

THE INHERITANCE OF THE PECULIAR PIGMENTATION OF THE SILKY FOWL.

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INTRODUCTION.

DURING the past six years we have been engaged upon a series of experiments connected with the inheritance of the peculiar pigmentation of the Silky Fowl. A brief account of the general features of this interesting case has already been published by one of us¹, but as our experiments are now concluded we are able to give in greater detail the evidence upon which our views are based. As a description of the Silky Fowl may be found in any of the standard works on poultry it is unnecessary for us to dwell upon the characters of the breed except in so far as they enter into this particular series of experiments. One of its most remarkable features is the extraordinary abundance of black pigment which is generally distributed among most of the mesodermal

¹ W. Bateson, *Mendel's Principles of Heredity*, 1909, p. 181.

tissues of the body. Seen through the thin epidermis this pigment gives the bird the appearance of a fowl with a black skin, deep purple comb and wattles, and dark slaty shanks. The iris is heavily pigmented, and the usually white earlobe takes on a more or less intense turquoise tint which is especially noticeable in the hens. The somatic peritoneum, the periosteum and pia mater are inky black from the pigment with which they are crowded. The splanchnopleure is much less pigmented, and the liver seen through this looks its normal colour. The muscles also have a blackish appearance, but we have not made any histological examination to determine the exact distribution of the pigment here. It is apparently confined to membranes of mesodermal origin, and is absent from the lungs, liver and other viscera, while at the same time the plumage is white. There is never any trace of it in the allantois, or other foetal membranes.

Our experiments with this breed were begun with the idea of investigating the nature of the form of comb by which it is characterised, but we had not proceeded far before it became evident that the inheritance of the peculiar pigmentation promised more interesting and novel results. As the case presents features unlike any hitherto met with elsewhere it will be convenient if we give a brief outline of the main results and of the interpretation before passing to a detailed examination of the experimental data.

GENERAL STATEMENT OF RESULTS.

The breed with which the Silky was originally crossed was a strain of Brown Leghorns which had been in our possession since 1899. The first indication of something unusual was the definite difference found in the reciprocal crosses between these two breeds. While the mating of Silky ♀ × Brown Leghorn ♂ resulted in chicks of both sexes with little pigmentation, the mating of Brown Leghorn ♀ × Silky ♂ gave a markedly different result. From this mating the ♂ chicks had only a little pigment and were indistinguishable from those resulting from the previous cross, but the ♀ chicks were all deeply pigmented, differing but little in this respect from a pure Silky¹. On breeding the F_1 birds together there resulted in either case an F_2 generation consisting of

¹ The F_1 chicks all had coloured plumage and subsequent breeding showed that the white of the Silky behaved as a simple recessive (cf. *Rep. Evol. Comm. Roy. Soc.* iv. 1908). Our experiments have led us to infer that the pigmentation is quite independent of the colour of the plumage.

pigmented F , ♀ as well as for the unpigmented. But when the F_1 ♂ was crossed with a Brown Leghorn ♀ about one in eight of the offspring were deeply pigmented *and these were always females*. To assist the reader in following this somewhat complicated case we append a rough scheme. It will be understood of course that the scheme gives no indication of the proportions in which the various classes are produced, neither for the moment do we attempt to differentiate between the various grades of pigmentation other than the fully pigmented state.

We may now state briefly the interpretation to which our various experiments have led us. We consider that three factors are involved of which two are directly concerned with the degree of pigmentation. These are (α) a *pigmentation* factor (P), and (β) an *inhibition* factor (I) which can prevent the full development of the pigmentation¹. The various grades of pigmentation met with depend upon the various compositions of the zygotes in regard to these two factors; e.g. a bird of the constitution $PPii$ will be fully pigmented, a bird of the constitution $PpIi$ will be slightly pigmented, while birds of the constitution $ppII$, $ppIi$, or $ppii$ will be unpigmented (see also p. 200).

The third element with which we are concerned in these experiments is *sex*. Here we have made certain assumptions. We regard the female as differing from the male in possessing a special element, F , of which the hereditary behaviour is like that of any other Mendelian factor. Moreover we consider that the female is always heterozygous for this factor so that the zygotic constitution of a female is Ff while that of a male is ff . Further we suppose that in such zygotes as are heterozygous for both F and I there occurs a repulsion between these two in gametogenesis so that F and I do not pass into the same gamete. We may allude to the cases of the inheritance of the *lacticolor* variety of *Abraaxas grossulariata*² and of the red eye of cinnamon canaries³ in which similar phenomena can be shown to follow the same system of descent.

It must be expressly stated that the suggestion that females are heterozygous for *femaleness* is offered without prejudice as to the possibility that males may also be heterozygous in *maleness*. The systems followed by the descent of colour-blindness⁴ in Man and by

¹ The condition of the gamete from which either or both of these factors are absent we shall denote in the conventional way by the use of the corresponding small letters p and i .

