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Studies on inheritance in poultry: I. The constitution of the White Leghorn breed.

BULLETIN 155

Agricultural Experiment Station

OF THE

Rhode Island State College

KINGSTON, R. I., U. S. A., JUNE, 1913.

The publications of the Station will be sent free to all who apply for them. Suggestions how the Station can aid the State are gladly received. Visitors are always welcome. Railway Station, Telegraph, Express and Post-Office—Kingston, R. I. Telephone, Narragansett Pier Exchange, 232-J.

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AGRICULTURAL EXPERIMENT STATION OF THE RHODE ISLAND STATE COLLEGE.

BULLETIN 155*

STUDIES ON INHERITANCE IN POULTRY: I. THE CONSTITUTION OF THE WHITE LEGHORN BREED.†

PHILIP B. HADLEY,
WITH THE ASSISTANCE OF DOROTHY W. CALDWELL AND C. H. MAGOON.

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*This bulletin constitutes a part of the Twenty-sixth Annual Report for the year ending June 30, 1913.

†Contribution No. 19, from the Division of Animal Breeding and Pathology of the Agricultural Experiment Station.

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I. Introduction.

In the history of plant and animal breeding it has been commonly observed that the mating of different varieties or species may produce offspring which, in certain respects, are unlike either parent. In some instances the qualities of this mixed, or heterozygous, individual are an improvement upon either parent form, just as superior strains of corn are in reality hybrid-products, or as the crosses between certain varieties of poultry yield birds of different plumage or of larger size than that of either parent. In the continued propagation of these desirable types, the plant or animal breeders have, however, encountered much difficulty. This difficulty deals primarily with the following circumstance: In the majority of cases the heterozygous form does not breed true; upon continued propagation it breaks up again into the parent types, and leaves only a certain proportion of heterozygous individuals which themselves, when bred further, behave in the same manner.* In other words, no method is known of "fixing" a heterozygous character,—of causing it to faithfully reproduce itself through successive generations. That knowledge of such a method would be a valuable addition to the theory and practice of both plant and animal breeding, no one can deny; whether it is possible, remains to be ascertained.

The many variable features possessed by domestic poultry and the ease with which crosses between diverse types can be made, render this group of animals especially favorable for studying the behavior, in inheritance, of such so-called heterozygous characters. At the outset of this investigation, in 1909, *barring* in fowls was selected as the character to be studied. The barred color-pattern in feathers was then tentatively regarded as a heterozygous condition arising

*A case in point is that of the Blue Andalusian fowl which is a "hybrid" product and never breeds true.

from the mixture of black and white. The problem was therefore, first of all, to produce this character *de novo*, as it were; or at least, to obtain it as a result of mating fowls which, in themselves or in their ancestry, were not known to possess the condition either in a fixed or in a transitional state; in other words, in selecting the material to be employed in the investigation, the use of Barred Plymouth Rocks and other barred breeds, as well as of their ancestors and their derivatives, was to be scrupulously avoided. Secondly, the problem was to so breed the birds manifesting the newly-produced character that it should be made a permanent acquisition of the breed.

As will appear in the following pages this end has in a measure been reached,—that is to say, a breed of barred fowl has been produced through the employment in breeding of factors found in birds which manifested no somatic barring. But the nature of the results secured is such as to call into question the truth of the very hypothesis upon which the investigation was originally based. In other words, the question is now raised whether we are justified in considering the type of barring revealed and studied in the experiments to be reported in the light of a heterozygous character. The recently-devised factor-hypothesis and its application to the principles of breeding and laws of heredity, together with the theory of unit-characters, has profoundly modified our views regarding the fundamental nature of the things that are inherited. Thus, to discover a factor for barring where it was not previously known to exist, and to produce such a factor (or such a pattern) *de novo* by the bringing together of simpler germinal elements, are manifestly two different operations. A discussion of the bearing of this consideration upon the results of the present investigation may well be deferred until the experimental data have been presented. It may be said here, however, that these data may not be valueless notwithstanding that their significance now appears to be different from that first assumed; and the investigation as a whole, though, perhaps not dealing with the actual "fixation" of a heterozygous character as first surmised may still have the merit of throwing new light upon one phase of the inheritance of the barred

color-pattern; and, in addition, of producing a new type of fowl through the isolation, and subsequent employment in breeding, of a previously hidden factor.

The barred color-pattern is doubtless a very old and a by no means uncommon form of marking in the plumage of both wild and domestic birds. With some modification it is present in the feathering of many of our game birds, but it is in one or two varieties of domestic fowl that the character is to be seen in the purest and most extended form. At the present day the Barred Plymouth Rocks, an American breed, represent by far the most perfect development of the barred pattern to be found in any species or variety of bird.

The origin of barring in domestic fowls is not easy to ascertain. It appears probable that the barring used in making the breed of Barred Plymouth Rocks as it is known to-day was derived from the American Dominiques. These birds, which possess less perfect barring than the Barred Plymouth Rocks, are stated by some to have inherited this marking from the "cuckoo" birds of England, but this point is not supported by available evidence. It must therefore be concluded that we are not acquainted with the manner by which the definite barred color-pattern was first introduced into the breeds of domestic fowl. So far as can be ascertained, however, no new breeds of barred fowl have been produced since the making of the American Barred Plymouth Rocks, in which, as has been stated, the Dominiques were the major component. A partial exception to this statement is found in the words of Wright (1910), who states that barred birds are sometimes the result of crosses between white birds and those of dark color. Wright assumes that barring is not a primary character [unit character], but a sort of mixture through which the breed of Dominiques may have been founded. He further observes that when once produced, this character "has a strong tendency to permanence." These opinions of Wright were based upon observations made from time to time in the poultry yard and without especial study. Within the past few years, however, the method of inheritance of many characters in fowl has been made by several

investigators the object of especial study and, among these characters, that of barring has received some consideration. We may therefore review briefly some of the recent work on this subject.

II. Historical Resumé.

Hurst (1905) was among the first to test the Mendelian principles of heredity with respect to characters of fowl. Although he did not make a particular study of barring he makes several references to the appearance of this color-pattern in cross-bred birds. Among other crosses was Houdan ♂ × White Leghorn ♀. This cross "gave 94 whites and 11 blacks; of these, 22 were apparently clear white, 72 white ticked with black, one black with white head, and 10 black ticked with white. In each case the tickings were slight and not extensive, so that in the ground color, the distinction between white and black was marked and discontinuous. In the first plumage all except two of the clear whites developed black ticks, similar to those that were born ticked; the blacks developed into 6 blacks and 5 'cuckoos;' 5 of the blacks were slightly ticked with white in the crest only, and in their plumage were indistinguishable from the Crève-cœur breed, the other black developed into a typical light Houdan; the 5 cuckoos were gray-white, barred with blue-black or white feathers; both the blacks and the cuckoos were distinctly shaded with brown. Curiously enough the 6 blacks were all pullets and the 5 cuckoos all cockerels!" But this result, as will be shown later, is wholly explainable on the ground that Hurst's White Leghorn ♀♀ were heterozygous for the barred plumage character, and that they were not pure for white.

Later, Hurst mated one of the cuckoo cockerels with two of the black pullets. From this mating, 43 chicks were hatched, all with black down-feathers. But 34 were ticked with white, 7 had white heads and 2 were strongly shaded gray. Of those hatched, 31 were reared and gave, in the first plumage, 17 cuckoos and 14 blacks. "Of the cuckoos, 7 were cockerels and 10 were pullets, and of the

blacks, 8 were cockerels and 6 were pullets, so that the correlation of black with ♀ and cuckoo with ♂ in F_1 was not maintained in F_2." Hurst states further that "the cuckoos were precisely similar to those of F_1, having a gray-white ground barred with blue-black, with odd black or white feathers. . . . The blacks were of two types, dark Houdans and Crèves, suggesting that the cuckoo male parent was giving off black gametes. No dominant whites appeared in this mating, suggesting that the cuckoo male parent was *not* giving off dominant white gametes."

It is interesting to note that the cuckoo ♂ mentioned above subsequently moulted into almost clear white, only one feather on the back being tipped with gray.

Besides the Houdan × White Leghorn cross, Hurst also crossed Black Hamburg ♂ with White Leghorn ♀. The progeny comprised 49 whites and 8 blacks; of these one was apparently clear white, 48 were ticked with black, and 8 were black with whitish throats. None of these chicks were raised for further observation, and Hurst draws no conclusions regarding the origin of the barred pattern described.

Davenport (1906) has also described a type of barring which appeared when certain black and white breeds were crossed. In these matings dominance of white was the usual result. Two White Leghorns crossed by a Black Minorca produced in F_1 only white birds, the ♀♀ having some black feathers White Leghorns crossed with Houdans gave only white progeny This result is at variance with Hurst's mentioned above. White Leghorns crossed with Red-backed game had "white offspring with some buff on breast." "On the other hand," Davenport continues (p. 75), "the white color of the Silky dominates over the dark color of the Frizzle in about only 23 per cent. of the hybrids."

Davenport states further that no barring resulted from crossing White Leghorn with Houdan or with Black Minorca. Barring in the male progeny did appear, however, in matings between the Tosa fowl and White Cochin, between White Leghorn Bantam and Dark Brahma, and in matings between White Leghorn Bantam and Rump-

less Game. "Of 26 hybrids between Black Cochin and White Leghorn, 8 were barred black and white, and these belonged equally to the two sexes."

With reference to barring, Davenport in his 1906 report concludes as follows: "Barring is a heterozygous condition found in hybrids from a white and black parent. It is provisionally regarded as a form of particulate inheritance as opposed to the alternative inheritance of the Leghorn × Minorca cross. This heterozygous condition when interbred, usually breaks up into white, uniformly pigmented, and barred, as in the case of the Tosa × White Cochin hybrids." As to the inheritance of white and dark plumage, Davenport states: "Aside from cases of barring and Andalusian coloration, white usually dominates over dark plumage. This is true in all cases where White Leghorn is employed as a white race, whether the other race is Game, Dark Brahma, Houdan or Minorca. When the Silky is used as the white race, white is sometimes recessive, but it must be acknowledged that the dark parents were not the same as were used with the Leghorn, but were a Game, Frizzle and Jungle fowl; consequently the results in the two series are not strictly comparable. . . . It is hardly conceivable that the white of the Silky is different from that of the Leghorn; so it must be concluded that the white inherited as a solid color is sometimes dominant and sometimes recessive, depending upon the race in which it inheres." On this point, we now have further light as will be indicated later in this paper.

In Davenport's later report (1909) upon inheritance of characteristics in domestic fowl, the application of the factor hypothesis is strongly evident, and, in the light of later researches, several of his earlier conclusions are modified or the results receive a somewhat different interpretation.

Among the Black × White crosses reported in this paper is the cross White Leghorn (♂?) × Black Minorca (♀?). In 154 offspring there appeared 116 white, black-white, or blue, and 38 black. Some of the latter contained more or less white, and among them were four

barred birds. This result approximates very closely the expected F_1 Mendelian ratio.* Since the birds that are heterozygous for white and black appear white, we have 75 per cent. of white birds. Apparently Davenport was not working with the pure-bred White Leghorn stock.

In a cross between White Leghorn and Black Cochin there appeared among 24 offspring, 10 white, 7 black and 7 barred. In this case Davenport assumes that the Leghorn was heterozygous for white (since half the progeny were not white) and heterozygous for barring. Subsequently the barred birds which resulted from the above cross, were mated together. This cross gave 23 white birds, 40 blacks or games, and 21 spangled, barred or blue. Regarding this result Davenport says: "On the assumption that the zygotic formula of both hens and cocks is BbN_2Ww (compatible with barred plumage), we get four-sixteenths of the offspring white, three-sixteenths mottled or barred, and nine-sixteenths black or game, thus approximating the observed result; *i. e.*, 21, 16, 47, as compared with 23, 21, 40. The result supports the hypothesis of a barring factor, B."

That Davenport obtained barred birds in a cross between White Leghorn Bantam and Dark Brahma has already been mentioned: Of 51 F_1 birds, 5 were barred. An attempt was made to fix the barring. The best cock bred from F_2 and the best females from F_1 or F_2 were used for the experiment. From this cross there were obtained 3 whites, 67 blacks, 37 of Dark Brahma type and 38 barred birds. "This result," says Davenport, "suggests the interpretation that one of the parents, probably the male, contains both heterozygous black and barring, while the other parent lacks the supermelanic coat and has homozygous barring. Then, of the offspring, half will be barred and half will be black, and consequently (since only the non-black show their barring), one-fourth will appear barred, one-fourth will appear of the Dark Brahma type and half will be pure black, or have the pattern obscured by the supermelanic coat."

Besides the studies on barring reported above, dealing chiefly with crosses between light and dark birds, the barring of the Plymouth

*Provided that the White Leghorns were heterozygous for white.

Rock breed of fowls has, within the past two or three years, received some consideration.

The fact has long been noticed by observant poultrymen that the progeny from crosses between Plymouth Rocks and dark non-barred breeds varied with respect to the barred color-pattern, according as the male bird belonged to one or the other race in question. Cushman (1893) was probably the first to report this circumstance. This writer made a large number of crosses between pure-bred fowls with the purpose of perfecting a good market roaster. Among his crosses were Indian Game ♂ × Barred Plymouth Rock ♀. Cushman (*l. c.*) gives a brief description of this cross and states that the cockerels had barred plumage whereas the pullets were all black.

It is probable that other poultrymen have observed similar results from such crosses, but without recording their observations. Yet the facts observed awakened little speculation until the attempt was made to place upon them an interpretation agreeing with the Mendelian view of heredity. Spillman (1908) then devised a Mendelian hypothesis to account for the facts observed in the inheritance of barring. This hypothesis may be briefly stated as follows:

1. When barring is present in *female* birds, they are heterozygous for this character; they are also heterozygous for the female sex character (*F*).

2. When barring is present in *male* birds, they may be either *heterozygous* or *homozygous* for this character; the males are always homozygous for the absence of the female sex character.

3. Barring (*B*) and the character, "femaleness" (*F*), never exist together in the same gamete.

This may be represented symbolically as follows:

Let *F* represent the female sex character (♀).

Let *f* represent the absence of femaleness, or the male sex character (♂).

Let *B* represent the factor for barring.

Let *b* represent the absence of the barring factor.

Employing these symbols, the zygotic formula of the Barred Plymouth Rock ♂ becomes

$$BBff,$$

forming gametes

$$Bf \cdot Bf$$

The zygotic formula of the ♀ becomes

$$BbFf,$$

forming gametes

$$Bf \cdot bF$$

since, by hypothesis, B and F (or their complementary combination, bf), cannot be present in the same gamete.

The matings occurring in the propagation of pure Barred Plymouth Rock stock would therefore be represented:

$$\begin{array}{l} ♂\ Bf \cdot Bf \times \\ ♀\ Bf \cdot bF = \\ \hline ♀♀\ BbFf, \text{ Barred} \\ ♂♂\ BBff, \text{ Barred} \end{array}$$

the ♀♀ being heterozygous for barring and the ♂♂ homozygous.

If, however, we have the mating between the Barred Plymouth Rock and some dark non-barred breed, such as the Rhode Island Red, the case is different, and the results vary accordingly as the ♂ is chosen from one breed or the other.

