	1	:	1	

Representing the above results by a diagram:

SSmm × ssMM
F₁ SmsM × ssmm
Gametes (Sm, sM) (sm)
SmsM SmSm sMsM Smsm sMsm
F₂ 2 : 1 : 1 1 : 1

The facts given in the preceding lines give an ample proof of the occurrence of complete repulsion between the **S** and **M** of **SM** zygotes in both sexes; thus, individuals homozygous with regard to the presence of both **S** and **M** are not possible; in other words, no gamete is able to carry over **S** and **M** simultaneously.

It must, however, be noted that the present case is open to another explanation, i. e. by the hypothesis of multiple allelomorphism. Let **S**, **M** and **R** denote striped, moricaud and double recessive (e. g. normal or plain) respectively on the assumption that any gamete bears one and only one of these factors, then the factors loaded in each zygote are always two, and the diagram above given must be modified as follows:

SS × MM
F₁ SM × RR
Gametes (S, M) (R)
SM SS MM SR MR
F₂ 2 : 1 : 1 1 : 1

Multiple allelomorphic relation of hereditary factors was suggested by CUÉNOT as early as 1903, and subsequently various authors have reported

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[1] Here occurs **M-Y** repulsion approximate to the ratio 1 : 3 : 3 : 1.

cases and attempted to explain them on this hypothesis. STURTEVANT (1913c) proved that almost all cases of so-called multiple allelomorphism can be considered as cases of complete coupling, though he was inclined to advocate the former hypothesis. On the contrary, PUNNETT (1915), who is aware of the inconsistency of this hypothesis with the universally adopted one of "presence and absence," adopts the theory of coupling.

The present case can not, however, be explained by the coupling hypothesis. To interpret the case as one of coupling, one would be forced to assume (1) that striped is **SM** in genetic constitution, in which **S** and **M** are completely coupled; (2) that moricaud is **sM**; (3) that double recessive is **sm**. The first assumption is evidently inconsistent with the fact mentioned before that the stripedd oes not involve the **M** factor at all, the characteristics of which must come to view if present. It follows that the case before us is a peculiar example of multiple allelomorphism which can not be explained by the theory of complete coupling. It does not, however, clash with the presence-absence hypothesis, if we assume a complete repulsion between **S** and **M** as was done above.

IV. COUPLING, REPULSION, AND SEXUAL DIMORPHISM OF GAMETIC SERIES. 1)

So far as characters are not sex-limited, the gametic distribution is generally assumed to follow an identical system in both sexes. The hybrid males and females give the offspring nearly in the same ratio when crossed with double recessive. A sharp contrast to this general rule was, however, discovered in the correlated inheritance of the cocoon colour and the larval marking. These characters are associated in such a manner that the association is partial in the male, and complete in the female, a fact of deep interest in connection with the genetics of sex and "gametic reduplication."

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1) Preliminary communications on this subject are found in two of my previous papers (1914a,b). An article containing more detailed statements was sent to the *Zeitschrift f. ind. Abst. u. Vererbungslehre* in April of 1914 through the kindness of Prof. BAUR, and the proof was read by Prof. HATTA. But I do not know whether the number of the journal containing the article has been published or not, for it was about that time that the great war broke out.

1) Correlation of Quail Factor and Yellow Cocoon Character.

In my previous papers I regarded the "normal" pattern as a unit character and denoted it by the symbol **N**. This was, however, incorrect; the normal is in reality a compound character brought about by the combination of **P** (plain) and **Q** (quail) factors as demonstrated above. On the other hand, the correlation of the normal marking (**PQ**) and the yellow colour (**Y**) was, as the following data show, the association of **Q** and **Y**, the **p** factor being transmitted independently (*cf.* Chapter **V**).

A. **Q-Y** Repulsion.

The cross between the normal white (**PPQQyy**) and the plain yellow (**PPqqYY**) gives rise to normal yellow F$_1$s (**PQyPqY**) which produced in F$_2$ generation three zygotic forms,— normal yellow, normal white and plain yellow in the ratio 2 : 1 : 1

PQyPqY × **PQyPqY**

a) Offspring of heterozygous normal yellows whose history is not exactly known.

	Normal yellow	Normal white	Plain yellow	Totals
N 4^1'12	168	77	81	326
N 4^2'12	154	72	62	288
N 4^3'12	136	86	68	290
H 2'12	80	30	28	138
H 5'12	123	88	61	272
Totals	661	353	300	1314

b) F$_2$ ex the cross normal white ♀♀ × plain yellow ♂♂

	Norm. yel.	Norm. wh.	Pl. yel.	Totals
H 12–1'13	178	82	87	347
H 12–2'13	136	83	84	303
H 12–3'13	38	16	11	65
H 12–4'13	159	63	64	286
H 12–5'13 (7 batches[1] in aggregate)	1057	539	487	2083

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[1] The "batch" is a group of eggs laid by a single female.

H 28′13	64	39	43	146
H 34–1′13	257	151	136	544
H 34–2′13	239	130	141	510
Totals	2128	1103	1053	4284

c) F_2 ex the cross plain yellow ♀♀ × normal white ♂♂.

	Norm. yel.	Norm. wh.	Pl. yel.	Totals
H 13–1′13	111	80	65	256
H 13–2′13	219	118	115	452
H 13–3′13	121	56	62	239
H 13–4′13	141	53	50	244
H 13–5′13 (13 batches in aggregate)	2321	1123	1117	4561
H 30–1′13	182	79	73	334
H 30–2′13	249	125	112	486
H 30–3′13	92	57	58	207
H 33–1′13	171	81	98	350
H 33–2′13	121	66	64	251
H 33–3′13	27	14	14	55
Totals	3755	1852	1828	7435

d) F_3 offspring derived from diheterozygous F_2s.

	Norm. yel.	Norm. wh.	Pl. yel.	Totals
C 30–1′14	55	30	28	113
C 33–1′14	24	21	13	58
C 33–2′14	118	58	65	241
O 3–1′14	135	76	74	285
O 3–2′14	163	68	86	317
O 3–3′14	37	20	21	78
Totals	532	273	287	1092

Summary of the results from the mating **PQyPqY** × **PQyPqY**.

	Normal yellow	Normal white	Plain yellow	Total
Observed	7076	3581	3468	14125
Expected	7063	3531	3531	14125
Ratio	2 :	1 :	1	

So far as the above results are concerned, the present case is hardly distinguishable from the ordinary one of complete repulsion occurring in both sexes. Crossings, however, were made reciprocally between F_1 individuals and double recessives, which revealed an extraordinary feature.

Crossing F_1 females with recessive males.

(**PQyPqY** ♀♀ × **PqyPqy** ♂♂)

	Normal white	Plain yellow	Totals
N 12'13	242	253	495
N 13'13	261	250	511
N 14'13	333	311	644
N 15'13	253	240	493
N 16'13	187	198	385
N 17'13	216	229	445
N 18'13	152	121	273
N 19'13	192	183	375
N 20'13	237	242	479
N 21'13	239	244	483
N 22'13	240	223	463
D 9–2'14	80	71	151
P 54–1'14	138	136	274
P 61'14	167	191	358

Grand totals of the results from the cross **PQyPqY** ♀ × **PqyPqy** ♂.

	Normal white	Plain yellow	Total
Actual numbers	2937	2892	5829
Expected	2914.5	2914.5	5829.0
Ratio	1 :	1	

Only two forms, normal white and plain yellow, were produced from the cross **PQyPqY** ♀ × **PqyPqy** ♂, so that it is evident that a complete repulsion between **Q** and **Y** occurs in oögenesis. Next let us examine the reciprocal cross.

Crossing F_1 males with recessive females.

(**PqyPqy** ♀♀ × **PQyPqY** ♂♂)

	Norm. yel.	Norm. wh.	Pl. yel.	Pl. wh.	Totals
H 43–1′13	39	117	121	40	317
H 43–2′13	34	64	76	37	211
N 1′13	42	130	134	44	350
P 62′14	49	208	157	36	450
P 67′14	46	133	139	38	356
P 68′14	70	175	129	27	401
Totals	280	827	756	222	2085

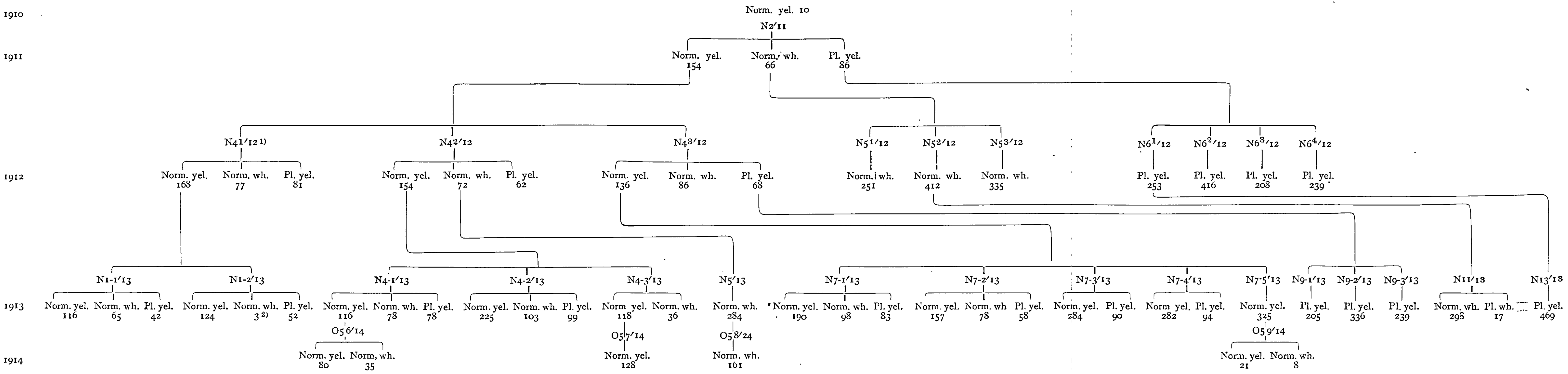
Thus a partial repulsion occurred in F_1 males instead of the complete one that took place in females of the same generation. As to the intensity of repulsion there is some fluctuation which makes it impossible at present to determine exactly the system of reduplication. For instance, H 43–1′13 shows a phenotypic ratio close to 1 : 3 : 3 : 1, whereas H 43–2′13 rather approaches to 1 : 2 : 2 : 1. In other lots there are found similar variations in the zygotic ratio, that is the gametic ratio of the heterozygous parents. The theoretical numbers calculated on the 1 : 3 : 3 : 1 basis are compared with the actual results:

	Normal yellow	Normal white	Plain yellow	Plain white	Total
Observed	280	827	756	222	2085
Expected	260.6	781.9	781.9	260.6	2085.0

The present case affords a strong basis for the argument that the crossing of F_1 individuals with double recessives not only facilitates the study of gametic distribution, but is indispensable for it, as has been repeatedly stated by various authors. But the results of mating various phenotypes among themselves also throw some light upon the subject, though the actual feature of gametic distribution is not fully manifested in this way alone.

If the **Q-Y** relation be of the ordinary kind of complete repulsion, all F_2 normal yellows should be heterozygous, to be split again in F_3 into three phenotypes, while the normal white and plain yellow offspring should necessarily be homozygous and breed true—processes to be effected in subsequent generations. But this expectation was not realised in my experiments, as is obvious in the following pedigree.

Table I.



1) As to the alteration of suffixes *cf.* p. 130.

2) Probably ramblers.

As the table shows, neither are normal yellow in F_3 and later generations necessarily heterozygous, nor normal white necessarily homozygous,— facts that disprove the occurrence of ordinary repulsion between the factors under consideration. According to the result obtained by crossing F_1 with double recessive, we may assume the dimorphic gametic series as

	PQY	PQy	PqY	Pqy
Sperm.	1 :	3 :	3 :	1
and				
Egg	0 :	1 :	1 :	0

then F_2 zygotes must be as follows :—

F_2 phenotypes		Their zygotic constitution
Normal yellow	8	1 PQYPQy 6 PQyPqY 1 PQYPqY
Normal white	4	3 PQyPQy 1 PQyPqy
Plain yellow	4	3 PqYPqY 1 PqYPqy

A) F_2 normal yellow yield various F_3 families according to the genetic constitution of the individuals mated.

F_2 matings				F_3 families
Males		Females		
Zygotes	Gametes	Zygotes	Gametes	
PQyPqY	1PQY : 3PQy : 3PqY : 1Pqy	PQyPqY	1PQy : 1PqY	Class I 2 normal yellow 1 normal white 1 plain yellow
PQyPqY	1PQY : 3PQy : 3PqY : 1Pqy	PQYPQy	1PQY : 1PQy	Class II 3 normal yellow 1 normal white
PQYPQy	1PQY : 1PQy	PQYPQy	1PQY : 1PQy	
PQYPQy	1PQY : 1PQy	PQyPqY	1PQy : 1PqY	
PQyPqY	1PQY : 3PQy : 3PqY : 1Pqy	PQYPqY	1PQY : 1PqY	Class III 3 normal yellow 1 plain yellow
PQYPqY	1PQY : 1PqY	PQYPqY	1PQY : 1PqY	
PQYPqY	1PQY : 1PqY	PQyPqY	1PQy : 1PqY	

PQYPQy	1PQY : 1PQy	PQYPqY	1PQY : 1PqY	Class IV all normal yellow
PQYPqY	1PQY : 1PqY	PQYPQy	1PQY : 1PQy	

The results in subsequent generations can likewise be explained. All of the four classes given above were actually observed.

B,C) F$_2$ normal white and plain yellow derived from the cross **PQyPQy** × **PqYPqY** were also not uniform in respect to the genetic constitution, some were homozygous, but others were heterozygous for one of the two allelomorphs under consideration.

F$_2$ normal white paired *inter se.*

F$_2$ matings				F$_3$ families
Males		Females		
Zygotes	Gametes	Zygotes	Gametes	
PQyPQy	PQy	PQyPQy	PQy	Class V all normal white
PQyPQy	PQy	PQyPqy	1PQy : 1Pqy	
PQyPqy	1PQy : 1Pqy	PQyPQy	PQy	
PQyPqy	1PQy : 1Pqy	PQyPqy	1PQy : 1Pqy	Class VI 3 normal white 1 plain white
F$_2$ plain yellow paired *inter se.*				
PqYPqY	PqY	PqYPqY	PqY	Class VII all plain yellow
PqYPqY	PqY	PqYPqy	1PqY : 1Pqy	
PqYPqy	1PqY : Pqy	PqYPqY	PqY	
PqYPqy	1PqY : 1Pqy	PqYPqy	1PqY : 1Pqy	Class VIII 3 plain yellow 1 plain white

The frequency of each class may be calculated as follows :—

A) Frequency of the occurrence of the various families in the offspring of normal yellow in the Class I lot of any generation.

Male		Female		
6 PQyPqY	×	6 PQyPqY		......36......giving rise to Class I
6 PQyPqY	×	1 PQYPQy	6	...13......giving rise to Class II
1 PQYPQy	×	1 PQYPQy	1	
1 PQYPQy	×	6 PQyPqY	6	

6 PQyPqY × 1 PQYPqY 6
1 PQYPqY × 6 PQyPqY 6 ...13......giving rise to Class III
1 PQYPqY × 1 PQYPqY 1

1 PQYPQy × 1 PQYPqY 1
1 PQYPqY × 1 PQYPQy 1 ... 2......giving rise to Class IV

We should expect to meet with the classes I, II, III, IV respectively 36, 13, 13, and 2 times in 64 families. The actual counts are

	Cases included in Table I	Other cases	Totals	Expect.
Class I	9	5	14	14.6
Class II	3	3	6	5·3
Class III	2	2	4	5·3
Class IV	1	1	2	0.8

B) Frequency of the different families in the offspring of normal white in the Class I lot of any generation.

Male Female
3 PQyPQy × 3 PQyPQy 9
3 PQyPQy × 1 PQyPqy 3 ...15......giving rise to Class V
1 PQyPqy × 3 PQyPQy 3
1 PQyPqy × 1 PQyPqy ...... 1......giving rise to Class VI

Actual results:

	Cases included in Table I	Other cases	Totals	Expected
Class V	4	3	7	7·5
Class VI	1	0	1	0.5

C) Frequency of the different families in the offspring of plain yellow in the Class I lot of any generation.

Male Female
3 PqYPqY × 3 PqYPqY 9
3 PqYPqY × 1 PqYPqy 3 15......giving rise to Class VII
1 PqYPqy × 3 PqYPqY 3
1 PqYPqy × 1 PqYPqp 1...........giving rise to Class VIII

The observed results were:

	Cases included in Table I	Other cases	Totals	Expected
Class VII	7	3	10	9.4
Class VIII	0	0	0	0.6

Though the number is not large enough, the expectation was fairly realised in all of the three forms A, B and C.

B. **Q-Y** Coupling.

When **Q** and **Y** are brought into a hybrid by the same parent, coupling occurs between these dominants. In contradistinction to the case of repulsion, all possible F_2 forms are produced in the ordinary as well as in the sexually dimorphic coupling, so that the actual proportion of gametes is almost impossible to make out so long as the breeding is confined *inter se.*[1]

F_2 offspring ex normal yellow × plain white.

(PQYPqy × PQYPqy)

	Norm. yel.	Norm. wh.	Pl. yel.	Pl. wh.	Totals
C 21'14	135	13	13	25	186
C 22'14	265	40	20	78	403
C 23'14	223	40	27	69	359
C 24'14	64	9	3	17	93
C 25–1'14	74	10	9	24	117
C 25–2'14	75	10	1	25	111
C 25–3'14	146	19	11	48	224
C 26–1'14	119	16	16	23	174
C 26–2'14	113	9	8	31	161
C 26–3'14	218	20	23	47	308
C 27–1'14	138	19	11	44	212
C 27–2'14	99	14	9	42	164
C 27–3'14	111	17	13 *	31 *	172
C 28–2'14	41	7	3	13	64

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1) I formerly regarded the coupling between **S** or **M** and **Y** as a case of the ordinary nature occurring in the frequency 7 : 1 : 1 : 7 in both sexes (1913 b).

C 28-4'14	241	24	27	56	348
O 42-2'14	159	7	12	35	213
O 42-3'14	117	8	6	28	159
Totals	2338	282	212	636	3468

F_2 normal yellow from the lots C 26-2 and C 27-1, and F_1 from N 6'14 were mated *inter se*, the offspring being reared in the summer of the same year. The results follow:

	Norm. yel.	Norm. wh.	Pl. yel.	Pl. wh.	Totals
C 41-1'14	68	7	6	19	100
C 41-2'14	9	1	1	2	13
C 41-3'14	175	—	—	—	175
C 42-1'14	43	2	1	13	59
C 42-2'14	103	6	12	19	140
C 42-3'14	29	2	3	4	38

Setting aside one uniform normal yellow family, C 41-3, and two small lots, C 41-2 and C 42-3, the totals of the rest are

Norm. yel.	Norm. wh.	Pl. yel.	Pl. wh.	Total
214	15	19	51	299

The results of back-crossing are given below.

PQYPqy ♀ × **PqyPqy** ♂

	Normal yellow	Plain white	Total
P 64'14	167	117	284

PqyPqy ♀♀ × **PQYPqy** ♂♂

	Norm. yel.	Norm. wh.	Pl. yel.	Pl. wh.	Totals
P 65'14	119	45	42	99	305
P 66'14	147	40	33	108	328
Totals	266	85	75	207	633

Thus F_1 females produced, when crossed with a double recessive, only two forms similar to the original parents, while F_1 males gave four possible forms in nearly the ratio 3 : 1 : 1 : 3, the expectation on that basis being 237 : 79 : 79 : 237.

Now if we assume the F_1 gametes as

	PQY		**PQy**		**PqY**		**Pqy**
Eggs	1	:	0	:	0	:	1
Sperm.	3	:	1	:	1	:	3

the succeeding zygotic series ought to be

11 : 1 : 1 : 3.

Comparing this ratio with my actual F_2 counts in 1914, we obtain

	Norm. yel.	Norm. wh.	Pl. yel.	Pl. wh.	Totals
Spring 1914	2338	282	212	636	3468
Summer 1914	214	15	19	51	299
Totals	2552	297	231	687	3767
Expect.	2590	235	235	706	3766

The theoretical figures are not far from the actual ones.

We can, however, assume another ratio, 5 : 2 : 2 : 5 (2.5 : 1 : 1 2.5); on this basis the zygotic ratio and calculated numbers are

	Norm. yel.	Norm. wh.	Pl. yel.	Pl. wh.	Total
Ratio	19 :	2 :	2 :	5	28
Expectation	2556	269	269	673	3767

It follows that, as in the case of repulsion, there is room for doubt as to the actual system of coupling in the male hybrid. Moreover, the zygotic proportions in various lots are not quite identical: whether such a fluctuation is or is not due to chance is to be decided by further experiments.

All individuals concerned in the above experiments were homozygous for the presence of **P** factor. Now I am to describe the cases in which the dominant individuals were homozygous for the absence of **P**, or were heterozygous for **P**. The results are quite the same with those given above, so far as the **Q-Y** coupling is concerned.

Triply heterozygous normal yellows (**PQYpqy**)
mated *inter se*.

		A 452′15	A 453′15	A 454′15	A 456′15	Totals
Normal yellow	PQY	143	169	146	147	605
Normal white	PQy	9	14	22	21	66

Plain yellow	PqY	13 *	11 *	14	10	48
Plain white	Pqy	36 *	48 *	46	38	168
Quail yellow	pQY	56	43	63	42	204
Quail white	pQy	3	1	5	4	13
Pale-quail yellow	pqY	5 *	4 *	5 *	1	15
Pale-quail white	pqy	10 *	16 *	13 *	16	55
Totals		275	306	314	279	1174

Triply heterozygous normal yellow females paired with absolute recessive, i. e. **PQYpqy** ♀♀ × **pqypqy** ♂♂.

		A 459'15	A 460'75	Totals
Normal yellow	PQY	95	85	180
Plain white	Pqy	82	86	168
Quail yellow	pQY	73	99	172
Pale-quail white	pqy	75 *	85 *	160
Totals		325	355	680

Absolute recessive females mated with triple hybrids, i. e. **pqypqy** ♀♀ × **PQYpqy** ♂♂.

		A 461'15	A 462'15	A 463'15	Totals
Normal yellow	PQY	71	49	56	176
Normal white	PQy	19	9	16	44
Plain yellow	PqY	15 *	11	13	39
Plain white	Pqy	47 *	38	61	146
Quail yellow	pQY	51	44	51	146
Quail white	pQy	30	16	10	56
Pale-quail yellow	pqY	16 *	22	11 *	49
Pale-quail white	pqy	55 *	36	59 *	150
Totals		304	225	277	806

Doubly heterozygous quail yellow females mated with absolute recessives, i. e. **pQYpqy** ♀♀ × **pqypqy** ♂♂.

	Quail yellow (pQY)	Pale-quail white (pqy)	Totals
A 425'15	264	244	508
A 426'15	228	224	452

Totals	492	468	960

An absolute recessive female mated with a double hybrid,

i. e. **pqypqy** ♀ × **pQYpqy** ♂.

