INHERITANCE OF EARLOBE COLOR IN POULTRY[1]

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INTRODUCTION

The earlobe of the chicken is a structure on the skin of the face just below the ear, the outline of which is marked by a slight thickening of the tissues. It is bare of feathers and may be the same color as the rest of the face for which the degree of redness is somewhat dependent upon the health of the bird. As is true of most of the head furnishings, this structure is larger in males than females.

For some breeds of poultry, more commonly those classified as Mediterraneans, the color of the earlobe differs from that of the rest of the skin of the face. In such cases it is of a pearl white color and although the histology of the tissue has not been studied the color appears to be due to a deposition of white material just beneath the epidermal layer. In the White-Faced Black Spanish breed the white color is extended to cover the entire face. In the breeds of the Mediterranean group the earlobe is proportionately larger than in most other breeds.

The poultry fancier has decreed that the earlobe must be all white or all red, making the color a breed characteristic. Since even slight variations from standard color constitute a show ring disqualification, uniformity of color has been rigidly selected for during a considerable period. For this reason most breeds are quite constant for earlobe color.

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Although the earlobe is one of the conspicuous furnishings of the head of the chicken, we find little mention of it in genetic literature. Numerous crosses have been made involving differences in earlobe color but practically nothing has been written upon the inheritance of its color variations. The variability of the F_1 generation and the complex nature of its factorial basis have probably been the conditions which have discouraged the undertaking of genetic investigations of this character.

This study is an attmpt to analyze as completely as our knowledge of the genetics of poultry will permit, the factorial basis of earlobe color.

BREEDS USED

Most of the conclusions of this paper are based upon the results of crosses of the Jersey Black Giant and the Single Comb White Leghorn breeds. However, in the course of other genetic studies, crosses of several breeds differing in earlobe color have been made and in all cases accurate records have been kept. The white-earlobe breeds used in this study were the Single Comb White Leghorn, Rose Comb Brown Leghorn, and Single Comb Buff Leghorn. The red-earlobe breeds were Jersey Black Giant, Barred Plymouth Rock, Single Comb Rhode Island Red, Dark Brahma, White Wyandotte and Silver Laced Wyandotte. The tables presented in the following discussion will indicate the crosses made of the various breeds.

CLASSIFICATION OF EARLOBE COLOR

Records of earlobe color were made at three months and six months of age. It was found that the description for the three-month age was not entirely reliable since changes in color sometimes took place afterwards. The description at the age of six months was used for classification since color attained at that age appeared to be the normal adult color. Any changes after this age were usually due to injury. The fact that only those individuals raised to the adult condition could be classified, accounts for the small numbers in some crosses.

The resulting offspring exhibited all gradations between entirely red and entirely white earlobes. For purposes of classification it became necessary to establish arbitrary groupings of the intermediate colors. Four grades were recognized; namely, white, predominately white, predominately red, and red. It is realized that there is some experimental error in using so crude a system of classification, but since it was the more accurately defined first and last grades that were of primary interest it seemed to satisfy the needs of the experiment at hand. The intermediate grades were not cases of blending of the red and white but the mingling of the two in varying proportions. The variations are probably quantitative ones depending upon the amount of white tissue deposited and the relative amounts of white and red are determined by the proportion of the surface of the earlobe covered by the white.

F_1 GENERATION

For study of the results of mating red and white earlobe breeds of poultry, data were available from ten different crosses. In table 1 are

TABLE 1

Distribution of earlobe color for the F_1 generation of various crosses.

RED EARLOBE MALES BY WHITE EARLOBE FEMALES

Mating	Females				Males			
	White	Predominately white	Predominately red	Red	White	Predominately white	Predominately red	Red
1 Black Giant male by White Leghorn female	1	20	27	2	2	17	24	1
2 Rhode Island Red male by White Leghorn female		2	21	1	1	1	19	3
3 Dark Brahma male by Brown Leghorn female	3	7	6	1	2	3	7	5
4 Barred Rock male by Brown Leghorn female	1	1	5	3	1	1		2
5 Barred Rock male by Buff Leghorn female	1	5	9	1	1	9	9	7
6 White Wyandotte male by Buff Leghorn female	6	2	1		1	7	1	
WHITE EARLOBE MALES BY RED EARLOBE FEMALES								
7 White Leghorn male by Black Giant female	12	11	6	1	12	11	7	
8 Brown Leghorn male by Silver Laced Wyandotte female.	3	4	5		3	3	5	2
9 Brown Leghorn male by Silver Pencilled Rock female	6	6	1		2	11	7	
10 White Leghorn male by Rhode Island Red female		9	19	3			14	9

shown the results of these crosses, six of which are matings of red earlobe males by white earlobe females and four in which the reciprocal relations were true. In two crosses, Jersey Black Giant by White Leghorn and Rhode Island Red by White Leghorn, reciprocal crosses of the same mating were available. A glance at table 1 will show that complete dominance of either color was not obtained. Also it is seen that the different matings of the same type (involving different breeds) are somewhat variable with respect to the proportions of red, white and intermediate colors. The small number of individuals involved in some matings may be responsible for the variability but later generations indicate that the various breeds may differ as to their genetic constitution for genes affecting earlobe color.