² Doncaster, L., *Reports to the Evolution Committee of the Royal Society*, iv. 1908.

³ Durham, F. M., *Reports to the Evolution Committee of the Royal Society*, iv. 1908.

⁴ *Mendel's Principles*, 2nd imp., 1909, p. 195, note.

that of the white eye recorded by Morgan in *Drosophila*¹ clearly point to the existence in those cases of a repulsion between a factor for maleness (*M*), and factors respectively for colour-blindness and for the red eye. The operation of the system of sex-limitation is similar in all these examples, the only difference being that in the one group the repulsion is from the factor *F*, in the other from the factor *M*.

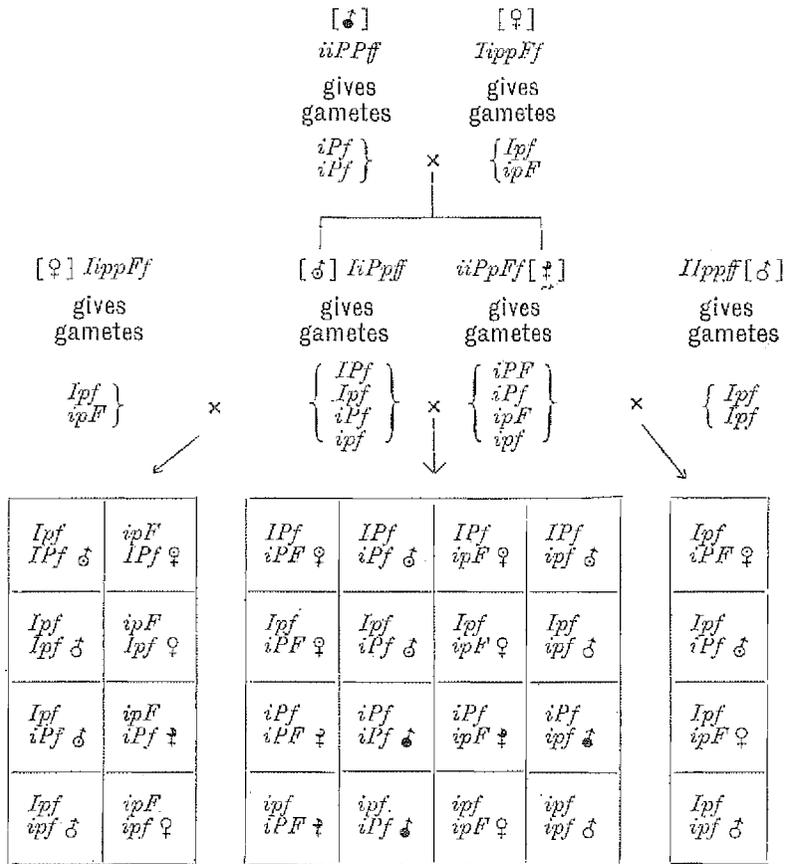


Fig. 3.

Recognition of the existence of factors both for femaleness and for maleness of course involves the assumption that ova bearing *F* can only be effectively fertilised by sperms not bearing *M*, and *vice versa*. For that supposition no independent evidence yet exists, and we note that

¹ Morgan, *Science*, 1910, N. S. xxxii. p. 120.

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Morgan¹ has made observations on *Cumingia* (Mollusca) distinctly unfavourable to it. At present however we think it is the most acceptable account of the facts ascertained both as to the heredity and the variability of sexual characters.

