GENETIC STUDIES IN POULTRY

X. CREAM PLUMAGE

By R. C. PUNNETT, F.R.S.

(With Plates 12–14)

CONTENTS

Introductory

Thirteen years ago I recorded some experiments dealing with blue egg colour derived from certain hens imported from Chili (Punnett, 1933). In the course of these experiments an unknown type of plumage colour made its appearance, and it is with this that the following brief account deals. In tracing the heredity of egg colour a Chilean hen of a nondescript light yellowish brown appearance was mated with a Gold-Pencilled Hamburgh cock. The F_1 birds were all gold with irregular pencilling. In a small F_2 generation bred subsequently there appeared some birds with a very pale creamy ground colour in addition to those of the normal gold type. The proportion in which these creams appeared pointed obviously to their being simple recessives to gold, and this was confirmed by the fact that they bred true in respect of the cream ground. The small stock of creams so obtained, though uniform in respect of ground colour, was highly diverse in the development and distribution of melanic pigment. With a view to further study it was decided to produce 'cream' forms of certain well-established types of plumage, and for this purpose the Buff and the Brown Leghorns were chosen. And here mention must be made of L. W. Taylor's work (1932) with birds which he also described as creams. He found the character to be recessive to gold, and I feel little doubt that we were simultaneously working with similar material. Our interpretations, however, are somewhat different; for while he regards the 'cream' gene as an inhibitor of gold I prefer to look upon gold as being due to a gene which intensifies cream. More recently Mr M. S. Pease has informed me that cream has turned up in one of his crosses, and it is not unlikely that the character is more widely spread than is generally realized.

The Buff Leghorn cross

A Buff Leghorn ♂ was mated with 2 cream ♀♀ in 1934 and gave only light gold offspring. An F_2 generation from 2 ♂♂ and 7 ♀♀ produced in the following years resulted in 113 golds and 45 cream. F_2 birds with the minimum of melanic pigment were selected to produce an F_3 generation in 1936. With one exception the chicks were all 'creamy' in down and developed into adults with cream plumage and very little melanic pigment. It was noted

that some of the ♀♀, particularly those with more melanic pigment, showed a slight gold tinge, whereas in the ♂♂ not only was this gold tinge never present, but the cream tinge was so faint that they could easily be mistaken for silvers (cf. Pl. 12, fig. 1). Subsequent experience confirmed this sexual difference. Reduction of melanic pigment, such as occurs in the 'Columbian' pattern, brings about a rich cream ground colour in the hen, whereas the corresponding cock might be said to mimic a silver, though a faint straw tinge in the hackles tends to become accentuated as the feathers age. I have bred many creams with the Columbian pattern, but I have never seen a cock with the cream ground colour characteristic of the hen, nor have I ever had a hen which, like the cock, could be mistaken for a silver. It would be interesting to carry out castration experiments with such a strain.

The Brown Leghorn cross

The object of this cross was to ascertain the appearance of the birds when cream was substituted for gold in the Brown Leghorn type of plumage. A Brown Leghorn ♂ was mated with 2 F_2 cream ♀♀ from the cream × Buff Leghorn cross, which of course had a type of plumage approaching the Columbian. In down the chicks showed a good deal of variation. Some were of a normal brown stripe; others were paler, sometimes with the stripe well marked, and others with the stripe so blurred that the down was of a more or less uniform golden brown. Such variation must, I think, be due to unanalysed differences in the make-up of the Columbian cream strain in spite of the fact that they showed little difference among themselves phenotypically. So far as was noted this variation was not connected with the sex of the chicks, but I do not wish to stress this point since little heed was paid to it at the time. The birds reared all grew up into golds with nondescript melanic markings which were more pronounced in the hens than in the cocks. Of these F_1 birds 2 ♂♂ and 10 ♀♀ were mated up in a single pen with the object of obtaining the cream black-red as quickly as possible. Of the 225 birds which survived long enough for colour determination 172 were golds and 53 were creams. The golds were discarded as soon as they could be recognized with certainty. As in the F_1 generation, down colour showed great diversity, but although points of interest arise in connexion with them I prefer not to discuss them since I have been unable to come to any definite conclusions.

