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Dominance in poultry
Feathered feet, Rose comb, Internal Pigment and Pile

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1. Introduction

In a previous report (Fisher 1935) I have described the results of an experiment with poultry, covering the years 1929–34, so far as these concerned the three factors for Crest, Polydactyly, and Barred plumage. It was hoped at that time that two further years' experimentation would enable the conclusions to be demonstrated decisively by the production of parallel broods consisting exclusively of homozygotes and heterozygotes, in which the differences between these genotypes, and the variability of each, could be directly observed. This would require at least one male and several female homozygotes of the same kind, material which I have not succeeded in breeding in any line.

Although the stock did well in 1934, the year in which in most lines intercrossing was first practised, the two following years were exceedingly unfavourable to propagation. In 1935, for example, from over fifty sittings of eggs, only fifteen chicks in all were reared to maturity. Little of consequence can, therefore, be added in respect of the three factors previously dealt with, and the present report will be given principally to the four remaining factors.

Two small broods were indeed raised in 1935 from a herniated hen, crossed with an uncrested cock, and from these the two birds which lived long enough developed crests, while six others, having single combs, could be diagnosed as Crested owing to the combs being abbreviated and bent posteriorly in a way which appears to be characteristic of single-combed Crested birds (Brandt 1936). There can be no doubt, therefore, that the herniated mother, as anticipated, was homozygous for Crest.

The homozygous Barred cock, bred in 1934, mated to barred hens, produced a brood of only two chicks, of which the one male was homozygous like his father, while the female also was barred.

Birds heterozygous for polydactyly have, in these experiments, so frequently shown normal feet that a test on no larger scale than these was bound to be inconclusive. Of the eleven chicks, bred from apparently homozygous mothers, no less than seven were four-toed, and none of these survived to provide the opportunity of showing that they carried the gene for polydactyly. The analogy of the cases of Feathered feet and of Rumplessness, for which larger numbers are, fortunately, available, and which are discussed below, suggests that in this case, also, we are dealing with no more than a failure to manifest the heterozygous condition in a high proportion of the small number of chicks which it was possible to breed.

We may now consider the results for the four remaining factors, Feathered feet, Rose comb, Black Internal pigment and Pile plumage, which, in the course of the experiment, were introduced into a stock of wild *Gallus gallus*. A brief summary of the entire results is given at the end of this paper (p. 46).

2. Feathered feet

The four Silky pullets used in 1929, for the primary cross, had feathered feet, but apparently were not all homozygous, for, out of thirty-four chicks bred, fourteen were unfeathered. Of the nine cross-bred pullets used in 1930 six were chosen as having feathered feet, but their progeny was not kept separate. Of the 144 chicks bred, forty-one showed feathering. Two of these

were crossed in 1931 with a wild cock, and the character continued to be readily classifiable at hatching. The author was, however, away for some months during this summer, and, on his return, birds with feathered feet could not be distinguished with certainty from their normal sisters. Consequently, in 1932, all surviving pullets from this pen were mated for a fourth crossing to the wild stock. In 1932 only a quarter of the chicks were expected to be feathered, and in fact the feathering was recovered in six out of thirty chicks. Two of the thirty, including one feathered cockerel, were polydactylous, showing that polydactyly had been carried by one of the 1931 birds in this pen.

Since the gene for feathered feet seemed in the wild stock to be already nearly recessive, it was thought desirable to obtain homozygotes without delay, although the extent of feathering was still very variable. In 1933, therefore, a feathered cock was mated to two feathered hens, none of these showing polydactyly. Again, one at least of the parents must have carried this factor, for it reappeared in the chicks from this mating.

Of the nineteen chicks bred, only three were without feather. Of the remainder, some showed the very weak and transient feathering which had given trouble in previous years, some a medium degree of feathering, while in others it was very strongly developed. These latter, it was noticed, displayed additional features distinguishing them from birds showing the medium degree of feathering. In the first place they were brachydactylous, having the fourth toe noticeably shorter than the second. The claw in particular of the fourth toe was dwarfed, and on examination it was found that the toe itself contained three phalanges instead of the normal four. The third phalanx, moreover, was the smallest of the series, contrary to what occurs in other cases when the third and fourth phalanges are fused to form a single bone.

The second characteristic feature was that the line of feathers which passed obliquely across the back of the foot, instead of terminating at the base of the fourth toe, was extended up to the second or third joint. One of the chicks which showed these features died in the shell, and three more during the first few weeks of life. Two, however, from a late brood (29 July) seemed likely to live. They were both females, and in them it was noticed that the feathering was persistent, and not soft, but bristly to the touch. One of these pullets died in November and the other, which was also polydactylous and Silky, broke her leg and had to be killed during the winter. She had always been lame, and the accident was doubtless due to the crippled condition of her feet.

There can be now little doubt that the six birds from this mating showing

the three combined characters of heavy feathering, extended feathering and brachydactyly were homozygotes for the gene for feathering. As, however, none of them survived, it was necessary to repeat the experiment in the following year. The 1933 broods had, however, shown that the attempt to obtain homozygotes in that year was somewhat premature; the strain had been by no means freed from factors introduced in the original Silky parent. Apart from the appearance of Polydactyly, recessive factors for Silky plumage and for Black plumage also made their appearance. With so much germinal material present of domesticated origin it was to be anticipated that the strain would be far from pure also in factors affecting the manifestation of the gene for feathered feet.