	Quail yel.	Quail wh.	Pale-quail yel.	Pale-quail wh.	Total
A 424′15	131	22	23	111	287

Thus we know that **Q-Y** coupling always occurs in the same form in the hybrids **PPQqYy**, **PpQqYy** and **ppQqYy.**

Summary of the data given above with respect to **Q-Y** coupling:

QYqy × **QYqy**

	QY	Qy	qY	qy	Total
Observed	3361	376	294	910	4941
Expected	3396.9	308.8	308.8	926.5	4941.0
Ratio	11 :	1 :	1 :	3	

QYqy ♀♀ × **qyqy** ♂♂.

	QY	Qy	qY	qy	Total
Observed	984	0	0	940	1924
Expected	962	0	0	962	1924
Ratio	1	:		1	

qyqy ♀♀ × **QYqy** ♂♂.

	QY	Qy	qY	qy	Total
Observed	719	207	186	614	1726
Expected	647	216	216	647	1726
Ratio	3 :	1 :	1 :	3	

The result from the cross **PqyPqy** ♀♀ × **PQYPqy** ♂♂ approximates the numbers expected on the 3 : 1 : 1 : 3 basis, as shown below:

	Norm. yel.	Norm. wh.	Pl. yel.	Pl. wh.	Total
Observed	266	85	75	207	633
Expected	237.4	79.1	79.1	237.4	633.0

2) Correlation of Moricaud Marking and Yellow Cocoon Character.

A. **M-Y** Repulsion.

The moricaud is epistatic to all other markings but the striped, to which it is hypostatic. In F_1 moricaud yellow produced by crossing moricaud white with normal or plain yellow, a repulsion similar to that described in the preceding section occurs between **M** and **Y** factors.

MymY × **MymY**

F_2 ex the cross moricaud white × normal yellow.

(**MPQymPQY** × **MPQymPQY**)

	Mor. yel. (MPQY)	Mor. wh. (MPQy)	Norm. yel. (mPQY)	Norm. wh. (mPQy)	Totals
C 34-1'14	82	33	45	0	160
C 34-2'14	72	36	35	0	143
C 34-3'14	82	51	55	0	188
Totals	236	120	135	0	491

F_2 ex the cross moricaud white × plain yellow.

(**MPQymPqy** × **MPQymPqY**)

	Mor. yel. (MPQY)	Mor. wh. (MPQy)	Plain. yel. (mPqY)	Plain. wh. (mPqy)	Totals
P 50-1'14	89	40	49	0	178
P 50-2'14	64	34	20	0	118
P 50-3'14	88	44	47	0	179
A 40'15	59	26	23	0	108
Totals	300	144	139	0	583
Grand totals (**MymY**×**MymY**)	536	264	274	0	1074
Expect.	537.0	268.5	268.5	0	1074.0
Ratio	2 :	1 :	1		

The results apparently show occurrence of complete repulsion, at least in one of the sexes. Now let us test the crosses diheterozygotes × double recessives.

MymY ♀ × **mymy** ♂

Diheterozygous females mated to plain white males.

(**MPQymPqY** ♀♀ × **mPqymPqy** ♂♂)

	Moricaud white (MPQy)	Plain yellow (mPqY)	Totals
Ex 2–7′14	164	164	328
A 493′15 (3 batches)	357	386	743
Totals	521	550	1071
Expect.	535·5	535·5	1071.0

Complete repulsion took place in the female hybrid, as shown by the fact that no other combinations than two parental types were produced.

mymy ♀ × **MymY** ♂

a) A diheterozygous male mated to a normal white female.

(**mPQymPQy** ♀♀ × **MPQymPQY** ♂♂)

	Mor. yel.	Mor. wh.	Norm. yel.	Norm. wh.	Total
D 5–1′14	33	123	142	37	335

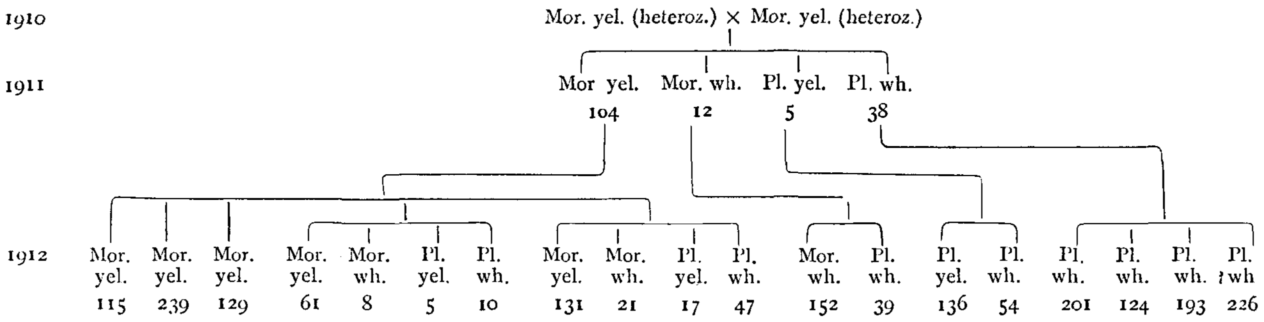
b) diheterozygous males (ex light normal yellow × moricaud white) mated to plain white females. (**mPqymPqy** × **MPQymPQY**)

	Mor. yel.	Mor. wh.	Norm. yel.	Norm. wh.	Totals
A 491′15	29	143	154 *	34 *	360
A 492′15	24	187	187 *	33 *	431
Totals	53	330	341	67	791
Grand totals (**mymy**♀ × **MymY**♂)	86	453	483	104	1126
Expect.	112.6	450.4	450.4	112.6	1126.0
	(1 :	4 :	4 :	1)	
	94	469	469	94	1126
	(1 :	5 :	5 :	1)	

B. **M**-**Y** Coupling.

In the heterozygotes produced by crossing moricaud yellow and normal or plain white, a coupling between **M** and **Y** takes place, as I have described in a previous paper of mine (1913 b). The reported cases are reproduced in Table II.

Table II.


1910
Mor. yel. (heteroz.) × Mor. yel. (heteroz.)
1911
Mor yel. 104
Mor. wh. 12
Pl. yel. 5
Pl. wh. 38
1912
Mor. yel. 115
Mor. yel. 239
Mor. yel. 129
Mor. yel. 61
Mor. wh. 8
Pl. yel. 5
Pl. wh. 10
Mor. yel. 131
Mor. wh. 21
Pl. yel. 17
Pl. wh. 47
Mor. wh. 152
Pl. wh. 39
Pl. yel. 136
Pl. wh. 54
Pl. wh. 201
Pl. wh. 124
Pl. wh. 193
Pl. ?wh 226

Further data were obtained in 1913, 1914 and 1915.

MYmy × **MYmy**

a) F_2 ex the cross normal white (**mPQymPQy**) ♀♀ × moricaud yellow (**MPQYMPQY**) ♂♂.

	Mor. yel. (MPQY)	Mor. wh. (MPQy)	Norm. yel. (mPQY)	Norm. wh. (mPQy)	Totals
H 19–1′13[1]	141	19	14	31	205
H 19–4′13 (6 batches)	1115	92	94	316	1617
H 21–1′13	220	14	18	56	308
H 21–2′13	108	14	10	29	161
H 21–3′13	269	24	35	73	401
H 21–4′13	113	14	11	37	175
H 21–5′13	57	16	12	36	121
H 21–6′13	188	7	13	55	263
H 21–7′13	130	16	11	45	202
H 21–8′13 (14 batches)	2954	253	257	853	4317
H 21–9′13 (6 batches)	1133	97	96	264	1590
Totals	6428	566	571	1795	9360

b) F_2 ex the cross moricaud yellow (**MPQYMPQY**) ♀♀ × normal white (**mPQymPQy**) ♂♂.

	Mor. yel. (MPQY)	Mor. wh. (MPQy)	Norm. yel. (mPQY)	Norm. wh. (mPQy)	Totals
H 20–1′13	163	13	15	55	246
H 20–2′13	120	7	9	31	167
H 22–1′13	154	16	7	47	224
H 22–2′13	191	16	20	40	267
H 22–3′13	123	11	13	38	185
Totals	751	63	64	211	1089

Data obtained in 1914.

F_2 ex the cross plain or normal white ♀♀ × moricaud yellow ♂♂

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[1] As to the alteration of suffixes see p. 130.

	Mor. yel.	Mor. wh.	Norm. or pl. yel.	Norm. or pl. wh.	Totals
C 19'14	158	20	11	41	230
C 20–2'14	149	18	9	54	230
O 14–2'14	137	18	4	41	200
O 17–1'14	88	7	12	30	137
O 40'14	177	12	17	49	255
Totals	709	75	53	215	1052

Datum obtained in 1915.

F_3 ex the cross moricaud yellow (**MPQYmPQY**) ♀ ×
quail white (**mpQympQy**) ♂

	Mor. yel.	Mor. wh.	Norm. yel.	Norm. wh.	Total
A 226'15	209	19	22	62	312

Grand totals of the results from the cross **MYmy** × **MYmy**:

	Mor. yel.	Mor. wh.	Non-mor. yel.	Non-mor. wh.	Total
Observed	8097	723	710	2283	11813
Expect. on 3 : 1 : 1 : 3	8121.4	738.3	738.3	2214.9	11812.9
Ratio	11 :	1 :	1 :	3	

The results of testing female hybrids are as follows:

MYmy ♀♀ × **mymy** ♂♂

a) A heterozygous moricaud yellow female mated to a normal white male (**MPQYmPQy** ♀ × **mPQymPQy** ♂).

	Mor. yel. (MPQY)	Norm. wh. (mPQy)	Total
P 42'14	69	69	138

b) A heterozygous moricaud yellow female mated to a plain white male (**MPQYmPQy** ♀ × **mPqymPqy** ♂).

	Mor. yel.	Norm. wh.	Total
P 44'14	89	90	179

c) Heterozygous moricaud yellow females mated to quail white males (**MPQYmPQy** ♀♀ × **mpQympQy** ♂♂).

	Mor. yel.	Norm. wh.	Totals
P 45-1′14	138	160	298
P 53′14	111	123	234

Grand totals of the results from the cross **MYmy** ♀ × **mymy** ♂:

	Mor. yel. (MY)	Non-mor. wh. (my)	Total
Observed	407	442	849
Expected	424.5	424.5	849.0

That a complete coupling occurs between the moricaud and yellow factors in the female heterozygotes is thus evident.

The results of testing the male hybrids follow:

mymy ♀ × **MYmy** ♂

a) Normal white females mated to heteroz. moricaud yellow males (**mPQymPQy** ♀♀ × **MPQYmPQy** ♂♂).

	Mor. yel. (MPQY)	Mor. wh. (MPQy)	Norm. yel. (mPQY)	Norm. wh. (mPQy)	Totals
H 39-5′13	61	26	24	64	175
H 53′13	188	54	65	176	483
M 4′13	116	45	51	121	333
M 5′13	162	78	69	159	468
P 43-1′14	134	52	44	99	329
P 43-2′14	110	45	43	122	320
P 46-1′14	130	57	60	160	407
P 46-2′14	138	59	52	129	378
P 48-1′14	142	57	67	142	408
P 48-2′14	191	66	69	179	505
P 52′14	174	59	78	200	511
A 158′15	102	17	23	91	233
Totals	1648	615	645	1642	4550

b) Plain white females mated to heteroz. moricaud yellow males (ex mor. yel. × norm. wh.) (**mPqymPqy** ♀♀ × **MPQYmPQy** ♂♂).

	Mor. yel.	Mor. wh.	Norm. yel.	Norm. wh.	Totals
M 3′13	174	67	59	173	473
D 15–′14	83	43	42	103	271
D 15–2′14	48	18	13	56	135
Totals	305	128	114	332	879

c) A quail white female mated to a heteroz. moricaud yellow male (ex mor. yel. × norm. wh.) (**mpQympQy** ♀ × **MPQYmPQy** ♂).

	Mor. yel. (MPQY)	Mor. wh. (MPQy)	Norm. yel. (mPQY)	Norm. wh. (mPQy)	Total
P 51′14	145	49	75	154	423

Grand totals of the results from the cross **mymy** ♀ × **MYmy** ♂.

	Mor. yel. (MY)	Mor. wh. (My)	Non-mor. yel. (mY)	Non-mor. wh. (my)	Total
Observed	2098	792	834	2128	5852
Expect. according to 3 : 1 : 1 : 3,	2194·5	731·5	731·5	2194·5	5852·0
to 5 : 2 : 2 : 5	2090	836	836	2090	5852

All the moricaud yellow hybrids which were used to produce these families were homozygous for the presence of both **P** and **Q**. The following results are, on the contrary, obtained from individuals heterozygous for **M**, **Y** and **P** (some also for **Q**), or from animals heterozygous for **M** and **Y** but homozygous for the absence of **P**.

a) Quadruply heterozygous moricaud yellow (**MPQYmpqy**) mated *inter se*.

		A 476′15	A 477′15	A 480–1′15	A 480–2′15	Totals
Moricaud yellow	MPQY	287	187	204	171	849
Moricaud white	MPQy	9	8	4	20	41
Plain yellow	mPqY	14 *	10	12	10	46
Plain white	mPqy	39 *	45	53	72	209
Moricaud-quail yellow	MpQY	63	60	72	69	264
Moricaud-quail white	MpQy	5	7	3	7	22
Pale-quail yellow	mpqY	4 *	7 *	5 *	4	20
Pale-quail white	mpqy	17 *	15 *	27 *	27	86

Totals	438	339	380	380	1537
Of which	MY	My	mY	my	
	1113	63	66	295	

b) Quadruply heterozygous moricaud yellow (**MPQYmpqy**) ♀♀ × absolutely recessive (**mpqympqy**) ♂♂

		A 472–1′15	A 472–2′15	A 475′15	A 479′15	Totals
Mor. yel.	MPQY	89	73	76	115	353
Mor. qu. yel.	MyQY	66	81	66	116	329
Pl. wh.	mPqy	81	72	67	101	321
Pal. qu. wh.	mpqy	78 *	66	63	109	316
Totals		314	292	272	441	1319
Of which		MY	my			
		682	637			

c) Absolute recessive ♀♀ (**mpqympqy**) × quadruply heteroz. moricaud yellow ♂♂ (**MPQYmpqy**)

		A 471′15	A 473′15	A 474′15	A 478′15	Totals.
Mor. yel.	MPQY	44	50	52	68	214
Mor. wh.	MPQy	6	6	8	18	38
Pl. yel.	mPqY	10	14	8	26	58
Pl. wh.	mPqy	49	53	59	52	213
Mor. qu. yel.	MyQY	50	59	42	46	197
Mor. qu. wh.	MyQy	6	12	6	18	42
Pal. qu. yel.	mpqY	9	6	9 *	15	39
Pal. qu. wh.	mpqy	59	57	52 *	69	237
Totals		233	257	236	312	1038
Of which		MY 411,	My 80,	mY 97,	my 450	

d) Triply heterozygous moricaud yellow (**MPQYmpQy**) paired *inter se.*

		A 80′15
Mor. yel.	MPQY	237
Mor. wh.	MPQy	15

Norm. yel.	mPQY	8
Norm. wh.	mPQy	74
Mor. qu. yel.	MpQY	79
Mor. qu. wh.	MpQy	10
Qu. yel.	mpQY	6
Qu. wh.	mpQy	22
Total		451

Of which MY 316 My 25 mY 14 my 96

e) Quail white (**mpQympQy**) ♀♀ × triply heterozygous moricaud yellow (**MPQYmpQy**) ♂♂.

		A 201'15	A 202'15	Totals
Mor. yel.	MPQY	93	89	182
Mor. wh.	MPQy	30	32	62
Norm. yel.	mPQY	25	19	44
Norm. wh.	mPQy	86	91	177
Mor. qu. yel.	MpQY	77	85	162
Mor. qu. wh.	MpQy	33	20	53
Qu. yel.	mpQY	27	20	47
Qu. wh.	mpQy	79	85	164
Totals		450	441	891

Of which MY 344 My 115 mY 91 my 341

f) Triply heterozygous moricaud-quail yellow (**MpQYmpqy**) paired *inter se*.

		A 481'15	A 482'15	A 483-1'15	A 483-2'15	Totals
Mor. qu. yel.	MpQY	240	310	236	200	986
Mor. qu. wh.	MpQy	13	14	25	10	62
Pal. qu. yel.	mpqY	15 *	18 *	22 *	13 *	68
Pal. qu. wh.	mpqy	70 *	78 *	64 *	63 *	275
Totals		338	420	347	286	1391

g) Triply heterozygous moricaud-quail yellow (**MpQYmpqy**) ♀ × pale-quail white (**mpqympqy**) ♂.

	Moricaud-quail yellow	Pale-quail white	Total
A 486'15	170	145 *	315

h) Pale-quail white (**mpqympqy**) ♀♀ × triply heterozygous moricaud-quail yellow (**MpQYmpqy**) ♂♂.

		A 484'15	A 485'15	Totals
Moricaud-quail yellow	MpQY	108	92	200
Moricaud-quail white	MpQy	23	20	43
Pale-quail yellow	mpqY	21 *	14	35
Pale-quail white	mpqy	110 *	100	210
Totals		262	226	488

i) A triply heteroz. moricaud-quail yellow (**MpQYmpQy**) ♀ × a plain white (**mPqymPqy**) ♂.

	Mor. yel. (MPQY)	Norm. wh. (mPQy)	Total
A 120'15	164	161	325

Summary of the above data regarding the **M-Y** coupling:

MYmy × **MYmy**

	MY	My	mY	my	Total
Observed	10512	873	858	2949	15192
Expect. accord. to 7 : 2 : 2 : 7	10550	844	844	2954	15192
Ratio	25 :	2 :	2 :	7	
Accord. to 3 : 1 : 1 : 3	10444.5	949.5	949.5	2848.5	15192
Ratio	11 :	1 :	1 :	3	

MYmy ♀ × **mymy** ♂

	MY	My	mY	my	Total
Observed	1423	0	0	1385	2808
Expected	1404	0	0	1404	2808
Ratio	1	:		1	

mymy ♀ × **MYmy** ♂

	MY	My	mY	my	Total
Observed	3053	1030	1057	3129	8269
Expected	3100.9	1033.6	1033.6	3100.9	8269.0
Ratio	3 :	1 :	1 :	3	

The above results satisfactorily prove the dimorphism of gametic series as regards the correlation of the moricaud pattern and the yellow colour. Complete coupling takes place in the female, partial coupling in the male. The coupling system in the male is of a low intensity, more or less approximating to 3 : 1 : 1 : 3.

3) Correlation of Striped Marking and Yellow Cocoon Colour.

A. **S-Y** Repulsion

A repulsion phenomenon similar to the one observed to occur between **Q** and **Y** or between **M** and **Y** also occurred when the two dominant characters, striped and yellow, are derived from different parents.

SysY × **SysY**

a) F_2 families ex the cross striped white (**SmPQy**·) × moricaud yellow (**sMPQY**)

	Striped yellow[1]	Striped white[1]	Moricaud yellow	Totals
O 51–1′14	30	15	23	68
O 51–2′14	122	65	77	264
O 51–4′14	116	51	58	225
O 51–5′14	43	15	20	78
Totals	311	146	178	635

b) F_2 ex the cross striped white (**SPQy**) × normal yellow (**sPQY**)

	Str. yel.	Str. wh.	Norm. yel.	Totals
A 34′15	61	38	38	137
A 35′15	67	31	24	122
A 36′15	108	48	50	206
Totals	236	117	112	465

---

1) Striped-moricaud included.

Grand totals of the results from **SysY** × **SysY.**

	Striped yellow (SY)	Striped white (Sy)	Non-striped yellow (sY)	Non-striped white (sy)	Total
Observed	547	263	290	0	1100
Expected	550	275	275	0	1100
Ratio	2 :	1 :	1		

SysY ♀ × sysy ♂

a) Triply heterozygous striped-moricaud yellow (**SmPQysMPQY**) ♀♀ × plain white (**smPqysmPqy**) ♂♂.

	Str. wh. (SmPQy)	Mor. yel. (sMPQY)	Totals
P 38–1′14	118	120	238
P 38–2′14	81	88	169
Totals	199	208	407

b) Triply heterozygous striped-moricaud yellow (**SmPQysMPQY**) × quail white (**smpQysmpQy**).

	Striped white (SmPQy)	Moricaud yellow (sMPQY)	Total
P 39′14	148	153	301

Grand totals of the results from the cross **SysY** ♀ × **sysy** ♂:

	Striped yellow (Sy)	Non-striped yellow (sY)	Total
Observed	347	361	708
Expected	354	354	708

sysy ♀ × SysY ♂

a) Quail white (**smpQysmpQy**) ♀ × triply heterozygous striped-moricaud yellow (**SmPQysMPQY**) ♂.

	Str. yel. (SmPQY)	Str. wh. (SmPQy)	Mor. yel. (sMPQY)	Mor. wh. (sMPQy)	Total
P 40–1′14	63	177	194	61	495

b) Quail white (**spQyspQy**) ♀ × diheterozygous striped-yellow (**SPQysPQY**) ♂.

	Str. yel.	Str. wh.	Norm. yel.	Norm. wh.	Total
P 40–2′14	49	161	178	58	446

Grand totals of the results from the cross **sysy** ♀ × **SysY** ♂:

	Striped yellow (SY)	Striped white (Sy)	Non-striped yellow (sY)	Non-striped white (sy)	Total
Observed	112	338	372	119	941
Expected	117.6	352.9	352.9	117.6	941.0
	(1 :	3 :	3 :	1)	

From these data we see that a complete repulsion takes place in the female, and the partial one in the male.

B. **S-Y** Coupling.

Since I published a short article (1914a) on the sexually dimorphic gametic series in striped-yellow coupling a host of data have been collected. In the following pages, both the figures contained in the paper just cited and those obtained since are given.

SYsy × **SYsy**

a) Diheterozygous striped yellow (**SPQYsPQy**) mated *inter se*.

	Str. yel. (SPQY)	Str. wh. (SPQy)	Norm. yel. (sPQY)	Norm. wh. (sPQy)	Totals
H 1–6'13 1)	204	23	12	54	293
H 1–8'13	247	26	24	65	362
H 1–9'13	60	3	10	18	91
H 29–1'13	240	22	35	63	360
H 29–2'13	140	15	23	48	226
H 29–3'13	300	35	33	91	459
H 29–4'13	239	38	40	55	372
H 29–5'13	342	36	41	94	513
H 29–6'13	242	50	24	54	370
H 29–7'13	195	31	29	39	294
H 29–8'13	275	37	36	63	411
C 15'14	171	15	20	47	253
C 17–1'14	211	22	16	71	320
O 1–2'14	108	3	10	26	147

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1) As to the alteration of suffixes of these lots, *cf.* p. 130.

O 2–3′14	73	8	10	12	103
O 22′14	118	13	14	34	179
O 23–2′14	198	32	31	59	320
O 25–2′14	61	6	3	19	89
O 25–3′14	131	9	15	42	197
O 27–1′14	289	32	27	70	418
O 27–2′14	283	30	29	83	425
O 33–1′14	235	27	33	69	364
O 33–2′14	231	25	20	62	338
O 34–1′14	139	12	9	16	176
O 34–2′14	139	18	16	62	235
O 55–1′14	332	22	26	87	467
O 55–2′14	280	25	36	75	416
O 55–3′14	241	21	22	79	363
P 76–1′14	226	15	14	47	302
P 76–2′14	177	14	18	53	262
P 76–4′14	205	18	18	53	294
P 83′14	102	11	11	33	157
P 84–1′14	44	8	7	8	67
P 84–2′14	125	11	16	45	197
A 78′15	115	8	10	42	175
A 79′15	159	9	9	50	227
A 211′15	118	11	13	33	175
A 212′15	271	18	18	72	379
A 214′15	157	13	18	52	240
Totals	7423	774	795	2044	11036

b) Triply heterozygous striped yellow (**SPQYsPqy**) mated *inter se*.