The zygotic formula of the R. I. Red ♂ (non-barred) would be

$$bbff,$$

forming gametes:

$$bf \cdot bf$$

while the formula of the Barred Rock ♀ is as shown above. This mating would therefore become:

$$\begin{array}{l} ♂\ bf \cdot bf \times \\ ♀\ bF \cdot Bf = \\ \hline ♂♂\ Bbff, \text{ Barred} \\ ♀♀\ bbFf, \text{ Black} \end{array}$$

In other words the ♂♂ would be barred (heterozygous) while the ♀♀ would be black.

The reciprocal cross would be represented

♂ *Bf* · *Bf* ×
♀ *bF* · *bf* =

♂♂ *Bbff*, Barred
♀♀ *BbFf*, Barred

both ♂♂ and ♀♀ being heterozygous for barring. In other words, all progeny are barred when the ♂ parent is homozygous for this character.

That Spillman's hypothesis could be verified in experimental results was first shown by Goodale (1909) in a brief paper reporting the results of matings between Buff Rocks and Barred Plymouth Rocks. In a subsequent note, Goodale (1910) states that in crosses between White Leghorn (♀) and White Plymouth Rock (♂), only white birds appeared in F_1; in a few of these faint bars developed. In F_2, however, there were white, black, gray and barred chicks, the latter resembling exactly the Barred Plymouth Rocks.

In addition to the instances of barring mentioned above, Pearl (1912) has reported, upon the authority of an English fancier*, the history of the "Cuckoo Pekins." This bantam breed, according to the authority cited, was produced from a mating of Black Pekin (♂) with White Booted (♀). One of the ♀ progeny showed "stone-colored bars on a milk-white ground." This bird was mated back to its sire, the Black Pekin. The cuckoo pullets from this mating were mated with a cuckoo cockerel derived from imported Chinese Cuckoo stock. Inbreeding was practiced until a permanent cuckoo variety was established. Regarding the origin of this barred pattern, Pearl assumes that it did not arise *de novo*, but that the barred factor was present in the White Booted parent. However this may be, one further point is of interest, namely, the question of the alleged transmission of barring from the White Booted ♀ to her daughter. As

*Mr. William F. Entwisle, who has published the account in his book, "Bantams," Wakefield, England, 1894 (?), p. 1–116.

will be shown later, this is contrary to the established method of inheritance of barring as it occurs in the Barred Plymouth Rock breed; and without more convincing evidence the case does not appear to warrant the assumption that barring of this sort is inherited in any other manner than that now generally accepted.

III. Experimental Results.

As has been stated, at the outset of this investigation barring was tentatively regarded as a heterozygous condition resulting from the mating of black with white fowls. Therefore the preliminary experiment involved chiefly the mating of these breeds with the aim of securing from some of the crosses a certain number of individuals possessing the barred color-pattern. These crosses were between the White Leghorn ♂ and the following black ♀♀: White-faced Black Spanish, Black Minorca, Black Langshan, Black Java, Black Hamburg and Black Cochin. The F_1 generation was bred in 1910. In 1911, the F_1 breeding was continued and in addition a number of the F_2 generation from some of the crosses were reared. In 1912, a greater number of the F_2 generation were reared, and also a number of other crosses were made between selected F_2 stock and several other varieties of fowl. It may be said in passing that all the stock used in the experiments was carefully selected from reputable breeders and was probably as pure-bred as any that could be obtained in the country. The breeds mentioned were chosen for the experiments first of all, because so far as could be ascertained from poultry literature none of them was known to be related to breeds possessing the barred color-pattern such as the Barred Plymouth Rocks or the Dominiques. The modern White Leghorn, though differing considerably from the older type, is usually stated to be a breed which has been mixed with others only to a slight extent; and it is therefore commonly regarded as "one of our purest breeds." As will be demonstrated later this conception is rather doubtful. So much regarding race-purity is not usually said of the Black Hamburgs,

Black Minorcas, Black Javas, Black Cochins, and Black Langshans, although the Black Spanish breed has probably been kept fairly pure. In no case, however, is it positively known that barred stock has entered into the formation of these breeds. It was therefore at first assumed that the appearance of barring in the progeny from these birds would indicate that this pattern had been formed *de novo* as a heterozygous condition, or that it was inherited from the white stock in which it existed as a cryptomere as in the case of the White Plymouth Rock breed. Whether this was a justifiable assumption will appear in the course of the experiments now to be described.*

CASE 1.—*White Leghorn* ♂ × *Black Hamburg* ♀. Nature of mating: *CCBBffII* × *CCbbFfii*. (For discussion, see p. 186).

White Leghorn ♂ 193A: Weight 5½ lbs., back of medium length; squirrel tail; body medium length, high on legs; high comb with six points, slightly thumb-marked and blade deficient in size; head long, eyes red; ear-lobes white but spotted with red; wattles of medium size with one fold in each; neck white with tendency to cream; back white; shanks, toes and beak pale yellow; spurs about one inch in length; no pattern observable on any of the feathers, which are also free from black ticking. (See Pl. I).

Black Hamburg ♀, 185A†: Weight 4 3/16 lbs., neck of good length; back long; tail carried high; body long but not deep; comb of good size, rather flat on top, spike with marked up-turn at rear; eyes dark hazel; ear-lobes bluish white and about half red; wattles very small, fine texture, smooth. Feathers of neck greenish black with purple barring; primaries dull black, secondaries and main tail feathers greenish black with some purple barring; body dull black; shanks dark slate; spurs about ⅓ inch long. (See Pl. III).

The data on the first set of W. L. × B. H. matings are summarized in the following table:

*It will be convenient to include in the present section only the actual experimental results. All discussion of the significance of these results, together with their explanation, is taken up in Section IV, p. 182.

†Black Hamburg 186A resembled 185A in nearly all points.

TABLE 1.—Showing the results in F_1 of crossing White Leghorn ♂ × Black Hamburg ♀♀ (1910 series.)

MATING NUMBER.	PARENTS.		PROGENY.		
	♂	♀	White.	Black.	With barred feathers.
201	193 A	185 A	22	0	1 ♂ 1 ♀
202	193 A	186 A	8	0	.....
211	193 A	*	19	0	2 ♂♂

*Female not identified, but one or the other of the above.

The data presented in Table 1 demonstrate that the white of the W. L. in all instances dominated over the black of the B. H. The progeny were not all pure white, however, since more than one-half of the F_1 generation (♂♂ and ♀♀ equally) showed black flecks in the white feathers. When the chicks were in down-feather the majority revealed one or more patches of black down on head, back or sides. Table 1 also shows that of the 49 birds recorded, 4 possessed one or more barred feathers, which were usually located on the back or among the wing coverts. In these cases the barring was usually clear and definite, although the pattern never reached to the base of the feather and frequently covered only the tip. No bird in F_1 was found to possess more than two or three such barred feathers. Of the four birds so characterized, three were ♂♂ and one was a ♀. In addition it should be noted that one bird showed a buff half-moon-shaped splash at the tip of one of the saddle-feathers.

Subsequent to making the series of crosses mentioned above, a second series was obtained in 1911. In this case one of the two B. H. ♀♀ was employed, but another W. L. ♂ was used, and B. H. ♀♀ from a different source were also introduced. The result of these matings is shown in Table 2.

TABLE 2.—Showing the results in F_1 of the second series of White Leghorn × Black Hamburg matings (Series of 1911).

MATING NUMBER.	PARENTS.		PROGENY.				
					With barred feathers.*		
	♂	♀♀	White	Black	♂	♀♀	?
8	1 A	4 A	14	0	1	4	0
9	1 A	5 A	4	0	0	1	0
10	1 A	6 A	9	0	0	0	0
11	1 A	7 A	20	0	0	0	1
27	1 A	186 A	14	0	1	1	0
Totals			61	0	2	6	1

*These birds are also listed in the white column since their plumage was mainly white (see text).

From Table 2 it appears that of 61 F_1 birds, all were white; but that 9 possessed one or more barred feathers. Of these 9, 6 were ♀♀, 2 were ♂♂, and the sex of the other was not ascertained. In this series there was about the same proportion of birds flecked with black and these were evenly distributed between the sexes.

CASE 1a.—[*White Leghorn* ♂ × *Black Hamburg* ♀] ♂ × [*White Leghorn* ♂ × *Black Hamburg* ♀] ♀. Nature of mating: *CCBbffIi* × *CCBbFfIi*. (For discussion, see p. 192).

Of the cross-bred fowls raised in 1910, ♂ 211M_2 and six ♀♀ were bred together in 1911.

> The cockerel was hatched as a pure white bird without trace of black down-feathering. Among the coverts of each wing was a single feather showing a buff-yellow bar; among the saddle feathers were a few showing some buff.
>
> Among the ♀♀, 201 G was a nearly pure white bird but showed a few splashes of black in wing coverts and saddle feathers; 201 L was hatched with a large patch of black down

feathers on the back, but became a pure white bird; 202 G showed many black-splashed feathers on back and wings; 211 B showed a very small amount of black ticking; 211 K was a pure white bird; 211 V showed a small amount of black ticking.

TABLE 3.—Showing the results obtained in F_2 from the mating of White Leghorn × Black Hamburg cross-breds (1911 series).

MATING NO.	♀♀	Total progeny.	White.	BLACK.			BARRED.			GRAY.
				♂	♀	?	♂	♀	?	
314	201 G	30	21	0	6	0	2	0	1	0
315	201 L	22	16	0	1	0	2	0	3	0
316	202 G	6	5	0	1	0	0	0	0	0
317	211 B	17	15	0	1	0	0	0	1	0
340	211 K	23	18	0	0	2	0	0	0	3
341	211 V	19	15	0	0	1	0	2	0	1
Actual totals		117	90	0	9	3	4	2	5	4
Expected totals		.....	$87\frac{2}{16}$	$7\frac{5}{16}$			$21\frac{15}{16}$			.....

The data presented in Table 3 show that the F_2 generation of W. L. × B. H. cross-breds is composed of black, white, gray and barred birds. If the gray, black and barred be considered together as "dark" individuals, it is then apparent that this group represents about one-fourth of the total number of fowls, while the group of white birds represents about three-fourths. This result is what we should expect in case of a pair of allelomorphic characters. It is evident that the white birds, although all appearing alike, include two sorts,—pure dominants (white), and birds that are heterozygous for black (usually flecked).

In 1912, another F_1 ♂, 8 L, was mated with 12 F_1 ♀♀. Both ♂ and ♀♀ resembled closely those used in the 1911 series of matings.

TABLE 4.—Showing the results obtained in F_2 from the mating of White Leghorn × Black Hamburg cross-breds (1912 series).

MATING NO.	♀♀	Progeny. (Total).	White.	Black.			Barred.		
				♂	♀	?	♂	♀	?
456	8 B, G, H, I	18	13	0	1	0	2	1	1
457	9 C	13	8	0	1	0	3	0	1
458	10 H, I	14	10	0	1	0	2	1	0
459	11 B, E, G	25	21	0	0	0	2	1	1
460	201G, L	67	54	0	3	1	5	3	1
Actual totals		137	106	0	6	1	14	6	4
Expected totals			$102\frac{2}{16}$	0	$8\frac{0}{16}$	....	$17\frac{2}{16}$	$8\frac{9}{16}$	....

It is further apparent in Table 4 that among the "dark" birds, the blacks (including the grays) and barred birds appeared in the ratio 7 : 24. It should be said here, however, that several of the chicks which are recorded as black were described when they were in down-feather. It is certain that had they lived barring would have appeared in some of them, and the ratio of barred to black birds would have been changed somewhat in favor of the barred group.

There was a marked variation in the amount of barring present in the barred individuals. The pattern invariably found clearest expression in the hackle feathers, wing coverts and tail coverts; the primaries always showed a barring that was inferior to that of the secondaries. It was also observed that the ground-color of the feathers was not so light as in the case of feathers from a Barred Plymouth Rock, but contained more gray or blue-gray, so that the pattern was less distinct. But aside from these differences the type of barred pattern observed in F_2 differed in no important respect

from that present in the Barred Plymouth Rocks. It corresponded well with the barring depicted in early illustrations (see Pearl, 1911, p. 306) of the Barred Plymouth Rock breed as it existed years ago, before it had been developed to the present state of perfection.

As has been stated, it is impossible to ascertain when chicks are in the down whether they may later develop barring. For this reason the ratio of black to barred birds as expressed in Table 3 probably does not represent the actual ratio. In order to avoid this source of error, there was made in 1912 a second series of crosses between F_1 W. L. $\times$ B. H. stock, reared in 1911 from new birds not employed in the 1910 matings. In compiling the records of these F_2 individuals no bird that was less than 3 weeks of age was entered. This precaution made it possible to discriminate carefully between black and barred birds, and results in some difference in the totals.

The results of this series of matings (Table 4) were essentially the same as in the 1911 series, save in the black : barred ratio. The barred birds showed the same sort of barring and all circumstances indicated that the appearance of this character in F_2 was in accordance with some definite law. This point is discussed in detail on p. 193, and we may now turn our attention to the results of other crosses involving the W. L. stock.

CASE 2.—*White Leghorn* ♂ $\times$ *Black Spanish* ♀. Nature of mating: *CCBBffII* $\times$ *CCbbFfii*. (For discussion, see p. 186).

In this series of matings the results of the 1910 and 1911 breeding are combined. In 1910, W. L. 193 A was employed; in 1911, W. L. 1 A.* In the 1910 matings, Black Spanish ♀♀ 181 A and 182 A were employed.† In 1911 B. S. ♀♀ 13 A, B and C were used.‡ The Black Spanish ♀ 181 A, typical of the others, was described as follows:

*Obtained from Charles J. Fogg, Waltham, Mass.

†Obtained from the Groesbeck Poultry Farms, Hartford, Conn.

‡Obtained from M. H. Lindsey, Northville, N. Y.

Black Spanish ♀, *181 A:* Weight $4\frac{3}{16}$ lbs., neck long, back of medium length; body of medium length, set well on legs; comb upright, four points, fine texture; head long and face deficient in white; eyes dark hazel; wattles are smooth and have a fine texture; wing coverts, back and tail coverts black with purple barring; primaries, secondaries and main tail feathers are dull black; body feathering has a dark brown cast; under-color dark slate.

TABLE 5.—Showing the results in F_1 of White Leghorn × Black Spanish matings (1910 and 1911 series).

MATING NO.	♂♂	♀♀	Total progeny.	White	With barred feathers.
197	193 A	181 A	10	10	0
198	193 A	182 A	24	24	0
14	1 A	13 A	18	18	1 ♀
15	1 A	13 B	1	1	1 ♂
16	1 A	13 C	6	6	1 ♂
Actual total			59	59	3

A glance at Table 5 makes it evident that the white of the W. L. dominated over the black of the B. S. as it did over the black of the B. H. The dominance was not perfect, however, since a small number of birds showed black fleckings; and three possessed feathers which were distinctly barred. These barred feathers appeared as follows: In one case two right secondaries and one tail feather had a single gray band across the tip. These barred secondaries remained in the adult plumage, but the barred tail feather was lost. In the second case the barred pattern was faintly present in one of the saddle feathers. In the third case a bird put up one barred wing covert which was moulted and never replaced.

CASE 2a.—[*White Leghorn* ♂ × *Black Spanish* ♀] ♂ × [*White Leghorn* ♂ × *Black Spanish* ♀] ♀. Nature of mating: *CCBbffIi* × *CCBbFfIi.* (For discussion, see p. 193).