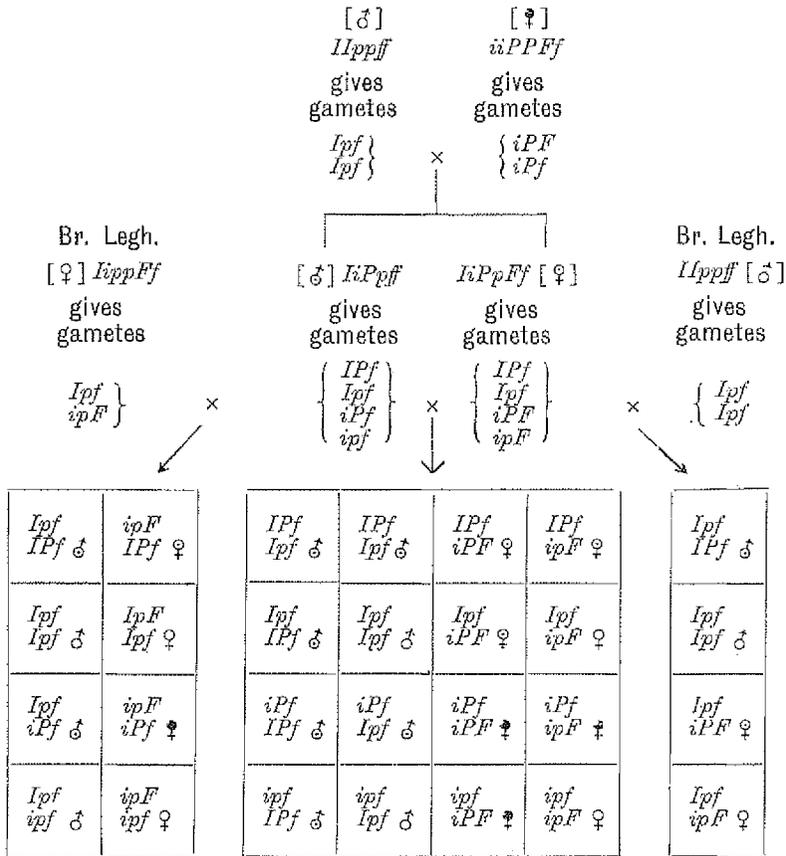


Fig. 4.

The Silky Fowl normally breeds true to the fully pigmented condition and we consequently represent the cocks and hens of this breed as *ffPPii* and *FfPPii* respectively. The Brown Leghorn on the other hand never produces pigmented birds and we therefore regard it as being entirely without the factor *P*. But it possesses the inhibitor factor *I*; and for reasons which will appear later the cock must be

¹ Morgan, Payne, and Browne, *Biol. Bull.* 1910, xviii. p. 76.

normally homozygous and the hen heterozygous for this factor. Constitutionally therefore we look upon the cocks and hens of this breed as being respectively $ffIIpp$ and $FfIIpp$. To illustrate what we imagine to happen in the several generations produced by mating a Silky ♂ with a Brown Leghorn ♀ as well as in the reciprocal cross we have drawn up the appended schemes (Figs. 3 and 4) for comparison with Figs. 1 and 2. These schemes also indicate the composition on our hypothesis of the generations shown and we may now proceed to test their validity by the facts witnessed in these and other forms of mating.

DETAILED RESULTS OF THE VARIOUS CROSSES.

1. The F_1 generation.

(a) From the Silky ♀.

[Nature of mating $FfPPii \times ffpII$.]

We have bred from Silky ♀ × Brown Leghorn ♂ on two occasions and in neither case had any of the chicks more than a slight amount of pigment (cf. Fig. 1). Many of these were reared and in the adult state were almost indistinguishable in general appearance from pure unpigmented birds. Careful examination however revealed traces of pigment as patches either on the wattle, skin, or shanks. In most cases the presence of some pigment was most readily detected beneath the skin in the periosteum of the femoro-tibial or of the tarso-metatarsal joints. Dissection showed that some pigment was nearly always present in the ribs and in the occipital region of the skull. There was frequently a little peritoneal pigment more especially in the region of the ribs and some in the occipital pia mater. The amount of pigment varies somewhat and may be very slight. In some cases the chicks are recorded in our notes as being without pigment, but most of these

TABLE I.

Reference	Nature of mating	Males			Females		
		Full	Some	None	Full	Some	None
1905 Pen 16, 349	Silky ♀ × Br. L. ♂	—	5	—	—	2	—
1907 „ 7, 495	„ „	—	8	—	—	8	—
1909 „ 7, 150	F_2 ♀ × „	—	7	—	—	13	—

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records refer to birds which were not killed and critically examined. The extent to which the pigment development is inhibited exhibits individual variation, and it is likely that in some birds the inhibition is so complete that they are indistinguishable from birds which lack the pigmentation factor. Here we may mention also that we bred from a fully pigmented F_2 hen (♀ 150, see p. 197) with results similar to those which we obtained from the Silky hens.

(β) *From the Silky ♂.*

[Nature of mating $FfppLi \times ffPPii$.]

Our original Silky ♂ was mated at different times with two pure Brown Leghorn hens. The F_1 males from this mating were precisely similar to those produced from the reciprocal cross. The F_1 hens however were nearly as deeply pigmented as the Silky (cf. Figs. 2 and 4). To the one exception, a slightly pigmented ♀ , we shall return later (p. 200).

TABLE II.

Reference	Nature of mating	Males			Females		
		Full	Some	None	Full	Some	None
1905 Pen 51, 404 } 1906 „ 18, 404 }	Br. L. ♀ \times Silky ♂	—	3	—	8	—	—
1908 „ 18, 281 } 1909 „ 18, 281 }		„ „	—	29	—	31	1

2. The F_2 generation.

(α) *From the Silky ♂.*

[Nature of mating $FfPpii \times ffPpIi$.]

In Figure 3 we have already indicated the results which are to be expected from this form of mating. One quarter of the total offspring should be completely unpigmented while the remainder should be equally divided between the fully pigmented and the partially pigmented classes, the expected ratio being three fully pigmented, three partially pigmented, and two unpigmented out of every eight birds. Moreover the ratio should be the same for each sex. In Table III the results of six such matings between F_1 birds are given. There is a slight excess of fully pigmented ♀ ♀ due to the unusually high proportion of such birds in one of the matings (1909, Pen 4, 329), but on the whole the facts are in close accord with expectation.