	Str. yel. (SPQY)	Str. wh. (SPQy)	Pl. yel. (sPqY)	Pl. wh. (sPqy)	Totals
C 11′14	229	23	30	66	348
O 46′14	219	23	24	71	337

P 73′14	55	9	7	17	88
P 75–1′14	139	11	14	40	204
P 75–2′14	95	7	10	27	139
P 82′14	67	7	3	17	94
A 62′15	165	9	14	52	240
A 73′15	164	16	12	43	235
A 74′15	307	20	30	77	434
A 76′15	128	17	11	36	192
A 216′15	122	9	7	31	169
A 220′15	118	10	5	26	159
Totals	1808	161	167	503	2639

c) Triheterozygous striped yellow (**SPQYspQy**) paired *inter se*.

		A 63′15	A 64′15	A 65′15	Totals
Str. yel.	SPQY	54	42	68	164
Str. wh.	SPQy	4	7	4	15
Norm. yel.	sPQY	8	7	5	20
Norm. wh.	sPQy	14	10	12	36
Str. qu. yel.	SpQY	21	18	49	88
Str. qu. wh.	SpQy	3	1	7	11
Quail yel.	spQY	4	2	3	9
Quail wh.	spQy	5	9	7	21
Totals		113	96	155	364

d) F_2 ex the cross pale-quail white (**spqy**) × striped yellow (**SPQY**).

		A 531′15	A 539′15	A 540′15	Totals
Str. yel.	SPQY	71	212	112	395
Str. wh.	SPQy	5	12	8	25
Pl. yel.	sPqY	7	7 *	10	24
Pl. wh.	sPqy	31	65 *	30	126
Str. qu. yel.	SpQY	51	81	40	172
Str. qu. wh.	SpQy	0	4	6	10

Pale-qu. yel.	spqY	6 *	6 *	2	14
Pale-qu. wh.	spqy	15 *	22 *	22	59
Totals		186	409	230	825

e) F_2 ex the cross plain white (**sPqy**) × striped-quail yellow (**SpQY**).

	A 532'15	A 533'15	Totals
Str. yel.	102	132	234
Str. wh.	11	12	23
Light norm. yel. 1)	8	8	16
Light norm. wh.	33	39	72
Str. qu. yel.	37	52	89
Str. qu. wh.	3	2	5
Light qu. yel. 1)	3	7	10
Light qu. wh.	7	12	19
Totals	204	264	468

f) F_2 ex the cross striped-quail yellow (**SpQY**) × quail white (**spQy**).

	Str. qu. yel.	Str. qu. wh.	Qu. yel.	Qu. wh.	Total
A 100'15	212	16	16	40	284

g) F_2 ex the cross pale-quail white (**spqy**) × striped-quail yellow (**SpQY**).

	Str. qu. yel.	Str. qu. wh.	Pale qu. yel.	Pale qu. wh.	Totals
A 511'15	225	21	15 *	47 *	308
A 512'15	148	14	15 *	50 *	227
Totals	373	35	30	97	535

Grand totals of the results from the cross **SYsy** × **SYsy**.

	Striped yellow (SY)	Striped white (Sy)	Non-striped yellow (sY)	Non-striped white (sy)	Total
Observed	10958	1075	1101	3017	16151
Expect. on the 3 : 1 : 1 : 3 basis	11104	1009	1009	3028	16150
	(11 :	1 :	1 :	3)	
On 5 : 2 : 2 : 5 basis	10959	1154	1154	2884	16151
	(19 :	2 :	2 :	5)	

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1) The appearance of light normal and quail instead of plain and pale-quail will be discussed in later pages.

SYsy ♀ × **sysy** ♂

a) Heterozygous females (**SPQYsPQy**) paired to normal white males (**sPQysPQy**).

	Str. yel. (SPQY)	Norm. wh. (sPQy)	Totals
H 58–1'13	208	215	423
H 58–2'13	208	233	441
H 58–3'13	167	152	319
P 4'14	166	168	334
Totals	749	768	1517

b) Heterozygous females (**SPQYsPQy**) mated to plain white males (**sPqysPqy**).

	Str. yel. (SPQY)	Norm. wh. (sPQy)	Totals
P 1–2'14	142	135	277
P 3'14	164	168	332
P 11'14	188	184	372
P 24–1'14	179	155	334
P 24–2'14	162	197	359
P 26–1'14	195	200	395
P 26–2'14	179	197	376
P 30–1'14	174	176	350
P 30–2'14	224	203	427
P 30–3'14	184	206	390
P 30–4'14	150	162	312
P 30–5'14	153	137	290
Totals	2094	2120	4214

c) Heterozygous females (produced from the cross str. yel. × normal wh.) mated to quail white males, i. e. **SPQYsPQy** ♀♀ × **spQyspQy** ♂♂.

	Str. yel. (SPQY)	Norm. wh. (sPQy)	Totals
P 5'14	59	86	145
P 19–1'14	170	159	329

P 19–2′14	144	136	280
P 25–1′14	166	164	330
P 25–2′14	212	216	428
Ex 2–8′14	154	132	286
Totals	905	893	1798

d) Quadruply heterozygous striped yellow (**SPQYspqy**) ♀♀ × pale-quail white (**spqyspqy**) ♂♂.

		A 536′15	A 537′15	Totals
Striped yellow	SPQY	58	80	138
Striped-quail yellow	SpQY	74	85	159
Plain white	sPqy	65	84 *	149
Pale-quail white	spqy	95 *	78 *	173
Totals		292	327	619

e) A triheterozygous striped yellow (**SPQYgspQyg**) ♀ × plain green (**sPqyGsPqyG**) ♂.

	Striped yellow (SPQYG)	Normal green (sPQyG)	Total
P 14′14	161	155	316

f) Triply heterozygous striped-quail yellow (**SpQYspqy**) ♀♀ × pale-quail white (**spqyspqy**) ♂♂.

	Str. qu. yel. (SpQY)	Pale qu. wh. (spqy)	Totals
A 515′15	209	220 *	429
A 516′15	225	207 *	432
Totals	434	427	861

g) Diheterozygous striped-quail yellow (**SpQYspQy**) ♀♀ × pale-quail white (**spqyspqy**) ♂♂.

	Str. qu. yel. (SpQY)	Quail wh. (spQy)	Totals
A 107′15	166	180	346
A 113′15	137	109	246
Totals	303	289	592

h) A diheterozygous striped-quail yellow (**SpQYspQy**) ♀ × plain white (**sPqysPqy**) ♂.

	Str. yel. (SPQY)	Norm. wh. (sPQy)	Total
A 116′15	171	174	345

Grand totals of the results from the cross **SYsy** ♀ × **sysy** ♂:

	SY	sy	Totals
Observed	5114	5148	10262
Expected	5131	5131	10262

Crossing of **SYsy** females with **sysy** males has resulted in the production of only two of the possible forms, viz. double dominant (**SY**) and double recessive (**sy**,) so that complete coupling must be assumed to occur in oogenesis. Let us now pass over to the examination of male gametic series.

sysy ♀ × **SYsy** ♂

a) Plain white females mated to heterozygous males (ex str. yel. × norm. wh.), i. e. **sPqysPqy** ♀♀ × **SPQYsPQy** ♂♂.

	Str. yel. (SPQY)	Str. wh. (SPQy)	Norm. yel. (sPQY)	Norm. wh. (sPQy)	Totals
H 45–2′13	88	45	55	97	285
S 8′13	113	39	33	148	333
S 9′13	94	35	39	94	262
D 6–1′14	35	19	23	49	126
D 11′14	46	29	22	77	174
P 2–1′14	159	37	53	152	401
P 2–2′14	150	58	47	173	428
P 16–1′14	95	36	61	119	311
P 22′14	139	61	64	106	370
P 27–1′14	173	65	62	169	469
P 27–2′14	126	54	54	138	372
P 28–1′14	73	35	20	79	207
P 28–2′14	129	69	46	148	392

P 28–3′14	167	74	62	152	455
P 31′14	117	71	71	128	377
A 184′15	119	40	48	100	307
Totals	1823	757	760	1929	5269

b) Quail white females mated to heterozygous males, i. e.

spQyspQy ♀♀ × **SPQYsPQy** ♂♂.

	Str. yel. (SPQY)	Str. wh. (SPQy)	Norm. yel. (sPQY)	Norm. wh. (sPQy)	Totals
S 1′13	171	67	67	190	495
S 2′13	186	92	101	198	577
S 3′13	204	61	80	181	526
S 11′13	143	73	78	135	429
P 7′14	228	69	31	188	516
P 15′14	190	79	76	168	513
P 21′14	155	81	96	147	479
P 35–1′14	129	45	55	118	347
P 35–2′14	153	46	49	170	418
Totals	1559	613	633	1495	4300

c) A pale-quail white (**spqyspqy**) ♀ × a triheterozygous striped yellow (**SPQYsPqy**) ♂.

	Str. yel. (SPQY)	Str. wh. (SPQy)	Pl. yel. (sPqY)	Pl. wh. (sPqy)	Total
A 279′15	108	27	41	126	302

d) Pale-quail white (**spqyspqy**) ♀♀ × tetraheterozygous striped yellow (**SPQYspqy**) ♂♂.

		A 534′15	A 535′15	Totals
Str. yel.	SPQY	49	45	94
Str. wh.	SPQy	18	13	31
Pl. yel.	sPqY	16 *	16	32
Pl. wh.	sPqy	47 *	48	95
Str. qu. yel.	SpQY	46	53	99

Str. qu. wh.	SpQy	8	10	18
Pal. qu. yel.	spqY	13 *	9	22
Pal. qu. wh.	spqy	51 *	38	89
Totals		248	232	480

e) Pale-quail white (**spqyspqy**) ♀♀ × triheterozygons striped-quail yellow (**SpQYspqy**) ♂♂.

		A 513′15	A 514′15	Totals
Str. qu. yel.	SpQY	93	42	135
Str. qu. wh.	SpQy	32	5	37
Pal. qu. yel.	spqY	32 *	15	47
Pal. qu. wh.	spqy	85 *	25	110
Totals		242	87	329

f) A pale-quail white (**spqyspqy**) ♀ × a diheterozygous striped-quail yellow (**SpQYspQy**) ♂.

	Str. qu. yel. (SpQY)	Str. qu. wh. (SpQy)	Quail yel. (spQY)	Quail wh. (spQy)	Total
A 105′15	124	31	51	95	301

g) Quail white (**spQyspQy**) ♀♀ × diheterozygous striped-quail yellow (**SpQYspQy**) ♂♂.

	Str. qu. yel. (SpQY)	Str. qu. wh. (SpQy)	Quail yel. (spQY)	Quail wh. (spQy)	Totals
A 114′15	176	35	45	186	442
A 115′15	138	46	44	136	364
A 122′15	165	36	60	157	418
Totals	479	117	149	479	1224

Grand totals of the results from the cross **sysy** ♀ × **SYsy** ♂:

	SY	Sy	sY	sy	Total
Observed	4421	1631	1735	4418	12205
Expect. on 3 : 1 : 1 : 3,	4576.9	1525.6	1525.6	4576.9	12205.0
on 5 : 2 : 2 : 5	4359	1743	1743	4359	12204

Heterozygous males used in above crossings were taken from various lots of the F_1, F_2 or F_3 generation derived from the cross striped yellow × normal or plain or quail or pale-quail white, and all the families mentioned showed more or less approximation to a definite ratio of phenotypes. It is therefore obvious that in heterozygous striped yellow males a partial coupling denoted by the formula 3 : 1 : 1 : 3 or the like takes place between striped and yellow factors.

4) Discussion.

In the cases of coupling and repulsion described in the foregoing pages, there is little doubt that two ancestral forms only occur in equal numbers in F_1 oogenesis, no "cross-over" being produced. On the other hand, F_1 male gametic series shows, when each family is taken separately, a good deal of variability. When, however, a number of families are mingled together the ratios seem to converge to the formula $n : 1 : 1 : n$ for coupling and $1 : n : n : 1$ for repulsion, where n represents a number ranging from 2.5 to 3.0. A similar variability of association intensity is also met with in *Drosophila*, in even higher degree, as can be seen in the paper of BRIDGES and STURTEVANT (1914). In the test of F_1 females from the cross black × curved, they reared 14 families, in which the percentage of cross-overs varied from 15.2 to 31.6 (*l. c.* p. 209) according to families. 15.2% of cross-overs corresponds to 1 : 5.6 : 5.6 : 1, and 31.6% corresponds to 1 : 2.2 : 2.2 : 1, on the assumption that the gametes are symmetrically distributed. A similar phenomenon occurred in experiments of GREGORY on *Primula* (1911 a, especially see pp. 127–129) and in those of PUNNETT on the sweet-pea (1913, especially see p. 86, Tables II and IX.)

From the literature on gametic reduplication we learn that the association was proved to be of the same intensity in both sexes of certain plants; the method of proof adopted being the crossing of the hybrids with double recessives. PUNNETT (1913) proved, for instance, such an association in the coupling (7 : 1 system) of blue factor and long pollen in the sweet-pea, while EMERSON (1911) made out a similar case in the colour correlation (complete coupling) of the maize. On the other hand, there are some authors who merely assumes the similarity of male and female gametic series without actually bringing them to the test mentioned above.

A few previous investigators maintain, however, dissimilar gametic distribution, in the male and female, of the factors that are not sex-limited in several species of plants and one of animals.

DE VRIES (1911, 1913) discovered *Oenothera* hybrids which were produced by reciprocal crossings and markedly different from each other, being apparently patroclinous or matroclinous; he says:

> "Hier werden von den sichtbaren Eigenschaften einige nur mittels des Pollens und nicht durch die Eizellen auf die Kinder vererbt. Demgegenüber gibt es andere Merkmale welche nur in den Eizellen, und nicht im Pollen übertragen werden. Oder allgemein: Im Pollen und in den Eizellen werden verschiedene erbliche Eigenschaften auf die Nachkommen übermittelt."

"Heterogamy" as this phenomenon is called by DE VRIES, or "allogamy" by SWINGLE (1911), was most striking, among various cases, in the crossing between *O. biennis* and *O. muricata*.

Allogamy in *Oenothera* is regarded by GOLDSCHMIDT (1913a) from the cytological point of view as due to merogony, but RENNER (1913) rejects this view.

GREGORY (1911 a) obtained the ratio 411 (magenta, green stigma) : 98 (magenta, red stigma) : 97 (red, green stigma) : 78 (red, red stigma) in *Primula*, and remarks as follows:

> "For the time being it may be pointed out that a very close approximation to the observed numbers is given by the assumption that a coupling of the form 7:1:1:7 is present in gametes of one sex only, gametes of the opposite sex being produced in equal numbers of all four kinds."

GREGORY'S view is criticized by TROW (1912), who maintains that the ratio obtained may be expected on the basis of 2 : 1 : 1 : 2 coupling occurring in the male and female alike.

SAUNDERS (1910, 1911) concludes from her elaborate researches on the doubling character in the flower of *Petunia* and *Matthiola* that there is a sexual dimorphism of gametes occurring in a way that she describes as follows:

> "...........although both in the single Stock which constantly throws doubles, and in the single *Petunia* which yield doubles when fertilized by a double, the pollen is homogeneous [ovules heterogeneous] in respect of some factor needed to produce singleness, the homogeneity is brought about by the absence of this factor in the Stock, by its presence in *Petunia*." (1910, p. 63.)

Thus in the Stock the female gametic series was assumed as n–1 XY : 1 Xy : 1 xY : n–1 xy, and the male gametic series as xy, where X and Y stand for the factors necessary for the manifestation of singleness.

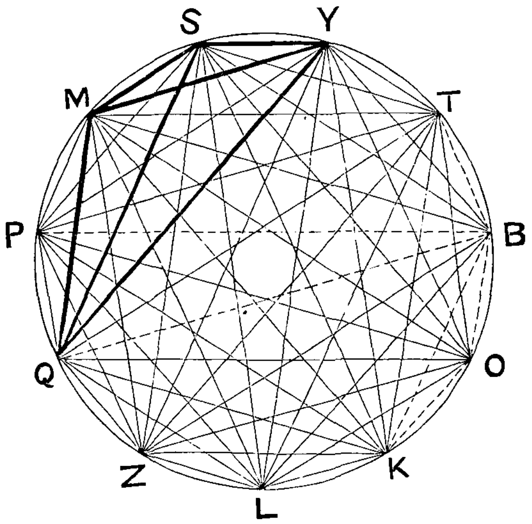
GOLDSCHMIDT (1913b) discussed this case and endeavoured to analyse it as an example of sex-limited inheritance, but SAUNDERS (1913) contends for her own position. In fact the total sterility of one (*Petunia*, female) or both sexes (*Matthiola*) of recessive (double-flowering) plants renders a direct test of gametic distribution difficult.

MORGAN and his collaborators found in *Drosophila* a number of cases in which male and female gametic series were decidedly different, that is the linkage is partial in the female and complete in the male. This case is, therefore, the only instance known so far, which shows a close resemblance to the present case in *Bombyx*. In both the fruit-fly and the silkworm, the gametic series were tested not only by inbreeding, but also by reciprocally crossing the diheterozygotes with double-recessive individuals; the results were in accordance in many respects in both cases. A notable contrast is however presented by these two species of the Insect, in that complete association took place in the male in the fly but in the female in the silkworm, while partial association occurred in the female of *Drosophila* and in the male of *Bombyx*.

The said difference strongly reminds us of two kinds of sex-limited inheritance (STURTEVANT, 1915 b). Sex-limited inheritance is explicable on the assumption that the female sex is the bearer of the linked character in some cases, and the male in others. Such a parallelism between sex-linked inheritance and linkage of non-sex-linked characters appears much interesting as well as suggestive.

V. NON-CORRELATED CHARACTERS.

The Mendelian factors concerned in the present experiments are eleven in all, i. e. **S, M, P, Q, Z, L, K, O, B, T** and **Y.**[1] Of these 11 factors the following 55 combinations are possible:



Text-fig. 5.

Of the combinations shown in the left, those connected by dotted lines have not been tested yet, while those factors connected by thick lines are correlated either positively or negatively in inheritance, and were described in the preceding pages. All other combinations show those which are transmitted independently of each other.

It may be interesting that there are so many independent characters in the silkworm which has chromosomes as numerous as 28 in haploid (YATSU, 1913), while in *Drosophila*, in which only 4 chromosomes are present in haploid condition (STEVENS, 1908), all the tested characters fall into 4 groups of linkage.

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1) Besides these, multiple factors are assumed for the normal and quail patterns, moulting character, etc. (See Chapter VI.)

Moulting Character. 1) (Three-moulting, **T**, *versus* four-moulting, **t.**)

There are a host of data which speak for the independent inheritance of moulting character; a few typical cases are given below.

a) **T** and **Y**, **T** and **P.**

Heterozygous 3-moulting plain yellows (**PpqqTtYy**) mated *inter se.*

		A 785'15			A 786'15		
		3-m. (T)	4-m. (t)	Totals	3-m. (T)	4-m. (t)	Totals
Pl. yel.	PqY	84	27	111	103	42	145
Pl. wh.	Pqy	28	10	38	40	18	58
Pal. qu. yel.	pqY	26	7	33	38	6	44
Pal. qu. wh.	pqy	10	6	16	15	2	17
Totals		148	50	198	196	68	264

	YT	**Yt**	**yT**	**yt**
Of which	251	82	93	36
Expected ratio	9 :	3 :	3 :	1
	PT	**Pt**	**pT**	**pt**
	255	97	89	21

A heterozygous 3-moulting plain yellow (**PpqqTtYy**) ♀ × a 4-moulting normal white (**PPQQttyy**) ♂.

			T	t	Totals
A 789'15	Norm. yel.	PQY	110	108	218
	Norm. wh.	PQy	112	104	216
	Totals		222	212	434

Reciprocal to the above cross:

			T	t	Totals
A 790'15	Norm. yel.	PQY	64	83	147
	Norm. wh.	PQy	92	93	185
	Totals		156	176	332
	Ratio		1 :	1	

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1) The moulting character is, on one hand, seriously affected by external circumstances, and, on the other hand, there is some indication that more than one allelomorphs are concerned in the character. Both causes act to bring about divergent zygotic ratios which are often met with in inheritance of this character. But in the present section, I shall deal with only those cases in which simple Mendelian ratio was realised. (*cf.* Chapter **VI.**)

b) **T** and **S.**

Heterozygous 3-moulting striped white (**SsPpQqTtyy**) mated *inter se*.

A 524′15		3-m.	4-m.	Totals
Striped	SPQy	91	31	122
Striped-quail	SpQy	52	12	64
Plain	sPqy	35	11	46
Pale-quail	spqy	14	4	18
Totals		192	58	250

Of which **ST** 143 : **St** 43 : **sT** 49 : **st** 15

Exp. ratio 9 : 3 : 3 : 1

A 4-moulting pale-quail white (**ssppqqttyy**) ♀ × a heterozygous 3-moulting striped white (**SsPpQqTtyy**) ♂.

A 523′15		T	t	Totals
Striped	SPQy	27	25	52
Striped-quail	SpQy	29	37	66
Plain	sPqy	27	23	50
Pale-quail	spqy	37	34	71
Totals		120	119	239

Of which **ST** 56 : **St** 62 : **sT** 64 : **st** 57

Exp. ratio 1 : 1 : 1 : 1

c) **T** and **M.**

A heterozygous 3-moulting plain white (**mmTtyy**) ♀ × a heterozygous 3-moulting moricaud yellow (**MmTtYy**) ♂.

A 491′15		T	t	Totals
Mor. yel.	MY	22	7	29
Mor. wh.	My	109	34	143
Pl. yel.	mY	123	31	154
Pl. wh.	my	28	6	34
Totals		282	78	360

Of which **MT** 131 : **Mt** 41 : **mT** 151 : **mt** 37

Exp. ratio 3 : 1 : 3 : 1

d) **T** and **Q.**

Heterozygous 3-moulting moricaud yellow (**MmPpQqTtYy**) mated *inter se.*

A 775′15		T	t	Totals
Mor. yel.	MPQY	151	39	190
Mor. wh.	MPQy	5	6	11
Pl. yel.	mPqY	12	7	19
Pl. wh.	mPqy	43	16	59
Mor. qu. yel.	MpQY	50	20	70
Mor. qu. wh.	MpQy	5	1	6
Pal. qu. yel.	mpqY	8	0	8
Pal. qu. wh.	mpqy	24	5	29
Totals		298	94	392

Of which **QT** 211 : **Qt** 66 : **qT** 87 : **qt** 28

Exp. ratio 9 : 3 : 3 : 1

e) **T** and **Z.**

A heterozygous 3-moulting moricaud-zebra yellow (**MmPPQQZzYyTt**) ♀ × a heterozygous 3-moulting quail white (**mmppQQzzyyTt**) ♂.