In 1911 one of the cross-bred ♂♂ (198 B) was bred to five of the cross-bred ♀♀ (197 K, 198 E, 197 A, 197 G and 198 A). The ♂ 198 B was white except for a very faint ticking of black on a few feathers. The 5 ♀♀ resembled the ♂ in all points of plumage. In 1912, the same ♂ was mated to 3 of the 1910 cross-breds and to 3 of the F_1 cross-bred ♀♀, produced in the 1911 matings between W. L. and B. S. stock. The results of these matings are presented in Tables 6 and 7.

TABLE 6.—Showing the results obtained in F_2 from the mating of White Leghorn × Black Spanish cross-breds (1911 series).

MATING NO.	♂	♀♀	Total progeny.	White.	BLACK.			BARRED.			Gray.
					♂	♀	?	♂	♀	?	
19	198 B	197 K	11	10	0	1	0	0	0	0	0
311	198 B	198 E	28	22	0	2	0	3	0	0	1
310	198 B	197 A	23	19	0	2	0	0	0	0	2
20	198 B	197 G	16	13	0	2	0	0	1	0	0
21	198 B	198 A	12	11	0	0	0	0	0	1	0
Actual totals			90	75	0	7	0	3	1	1	3
Expected totals			.....	$67\frac{8}{16}$	0	$5\frac{10}{16}$	...	$11\frac{4}{16}$	$5\frac{10}{16}$	...	.....

In 1912, similar matings between W. L. × B. S. cross-breds were made with the results shown in Table 7. Combined results for the two years are given in Table 8.

TABLE 7.—Showing the results obtained in F_2 from the mating of White Leghorn × Black Spanish cross-breds (1912 series).

MATING NO. ♂	♀♀	Total progeny.	White.	BLACK.			BARRED.			Gray.
				♂	♀	?	♂	♀	?	
467..... 198 B	14 D, S, T	85	69	0	6	2	7	1	0	0
468..... 198 B	197 A, G	65	61	0	4	0	0	0	0	0
469..... 198 B	198 E	41	31	0	3	0	4	0	0	3
Actual totals.....		191	161	0	13	2	11	1	0	3
Expected totals.....			$143\frac{4}{16}$	0	$11\frac{15}{16}$	..	$23\frac{4}{16}$	$11\frac{15}{16}$	.....	

TABLE 8.—Combined results from Tables 6 and 7.

SERIES.	Total progeny.	White.	BLACK.			BARRED.			Gray.
			♂	♀	?	♂	♀	?	
1911.....	90	75	0	7	0	3	1	1	3
1912.....	191	161	0	13	2	11	1	0	3
Actual totals.....	281	236	0	20	2	14	2	1	6
Expected totals.....	.....	$210\frac{3}{16}$	0	$17\frac{9}{16}$	....	$35\frac{3}{16}$	$17\frac{9}{16}$	.....	

We thus observe from the results presented in Tables 6, 7 and 8 that barred birds made their appearance in the F_2 generation of the W. L. × B. S. cross. The fairly wide departure from the expected ratios will be discussed on a later page.

CASE 3.—*White Leghorn* ♂ × *Black Minorca* ♀. Nature of mating: *CCBBffII* × *CCbbFfii*. (For discussion, see p. 186).

The ♂ used in this experiment was 193 A, previously described.

Black Minorca ♀, 183 A: Weight $6\frac{1}{16}$ lbs., neck flat, back of good length; body of medium length; comb, large with serrated blade, five points,—falls half on each side; eyes light hazel; ear-lobes bluish white, mottled with red; wattles of fine texture, small; wing-coverts and tail-coverts greenish with purple barring; primaries, secondaries and main tail feathers are dull black; body feathers are very dark brown; under-color slate; shanks are dark slate. Black Minorca ♀ 184 A was similar in all important respects to 183 A.

As a result of this cross all the F_1 birds were white. Many showed black tickings and one ♂ put up a barred feather. This bird was hatched as a white chick with a small patch of black down on the back. Later a buffy tinge developed over some of the wing coverts.

CASE 3a.—[*White Leghorn* ♂ × *Black Minorca* ♀] ♂ × [*White Leghorn* ♂ × *Black Minorca* ♀] ♀. Nature of mating: *CcBbffIi* × *CcBbFfIi*. (For discussion, see p. 193).

Of the W. L. × B. M. cross-breds raised in 1910, ♂ 200 C, which put up one barred feather the first year, was mated in 1911 with two of his sisters, 199 E and 200 D. These two ♀♀ were white but showed many feathers that were ticked with black. The results of this cross are presented in Table 9.

TABLE 9.—Showing the results obtained in F_2 from the mating of White Leghorn × Black Minorca cross-breds.

MATING NO.	♂	♀♀	Total progeny.	White.	BLACK.			BARRED.		
					♂	♀	?	♂	♀	?
312	200 C	199 E	10	9	0	0	1	0	0	0
313	200 C	200 D	7	5	0	1	0	1	0	0
Actual totals			17	14	0	1	1	1	0	0
Expected totals			.....	$12\frac{12}{16}$	0	$1\frac{1}{16}$	...	$2\frac{2}{16}$	$1\frac{1}{16}$	...

From the data presented in Table 9 it is apparent that, as was the case with the W. L. × B. H. and the W. L. × B. S. cross-breds, here also we have both black and barred birds thrown out in F_2. But, whereas in the earlier matings the dark : light ratio came very close to Mendelian expectations, in the present case the departure is more noticeable. It is probable, however, that observation of a larger number of birds would have yielded results closer to the expected.

The one barred bird resulting from this cross, 313 C, was a ♂. Its general coloration was gray but barring was well manifested in feathers of the hackle and back and in the wing coverts. No barring was present in the primaries but it could be distinguished faintly in the secondaries.

CASE 3b.—[*White Leghorn* ♂ × *Black Minorca* ♀] ♂ × *Black Minorca* ♀. Nature of mating: *CcBbffIi* × *CCbbFfii*. (For discussion, see p. 194).

In addition to the foregoing, the results of a cross between an F_1 ♂ and pure-bred, Black Minorca ♀♀ may be reported. The ♂ 200 C as previously stated showed on the right flank a feather barred over one-half. The B. M. ♀♀ were those used in the F_1 matings. In Table 10 are presented the data relative to this back-cross.

TABLE 10.—Showing the results of the cross: [White Leghorn ♂ × Black Minorca ♀] ♂ × Black Minorca ♀.

MATING NO.	♂	♀♀	Total progeny.	White.	BLACK.		BARRED.	
					♂	♀	♂	♀
325	200 C	183 A	5	3	0	1	1	0
326	200 C	184 A	1	0	0	1	0	0
Actual totals			6	3	0	2	1	0
Expected totals				3	¾	¾	¾	¾

In Table 10 it is shown that of 6 birds resulting from this cross 2 were black ♀♀ and one was a barred ♂. The latter developed into a well barred adult bird (325 B). The pattern was clearest in wing coverts, tail coverts and hackle feathers. On the primaries barring was faint but clearer on the secondaries. The general coloration was slightly brownish.

CASE 3c.—$\sigma \left\{ \frac{[White\ Leghorn\ \sigma \times Black\ Minorca\ \varphi]\ \sigma}{Black\ Minorca\ \varphi} \right\} \times$ *Black Minorca* ♀. Nature of mating: *CCBbffii* × *CCbbFfii*. (For discussion, see p. 195).

In case the barred, cross-bred cockerel, 325 B, possessed the barred character in heterozygous condition (as represented in the zygotic formula *CCffBbii*) it is to be expected that, when mated with pure Black Minorcas, one-half of his progeny would be barred. In the season of 1912 this mating was made with the results presented in Table 11.

TABLE 11.—Showing the results obtained from the cross indicated above.

MATING NO.	♂	♀♀	Total progeny.	BLACK.			BARRED.		
				♂	♀	?	♂	♀	?
472	325 B	184 A	13	4	2	0	4	3	0
473	325 B	34 A, B	53	12	13	3	9	12	4
Actual totals			66	16	15	3	13	15	4
Expected totals				16½	16½	....	16½	16½	....

The results of this cross demonstrate that the mating of the barred ♂, 325 B, with the pure-bred Black Minorca ♀♀ gave one-half barred and one-half black progeny; and that the barred and black birds were about equally divided between the sexes.

CASE 3d.—♂ $\left\{\frac{[White\ Leghorn\ ♂ \times Black\ Minorca\ ♀]\ ♂}{Black\ Minorca\ ♀}\right\} \times$ ♀ [*White Leghorn* ♂ × *Black Minorca* ♀]. Nature of mating: *CCBbffii* × *CCBbFfIi*. (For discussion, see p. 196).

In this instance, the barred cross-bred cockerel, 325 B, was bred to one of the ♀♀ which resulted from the first W. L. × B. M. cross. The results are presented in Table 12.

TABLE 12.—Showing the results of the mating indicated above.

MATING NO.	♂	♀	Total progeny.	White.	BLACK.			BARRED.		
					♂	♀	?	♂	♀	?
474	325 B	200 D	34	17	1	1	2	7	2	4
Expected totals				17	0	$4\frac{1}{2}$	...	$8\frac{3}{4}$	$4\frac{1}{4}$	...

In Table 12 it is shown that one-half of the progeny of 325 B were dark and one-half light. Of the darks one-fourth were black and three-fourths barred.

CASE 3e.—♂ $\left\{\frac{[White\ Leghorn\ ♂ \times Black\ Minorca\ ♀]\ ♂}{Black\ Minorca\ ♀}\right\} \times$ ♀ $\left\{\frac{(White\ Leghorn\ ♂ \times Black\ Minorca\ ♀)\ ♂}{Black\ Minorca\ ♀}\right.$ Nature of mating: *CCBbffii* × *CCbbFfii*, black, and *CCbbFfIi*, white, or *CCBbFfIi*, white. (For discussion, see p. 198).

In this case the barred cross-bred ♂, 325 B, was mated with two of his sisters, 325 A and 325 E. Female 325 A was clear black with blue-black beak and shanks and a slight green tinge to the plumage. Female 325 E was a white bird with light shanks and beak. The results of these matings are given in Table 13.

TABLE 13.—Showing the results of the crosses indicated above.

MATING NO.	♂	♀♀	Total progeny.	White.	BLACK.			BARRED.		
					♂	♀	?	♂	♀	?
470.....	325 B	325 A (black)	43	0	6	8	4	10	12	3
			Expected..	0	10¾	10¾	...	10¾	10¾	...
				Totals.	21½			21½		
471.....	325 B	325 E (white)	50	25	2	6	5	5	4	3
			Expected*.	25	6¼	6¼	...	6¼	6¼	...
				Totals.	12½			12½		

*Provided the zygotic constitution of the ♀ 325 E is CCbbFfIi.

From the data presented in Table 13 it is apparent that in the mating of 325 B with his black sister, 325 A, there was a tendency to produce equal numbers of black and barred progeny; and that the sex-ratio between these groups approximated 1 : 1.

In the mating of 325 B with his white sister, 325 E, half the progeny were white, while the other half included both black and barred birds in equal numbers and equally divided between the sexes.

CASE 3f.—♂ $\left\{ \frac{(\textit{White Leghorn} \ ♂ \times \textit{Black Minorca} \ ♀) \ ♂}{\textit{Black Minorca} \ ♀} \right\} \times$ *Black Java* ♀. Nature of mating: *CCBbffii* × *CCbbFfii*. (For discussion, see Case 5, p. 203).

Among the self-colored birds with which the barred cross-bred ♂ 325 B, was mated during the season of 1912 were the Black Java ♀♀ 335 C and F. The results of this mating are given in Table 14.

TABLE 14.—Showing the results of the mating indicated above.

MATING NO.	♂	♀♀	Total progeny.	BLACK.		BARRED.		
				♂	♀	♂	♀	?
477	325 B	335 C, F	52	11	16	10	14	1
Expected totals				13	13	13	13	....
Expected grand totals				26		26		

From the data presented in Table 14 it is clear that one-half of the progeny from this cross were black and one-half were barred; and that the black and the barred birds were about equally divided between the sexes. Similar results were obtained from mating the cross-bred ♂, 325 B, with Black Hamburg ♀♀. One of the ♂♂, 477 V, resulting from the Black Java cross, was mated in 1913 with a pen of barred ♀♀. This mating is considered in Case 5, p. 203.

CASE 4.—*White Leghorn* ♂ × *Black Java* ♀. Nature of mating: *CCBBffII* × *CCbbFfii*. (For discussion, see p. 186).

In other series of crosses bred in 1911, 1912 and 1913, the W. L. ♂, 193 A, used in the previous experiments, was mated with several B. J. ♀♀.

> *Black Java* ♀, *187 A:* Weight $7\frac{7}{8}$ lbs., good form but slightly lacking in breast; beak black shading into yellow at base; eyes hazel; ear-lobes are three-fourths white; wattles red; small amount of purple barring on feathers of neck, wing coverts and tail coverts; primaries, secondaries and main tail feathers are dull black; under-color dark slate; shanks and feet yellow. The other Black Java ♀♀, 188 A, 230 A and 231 A, resembled the bird described above in all important points.

The result of this series of matings shows that as in earlier cases the white of the W. L. was dominant over the black of the Java; fur-

ther, that as in other crosses, birds possessing a few barred feathers appeared in F_1. Of these birds two were ♂♂ in which the barred pattern appeared in the coverts or saddle feathers.

CASE 4a.—[*White Leghorn* ♂ × *Black Java* ♀] ♂ × [*White Leghorn* ♂ × *Black Java* ♀] ♀. Nature of mating: *CcBbffIi* × *CcBbFfIi*. (For discussion, see p. 193).

In the season of 1912 the cross-bred ♂ 25 C was mated with cross-bred ♀♀ of similar constitution. The cockerel was a solid white bird except for one feather in the middle of the back which showed barring on one-half. Of the ♀♀ used, 25 B showed at the age of one month slight barring in the right secondary coverts and in two secondaries. At the age of five months the barring had disappeared. Female 25 I showed a few dark saddle feathers but no barring. Female 203 B was a pure white bird.

TABLE 15.—Showing the results in F_2 of the White Leghorn × Black Java cross-breds (1912 series).

MATING NO.	♂	♀♀	Total progeny.	White.	BLACK.			BARRED.		
					♂	♀	?	♂	♀	?
481	25 C	25 B	33	26	0	1	0	2	1	3
482	25 C	25 I	38	27	0	3	0	5	2	1
483	25 C	203 B	44	38	0	2	1	1	2	0
Actual totals			115	91	0	6	1	8	5	4
Expected totals				$86\frac{4}{16}$	0	$7\frac{3}{16}$	...	$14\frac{6}{16}$	$7\frac{3}{16}$	...
Expected grand totals			.....	$86\frac{4}{16}$	$7\frac{3}{16}$			$21\frac{9}{16}$		

In 1912 other crosses between W. L. a ıd B. J. stock were made. These involved the use of W. L. ♂, 1 A. As expected, the first

generation, raised in 1912, was composed entirely of white birds. The results in F_2 (1913) are shown in Table 16.

TABLE 16.—Showing the results in F_2 from the mating of White Leghorn × Black Java cross-breds (1913 series).

MATING NO.	♂	♀♀	Total progeny.†	White.	Black.†	Barred.*
553	463 A	463 E, F, J	30	18	3	9
554	463 A	464 K, N, Q	47	37	2	8
Actual totals			77	55	5	17
Expected totals				$57\frac{12}{16}$	$4\frac{13}{16}$	$14\frac{7}{16}$

*The sex of the black and the barred birds could not be ascertained in time to report in this publication.

†Over 3 weeks old when described.