Of the cream F_2 birds reared to maturity the darkest of the pullets closely approached the general coloration of the Brown Leghorn ♀. These were all brown striped in the down. But of the few cream cockerels successfully reared from brown-striped downs not one approached the Brown Leghorn ♂ in plumage. They were of a predominantly light type, a good deal splashed with chestnut and black. The bird figured on Pl. 12, fig. 2 represents such a 'splashed' bird though in this case the splashing is more reduced than usual.

Failure to recover the Brown Leghorn type of plumage in the F_2 ♂ necessitated a further mating in the following year. For this purpose a 'splashed' F_2 ♂ was mated with 7 F_2 pullets all with plumage approaching that of the Brown Leghorn ♀. These pullets were all dark-shanked whereas the ♂ was a heterozygous light-shanked bird. The interest of this will appear later. From this mating all of the chicks hatched out brown striped. Ninety of these were reared to the adult or nearly adult stage, viz. 52 ♀♀ and 38 ♂♂. Both ♂♂ and ♀♀ could be divided with fair accuracy into two classes. For the ♀♀ the distinction was breast colour which was either full or nearly full salmon, or else was either pale salmon or only salmon tinged. For the ♂♂ the two classes were concerned with general plumage type,

whether splashed, as in the male parent, or approaching nearly to the Brown Leghorn type as shown on Pl. 12, fig. 3. In either sex the two classes were of approximately the same size and evidently depended on the transmission by the male parent of some inhibitory element occurring in the Columbian pattern for which he must have been heterozygous.

Here we may revert for a moment to the point raised above in connexion with shank colour. The male parent, as already noted, was heterozygous for both shank colour and the inhibitor of plumage pigmentation. In respect of these two pairs of characters his 38 sons may be classified as follows:

	Dark shanks	Light shanks
Light plumage	6	14
Dark plumage	13	5

Though the figures suggest a linkage between these two inhibitors the numbers are few, and I have given them with the idea that it may draw the attention of some future worker to this point.

The figures for the two classes of ♀♀, though still suggestive of linkage, are not so marked. On the supposition that the 'Columbian' inhibitor here inhibits the production of salmon on the breast the classified figures are:

	Dark shanks	Light shanks
Pale salmon	15	12
Full salmon	16	9

The excess of dark-shanked birds tends to mask the somewhat more frequent association of pale breast with light shanks.

However, the chief interest of the above mating is that not only pullets but cockerels also were produced which were very close to the Brown Leghorn type of plumage. In the following year two pens were mated up, each with a ♂ and 2 ♀♀ of birds nearest to the type desired. From these was ultimately established a strain with typical Brown Leghorn plumage, but on a cream ground instead of on a gold one. In such a strain the hen closely resembles a silver grey, though close inspection shows that the general tint is just a shade warmer, though less warm than in the Brown Leghorn, and that the neck hackles are straw tinged. In the cock, however, with his more abundant hackles, the distinction is far more obvious. For the white edging of these feathers (Pl. 14, fig. 4) in place of the normal gold (Pl. 14, fig. 3) brings about a very different appearance. Again, the chestnut of the wing covers is not so intense as in the Brown Leghorn (cf. Pl. 14, figs. 5 and 6, and figs. 7 and 8). Nevertheless, though less intense, chestnut in the Brown Leghorn remains chestnut in its cream counter-part. The difference in ground colour between cream and gold offers a chance of distinguishing in a black-red between coloration due to gold and that due to chestnut. Such a test is the outer web of the secondaries which in the Brown Leghorn is of a bright gold-brown. On Pl. 14, figs. 1 and 2 are shown two corresponding secondaries of a normal Brown Leghorn ♂ and a cream. The bright brown outer web of the former is replaced in the latter by white. The inference is that in the black-red ♂ this part of the colour scheme is dependent on the development of gold pigment, and is independent of chestnut.