A 615′15		3-m. (T)	4-m. (t)	Totals
Mor. zeb. yel.	MPQZY	68	20	88
Mor. yel	MPQzY	67	26	93
Zebr. wh.	mPQZy	67	26	93
Norm. wh.	mPQzy	55	23	78
Totals		257	95	352

Of which **ZT** 135 : **Zt** 46 : **zT** 122 : **zt** 49

Exp. ratio 3 : 1 : 3 : 1

(f **T** and **L.**

A heterozygous 3-moulting multilunar yellow (**LlYyTt**) ♀ × a heterozygous 3-moulting multilunar white (**LlyyTt**) ♂.

A 745′15		3-m. (T)	4-m. (t)	Totals
Multil. yel.	LY	88	39	127

Multil. wh.	Ly	95	31	126
Norm. yel.	lY	24	10	34
Norm. wh.	ly	28	12	40
Totals		235	92	327

Of which **LT** 183 : **Lt** 70 : **lT** 52 : **lt** 22

Exp. ratio 9 : 3 : 3 : 1

g) **T** and **K.**

Heterozygous 3-moulting knobbed zebra whites (**ZzKkyyTt**) mated *inter se.*

A 763′15		3-m. (T)	4-m. (t)	Totals
Knobbed zebra	ZKy	135	51	186
Smooth zebra	Zky	56	17	73
Knobbed normal	zKy	45	17	62
Smooth normal	zky	15	6	21
Totals		251	91	342

Of which **KT** 180 : **Kt** 68 : **kT** 71 : **kt** 23

Exp. ratio 9 : 3 : 3 : 1

h) **T** and **O.**

Heterozygous 3-moulting opaque normal (**PPQqOoTt**) paired *inter se.*

A 67′15		3-m. (T)	4-m. (t)	Totals
Normal opaque	PQO	162	49	211
Normal oily	PQo	46	21	67
Plain opaque	PqO	44	13	57
Plain oily	Pqo	11	7	18
Totals		263	90	353

Of which **OT** 206 : **Ot** 62 : **oT** 57 : **ot** 28

Exp. ratio 9 : 2 : 3 : 1

i) **T** and **B.**

Not yet fully elucidated.

Melanism.[1] (Melanic, **B**, *v.* chocolate, **b.**)

In the presence of **B**, the pigment colour of the patterns is melanic, as is the case with ordinary strains, while in its absence the markings are chocolate (*cf.* p. 132).

a) Behaviour of **B** towards **O**, **K**, and **Q** has not been tested yet.

b) **B** and **P**, **B** and **Y**.

Heterozygous 3-moulting melanic normal yellows (**PpQQBbTtYy**) mated *inter se*.

A 735′15		3-m. (T)	4-m. (t)	Totals
Mel. norm. yel.	PQBY	21	49	70
Mel. norm. wh.	PQBy	6	14	20
Mel. qu. yel.	pQBY	7	13	20
Mel. qu. wh.	pQBy	6	9	15
Choc. norm. yel.	PQbY	4	6	10
Choc. norm. wh.	PQby	1	2	3
Choc. qu. yel.	pQbY	3	3	6
Choc. qu. wh.	pQby	1	1	2
Totals		49	97	146

Of which **PB** 90 : **Pb** 13 : **pB** 35 : **pb** 8

BY 90 : **By** 35 : **bY** 16 : **by** 5

Exp. ratio 9 : 3 : 3 : 1

c) **B** and **L.**

Heterozygous melanic striped-multilunar yellows (**SsPPQqLlBbYy**) mated *inter se.*

A 759′15		Melanic (B)	Chocol. (b)	Totals
Str. multil. yel.	SPQLY	16	10	26
Str. multil. wh.	SPQLy	2	1	3
Multil. yel.	sPqLY	5	1	6
Multil. wh.	sPqLy	6	1	7

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[1] That the chocolate character mendelizes as a simple recessive to the melanic was first made out by TOYAMA (1909).

Str. yel.	SPQlY	4	2	6
Str. wh.	SPQly	2	0	2
Pl. yel.	sPqlY	2	0	2
Pl. wh.	sPqly	2	0	2
Totals		39	15	54

Of which **LB** 29 : **Lb** 13 : **lB** 10 : **lb** 2

Exp. ratio 9 : 3 : 3 : 1

d) **B** and **Z.**

Heterozygous melanic normal zebras (**PPQQZzBbyy**) mated *inter se.*

		A 736'15	Exp. ratio
Mel. norm. zebr.	PQZB	43	9
Choc. norm. zebr.	PQZb	8	3
Mel. norm.	PQzB	16	3
Choc. norm.	PQzb	3	1
Total		70	

e) **B** and **S.**

Heterozygous melanic striped yellows (**SsPPQQBbYy**) mated *inter se.*

		O 23–1'14	O 35–1'14	P 29'14	Totals
Mel. str. yel.	SPQBY	116	96	164	376
Mel. str. wh.	SPQBy	14	22	10	46
Mel. norm. yel.	sPQBY	8	15	9	32
Mel. norm. wh.	sPQBy	34	22	74	130
Choc. str. yel.	SPQbY	37	36	39	112
Choc. str. wh.	SPQby	2	2	5	9
Choc. norm. yel.	sPQbY	5	4	5	14
Choc. norm. wh.	sPQby	9	10	14	33
Totals		225	207	320	752

Of which **SB** 422 : **Sb** 121 : **sB** 162 : **sb** 47

Exp. ratio 9 : 3 : 3 : 1

f) **B** and **M.**

Heterozygous melanic moricaud yellows (**MmPPQQBbYy**) mated *inter se.*

C 34–3'14		Mel. (B)	Choc. (b)	Totals
Mor. yel.	MPQY	63	19	82
Mor. wh.	MPQy	39	12	51
Norm. yel.	mPQY	39	16	55
Totals		141	47	188

Of which **MB** 102 : **Mb** 31 : **mB** 39 : **mb** 16

Exp. ratio 9 : 3 : 3 : 1

Opacity. (Opaque, **O**, *v.* transparent, **o**.)

In ordinary silkworm larvae the skin is, as a whole, powdery white owing to the presence of guanin-like granules in the epidermal cells. Only on the ventral side, especially the internal side of abdominal legs, on the mid-dorsal line over the heart, the cells contain less granules, so that the skin looks more or less transparent. There is, however, a strain known as "oily" or transparent-skinned, in which the white granules are very scanty or entirely absent from the epidermis, so that the whole skin is so transparent as to make the internal organs and tissues visible from outside with the exception of the patterned portions and the opaque hard parts (the head-case etc.). The "oily" character is always apparent after the first moult.

a) Heterozygous knobbed zebra opaque yellows (**ZzKkOoyY**) mated *inter se.*

		A 764'15		A 765'15	
		Opaque (**O**)	Oily (**o**)	Opaque (**O**)	Oily (**o**)
Knob. zebr. yel.	ZKY	96	31	69	24
Knob. zebr. wh.	ZKy	33	10	30	4
Zebr. yel.	ZkY	32	9	12	5
Zebr. wh.	Zky	12	10	4	1
Knob. pl. yel.	zKY	30 *	9 *	24 *	6 *
Knob. pl. wh.	zKy	14 *	0	8 *	3 *
Pl. yel.	zkY	6 *	0	6 *	2 *
Pl. wh.	zky	5 *	0	0	0

Totals		228	69	153	45
Of which	**OK** 304 :	**Ok** 77 :	**oK** 87 :	**ok** 27	
Exp. ratio	9 :	3 :	3 :	1	

b) **O** and **S**, **O** and **Y.**

Heterozygous striped opaque yellows (**SsPPQqOoYy**) mated *inter se.*

		A 69'15	A 70'15	A 71'15	Totals
Str. opaq. yel	SPQOY	164	178	236	578
Str. oil. yel.	SPQoY	39	50	62	151
Str. opaq. wh.	SPQOy	12	18	31	61
Str. oil. wh.	SPQoy	1	2	11	14
Pl. opaq. yel.	sPqOY	13	15	22	50
Pl. oil. yel.	sPqoY	6	2	15	23
Pl. opaq. wh.	sPqOy	44	55	57	156
Pl. oil. wh.	sPqoy	6	16	25	47
Totals		285	336	459	1080
Of which	**SO** 639 :	**So** 165 :	**sO** 206 :	**so** 70	
	OY 628 :	**Oy** 217 :	**oY** 174 :	**oy** 61	
Exp. ratio	9 :	3 :	3 :	1	

c) **O** and **P**, **O** and **Q.**

Heterozygous normal opaque yellwos (**PpQqOoYy**) mated *inter se.*

A 768'15		Yel. (Y)	Wh. (y)	Totals
Norm. opaq.	PQO	79	21	100
Qu. opaq.	pQO	21	6	27
Pl. opaq.	PqO	23	9	32
Pal. qu. opaq.	pqO	9	2	11
Norm. oil.	PQo	17	6	23
Qu. oil.	pQo	6	4	10
Pl. oil	Pqo	8	4	12
Pal. qu. oil.	pqo	2	0	2
Totals		165	52	217

Of which **PO** 132 : **Po** 35 : **pO** 38 : **po** 12

QO 127 : **Qo** 33 : **qO** 43 : **qo** 14

Exp. ratio 9 : 3 : 3 : 1

d) **O** and **M**, **O** and **L**.

Heterozygous multilunar-moricaud opaque yellows (**MmPPQqLlOoYy**) mated *inter se*.

A 769'15		Opaque (**O**)	Oily (**o**)	Totals
Multil. mor. yel.	MPQLY	32	13	45
Multil. mor. wh.	MPQLy	2	0	2
Mor. yel.	MPQlY	15	5	20
Mor. wh.	MPQly	1	0	1
Multil. norm. yel.	mPQLY	1	1	2
Multil. norm. wh.	mPQLy	7	2	9
Norm. yel.	mPQlY	2	4	6
Norm. wh.	mPQly	1	0	1
Totals		61	25	86

Of which **MO** 50 : **Mo** 18 : **mO** 11 : **mo** 7

LO 42 : **Lo** 16 : **lO** 19 : **lo** 9

Exp. ratio 9 : 3 : 3 : 1

e) **O** and **Z**.

Heterozygous plain-zebra opaque yellows (**PPqqZzOoYy**) mated *inter se*.

A 767'15		Opaque (**O**)	Oily (**o**)	Totals
Pl. zebr. yel.	PqZY	62	20	82
Pl. zebr. wh.	PqZy	23	5	28
Pl. yel.	PqzY	20	9	29
Pl. wh.	Pqzy	5	5	10
Totals		110	39	149

Of which **ZO** 85 : **Zo** 25 : **zO** 25 : **zo** 14

Exp. ratio 9 : 3 : 3 : 1

Knobbedness. (Knobbed, **K**, *v.* smooth, **k.**)

The presence of knobs is a striking characteristic of the Chinese race *Lung-chiao tsan,* which means "Dragon-horned silkworm". No prominent peculiarity is seen in the larvae until they have passed through the third moult, when the knobs come forth for the first time, and their full development is attained only in the last stage of larval life. The knobs are large, paired evaginations of the skin formed on the subdorsal lines of at least four segments, II, III, V, VIII; sometimes they are present in all the segments from II to XI. The remnants of certain knobs are still visible in the pupal and imaginal stages.

a) **K** and **Z.**

Heterozygous knobbed normal-zebras (**PPQQZzKkyy**) mated *inter se.*

		A 763′15	Exp. ratio
Knob. norm. zebr.	PQZK	186	9
Smooth norm. zebr.	PQZk	73	3
Knob. norm.	PQzK	62	3
Smooth norm.	PQzk	21	1
Total		342	

b) **K** and **S.**

Heterozygous striped knobbed (**SsPPQQKk**) mated *inter se.*

		A 762′15	Exp. ratio
Str. knob.	SPQK	106	9
Str. smooth	SPQk	44	3
Norm. knob.	sPQK	39	3
Norm. smooth	sPQk	5	1
Total		194	

c) **K** and **P**, **K** and **Q.**

Heterozygous normal knobbed whites (**PpQqKkyy**) mated *inter se.*

A 760′15		Knobbed (K)	Smooth (k)	Totals
Normal	PQ	74	19	93

Plain	Pq	35	6	41
Quail	pQ	18	5	23
Pale-quail	pq	14	4	18
Totals		141	34	175

Of which **PK** 109 : **Pk** 25 : **pK** 32 : **pk** 9

QK 92 : **Qk** 24 : **qK** 49 : **qk** 10

Exp. ratio 9 : 3 : 3 : 1

d) **K** and **M**, **K** and **L**, **K** and **Y**.

Heterozygous multilunar-moricaud knobbed yellows

(**MmPpQQLlKkYy**) mated *inter se*.

A 761'15		Yellow (Y)	White (y)	Totals
Knob. multil. mor.	MPQLK	56	13	69
Multil. mor.	MPQLk	37	7	44
Knob. mor.	MPQlK	23	1	24
Mor.	MPQlk	10	0	10
Knob. multil. mor. qu.	MpQLK	22	0	22
Multil. mor. qu.	MpQLk	10	0	10
Knob. mor. qu.	MpQlK	11	1	12
Mor. qu.	MpQlk	5	1	6
Knob. multil. norm.	mPQLK	4	11	15
Multil norm.	mPQLk	3	21	24
Knob. norm.	mPQlK	2	6	8
Norm.	mPQlk	0	1	1
Knob. multil. qu.	mpQLK	1	8	9
Multil. qu.	mpQLk	3	4	7
Knob. qu.	mpQlK	0	0	0
Qu.	mpQlk	0	0	0
Totals		187	74	261

Of which **LK** 115 : **Lk** 85 : **lK** 44 : **lk** 17

KY 119 : **Ky** 40 : **kY** 68 : **ky** 34

MK 127 : **Mk** 70 : **mK** 32 : **mk** 32

Exp. ratio 9 : 3 : 3 : 1

As the observed numbers are somewhat remote from the expected, some other examples are given below.

Heterozygous knobbed multilunar-normal (**PpQqLlKkyy**) mated *inter se.*

A 747'15		Knobbed (K)	Smooth (k)	Totals
Multil. norm	PQL	69	30	99
Norm.	PQl	35	12	47
Multil. pl.	PqL	0	9	9
Pl.	Pql	28	3	31
Multil. qu.	pQL	40	13	53
Qu.	pQl	0	2	2
Multil. pal. qu.	pqL	13	4	17
Pal. qu.	pql	0	0	0
Totals		185	73	258

Of which **LK** 122 : **Lk** 56 : **lK** 63 : **lk** 17

Exp. ratio 9 : 3 : 3 : 1

A heterozygous knobbed multilunar-zebra yellow (**PPQQZzLlKkYy**) ♀ × her white brother (**PPQQZzLlKkyy**) ♂.

A 754'15		Yel. (Y)	Wh. (y)	Totals
Knob. multil. zebr.	PQZLK	44	42	86
Multil. zebr.	PQZLk	30	22	52
Knob. zebr.	PQZlK	14	17	31
Zebr.	PQZlk	3	4	7
Knob. multil.	PQzLK	15	18	33
Multil.	PQzLk	7	2	9
Knob. norm.	PQzlK	4	8	12
Norm.	PQzlk	0	1	1
Totals		117	114	231

Of which **LK** 119 : **Lk** 61 : **lK** 43 : **lk** 8

KY 77 : **Ky** 85 : **kY** 40 : **ky** 29

Exp. ratio 3 : 3 : 1 : 1

Summary of the above three families :

LK[1] 356 : **Lk** 202 : **lK** 150 : **lk** 42

which agrees roughly with the normal ratio 9 : 3 : 3 : 1.

Multilunar Pattern (L).

By "multilunar" I mean the type of marking which is composed of at least four pairs of large, yellowish spots of round shape occurring on the dorsal side of the larva. It is interesting that the lunar spots correspond in position and number to those of the knobs in the multilunar knobbed strain.

a) **L** and **Z.**

As to the hereditary behaviour there is, as already stated, a great resemblance between the multilunar and zebra, but these two characters are transmitted quite independently of each other.

Heterozygous multilunar-zebra whites (**PPQqZzLlyy**) mated *inter se*.

A 748'15		Multil. (L)	Non-multil. (l)	Totals
Norm. zebr.	PQZ	69	30	99
Norm.	PQz	27	7	34
Pl. zebra.	PqZ	64	13	77
Pl.	Pqz	5	6	11
Totals		165	56	221

Of which **ZL** 133 : **Zl** 43 : **zL** 32 : **zl** 13

Heterozygous multilunar-zebra yellows (**PPQQZzLlYy**) mated *inter se*.

A 751'15		Multil. (L)	Non-multil. (l)	Totals
Norm. zebr. yel.	PQZY	67	30	97
Norm. zebr. wh.	PQZy	23	11	34
Norm. yel.	PQzY	27	8	35
Norm. wh.	PQzy	6	4	10
Totals		123	53	176

Of which **ZL** 90 : **Zl** 41 : **zL** 33 : **zl** 12

A 754'15 (p. 199) 138 : 38 : 42 : 13

Summary of the above three families :

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[1] The deficit of **LK** and excess of **Lk** are perhaps accidental.

	ZL		**Zl**		**zL**		**zl**
	361	:	122	:	107	:	38
Expected ratio	9	:	3	:	3	:	1

A heterozygous multilunar-zebra yellow (**PPQqZzLlYy**) ♀ × a quail yellow (**ppQqzzllYy**) ♂.

A 750′15		Mult. (L)	Non-multil. (l)	Totals
Norm. zebr. yel.	PQZY	50	43	93
Norm. zebr. wh.	PQZy	15	14	29
Norm. yel.	PQzY	68	56	124
Norm. wh.	PQzy	13	16	29
Pl. zebr. yel.	PqZY	30	27	67
Pl. zebr. wh.	PqZy	12	10	22
Pl. yel.	PqzY	40	10	40
Pl. wh.	Pqzy	5	14	19
Totals		233	190	423

	ZL		**Zl**		**zL**		**zl**
Of which	117	:	116	:	94	:	96
Exp. ratio	1	:	1	:	1	:	1

b) **L** and **Q.**

	QL	**Ql**	**qL**	**ql**	Totals
A 747′15 (p. 199)	152	49	26[1]	31[1]	258
A 748′15 (p. 200)	96	37	69	19	221
Totals	248	86	95	50	479
Expected ratio	9 :	3 :	3 :	1	

c) **L** and **P.**

Heterozygous multilunar-plains (**PpqqLlyy**) mated *inter se*.

		A 741′15	Exp. ratio
Multil. pl.	PqL	125	9
Plain	Pql	44	3
Multil. pal. qu.	pqL	32	3

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[1] In **PqL** form the **L** pattern is so light in tone that it is likely to be mistaken for **Pql** by careless eyes (*cf.* p. 145). The deficit of **qL** and the excess of **ql** class are very probably due to this error.

Pal. qu.	pql	15	1
Total	·	216	

d) **L** and **M.**

Heterozygous multilunar-moricaud opaque yellows (**MmLlOoYy**) paired *inter se.*

		A 752′15	A 769′15	Totals
Multil. mor. opaq. yel.	MPQLOY	45	32	77
Multil. mor. opaq. wh.	MPQLOy	6	2	8
Multil. mor. oil. yel.	MPQLoY	15	13	28
Multil. norm. opaq. yel.	mPQLOY	2	1	3
Mor. opaq. yel.	MPQlOY	13	15	28
Multil. mor. oil. wh.	MPQLoy	1	0	1
Multil. norm. oil. yel.	mPQLoY	1	1	2
Norm opaq. yel.	mPQlOY	0	2	2
Multil. norm. opaq. wh.	mPQLOy	8	7	15
Mor. oil. yel.	MPQloY	8	5	13
Mor. opaq. wh.	MPQlOy	2	1	3
Multil. norm. oil. wh.	mPQLoy	1	2	3
Mor. oil. wh.	MPQloy	0	0	0
Norm. opaq. wh.	mPQlOy	4	1	5
Norm. oil. yel.	mPQloY	1	4	5
Norm. oil. wh.	mPQloy	2	0	2
Totals		109	86	195

Of which **ML** 114 : **Ml** 44 : **mL** 23 : **ml** 14

Exp. ratio 9 : 3 : 3 : 1

e) **L** and **S.**

Heterozygous multilunar-striped yellows (**SsPPQqLlYy**) mated *inter se.*

A 759′15		Yel. (Y)	Wh. (y)	Totals	Exp. ratio
Multil. str.	SPQL	26	3	29	9

Striped	SPQl	6	2	8	3
Multil. pl.	sPqL	6	7	13	3
Plain	sPql	2	2	4	1
Totals		40	14	54	

f) **L** and **Y.**

LlYy × LlYy

	LY	Ly	lY	ly	Totals
A 761'15 (p. 198)	136	64	51	10	261
A 751'15 (p. 200)	94	29	38	15	176
Totals	230	93	89	25	437
Exp. ratio	9 :	3 :	3 :	1	

LlYy ♀♀ × llyy ♂♂

	LY	Ly	lY	ly	Totals
A 755'15	9	17	27	15	68
A 756'15	102	97	84	90	373
A 758'15	91	67	66	80	304
Totals	202	181	177	185	745
Exp. ratio	1 :	1 :	1 :	1	

Zebra Pattern (Z).[1]

This is characterized by the segmental, narrow black bands on the dorsum, and the paired black spots on the ventro-lateral sides of the head and each body segment, of which those on segments IV–VI are most prominent.

a) **Z** and **P.**

Heterozygous normal-zebra yellows (**PpQQZzYy**) mated *inter se.*

		A 562'15	A 601'15	A 602'15	Totals	Exp. ratio
Norm. zebr. yel.	PQZY	150	153	144	447	27
Norm. zebr. wh.	PQZy	50	61	34	145	9
Quail zebr. yel.	pQZY	58	51	40	149	9
Norm. yel.	PQzY	21	50	36	107	9

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[1] This pattern has often been designated by TOYAMA as "striped".

Quail zebr. wh.	pQZy	14	17	4	35	3
Norm. wh.	PQzy	6	21	16	43	3
Quail yel.	pQzY	9	11	15	35	3
Quail wh.	pQzy	9	8	4	21	1
Totals		317	372	293	982	

Heterozygous normal-zebra whites (**PpQQZzyy**) inbred.

	Norm. zebr. (PQZ)	Normal (PQz)	Quail zebr. (pQZ)	Quail (pQz)	Totals
A 591′15	201	89	80	25	395
A 592′15	169	79	66	14	328
Totals	370	168	146	39	723
Exp. ratio	9 :	3 :	3 :	1	

b) **Z** and **Q.**

Heterozygous normal-zebra whites (**PpQqZzyy**) inbred.

		A 581′15	Exp. ratio
Norm. zebr.	PQZ	198	27
Pl. zebr.	PqZ	74	9
Qu. zebr.	pQZ	75	9
Normal	PQz	73	9
Pal. qu. zebr.	pqZ	29	3
Plain	Pqz	16	3
Quail	pQz	20	3
Pal. qu.	pqz	9	1
Total		494	

c) **Z** and **M.**

Heterozygous moricaud-zebra yellows (**MmPPQQZzYy**) inbred.