The data presented in Table 16 indicate that in F_2 of the cross under discussion, white, barred and black birds appeared in the ratio 55 : 17 : 5.

CASE 5.—♂ $\left\{ \begin{array}{c} \left\{ \begin{array}{c} (White\ Leghorn\ ♂ \times Black\ Minorca\ ♀)\ ♂ \\ \hline Black\ Minorca\ ♀ \end{array} \right\} ♂ \\ \hline ♀\ Black\ Java \end{array} \right\} \times$ *Cross-bred ♀♀, heterozygous for barring.* Nature of mating: *CCBbffii* × *CCBbFfii.* (For discussion, see p. 203).

Male 477 V was a fairly well-barred bird but with dark under-color. The general tone had a brownish tinge. The ♀♀ mated with him had the ancestry given below:

461 E.—$\dfrac{♂\quad [Wh.\ Leghorn\ ♂ \times Blk.\ Hamburg\ ♀]}{♀\ \left\{ \begin{array}{c} (Wh.\ Leghorn\ ♂ \times Blk.\ Hamburg\ ♀)\ ♂ \\ \hline (Wh.\ Leghorn\ ♂ \times Blk.\ Hamb.\ ♀)\ ♀ \end{array} \right\}}$

343 B, E.—Out of mating given in Case 3e; from black ♀.

344 B.—Out of mating given in Case 3e; from white ♀.

$$\left.\begin{array}{l}472\text{ E.}\\ 473\text{ F.}\end{array}\right\} \frac{♂\left\{\dfrac{(\textit{White Leghorn } ♂ \times \textit{Black Minorca } ♀)\ ♂}{\textit{Black Minorca } ♀}\right\}}{♀\ \textit{Black Minorca.}}$$

$$474\text{ G.—}\frac{♂\left\{\dfrac{(\textit{White Leghorn } ♂ \times \textit{Black Minorca } ♀)\ ♂}{\textit{Black Minorca } ♀}\right\}}{♀\ (\textit{White Leghorn } ♂ \times \textit{Black Minorca } ♀)}$$

$$476\text{ A.—}\frac{♂\left\{\dfrac{(\textit{White Leghorn } ♂ \times \textit{Black Minorca } ♀)\ ♂}{\textit{Black Minorca } ♀}\right\}}{♀\ \textit{Black Hamburg}}$$

477 E, P, S.—Same ancestry as 477 V.

The results of these matings, which were made in the season of 1913, are presented in Table 17.

TABLE 17.—Showing the results obtained from the matings described above.

MATING NO.	PARENTS. ♂	PARENTS. ♀♀	Total progeny.*	BLACK.†	BARRED.†
541	477 V	461 E	40	15	25
542	477 V	343 B	17	6	11
543	477 V	343 E	14	3	11
544	477 V	344 B	2	0	2
545	477 V	472 E	10	4	6
546	477 V	473 F	29	10	19
547	477 V	474 G	1	0	1
548	477 V	476 A	27	7	20
549	477 V	477 E	33	13	20
550	477 V	477 P	30	7	23
551	477 V	477 S	27	5	22
552	477 V	347 E	17	5	12
Actual totals			247	75	172
Expected totals			.....	62	185

*Over 3 weeks old when described.

†The sex of the black and the barred birds could not be ascertained in time to report in this publication.

IV. General Discussion of Results.

The experimental data presented in the foregoing pages make it clear that a type of barred plumage-pattern has arisen in F_2 from the mating of white with black birds. First of all we may ask: Where did this barring, manifested in a few feathers of a small number of F_1 individuals but appearing as a fully developed barred pattern in a certain proportion of F_2 progeny, have its origin? As stated at the beginning of this paper it was tentatively assumed, when the present investigations were planned in 1909, that barring represented a heterozygous condition resulting from the crossing of light colored with dark colored birds. This tentative assumption was based on the fact that breeders* have commonly made the observation that the crossing of Blacks × Whites occasionally gave some birds with good barring. Thus the barred plumage-pattern was considered by some as a mosaic made up of black and white. It is now clear, however, that this view is not supported by any evidence supplied by the present investigations. In F_1, contrary to expectation, the degree of dominance of white in all the White Leghorn × Black crosses was so great that the presence of black pigment was usually manifested only as flecks on an otherwise pure white plumage, or, in a smaller number of cases, as a partly barred feather among the white. If the barred pattern were of the nature of a mosaic, it should appear most definitely in F_1; one would not be led especially to anticipate its appearance in F_2,—at least in a well developed condition. But as shown in all the tables giving data on the F_2 birds this is exactly where the most extended and most clear-cut barring did appear.

In contrast to the view outlined above, several other investigations† dealing with the type of barring found in Barred Plymouth Rocks have shown that this character as there found may behave in inheritance like a unit-character; it is separately heritable. In other words, birds that show this barred pattern may be assumed to possess the *factor* for barring; and without the presence of this factor in the

*See Davenport (1906); Wright (1905); Hurst (1905).
†Goodale (1909); Pearl and Surface (1910).

zygote, barring cannot appear. Thus the outcome of the first season's breeding of black with white birds, when coupled with the evidence of the existence of a barring factor, *B*, supplied by other breeders, demanded a change in view regarding the origin of the barring in question; at least it required a consideration of the possibility that a *factor* for barring might be present in one of the parent breeds used in the experiments.

If a factor for barring were present in any of the parent breeds it seemed probable that it did not exist in the black ♀♀, since experience has shown that the black pigment possessed by these birds would cause the barring factor to be revealed even if it existed in a heterozygous condition.* Hence it was assumed that it might be present in the W. L. ♂; and it became the aim of the investigation to test this point experimentally; furthermore to ascertain the behavior of this type of barring in F_2 and subsequent generations; also to produce, by the breeding of selected birds possessing the requisite gametic constitution, a barred breed, wholly distinct (at least with respect to the origin of the barred pattern) from the Barred Plymouth Rocks. To what extent these results have been accomplished will appear in the following pages.

First, however, it is desirable to consider in some detail the probable zygotic constitution of the black and white fowls concerned in the experiments, since the expression of the factor for barring is dependent as will be shown, upon the presence or absence of several other factors,—especially the factors for sex and for the inhibition of black pigmentation. We may therefore inquire, first, as to what factors, among those with which we are especially concerned, are present in the birds used in the matings already described.

*For instance, it is well known that if pigment be added to the White Plymouth Rock, as a result of mating with black breeds, the barring will be revealed in F1.

It seems probable that we have to deal with at least four different factors: (1) a factor for black pigmentation, C*, (2) a factor for the inhibition of pigmentation, I; (3) a factor for sex (F, female; f, male); and (4) a factor for barring, B.

With reference to these factors, what then is the zygotic constitution of the black ♀♀? First, we can assume that they are homozygous for black pigmentation (CC)*; second, that they are homozygous for the absence of barring (bb); further, that they are homozygous for the absence of the inhibiting factor (ii) which factor, in the case of the W. L., as will appear, prevents the black pigment from showing. Finally, we will assume that they are heterozygous for the female sex (Ff). The zygotic formula of these birds could therefore be written $C_2b_2Ffi_2$.

Making use of these symbols we may now consider the zygotic formula for the W. L. ♂. The W. L. breed of fowls is usually regarded as a "pure" white variety, sometimes called the dominant white or D-white, since in matings with dark birds the white appears to dominate over black. But, if we regard the white plumage as an *absence of pigmentation* it is manifestly illogical to say that the absence of a character can be dominant over its presence. Therefore another explanation must be sought for the apparent dominance of white, and we may assume with Bateson and Punnett (*op. cit.*) that the dominance of white is due to the inhibiting factor I, which has the

*It appears from the work of Bateson and Punnett (1908) on the D-whites and the R-whites, that black pigmentation in poultry may not always be due to a single factor. There may be present a general factor for color, C, and in addition factors for special pigmentations, such as buff, red or black. The latter, as suggested by Davenport and others may be conceived of as partaking of the nature of an enzyme, which, as a result of its action upon C, produces the color in question. According to this view the presence of both factors would be required if the bird is to show pigmentation. For instance, with reference to the inheritance of color in birds possessing two kinds of pigments, we might need to consider three sorts of factors: the general color factor, C, and two special color factors, which working upon C, might produce, the one red, the other black pigment. The explanation of color-inheritance in poultry may eventually be found not even so simple as this; but it is apparent from results already attained that, as in the case of the inheritance of certain colors in the sweet pea, several factors may be involved. In the present case, however, we are concerned on the one hand, only with the presence of black pigmentation (or its potential possibility of appearance, other factors permitting) and, on the other hand, with the apparent absence of black. For this reason, and to avoid complexity, it will be sufficient for present considerations to assign to the black pigmentation a single factor, and this we will term C, with the understanding that in reality this character may be dependent upon the action of two factors instead of one. These might be compared with the factors which Davenport (1909) calls C and N; or to factors which Bateson and Punnett (1908) refer to as X and Y.

power to repress the manifestation of black pigment in the plumage; and this power is still present, although lessened, when I_2 is diluted to a heterozygous condition, Ii, as is the case in F_1 of the W. L. $\times$ Black cross-breds.

With our recognition of the fact that the W. L. ♂ carries inhibiting factors which repress the manifestation of black in the plumage of the progeny from matings with black breeds, the results of certain matings lead to the question whether the W. L. in its own somatic cells, possesses the elements of black pigmentation. Without now entering into a discussion of this point, which is considered in detail on a later page, it may be said that evidence derived from breeding experiments yet to be presented indicates that the W. L. ♂ carries in its germ cells the factor or factors for black pigmentation. This view will be found in harmony with the experimental results already given and with others to be mentioned subsequently.

Looking at the problem in this light the W. L. may be regarded not as an actually white bird, but as a black one in which an inhibiting factor prevents the black from appearing. We may then tentatively assume that the W. L. ♂ is homozygous for black pigmentation, and at the same time homozygous for the inhibiting factor. Of course, were the W. L. ♂ heterozygous for C, the visible results in F_1 would be approximately the same.

With respect to the factor for sex, assuming a Mendelian interpretation of this phenomenon, we may tentatively regard the W. L. ♂ as homozygous (ff) for the absence of the female sex factor, the ♀♀ as heterozygous (Ff) for F.

We come now to the relation of the W. L. ♂ to the factor for barring. If the W. L. carries barring at all, it might be assumed that it is either homozygous (BB) or heterozygous (Bb) for this character; and the theoretical results from crossing will vary with the possibility which we assume to hold true. In deciding this point we may take into consideration the probable manner of inheritance of barring in the W. L. breed provided this breed does actually carry, more or less regularly, the factor for the barred plumage pattern. Analogy with

the Barred Plymouth Rocks permits the assumption that the W. L. ♂♂ are homozygous (BB) while the ♀♀ are heterozygous (*Bb*) for this character. This circumstance would maintain the barred pattern under conditions of equilibrium in both sexes in successive generations; and logically we cannot assume otherwise if our experimental birds belong to pure-bred stock. On this assumption, the complete zygotic formula for the W. L. ♂ would be $C_2B_2f_2I_2$, while that of the ♀ would be C_2BbFfI_2, since the ♀ is assumed to be heterozygous for both female sex and barring, and homozygous for the inhibiting factor. On the basis of these assumptions (which, it must be fully understood, are for the moment merely assumptions, used to frame a working hypothesis) we may now turn to a more detailed consideration of the special cases.

A. DISCUSSION OF THE SPECIAL CASES.

Cases 1, 2, 3 and 4.—On the basis of the assumed zygotic formulæ previously stated, what is the expected result of crossing the W. L. ♂ with the black ♀♀? The W. L. ♂ forms only one type of gamete,—CBfI, while the black ♀♀ form two types, CbFi and Cbfi. The mating may then be represented

♂ *CBfI* · *CBfI* ×
♀ *Cbfi* · *CbFi* =

♂ ♂ C_2Bbf_2Ii, white
♀ ♀ $C_2BbFfIi$, white

In other words, the first cross between the W. L. ♂ and the black ♀♀ gives birds that are all white and heterozygous for the barring factor and for *I*. It has been stated in the description of the experiments that a few F_1 birds put up one or two barred or partly barred feathers. This may be explained on the grounds that the dominance of the inhibiting factor, *I*, was not complete when, as in F_1, it existed in a heterozygous or simplex condition. Where a little black was permitted to show, there it filled out the pattern of a barred feather. When the black was inhibited to a still greater degree, the pigment

appeared only as minute ticks on an otherwise white plumage. In this respect no difference was observed between ♂♂ and ♀♀. Davenport (1909) has reported that in certain crosses involving a W. L. Bantam ♂ and certain black ♀♀ the ticking was chiefly in the ♀♀.

We may now compare the results of the present matings with some similar cases reported by other investigators. First, among those who have used the W. L. may be mentioned Davenport (1906) who reports the following instances:

1. *W. L. (Bantam)* ♂ × *Dark Brahma* ♀. Result: 16 white, or white splashed; 5 black; 7 barred and 3 of the Brahma type. All of the blacks were ♀♀, while of the barred birds, 3 were ♂♂, 2 ♀♀ and 2 of unknown sex.

2. *W. L. (Bantam)* ♂ × *Black Cochin (Bantam)* ♀. Result: 10 white, 7 black and 7 barred.

3. *Single Comb W. L.* ♂ × *Houdan* ♀. Result: Of 41 individuals, all were white with traces of black.

In the following cases, Davenport mated various ♂♂ with White Leghorn ♀♀:

4. *Black-breasted Red Game Bantam* ♂ × *W. L. (Bantam)* ♀. Result: Among 24 individuals were 12 dark and several barred birds.

5. *Buff Cochin Bantam* ♂ × *W. L. (Bantam)* ♀. Result: Among 31 offspring were 9 white, 9 white and buff, 4 white and black, 2 white, black and buff, 4 black and buff, and 3 black. No barred birds were reported for this cross.

6. *R. C. Black Minorca* ♂ × *S. C. W. L.* ♀. Results: Of 83 birds, 74 were white and 9 were pigmented. Davenport states, however, that one of the Leghorns used (B) in this cross gave all the dark progeny, while the other two Leghorn ♀♀ (A and C) gave only white.

To the above cases in which the W. L. ♀ was used, Hurst (1905) adds the following cases:

7. *Houdan* ♂ × *W. L.* ♀. Results: 94 whites and 11 blacks. Of the blacks there were 6 pure blacks (♀♀) and 5 barred (♂♂).

8. *Black Hamburg* ♂ × *W. L.* ♀. Results: Of 57 individuals (in downfeathers) 49 were white and 8 were black.

Regarding the eight instances reported by Davenport and by Hurst, the following may be said:

Instance 1.—Davenport's W. L. Bantam ♂ was undoubtedly heterozygous for both *B* and *I*. The pure-bred W. L. ♂ must be

regarded as homozygous for *I*. If the W. L. Bantam in question possessed the constitution C_2Bbf_2Ii, one would expect in F_1 equal numbers of dark and light birds; and each sort would be equally divided between the sexes. Of the dark birds, half should be barred and half non-barred. The actual and the expected results can be represented as follows:

RESULTS.	White.	Black.	Barred.	Brahma.
Actual	16	5	7	3
Expected	15½	7¾	7¾	(?)

It is clear that, on this interpretation, there is close correspondence between the actual and expected in Davenport's first instance, second series (*l. c.*, p. 37), in which the ♂ parent was the W. L. Bantam

Instance 2.—In this case, Davenport's results are explainable on the hypothesis made for Instance 1. If the constitution of the W. L. Bantam were C_2Bbf_2Ii, we should have the following ratios:

RESULTS.	Total.	White.	Barred.	Black.
Actual	24	10	7	7
Expected	.....	12	6	6

This explanation is also in accord with Davenport's results in mating the same W. L. Bantam ♂ with W. L. ♀♀ (Davenport's Nos. 127 and 128).