TABLE III.

Reference	Nature of mating	Males			Females		
		Full	Some	None	Full	Some	None
1907 Pen 15, 283	$F_1 \text{♀ (full pig.)} \times F_1 \text{♂}$	11	6	4	9	11	9
„ 23, 114	„	2	6	1	6	3	3
1907} „ 22, 121	„	6	7	6	6	6	4
1908} „ 5, 467	„	7	—	4	11	8	4
1909 „ 4, 329	„	11	13	9	22	8	6
„ 22, 148	„	3	3	3	5	2	1
1909} „ 20, 374	„	11	20	7	15	17	11
Total		51	55	34	74	55	38
Expectation		52.5	52.5	35	62.5	62.5	42

(β) From the Silky ♀.

[Nature of mating, $FfPpIi \times ffPpIi$.]

As indicated in Figure 4 expectation is here different from that in the preceding case where the F_1 ♀ was from the cross Brown Leghorn ♀ \times Silky ♂. The slightly pigmented F_1 ♀ is here heterozygous for the inhibitor factor, I , and there comes into play the repulsion between I and F so that all the male gametes produced by such birds contain I , while this factor is carried by none of the female gametes. From this mating therefore we should not expect any fully pigmented males since every bird of this sex must contain I . Nevertheless, as the data in Table IV show, many of the males resulting from this mating were recorded as being heavily pigmented. By far the greater number of chicks in this generation were killed and recorded on hatching, and a peculiarity of the ♂♂ booked as fully pigmented lay in the fact that the toes of these birds were always light in colour. We regard these birds as of

TABLE IV.

Reference	Nature of mating	Males			Females		
		Full	Some	None	Full	Some	None
1906 Pen 9, 467	$F_1 \text{♀ (unpig.)} \times F_1 \text{♂}$	1	3	1	2	—	2
1907 „ 11, 459	„	6	8	1	5	11	1
„ 20, 461	„	2	14	8	10	7	4
1908 „ 19, 459	„	—	2	3	2	3	—
„ 19, 393	„	3	14	8	5	7	6
„ 22, 467	„	—	1	—	4	—	—
Total		12	42	21	28	28	13
Expectation		18.75	37.5	18.75	26	26	17

the constitution $ffPPII$ or $ffPPIi$ and suppose that in the presence of a double dose of the pigmentation factor the effects of the inhibitor are in considerable measure overcome in the younger stages. In corroboration of this view we may state that we reared several of these deeply pigmented ♂♂ and that they all became far less heavily pigmented in appearance as they approached maturity. In external appearance indeed they showed little more pigmentation than the F_1 cocks. This explanation is the natural one if we regard the constitution of the slightly pigmented F_1 ♀ as $FfPpIi$, and further evidence (p. 198) in favour of this view will be adduced from an entirely different set of experiments.

3. $F_1 \times$ Brown Leghorn.

(a) *Brown Leghorn* ♀ \times F_1 ♂.

[Nature of mating, $FfppIi \times ffPpIi$.]

On our hypothesis this form of mating should give a specific result, for while the ♂♂ should all be either without, or with comparatively little, pigment, one quarter of the ♀♀ should be fully pigmented (cf. Figs. 3 and 4). We have bred a considerable number of birds (nearly 700) in this way, and the figures given in Table V show that this expectation is closely realised. None of the 336 ♂♂ produced

TABLE V.

Reference	Nature of mating	Males			Females		
		Full	Some	None	Full	Some	None
1906 Pen 9, 207	Brown ♀ \times F_1 ♂	—	28		8	29	
„ 33, 248	„	—	8		1	1	
„ 33, 159	„	—	13		5	13	
1907 „ 11, 203	„	—	34		8	24	
„ 12, 264	„	—	13		3	8	
„ 12, 159	„	—	19		3	18	
„ 15, 347	Br. L. ♀ \times F_1 ♂	—	34		11	37	
„ 16 ♀ \times Br. L.	Brown ♀ \times F_1 ♂	—	18		2	14	
„ 20, 129	„	—	22		7	19	
„ 22, 101	„	—	42		8	28	
„ 23, 98	„	—	24		7	18	
1908 „ 5, 101	„	—	17		3	20	
„ 16, 345	Br. L. ♀ \times F_1 ♂	—	20		7	16	
„ 22, 129	Brown ♀ \times F_1 ♂	—	40		8	31	
1909 „ 20, 347	Br. L. ♀ \times F_1 ♂	—	4		1	4	
	Total	—	336		82	280	
	Expectation	—	336		90.5	271.5	

were deeply pigmented, while of the 362 ♀♀ 82 were deeply pigmented, a proportion approximating fairly closely to the expected quarter. We should add that owing to a deficiency of pure Brown Leghorns some of the hens used were light-shanked brown birds of Brown Leghorn extraction. With regard to the transmission of pigmentation these behaved similarly to the pure race.