Variability of the F_1 Generation

In most crosses it is seen that all four grades of earlobe color are found in the F_1 generation. It is of interest to determine whether these variations are due to variability in dominace or lack of homozygosity. Either or both conditions may contribute to the variability of the F_1 individuals. Since a large number of F_1 individuals were not mated, only a limited amount of data are available for determining whether F_1 individuals differing in earlobe color actually differ in genetic constitution. From the cross of Jersey Black Giant by White Leghorn three F_1 females were mated to the same male. One of these females had red earlobes while the earlobes of the other two were predominately white. Only female offspring are listed here since it will later be shown that sex-linked factors are also involved in this cross. The ratios of the earlobe colors of the female offspring were as follows:

Hen Number	*White*	*Predominately white*	*Predominately red*	*Red*
5388–Red Earlobe		7	6	1
5415–Predominately White	3	3	1	
5452–Predominately White	3	9	2	

It will be seen that the offspring differ in accordance with differences among the F_1 parents.

Two F_1 males were backcrossed to several Jersey Black Giant females. One having predominately red earlobes produced female offspring which were classified as follows; 14 predominately white; 54 predominately red and 28 red. The other which had predominately white earlobes gave the following distribution of earlobe colors; 10 predominately white, 23 predominately red and 7 red. Here again the distribution of color among the offspring differed in accordance with the difference between the two F_1 males.

In the cross of Brown Leghorn by Silver Penciled Rocks two F$_1$ males were used. They were full brothers but one had earlobes classified as white and the other as predominately white. For certain other genetic studies, the two males were each mated to F$_1$ females from cross of Brown Leghorn by Buff Leghorn and Brown Leghorn by Rhode Island Red. In table 2 the results of these matings are shown. Male 987M which had the entirely white earlobes produced offspring whose earlobes showed a greater amount of white than did the progeny of 989M. In the first mating shown in table 2 the autosomal constitution of the offspring was such that most of the earlobes were white but the few which were not entirely white came from male 989 M. In the second mating more earlobes appeared which showed varying degrees of red and here the offspring of 989 M had earlobes which averaged considerably more red. Since these two males were full brothers the difference in their genetic constitution with respect to factors influencing earlobe color must have been due to heterozygosity for these factors on the part of one or oth parents.

TABLE 2

Variability of earlobe color of F_1 individuals. Results of mating two F_1 males differing in earlobe color to similar lots of females; showing that the variability in the F_1 generation is due to differences in their genetic constitution.

MATED TO F$_1$ FEMALES FROM BROWN LEGHORN—BUFF LEGHORN CROSS

Male Number	Females				Males			
	White	Predominately white	Predominately red	Red	White	Predominately white	Predominately red	Red
987M (white earlobe)	53				42			
989M (predominately white)	21	3	1		52	3		

MATED TO F$_1$ FEMALES FROM BROWN LEGHORN—RHODE ISLAND RED CROSS

Male Number	Females				Males			
	White	Predominately white	Predominately red	Red	White	Predominately white	Predominately red	Red
987M	38	9	2	1	31	3		
989M	21	16	4	2	20	9	3	

The foregoing data seem to indicate that the offspring of F$_1$ individuals varying in earlobe color, tend to vary in the same direction as their parents. This may be due to the fact that the parental stock was not entirely homozygous for the factors involved and that we are dealing with a multiple factor situation. Since the breeds used seldom showed by their own variability any indication of heterozygosity it would be difficult to establish homozygosity before crossing. These factors although exerting no apparent influence in the pure breed, did appear to be effective when the other factors were in a heterozygous condition.

SEX-LINKED FACTORS

Reciprocal F_1 matings of the same cross may be utilized to determine whether factors influencing earlobe color are carried by the sex-chromosome. In two crosses, White Leghorn by Jersey Black Giant and White Leghorn by Rhode Island Red, data from reciprocal crosses are available for comparison. Variability of the genetic constitution of individuals of a breed is here a source of error but it is believed that individuals of a single strain do not differ greatly in their constitution with respect to the major factors for earlobe color. If sex-linked factors affecting earlobe color are operative we would expect the female offspring of reciprocal crosses to differ. Since in the chicken, the male is the homogametic and the female the heterogametic sex, the female offspring of any cross receive their only Z- or sex-chromosome from the father. Since the female has only one Z-chromosome she should exhibit all sex-linked characters of her father. Thus if there are sex-linked factors affecting earlobe color, females from reciprocal F_1 crosses should differ in accordance with the effects of these factors in conjunction with those carried by the autosomes when in a heterozygous condition.

Matings 1 and 7 and 2 and 10 of table 1 afford data for comparison of the results of reciprocal F_1 crosses. For the first-mentioned matings the daughters of the white earlobe male show more white in the earlobes than those of the reciprocal mating in which the father had red earlobes. For the second case (Rhode Island Red by White Leghorn) there is only a very slight difference between the reciprocal crosses but such difference as exist are in the same direction as the other two reciprocals. If these differences may be taken as significant they would seem to indicate that some determiners for earlobe color are located in the Z-chromosome. It should be noted, however, that in the cross of Jersey Black Giant by White Leghorn the male offspring of reciprocal crosses differ in the same manner as do the females. Since all sons receive a Z-chromosome from each parent, the male offspring of reciprocal crosses should not differ with respect to the sex-linked factors. So from the F_1 generation no conclusions can be drawn regarding the existence of sex-linked factors affecting earlobe color. From the distribution of F_1 males it cannot be said that either color of earlobe is dominant. Most of the F_1 individuals have earlobes which are intermediate in color.