THE RHODE ISLAND RED CROSS

Some experiments were made by crossing Rhode Island Red with cream—the idea behind them being to ascertain the extent to which the chestnut element in the Rhode Island Red make-up could be separated from the gold basis on which it was developed. The Rhode

Island Red was crossed with the pale cream derived from the Buff Leghorn cross. For various reasons the work was not carried far, but enough evidence was collected to show that the chestnut element in the Rhode Island Red could be shifted from its normal gold on to a cream basis. Hens were bred in which the chestnut was fairly evenly spread on a cream basis to give a cold form of chestnut. But so far as the work went no fully chestnut ♂ was bred. Even in birds with the most chestnut there was always a considerable admixture of cream feathers irregularly dispersed in the plumage.

Genetical relation of silver, gold and cream

Gold and cream form an allelomorphic pair, but, as is well known, gold and silver also form an allelomorphic pair which is extensively used for sex-linkage in commercial breeding. Either we must suppose that silver, gold and cream form an allelomorphic series located in the sex chromosome, or else we must consider that we are dealing with two independent pairs, one situated in the sex chromosome and the other in an autosome. And if the latter supposition turns out to be the more likely one, what is the fourth term required to constitute our two allelomorphic pairs?

We may consider first the hypothesis of a triple allelomorphic series situated in the sex chromosome. This hypothesis was put to an experimental test in the following way. By a happy chance a silver Light Sussex ♀ was found which on mating with a cream ♂ gave only silver ♂♂ and cream ♀♀. Such ♂♂ must be silver on cream, and one of them mated back to cream ♀♀ gave silvers and creams of both sexes. A silver hen from this mating (i.e. silver on cream) was mated with a gold Rhode Island Red ♂. If silver, gold and cream form an allelomorphic series in the sex chromosome the ♂♂ from this mating should receive silver from their mother and gold from their father, i.e. cream from neither parent. Hence such ♂♂ mated to cream ♀♀ should give silvers and golds of both sexes, *but no creams*. Actually this mating gave 13 silvers, 9 golds and 8 creams, both sexes being represented in each colour class. Clearly this disproves the hypothesis of an allelomorphic series in the sex chromosome. But the figures accord reasonably well with the assumption of two independent allelomorphic pairs where expectation would be silvers, golds and creams in the ratio 2 : 1 : 1.*

The question now remains as to what these two pairs are. Evidently silver is one member of a pair located in the sex chromosome. And in view of the fact that the Light Sussex hen already mentioned did not transmit gold when mated with a cream ♂, I incline to consider that the sex-linked pair should be regarded as a silver-cream pair. Hence, since the experimental evidence excludes the hypothesis of a multiple series in the sex chromosome, we must suppose that 'gold' is located in an autosome. If so, the most natural way of regarding it is to suppose that it is an intensifier of cream, transforming it to gold, and that it is allelomorphic to something which does not bring about the intensification of cream to gold. What that something may be we have at present no means of deciding. For the present we can only regard it as absence of the intensifier.

An alternative view is, of course, to suppose that gold and cream form an allelomorphic pair in some autosome, and that either may be inhibited by the 'silver' factor in the sex

* While this experiment was in progress I learned from Mr M. S. Pease that he had obtained the following evidence telling against the supposition of a multiple allelomorphic series. A gold hen carrying cream when mated with a cream cock gave golds and creams of both sexes. On the supposition of multiple allelomorphs one would have expected all the male chicks to be gold and the females to be cream.

chromosome. In that case we are left with the problem of deciding what the allelomorphic pair to the 'silver' inhibitor may be, and at present we can on this view regard it only as the absence of the inhibitor. A decision between these two views might be provided if we could establish a linkage between gold and cream and some other autosomal pair. That must remain for future work to decide. The only data that I can at present offer are negative, though for the benefit of future workers it may be worth while to set them out below.

