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On certain characteristics of the Silk-worm which are apparently non-Mendelian.

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Since the discovery and confirmation of Mendelian principles in 1900 by three independent workers, Correns, Tschermak and De Vries, a great many experiments have been carried on by many eminent biologists. As a result, the theory now stands on firm ground, supported by many facts verified by experiments which have been systematically carried out, and thus has been rendered possible that rapid advance which has taken place in the science of Genetics.

In the first part of the last ten years when there were only a few experiments systematically carried on after Mendelian methods, there were enumerated many non-Mendelian cases in the inheritance of characteristics, and even now some anomalous cases exist; but as the experiments advanced in number and became more accurate, we gradually perceived that we could easily show these so-called anomalous cases to be in accordance with the Mendelian Theory.

In the breeding of silk-worms, we have found certain cases in which Mendelian characteristics show themselves to be non-Mendelian in heredity. I shall describe them in the following pages.

Before entering upon the subject, we shall enumerate the normal Mendelian characteristics found in the silk-worm during the last five years. In my first experiments on the breeding of silk-worms published in 1906, we came to the conclusion that "of various characteristics of the silk-worm, some strictly follow Mendel's laws (colours of cocoons, larval markings etc.), while others obey certain other laws which are not to be clearly formulated as Mendel's (such as voltine characters)", concerning the latter of which McCracken[1]) arrived at the same conclusion in her paper published in 1909. An investigation made by Kellogg[2]) (1908) gave a similar result. He says "Larval colour-pattern differences are consistently and rigorously alternative and Mendelian in inheritance" and "cocoon colours tend to be alternative and Mendelian in behaviour but are inconsistent as to dominancy and recessiveness and numerical proportions, and may even break down and blend, or one colour be otherwise influenced or modified by the presence, in a mating, of another. Thus sweeping generalizations concerning the inheritance behaviour of the cocoon colours tending to class them unqualifiedly in the Mendelian category can not be made. The tendency is for them to behave in Mendelian manner, but it is a tendency subject to numerous, marked and various inconsistencies and irregularities."

Now we shall briefly enumerate the various characteristics of silk-worms studied by us since 1907.

Larval Characteristics.

1. "Exuviation." Certain breeds of the silk-worm moult four times during their larval stage, while others only moult three times. We call the former tetra-moulting worms and the latter tri-moulting. Most of the good breeds now in vogue belong to the former class. These are Mendelian characteristics, the tetra-moulting being recessive to the tri-moulting There are found sometimes tri-moulting worms among ordinary tetra-moulting ones. In this case, the characteristic is not transmissible to the offspring. We believe now that it is caused by certain external influences.

2. The colour of the blood. In the silk-worm, there are two sorts of breeds, the one being yellow-blooded and the blood of the other being colourless. All the former spun yellow or some other coloured cocoons, while the latter are mostly white cocooners, rarely green or canary yellow cocooners. These characteristics come also in the Mendelian category, the yellow blooded being dominant towards the colourless. Most European yellows belong to this category. All the green breed are colourless.

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1) McCracken, J. — Heredity of the race-characters univoltism and bivoltinism in the silk-worm. 1909.

2) Kelogg, L. — Inheritance in silk-worms. 1908.

3. Blue worms. In Japanese or Chinese breeds, we often found certain blue worms, characterized by the special blue colour of the skin, its cause being the absence of special pigments in the hypodermal cells. This is also a Mendelian characteristic and recessive to the normal-skinned characteristic.

4. "Knobbed" or "Dragon-horned" worms. In the larvae of certain Chinese breeds called "Dragon-horned", the worm has a pair of small knobs or horns on the dorsal part of certain segments. These knobs are only an evagination of hypodermal epithelium together with the cuticle, and are generally found on the second, third, fifth and eighth, sometimes on the sixth or seventh, and more rarely on the other segments. This is also a Mendelian characteristic dominant to the normal one. Quajat's[3]) results are quite in accordance with ours.

5. Spotted worms. These are characterized by the presence of a pair of large yellowish brown or greenish brown spots on the dorsal part of certain segments of the worm. As to their number, it varies greatly according to the individual. Thus certain worms have the pair of spots in every segment except the anal segment, while some others bear a pair of the spots on the fifth and eighth segments. Normally they are provided with the spots on the 5th, 7th, 8th and 9th. This is also a Mendelian characteristic, dominant to the absence of this characteristic.