The results of various crosses of the White Leghorn and Jersey Black Giant are given in table 3 for the purpose of showing whether important sex-linked factors are involved in the determination of earlobe color. Because of the variety of F_2 matings made in the cross this set of data is most satisfactory for analyzing the situation. In this table symbols are used to indicate the genetic constitution of each parent and the male and female offspring. The symbols in bold-face type indicate the origin of the two members of any pair of autosomes which may carry major factors influencing earlobe color. The symbols in italics show the origin of the Z-chromosome. The letter W in bold-face type signifies that the particular autosome was derived from the white earlobe parent while the same letter in italics marks a Z-chromosome originating in the white earlobe parent. The letter R is used in the same manner to indicate chromosomes originating in the red earlobe parent. Under the son and daughter headings are found listed all possible genotypes with reference to the sex chromosomes and any one pair of autosomes.

TABLE 3

Results of the various crosses of White Leghorns and Jersey Black Giants for the study of inheritance of earlobe color.

SIRE	DAM	SONS	DAUGHTERS	WHITE	PREDOMINATELY WHITE	PREDOMINATELY RED	RED
1 Giant **RR** *RR*	Leghorn **WW** *W*	**RW** *RW*	**RW** *R*	♀ 1 ♂ 2	20 17	27 24	2 1
2 Leghorn **WW** *WW*	Giant **RR** *R*	**RW** *RW*	**RW** *W*	♀ 12 ♂ 12	11 11	6 7	1
3 F_1 **RW** *RW*	F_1 (*G*♂×*L*♀) **RW** *R*	$\left.\begin{array}{l}\mathbf{RR}\\\mathbf{RW}\\\mathbf{WW}\end{array}\right\}\begin{array}{l}RR\\RW\end{array}$	$\left.\begin{array}{l}\mathbf{RR}\\\mathbf{RW}\\\mathbf{WW}\end{array}\right\}\begin{array}{l}R\\W\end{array}$	♀ 10 ♂ 2	27 28	17 36	1 10
4 F_1 **RW** *RW*	F_1 (*L*♂×*G*♀) **RW** *W*	$\left.\begin{array}{l}\mathbf{RR}\\\mathbf{RW}\\\mathbf{WW}\end{array}\right\}\begin{array}{l}RW\\WW\end{array}$	$\left.\begin{array}{l}\mathbf{RR}\\\mathbf{RW}\\\mathbf{WW}\end{array}\right\}\begin{array}{l}R\\W\end{array}$	♀ 16 ♂ 30	51 42	34 28	10 8
5 F_1 **RW** *RW*	Giant **RR** *R*	$\left.\begin{array}{l}\mathbf{RR}\\\mathbf{RW}\end{array}\right\}\begin{array}{l}RR\\RW\end{array}$	$\left.\begin{array}{l}\mathbf{RR}\\\mathbf{RW}\end{array}\right\}\begin{array}{l}R\\W\end{array}$	♀ . . ♂ . .	14 3	54 29	28 56
6 F_1 **RW** *RW*	Leghorn **WW** *W*	$\left.\begin{array}{l}\mathbf{RW}\\\mathbf{WW}\end{array}\right\}\begin{array}{l}RW\\WW\end{array}$	$\left.\begin{array}{l}\mathbf{RW}\\\mathbf{WW}\end{array}\right\}\begin{array}{l}R\\W\end{array}$	♀ 17 ♂ 22	10 2	1 1	. . . .
7 Leghorn **WW** *WW*	F_1 (*G*♂×*L*♀) **RW** *R*	$\left.\begin{array}{l}\mathbf{RW}\\\mathbf{WW}\end{array}\right\}RW$	$\left.\begin{array}{l}\mathbf{RW}\\\mathbf{WW}\end{array}\right\}W$	♀ 31 ♂ 33	1 3	. . 3	. . . .

The histograms of figure 1 show graphically the distribution of earlobe color for both males and females of the last five matings of table 3. The solid line represents the distribution for the females and the dash line for the males. The four sections of each histogram represent the four grades of earlobe color; namely, white, predominately white, predominately red and red. The left hand section of each histogram is for white and the other grades follow in the order just given. Below each diagram is indicated the origin of the Z-chromosomes in the two sexes. In each mating, the genetic constitution of males and females with respect to autosomal genes is, of