		A 611′15	A 612′15	A 613′15	Totals
Mor. zebr. yel.	MPQZY	121	127	141	389
Mor. zebr. wh.	MPQZy	17	9	7	33
Norm. zebr. yel.	mPQZY	4	13	18	35

Norm. zebr. wh.	mPQZy	29	50	41	120
Mor. yel.	MPQzY	45	53	53	151
Mor. wh.	MPQzy	3	5	6	14
Norm. yel.	mPQzY	7	2	3	12
Norm. wh.	mPQzy	12	10	13	35
Totals		238	269	282	789

Of which **MZ** 422 : **Mz** 165 : **mZ** 155 : **mz** 47

Exp. ratio 9 : 3 : 3 : 1

A heterozygous moricaud-zebra yellow (**MmPPQQZzYy**) ♀ × a quail white (**mmppQqyy**) ♂.

		A 615'15	Exp. ratio
Mor. zebr. yel.	MPQZY	88	1
Mor. yel.	MPQzY	93	1
Norm. zebr. wh.	mPQZy	93	1
Norm. wh.	mPQzy	78	1
Total		352	

A pale-quail white (**mmppqqzzyy**) ♀ × a heterozygous moricaud-zebra yellow (**MmPPQqZzYY**) ♂.

		A 620'15	Exp. ratio
Mor zebr. yel.	MPQZY	90	1
Mor. yel.	MPQzY	108	1
Plain-zebr. yel.	mPqZY	88	1
Plain yel.	mPqzY	94	1
Total		380	

d) **Z** and **S**.

Heterozygous striped-zebra yellows (**SsPPQQZzYy**) inbred.

		A 551'15	A 552'15	A 553'15	Totals
Str. zebr. yel.	SPQZY	162	133	143	438
Str. zebr. wh.	SPQZy	10	17	12	39
Str. yel.	SPQzY	45	38	54	137

Str. wh.	SPQzy	3	10	1	14
Norm. zebr. yel.	sPQZY	19	6	6	31
Norm. zebr. wh.	sPQZy	47	34	50	131
Norm. yel.	sPQzY	6	4	5	15
Norm. wh.	sPQzy	10	13	18	41
Totals		302	255	289	846
Of which	**SZ** 477 :	**Sz** 151 :	**sZ** 162 :	**sz** 56	
Exp. ratio	9 :	3 :	3 :	1	

Heterozygous striped-zebra yellow (**SsPPQQZzYy**) ♀♀ × pale-quail white (**ssppqqzzyy**) ♂♂.

		A 558′15	A 559′15	A 560′15	Totals	Ratio
Str. zebr. yel.	SPQZY	109	100	73	282	1
Str. yel.	SPQzY	117	102	89	308	1
Norm. zebr. wh.	sPQZy	91	89	75	255	1
Norm. wh.	sPQzy	89	111	94	294	1
Totals		406	402	331	1139	

Pale-quail white (**ssppqqzzyy**) ♀♀ × heterozygous striped-zebra yellow (**SsPPQQZzYy**) ♂♂.

		A 556′15	A 557′15	Totals
Str. zebr. yel.	SPQZY	14	42	56
Str. zebr. wh.	SPQZy	3	12	15
Str. yel.	SPQzY	19	39	58
Str. wh.	SPQzy	5	12	17
Norm. zebr. yel.	sPQZY	3	12	15
Norm. zebr. wh.	sPQZy	21	47	68
Norm. yel.	sPQzY	4	12	16
Norm. wh.	sPQzy	18	39	57
Totals		87	215	302
Of which	**SZ** 71 :	**Sz** 75 :	**sZ** 83 :	**sz** 73
Exp. ratio	1 :	1 :	1 :	1

ZzYy × ZzYy

	ZY	Zy	zY	zy	Totals
A 551'15	181	57	51	13	302
A 552'15	139	51	42	23	255
A 553'15	149	62	59	19	289
A 561'15	187	58	69	19	333
A 562'15	208	64	30	15	317
A 601'15	204	78	61	29	372
A 602'15	184	38	51	20	293
A 611'15	125	46	52	15	238
A 612'15	140	59	55	15	269
A 613'15	159	48	56	19	282
Totals	1676	561	526	187	2950
Exp. ratio	9 :	3 :	3 :	1	

ZzYy ♀♀ × zzyy ♂♂

	ZY	Zy	zY	zy	Totals
A 555'15	89	85	88	87	349
A 558'15	109	91	117	89	406
A 559'15	100	89	102	111	402
A 560'14	73	75	89	94	331
A 603'15	120	108	77	108	413
A 615'15	88	93	93	78	352
Totals	579	541	566	567	2253
Exp. ratio	1 :	1 :	1 :	1	

zzyy ♀♀ × ZzYy ♂♂

	ZY	Zy	zY	zy	Totals
A 554'15	95	91	87	91	364
A 556'15	17	24	23	23	87
A 557'15	54	59	51	51	215
A 616'15	49	80	68	78	275
A 617'15	71	60	53	59	243

A 618′15	91	98	82	69	340
A 619′15	97	98	104	110	409
Totals	474	510	468	481	1933
Exp. ratio	1 :	1 :	1 :	1	

The results above given evidently prove the independent transmission of **Z** and **Y** factors. This conclusion is in exact conformity with the results obtained by Coutagne (1903, p p. 129– 130) and by Toyama (1906 a).

Plain-coated (P).

a) **P** and **Q.**

PpQq × PpQq

	PQ	Pq	pQ	pq	Totals
A 452′15	152	49	59	15	275
A 453′15	183	59	44	20	306
A 454′15	168	60	68	18	314
A 456′15	168	48	46	17	279
Totals	671	216	217	70	1174
Exp. ratio	9 :	3 :	3 :	1	

PpQq ♀♀ × ppqq ♂♂

	PQ	Pq	pQ	pq	Totals
A 459′15	95	82	73	75	325
A 460′15	85	86	99	85	355
Totals	180	168	172	160	680
Exp. ratio	1 :	1 :	1 :	1	

b) **P** and **S.**

SsPp × SsPp

	SP	Sp	sP	sp	Totals
A 63′15	58	24	22	9	113
A 64′15	49	19	17	11	96
A 65′15	72	56	17	10	155
Totals	179	99	56	30	364
Exp. ratio	9 :	3 :	3 :	1	

SsPp ♀♀ × **sspp** ♂♂

	SP	Sp	sP	sp	Totals
A 536′15	58	74	65	95	292
A 537′15	80	85	78	84	327
Totals	138	159	143	179	619
Exp. ratio	1 :	1 :	1 :	1	

c) **P** and **M**.

MmPp × **MmPp**

	MP	Mp	mP	mp	Totals
A 476′15	296	68	53	21	438
A 477′15	195	67	55	22	339
A 480–1′15	208	75	65	32	380
A 480–2′15	191	76	82	31	380
Totals	890	286	255	106	1537
Exp. ratio	9 :	3 :	3 :	1	

MmPp ♀♀ × **mmpp** ♂♂

	MP	Mp	mP	mp	Totals
A 472–1′15	89	66	81	78	314
A 472–2′15	73	81	72	66	292
A 475′15	76	66	67	63	272
A 479′15	115	116	101	109	441
Totals	353	329	321	316	1319
Exp. ratio	1 :	1 :	1 :	1	

d **P** and **Y**.

Heterozygous normal yellows (**PpQQYy**) inbred.

	Norm. yel. (PQY)	Norm. wh. (PQy)	Qu. yel. (pQY)	Qu. wh. (pQy)	Totals
C 7′14	52	16	19	8	95
C 36–1′14	77	29	28	3	137
C 39–1′14	139	35	40	15	229
C 39–2′14	87	22	24	3	136
C 39–3′14	93	44	44	16	197

C 40–1′14	54	24	19	6	103
C 40–2′14	62	16	18	10	106
A 451′15	154	53	50	22	279
A 455′15	136	49	51	13	249
Totals	854	288	293	96	1531
Exp. ratio	9 :	3 :	3 :	1	

Heterozygous normal yellow (**PpQqYy**) ♀ × quail white (**ppQQyy**) ♂.

		A 458′15	Exp. ratio
Norm. yel.	PQY	108	1
Norm. wh.	PQy	119	1
Quail yel.	pQY	104	1
Quail wh.	pQy	93	1
Total		424	

Quail white (**ppQQyy**) ♀ × heterozygous normal yellow (**PpQqYy**) ♂.

		A 457′15	Exp. ratio
Norm. yel.	PQY	39	1
Norm. wh.	PQy	49	1
Quail yel.	pQY	49	1
Quail wh.	pQy	54	1
Total		191	

VI. MULTIPLE FACTORS⁽¹⁾; COMPOUND NATURE OF UNIT CHARACTERS.

1) Multiple Factors Concerning the Normal, Quail and Other Markings.

There is a great variability of pigment intensity in the normal, quail, striped and moricaud patterns, and the most abundant data on this point have been obtained from the normal type. In this we find almost every gradation from the lightest to the darkest, apparently presenting a continuous variation. From breeding experiments it has been learned that the characteristics of certain subtypes are transmitted to the offspring, while those of others are not reproduced in the progeny i. e. they are merely due to fluctuation. It is, however, by no means easy sharply to distinguish the subtypes of two categories. Provisionally I have divided the normal, according to the heritable characteristics, into four subtypes: namely normal 1, 2, 3 and 4.

Normal 1. This subtype represents the lightest normal, and the range of fluctuation is wide; the lightest are almost totally destitute of the "eye-spots" and "semilunules" and hardly distinguishable from the pure plain, while the darkest are provided with easily perceivable "eye-spots" and "semilunules". Between these two extremities every grade of marking intensity is exhibited (Figs. 44, 49).

Normal 2. With distinct "eye-spots", whose outlines are however more or less indefinite; anterior "semilunules" always present, posterior ones often absent. There is also a certain fluctuation (Figs. 43, 48).

Normal 3. The most common subtype; the "eye-spots" distinct and conspicuous, the "semilunules" well defined; the body surface looks, as a rule, clean owing to dots being scanty (Figs. 42, 47).

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1) It may not be proper, in the strict sense of the term, to regard the cases described in the present chapter as regards patterns and cocoon colours as examples of multiple factors or plural factors (SHULL, 1914), because I assume in these cases neither the so-called "gleichsinnige Faktoren" nor the factors which co-operate in furthering the development of *a certain character*, but I assume the existence of *different genes* respectively for the different subtypes of the marking and colour. Notwithstanding, I believe it is convenient to take the term in a broader sense and as including such cases as are described in the present paper.

Normal 4. The dark normal; in extreme case the "eye-spots" are deep-black, and the "frontal patch" enclosed by them is intensely dark brown, so that the "eye-spots" become apparently confluent, while the lightest examples of this subtype approaches to 3, but are distinguished from the latter by the darker "eye-spots" and a thicker distribution of the dorsal dots. Many intermediate forms exist between these two extremities (Figs. 39, 40, 41, 46).

It must be admitted that the above classification is to some extent arbitrary, for two adjoining subtypes are often difficult to separate, fluctuating one into the other; moreover, it is not impossible that the present classification may be unsatisfactory, and further subdivision is needed.

The normal marking is a compound character, as stated elsewhere, being composed of the two factors **P** and **Q**. Experiments have been made with the object of bringing out the component which causes the variation of the normal marking. A few data are, however, sufficient to show that the variability of the normal is due to that of the **Q** gene, whereas the **P** subserves as a negative factor or partial suppressor of the **Q** pattern (p. 144). In fact, almost all the subtypes exactly corresponding to those of the normal are found in the quail. We will denote these quail subtypes by the symbols $\mathbf{Q}^1$, $\mathbf{Q}^2$, $\mathbf{Q}^3$, $\mathbf{Q}^4$. The following data show the relation between normal and quail subtypes.

A 18′14 Plain × A 21–5′14 quail (Q^1)

A 258′15 Normal (1) Plain

239 52

A 411′15 Normal (1) Quail (1)

258 83

P 94–2′14 Normal (2) × A 18′14 Plain

A 167′15 All normal (2)

342 ♀ × A 255′15 Plain ♂

Normal (2) Normal (1) and plain

230 218

Plain × Quail (Q^3)

A 196′15 Normal (3)

241 (all)

Pale-quail ♀ × ♂

A 464′15	Normal (3)	Normal (1)	Quail (Q^3)	Quail (Q^1)
	49	65	74	46

The result is that the colour intensity of the normal offspring ex the cross plain × quail depends upon the marking intensity of the quail parent. It follows that the normal subtypes 1, 2, 3 and 4 may be represented as $\mathbf{PQ}^1$, $\mathbf{PQ}^2$, $\mathbf{PQ}^3$ and $\mathbf{PQ}^4$ respectively. It must be noted that the "eye-spots" of the normal subtypes are, as a rule, a little lighter than those of the corresponding quail subtypes, owing to the "palliating" function of **P**. This factor acts, as mentioned in Chapter **II**, as a suppressor of the irregular lines and dots characteristic to the **Q** pattern, and may at the same time tend to diminish the intensity of the "eye-spots" though in a slight degree.

A 22′14 Pale-quail × P 80′14 Striped

A 278′15	Striped	Striped-quail	Normal (PQ^3)	Quail (pQ^3)
	88	87	98	115

♀ × A 99′15 Pale-quail ♂

A 460′15	Normal (PQ^3)	Plain	Quail (pQ^3)	Light quail (pQ^1) and pale-quail (pq)
	85	86	99	85

As already stated (Chapter **V**), **P** and **Q** are quite independently distributed in the gametogenesis, and we should expect the presence of *light normal* ($\mathbf{PQ}^1$) in the above family (A 460′15) in which a number of *light quails* ($\mathbf{pQ}^1$) appeared. Contrary to expectation, no individuals of light normal type appeared in this case. This can not be interpreted otherwise than by the assumption that the individuals with the genetic constitution $\mathbf{PQ}^1$ (light normal) really occurred, but that the "eye-spots" were palliated by the **P** factor to so extreme a degree as to make them indistinguishable from pure plain. Quite similar case is met with in A 454′15 A 460′15 A 463′15 (p. 134), A 536′15

(p. 141), A477′15 A 480–1′15 A472–1′15 A479′15 A474′15 A478′15 (p. 143) etc. Even in cases in which light normal come to view, the percentage of the light normal to the plain is always lower than that of the light quail to the pale-quail: the phenomenon must also be caused by the peculiar action of **P**. Whether a plain is "specious" or not, may be *conjectured* by its pedigree or through further breeding.

True or pure plain:

M 37′14 Plain
Plain
A 16′15 151
A 17′15 287
A 99′15 Pale-quail ♀ × ♂
A 382′15 Plain [1]
245
Plain Pale-quail
A 770′15 206 69
A 771′15 262 84

A 22′14 Pale-quail × A 18′14 Plain
A 251′15 Plain
316
A 391′15 Plain Pale-quail
308 82

Apparent or specious plain:

H 44–1′13 Striped × X 2–4′13 Normal (PQ^3)
N 6′14 Striped Normal (PQ^3) + light normal (PQ^1)
182 189
Light normal (PQ^1) Plain

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[1] There were 4 lightest normal.

N 15-1'14 34 21
A 96'15 Light normal (PQ^1) Plain
18 **175**

A 18'14 Plain
A 92'15 Normal (PQ^1) Plain
(4 batches) 95 797

O 92'14 Quail (pQ^1) × A 18'14 Plain
A 250'15 **Plain** 103
A 371'15 Light normal (PQ^1) + plain (majority) Quail (pQ^1)
356 106

A 22'14 Pale-quail × A 18'14 normal (PQ^1)
A 255'15 Extremely light normal[1] + plain[2]
413
A 392'15 Normal (lightest) and plain Quail (lightest) and pale-quail
318 104

There is, however, another way in which the intensity of the "eye-spots" is reduced: the spots may be lighter in the simplex condition of **Q** factor than in its duplex condition. The following datum speaks for the assumption that **QQ** develops the "eye-spots" more intensely than **Qq.**

A 22'14 Pale-quail (pq) × Light normal (PQ^1)
A 257'15 Plain (PpQ^1q) 240[2] (all)

In this case the **P** gene is already present in the *normal* parent and the heterozygosis of this negative factor can not be agent that causes the "eye-spots" to fade; the factor that plays this rôle must be **Q** which is in heterozygous condition in the offspring. The heterozygotic effect of **Q** on pattern development is, however, often inconspicuous, especially in normal and quails of the higher subtypes: the palliating action of **P** is also usually distinct in

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1) The majority of them had only two dark vertical lines in the place of the "eye-spots".

2) These were destitute of even a trace of "eye-spots".

lighter normal subtypes, but often not so in darker ones.

When plain or pale-quail is crossed with either striped or moricaud or distinctly marked normal or quail, we are to expect in F_2 neither lighter normal nor lighter quail, provided that no subordinate (i. e. hypostatic) quail factors are contained in the epistatic parent. Such was actually the case with the lots A 74'15 A 76'15 (p. 177), A 279'15 (p. 182) etc. Several additional examples are given below.

A 22'14 Pale-quail × P 94'14 Normal (PQ^3)
A 272'15 Normal (PQ^3)
176 × A 99'15 Pale-quail
A 375'15 Normal (PQ^3) Quail (pQ^3) Plain (Pq) Pale-quail (pq)
126 117 116 95

O 76-2'14
Normal (PQ^3) Normal (PQ^4)
126 145
O 87'14 Normal (PQ^3) Plain (Pq) O 86'14 Normal (PQ^4)
40 12 35
♀ × A 17'14 Plain ♂
A 163'15 Normal (PQ^3) Plain (Pq)
31 37

H 20-1'13 Moricaud × X 6-1'13 Quail
P 45-1'14 Moricaud Normal
138 160
P 86'14 Moricaud Moricaud-quail Normal Quail
82 24 33 14
A 22'14 Pale-quail ♀ × ♂
A 275'15 Moricaud Moricaud-quail
66 70
A 99'15 Pale-quail ♀ × ♂

	Moricaud	Moricaud-quail	Plain	Pale-quail
A 473'15	56	71	67	63

The cases above given are, in fact, rather exceptional; and usually light normal or light quails appear in the progeny of similar crosses, beside the parental forms.

Pale-quail ♀ × Striped-quail ♂

	Striped-quail	Quail
A 105'15	155	146

Pale-quail ♀ × ♂

	SpQ	spQ¹	spq
A 513'15	125	60	57
A 514'15	47	8	32

♂ × ♀

	SpQ	spQ¹	spq
A 502'15	294	69	36
A 511'15	246	30	32

♀ × Pale-quail ♂

	SpQ	spQ¹ + spq
A 515'15	209	220
A 516'15	225	207

A 22'14 Pale-quail × P 86'14 Moricaud

	Moricaud	Moricaud-quail
A 275'15	66	70

A 99'15 Pale-quail ♀ × ♂

	Mor.	Mor. qu.	Pl. + light norm.	Pal. qu. + light qu.
A 474'15	60	48	67	61

♂ × A 99'15 Pal. qu. ♀

	Mor. qu.	Light qu. + pal qu.
A 483-1'15	261	86
A 483-2'15	210	76

	Mor. qu.	Light qu. × pal. qu.
A 484'15	131	131

P 87'14 Plain × Ex 2-9'14 Moricaud

	Moricaud	Normal (PQ¹)
A 188'15	106	92

A 183'15 Plain ♀ × ♂

	Mor.	Light norm. (PQ¹) + plain
A 491'15	172	188
A 492'15	211	220

♀ × A 183'15 Plain ♂

	Mor.	Light norm. (PQ¹) + plain
A 493'15	357	386

P 86′14 Moricaud-quail × A 18′14 Plain

A 120′15 Moricaud Normal

Pale-quail ♀ × ♂ 164 161

	Mor.	Mor. qu.	Norm.(mPQ^1) + pl.	Qu.(mpQ^1) + pal. qu.
A478′15	86	64	78	84

	Mor.	Mor. qu.	Norm.(PQ^1) + pl.	Qu.(pQ^1) + pal. qu.
A476′15	296	68	53	21
A477′15	195	67	55	22

In the offspring of the crossings of pale-quail with normal, moricaud and striped, the light normal or light quail appeared in the majority of cases; similar results came out in the crossings of plain with those epistatic forms named above. Hence it may be inferred that the majority of these epistatic parents have contained the lightest quail factor ($\mathbf{Q}^1$) together with **Q** of a higher subtype ($\mathbf{Q}^3$ or $\mathbf{Q}^4$).

One may imagine this case to be an example of the "modification" of genes due to crossing (Gates, 1915). But this seems improbable in the silkworm, (1) because the *darker* offspring are pigmented as intensely as the darker *parent*, i. e. no marked reduction of pattern development is recognizable, and (2) because there are at least certain cases in which *no* light normal or light quail appeared.

The appearance of light normal and quail was also met with frequently in experiments on coupling and repulsion (Chapter **IV**) and the non-correlated inheritance (**II**, **V**): such cases are marked with $_*$[1]. In these cases I have distinguished the lighter subtypes from distinctly marked ones and counted the lightest normal and lightest quails with the plains and pale-quails respectively, because they agree in being destitute of **Q** factor of the higher subtypes ($\mathbf{Q}^3$, $\mathbf{Q}^4$). Heretofore the result of analysis on this way have been adequate and satisfactory.

The light normal and light quails which appeared in the above crosses

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[1] The families free from * would have not been necessarily homogeneous in respeet of their plain and pale-quail classes: in certain families it was not noticed if there were present some individuals with lightest "eye-spots"; such families are involved within the non-asterisked group.

have now to be considered. Before proceeding further, however, we shall examine the interrelation of various quail or normal subtypes.

P 94–1′14 Normal (PQ^4) ♀ × N 15–3′14 Normal (PQ^1) ♂
A 150′15 Normal (PQ^4)
233

P 84–2′14 Normal (PQ^1) × P 94–1′14 Normal (PQ^4)
A 151′15 Normal ($PQ^{3\cdot4}$)
228

A 441′15 Normal ($PQ^{3\cdot4}$) Normal (PQ^1) Plain (Pq)
263 37 45

P 87′14 Normal (PQ^1) ♀ × A 21′14 Quail (pQ^3) ♂
A 193′15 All normal (PQ^3)
305

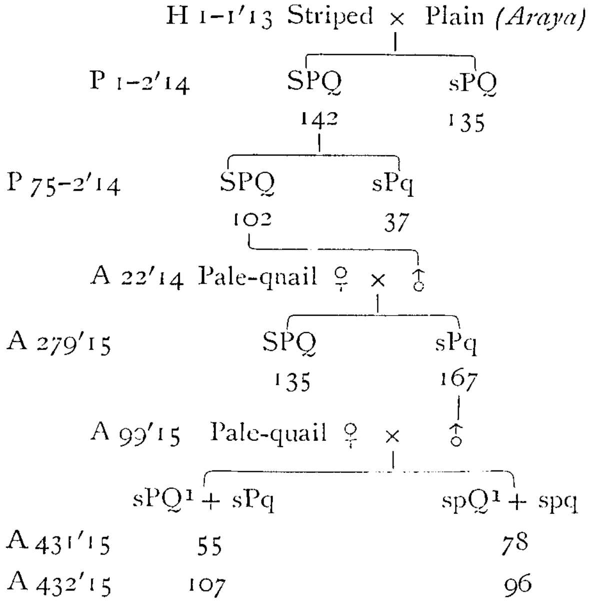
Quail (pQ^3) ♀ × O 88′14 Normal (PpQ^1) ♂
Normal (PQ^3) Quail (pQ^3)
A 209′15 121 127

It is evident that a higher subtype is epistatic to a lower one, i. e.

$$\mathbf{Q}^4 > \mathbf{Q}^3 > \mathbf{Q}^2 > \mathbf{Q}^1,$$

so that the occurrence of such forms as $\mathbf{Q}^3\mathbf{Q}^3\mathbf{Q}^1\mathbf{Q}^1$, $\mathbf{Q}^3\mathbf{Q}^3\mathbf{qq}$, or any other combinations of subordinate factors must be possible. Consequently there may exist in the striped, moricaud, normal and quail types various strains which are different from one another as regards the quail factors involved. Now a moricaud of the genetic constitution $\mathbf{MMQ}^3\mathbf{Q}^3\mathbf{Q}^1\mathbf{Q}^1$ is to yield, when crossed with a pale-quail, F_2 animals of such phenotypes as moricaud, moricaud-quail, *light normal, light quail,* plain and pale-quail, if $\mathbf{Q}^1$ is not completely coupled with **M**. This was, in fact, the result in the majority of such crossings. On the other hand, if a moricaud of the constitution $\mathbf{MMPPQ}^3\mathbf{Q}^3\mathbf{qq}$ is crossed with a pale quail, F_2 zygotic series will be represented by moricaud, moricaud-quail, plain and pale-quail, but will contain neither light normal nor light quail. This was realised in A 473′15 (p. 143) and some other families. Similar results may be expected for the other markings, i. e. striped, normal and quail.