(β) F_1 ♀ (*unpigmented*) × *Brown Leghorn* ♂.

[Nature of mating, $FfPpIi \times ffppII$.]

Two F_1 ♀♀ of this nature were crossed with a Brown Leghorn ♂ and gave 26 ♂♂ and 18 ♀♀ of which none were deeply pigmented. This again fits in with our hypothesis (cf. Fig. 4), for no deeply pigmented birds are to be looked for from this mating.

4. F_1 × Fully pigmented ($PPii$) birds.

(α) F_1 ♂ × $PPii$ ♀.

[Nature of mating, $FfPPii \times ffPpIi$.]

The expected result from this form of mating is equal numbers, in both sexes, of chicks with deep pigmentation and of chicks with some pigmentation. We have made this mating twice with the following results:

TABLE VI.

Reference	Nature of mating	Males		Females	
		Full pigmentation	Some pigmentation	Full pigmentation	Some pigmentation
1906 Pen 33, 349	Silky ♀ × F_1 ♂	5	2	3	5
1909 ,, 17, 114	F_2 full pig. ♀ × F_1 ♂	20	18	19	22
	Total	25	20	22	27
	Expectation	23.5	23.5	23.5	23.5

These results are obviously in close accord with expectation, but it must be mentioned that ♀ 114 also gave one ♀ chick recorded as *without pigmentation*.

(β) F_1 ♀ (*slightly pigmented*) × *Silky* ♂.

[Nature of mating, ♀ ♂ $PpIi \times \text{♂♂} PPii$.]

Since on the hypothesis the gametes produced by the F_1 ♀ are $\text{♀} Pi$, $\text{♀} pi$, $\text{♂} PI$, and $\text{♂} pI$ it follows that all the female chicks will contain P without I , while of the male chicks all will be heterozygous for I while half will be homozygous for P . In discussing the nature of the

F_2 generation from this type of F_1 ♀ we have already seen reason for supposing that the male chicks of the constitution $PPii$ are practically fully pigmented on hatching, but that the pigment becomes much reduced with advancing age. Hence the expectation for the present type of mating is that all the ♀♀ will be deeply pigmented, and that the ♂♂ will hatch either as deeply pigmented chicks, or as chicks with some pigment only—these two classes being produced in equal numbers. Table VII gives the results of the two cases in which we have made this mating. While the general result is in accordance with expectation the Table shows that there are two ♀♀ from each mating which are not fully pigmented. To these exceptions we shall recur later (p. 200).

TABLE VII.

Reference	Nature of mating	Males			Females		
		Full	Some	None	Full	Some	None
1907 } 1908 } Pen 18, 459	F_1 ♀ (slight pig.) × Silky ♂	12	13	—	28	2	—
1907 } 1908 } " 9, 467	" "	12	18	—	28	2	—
1909 } " 16, 467	" "						
Total		24	31	—	56	4	—
Expectation		27.5	27.5	—	60	—	—

(γ) F_1 ♀ (fully pigmented) × Silky ♂.

[Nature of mating, ♀ ♂ $Pp ii$ × ♂ ♂ $PP ii$.]

Since the gametes of neither parent carry the inhibitor factor and since those of one parent all contain the pigmentation factor, the expected result of this mating is fully pigmented chicks only, of both sexes. The mating has been made on three occasions and as Table VIII shows the results are in accordance with expectation.

TABLE VIII.

Reference	Nature of mating	Males Full pig- mentation	Females Full pig- mentation
1907 Pen 18, 121	F_1 ♀ full pigmentation × Silky ♂	17	3
1907 } 1908 } " 18, 114	" "	10	15
1907 } 1908 } " 9, 235	" "	15	19

We have already alluded to the deeply pigmented hens which resulted from crossing the F_1 ♂ with the Brown Leghorn ♀. On our

hypothesis these birds are in constitution $FfPpii$ and consequently should give the same result as the deeply pigmented F_1 ♀ when crossed with a pure Silky ♂. We have made this cross on two occasions and in accordance with expectation all the chicks were deeply pigmented (cf. Table IX).

TABLE IX.

Reference	Nature of mating	Males		Females	
		Full pigmentation		Full pigmentation	
1907 Pen 18, 344	♀ $Ppii$ × Silky ♂	11		12	
1907 „ 9, 376	„ „	10		12	

5. Crosses with deeply pigmented F_2 birds.

In the course of our experiments we have made crosses with two deeply pigmented F_2 birds, viz. ♂ 40 (from Pen 15, 283 of 1907) and ♀ 150 (from Pen 23, 114 of 1907). Each of these birds was as deeply pigmented in the adult stage as the pure Silky, and when bred together they gave only fully pigmented offspring (12 ♂♂ and 21 ♀♀). ♂ 40 was also mated with a pure Brown Leghorn ♀ and gave 21 ♂♂ with some pigment together with 33 deeply pigmented ♀♀. But he is recorded as giving also one deeply pigmented ♂ and 2 ♀♀ which were not deeply pigmented. To these exceptions we shall return and will merely state here that we regard them as due to a peculiarity in the behaviour of the Brown Leghorn hen. ♀ 150 behaved like a pure Silky when crossed with a Br. L. ♂ (p. 192), and we look upon both these F_2 birds as of the constitution $PPii$.