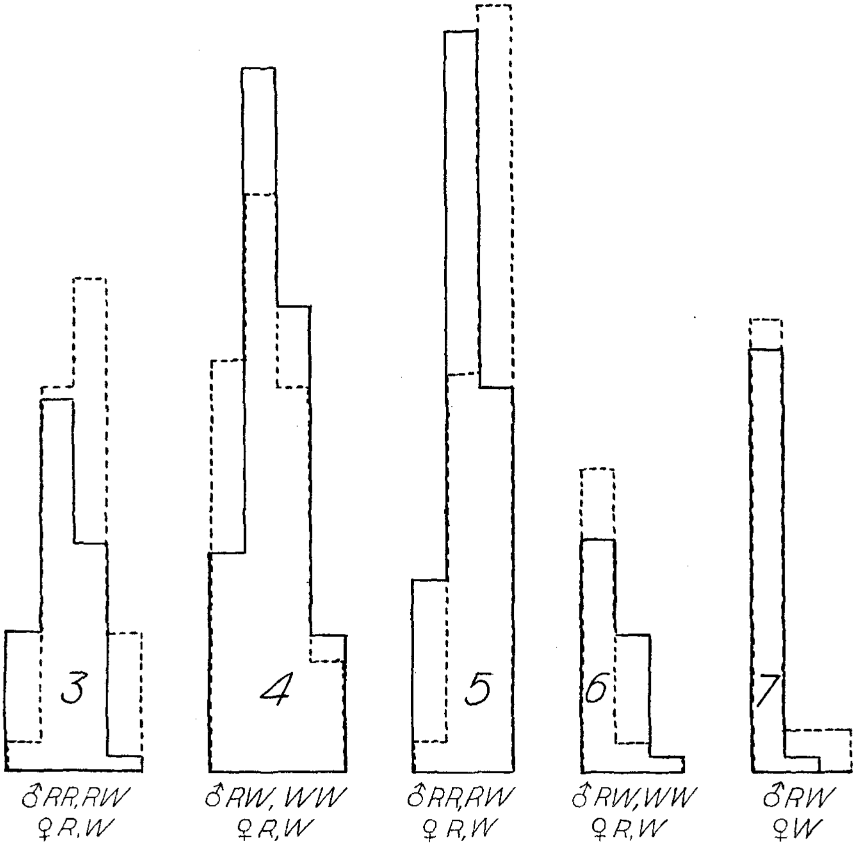

FIGURE 1.—The effect of sex-linked determiners upon earlobe color. The histograms present graphically a comparison of the distribution of earlobe color for males and females of the last five matings in table 3. The solid line indicates the distribution for females and the dash line for males. The letters below the graphs indicate the origin of the sex-chromosomes for the two sexes, *R* being for chromosomes originating in the red earlobe stock and *W* for those from the white earlobe stock.

course, the same. If differences between the two sexes are consistently associated with differences in origin of the sex chromosomes then it may be held that they are due to varying constitutions of the individuals from which the chromosomes came.

For all matings except the last it will be seen that the females are identical with respect to their Z-chromosomes, half receiving their only sex chromosome from the red and half from the white earlobe breed. In the histogram for mating 3 it will be seen that the earlobes of the males vary more in the red direction than do those of the females. Here half of the males are homozygous for sex chromosomes from the red earlobe stock while the other half are heterozygous. The two sexes are identical with respect to their autosomal constitution so if we assume that the diploid condition as found in the male is more effective than the haploid in the female, then the males should vary more in the red direction than do the females. In mating 4 it will be noted that the males are equally divided between those homozygous for the "white" chromosome and those heterozygous for the sex-linked factors. If the factors carried by the sex chromosome influence earlobe color, then it would be expected that the males would have whiter earlobes than those in the previous mating(since the autosomal constitution of the two matings are the same) and that they should be whiter than those of their sisters. An examination of histograms 3 and 4 will prove that both these conditions are met. The females of these two matings are identical with respect to both sex chromosomes and autosomes and their histograms also are quite similar.

The histograms 5 and 6 are for matings of the same designation in table 3. It will be seen that since in mating 5 the males are half homozygous for the "red" chromosome and half heterozygous they should have earlobes which are less white than their sisters. In mating 6, the formulas of their sex chromosomes would indicate that the males should have whiter earlobes than their sisters. The histograms for these two matings show the distribution of color of earlobes for the two sexes to be in agreement with their sex chromosomal composition.

The last histogram which represents the distribution of earlobe color for mating 7 shows practically no difference between the color of earlobes of the two sexes. It will be noted that the males are all heterozygous for any factors on the sex chromosome influencing earlobe color. This result is in agreement with the reciprocal F_1 matings. These two matings indicated in table 3 as 1 and 2 show the distribution of earlobe color to be quite similar for the two sexes.

The results in table 3 and figure 1 show fairly clearly that sex-linked factors are operative in influencing earlobe color. It would seem, however, that the determiners for earlobe color carried by the Z-chromosome are effective only when they are in a homozygous and diploid condition. It is true, at least, that in all matings where half of the male offspring were homozygous for genes of the red or white earlobe stock they differed from the females in earlobe color in the expected direction. In matings where the males were all heterozygous for sex-linked determiners there was no difference between the earlobe color of the males and females.

In crosses of other breeds the matings are not as complete as the one involving Jersey Black Giants and White Leghorns. The matings of Rhode Island Reds and White Leghorns shown in table 4 indicate that sex-linked factors are not operative. An examination of these matings shows that although the sons of the two F₂ matings differ in their sex chromosomes, their earlobe colors are quite similar and differ but little from those of their sisters.