Instance 3.—The results in F_1 are in full accord with the present hypothesis. Apparently the W. L. ♂ was homozygous for *I*.

Instance 4.—If we assume that the W. L. Bantam was heterozygous for *I* and *B*, and that *B* is, in this case, a sex-limited character, we should expect to find, among 24 individuals, 12 white and 12 dark; of the latter, 6 would be black ♀♀ and 6 barred ♂♂. Actually Davenport obtained 12 whites, and 12 darks. Of the darks, some (actual numbers not given) were barred and these were all ♂♂. This explanation places Davenport's results in full accord with the present hypothesis.

Instance 5.—The results of this mating are consistent with the explanation furnished in this paper, and suggested in Davenport's report (*op. cit.*, p. 82). The only possible difference is one of interpretation, in that we may regard the W. L. Bantam as heterozygous for *I*, instead of "heterozygous in white" as indicated by Davenport.

Instance 6.—In the case of the ♀♀ A and C the results are as expected. Both birds were apparently homozygous for *I*. As Davenport states, "B's germ cells were probably mixed;" it was doubtless heterozygous for *I*.

Instance 7.—From the first cross mentioned by Hurst (*op. cit.*, p. 133) we should expect nothing but white birds. The fact that 6 blacks and 5 "cuckoos" were observed in F_1 demonstrates, as suspected by Hurst, the "mixed" nature of some of the stock. If, as was the case in Davenport's Instance 4, these impure W. L. ♀♀ were heterozygous for both *I* and *B*, then we would expect exactly the "curious" results obtained by Hurst. The heterozygous barring of the "mixed" ♀ or ♀♀ would be transmitted only to the ♂♂ while it is most improbable that the ♀♀ could derive barring from the Houdan ♂ [$C_2b_2f_2i_2$].

Instance 8.—In Hurst's Experiment 2 (*op. cit.*, p. 134) one would expect all the progeny to be white, or white flecked with black. The fact that black birds resulted from this cross indicates that some of the W. L. ♀♀ were not pure for *I*. The expected results are as in Instance 7, and the fact that Hurst reports no barred ♂♂ is doubtless due to the circumstance that the 8 blacks did not live long enough to develop barring. The sex-ratios are not reported.

In conclusion, it may be said regarding the above cases that the F_1 results of both Davenport's and Hurst's matings of W. L. stock with various black breeds are fully explainable on the hypothesis advanced above: that the W. L. ♂♂ are normally homozygous for *B* and *I*, while the ♀♀ are homozygous for *I* but heterozygous for *B*. Many of the birds used by both Davenport and Hurst were manifestly impure with respect to several factors.

CASES 1a, 2a, 3a and 4a.—What now happens when the F_1 cross-breds from any of the matings presented in Cases 1, 2 and 3 are mated among themselves? The white cross-bred ♂♂ as we have seen possess the zygotic constitution

$$C_2Bbf_2Ii$$

while the ♀ cross-breds are

$$C_2BbFfIi$$

The ♂ forms gametes,

$$CBfI \cdot CBfi \cdot CbfI \cdot Cbfi$$

Since the ♀ is heterozygous for three pairs of characters, eight sorts of gametes might be expected:

$$CBfI \cdot CBFI \cdot CbFI \cdot CBFi$$
$$CBfi \cdot CbfI \cdot CbFi \cdot Cbfi$$

But it has been pointed out on a previous page that in the case of the Barred Plymouth Rocks there is good reason for assuming that the factors *B* and *F* never pass together into the same gamete; that there is some sort of a repulsion between these factors. In the case of the Barred Plymouth Rocks this results in black, or at least non-barred ♀♀ when B. P. R. ♀♀ are crossed by the ♂ of a non-barred breed. Since we have observed in the data already presented a certain proportion of black ♀♀ are produced in F_2, we may tentatively assume that in the White × Black crosses being described there exists a similar incompatibility between the factors, *B* and *F*. It may therefore be supposed that of the 8 sorts of gametes that might be formed by the ♀ cross-bred (with the zygotic formula, $C_2BbFfIi$), there are actually formed only four; in other words, we may eliminate from consideration all possible gametic combinations containing both

B and *F*, together with their complementary gametic combinations. Looking at the matter in this light we have formed by the cross-bred ♀♀ only the following gametes:

$$CBfI \cdot CbFi \cdot CBfi \cdot CbFI$$

The mating between the F_1 ♂ and the F_1 ♀♀ may therefore be represented as follows:

♂ $CBfI \cdot Cbfi \cdot CBfi \cdot CbfI \times$
♀ $CBfI \cdot CbFi \cdot CBfi \cdot CbFI =$

♂♂
- $C_2B_2f_2I_2$ (1), white
- $C_2Bbf_2I_2$ (1), "
- C_2Bbf_2Ii (2), "
- $C_2B_2f_2Ii$ (2), "
- $C_2Bbf_2i_2$ (1), barred
- $C_2B_2f_2i_2$ (1), "

♀♀
- C_2BbFfI_2 (1), white
- $C_2b_2FfI_2$ (1), "
- $C_2BbFfIi$ (2), "
- C_2b_2FfIi (2), "
- $C_2b_2Ffi_2$ (1), black
- C_2BbFfi_2 (1), barred

The data presented above may be summarized as follows:

CHARACTER.	♂	♀	Total.
White	6	6	12
Black	0	1	1
Barred	2	1	3
Totals	8	8	16

In other words, among every 16 birds in F_2 we may expect 12 whites, 3 barred and one black. The whites should be equally

divided between the sexes; 2 of the three barred birds should be ♂♂ and all black birds should be ♀♀; moreover, one of the barred males should be homozygous for the barring factor while the other ♂ and the ♀ should be heterozygous. Other birds both ♂ and ♀ carry the barring factor but do not visibly manifest the barred pattern because they are either homozygous or heterozygous for *I*,—a circumstance which prevents the appearance of the pigment and therefore of the barring also.

Having thus outlined the expected results in the F_2 generation from White × Black crosses, provided the White Leghorn ♂ was actually homozygous for barring and actually possessed the inhibiting factor *I*, we may now attempt to ascertain to what extent these theoretical results agree with the experimental data and furnish an interpretation for them.

CASE 1a.—*White Leghorn* × *Black Hamburg*, F_2.—(Tables 3 and 4, pp. 167 and 168). First of all it is apparent that the ratio 3 white: one dark is closely realized among the 117 birds included in Table 3 and in the 137 birds comprising Table 4. In the 1911 series (Table 3) the actual results were 90 white : 27 dark, and the expected results 88 : 29. Whereas we should expect only 7 + blacks (all females) we actually have 12 (16 including the grays), including 9 ♀♀ and 3 in which the sex was not ascertained. In explanation of this discrepancy it may be said that in young chicks under 2 weeks of age, it is difficult to distinguish accurately the blacks from the barred. In case chicks die during the first week or two, all those which might later develop barring must be described as black. There can therefore be no doubt that several of the birds described as black would have become barred if they had lived. The only way seen at present to avoid this difficulty is to embody in the tables no chicks which die when less than 3 weeks of age. This plan was adhered to in the formulation of Table 4.

Regarding the barred birds, it is clear that more are called for (21+) than actually appeared (11); but as already explained, the deficiency would probably have been made up by addition of the

individuals from the "black" column, if these had lived long enough to develop their barring. It is apparent, however, that the ratio of ♂♂ to ♀♀ is in the right sense.

Turning now to the results of similar matings presented in Table 4, it is apparent that the experimental results conform more closely to the expected. In this case all the chicks were over three weeks old when described. The obtained ratio of whites to blacks is 106 : 31, while the expected is 102 : 35. The actual ratio of black to barred birds was 7 : 24, while the expected was 8+ : 25+. As was to be expected no black ♂♂ appeared while the number of barred ♂♂ was approximately twice the number of the barred ♀♀ (14:6), the expected being 17+ : 8+.

It is thus clear that when only chicks over three weeks old are included in the tables the actual and the expected ratios find close agreement, and appear to demonstrate the correctness of the view that the ♂ W. L. is homozygous for the barred plumage pattern.

CASE 2a.—*White Leghorn* × *Black Spanish*, F_2.—(Tables 6, 7 and 8, pp. 171 and 172). The 1911 results presented in Table 6 show a predominance of whites and a deficiency of both black and barred birds. These matings were repeated in 1912 to ascertain whether the same defective ratios were present. Table 7 makes it appear that both the excess of whites and deficiency of dark are still apparent, although in the case of the progeny of 14 D, S and T* the experimental results are closer to the expected. What circumstance causes the defective ratios shown in the totals in Table 9, cannot at present be stated. In this instance, some unsuspected factor may be at work.

CASE 3a.—*White Leghorn* × *Black Minorca*, F_2.—(Table 9, p. 173). Although only a small number of individuals were raised from this mating, the experimental results, as in the case of W. L. × B. H., F_2, are seen to correspond well with the expected.

CASE 4a.—*White Leghorn* × *Black Java*, F_2.—(Tables 15, 16, p. 179, 180). There is seen in the 1912 cross-breds a slight deficiency in

*These ♀♀ were raised from the Black Spanish mothers of F_1 in the season of 1911.

the white and in the barred birds. But the ratios have an approximate agreement and the sex-ratios are all in the expected sense. In Table 15, showing the F_2 results of the 1913 series, it appears that the experimental results come very close to the expected.

CASE 3b.—(*White Leghorn* × *Black Minorca*) ♂ × *Black Minorca* ♀. (Table 10, p. 174). It has been shown in Table 10 that when the White Leghorn × Black Minorca F_1 ♂ was bred back to pure Black Minorca ♀♀, the offspring included white, black and barred birds. We may now submit this case to Mendelian analysis, making use of the same factors as those employed in the discussion of F_2. Assuming the zygotic formula of the F_1 cross-bred ♂ to be C_2BbF_2Ii, and that of the black ♀ to be $C_2b_2Ffi_2$, the mating may be represented:

♂ *CBfI* · *Cbfi* · *CBfi* · *CbfI* ×
♀ *CbFi* · *Cbfi* =

♂♂
- C_2BbF_2Ii, white
- $C_2b_2f_2i_2$, black
- $C_2BbF_2i_2$, barred
- $C_2b_2f_2Ii$, white

♀♀
- $C_2BbFfIi$, white
- $C_2b_2Ffi_2$, black
- C_2BbFfi_2, barred
- C_2b_2FfIi, white

Thus, according to the present hypothesis, there would appear in F_2, in every lot of 8 birds, the following types:

CHARACTER.	♂	♀	Total.
White	2	2	4
Black	1	1	2
Barred	1	1	2
Total	4	4	8

Now how do the observed results compare with the expected? In Table 10 (p. 174), have been presented the experimental results which should test the present theory. It is there shown that of 6 birds half were white and half dark; of the darks two were black and one was barred. The number of individuals described is too small to be of great value but it appears that the trend of the data is towards the verification of the hypothesis which has been assumed to cover these cases.

CASE 3c. ♂ $\left\{ \frac{[White\ Leghorn\ ♂ \times Black\ Minorca\ ♀]\ ♂}{Black\ Minorca\ ♀} \right\} \times$ *Black Minorca* ♀.—(Table 11, p. 175). Under the heading of Case 3b (Table 10) it has been shown that the mating (W. L. × B. M.) ♂ $[C_2Bbf_2Ii]$ × Black Minorca ♀ $[C_2b_2Ffi_2]$ gives one-eighth ♂♂ that are heterozygous for barring and lack the black-inhibiting factor *I*. Using as a breeding unit a ♂ having the zygotic constitution $C_2Bbf_2i_2$, it should be possible, if the theoretical deductions are correct, to build up a group of barred ♀♀ possessing the barring originally derived from the W. L. ♂. The first step in this process would be to demonstrate that ♂ 325B actually was heterozygous for the barring factor, and would transmit this character to his offspring; then to produce heterozygous ♀♀, free from *I*, and a homozygous ♂ possessing the zygotic formula $C_2B_2f_2i_2$,—in other words, the constitution of the pure-bred B. P. R. ♂. To accomplish the first step mentioned above ♂ 325B was mated with a number of black ♀♀, including Black Minorcas. Since these fowls have the zygotic constitution $C_2b_2Ffi_2$, compatible with the absence of barring, and of the inhibiting factor, the cross should bring out a certain number of ♀♀ manifesting heterozygous barring. This has appeared to be the case. The mating as made may be represented as follows:

The ♂ 325B, $[C_2Bbf_2i_2]$ may be assumed to form gametes,

$$CBfi \cdot Cbfi$$

and the black ♀♀ to form gametes,

$$CbFi \cdot Cbfi.$$

Since both ♂ and ♀ are now homozygous for *C* and *i*, these symbols may be left out of the mating formulæ:

♂ *Bf* · *bf* ×
♀ *bF* · *bf* =

♀ b_2Ff — black
♀ *BbFf* — barred
♂ b_2f_2 — black
♂ Bbf_2 — barred

In other words, provided ♂ 325B was actually heterozygous for barring, this mating should give equal numbers of barred and black birds, equally divided between the sexes. When we compare with these theoretical deductions the experimental results presented in Table 11, p. 175, it is apparent that there is close correspondence. Similar results were obtained from mating of ♂ 325B with Black Java ♀♀ (Case 3f) and Black Hamburg ♀♀. These matings served to give a number of ♀♀ heterozygous for the barred plumage-pattern, and freed from the pigment-inhibiting factor; and these fowls as described in Case 5 were mated in the season of 1913 with ♂ 477 V, a bird which showed better barring than 325B. The data on the results of these crosses are reported on p. 180.

CASE 3d.—♂ $\left\{\frac{(\textit{White Leghorn}\ ♂ \times \textit{Black Minorca}\ ♀)\ ♂}{\textit{Black Minorca}\ ♀}\right\} \times$ (*White Leghorn* ♂ × *Black Minorca* ♀) ♀.—(Table 12, p. 176). Another method of testing the heterozygous nature of ♂ 325B for the barring factor was to mate this bird with (W. L. × B. M.) F_1 ♀♀. These we assume are, themselves, heterozygous for the barring factor and have the zygotic constitution $C_2BbFfIi$, a formula compatible with barred plumage rendered obscure by the presence of inhibiting factor *I*. These birds form gametes

CbFi · *CbFI* · *CBfI* · *CBfi*

In this case the presence of the inhibiting factor *I*, in a heterozygous condition, would interfere with the manifestation of the barred color-pattern in one-half the progeny which would therefore be white.

Among the other half, lacking the inhibiting factor, a part should be barred and the remainder black.

If we assume that ♂ 325B, having the constitution $C_2BbF_2i_2$, forms gametes

$$CBfi \cdot Cbfi$$

and that the ♀♀ [$C_2BbFfIi$] form gametes

$$CBfi \cdot CBfI \cdot CbFi \cdot CbFI$$

the mating may be represented:

♂ $CBfi \cdot Cbfi \times$

♀ $CBfi \cdot CBfI \cdot Cbfi \cdot CbFI$

♂♂
- $C_2B_2f_2Ii$, white
- C_2Bbf_2Ii, white
- $C_2B_2f_2i_2$, barred
- $C_2Bbf_2i_2$, barred

♀♀
- $C_2BbFfIi$, white
- C_2b_2FfIi, white
- $C_2b_2Ffi_2$, black
- C_2BbFfi_2, barred

The data presented above may be summarized as follows:

CHARACTER.	♂	♀	Total.
White	2	2	4
Black	0	1	1
Barred	2	1	3
Total	4	4	8

In other words, among every 8 birds resulting from this cross, we should expect to find 4 whites, one black and 3 barred. Of the 4 white, one should be homozygous and 2 heterozygous for barring;

and of the barred birds one ♂ should be homozygous, one heterozygous, and one ♀ heterozygous for this character.