As has been stated in a foregoing page, a $\mathbf{PQ}^1$ animal often looks like a plain ($\mathbf{Pq}$) but it is only a "specious" plain; a $\mathbf{pQ}^1$ individual also may sometimes be mistaken for a pale-quail ($\mathbf{pq}$), both owing to the fluctuation before spoken of. The offspring ought to contain some light normal and light quails, when such a specious plain or a specious pale-quail is crossed with any other marking types irrespective of the presence or absence of the $\mathbf{Q}^1$ factor in the latter.



The fact described in the present and just preceding paragraphs may be expressed by diagrams as follows:

Taking the case of crossing with $\mathbf{PQ}^3$ normal;

Distinct normal (PQ^3q) × specious pale-quail (pqQ^1)

or

Distinct normal (PQ^3Q^1) × true pale-quail (pq)

F_1 Distinct normal (PpQ^3Q^1q)

	Distinct norm.	Distinct qu.	Light norm.	Light qu.	Plain	Pal. qu.
F_2	(PQ^3)	(pQ^3)	(PQ^1)	(pQ^1)	(Pq)	(pq)
	36	12	9	3	3	1

Distinct normal (PQ^3q) × specious plain (PQ^1)

or

Distinct normal (PQ^3Q^1) × pure plain (Pq)

F_1 Distinct normal (PQ^3Q^1q)

F_2	Distinct norm. (PQ^3Q^1)	Distinct norm. (PQ^3q)	Light norm. (PQ^1)	Plain (Pq)
	9	3	3	1

The facts for other kinds of normal hybrids such as $\mathbf{PQ^4Q^1}$ (M 46–1′14, A 23′15) $\mathbf{PQ^{3\text{-}4}Q^2}$ (M 46–3′14), $\mathbf{PQ^2Q^1}$ (M 47–1′14, A 442′15) are given below.

B 7′13 Dark normal yellow

M 46–1′14	Dark norm. yel. (PQ^4Y)	Dark norm. wh. (PQ^4y)	Light norm. yel. (PQ^1Y)	Light norm. wh. (PQ^1y)
	77	57	25	11
A 23′15	PQ^4Y	PQ^4y	PQ^1Y	PQ^1y
	24	10	11	3

B 7′13 Dark normal yellow

M 46–3′14	Dark norm. yel. ($PQ^{3\text{-}4}Y$)	Dark norm. wh. ($PQ^{3\text{-}4}y$)	Light norm. yel. (PQ^2Y)	Light norm. wh. (PQ^2y)
	37	8	8	5

B 7′13 Light normal yellow

M 47–1′14	Lighter norm. yel. (PQ^2Y)	Lighter norm. wh. (PQ^2y)	Lightest norm. yel. (PQ^1Y)	Lightest norm. wh. (PQ^1y)
	130	45	50	17

A 175′15 PQ^2Y

A 442′15	PQ^2Y	PQ^2y	PQ^1Y	PQ^1y
	140	51	69	15

We shall now examine the behaviour of subordinate quail factors towards **Y** character. All the cases of **Q-Y** coupling and repulsion which were described under Chapter **IV**, concern the correlation between **Q** genes of higher subtypes ($\mathbf{Q^3}$,$\mathbf{Q^4}$) and **Y.** Here follow several cases of correlated inheritance between the **Q** of lower subtypes ($\mathbf{Q^1}$, $\mathbf{Q^2}$) and **Y** factor.

Coupling:

H 44-1'13 Striped white × X 2-4'13 Normal yellow

	Striped yellow	Distinct normal yellow + light normal yel.
N 6'14	182	189

	Light normal yellow (PQ^1Y)	Light normal white (PQ^1y)	Plain yellow (PqY)	Plain white (Pqy)
N 15-1'14	32	2	3	18
N 15-3'14	130	11	6	24
A 94'15	113	13	6	39

F 5'14 Normal (PQ^2)

438

	Norm. yel. (PQ^{1-2})	Norm. wh. (PQ^{1-2})	Pl. yel. (Pq)	Pl. wh. (Pq)
C 27-1'14	138	19	11	44
C 42-1'14	43	2	1	13
C 42-2'14	103	6	12	19
C 42-3'14	29	2	3	4

F 4'13 Normal (PQ^2)

169

	Norm. yel. 1)	Norm. wh.	Pl. yel.	Pl. wh.
C 26-2'14	113	9	8	31

	Norm. yel. (PQ^2Y)	Norm. wh. (PQ^2y)	Pl. yel. (PqY)	Pl. wh. (Pqy)
C 41-1'14	68	7	6	19

Repulsion:

P 87'14

Light norm. yel. (PQ^1Y)	Light norm. wh. (PQ^1y)	Pl. yel. (PqY)
54	24	18

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1) Marking intensity of these normal was not recorded.

Plain wh. ♀ × ♂
(Pqy)

	Light norm. yel. (PQ^1Y)	Light norm. wh. (PQ^1y)	Plain yel. (PqY)	Plain wh. (Pqy)
A 179′15	43	104	116	52
A 182′15	39	128	95	45

The above experiments clearly show that coupling and repulsion similar to those observed in distinctly marked normal and quail, occur between the **Y** and $\mathbf{Q}^1$ or $\mathbf{Q}^2$ factor responsible for lighter normal and quails.

Some families in my experiments apparently showed the independent inheritance of darker quail factors ($\mathbf{Q}^3$, $\mathbf{Q}^4$) and **Y**, when lighter quail factors ($\mathbf{Q}^1$, $\mathbf{Q}^2$) are involved; while some others gave rise to coupling or repulsion under a similar circumstance. Beside this, the interrelations of subordinate quail factors, and their behaviour towards **S**, **M**, **q** etc. are still open question: these obscure points are to be manifested by future experiments.

The striped and moricaud strains are also not free from variation, and families are often met with which consist of different subtypes in respect of marking intensity. Fig. 60 represents a series showing such a variation in the moricaud in the third larval stage, and Fig. 50 represents a variation in the normal marking in the same stage. It will be seen that the lightest moricaud is somewhat difficult to distinguish sharply from the darkest normal, though the difference between the moricaud and normal becomes so marked in later stages that two strains can scarcely be confused. Whether such a variation of the striped and moricaud is due to the variation of **S** and **M**, or due to that of **Q** gene, as in the case of quail and normal, is almost impossible to assert, as **Q** is completely coupled with **S** and **M** as already mentioned.

2) Compound Nature of Unit Characters.

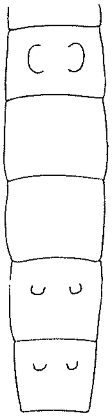
The essential feature of the normal marking consists of three pairs of spots, i. e. the "eye-spots" on the segment II, the anterior "semilunules" on V, and the posterior on VIII. The "eye-spots" and anterior "similunules" are usually of very nearly the same colour intensity, while the posterior “semilunules” are less conspicuous both as regards size and tint, and are often absent in lighter normal.

In certain strains, however, the “eye-spots” and anterior “semilunules” are unequally developed, either the former or the latter being more intensely pigmented than the other. This peculiarity is transmissible.

From the summer culture of 1914, I selected a number of normal-patterned larvae with “eye-spots” of $\mathbf{pQ}^2$ subtype and anterior “semilunules” of $\mathbf{pQ}^1$ and mated them among themselves. The normal offspring produced by these matings were 257 in number in A 141'15, and 243 in A 145'15 and all bred true in having the “eye-spots” darker than the anterior “semilunules”. Similar result was obtained with the lots A 147'15, A 373'15 and A 442'15 (Figs. 63, 64).

On the contrary, there are some strains in which the “eye-spots” are markedly lighter than the anterior “semilunules”. For instance, the quails (55 in number) in A 674'15 were $\mathbf{Q}^1$ as regards the “eye-spots”, but $\mathbf{Q}^2$ in respect of “semilunules”. A Japanese race *Arayahime* is plain or lightest normal so far as the “eye-spots” are concerned, but traces of “semilunules” are always present and darker in colour than the “eye-spots”. The said family A 674'15 was, in fact, the offspring of a crossing of *Arayahime* and pale-quail. A 142'15 and A 372'15 belong also to this category (Figs. 65, 66).

In various strains of normal, there is occasionally met with a peculiar type which is provided with third semilunular spots on segment IX, as large as the second (posterior “semilunules”) (Fig. 62). In the summer of 1914, I separated the larvae of this type from those of the ordinary type in the families C 29–1,2,3,4'14 and mated them among themselves, with the following results. Two matings of the ordinary type gave 564 individuals (A 60'15), of which 460 were normal, 54 quail, and 50 plain and pale-quail not a single larva being provided with the third “semilunules”. A mating of the individuals with “semilunules” on segment IX, gave 223 offspring in all, of which 161 individuals were normal, and 62 plain (A 59'15). Not only all the normal of this family had the extra "semilunules" 1), but the plain larvae possessed C Ↄ shaped traces of the spots on segment IX, as well as on V and VIII 2) (Text-fig. 6). A plain male from this family was crossed with a quail female from A59′15 3) (ex C29–1,2,3,4′14, i. e. with a common ancestor with her mate), the resulting family, A353′15, consisted of 106 normal with the third "semilunules" and 29 normal without the spots in question (ratio about 3 : 1) From these facts it is evident that (1) the third "semilunules" are heritable and (2) the type with this mark is a simple dominant over the oridinary type. It is an interesting fact that the extra "semilunules" are often found in wild silkworms, *Bombyx mori* var. *mandarina*, the assumed ancestor of the domestic forms, though the wild type is moricaud in marking (Fig. 61). 4)

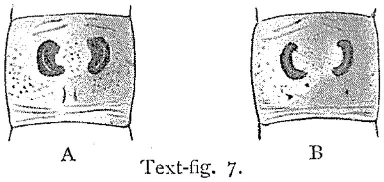


Text-Fig. 6.

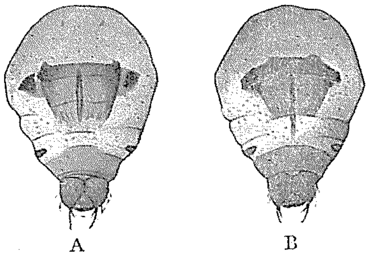
Normal of the *Bagdad* and some other European races are peculiar in having "semilunules" of a "blurred" appearance (Text-fig. 7, A), in contrast to their sharp outlines in Japanese normal (B).

The distribution of the dorsal dots vary considerably in different strains, even among those in which the "eye-spots" or "semilunules" are of about the same intensity.

In the normal of some strains (A 283′15, A 314′15) the subdorsal dots were unusually distinct. In some of the normal larvae from the families A 155′15 and A 318′15, the



Text-fig. 7.



A, ordinary type; B, modified type.

Text-fig. 8.

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1) In a few individuals the spot was present on one side only. Similar asymmetry frequently occurs in the multilunar pattern.

2) The presence of similar traces on segments V and VIII only is by no means rare in ordinary plain strains.

3) The extra "semilunules" were not taken note of in this family, but it is possible that the animal mated possessed the spots in question, and was heterozygous in this character.

4) In my experiments some domestic moricaud larvae were also found provided with extra semilunular spots.

blank space of the "eye-spots" was filled up (Text-fig. 8). All these traits have been proved to persist in the offspring.

The facts above given are, perhaps, enough to show that one or both of the complementary factors (**P**,**Q**) of the normal marking may be subject to minor changes which are inherited to the offspring. I am consequently forced to conclude that the so-called unit characters are not *unit* in the strict sense, but are of compound nature somewhat comparable to chemical compounds. There are one or more genes which are indispensable for the development of the essential features of a given character; they correspond, I venture to assume, to the element or elements forming the nucleus of a chemical compound. This genetic nucleus combines with a number of determinants or groups of them which correspond to the chemical radicles, and forms a compound. The cluster of genes thus combined may be inherited as such and appears as a "unit character", but it may also undergo slight changes caused by the dropping off of one or more than one genes or radicles or their replacement by another, or rearrangement of them in consequence of some physiological disturbance, say, in chromosomes. Any variations must be genetic in nature, as far as they are transmissible, yet they do not alter, the essential feature of the character, unless the variations affect the factor-nucleus itself. The forms produced by minor genetic variations may be compared to chemical isomers and derivatives.1)

3) Multiple Factors Concerning the Moulting Character.

Silkworms usually pass through four moults before spinning cocoons, i. e. they are 4-moulters. There are, however, some races which spin, as a rule, already after the third moult and are, therefore, 3-moulters. These 3-moulters are not distinguishable from the 4-moulters until the second moult which is gone through by the latter earlier. In the 3-moulters, the third and fourth stages last, moreover, a few days longer than in the 4-moulters which have, however, to moult once more, and commence to spin ("mount") 2 to 5 days

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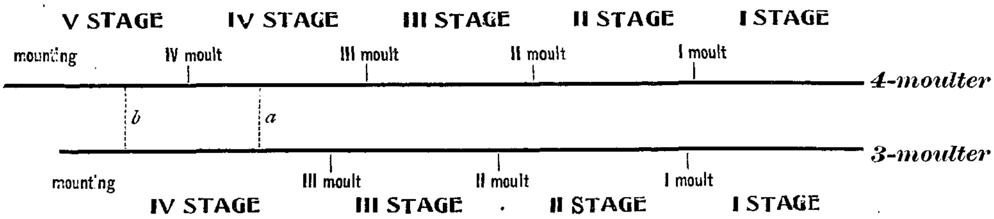
1) Whether the present cases are comparable with those enumerated by Castle (1912) as examples of the inconstancy of unit characters, is still doubtful.

later than the 3-moulters. The following diagram may illustrate more clearly the differential development of the two strains.



Text-fig. 9.

Owing to its great variability, the body size or weight can not be taken as the criterion for distinguishing 3-moulters from 4-moulters. The size of the head-case, on the other hand, does not show any marked increase during the same stage; and further the individual variation is less extensive as compared to the body size. The head-case grows at every moult, and in a full-grown 4-moulter (fifth stage) the head is larger than in a full-grown 3-moulter (fourth stage), though the head-size of 3-moulter exceeds that of a 4-moulter of the corresponding stage (e. g. fourth or third). Taking the *a* period in the diagram, for instance, the large-headed 3-moulters are not difficult to distinguish from the small-headed 4-moulters. On the contrary, taking the *b* period in the figure, the relative size of the head in the two strains is just the reverse. I mention this because the distinguishing criterion is so important for avoiding errors that may otherwise vitiate the results of experiments. There were in my experiments, only a few cases which rendered the distinction uncertain on account of considerable fluctuation in the head size.

The moulting character is constant to some extent; I have in my possession several strains which bred true in regard to this character for generations. Moreover, the character is Mendelian, 3-moulting dominating over 4-moulting. The cases of simple Mendelian inheritance are shown below.

Chinese 3-moulters (*"Sze-chuan"* race) were crossed with Japanese 4-moulters (pale-quail strain); F_1 generation consisted of 3-moulters only. The F_1 individuals were mated *inter se*, as well as cross-bred with the recessives with following results.

F_1 3-moulters mated *inter se.*

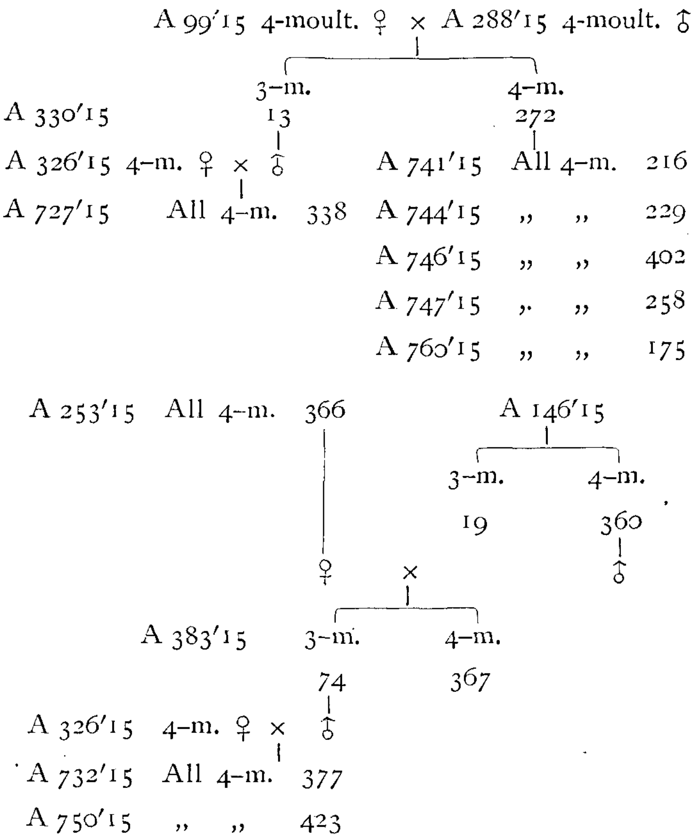
	3-moult.	4-moult.	Ratio		
A 785'15	148	50	3	:	1
A 786'15	196	68	2.9	:	1
A 787'15	173	60	2.9	:	1
A 788'15	231	48	4.8	:	1
Totals	748	226	3.3	:	1
Expect.	730.5	243.5	3	:	1
	F_1 3-moulters × 4-moulters.				
A 783'15	169	157	1.1	:	1
A 784'15	161	207	1	:	1.3
A 789'15	222	212	1.1	:	1
Totals	552	576	1	:	1
Expect.	564	564	1	:	1
	4-moulters × F_1 3-moulters.				
A 782'15	212	194	1.1	:	1
A 790'15	156	176	1	:	1.1
Totals	368	370	1	:	1
Expect.	369	369	1	:	1

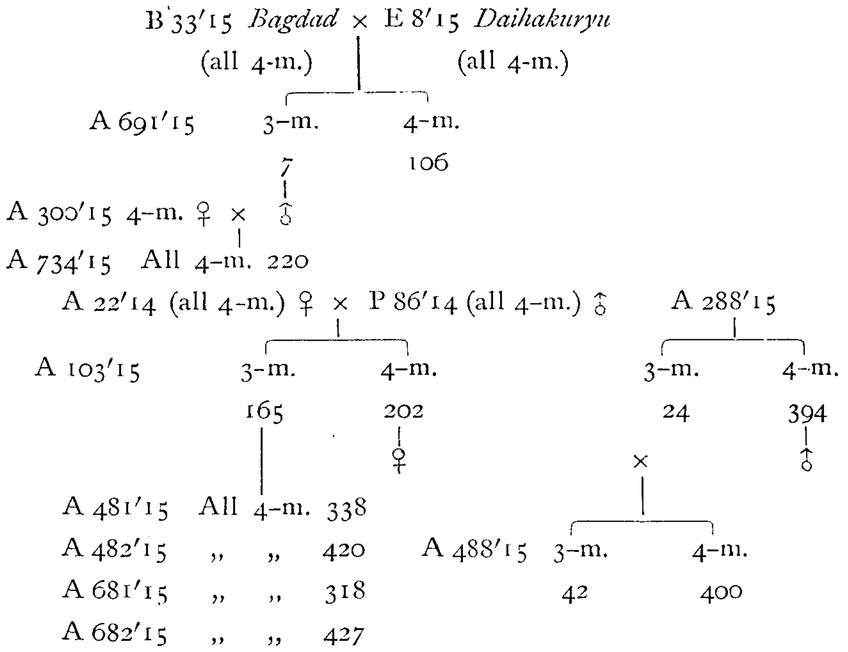
I have many other cases which gave monohybrid ratio in inheritance of moulting character, but they need not, I believe, be added here.

The moulting character is, on the other hand, subject to variation under environmental agencies. In some cases, 3-moulters or 5-moulters are found in families which are normally 4-moulting. Though usually small in number, the variants may sometimes attain a high percentage. In 1911, in Nagano Province, for instance, 5-moulters appeared unexpectedly and were so numerous as to draw general attention; the event is to be ascribed to certain physiological disorders caused by the volcanic ashes which repeatedly covered the mulberry-field during the year, as is demonstrated later by YOKOTA(1912) and KAWASE and KARASAWA (1915) in their experiments in which the 5-moulters were produced from 4-moulting races by feeding them with leaves sprinkled with coal- or volcanic ashes.

In 1912, I obtained from Mr. YOKOTA eggs deposited by 5-moulting variants, from which five batches were hatched and reared separately. Of the more than 1000 larvae, not a single one bred true; similar results have been obtained by various authors. In fact there is, so far as I am aware, no constant 5-moulting strain, and the all silkworm races are 4-moulters if not they are 3-moulters.

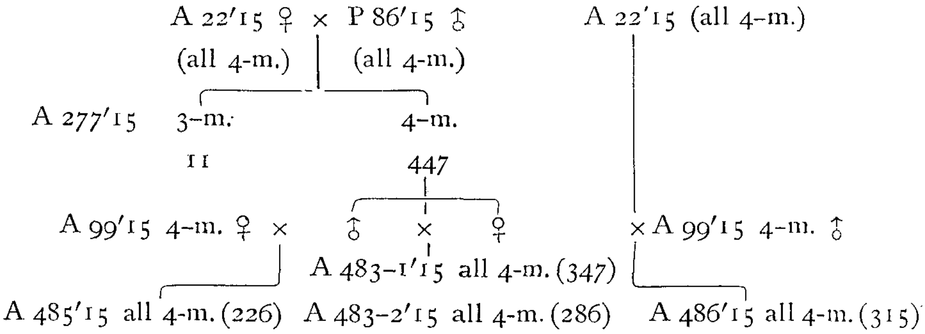
In the course of my experiments, I have noticed that 4-moulting families often yielded small numbers of 3-moulters, which did not transmit their moulting character to the offspring.