6. The $ppii$ strain.

In this account we have so far been concerned with the results of various crosses between the Silky and the Brown Leghorn breeds. By a happy accident we are able to adduce independent and cogent evidence in favour of the interpretation which we have put forward. In 1907 we bought a Silky ♂ which proved to be heterozygous for P (i.e. $Ppii$). Mated with an Egyptian hen, a brown bird with light coloured shanks, he gave *unpigmented as well as deeply pigmented hens*. Two of these unpigmented birds were mated back to the heterozygous Silky ♂ in 1908 and as was expected gave deeply pigmented and unpigmented birds of both sexes, viz. 18 ♂♂ deeply pigmented, 15 ♂♂ unpigmented, 21 ♀♀ deeply pigmented, 17 ♀♀ unpigmented. In this way we were able to establish a strain of birds *containing neither*

the pigmentation nor the inhibiting factor in either sex. These birds, on our system of notation, must be represented as *ppii*, and the possession of such a strain provided us with the means of testing the constitution of the F_1 (Silky \times Brown Leghorn) birds in the simplest and most direct way.

The F_1 ♂ on the hypothesis produces four kinds of gametes in equal numbers, viz. *fPI*, *fPi*, *fpI* and *fpI*. Crossed with *Ffppii* such a bird should give in both sexes equal numbers of birds with and without pigment. Again among the pigmented birds there should be equal numbers of deeply pigmented birds, and of birds with a small amount of pigment only. Table X shows that these expectations were closely realised in fact.

TABLE X.

Reference	Nature of mating	Males			Females		
		Full	Some	None	Full	Some	None
1909 Pen 4, 408	♀ <i>ppii</i> \times F_1 ♂	1	3	1	—	3	4
„ 17, 274	„ „	8	8	16	6	6	20
„ 22, 261	„ „	5	4	5	3	3	8
Total		14	15	22	9	12	32
<i>Expectation</i>		13	13	25	13	13	27

We have also made a similar set of experiments to test the gametic output of the slightly pigmented F_1 ♀ (ex Silky ♀ \times Br. L. ♂). The constitution of such birds on the hypothesis is *FfPpIi* and owing to repulsion between *F* and *I* the gametes produced are of four kinds only, viz. *FPi*, *Fpi*, *fPI*, *fpI* (cf. p. 188). Mated with ♂♂ of the constitution *ppii* such birds should give equal numbers of pigmented and unpigmented chicks in both sexes. And since the female gametes which contain *P* all lack the inhibiting factor, all the ♀♀ pigmented

TABLE XI.

Reference	Nature of mating	Males			Females		
		Full	Some	None	Full	Some	None
1909 Pen 3, 467	F_1 (slight pig.) ♀ \times ♂ <i>ppii</i>	—	1	2	—	1	4
1909 } 1910 }	„ 13, 459 „ „	—	11	9	16	2	12
1909 } 1910 }	„ 25, 393 „ „	—	23	17	24	—	21
1910 „ 22, 4 ♀♀	♀ <i>PpIi</i> \times ♂ <i>ppii</i>	1	67	67	81	1	56
Total		1	102	95	101	4	93
<i>Expectation</i>		—	99	99	99	—	99

at all should be deeply pigmented. On the other hand all the male gametes of the F_1 ♀ which contain P contain also I , and consequently none of the pigmented ♂♂ produced should be deeply pigmented. Table XI which gives the details of four such experiments shows how closely this expectation is realised, and offers strong corroborative evidence of the view here taken of the nature of the gametes produced by this type of F_1 ♀. The five exceptions recorded we shall refer to again (p. 200).

THE CONSTITUTION OF THE BROWN LEGHORN HEN.

While the Brown Leghorn ♂ is homozygous for the inhibiting factor, the ♀ is on our hypothesis always heterozygous for this factor. And since we assume repulsion to take place during gametogenesis between the factors F and I it follows that she produces two kinds of gamete, viz. Fpi and fPI . The possession of the $ppii$ strain enabled us to devise a pretty experiment to test this view. By mating a Brown Leghorn ♀ with a cock of the constitution $ffppii$ we obtained a number of unpigmented chickens of both sexes. On our hypothesis only the ♂♂ should receive the inhibiting factor, being in constitution $ffppIi$, while the ♀♀ should be $Ffppii$, and consequently lacking the inhibiting factor. This difference between the sexes with regard to the inhibiting factor should be brought out by a cross with fully pigmented homozygous birds ($PPii$), for while the females should give only fully pigmented chicks, the males may be expected to produce fully pigmented and partially pigmented chicks of both sexes in equal numbers. During the present year a cockerel (ex Br. Leg. ♀ × $ppii$ ♂) was mated with a pure Silky hen, and four sister pullets were put with an F_2 fully pigmented ♂ (No. 40, ex Pen 15, 283 of 1907) already shown to be $PPii$ in constitution. The results are shown in Table XII and are in accordance with expectation:

TABLE XII.