SOME LINKAGE DATA

A mating was made between a ♂ which was single-combed (**r**), non-crested (**cr**) and proved not to carry the factor for blue egg (**b**), and 4 ♀♀, all of which were rose-combed (**R**), crested (**Cr**) and layers of blue eggs (**B**) in respect of which three characters they were heterozygous. At the same time all of the birds were heterozygous for cream (**Gg**). Symbolically the ♂ was $\frac{\mathbf{r\ cr\ b\ G}}{\mathbf{r\ cr\ b\ g}}$ and the ♀♀ were $\frac{\mathbf{r\ cr\ b\ G}}{\mathbf{R\ Cr\ B\ g}}$. The results for the various characters were as tabulated below:

Rose		Single		
Blue	Non-blue	Blue	Non-blue	(Coupling series)
13	13	10	13	
Rose		Single		
Crest	No crest	Crest	No crest	(Coupling series)
30	28	24	29	
Rose		Single		
Gold	Cream	Gold	Cream	(Repulsion series)
53	15	42	21	
Crest		No crest		
Blue	Non-blue	Blue	Non-blue	(Coupling series)
19	17	12	9	
Crest		No crest		
Gold	Cream	Gold	Cream	(Repulsion series)
36	18	41	16	
Blue		Non-blue		
Gold	Cream	Gold	Cream	(Repulsion series)
15	8	18	8	

Data have already been accumulated to show that three of the allelomorphic pairs here dealt with, viz. rose-single, crest-non-crested and blue-non-blue, are located in different autosomes (Hutt & Lamoreux, 1940). The data tabulated above, though scanty, offer no grounds for supposing that the gold-cream pair is located in any of these three autosomes.

A few further data are available in connexion with the rose-single pair. A gold RC ♂ heterozygous for cream of constitution $\frac{\mathbf{R\ g}}{\mathbf{r\ G}}$ was mated with two SC cream hens to give

Gold rose	9
Gold single	11
Cream rose	7
Cream single	6

At present the data given above are all that I can offer in connexion with the gold-cream pair, and although they show no obvious linkage with rose, crest or blue egg it should be borne in mind that these three characters are all located near the extreme end of their respective chromosomes. It is, therefore, not impossible that further data involving genes located elsewhere on one or other of these chromosomes may disclose a linkage for the gold-cream pair.

SUMMARY

A type of plumage hitherto unrecorded in this country is described, viz. 'cream', which behaves as a simple recessive to gold. Silver, gold and cream do not constitute an allelomorphic series in the sex chromosome, but the three types of plumage depend upon two allelomorphic pairs of which one is located in the sex chromosome and the other in an autosome. The possible nature of these two pairs is discussed in the text.

Since 1942 part of the cost of these experiments has been met by grants from the Government Grants Board of the Royal Society, to which Board I wish to place on record my acknowledgement.

REFERENCES

HUTT, F. B. & LAMOREUX, W. F. (1940). *J. Hered.* **31**, 231, 235.
PUNNETT, R. C. (1933). *J. Genet.* **27**, 465–70.
TAYLOR, L. W. (1932). *Proc. 5th Int. Congr. Genet. Ithaca.* 197–9.

EXPLANATION OF PLATES 12—14

PLATE 12

Dorsal view of three male birds.