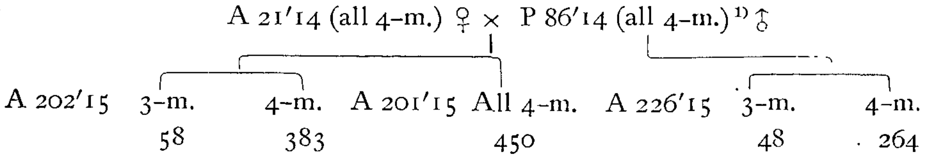




In A 103'15 (ex 4-m. × 4-m.) 3-moulting variants attain about 45% of the whole family, and yet they do not inherit the acquired character, namely they are mere somatic variants.

Several other examples in which 3-moulters appeared in small numbers in the families descended from 4-moulting parents, are given below.





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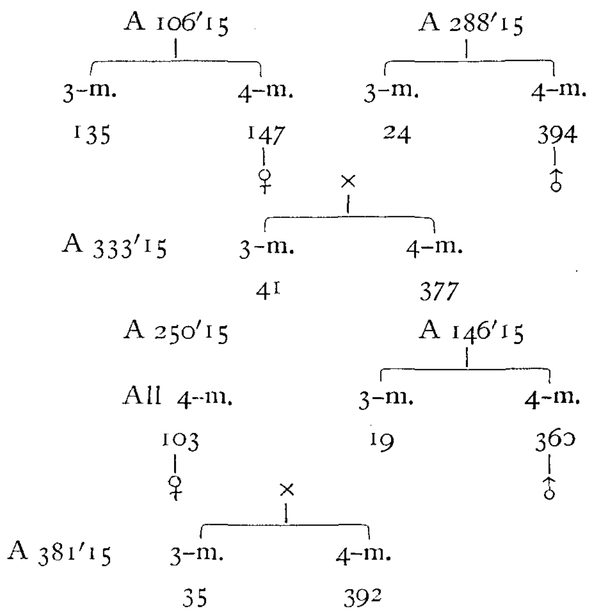
[1] The reciprocal cross of this produced only 4-moulters (441 in number) (A 203'15).



There is some indication of positive correlation between the male sex and 3-moulting variants. Of the 58 3-moulters in A 202′15 only 14 were allowed to complete their development, and of these 13 were male, and 1 female; of 24 3-moulters in A 288′15, 7 emerged as moths and were all males; the 41 3-moulters in A 333′15 consisted of 30 males and 11 females; of the 74 sports of A383′15 26 individuals completed their development and all were males (1).

Apart from the sporting, the moulting character seems to do not always behave in inheritance so simply as in the examples given at the beginning of the present section. In the course of my experiments, pretty complex examples have very frequently been met with, the more important of which are cited here.

1) Heterozygous 3-moulters yielded by inbreeding, 3- and 4-moulters in ratios approximate to 1 : 1 instead of the ordinary 3 : 1.

2) Heterozygous 3-moulters produced, when crossed with recessive 4-moulters, various abnormal ratios; in some cases the recessives fell far behind

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1) In ordinary cases the sex-ratio in the silkworm is more or less approximate to 100 : 100.

the dominants in number; in others, the former far exceeded the latter.

3) Extraordinary ratios of 3- and 4-moulters appeared as results of the mating of 3-moulters and 3-moulters.

4) The two forms (3- and 4-moulters) appeared nearly in equal numbers as a result of crossing 4-moulter × 4-moulter.

In the following lines are given some examples of such abnormal proportions, met with in my experiments.

3-moulters × 3-moulters.

	3-m.	4-m.	Ratio
O 25-1'14	97	70	1.4 : 1
O 25-2'14	53	36	1.5 : 1
O 25-3'14	117	80	1.5 : 1
O 26-1'14	126	191	1 : 1.5
O 34-2'14	122	113	1.1 : 1
O 40'14	125	130	1 : 1
N 14-1'14	45	40	1.1 : 1
N 15-1'14	20	35	1 : 1.8
N 15-3'14	85	86	1 : 1
P 73'14	37	51	1 : 1.4
P 75-1'14	166	38	4.4 : 1
P 75-2'14	44	95	1 : 2.2
P 81'14	58	45	1.3 : 1
P 84-1'14	57	10	5.7 : 1
P 84-2'14	106	91	1.2 : 1
A 533'15	221	43	5.1 : 1
A 621'15	197	33	6 : 1
A 764'15	139	158	1 : 1.1
A 725'15	12	59	1 : 4.9
A 726'15	4	41	1 : 10

3-moulter ♀♀ × 4-moulter ♂♂.

N 6'14	295	76	3.9 : 1

P 1–1'14	81	324	1 : 4
P 1–2'14	33	244	1 : 7.4
P 3'14	51	281	1 : 5.5
P 4'14	59	275	1 : 4.7
P 14'14	83	233	1 : 2.8
P 19–2'14	81	199	1 : 2.5
P 30–1'14	57	293	1 : 5.1
P 30–3'14	57	333	1 : 5.8
P 30–5'14	41	249	1 : 6.1
P 33'14	86	255	1 : 3
P 36–2'14	85	236	1 : 2.8
P 54–1'14	25	259	1 : 10
P 57'14	53	338	1 : 6.4
P 64'14	74	210	1 : 2.8
P 70'14	64	158	1 : 2.5
P 71–2'14	32	421	1 : 13.2
Ex 2–7'14	102	226	1 : 2.2
	4-moulter ♀♀ × 3-moulter ♂♂.		
N 11–1'14	99	372	1 : 3.8
P 2–3'14	84	281	1 : 3.4
P 15'14	44	469	1 : 10.7
P 16–2'14	42	398	1 : 9.5
P 21'14	41	438	1 : 10.7
P 34'14	150	67	2.2 : 1
P 35–1'14	33	314	1 : 9.5
P 40–2'14	64	382	1 : 6
P 41'14	66	316	1 : 4.8
P 43–1'14	88	241	1 : 2.7
P 46–1'14	44	363	1 : 8.3
P 48–1'14	95	313	1 : 3.3
P 48–2'14	35	470	1 : 13.4
P 60'14	27	446	1 : 16.5

P 65′14	92	213	1 : 2.3
P 67′14	31	325	1 : 10.5
P 68′14	44	357	1 : 8.1
	4-moulters × 4-moulters.		
A 114′15	212	230	1 : 1.1
A 128′15	131	107	1.2 : 1
A 129′15	93	93	1 : 1
A 211′15	83	92	1 : 1.1
A 212′15	205	174	1.2 : 1
A 245′15	234	187	1.3 : 1
A 246′15	217	241	1 : 1.1
A 279′15	152	150	1 : 1

To what extent the above cases owe their abnormal phenotypic ratios to intransmissible fluctuation, and to what extent owe to the genetic cause, is a difficult question to solve. The multiple factor theory is applicable to the question only when some of these cases, at least, have been proved to be neither due to fluctuation, nor accidental, but due to genetic recombination. Many of these abnormal cases, if not all, can be interpreted, for instance, on the assumption that either 3- or 4-moulting arises according as two conditional factors, $\mathbf{T}^a$ and $\mathbf{T}^b$, are present simultaneously or not. Some such hypothesis assuming the presence of more than one allelomorphs in the inheritance of moulting character appears to me at present to be the most plausible.

4) Multiple Factors Concerning Colour and Other Cocoon Characters.

The silkworm cocoons may be divided into two distinct groups, coloured and colourless. The colourless or white cocoons are further subdivided into dominant and recessive whites (TOYAMA 1912 a, TANAKA 1913 a). Two subdivisions are recognized also in the coloured cocoons, namely the yellow and green. The "green" colour of the cocoon might rather be classed in the yellow series according to the general nomenclature of colours, yet the yellow-cocoon spinner is yellow-blooded and hence yellow-legged, in contrast to the green-cocoon spinner in which the haemolymph and the abdominal legs are never yellow. Consequently these two strains are readily distinguishable, already in the larval stage, whereas it is by no means easy to distinguish the green and white before spinning.

The yellow character is dominant over the green, but the dominance is not complete, the cocoons of **YG** individuals being intermediate of those of **YY** and **GG** parents in colour, on account of the simultaneous development of the two colours.

Not only in my previous papers, but also in the preceding pages of the present communication, I have, for the sake of simplicity, dealt with the yellow as a simple character. Various sorts of colour subtypes can, however, be recognized in the yellow as well as in the green series: to speak more fully, orange [1], cadmium yellow, chrome yellow, salmon, salmon-buff, cream and many intermediate colour subtypes are involved in the yellow type; while citron yellow, sulphur yellow, primrose yellow, greenish white, and many intergrades belong to the green series. The majority of these colour races transmit their characteristics, as is learned by my unpublished experiments; they are therefore undoubtedly dependent upon respectively different factors.

The inter-crossing of different subtypes often gives monohybrid F_2 ratio, whereas in some other cases, it gives rise to a widely ranging variability in the cocoon colour, a "breaking up" being brought about. This is a fact which speak for the existence of several allelomorphs for the yellow and green colours. More detailed account on the inheritance of yellow and green characters will appear on a future occasion.

There are some reasons to believe that the multiple factor hypothesis fits in best for the inheritance of shape and size of cocoons, thickness and length of cocoon-fibres ("baves") and other quantitative characters in the silkworm. My experiments in this direction is now in progress.

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[1] According to the nomenclature of colours by Ridgway (1886).

VII. ON MOSAICS AND GYNANDROMORPHS.

In the spring culture of 1914, I obtained four larvae apparently mosaic in morphological character, as the following descriptions show.

Mosaic 1 (Fig. 68). The pattern was decidedly different on both sides of the longitudinal median line, the right being moricaud, and the left normal. The boundary was distinct, and the characteristics were not intermingled in any way.

Mosaic 2 (Fig. 69). Normal-patterned on both sides, but the skin of the left side presented a transparent or "oily" character, as it is commonly called, while the right side was of the ordinary opaque white colour. The epidermal abnormality of the left side was, however, not uniform; the transparent areas formed patches surrounded by the normal white portions.

Mosaic 3 (Figs. 70, 71). On the right side, the anterior half of the body (to segment VII) had the ordinary black stripes, in segment VIII the black areas predominanted over the white ones, while in the hinder segments the pattern was almost perfectly normal. On the left side, the anterior segments were practically normal-patterned, provided with a few small scattered black spots. From segment VII backwards, especially in the hinder segments, the black areas generally predominated over the normal ground colour, though their arrangement was very irregular. Nevertheless the unilateral distribution of the marking is quite obvious, the median line forming the boundary. On the ventral surface of the anterior segments as far backward as VII, the ventral spots characteristic of **S** type are ◀ shaped and confined to the right side, while in the hinder segments the spots are complete and equally developed on either side of the median line.

The specimen spoken of was killed and preserved, and the gonads were sectioned and mounted for microscopical study, which showed that the right gonad was an ovary, while the left was a testis.

Mosaic 4. The larval pattern was normal, but the two sides of the body differed to marked degree in the intensity of their patterns, the right side being darker. The unilateral development of the pattern was very evident, and there was no intermingling of the characteristics of the two sides.

Mosaic 5 (Fig. 72). In the summer culture of the same year, one more mosaic monster was obtained. On the left side of this individual the pattern was striped-black in segments II, III, IV, V, X and XI; in the rest, the black was, roughly speaking, equal tot he normal in area. On the right side of the body, in segments III, VII and VIII black areas were likewise equal to the white (normal). In the other segments of the same side, the white area evidently predominated over the black.

Of these five mosaic silkworms all but the third one died of disease, and their sex could not be ascertained.

In 1915, several more specimens were obtained; they are described below.

Mosaic 6. This example is interesting on account of its being a mosaic of size as well as of colour. On the dorsum, the left half of the head and body anterior to segment VIII differs markedly from the right in being dwarfed, the "eye-spots" and anterior "semilunules" of the respective sides were naturally proportionate to that size difference. The five hinder segments appeared to be normal and bilaterally symmetrical. On the ventral side, the mosaic character extended further backwards; the left half of all the segments including the thoracic as well as abdominal legs (the so-called anal leg included) were much smaller as compared with their counterparts of the opposite side. All the head appendages exhibited a similar asymmetry. The five anterior stigmata of the right side were remarkably bigger than the corresponding ones of the opposite side, which were equal in diameter to the remaining ones of the right.

The coloration also partook of the asymmetry. On the dorsal side, the section anterior to segment VIII was opaque white on the right side, while on the left and the rest of the right side the body was oily. On the ventral side, the opaque right half, and the transparent left were sharply marked off from each other by the ventral median line throughout the entire length of the body.

This curious example was found among a lot of pure breed of the Japanese race *O-awo* noted for its large size. To my regret, the larva was lost before the sex could be ascertained and either a photograph or a sketch had been taken.

Mosaic 7. A light normal-patterned larva, yellow-footed. Right half of body normal opaque, left transparent, some intermingling of the characters. Female on both sides.

Mosaic 8. A green-cocooner with lightest normal pattern, of the Japanese breed *Watako*. No abnormality was recognized on the back, but the skin of the ventral side was marked in the left half with a number of transparent patches of irregular outlines. The mosaic is confined to segments I–VIII, the hinder ones remaining normal. Female.

Mosaic 9. On the dorsal surface, there are present in the left half, a number of detached transparent patches which become more extensive in the posterior segments. The caudal horn pointed toward the left instead backwards. Ventral side opaque white and symmetrical. Female.

Mosaic 10. Multilunar-zebra-normal, yellow. The right side was entirely free from multilunar spots, which occurred on the left side in II, III, V, VII and VIII segments. No abnormality regarding **Z** and **PQ** patterns. Sex unknown.

Mosaic 11 (Fig. 73). The larva is practically moricaud-quail, but the moricaud character is absent here and there in the left of the body, leaving many irregularly shaped white patches. The gonads were not examined.

Some instances of mosaic and gynandromorphous individuals are found in the literature on silkworms. Toyama (1906a), whose descriptions on the subject are best known, had two examples, both found among the F_1 offspring of the cross zebra ♀ × normal ♂. In both the right side was zebra and female and the left normal and male.

Ikeda (1908) mentions two mosaics, one of which had normal right and moricaud left, whereas the other was a mosaic gynandromorph, i. e. the right side was normal and female, and the left side plain and male.

Recently TAKAHASHI (1914) has described four mosaic specimens of the silkworm. One was a combination of moricaud right and normal left, but was male on both sides. The second was normal-patterned, but had oily skin on the left side, and opaque white on the right; it was a female. The third specimen showed oily patches on the right side, and was female on both sides. The fourth individual was normal in marking and showed no abnormality on the dorsal side. On the ventral, however, the left was transparent-skinned, the right being ordinary opaque. This individual was a gynandromorph, male on the right and female on the left.

The views of previous authors on the cause of gynandromorphism are pretty divergent. BOVERI (1915) attempts to explain it by partial merogony, LANG (1912) by mutation in the sex-chromosome. GOLDSCHMIDT (1912) by "Potentialdifferenz" of sex-factors, and MORGAN (1913) by polysperm fertilization. Having worked recently on a gynandromorph of the fruit-fly, MORGAN (1914h, 1916) comes to view that "gynandromorphs and mosaics may arise through a mitotic dislocation of the sex-chromosomes."

The silkworm mosaics and gynandromorphs must, I believe, be explained by mutations taking place in the course of ontogeny. By the term "mutation" I do not like to mean a sudden elimination or addition of certain factor or factors, but some reorganization or disturbance taking place among somatic cells or chromosomes, by which certain factor or factors are suppressed, or suppressed factors called into activity.

The mutation may affect either non-sexual characters only (simple mosaic), or the sex-factor only (simple gynandromorph 1)), or both (mosaic gynandromorph).

We have sharply marked off "right-left mosaics" 2) on one hand, and more or less irregular mosaics 3) on the other. It would not be unreasonable to

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1) Gynandromorphs which are not mosaic in somatic characters at all, are at least theoretically possible in the silkworm as in other animals. That such examples have not been described until now is perhaps due to the circumstance that they would very likely be overlooked, presenting, as they would, to the observer no marked external difference from the normal unisexual larvae.

2) Mosaics 1, 4, 6, 10 etc.

3) Mosaics 2, 3, 5, 7, 8, 9, 11 etc.

assume that the antagonistic characters are the more irregularly intermingled the later the mutations occur in blastomeres. From this point of view, the "right-left mosaic" should be produced by a single early or major mutation, while other mosaics should be produced by a major and some later or minor mutations ("mutation epidemic" !). The specimens given in Figs. 74, 75 and 76 may be regarded as have resulted from some minor mutations preceded by no major one.

The mosaic 6 interests us, because it assists to a fuller understanding of the size inheritance in the silkworm. Under ordinary circumstances, the proving of this inheritance meets with insurmountable difficulty, because it is practically impossible to place the individuals under exactly the same condition. The present case is, of course, quite free from this objection, and yet one side is markedly smaller than the other.

VIII. SUMMARY.

The more important results of this paper may be summed up as follows.

1) The genetic factors for larval markings in the silkworm are six:

S ....striping factor, **P** ....plain factor,
M...........moricaud factor, **Z** ....zebra factor,
Q ....quail factor, **L** ....multilunar factor.

2) The zygotic constitutions of the more common markings are as follows:

Striped	**SmPQzl**	Normal-zebra	**smPQZl**
Moricaud	**sMPQzl**	Multilunar-plain	**smPqzL**
Normal	**smPQzl**	Multilunar-normal	**smPQzL**
Quail	**smpQzl**	Multilunar-normal-zebra	**smPQZL**
Plain	**smPqzl**	Striped-quail	**SmpQzl**
Pale-quail	**smpqzl**	Moricaud-quail	**sMpQzl**
Plain-zebra	**smPqZl**	Striped-quail-zebra	**SmpQZl**
Striped-zebra	**SmPQZl**	Multilunar-quail-moricaud	**sMpQzL**
etc.		etc.	

3) **Q** factor is completely coupled with **S** and **M** in both sexes.

4) The presence of **Q** factor favours pigment formation in the epidermis, whereas the presence of **P** has opposite effect and lead to partial suppression of pigment development. So that **pQ** animal is more intensely pigmented than **PQ**, and **PQ** than **pq**, and **pq** than **Pq**; **L** pattern is likewise more fully developed in **pQL** and **PQL** than in **pqL**, and **pqL** than in **PqL**. The development of **Z** pattern is, on the contrary, scarcely affected by the presence of **P** or **Q**.

5) The striped character is dominant to the moricaud, but in certain parts of the body, the moricaud or recessive pattern is apparently developed in the striped hybrid. Similarly the quail factor is partially dominant and partially recessive to the plain. These facts show that the relation of dominance and recessiveness is more complex than is generally supposed.

6) Bringing forth individuals homozygous for the presence of both **S** and **M** is impossible in consequence of complete repulsion occurring between them. This case might be taken as an example of multiple allelomorphism.

7) Coupling and repulsion take place between the yellow (cocoon or haemolymph colour) and either one of the following markings:

1) Quail,
2) Normal,
3) Striped,
4) Striped-quail,
5) Moricaud,
6) Moricaud-quail.

It is not impossible to imagine that all these cases of coupling and repulsion are nothing other than the correlation of **Q** and **Y**, because the **Q** factor is common to all of these markings.

8) Coupling and repulsion in the silkworm are peculiar in being complete in the female, but partial in the male: this phenomenon may be called "dimorphism of gametic series." In connection with this subject, more than 101,000 larvae have been raised in the last four years.

9) Partial coupling and repulsion in the male are comparatively low in intensity; the ratios are usually approximate respectively to 3 : 1 : 1 : 3 and

1 : 3 : 3 : 1, though the ratios fluctuate to a certain extent.

10) Similar dimorphism of gametic series was observed by T. H. MORGAN and his collaborators in the fruit-fly; but in this insect, coupling and repulsion were complete in the *male*, and partial in the *female*, in contrast to what has been observed in the silkworm.

11) Independent inheritance has been proved between the following factors:

T (3-moulting) and **O** (opaque skin)
T and **L**
T and **Q**
T and **M**
T and **Y**
B and **Z**
B and **S**
O and **K**
O and **L**
O and **Q**
O and **M**
O and **Y**
K and **Z**
K and **P**
K and **S**
L and **Z**
L and **P**
L and **S**
Z and **Q**
Z and **M**
Z and **Y**
P and **M**
P and **Y**
T and **K** (knobbed)
T and **Z**
T and **P**
T and **S**
B (malanic) and **L**
B and **P**
B and **M**
B and **Y**
O and **Z**
O and **P**
O and **S**
K and **L**
K and **Q**
K and **M**
K and **Y**
L and **Q**
L and **M**
L and **Y**
Z and **P**
Z and **S**
Q and **P**
P and **S**

12) A wide range of variation is found in the pigment intensity of the normal and quail types. Certain variations transmit their characteristics to the offspring: such heritable variations are probably due to the existence of

several quail factors, say, $\mathbf{Q}^1$, $\mathbf{Q}^2$, $\mathbf{Q}^3$ and $\mathbf{Q}^4$, of which $\mathbf{Q}^1$ is responsible for the lightest, and $\mathbf{Q}^4$ for the darkest normal and quail.

13) Besides these genetic variations, there are considerable intransmissible fluctuations in each subtype.

14) The presence of **P** or the heterozygous condition of **Q** may sometimes cause a reduction of "eyebrows" in the light normal and light quail, and gives rise to "specious plain" and "specious pale-quail."

15) Light normal or quails ($\mathbf{Q}^1$ subtype) are often produced in crossing one of the $\mathbf{Q}^3$ or $\mathbf{Q}^4$ type markings (darker normal, darker quail, striped, moricaud) with one of the **q** type patterns (plain, pale-quail), a fact which is explicable on the basis of multiple factor hypothesis.

16) Moricaud und striped markings are also subject to variation within certain limits.

17) There are various strains of the *normal* marking which differ from each other in minor points; these differences, though insignificant, are transmitted to the offspring. This fact shows that the so-called unit characters are not "unit" in strict sense but are comparable to chemical compounds; modified strains may be compared with isomers or derivatives.

18) Several heritable gradations of colour are distinguishable in yellow and green cocoons. These colour differences depend upon different genetic factors for various subtypes.

19) Moulting character is highly variable according to environmental influences, and naturally there may exist many "specious" 3-moulters as well as "specious" 4-moulters which do not inherit their apparent or acquired characters to the offspring.

20) In order to explain the unusual phenotypic ratios which are often met with in the inheritance of moulting character, I assumed two conditional factors, $\mathbf{T}^a$ and $\mathbf{T}^b$, the simultaneous presence of which gives 3-moulters. Owing to the high variability of this character, the above assumption is still tentative.

21) Mosaic of somatic characters does not necessarily accompany the mosaic of sexual characters, i. e. gynandromorphism.

22) I believe mosaics are produced by mutations, either major or minor, occurring in the segmenting cells in different stages of embryonal development. By "mutation" I mean assumed sudden check of physiological functions of a gene or genes, or a sudden revival of them in the egg-cells.

23) Mosaic abnormality in the silkworm are not only known with regard to various larval patterns (striped, moricaud, normal, plain, quail, zebra, multilunar), body colour (opaque and oily) and sex, but even size mosaic has been observed, though only once.

24) Mosaics appeared in hybrids as well as in pure breeds, but they are more frequent in the former.

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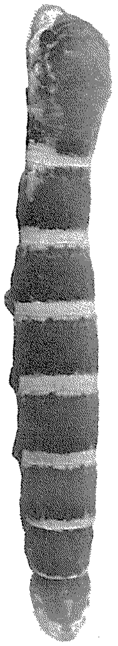
Explanation of Plate I.