6. Striped characteristic. Worms who are decorated with these markings are called striped or zebra worms. They are found in breeds reared in Japan, China, India, Siam, Korea, Europe or Turkey. This is also a Mendelian characteristic, dominant to the non-striped characteristic.

7. The red and dark worms[4]). In normal breeds, the worms in the first larval stage are brownish black, but now and then we find orange-red worms whose larval markings in advanced stages are reddish brown, contrary to the normal dark or brownish black colour. This is a Mendelian characteristic recessive to the normal dark.

8. Moricaud or "bear" worms. These are found in certain European, Turkish, Japanese, Chinese or tropical breeds.

9. Chinese black worms, characterized by the dark markings which cover all the dorsal part of the larval body except the inter segmental region, where it is white, and consequently it looks like a black worm striped with white rings.

10. Normal patterned worms. These are generally found in nearly every breed. The ground colour of the body is nearly white, marked with fine spots or faint markings. Conspicuous

3) Quajat-Gulla reproduzione degli incroci. 1911.

4) Toyama, K. — A sport of the silk-worm and its hereditary behaviour. 1909.

markings are those of the eye-brow on the second segment, a pair of horse-shoe shaped markings on the fifth, and a pair of roundish markings on the eighth.

11. "Smudged" or "Kasuri" worms. These are found in Japanese breeds. They are characterized by the presence of markings like light smudges over the dorsal part of the body.

12. Pale worms, which have lost nearly all the markings.

13. Pale smudged worms which are the pale form of the smudged worms just referred to.

These latter six kinds (Nos. 8—13) of markings may be divided into two classes, one of these having "special markings" and the other having no special markings. By the words "special markings", we mean those markings which are found on the second segment or the "eyebrow", a pair of horse-shoe-shaped ones on the fifth, segment, and a pair of roundish ones on the eighth. The other markings which decorate the general surface of the body will be called "general markings", except certain markings which are found on the ventral side of the segments.

The moricaud, Chinese black, normal-patterned, and smudged worms, belong to the category which possess the special markings, and the latter two, pale and pale smudged, to the category of those which do not possess the special markings. They are Mendelian allelomorphs, the presence being dominant towards the absence.

In the general markings, the Chinese black stands first in dominancy, then in order come the moricaud, the normal smudged, pale, and pale smudged markings.

The relation between normal, smudged, pale, and pale smudged is very interesting because if we cross certain pale worms with smudged worms, the results will be the production of all normal F_1 which gave in F_2 9 normals: 3 smudged: 3 pales and 1 pale smudged. In the mating between pale and pale-smudged, the F_1 is all pale worms, which segregate into 3 pales to 1 pale-smudged in F_2. The phenomena of inheritance are quite the same as those observed by Bateson in fowls and many plants[5]).

In the silk-worm larvae we may therefore enumerate the following Mendelian characteristics:

Dominant.	Recessive.
1. Trimoulting characteristic.	Tetra-moulting characteristic.
2. Yellow blood characteristic.	The absence of yellow colour characteristic.
3. The presence of some pigments in the hypoderm.	The absence of pigments.
4. The presence of knobs.	„ „ „ knobs.
5. The presence of spotted markings.	„ „ „ spotted markings.

5) Bateson, W. — Mendel's principles of Heredity. 1909.

Dominant.	Recessive.
6. The presence of striped markings.	The absence of striped markings.
7. Dark worms.	Orange-red worms.
8. The presence of the special markings.	The absence of the special markings.

General Markings.

9. Chinese black.	Moricaud.
10. Moricaud.	Normals.
11. Normals.	Smudged.
12. Smudged.	Pale.
13. Pale.	Pale-smudged.

Colour-characteristics of the Cocoon.

Now we shall observe the colour of cocoons. Regarding the relation between Japanese white and European yellow, as we have already reported in my previous papers, the yellow is dominant to the white. The Japanese white is also recessive to the Japanese yellow (Onodahime). When we crossed European yellow, Papillons noirs with Japanese divoltine white, the segregation is quite complete and they gave the proportion of yellow and white in each mating, as demanded by the Mendelian theory and the yellow is dominant to the Japanese white. On the contrary, European whites, such as Italian white, and Sina blanc, are dominant to Japanese or European yellows.