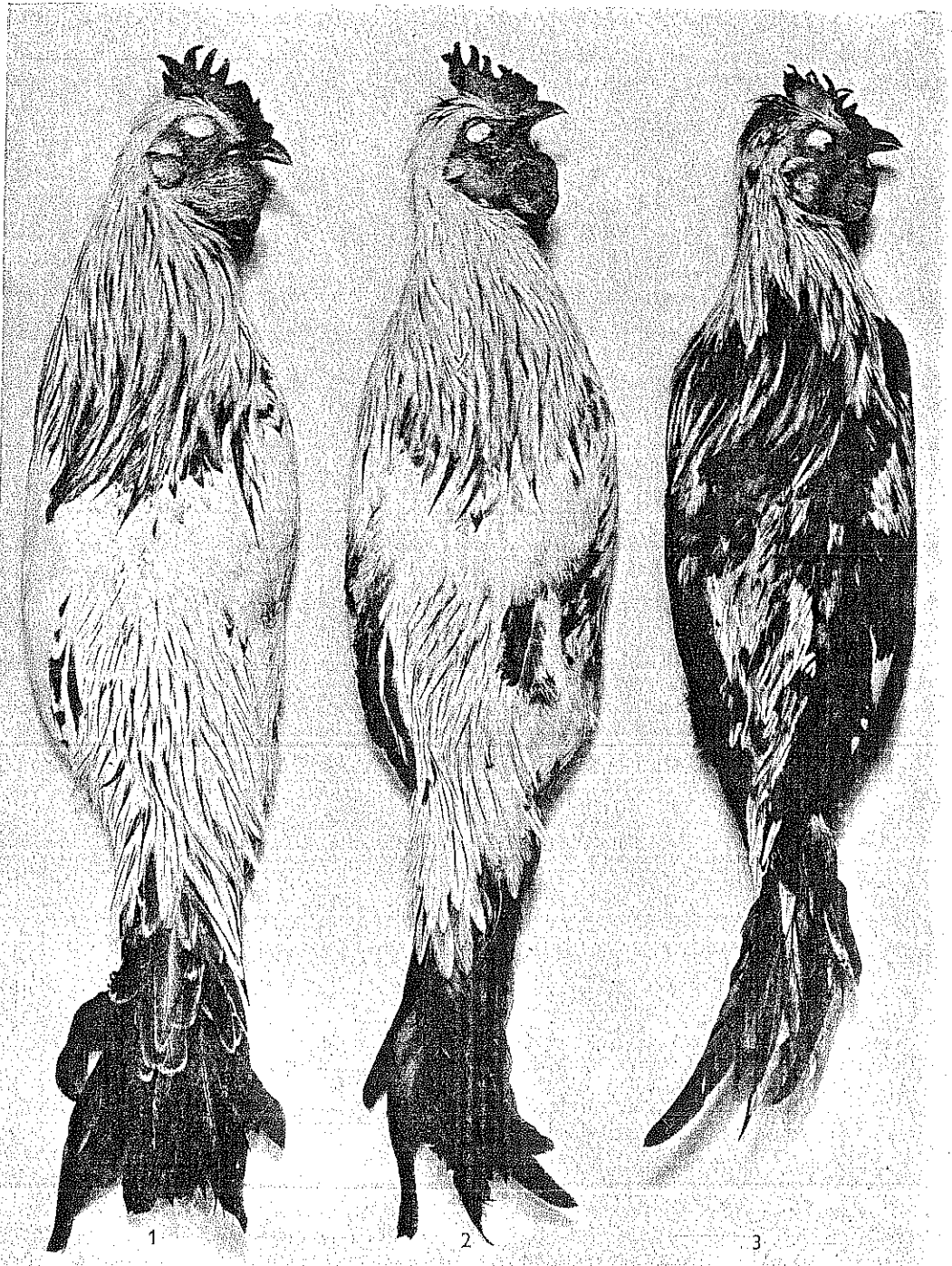
Fig. 1. 'Cream' cock with Columbian type of plumage. There is rather more melanic pigment in this bird than in the majority of those bred.
Fig. 2. 'Splashed' cream cock. Such birds generally show more chestnut and more melanic pigment than the one figured.
Fig. 3. Cream cock with Brown Leghorn type of plumage.