Fundamental or Primary Markings.

Fig. 1. Striped (SmPQzl), dorsal.
Fig. 2. ditto, ventral.
Fig. 3. Moricaud (sMPQzl), dorsal.
Fig. 4. ditto, ventral.
Fig. 5. Normal (smPQzl), dorsal.
Fig. 6. ditto, ventral.
Fig. 7. Plain (smPqzl), dorsal.
Fig. 8. ditto, ventral.
Fig. 9. Quail (smpQzl), dorsal.
Fig. 10. ditto, ventral.
Fig. 11. Pale-quail (smpqzl), dorsal.
Fig. 12. ditto, ventral.
Fig. 13. Zebra (smPqZl), dorsal.
Fig. 14. ditto, ventral.
Fig. 15. Multilunar (smPQzL), ventral.
Fig. 16. ditto, dorsal.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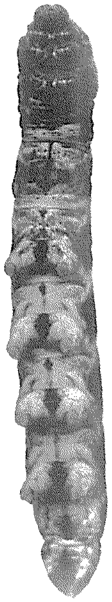
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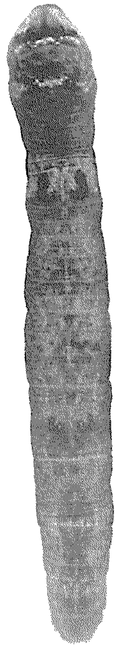
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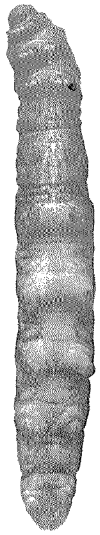
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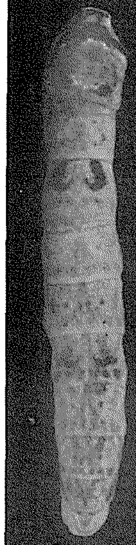
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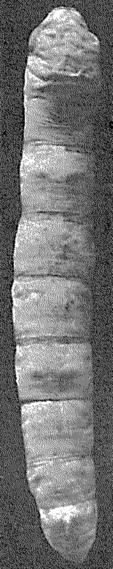
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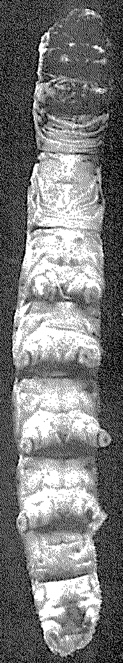
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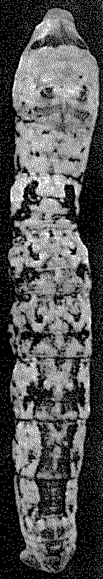
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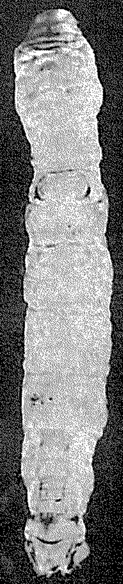
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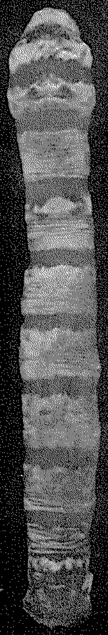
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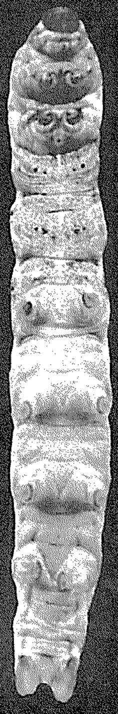
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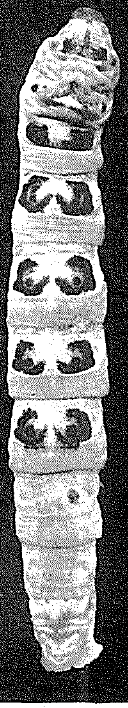
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Explanation of Plate II.

Combined or Secondary Markings.

Figs. 17–19. Striped-moricaud hybrids (SMPQzl). The marking is practically striped, but the characteristic pattern of the moricaud is visible on the intersegmental regions, on the under-surface of anterior body segments, and on the head-case.

Fig. 20. F_1 hybrid of the domestic striped and wild silkworm (*B. m. mandarina*, moricaud), dorsal. Combined development of S and M characters is also visible here.

Fig. 21. Multilunar-moricaud (sMPQzL), dorsal.

Fig. 22. Multilunar-striped (SmPQzL), dorsal.

Fig. 23. Striped-zebra (SmPQZl), dorsal. The characteristic bands and spots of zebra-type are visible, first of all, on the head-case, *on the dorsal of segments III and IV, on the ventral of* segments IV and V. (*cf.* Fig. 27.)

Fig. 24. Striped-quail (SmpQzl), dorsal.

Fig. 25. Moricaud-quail (sMpQzl), dorsal.

Fig. 26. ditto, ventral.

Fig. 27. Striped-zebra (SmPQZl), ventral.

Fig. 28. Moricaud-zebra (sMPQZl), dorsal.

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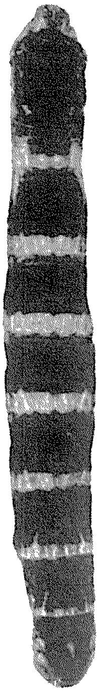

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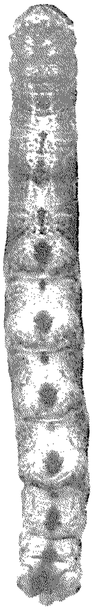

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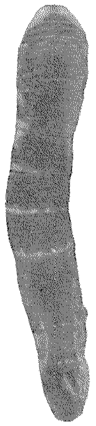

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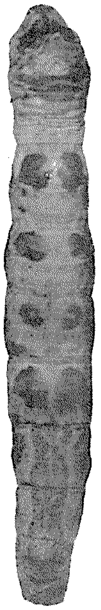

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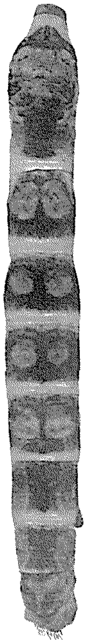

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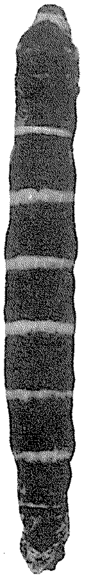

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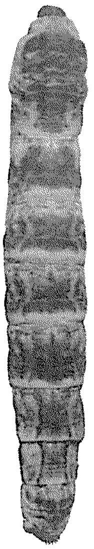

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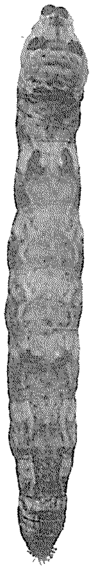

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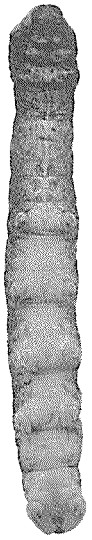

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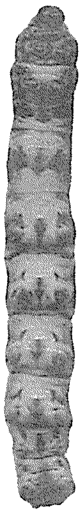

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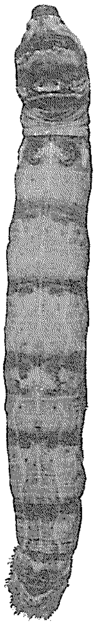

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Explanation of Plate III.

Combined or Secondary Markings—*Continued.*

Fig. 29. Quail-zebra (smpQZl), dorsal.

Fig. 30. ditto, ventral.

Fig. 31. Multilunar-quail (smpQZL), lunar spots as numerous as 7 pairs, dorsal.

Fig. 32. Zebra-normal (smPQZl), dorsal.

Fig. 33. Zebra-normal, knobbed (smPQZlK), dorsal.

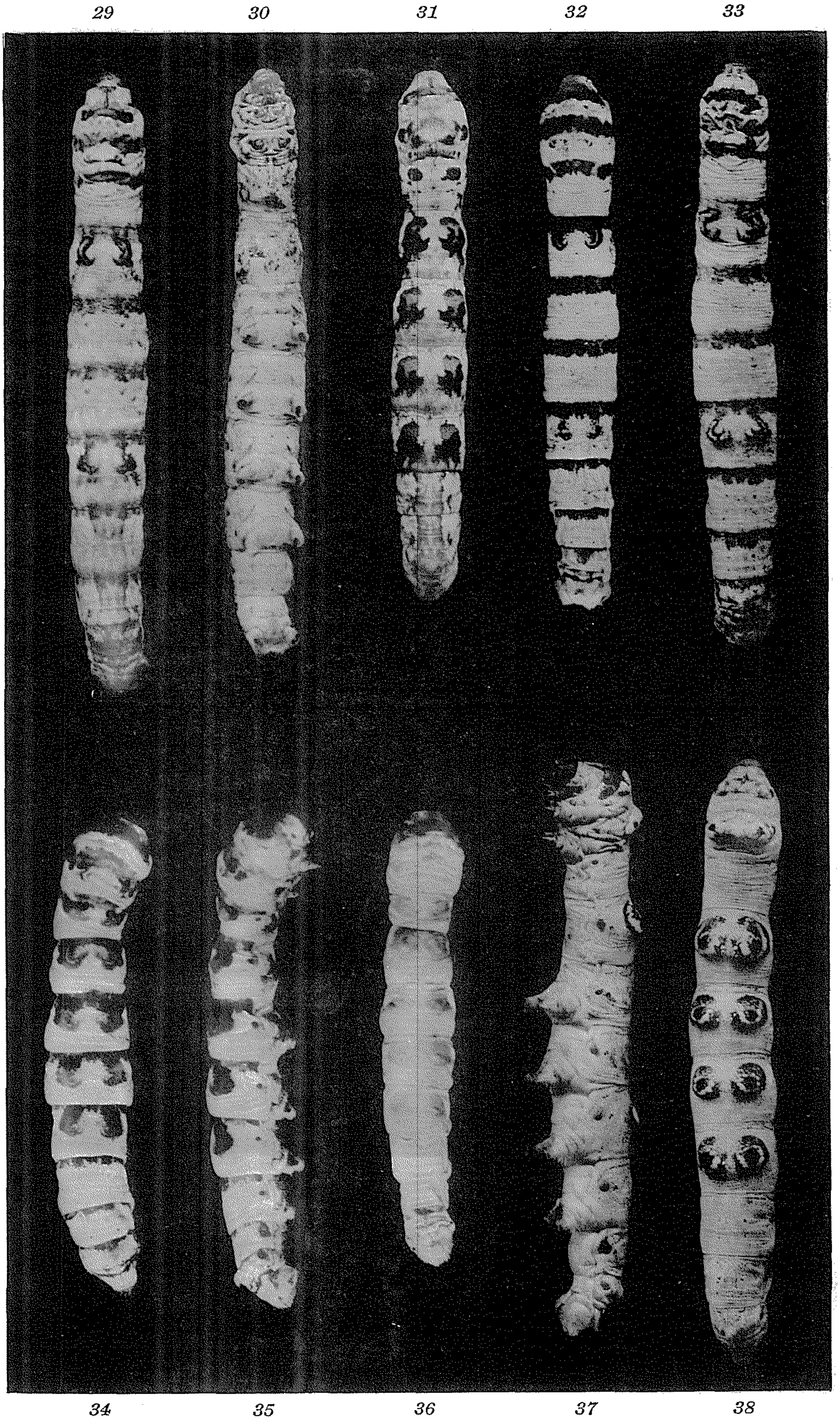
Fig. 34. Multilunar-normal-zebra (smPQZLk), dorsal; lunar spots 7 pairs.

Fig. 35. ditto, lateral.

Fig. 36. Multilunar-plain (smPqzL), dorsal.

Fig. 37. Normal (smPQzlK), knobbed, lateral.

Fig. 38. Multilunar-normal, knobbed (smPQzLK) dorsal; lunar spots and knobs 6 pairs.



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Explanation of Plate IV.

Variation of Normal Marking.

Figs. 39–41. Normal of PQ^4 subtype, showing fluctuation.

Fig. 42. A normal of PQ^3 subtype or moderate intensity.

Fig. 43. A PQ^2 normal.

Fig. 44. A PQ^1 normal.

Fig. 45. A plain.

Figs. 46–49. Variation of the "eye-spots" or "eyebrows".

Fig. 46 (a, b). PQ^4 normal.

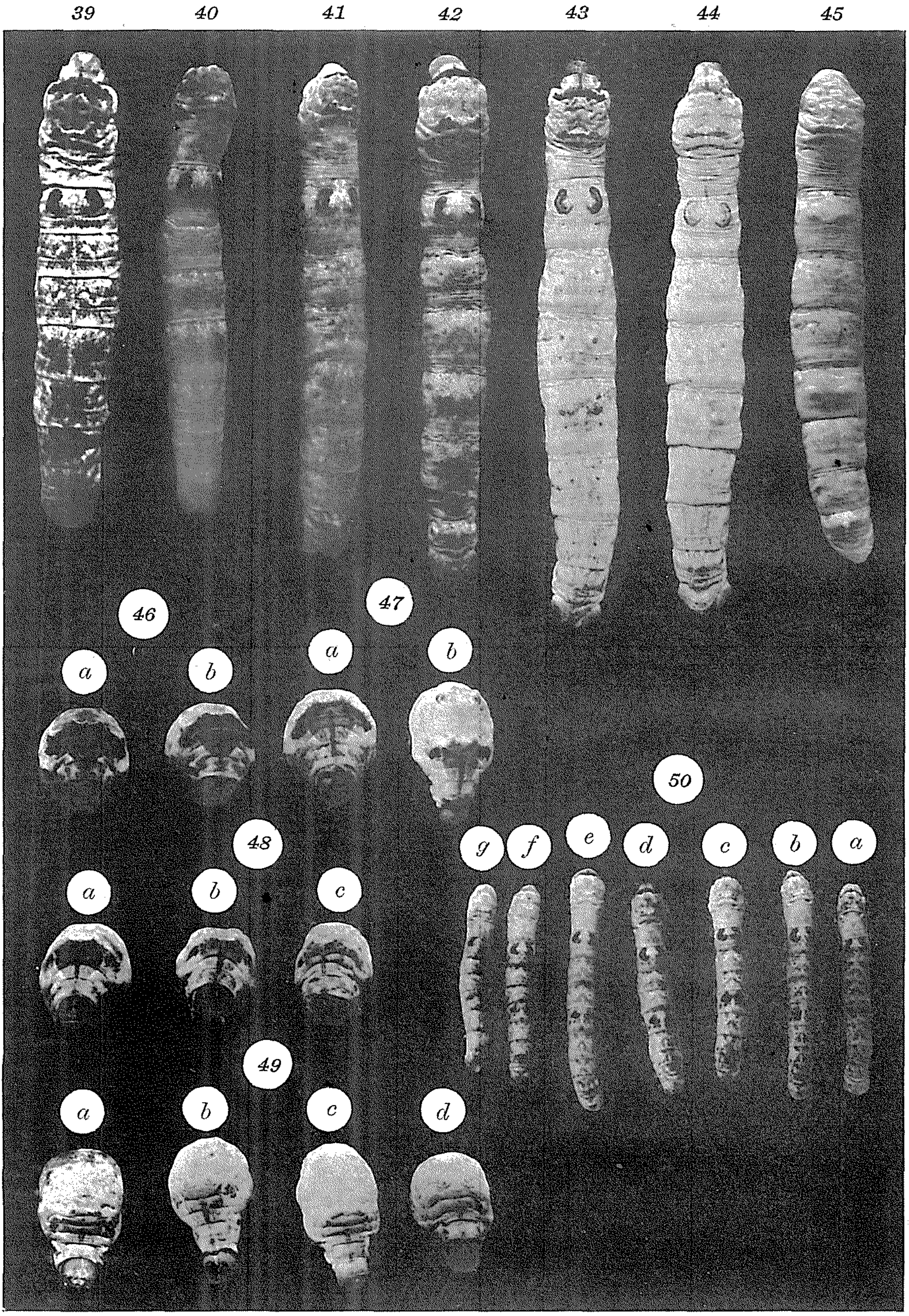
Fig. 47 (a, b). PQ^3 normal.

Fig. 48 (a–c). PQ^2 normal.

Fig. 49 (a–d). PQ^1 normal, d representing a "specious" plain.

Fig. 50 (a–g). Variation of normal pattern in the third larval stage, the pattern pigment ranging from the darkest (a) to the lightest (g).

Pl. IV.



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Explanation of Plate V.

Variation of Moricaud and Quail Markings; Modified
Normal and Quails.

Figs. 51–53. Variation in full-grown moricauds, ranging from the lighter (51) to the darker (53).

Fig. 54. Pale-quail.

Fig. 55–58. Variation in quails.

Fig. 55. pQ^1 quail.

Fig. 56. pQ^2 quail.

Fig. 57–58 pQ^3 quails.

Fig. 59 (a–c). "Eye-spots" of pQ^1 (b, c) and pQ^2 (a) quails.

Fig. 60 (a–f). Variation of moricaud pattern in the third larval stage (*cf.* Fig 50).

Fig. 61. A wild silkworm with the extra "semilunules".

Fig. 62. A normal with the extra or third "semilunules" (l) on segment IX.

Figs. 63–64. Normal the "eye-spots" of which are darker than the "semilunules". Posterior "semilunules" are entirely lost in both individuals, anterior "semilunules" are very light (63) or absent (64), whereas, "eye-spots" are much more distinct.

Fig. 65. A normal provided with distinct "semilunules" and far lighter "eye-spots".

Fig. 66. A quail in which "eye-spots" are nearly absent, while two pairs of "semilunules" and other spots are very distinct.

Fig. 67. A quail with equally developed "eye-spots" and "semilunules".

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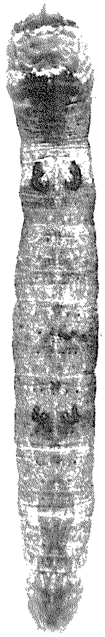

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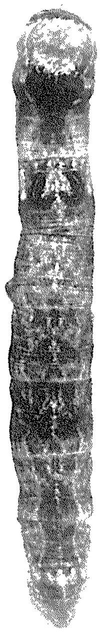

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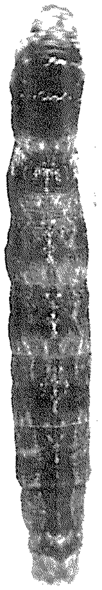

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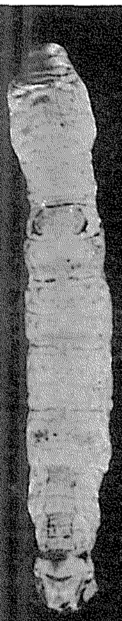

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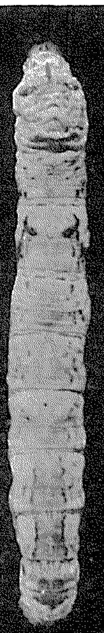

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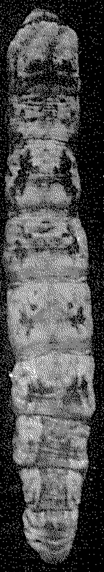

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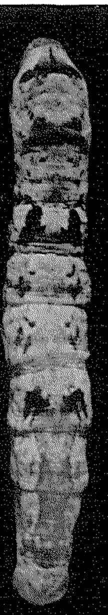

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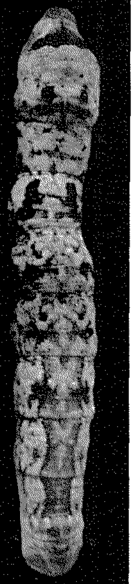

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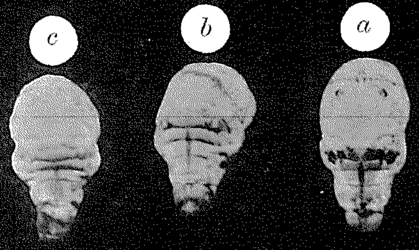

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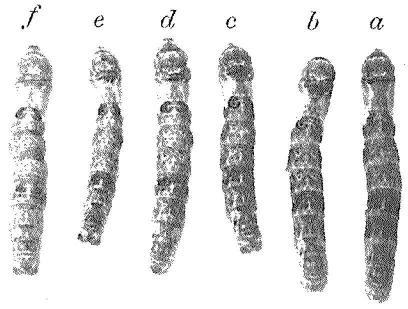

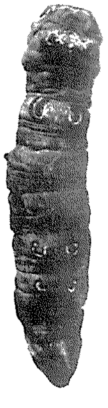
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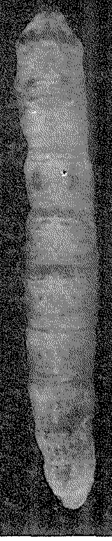
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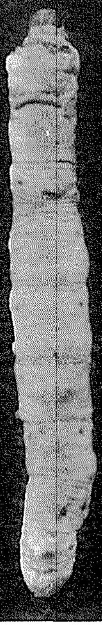
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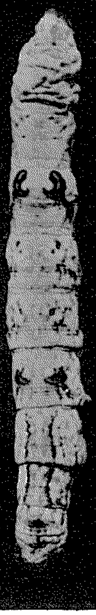
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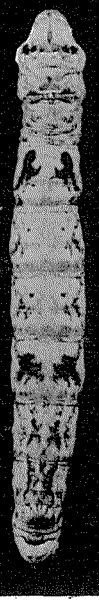
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Explanation of Plate VI.

Mosaic Monsters.

Fig. 68. A "rgiht (moricaud)- left (normal) mosaic".

Fig. 69. A normal-marked larva; the dark spots on the left half represent the "oily" areas.

Fig. 70. A striped-normal mosaic; the right anterior and left posterior quarters are practically striped, the right posterior and left anterior quarters are, for the most part, normal-marked.

Fig. 71. ditto, ventral view; the median spots anterior to segment VIII are in asymmetrical form.

Fig. 72. A striped-normal mosaic. In segments VI, VII and VIII the striped (black) and normal (white) characters are interspersed on both sides; in the other segments the right is, speaking in general, normal, the left striped.

Fig. 73. Moricaud-quail mosaic. In the left half, the moricaud pattern is absent in portions as shown by white patches scattered about.

Figs. 74–76. Striped larvae with white patches, the distribution of which seems scarcely influenced by the axis of symmetry.

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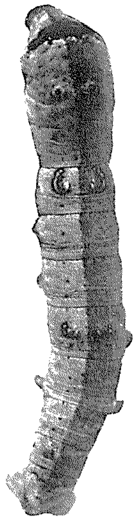

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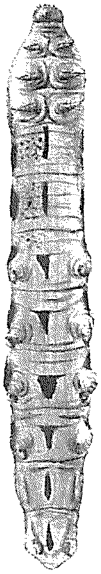

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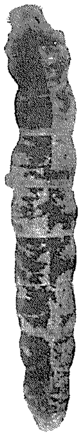

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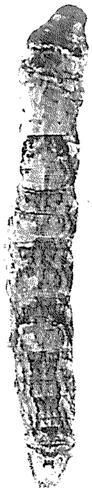

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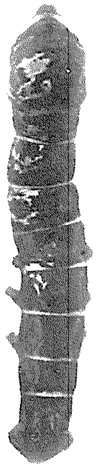

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