The experimental data presented in Case 3c may now be compared with these theoretical results. In Table 12, it was demonstrated that of 34 birds raised 17 were white and 4 were black, while 13 were barred as shown in the following diagram:

CHARACTER.	♂	♀	?	TOTALS.	
				Actual.	Expected.
White			17	17	17
Black	1	1	2	4	4¼
Barred	7	2	4	13	12¾
Totals	8	3	23	34	34

It will thus be seen that the correspondence between the actual and the theoretical results is very close.

CASE 3e.—♂ $\left\{ \frac{(White\ Leghorn\ ♂ \times Black\ Minorca\ ♀)\ ♂}{Black\ Minorca\ ♀} \right\} \times$ ♀ $\left\{ \frac{(White\ Leghorn\ ♂ \times Black\ Minorca\ ♀)\ ♂}{Black\ Minorca\ ♀} \right\}$—(Table 13, p. 177).

The experimental data presented under the head of Cases 3c and 3d made it apparent that ♂ 325B was actually heterozygous for the barring factor, and had the zygotic constitution, $C_2Bbf_2i_2$. The next step in the process of obtaining (from the 325 group) the barring factor in a pure, homozygous condition was to obtain a ♀ crossbred heterozygous for this character.

Under the heading of Case 3b it has been shown that from the mating (White Leghorn × Black Minorca) ♂ × Black Minorca ♀ there were produced, along with the barred ♂ 325B, black ♀♀ and

white ♀♀. From the mating in question one of each sort lived to maturity, black ♀ 325A and white ♀ 325E. A consideration of the analysis presented on p. 177, made it seem probable that 325A did not possess the barring factor, its zygotic formula being $C_2b_2Ffi_2$. The white ♀ 325E, however, might have had the zygotic constitution $C_2BbFfIi$ (compatible with a barred plumage rendered obscure by the presence of *I*); or the constitution C_2b_2FfIi (compatible with the total absence of the barring factor). We may now consider the details of these two matings, with the aim of demonstrating the actual zygotic constitution of the black and the white female cross-breds mentioned above, both being full sisters of ♂ 325B.

First Instance.—♂ *325B* (*barred*) × ♀ *325A* (*black*): As indicated above, ♂ 325B [$C_2Bbf_2i_2$] may be considered to form gametes

$$CBfi \cdot Cbfi$$

while the black ♀ 325A (his sister) [$C_2b_2Ffi_2$], forms gametes

$$CbFi \cdot Cbfi$$

The mating would then be represented:

♀ $CbFi \cdot Cbfi$ ×
♂ $CBfi \cdot Cbfi$ =

♀ $C_2b_2Ffi_2$, black
♀ C_2BbFfi_2, barred
♂ $C_2b_2f_2i_2$, black
♂ $C_2Bbf_2i_2$, barred

In other words, among every four birds two would be black and two would be barred; and in each of these groups there would be one ♂ and one ♀. Each of the barred birds would be heterozygous for this character. The expectation may be represented as follows:

CHARACTER.	♂	♀	Total.
Black	1	1	2
Barred	1	1	2
Totals	2	2	4

When we compare these deductions with the results actually obtained in experiments as presented on p. 177, it is apparent that the experimental results come fairly close to the expected. Of 43 birds described when over 3 weeks old, 25 were barred and 18 were black; and in each group the sex-ratios were approximately 1 : 1.

Second Instance.—♂ 325B (barred) × ♀ 325E (white); first possibility: We may consider first the case in which ♀ 325E is assumed to have the zygotic formula $C_2BbFfIi$, compatible with heterozygous barring rendered obscure by heterozygous *I*. As before, ♂ 325B may be assumed to form gametes,

$$CBfi \cdot Cbfi$$

while the ♀ 325E, forms gametes,

$$CbFI \cdot CbFi \cdot CBfI \cdot CBfi$$

The mating would then be represented:

♀ $CbFI \cdot CbFi \cdot CBfI \cdot CBfi \times$
♂ $CBfi \cdot Cbfi =$

♂♂
- C_2Bbf_2Ii, white
- $C_2B_2f_2Ii$, white
- $C_2Bbf_2i_2$, barred
- $C_2B_2f_2i_2$, barred

♀♀
- C_2b_2FfIi, white
- $C_2BbFfIi$, white
- C_2BbFfi_2, barred
- $C_2b_2Ffi_2$, black

These data may be summarized as follows:

CHARACTER.	♂	♀	Totals.
Black	0	1	1
White	2	2	4
Barred	2	1	3
Totals	4	4	8

It is thus apparent that in the mating under consideration among every 8 birds we may expect to have 4 white and 4 dark. Of the whites, 2 will be ♂♂ and 2 ♀♀. Of the darks, one will be black and 3 barred; the black bird and one of the barred birds will be ♀♀. It appears that the expectation of producing a ♂ homozygous for barring would here be attained. One out of every 8 birds (or one among every 3 barred ♂♂) should be homozygous for *B*.

We may now compare with these theoretical data the results obtained in the actual cross. As shown in Table 13 (p. 177), among 50 birds, 25 were white and 25 dark. Of the darks, 13 were black and 12 were barred. According to expectation we should have among 48 progeny the same proportion of light and dark birds, but the barred should stand in proportion to the blacks as 18 to 6; and all the blacks should be ♀♀. It is at once apparent that these expectations are by no means fulfilled, and we may therefore turn to a consideration of the second possible interpretation involving a different zygotic constitution for ♀ 325E.

Second Instance.—♂ 325B (barred) × ♀ 325E (white); second possibility: On p. 177 reference has been made to the fact that ♀ 325E, so far as appearance was concerned, might have been heterozygous for the barring factor or might lack it. In the previous instance the case has been considered in which the bird was assumed to be heterozygous for B. In the present instance we may consider the probable results of mating in case 325E lacked this factor but was heterozygous for *I*,—in other words, possessed the zygotic constitution C_2b_2FfIi. The ♂ 325B would form gametes as previously shown while the ♀ might be assumed to form gametes

$$CbFI \cdot CbFi \cdot CbfI \cdot Cbfi$$

The mating would then be represented:

♀ $CbFI \cdot CbFi \cdot CbfI \cdot Cbfi \times$
♂ $CBfi \cdot Cbfi =$

♂♂ {
- $C_2b_2f_2Ii$, white
- C_2Bbf_2Ii, white
- $C_2Bbf_2i_2$, barred
- $C_2b_2f_2i_2$, black

♀♀ { C_2b_2FfIi, white
$C_2BbFfIi$, white
C_2BbFfi_2, barred
$C_2b_2Ffi_2$, black

These data may be summarized as follows:

CHARACTER.	♂	♀	Totals.
Black	1	1	2
White	2	2	4
Barred	1	1	2
Totals	4	4	8

From this it appears that among every 8 birds resulting from such a cross as that being considered we should expect to have 4 whites and 4 darks. Of the white birds 2 would be ♂♂ and 2 ♀♀. Of the dark birds 2 would be barred and 2 black, each group being equally divided between the sexes.

We may now compare with these data the results obtained in the cross 325B × 325E presented on p. 177, and attempt to decide regarding the actual zygotic constitution of 325E. The actual and expected results were as follows:

CHARACTER.	♂	♀	Sex. (?)	Totals.	Expected.
White	?	?	.....	25	25
Black	2	6	5	13	12½
Barred	5	4	3	12	12½
Totals	.....	.....	.....	50	50

It is at once apparent that there is close relation between the actual and the expected results in these cases, thus verifying the constitution of 325E as C_2b_2FfIi. It is therefore clear that neither 325A nor 325E could be used in further matings to produce a barred strain. This purpose was served, however, by the barred ♀♀, daughters of 325B, secured in the 1912 matings from the black mothers. These were mated in 1913, not with 325B, but with one of his sons, 477V, a bird which possessed a somewhat clearer pattern, and was chosen as one which might be homozygous for barring. The details of these crosses are as follows:

CASE 5.—$$♂ \left\{ \frac{\left\{ \frac{(\textit{White Leghorn} \times \textit{Black Minorca})\ ♂}{\textit{Black Minorca}\ ♀} \right\} ♂}{♀\ \textit{Black Java}} \right\} \times \textit{Cross-}$$

bred ♀♀, heterozygous for barring (Table 16, p. 177). Since the ♂ 477V and the barred ♀♀ are homozygous for both C and i, these symbols now may conveniently be left out of the mating formulæ, which may be given as follows:

The zygotic constitution of the ♂ 477V is

$$Bbf_2$$

forming gametes

$$Bf \cdot bf$$

The constitution of the ♀♀ is

$$BbFf$$

forming gametes

$$bF \cdot Bf$$

The mating may therefore be represented:

$$\begin{array}{l} ♀\ Bf \quad bF\ \times \\ ♂\ Bf \quad bf\ = \\ \hline ♂\ Bbf_2, \text{ barred} \\ ♂\ B_2f_2, \text{ barred} \\ ♀\ b_2Ff, \text{ black} \\ ♀\ BbFf, \text{ barred} \end{array}$$

These expected results may be summarized, and compared with the actual results, as shown below:

CHARACTER.	Expected ♂♂	Expected ♀♀	Expected totals.	Actual totals.
Black	0	1	1	74
Barred	2	1	3	175
Totals	2	2	4	249

When the actual results (Table 17, p. 181) are compared with the expected it is clear that there is a close agreement. At the time this paper goes to press, it is impossible because of the immaturity of the stock to ascertain the sex-ratios and their relation to barring. It may be stated, however, that the 1913 progeny undoubtedly contains the expected proportion of ♂♂ homozygous for barring. It already appears possible to predict which these birds are by means of their lighter color. In this young stock there have already appeared birds which possess a much better grade of barring than any observed in the earlier stages of the investigation. To what extent selection for two or three years may be effective in further improving the character of the barred pattern remains of course to be ascertained. Suffice it to say at present that the mating described in Case 5 has finally yielded the expected ♂♂ homozygous, and ♀♀ heterozygous, for the barring factor; and these birds will now be used as selection-material for further improvement of the character under discussion.

B. DISCUSSION OF ADDITIONAL DATA NOT INCLUDED IN THE FOREGOING CASES.

During the course of these investigations a few other matings bearing upon the constitution of the White Leghorn have been made. These may be discussed briefly at this time, although the detailed results must await further breeding. These data relate to (1) the

constitution of the W. L. ♀ with reference to the factor *I;* (2) the presence of factor *C*, or other factors for black pigmentation, in the W. L. ♂; (3) the possible identity between the factor *I* in the W. L. and Bateson and Punnett's factor *I*, of the Brown Leghorn,—an inhibitor of the Silky type of mesodermal pigmentation in crosses between the B. L. and W. S.; (4) the possible occurrence of barring in other breeds of fowl possessing the "R-white." These points may be taken up in the order of their presentation.

1.—*The constitution of the White Leghorn ♀♀ with respect to factor I.*—In order to throw light on this point crosses were made during the season of 1913 between the B. H. ♂ and W. L. ♀♀, these being the reciprocal of crosses mentioned earlier in this paper. F_1 gave only white birds, thus indicating the homozygous nature of the W. L. ♀♀ for the inhibiting factor. This result was naturally expected.

2.—*The factor for black pigmentation in the W. L. ♂.*—It has been assumed in this study that the W. L. ♂ is essentially a black bird in which the pigmentation is obscured by the action of the inhibiting factor *I*. It is now necessary to present the data upon which this assumption is based. First it may be said that this assumption regarding the zygotic constitution of the W. L. is in harmony with the majority of the experimental results already presented. To assume that the W. L. ♂ lacks the factor for black pigmentation is not in agreement with the results observed. But it has seemed possible to throw light upon this matter by other means. If the W. L. ♂ were mated witn an R-white, such as the White Plymouth Rock, F_2 should yield some pigmented birds in which the factors *I* and *C* had become separated from each other. We may tentatively regard the zygotic constitution of the W. P. R. ♀ as c_2BbFfi_2 forming gametes

$$cBfi \cdot cbFi$$

The mating would then be represented:

♂ $CBfI \cdot CBfI \times$
♀ $cBfi \cdot cbFi =$

♀ $CcBbFfIi$ — white
♂ CcB_2f_2Ii — white

In an actual mating of this sort, of 63 F_1 individuals all were white. Of this number, however, 5 showed one or more barred feathers. Except in the case of one ♀ the sex of these birds was not ascertained. Many of the F_1 generation, as chicks, showed patches of black down feathers, but when the birds had matured all barred feathers had disappeared and both sexes were pure white except for occasional black ticks. It is thus evident that, even in F_1, *pigment appeared from some source*, although the parent breeds were in appearance pure white. This result is explainable on the ground of the dilution of the *II* of the W. L. to *Ii* in the cross-breds. Better evidence is however, to be derived from observations on the F_2 individuals.

In obtaining the F_2, cross-bred ♂ 463A employed, was an almost white bird, and may be assumed to form gametes of four sorts, as follows:

$$CBfI \cdot CBfi \cdot cBfI \cdot cBfi$$

while the cross-bred ♀♀ (463 E, F, J; 464 K, I, N, Q) may be assumed to form gametes of eight sorts:

$$CBfI \cdot CBfi \cdot cBfI \cdot cBfi$$
$$CbFI \cdot CbFi \cdot cbFI \cdot cbFi$$

The mating may be represented as follows:

♀ $CBfI \cdot CBfi \cdot cBfI \cdot cBfi \cdot CbFI \cdot CbFi \cdot cbFI \cdot cbFi \times$
♂ $CBfI \cdot CBfi \cdot cBfI \cdot cBfi =$

♀♀	C_2BbFfI_2 (1), white
	$C_2BbFfIi$ (2), white
	$CcBbFfI_2$ (2), white
	$CcBbFfIi$ (4), white
	c_2BbFfI_2 (1), white
	$c_2BbFfIi$ (2), white
	c_2BbFfi_2 (1), white
	C_2BbFfi_2 (1), barred
	$CcBbFfi_2$ (2), barred

♀♀ { $C_2B_2f_2I_2$ (1), white
$C_2B_2f_2Ii$ (2), white
$CcB_2f_2I_2$ (2), white
CcB_2f_2Ii (4), white
$c_2B_2f_2I_2$ (1), white
$c_2B_2f_2Ii$ (2), white
$c_2B_2f_2i_2$ (1), white
$C_2B_2f_2i_2$ (1), barred
$CcB_2f_2i_2$ (2), barred }

The data given above may be summarized in the following table:

CHARACTER.	♂	♀	Total.
White	13	13	26
Barred	3	3	6
Total	16	16	32

It is thus apparent that among every 32 F_2 individuals, one would expect to obtain 6 barred birds, equally divided between the sexes. The results may now be compared with the expectations as follows:

CHARACTER.	Actual.	Expected.
Barred	11	$11\frac{7}{16}$
White	50	$49\frac{9}{16}$
Totals	61	61

These results appear to justify the view that either the W. L. ♂ or the W. P. R. ♀♀ must be homozygous for the factor for black pigmentation. Since we know that whenever black pigmentation is

added to the barred pattern possessed as a cryptomere by the W. P. R. breed, the barring appears, we are forced to the conclusion that this breed does not normally carry this factor for black pigmentation but that the character lies dormant in the W. L. stock reappearing when it is freed from its inhibitor *I*. The fact that no black individuals, ♂♂ or ♀♀, but only barred (and white) birds arose from this cross in F_2 is additional proof of the homozygous condition of the W. L. ♂ with respect to the factor for barred plumage pattern.