TABLE 4

Results of crosses of White Leghorn by Rhode Island Red.

SIRE	DAM	SONS	DAUGHTERS	WHITE	PREDOMINATELY WHITE	PREDOMINATELY RED	RED
Red **RR**RR	Leghorn **WW**W	**RW**RW	**RW**R	♀ .. ♂ 1	2 1	21 19	1 3
Leghorn **WW**WW	Red **RR**R	**RW**RW	**RW**W	♀ .. ♂ ..	9 ..	19 14	3 9
*F*₁ **RW**RW	*F*₁ (*Rd*♂×*L*♀) **RW**R	**WW** **WR** } RW **RR** RR	**WW** **WR** } R **RR** W	♀ 5 ♂ 3	12 13	22 23	7 7
*F*₁ **RW**RW	*F*₁ (*L*♂×*Rd*♀) **RW**W	**WW** **WR** } RW **RR** WW	**WW** **WR** } R **RR** W	♀ 2 ♂ 5	4 9	16 15	6 11

In table 5 are shown the F₂ results from crosses of Brown Leghorn by Silver Penciled Rocks. Here the white earlobe is carried by the Brown Leghorns and the red by the Penciled Rock. A comparison of the distribution of earlobe color and the sex-chromosomes indicates slightly that sex-linked factors may be involved but evidence supporting this view is not found in all matings.

TABLE 5

Results of crosses of Brown Leghorns by Silver Penciled Rocks.

SIRE	DAM	SONS	DAUGHTERS	WHITE	PREDOMINATELY WHITE	PREDOMINATELY RED	RED
F_1 $\boldsymbol{RW}RW$	$F_1(L♂ \times Rd♀)$ $\boldsymbol{RW}W$	$\left.\begin{matrix}\boldsymbol{WW}\\ \boldsymbol{RW}\\ \boldsymbol{RR}\end{matrix}\right\}\begin{matrix}RW\\ WW\end{matrix}$	$\left.\begin{matrix}\boldsymbol{WW}\\ \boldsymbol{RW}\\ \boldsymbol{RR}\end{matrix}\right\}\begin{matrix}R\\ W\end{matrix}$	♀21 ♂32	26 26	14 5	1 1
F_1 $\boldsymbol{RW}RW$	Br. Leghorn $\boldsymbol{WW}W$	$\left.\begin{matrix}\boldsymbol{RW}\\ \boldsymbol{WW}\end{matrix}\right\}\begin{matrix}RW\\ WW\end{matrix}$	$\left.\begin{matrix}\boldsymbol{RW}\\ \boldsymbol{WW}\end{matrix}\right\}\begin{matrix}R\\ W\end{matrix}$	♀59 ♂59	4 1	2 ..	.. ..
F_1 $\boldsymbol{RW}RW$	S. P. Rocks $\boldsymbol{RR}R$	$\left.\begin{matrix}\boldsymbol{RW}\\ \boldsymbol{RR}\end{matrix}\right\}\begin{matrix}RW\\ RR\end{matrix}$	$\left.\begin{matrix}\boldsymbol{RW}\\ \boldsymbol{RR}\end{matrix}\right\}\begin{matrix}R\\ W\end{matrix}$	♀ 2 ♂ 1	2 1	4 2	1 4

Table 6 gives the data for the F_2 results of mating Buff Leghorn by White Wyandotte and Buff Leghorn by Barred Plymouth Rock. In the former cross there is evidence that sex-linked factors are involved in bringing about the difference in earlobe color. The data shown for the Buff Leghorn-Barred Plymouth Rock cross, if checked for the correspondence in distribution of sex chromosomes and earlobe color, furnish no evidence for the view that sex-linked factors are here operative.

TABLE 6

Results of crosses of Buff Leghorn by White Wyandotte and Barred Plymouth Rock.

WYANDOTTE×BUFF LEGHORN

SIRE	DAM	SONS	DAUGHTERS	WHITE	PREDOMINATELY WHITE	PREDOMINATELY RED	RED
F_1 $\boldsymbol{RW}RW$	$F_1(Wy♂ \times L♀)$ $\boldsymbol{RW}R$	$\left.\begin{matrix}\boldsymbol{WW}\\ \boldsymbol{RW}\\ \boldsymbol{RR}\end{matrix}\right\}\begin{matrix}RW\\ RR\end{matrix}$	$\left.\begin{matrix}\boldsymbol{WW}\\ \boldsymbol{RW}\\ \boldsymbol{RR}\end{matrix}\right\}\begin{matrix}R\\ W\end{matrix}$	♀85 ♂40	15 38	3 5	.. 3
F_1 $\boldsymbol{RW}RW$	W. Wyandotte $\boldsymbol{RR}R$	$\left.\begin{matrix}\boldsymbol{RW}\\ \boldsymbol{RR}\end{matrix}\right\}\begin{matrix}RW\\ RR\end{matrix}$	$\left.\begin{matrix}\boldsymbol{RW}\\ \boldsymbol{RR}\end{matrix}\right\}\begin{matrix}R\\ W\end{matrix}$	♀ 2 ♂	9 1	12 8	5 13