As the results of many series of experiments we are justified in saying that there are two kinds of white breeds in the silk-worm, one being dominant and the other recessive towards the same yellow. As far as our experiments went, the majority of European whites are dominant, some of them being a mixture of both dominant and recessive whites. Most Oriental whites, on the contrary, are recessive to the yellow and some other coloured cocooners.

If the crossing were made between such a mixed white breed with yellows, the results would be quite different from that obtained by normal mono-hybrid.

Let us now represent the dominant white by WW and the recessive white by ww and the yellow by YY. In a mixed white, we may infer that there exist three kinds of whites having different zygotic compositions, WW, Ww and ww. Hence in the F_1 derived from the white $\times$ the yellow, we expect to have the following gametic combinations:

1. $WW \times YY = WY =$ all white F_1.
2. $Ww \times YY = WY + wY =$ a mixture of white and yellow in an equal proportion.
3. $ww \times YY = wY =$ all Yellow F_1.

The first or homozygous dominant white mated with yellow gives all white F_1, the second or heterozygous white mated with yellow, a mixed F_1, consisting of yellow and white in equal proportions, and, lastly, the third or homozygous recessive mating, all yellow F_1. Hence in such white-yellow matings, F_1 will consist of three kinds of offspring.

As the composition of all white F_1 is WY, the F_2 will be 3 whites: 1 yellow, while all yellow F_1 whose composition is wY will give diametrically opposite results; namely 1 white: 3 yellows in F_2. The posterity of these series will follow the mono-hybrid principle, in the former, white always behaving as dominant, and in the latter, as recessive.

In the series in which the F_1 is a mixed offspring of white and yellow, both white and yellow segregate again into their components and thus the phenomena of inheritance seem to be quite inconsistent with Mendelian principles, if we considered them to be a case of Monohybrid back-crosses, 1 W : 1 Y. As the formula shows, however, both of them are heterozygous, and therefore their segregation in F_2 is consistent with Mendelian principles, and the white is dominant in the white series, and recessive in the yellow series.

Thus the order of inheritance of mixed white mated with yellow will be represented as below:

Mixed White × Yellow.

	(1.)	(2.)	
F_1	All W	(1 W	: 1 Y)
F_2	(3 W : 1 Y)	(3 W : 1 Y)	(1 W : 3 Y).

	(3.)
F_1	All Y
F_2	(1 W : 3 Y).

(4.)

(F_1 white × F_1 yellow.)

F_1	(1 W	: 1 Y)
F_2	(3 W : 1 Y)	(1 W : 3 Y).

The results of experiments made by Coutagne and Kellogg may come in the same category. We shall now quote their results graphically summarized from their original papers[6]).

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6) Coutagne, G. — Recherches expérimentales sur l'hérédité chez les vers a soie. 1902.

Kellogg, V. L. — Inheritance in silk-worms. 1908.

Coutagne's results.

White × Yellow.

(1.)

F_1	All W (1,750)
Expectation	All white
F_2	White (75,5 %) + Yellow (27,5 %)
Expectation	75 % + 25 %.

(2.)

F_1	(White (818) +	Yellow [849])		(F_1 Y × pure W)
Expectation	833,5 +	833,5		
F_2	W (1,016) + Y (432)	W (624) + Y (645)	W (359) + Y (964)	All W
Exspectation	(1,086 + 362)	(634,5 + 634,5)	($330^3/_4$ + $992^1/_4$)	all w.

(3.)

All White F_1 × pure yellow.

F_1	W (257) +	Y (307)
Expectation	1 W +	1 Y
F_2	W (710) + Y (247)	W (6?) + Y (871)
Expectation	W ($717^3/_4$) + Y ($239^1/_4$)	All yellow.

(4.)

F_1	All Yellow
Expectation	All yellow
F_2	0.

Kellogg's results.

(Bagdad white × Istrian yellow.)

(1.)

F_1	All W.
Expectation	(all white)
F_2	W (139) + Y (32)
Expectation	(3 W + 1 Y).

(2.)

F_1	All Y
Expectation	(All yellow)
F_2	W (52) + Y (125)
Expectation	(1 W + 3 Y).

(3.)