Reference	Nature of mating	Males			Females		
		Full	Some	None	Full	Some	None
1910 Pen 8, 150	Silky ♀ × ♂ (ex Br. L. ♀ × $ppii$ ♂)	1	4	—	3	3	—
„ 24, 4 ♀ ♀	♀ ♀ (ex Br. L. ♀ × $ppii$ ♂) × ♂ $PPii$	18	—	—	26	—	—

EXCEPTIONS.

In our account we have mentioned certain exceptions which occurred in several of the various matings. These are :

Table II, p. 192 .	ex Br. L. ♀ × Silky ♂	1 ♀ partially pigmented
p. 197 .	ex Br. L. ♀ × <i>PPii</i> ♂, <i>F</i> ₂	{ 2 ♀ ♀ partially pigmented 1 ♂ fully pigmented
Table VII, p. 196 .	ex <i>F</i> ₁ (<i>PpIi</i>) ♀ × Silky ♂	4 ♀ ♀ partially pigmented
Table XI, p. 198 .	ex <i>F</i> ₁ (<i>PpIi</i>) ♀ × <i>ppii</i> ♂	{ 4 ♀ ♀ partially pigmented 1 ♂ fully pigmented

In all these cases the ♀ ♀ should have been fully pigmented and the ♂ ♂ should have been partially pigmented on our hypothesis. It will be noticed that wherever these exceptions occurred the mother was a bird heterozygous for both *F* and *I*. These cases raise the question whether the normal repulsion between *F* and *I* in such birds may not occasionally break down, and whether in addition to *Fi* and *fI* gametes they may not produce *FI* and the complementary *fi* gametes. This appears the more likely as in two out of the four cases a fully pigmented ♂ also appeared as an exception; and in Table VII even if such birds appeared they would not be noticed, since fully pigmented ♂ ♂ are one of the classes normally produced from the mating of slightly pigmented *F*₁ ♀ and the Silky ♂. We incline therefore to think that upon occasion the repulsion between factors may be imperfect, though whether this imperfection is sporadic, or whether it can be conceived as part of some orderly scheme we do not yet know enough to say.

THE GRADES OF PIGMENTATION.

The dependence of pigmentation upon the presence or absence of two factors (*P* and *I*), as well as upon the heterozygous or homozygous condition of the individual with regard to either or both of them, would naturally lead the observer to look for a considerable range of variation in the pigmented condition. For in the full zygotic series are the nine possible combinations, *PPii*, *Ppii*, *PPII*, *PPIi*, *PpII*, *PpIi*, *ppII*, *ppIi*, *ppii*. The great majority of the chicks with which we dealt in these experiments were killed and recorded on hatching, and our practice was to refer them in so far as pigmentation was concerned to one of the following grades, viz. none, faint, slight, some, moderate, much, full, very full. Though not corresponding accurately to the various zygotic constitutions, these empirical grades nevertheless

afford some indication of them. Where P is not present the bird is always unpigmented, though with regard to I it may be either II , Ii , or ii . Where I is absent the bird is nearly always fully pigmented whether homozygous or heterozygous for P , though it is probable that chicks recorded as with much pigment may sometimes have been in constitution $Ppii$. The birds classed as "very fully" pigmented were probably in most cases $PPii$ though sometimes they may have been exceptionally deeply pigmented birds of the constitution $Ppii$. Where both P and I are present some pigment would appear to be always present though the amount is subject to fluctuation. Thus F_1 birds of both sexes (ex Silky ♀ × Brown Leghorn ♂), and the ♂ birds (ex Brown Leghorn ♀ × Silky ♂) are of the constitution $PpIi$, but in respect of the intensity of their pigmentation they might belong to either of our three classes "slight," "some," or "moderate," and our experience has been that these classes grade very much into one another. Birds with "much" pigmentation are in general either $PPII$ or $PPIi$, though an occasional bird of the $PpIi$ class might be referred to this group. The class $PpII$ is doubtless to be found among the birds with "faint" or "slight" pigmentation.

The grade of pigmentation would also appear to differ somewhat in the two sexes, for among birds similarly constituted for these two factors P and I the females are generally a little more pigmented than the males¹.