There may be, however, one other possible explanation of the appearance of black-pigmented feathers in F_1 birds and a certain proportion (6 in 32) of barred individuals in F_2. It is conceivable that the W. L. ♂ and the W. P. R. ♀ each contain one of the factors whose fusion is necessary for the full manifestation of black pigmentation. Bateson and Punnett (*op. cit.*) have described a case in which the mating together of two R-whites produced progeny all of which were dark colored. These factors may be designated *X* and *Y* and it may be assumed that, while neither alone can determine black pigmentation, *X* and *Y* working together (*i. e.*, *XY*) are able to bring it about. In case the W. L. ♂ was homozygous for the factor *X*, and the W. P. R. ♀ homozygous for the factor *Y*, all the offspring would be *XY*,—compatible with black pigmentation. But upon the assumption that the W. L. ♂ is I_2, this pigment would not be manifested in the F_1 individuals. Making use of this hypothesis the W. L. ♂ would be $B_2f_2I_2X_2y_2$ forming gametes

$$BfIXy \cdot BfIXy$$

while the W. P. R. ♀♀, having the zygotic constitution $BbFfi_2x_2Y_2$, would form gametes

$$Bfix Y \cdot bFix Y$$

The mating would then be expressed:

♂ $BfIXy \cdot BfIXy \times$
♀ $Bfix Y \cdot bFix Y =$

♂♂ $B_2f_2IiXxYy$, white
♀♀ $BbFfIiXxYy$, white

All of the F_1 individuals are heterozygous for *I*, *X* and *Y*. The

presence of *X* and *Y* together would determine pigmentation, but this would be obscured by *I*, although in heterozygous condition. It is conceivable, however, that *Ii* might permit a small amount of black to appear in the early feathering of F_1; and this condition was actually found to occur as also pointed out by Goodale (1910). In this paper it has been shown to hold for F_1 in nearly all of the White × Black crosses.

In the production of F_2 of the cross under discussion, a ♂ F_1 white cross-bred [$B_2f_2IiXxYy$] would form gametes of 8 sorts:

$$BfIXY \cdot Bfixy \cdot BfIXy \cdot BfixY$$
$$BfIxy \cdot BfiXY \cdot BfIxY \cdot BfiXy$$

while F_1 cross-bred ♀ [BbFfIiXxYy] would form 16 kinds of gametes:

$$BfIXY \cdot Bfixy \cdot BFIXY \cdot bFixy$$
$$BfIXy \cdot BfixY \cdot bFIXy \cdot bFixY$$
$$BfIxY \cdot BfiXY \cdot bFIxY \cdot bFiXY$$
$$BfIxy \cdot BfiXy \cdot bFIxy \cdot bFiXy$$

This mating would give 128 individuals possessing 27 different zygotic constitutions as follows:

♂ COMBINATIONS.

$B_2f_2I_2X_2Y_2$ (1), white
$B_2f_2IiXxYy$ (8), white
$B_2f_2I_2X_2Yy$ (2), white
$B_2f_2IiXxY_2$ (4), white
$B_2f_2I_2XxYy$ (4), white
$B_2f_2IiX_2Y_2$ (2), white
$B_2f_2I_2XxY_2$ (2), white
$B_2f_2IiX_2Yy$ (4), white
$B_2f_2IiXxy_2$ (4), white
$B_2f_2I_2X_2y_2$ (1), white
$B_2f_2I_2Xxy_2$ (2), white
$B_2f_2IiX_2y_2$ (2), white
$B_2f_2Iix_2Yy$ (4), white
$B_2f_2Iix_2Y_2$ (2), white
$B_2f_2I_2x_2Yy$ (2), white
$B_2f_2I_2x_2Y_2$ (1), white
$B_2f_2Iix_2y_2$ (2), white
$B_2f_2I_2x_2y_2$ (1), white
$B_2f_2i_2x_2y_2$ (1), white
$B_2f_2i_2x_2Yy$ (2), white
$B_2f_2i_2X_2y_2$ (1), white
$B_2f_2i_2Xxy_2$ (2), white
$B_2f_2i_2x_2Y_2$ (1), white
$B_2f_2i_2XxYy$ (4), barred
$B_2f_2i_2XxY_2$ (2), barred
$B_2f_2i_2X_2Y_2$ (1), barred
$B_2f_2i_2X_2Yy$ (2), barred

Females, heterozygous for *B* and *F*, would be formed in the exactly same number and proportion as those indicated above for the ♂ ♂.

From this analysis it is apparent that among every 128 individuals 18 would be barred and 110 white, both the barred and the white birds being equally divided between the sexes as follows:

CHARACTER.	♂	♀	Total.
White	55	55	110
Barred	9	9	18
Total	64	64	128

In the following table, we may compare the actual with the expected results in F_2 as formulated upon the present hypothesis:

RESULTS.	White.	Barred.	Total.
Actual	50	11	61
Expected*	$49\frac{9}{16}$	$11\frac{7}{16}$	61
Expected†	$52\frac{27}{64}$	$8\frac{37}{64}$	61

*Provided the W. L. ♂ possesses the primary color factor, *C*, and the W. P. R. ♀ ♀ possess no contributing pigmentation factor whatever.

†Provided the W. L. ♂ possesses the "*X-factor*" and the W. P. R. ♀ ♀ the "*Y-factor*."

It is apparent from the summary presented above that on the basis of the single-factor hypothesis we should obtain 12 barred individuals in every 64, while on the double-factor hypothesis we should obtain only 9 in 64. The experimental results, comprising observations on 61 F_2 individuals, are slightly in favor of the former view. It must be borne in mind, however, that the difference between the two groups of expected results is slight, and final conclusions must be deferred

until data are obtained on a larger number of F_2 birds than form the basis of present comparisons.

3.—*On the nature of the factor I of the White Leghorn fowl.*—Heretofore in this series of experiments the inhibiting factor has been observed only in its effect upon the factor (or factors) for black pigmentation of the feathers, and (still unpublished) of the beaks and shanks (epidermal pigmentation). Whether factor *I* has the power to inhibit in all cases other colors, such as buff and red, cannot be stated definitely at this time.* But one other point of interest has been raised with reference to the factor *I* as a result of reciprocal matings between the W. L. and W. S. breeds. The experimental data may be presented as follows:

From the cross, W. L. ♂ × W. S. ♀ all the progeny were white with the exception of a few minute black flecks and an occasional suffusion of buff on the breast or wing coverts. The ♂♂ and ♀♀ were exactly alike in appearance, not only with respect to the pigmentation of the feathers, beaks and shanks (epidermal), but also with respect to the typical mesodermal pigmentation of the W. S.

In the cross W. S. ♂ × W. L. ♀ the results were different: With respect to plumage pigmentation, both ♂♂ and ♀♀ were heavily splashed with black. The pigmentation was perhaps more apparent on the ♂ ♂. With respect to the Silky type of pigmentation, the heavily pigmented birds (eyes, beak, shanks, wattles, pleura, peritoneum, etc.), were invariably ♀♀. It is apparent that these results (so far as they relate to the inhibition of mesodermal pigmentation in the ♂♂), are in accord with the findings of Bateson and Punnett (*op. cit.*) from observation of reciprocal crosses between the Brown Leghorn and W. S.

The results obtained by the present writer make it appear that the W. L. ♀, as well as the B. L. ♀, possesses in heterozygous condition a factor for the inhibition of the Silky pigmentation; and that the

*It can now be stated, as a result of later work, that the red of the Rhode Island Red breed, is recessive to, and the buff of the Buff Leghorn and Buff Wyandotte dominant over, the white of the White Leghorn.

inheritance of this inhibiting character is sex-limited, being transmitted from the ♀♀ to the ♂♂ only.

The differences in plumage-color (*i. e.*, heavily splashed F_1 birds from the W. S. ♂ × W. L. ♀ mating, etc.) are more difficult to explain and no attempt will be made to do so at this time.

In conclusion it may be merely pointed out that the factor which inhibits black pigmentation in the plumage corresponds with Bateson's and Punnett's inhibitor of Silky pigmentation in so far as its effect is observed only in W. S. ♂ × W. L. ♀ matings. But the factors seem to be distinct in that, while the inhibitor of Silky pigmentation is strictly sex-limited (preventing deep pigmentation in the F_1 ♂♂ from W. S. ♂ × B. L. ♀), the W. L. inhibitor of black in plumage does not appear to be sex-limited, since the F_1 from the W. S. ♂ × W. L. ♀ cross are also deeply splashed with black. It therefore appears that the White Leghorn breed of fowls possesses at least two distinct color-inhibiting factors,—one for the Silky type of pigmentation, the other for black pigmentation in the plumage. These points require further study.

4.—*The presence of the barred pattern in other breeds of fowl characterized by the R-white.* Outside of the White Plymouth Rocks, which as is well known possess barring as a cryptomere, only two other breeds characterized by the R-white have yet been tested for their possession of the barring factor. These are (1) the White Silky, (2) the White Minorca.

In the first of these crosses between the W. S. ♂ and B. H. ♀, of 9 individuals all were black; these manifested also the dark shanks, skin, and crest of the Silky. In F_2 the results were:

Black, including 2 blue	33
White	10
Game pattern, variously modified	9

Thus the expected 3:1 ratio appears among the black and the white birds with no observed manifestation of the barred pattern. No attempt will be made at this time to explain the appearance of

the games.* It suffices the present purpose to state that the barred pattern did not appear in either F_1 or F_2 of the White Silky × Black Hamburg crosses.

In F_1 of the matings between a White Minorca ♂ and Black Hamburg ♀ all the progeny were black, the ♂♂ manifesting red saddle feathers. In F_2 of this cross (1913) the results were: black 78, white 27, the expected being: black 78¾, white 26¼. No barring appeared in either F_1 or F_2.

V. General Summary and Conclusions.

1.—In reviewing as a whole the results of the many crosses described in the foregoing pages it becomes apparent that, as was stated at the outset, the original aim of the investigation has not been realized. The main purpose was (in 1909) to produce, and then to "fix" the barred plumage pattern by means of suitable matings of white with dark birds, it being assumed tentatively that the barred plumage pattern might represent, as many breeders have supposed, a heterozygous condition of black and white,—a sort of a mosaic in the same feather. It is true that a part of the aim has been attained, in so far as a completely barred pattern was actually secured in F_2; and a pure strain of barred fowls has been built up from these barred F_2 individuals. But a consideration of the nature of this barring, together with a careful study of its manner of inheritance in the numerous crosses mentioned above, leaves no doubt that it could not have been produced *de novo* from the White × Black matings as first suspected, but that it had its origin in a *factor for barring* present in the gametes of the W. L. ♂. The evidence already presented indicates therefore that the W. L. ♂ is homozygous for this character *B*, while the ♀ is heterozygous. It also indicates that the W. L. ♂ carries a factor, *C*, or possibly other factors, for black pigmentation. This circumstance would naturally bring out the barred pattern were it not for the presence of an inhibiting fact, *I*, which represses the manifestation of black,—a factor for which the W. L. ♂ is also homozygous.

*This point, together with others which have arisen in the course of the investigations, will be considered in detail in a later publication.

2.—The zygotic constitution of the W. L. ♂ with respect to barring and the other factors concerned has thus been given provisionally as $C_2B_?f_2I_2$, and the ♀ as $C_2Bb_2FfI_2$. To what extent the W. L. stock of this country and Europe possesses this formula cannot now be definitely stated. All that may be said on this point at present is that the data presented in this paper are based on experiments which made use of some of the best W. L. stock obtainable.*

3.—The possible *origin* of the factor for barring in the W. L. has not been considered in these pages and it is probably useless to speculate on this point until we have more authoritative information relating to the foundation of this breed and to the manner of production of the various strains now scattered about the country. Among them all there may exist several variations in zygotic constitution.

4.—The result of the reciprocal crosses between the W. L. and W. S. indicates that ♂♂ of the former breed (as is also the case with the Brown Leghorn ♂) possess a factor which inhibits Silky pigmentation (mesodermal). The ♀♀ are heterozygous for this character, which is sex-limited in its inheritance. These "inhibiting factors," apparently possessed by the Leghorn breed of fowls as a whole, are of considerable interest and deserve further study. In the hands of the intelligent breeder, they suggest an effective instrument for controlling the manifestation of a variety of characters in poultry.

5.—Finally it may be said that the data reported in this paper explain certain curious results obtained by both Davenport and Hurst (*op. cit.*) with respect to barred progeny. They furthermore give an explanation for the interesting phenomenon occasionally observed by poultrymen,—the appearance of "cuckoo" progeny in F_1 or F_2 from supposedly non-barred parents; also for the otherwise unexplainable circumstance that barred ♀♀ have arisen from

*Since the results presented in the body of this paper were secured, two other W. L. males have been tested, one coming from Professor James E. Rice of the Cornell Agricultural College and Experiment Station; the other from Professor Harry Lewis of the New Jersey Agricultural Experiment Station. Both were found to possess the barring factor as indicated by the appearance of barred feathers in the F_1 individuals.

barred mothers in the case of crosses with W. L. ♂♂, it being now commonly assumed that the sex-limited character, barring, is inherited by ♀♀ from the ♂ only.

As to the production of the barred pattern *de novo*, it has been indicated that barring was *not* obtained from two cases of matings between Blacks (Hamburg) and recessive Whites (Silky and Minorca). That the barred character can be produced, or "synthesized" from breeds not possessing the factor for barring now seems improbable; and we can agree with Correns (1905, p. 13) when he says: "Wo Mosaikbildung *als Regel* bei einem Bastard auftritt, war sie schon in einem der Eltern oder in beiden, aktiv oder latent, vorhanden."

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VII. Description of Plates.

PLATE I.

Figure 1. White Leghorn ♂, 193 A.
Figure 2. White Leghorn ♂, 1 A.

PLATE II.

Figure 3. White Leghorn × Black Hamburg, F_1 ♀, 10 I.
Figure 4. White Leghorn × Black Hamburg, F_1 ♂, 211 M_2.

PLATE III.

Figure 5. White Leghorn × Black Hamburg, F_2 ♀, 315 S.
Figure 6. Barred F_3 ♂, 477 V. (See text, p. 180).
Figure 7. Black Hamburg ♀, 5 A.
Figure 8. Barred F_2 ♂, 325 B. (See text, p. 175).