F_1	W (41) + Y (30)		
Expectation	(1 W + 1Y)		
F_2	W (216) + Y (108)	W (283) + Y (315)	W (65) + Y 255)
Expectation	(3 W + 1 Y)	(1 W + 1 Y)	(1 w + 3 y).

4.

	(F_1 W × F_1 Y)
F_2	W (66) + Y (41)
Expectation	(1 w + 1 y).

W = White, Y = Yellow.

As we expected, both Coutagne's and Kellogg's results gave three sorts of F_1 broods: namely, all White, all Yellow, and a mixture of both white and yellow in an approximate proportion of 1 W : 1 Y. In the white F_1 series, the white behaved as dominant and in the yellow series the white is recessive towards yellows, their proportion being approximate to the expected number, while F_1 white mated with F_1 yellow gave a mixed F_2. In the third series of Coutagne's summary, there are found six white cocoons in F_2 yellow matings which are not demanded by the theory, and in certain of Kellogg's matings the proportion of white and yellow does not accord well with the ratio which our hypothesis demands. The former was possibly due to some accident, and the latter to the small number of worms reared in each mating.

Certain egg-characteristics.

Lastly, we shall notice the phenomena of inheritance observed in certain egg-characteristics in which the results seemed to us to be more irregular than in the case of varying dominance of cocoon-colour quoted above.

The ordinary colour of Japanese silk-worm eggs is a light greenish-white when newly laid. With the formation of the blastoderm, it gradually becomes of a brownish tint which at last turns into brownish-slate shaded with some light pink or purple. This is the normal colour of the egg of the Japanese breeds used in our experiments.

Among these normal eggs, we find sometimes many variants which are decidedly different from the normal ones, for instance, light brown, bluish-grey, orange, light orange, greenish white, crimson-red, and many others.

As to the shape the normal one is oval, slightly pointed at one end where a micropyle is situated. It is slightly flattened

and its surface is convex when newly laid but after a few days it becomes depressed in the middle, thus producing the characteristic form which is familiar to us. As in the colour, there are many variants, the one with which we made our experiments being a spindle-shaped variant derived from a normal-egged breed.

As the egg consists of the shell, vitelline membrane, serosa and yolk, each of which is coloured or shaded with certain tints or pigments, except the vitelline membrane, the colour of the egg is formed by the combination of those colours. In the case of the variants enumerated above, the colour is mostly influenced by the serosa, in which plenty of pigments are deposited, the colour of the shell and yolk playing a very small part in forming the colour of the egg, since most shells are white or only slightly shaded, except that of the green breed in which we find deep green coloured shells.

In the newly laid egg, the colour of the yolk plays an important part in forming the colour of the egg.

As to the shape, the shell is the chief factor in determining it. Those characteristics such as whitish grey eggs and spindle-shaped eggs belong to this category.

Now, then, let us quote here the results of line breeding on breeds possessing certain special egg characteristics.

Serie I.

The light brown egg.

In the winter of 1907, we obtained certain batches of eggs, some of them being light brown and the others normal brownish slate. Both of them were derived from a divoltine white called "Shinkawachi". Each of them, when inbred, gave the antagonistic characteristic in the following order:

Parent Eggs	Normal coloured eggs		
F_1	(Brown	+	Normal)
F_2	All divoltine White[7])		All divoltine White
F_3	N (10) + B (30) + M (36)		B (10) + N (10) + M (18)
F_4	All W		B (14) + N (28) + M (16)
F_5	All B (64)		B (1) + N (6) + W (48)
F_6	All W		N (6) + W (33)
F_7	All B (572)		N (25) + W (4).

B = brown batch; N = normal; W = divoltine white; M = mixed batch of brown and normal.

7) In di-, tetra- or multivoltine breeds, the eggs laid by the spring brood generally do not develope any dark pigments in the serosa and therefore they remain pale white in colour until the embryo is developed. This is a normal characteristic of these breeds.

Each batch laid by a mating was reared separately, but both the brown and normal colour-characters produced the antagonistic characteristics for certain generations, and at last both became a constant form.

Series II.

The Whitish Grey Egg.

This is also a variant derived from the divoltine normal-egged race called "Chusu". This is characterized by the special structure of the shell. In the ordinary breed, it is elastic and translucent and the surface is smooth. That of the variant, on the contrary, is thick and rather brittle, with the surface irregularly corrugated. It is opaque, and the colour of the serosa can hardly be seen through the shell in consequence of which a peculiar whitish colour is produced. There is no depression in the middle.