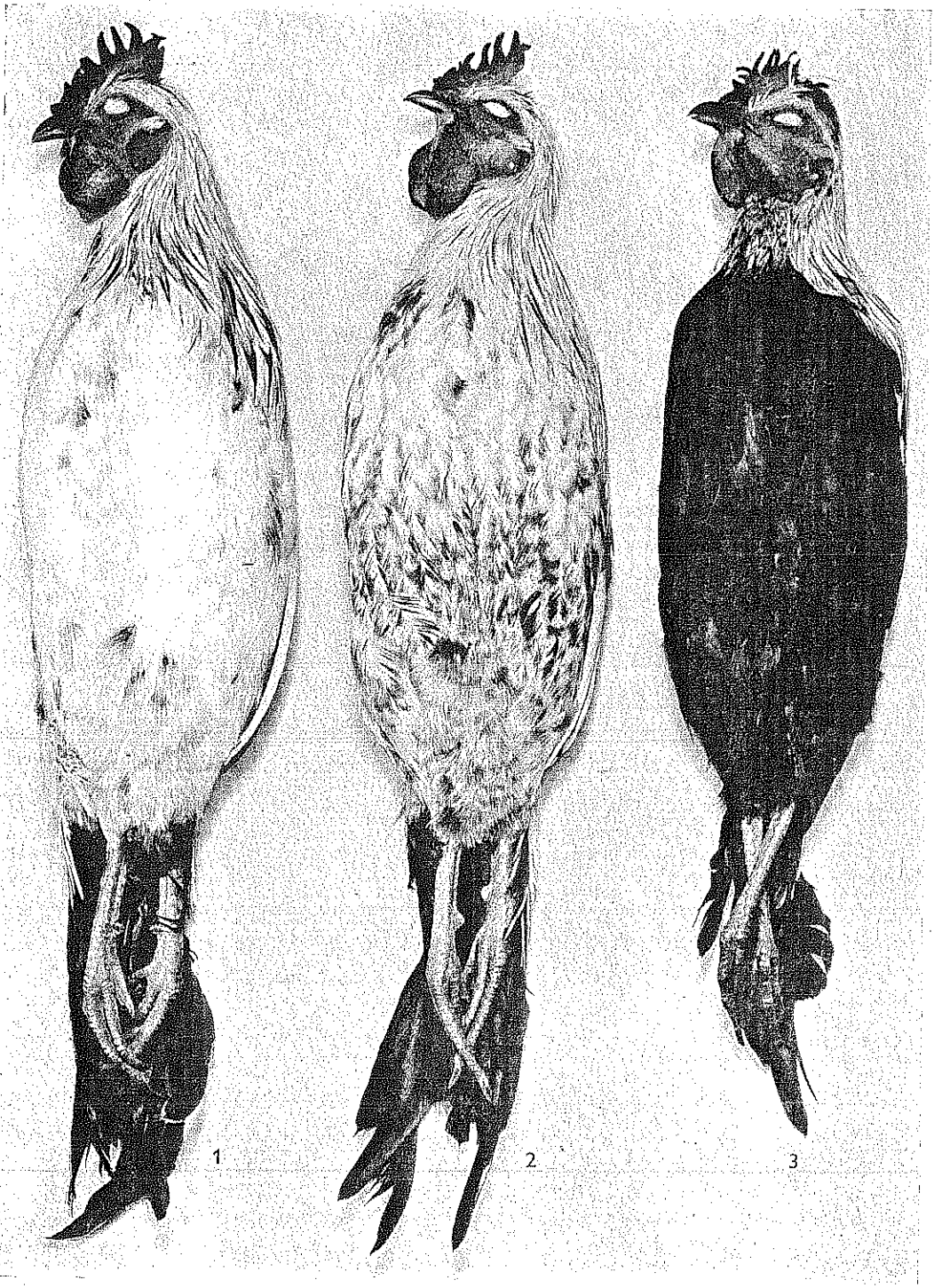
PLATE 13

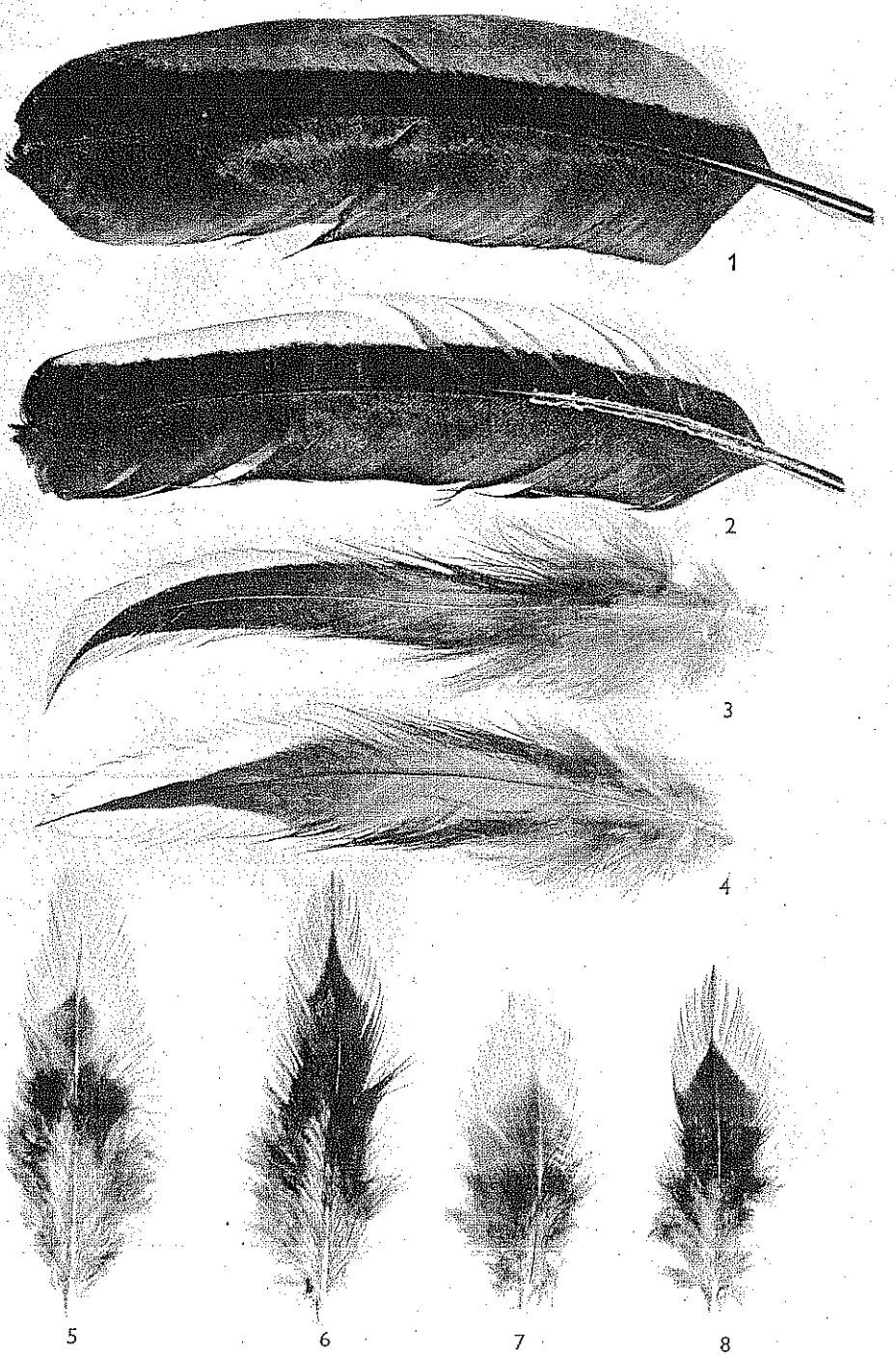
Ventral view of the three birds figured on Pl 12.

PLATE 14

Corresponding feathers from a pure Brown Leghorn cock and from a cream with the Brown Leghorn type of plumage.
Figs. 1, 2. Secondaries.
Figs. 3, 4. Neck hackle.
Figs. 5–8. From wing coverts. Figs. 5 and 7 are from a cream and Figs. 6 and 8 from a Brown Leghorn.


1
2
3


1
2
3


1
2
3
4
5
6
7
8