BARRED ROCK×BUFF LEGHORN

SIRE	DAM	SONS	DAUGHTERS	WHITE	PREDOMINATELY WHITE	PREDOMINATELY RED	RED
F_1 $\boldsymbol{RW}RW$	$F_1(Rk♂ \times L♀)$ $\boldsymbol{RW}R$	$\left.\begin{matrix}\boldsymbol{WW}\\ \boldsymbol{RW}\\ \boldsymbol{RR}\end{matrix}\right\}\begin{matrix}RW\\ RR\end{matrix}$	$\left.\begin{matrix}\boldsymbol{WW}\\ \boldsymbol{RW}\\ \boldsymbol{RR}\end{matrix}\right\}\begin{matrix}R\\ W\end{matrix}$	♀14 ♂12	15 12	20 11	15 9
F_1 $\boldsymbol{RW}RW$	Buff Leghorns $\boldsymbol{WW}W$	$\left.\begin{matrix}\boldsymbol{WW}\\ \boldsymbol{RW}\end{matrix}\right\}\begin{matrix}RW\\ WW\end{matrix}$	$\left.\begin{matrix}\boldsymbol{WW}\\ \boldsymbol{RW}\\ \boldsymbol{RR}\end{matrix}\right\}\begin{matrix}R\\ W\end{matrix}$	♀42 ♂39	12 13	5 4	1 2

AUTOSOMAL FACTORS

The data already presented indicate that sex-linked factors are involved in determining earlobe color in some breeds. In some cases their influence appeared to be slight and in other crosses there was no evidence for sex-linkage of factors responsible for the existing differences in earlobe color. These results would lead one to expect evidence for autosomal factors for color of the earlobe. If so the data already presented in table 3 should afford such evidence. The columns giving the genotypes of the male and female offspring show some instances where the constitution with respect to the sex chromosome are identical but where differences in the autosomal constitution exist. The female offspring of matings 4 and 5 offer material for a comparison of this sort. Although their sex chromosomal constitution is the same we find a wide difference in their earlobe color. Associated with this difference in distribution of color of earlobes we see that there is a difference in the autosomal constitution of the two lots of females. Those in mating 4 have the three genotypes which result from mating two heterozygous individuals, one-fourth homozygous for white, one-half heterozygous, and one-fourth homozygous for red. In mating 5, half the females are homozygous for red and half heterozygous, none being homozygous for white. The great difference found here shows that the major factors involved are probably autosomal in location.

A still greater difference is shown by matings 5 and 6. Here the female offspring of the two matings have identical sex-chromosomal composition but differ considerably in the origin of their autosomes. In 5 half are homozygous for factors of the autosomes from the red earlobe parent while in 6 half are homozygous for factors from the white earlobe stock. In each case half of the offspring are also heterozygous. Since mating 6 produces no phenotypes homozygous for the R-factor we would expect it to differ from mating 5 to a greater degree than does mating 4. These relations are in agreement with differences in the factorial constitution of their autosomes. Matings 5 and 6 are reciprocal back crosses to the parent stocks and since in mating 6 a higher percentage of whites occur than reds in mating 5 there is evidence that at least some of the white autosomal factors are partially dominant to the red.

The evidence is fairly conclusive that at least one pair of autosomal factors is effective in determining earlobe color. A comparison of the results of matings 2 and 7 seems to indicate that more than one pair of autosomal factors are operative. The female offspring of the two matings have identical constitution with respect to the sex chromosomes. They differ in that in mating 2 all are heterozygous for autosomal factors while in mating 7 half are of this constitution and half are homozygous for any given pair of autosomes from the white earlobe parent. If only one pair of autosomes are involved in determining earlobe color, then half of the female offspring in mating 7 should have earlobes the color of which show a distribution similar to that in mating 2. The data show that practically all of the females in mating 7 have white earlobes. Most of the expected intermediates are missing. This shortage of intermediates might be expected if there exists another autosomal factor which segregates independently of the first. If either autosomal factor in a homozygous condition is capable of producing birds with white earlobes but few earlobes other than white would be expected. It thus seems probably that more than one pair of autosomal factors are operative.

LINKAGE OF SEX-LINKED DETERMINERS

Since it has been shown that both autosomal and sex-linked factors are involved in determining earlobe color it is of interest to know whether earlobe color shows linkage with other known characters. The fact that some of its determiners show sex-linked behavior suggests that earlobe color should show linkage with some member of the sex-linked group. Since something is known of the distribution of the sex-linked factors it is possible to determine with some degree of accuracy the relative position of at least the major sex-linked factors influencing earlobe color. The writer (Anatomical Record **29**: 143–144) has shown that the factors for the sex-linked character determining rate of feathering is widely separated on the sex chromosome from those for barring and shank color. Hence, a cross involving these characters and differences in earlobe color should show in which end of the sex chromosome the sex-linked factor for earlobe color lies.