In the spring of 1909, we reared two batches of the variant. They, paired inter se, gave the following result, which is nearly similar to that given in the preceding table.

$$
\begin{array}{ll}
F_1 & \overbrace{\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad}^{G} \\
F_2 & \overbrace{\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad}^{(N \quad + \quad G)} \\
F_3 & \overbrace{N + \overbrace{(N + G)}} \qquad\qquad \overbrace{(N + G)} \\
F_4 & \overbrace{\text{all } N} \qquad\qquad \overbrace{(N + G + BG)} \\
F_5 & \overbrace{\text{all } N} \qquad\qquad \overbrace{(G + BG) \quad (N + G + BG)} \\
F_6 & \overbrace{\text{all } N} \qquad\qquad \overbrace{(G + BG)}.
\end{array}
$$

G = Greyish white; N = Normals; Gb = a new form.

Series III.

The spindle-shaped egg.

This is also a variant derived from the univoltine Japanese white, which usually lays oval eggs. The egg is a long spindle-shaped one and is slightly pointed at both ends. There is no depression in the middle, which is a characteristic common to ordinary silk-worm eggs.

The first generation, was reared in the spring of 1909. They gave all normal-shaped eggs without any exception. The second generation derived from the normal eggs gave two sorts of batches, 33 being normal and 13 spindle-shaped batches.

Both of them again produced the antagonistic characteristic in the next generation. Thus

$$
\begin{array}{ll}
F_1 & \overbrace{\text{Sp (1)}} \\
F_2 & \overbrace{N} \\
F_3 & \overbrace{\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad}^{(N \quad + \quad Sp)} \\
F_4 & \overbrace{(N + Sp)} \qquad \overbrace{(N + Sp)}.
\end{array}
$$

Sp = spindle-shaped; N = normal.

When we crossed those variants above described with normal-egged breeds, the results were nearly the same except the production of pure normal form in F_2.

Such phenomena of inheritance might be mistaken as non-Mendelian, since both characteristics produce antagonistic characteristics and seem to be neither dominant nor recessive.

Are they really non-Mendelian?

Let us consider the results of the other series of our experiments and our opinions deduced from them.

Series IV.

Reciprocal crosses between certain breeds which have special colour characteristics of the egg.

1. Chinese "Joken" and Japanese "Aobiki".

The former has a special greenish characteristic and certain other characteristics such as lustre and shade, which are quite wanting in the latter breed.

In this cross, Chinese females mated with Japanese males gave all Chinese characterized eggs, on the contrary, the reversed matings all Japanese coloured eggs. This cross was repeated with various breeds, the result being always the same.

2. Japanese green and normal white.

The former have a greenish shade while the latter have not. The shell is also more or less tinted with green in the former, some shells very slightly; while the shell of the latter is quite devoid of any greenish tint.

The results of reciprocal crosses are the same as in the former cross, that is to say, green females mated with normal males gave eggs which are entirely the same as those of pure green breeds. The contrary is the case when normal females are used.

3. A light brown-egged breed and a normal-egged breed. The results are entirely the same, the phenomena of inheritance are quite maternal, no paternal influence was observed.

4. Theophila mandarina × Bombyx mori.

In this case, the same holds good in any mating.

5. Papillons noirs × Tetravoltine white.

This is another example of matroclinous inheritance.

In those cases above mentioned, even the eye of experienced breeders could not distinguish the pure-bred eggs from cross-bred ones.

6. In the case of albinos, the phenomena are a little different from those described above.

In our experiments, we made use of three kinds of albinos, one derived from a Japanese normal univoltine white called "Chusu"

and the other from a cross between Theophila mandarina and Bombyx mori (Tetravoltine white), both of them being established as a constant form by ourselves, and the third, a breed extracted from a Chinese univoltine white by Ishiwata.

Of females from the first and the third albinos mated with normal males, some gave characteristic white eggs, some a mixture of both white and many other light coloured eggs, that is to say, some intermediate coloured ones, rarely normal light coloured eggs; but they are never so dark as pure normal dark coloured eggs. The reversed mating gave, on the contrary, all normal coloured eggs, no influence of an albinotic character could be seen.