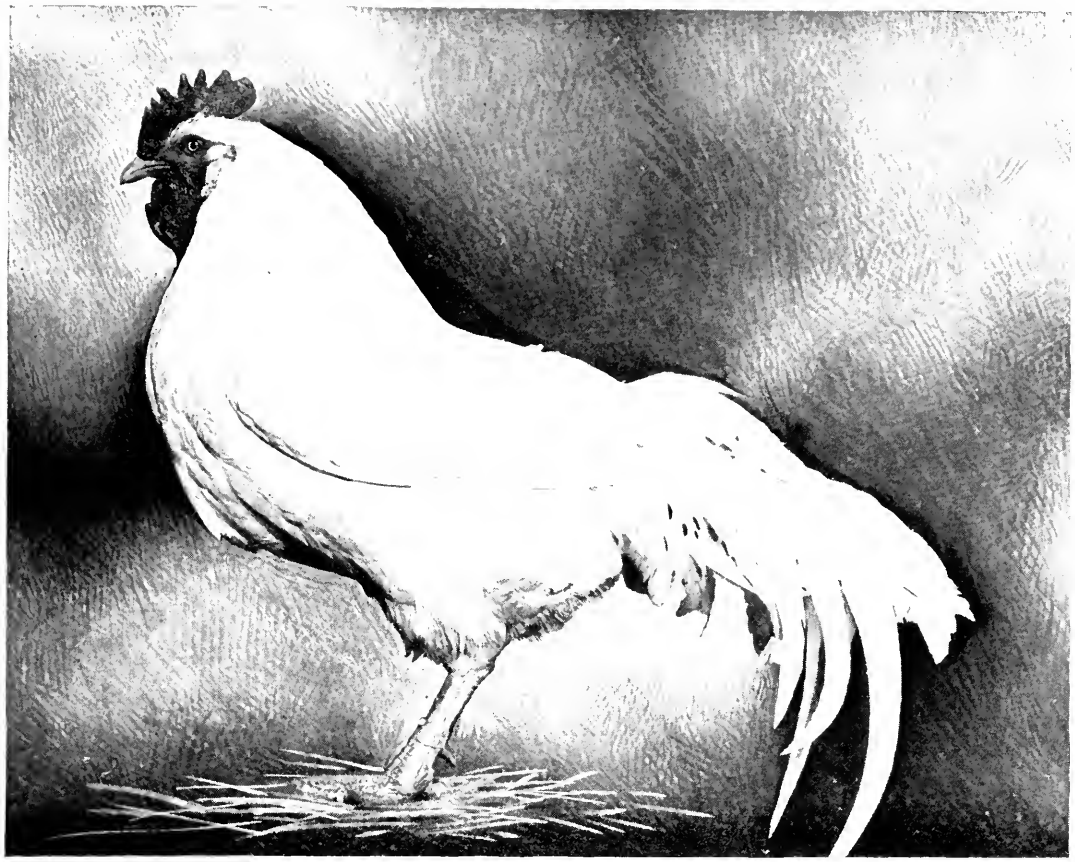
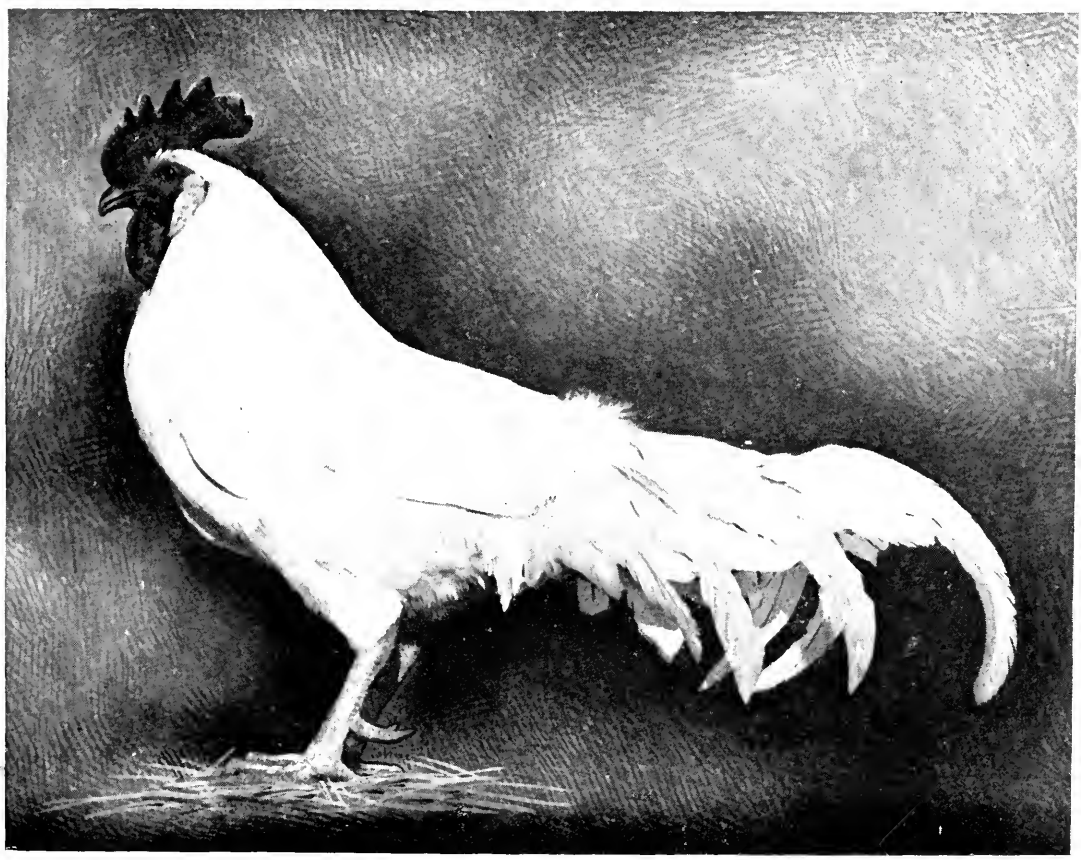


FIG. 1



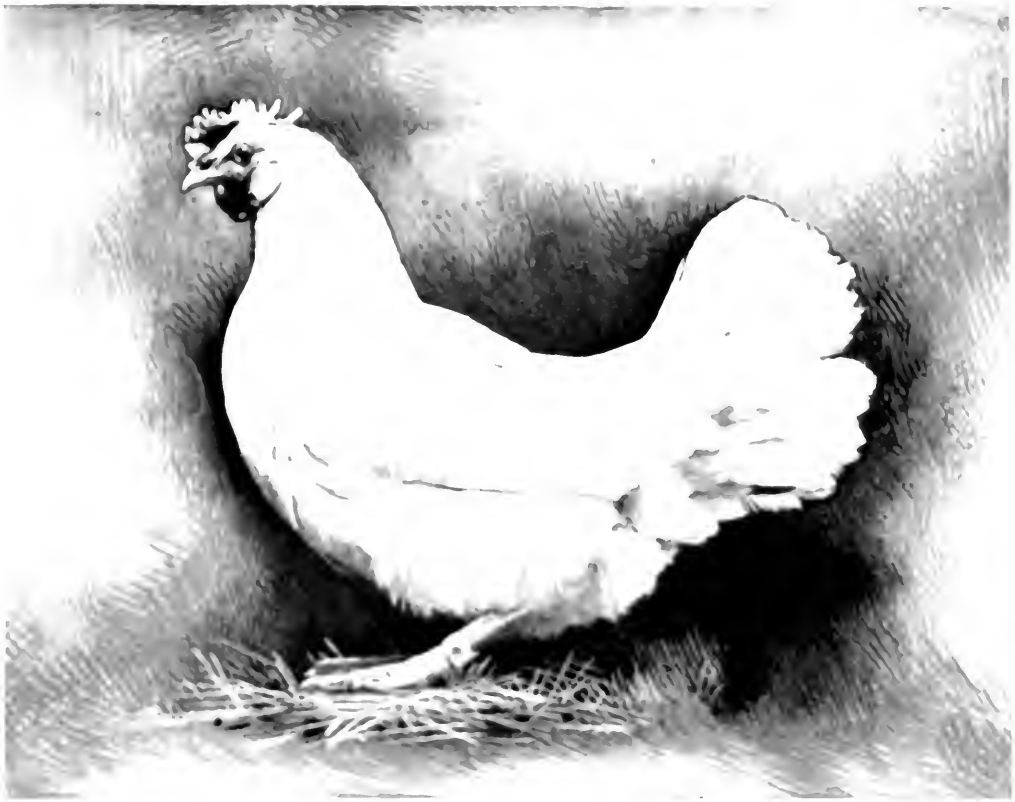


FIG. 3

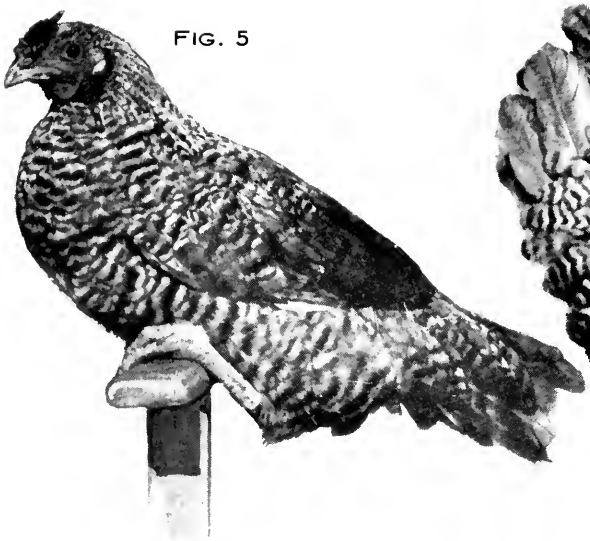


FIG. 5

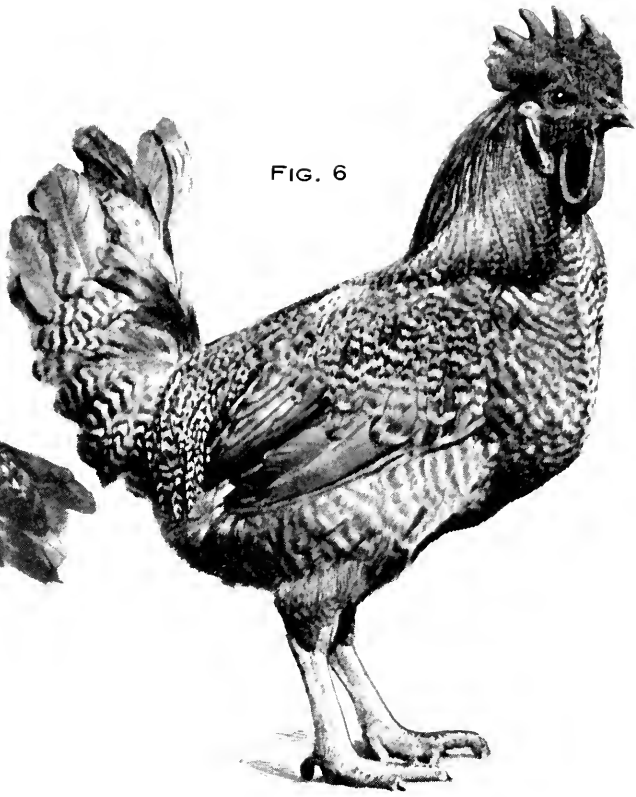


FIG. 6

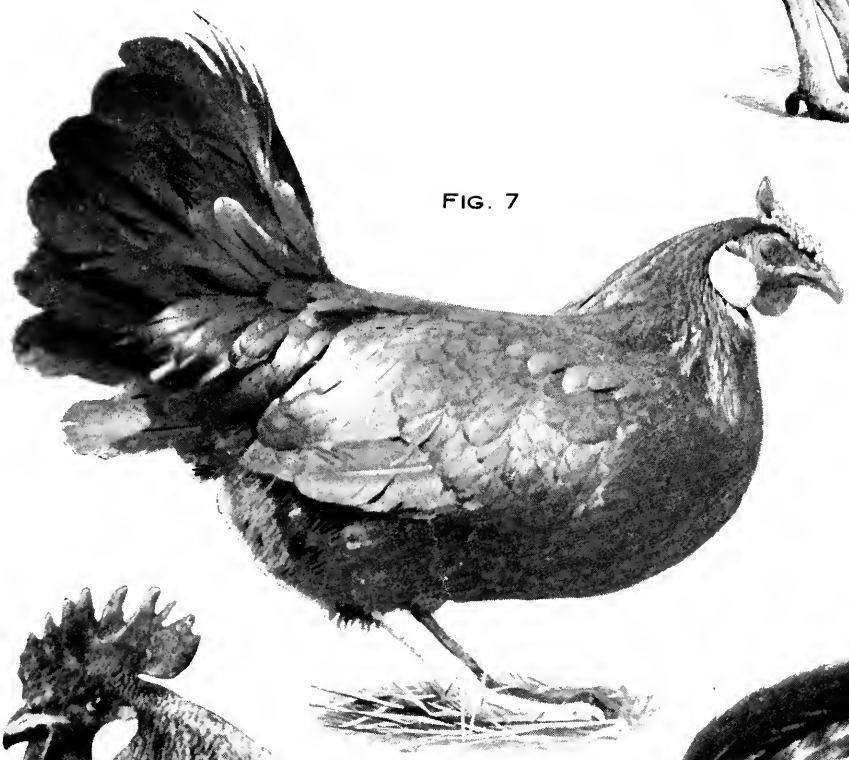


FIG. 7

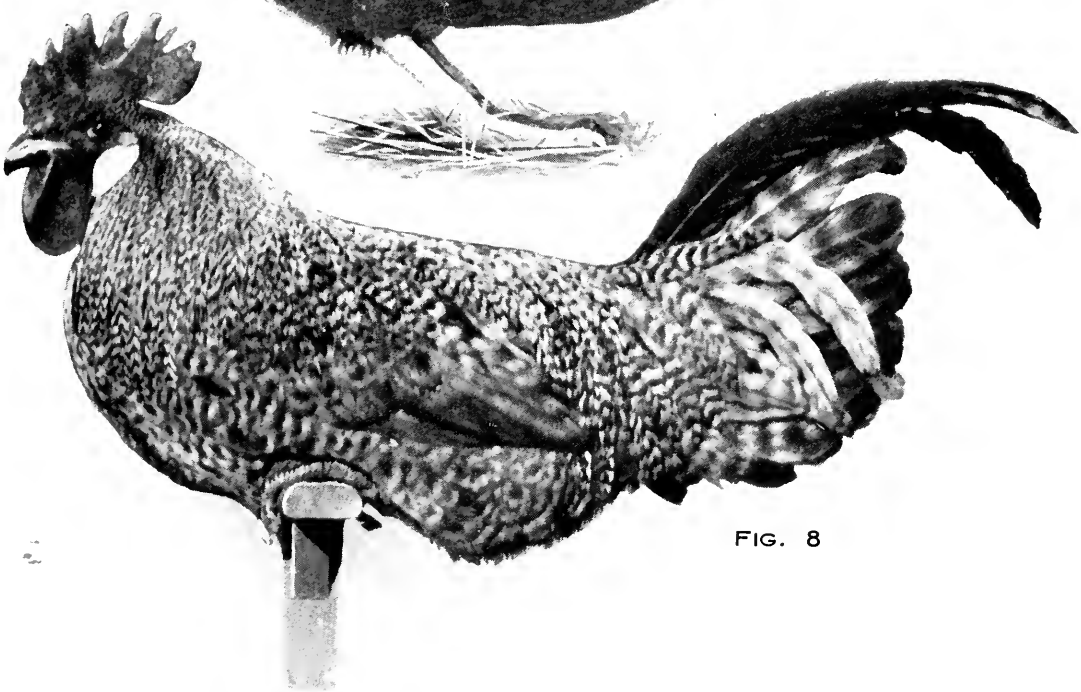


FIG. 8

CONTRIBUTIONS FROM THE DIVISION OF ANIMAL BREEDING AND PATHOLOGY.

SERIES BEGINNING 1909.

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