In table 7 are shown the linkage relations of earlobe color with rate of feathering and shank color, and rate of feathering and barring. These data are from the F_2 generation of crosses of the Jersey Black Giant and White Leghorn. In the table are included only the crossover classes, first for rate of feathering and shank color, and then rate of feathering and barring. Since the original combinations were rapid feathering and yellow shanks, and slow feathering and dark shanks, the crossover classes in the first section of the table are slow feathering-yellow and rapid feathering-dark. In the original crosses white earlobe entered with yellow shanks and rapid feathering. Since the determiners for yellow and rapid have been shown to occupy distant sections of the sex chromosome, the crossover classes in table 7, representing breaks in the sex chromosome between these points should indicate the position of the sex-linked determiners for earlobe color in relation to these two factors. When the determiners for yellow and rapid separate in crossing over, the determiners for white earlobe will go most frequently with the point with which it is most closely associated. Thus, since the original combination was yellow shank and rapid feathering, the two crossover classes will include each character combined with the allelomorph of the other and the group having the whiter earlobes will show which of these two points the earlobe color factor lies nearer.

Figure 2A shows the probable relation upon the sex chromosome of factors for rate of feathering and shank color. The diagrams 2B and 2C show the sex chromosome following the phenomenon of crossing over, B indicating the most frequent grouping of characters providing the gene influencing earlobe color is in the same end with that for rate of feathering. The situation when the determiner for earlobe color is in the opposite end is shown in C. If the situation shown in B be the true one,

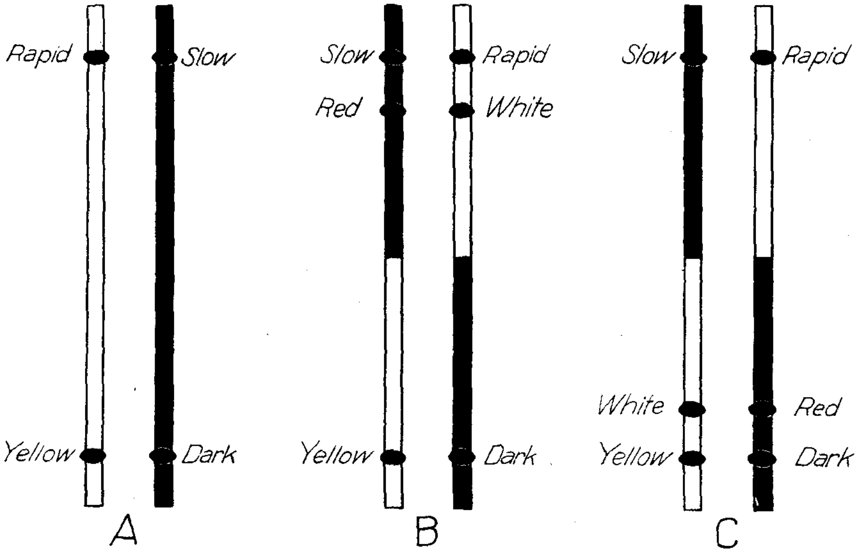

FIGURE 2.—Diagrams showing the various crossover combinations depending upon which end of the chromosome the sex-linked factor for earlobe color is located. Figure 2A gives the probable location of the factors for rate of feathering and shank color. Figure 2B gives the most frequent crossover combinations when the earlobe color factor is nearer the gene for rate of feathering while figure 2C shows the situation where it is located nearer the gene for shank color. In table 7 are found the data for these linkage relations.

then the crossover group rapid-dark should be whiter than its reciprocal slow-yellow. If the diagram C represents the true relation then the conditions stated above would be reversed, the crossover group slow-yellow being the whiter.

Table 7 shows the crossover group slow-yellow to be whiter than its reciprocal and hence substantiates the view that the sex-linked determiner for earlobe color is located in the chromosome nearer the shank color determiner than that for rate of feathering.

TABLE 7

Linkage relations of sex-linked factors for earlobe color.

	RELATION TO RATE OF FEATHERING AND SHANK COLOR			
Crossover group	Earlobe color			
	White	Predominately white	Predominately red	Red
Rapid dark	4	17	13	5
Slow yellow	16	22	11	4
	RELATION TO RATE OF FEATHERING AND BARRING			
Rapid non-barred		4	9	4
Slow barred	1	3	3	3

It has also been shown (WARREN 1924) that the determiner for barring is also distantly separated from the rate of feathering gene and probably located near the gene for shank color. If this be true then earlobe color should show relations to this factor similar to those found for shank color. The original combination was white earlobe, rapid feathering, barred plumage so the barred-slow crossover group should be whiter than the group rapid-non-barred. There is a slight difference in distribution in the expected direction. Since the numbers involved are small these results cannot be held to be conclusive but may be taken as a suggestion of the possible relations. Also, since the effects of the sex-linked determiners have been shown to be slight in the presence of the autosomal factors, large differences could not be expected in the data shown in table 7.

LINKAGE OF AUTOSOMAL FACTORS

It is also possible to determine whether linkage relations exist between any autosomal earlobe color factors and factors for certain known autosomal characters. Several autosomal characters were involved in the crosses, but for only two have the linkage been measured since in most instances the characters were not sufficiently clean-cut in their segregation to permit accurate classification. No autosomal linkage groups have yet been determined in poultry so it is not known whether the characters used belong to the same or different linkage groups. Although dominant white and extended black plumage colors have been treated as an allelomorphic pair the evidence substantiating this assumption is not entirely conclusive. This fact should not however influence the results.