Some albinotic forms derived from the second albino: namely the albino derived from the cross, "Theophila × Bombyx" behaved in a normal Mendelian way, the white being recessive towards the normal coloured ones. In this case, reciprocal crosses gave the same results, that is to say, only dominant characteristics make their appearance in F_1.

The results of the reciprocal matings above described, taught us that there are certain egg-characteristics which behaved as matroclinous in inheritance, and even dominant ones when belonged to males remained dormant in the offspring. As regards dominancy and recessiveness, some are perfect, while others are imperfect, in the latter some intermediate or mixed forms will be produced. We found also that the segregation of parental characteristics in the offspring takes place in the same way as Mendelian characteristics do.

As to the causes of the matroclinous inheritance above described, there may be two.

a) Where the origin of egg-characteristics is due to the shell or yolk, which are the products of the female parent before fertilization takes place; and, b) where their origin is due to the pigment of the serosa, which is derived from the conjugation of paternal and paternal nuclei. In the former, it is quite natural that the egg-characteristics should be matroclinous in inheritance, and in the latter, we attribute it in agreement with de Vries' theory, to the migration of maternal pangens to the cytoplasm before the entry of a spermatozoon into the egg, and thus paternal pangens have no, or very little, influence upon the characteristics of the eggs.

Now we return to Mendelian questions. Suppose there are some characteristics which are predetermined by the maternal gens before fertilization takes place. In such a case, even the dominant characteristic, when belonging to males, will not act as a potent characteristic in the offspring. If D represents a dominant factor and R a recessive, their reciprocal crosses would give diametrically opposite results as shown below:

			outer appearance	zygotic composition
F_1	D × R	=	D	DR
F_1	R × D	=	R	DR.

In the case where the female is recessive, the resulting F_1 eggs will be all R in their appearance and in the reversed mating all D. Zygotically, however, they are both the same; namely DR in their composition.

Moths derived from F_1 D, or R eggs whose zygotic composition is DR when mated *inter se* will give the following combination in F_2.

$$DR \times DR = DD + 2RD + RR.$$

Considered zygotically, therefore, F_2 eggs will be of three kinds, DD, DR, and RR but to outward appearance they are all D, no R ones, since all the females have the composition DR in which D only is an active factor in determining the character of the egg which is formed in the body of the female before fertilization takes place, provided that dominancy is perfect. If this is not the case, there would be produced some batches in which both D and R forms are mixed together.

In spite of being all D in F_2, the moths derived from F_2 worms have a different composition; namely DD, DR, and RR. As we have no means of distinguishing them from one another by outward appearance, we should expect to have a random mating between them. They will give the following combination in F_3.

			Outward appearance	Zygotic composition
1.	♀ DD × ♂ DD	=	D	DD
2.	♀ DD × ♂ DR	=	D	(DD + DR)
3.	♀ DD × ♂ RR	=	D	DR
4.	♀ DR × ♂ DD	=	D	(DD + DR)
5.	♀ DR × ♂ DR	=	D	(DD + DR + RR)
6.	♀ DR × ♂ RR	=	D	DR + RR
7.	♀ RR × ♂ DD	=	R	DR
8.	♀ RR × ♂ DR	=	R	(DR + RR)
9.	♀ RR × ♂ RR	=	R	RR

By the reasoning above stated, those females with the composition of DD or DR will give all D F_3 eggs and those with RR all R eggs, in spite of their males being DD, DR or RR.

Hence F_3 eggs derived from F_2 D eggs should be D and R, that is to say, some matings will produce all D batches, others all R eggs, and if all the moths were reared the proportion of D and R batches produced in F_3 will be 2D : 1R.

In the F_3 D series above quoted, two (matings Nos. 5 and 6) will disintegrate into R and D forms as there are RR females, while the remaining four in which the zygotic compositions of females are DD or DR, the F_4 eggs will be all D. Hence F_4 of

the dominant lineage will be D and (D + R), that is to say, certain lineages will gave all D F_4 eggs, while others will give both D and R batches in certain proportions.