This case of the Silky pigmentation is interesting in connection with the production of intermediate forms. In an F_2 family bred from Silky ♀ × Brown Leghorn ♂ all the nine possible zygotic combinations of P and I occur in one or other sex. It would be possible to choose birds of such breeding and to arrange them in a series exhibiting continuous gradation from full pigmentation to none at all. Yet we now know that such a series is due to the interaction of three definite factors (inclusive of the sex factor), and that the continuity in variation manifested is in reality founded upon a discontinuous basis. Moreover we may point out that the mating of partially pigmented males of the constitution $PPIIff$ with partially pigmented females of the constitution $PPIiHf$ would result in the establishing of a race breeding true to an intermediate condition of pigmentation in spite of the underlying discontinuity involved.

¹ This fact is interesting in connection with the common experience of fanciers that in black-feathered breeds which have yellow skins, it is easy to obtain males with clear yellow shanks, but the females almost always have some black pigment in the shanks.

SILKY CROSSES OTHER THAN WITH THE BROWN LEGHORN.

During the course of our experiments we have crossed the Silky with other fowls beside the Brown Leghorn, but as the crosses with the last named promised the most definite results our attention and resources were mainly devoted to these. We may however mention a few points of interest which have arisen in connection with some of the other crosses.

Our original Silky ♂ was mated in 1906 to a white Rosecomb bantam. All the chicks (5 ♂♂ and 7 ♀♀) were deeply pigmented on hatching though as they reached maturity the pigment became less marked in the cockerels. A few cases are already on record in which a Silky was crossed with another breed and all the resulting offspring of both sexes were deeply pigmented¹. It is worthy of note that in such cases the breed with which the Silky was crossed possessed dark shanks. This was certainly so for the Spanish used by Tegetmeier and Darwin as well as for the Rosecombs used by ourselves; and we infer, though this is not explicitly stated, that it was also true for the frizzled fowls used by Davenport.

We may mention two cases from our experiments which are consistent with this view. When a Silky ♂ was mated with a dark-shanked mongrel ♀ (F_2 ex White × Brown Leghorn) 2 out of the 13 male chicks produced were fully pigmented. The remaining 11 male chicks exhibited a varying amount of pigment, while all the 11 female chicks showed the full pigmentation (1906, Pen 18, 150). In the other case an \bar{F}_1 ♂, ex Silky ♀ × Brown Leghorn ♂, was also crossed with a dark-shanked mongrel Leghorn hen bred similarly to the last (1906, Pen 9, 604). Out of the 19 male chicks from this mating two were deeply pigmented, while with light-shanked hens the cock gave the usual result (cf. p. 194). We must suppose therefore that the factor or factors upon which shank pigmentation depends can influence the factors concerned with the development of the pigment found in the Silky fowl, but at present we do not know sufficient about the nature of these factors to make any more definite statement.

Though our experiments have led us to infer that the strain of Brown Leghorns with which we worked was homogeneous in respect of the factor modifying pigmentation we nevertheless have evidence

¹ Cf. Tegetmeier, *The Poultry Book*, 1873, p. 268; Darwin, *Animals and Plants*, 2nd edit., 1899, p. 253; Davenport, *Inheritance in Poultry*, 1906, p. 60.

suggesting that this is not necessarily the case for all light-shanked birds. An example may serve to illustrate our meaning. During 1908 and 1909 the fully pigmented F_2 ♂ mentioned on p. 197 was crossed with a Brown Leghorn ♀ and gave a typical result, viz. slightly pigmented ♂♂ and fully pigmented ♀♀. During both of these seasons he was also run with a light-shanked ♀ belonging to our recessive white strain¹. With her he gave 19 male chicks varying from slight to moderate pigmentation, but of the 18 female chicks 8 were fully pigmented and 10 showed only a slight to moderate amount of pigment (1908-9, Pen 24, 53). From this and other similar experiments it seems natural to infer that some light-shanked hens may carry other factors capable of modifying the Silky pigmentation besides that which we have been able to demonstrate in the Brown Leghorn.

Lastly we may refer to a cross which we made between our original Silky cock and a hen which was homozygous for the dominant white factor (1907, Pen 18, 397). All the offspring (18 ♂♂ and 22 ♀♀) showed some pigment, sometimes a good deal, and this as a rule was distributed in small irregular patches, but we were unable to notice any difference between the two sexes. We think it not unlikely that the hen used was potentially a dark-shanked bird, and that the offspring of both sexes would have exhibited full pigmentation had not its development been in some way checked by the dominant white factor. The results however were complex and lack of opportunity prevented us from following up the cross, but we have thought it worth placing these cases on record since they indicate that radical differences in constitution may exist among light-shanked birds, and that the behaviour of our strain of Brown Leghorns with regard to the Silky pigmentation is not necessarily typical of birds with unpigmented shanks.

¹ An account of the origin of this strain will be found in *Reports to the Evolution Committee of the Royal Society*, III, p. 19, IV, p. 28.