Any character, the factor for which lies in the same chromosome with autosomal earlobe factors, should in segregation more frequently be associated with the earlobe color with which it originally entered. Thus in a cross involving white and black plumage and red and white earlobes, since white plumage and white earlobe entered the cross together, it is expected that in the F_2 generation the white plumage segregates will have the whiter earlobes, providing the factors for these two characters are in the same chromosome. The segregation of rose and single comb should in the same manner indicate their linkage relations with earlobe color. If no linkage exists the distribution of earlobe color among the classes of segregates should be a random one. Table 8 shows the distribution of earlobe color for F_2 segregates of black and white plumage and rose and single comb. It will be noted that the distribution of earlobe color for the two members of each group is practically identical, thus indicating that the determiners for these characters are not carried by any chromosomes bearing the major autosomal determiners for earlobe color.

TABLE 8

Linkage relations of autosomal factors for earlobe color

CONTRASTED PAIR	EARLOBE COLOR			
	White	Predominately white	Predominately red	Red
White		9	46	44
Black		8	35	35
Rose	67	56	16	2
Single	29	21	9	1

LINKAGE RELATIONS OF EARLOBE COLOR AND EGG COLOR

In the established breeds and varieties of poultry white egg shell color has usually been associated with white earlobe color, while the red earlobe breeds usually lay eggs of the darker shades. This has led practical breeders to hold that there is some relation between earlobe and egg color. The apparent linkage might be due to close association of the determining genes on the chromosome or to the existence of a single factor which controls the pigmentation of both the egg and earlobe. If the existing association between earlobe and egg color is a chance one, the linkage should be broken by segregation.

To determine the nature of the association between these two characters 62 F_2 females chosen at random from the cross Jersey Black Giant by White Leghorn were tested for egg color. For classifying (the egg colors) a color chart was made grading from white to the darkest brown shade. The color grade was determined by taking the average color of five eggs laid during the first month of production. Other studies have shown that egg color varies somewhat with the period of production and for that reason the selection was limited to the first month.

In table 9 is shown the distribution of egg color for the 62 females, grouped according to earlobe color. Grade 1 is white and the succeeding grades become progressively darker. It is seen that individuals falling into the four grades of earlobe color lay eggs of practically the same average color and hence there is no evidence for any conditions which tend to associate white earlobe with white egg color. This would seem to show that the existing association is entirely a chance one. It is possible that this association may bear some relation to the origin of breeds of poultry.

TABLE 9

Showing independent assortment of factors for earlobe color and egg shell color.

EARLOBE COLOR	EGG COLOR GRADES								
	1	2	3	4	5	6	7	8	9
White	..	..	1	1	4	..	1	1	..
Predominately white	2	2	2	5	8	5	1	..	1
Predominately red	..	1	4	4	6	4	2	..	..
Red	2	1	..	1	2	1	1	..	..

GENERAL DISCUSSION

The experiments discussed indicate that earlobe color is dependent upon several genetic factors. The fact that all grades of earlobe color are found in the F_1 generation from crossing most white and red earlobe breeds would lead one to expect a complex situation.

It also seems probable that individuals of a single strain of a breed may differ in some of the minor factors influencing earlobe color. The results of the F_2 generation indicated that individuals of some breeds were not homozygous for all factors for earlobe color. Greater differences in factorial constitution probably exist between breeds. Crosses of the Rhode Island Red breed showed no evidence of its carrying sex-linked earlobe color determiners while crosses of other breeds indicated genes of this chromosome to be operative. The differences in genetic constitution of individuals of a breed do not seem to affect the major earlobe color factors since the breeds dealt with seldom produced individuals varying from the standard.

From crosses of the Single Comb White Leghorn and Jersey Black Giant breeds there is evidence for the existence of at least three factors influencing earlobe color. A sex-linked factor is operative but seems to play a minor role since its influence was slight and exhibited only when in a homozygous diploid condition and acting with some of the autosomal factors in a heterozygous condition. The major earlobe color factors are autosomal and there is evidence that at least two factors of this group are operative. This complex situation is probably only the natural result of the manner in which the color has been fixed. Since the slightest variation from either white or red constitute a breed disqualification any modifying factor which tended to maintain the constancy of the desired color was seized upon and by selection incorporated in the genetic constitution of the breed.

SUMMARY

1. Earlobe color has a complex factorial basis.
2. Breeds having the same earlobe color may differ considerably in their genetic constitution with respect to this character.
3. Individuals of a single breed and strain may differ in some of the minor genetic determiners.
4. The Jersey Black Giant and White Leghorn breeds differ in at least three factors determining earlobe color, one sex-linked and two autosomal.
5. It was possible to estimate roughly the position upon the sex chromosome of the sex-linked factor.
6. The autosomal factors for earlobe color showed no linkage with those for any autosomal characters which the crosses permitted testing.
7. There was no evidence of any linkage between the factors for earlobe color and egg color.