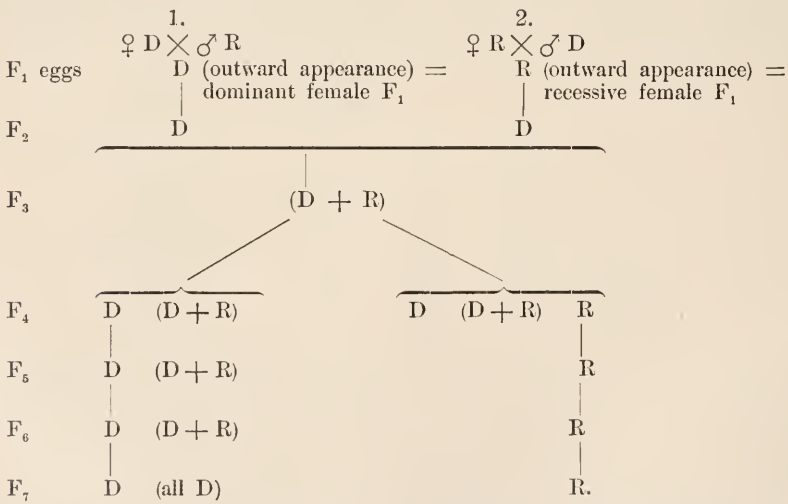
In the F_3 R series, those derived from the mating No. 7 in the above formulae will produce all F_4 D eggs, those from mating No. 8 a mixture of D and R batches, and lastly, those from mating No. 9 will give all R batches in F_4. Thus the F_4 of the R series will be D, (D + R), and RR, or some matings giving all D batches in F_4, some a mixture of D and R batches while the others are all R eggs.

If we eliminate the lineage which produced the antagonistic characteristics in both D and R series and keep only those which gave all uniform batches, the result would be:

In the D series, we may eliminate the lineage No. 3 which produced R batches in F_5 and in F_6 we may again take away the lineages Nos. 2 and 4 which will produce R batches. And thus we are able to establish a constant dominant form in F_7.

In the R series, if we keep the lineage which gave all R batches in F_4, it will be extracted as a constant R form, since, as we see from the formula before mentioned, it is RR in its composition.

The order of inheritance above described may graphically be summarized as below:



Let us now compare the results obtained by calculation according to Mendelian principles, with those actually obtained by us.

In the first series of line breedings before mentioned, if we considered the brown batch to be the F_1 eggs of the female brown series, the results are nearly the same, with a few irregularities possibly caused by the appearance of the divoltine white, which

prevents the proper elimination of the antagonistic characteristics. In the second series, if we take the grey batch as the F_2 D batch the results agree well with one another, and the grey form is dominant to the normal. In this case, however, there is a third characteristic accompanied by the dominant forms. If we consider them as a single characteristic, we get a pure Mendelian result.

Similarly in the third series, if we take the spindle-shaped eggs as the recessive female F_1, their successive generations are in good accordance with the formula demanded by the principle, excepting in the absence of uniform F_4 D eggs. This might be due to the small number of worms reared in this case, since flacherie made great havoc among them; and thus most of the worms during the fifth stage died, and we only obtained a small number of moths.

Brood characteristics ("Voltinism") of the silk-worm.

The phenomena of inheritance of the brood of the silk-worm also afford-another example of matroclinous inheritance. In my opinion, they come in the same category of inheritance above referred to, but the phenomena are more complicated than in the former cases because the divoltine characteristic is easily disturbed by the influence of temperature during the embryonic stage.

As is well known among Japanese breeders, divoltine breeds may be changed into uni-, di- or multivoltine, by the influence of the temperature during the incubation of the egg. As far as we have experimented, if we expose the eggs to a temperature of about 80° F. and upwards, all the worms which emerge from them will give moths which lay univoltine eggs without exception, while the embryo developedunder a temperature of about 65° F. or less, gave moths which laid all divoltine or multivoltine eggs. Hence the result of experiments made on the subject of brood-character might give rise to great mistakes unless we pay special attention to the temperature during the development of the embryo. On the other hand, the univoltine characteristic was not so easily influenced by the temperature as the divoltine was.

So we come at last to the conclusion that nearly all the characteristics of the silk-worms studied by us since 1900, even those which seem to be non-Mendelian, nevertheless really are Mendelian.

Über intermediäre und alternative Vererbung.

Von Dr. J. Grofs (Neapel).

1. Einleitung.

In zwei früheren Arbeiten habe ich versucht, der heute von fast allen Vererbungsforschern geteilten Auffassung, die in den

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