In 1934 two of the cocks from 1933 were tested by outcrossing and both were shown to be heterozygous. One of them, a weakly feathered male, was also mated with two weakly feathered sisters and gave a brood of six, four strongly feathered, one weakly, and one without feathers. Of the four strongly feathered, one, a Silky, died at 10 weeks old, but the remaining three, a cock and two hens, appeared to be typical homozygotes, showing brachydactyly and extension of the feathering with its stiff bristle-like texture. The male, unfortunately, died during the winter, but the two females, one of which was polydactylous, were available for mating in 1935 and 1936.

With males from lines from which feathering was absent, they gave the numbers shown in Table I.

TABLE I. CLASSIFICATION OF CHICKS FROM HOMOZYGOUS MOTHERS

		F	+
1935		3	1
1936	**H**	7	0
	O	0	1
	U	7	3
	Bb	9	0
	Total	26	5

The great excess of chicks with feathered feet shows that the mothers are not segregating in the ratio 1 : 1 as they would do if they were heterozygous. The presence of five chicks with unfeathered feet does, however, require explanation. In both years it was observed that some of the chicks, though classified soon after hatching, showed feathering in the minimal degree capable of detection, namely, a single down feather on one foot only, the other foot being unfeathered. With manifestation at this level it is not improbable that at least as many chicks carrying the feathered gene should

fail to show any phenotypic effect whatever. The gene for feathered feet is, in fact, behaving almost as much like a recessive as a partial dominant, and may completely fail to show itself, just as polydactyly has been shown in this same line to do. A parallel back-cross in 1936 with hens classified as heterozygous gave, in fact, seven feathered to nine normal, numbers which, apart from emphasizing the contrast with those judged to be homozygous, show a small excess among the unfeathered.

In respect of modification of dominance, the feathered line yielded some other interesting results. One of the cocks outcrossed in 1934 was found to give chicks rather strongly feathered, with the third and fourth phalanges of the fourth toe fused, as though displaying an initial stage of brachydactyly. Such an effect on heterozygotes, causing them somewhat to resemble the homozygote, is exactly what should be expected on the view that dominance is very liable to modification. The matings of this cock with heterozygous mates are summarized in Table II, in which distinction is drawn between the two types of heterozygotes, the strongly feathered with fused phalanges, and the weakly feathered.

TABLE II. MATINGS SHOWING TWO SORTS OF HETEROZYGOTES

	Brood	No feathers	Weakly feathered	Somewhat strongly feathered, fused phalanges	Very strongly feathered, extended, brachydactylous
1934	**J**	1	1	—	4
1935	**G**	—	1	4	—
	S	3	—	2	—
	W	1	3	2	2
	Bb	6	—	3	2
	Total	10	4	11	4
1936	**B**	1	—	3	1
	T	5	3	4	2
	Total	6	3	7	3
3 years		17	8	18	11

The supposition of a single modifying factor carried by the male only would give an expectation of 13·5 in each class. The deviations above give $\chi^2 = 5{\cdot}111$ for 3 degrees of freedom, which is not significant. The excess of strongly feathered heterozygotes does, however, suggest that one of the hens may have carried the modifier. We should expect, however, that the weakly feathered class would be depleted by the classification of several of the weak heterozygotes as non-feathered.

Summary for feathered feet

In wild stock the mutation for feathered feet shows itself in the heterozygote by a very weak and transient feathering. This may usually be recognized at hatching, but is often imperceptible later.

The homozygotes show a strong feathering, extended up the fourth digit, retained to adult life, bristly in texture, and accompanied by brachydactylous (three-jointed) fourth toes. The third joint and the claw are especially dwarfed. Occasional feathers sometimes appear on the distal joint of the third toe.

The mutation is thus nearly, but not quite, recessive. In comparison with the nearly recessive mutant Barred, Feathered feet seems slightly the more recessive.

Although the experiment was not sufficiently extensive, and was not carried far enough to analyse the causes of variation among heterozygotes, the observations agree in detail with the view that one dominance modifier from the domestic strain was still segregating in some of the test progenies.

3. Suppression of the heterozygous and change of the homozygous manifestation of an incompletely dominant gene

Extensive breeding experiments reported by Dunn and Landauer with the mutant for Rumplessness have revealed a series of remarkable facts bearing on the modification of both heterozygotes and homozygotes. The mutant had at first been described as "dominant"; Dunn and Landauer found in the stocks first examined that the term was apparently justified:

> In our original material and in the experience of other investigators this gene behaved as a "dominant". Fowls heterozygous for the gene lacked the free caudal vertebrae, one or two synsacral vertebrae, the fleshy rump, the tail feathers and the uropygial gland. This condition, which was likewise characteristic of the few known homozygotes examined, we referred to as complete rumplessness.

When this stock was outcrossed to normal breeds, dominance tended to disappear, and intermediate heterozygotes began to predominate.

> The factors responsible for these modifications towards normal proved to be hereditary, and after selection and inbreeding among members of the modified stock, ratios approaching $\frac{1}{4}$ complete rumpless : $\frac{1}{2}$ intermediate rumpless : $\frac{1}{4}$ normal were obtained from *inter se* matings of intermediates; while from matings of intermediates by normals from the same stock there resulted chiefly normals and intermediates, with very few complete rumpless.

By an outcross to a non-rumpless breed, followed by selection, Dunn and Landauer had produced a condition closely analogous to that of Crest,

Pile, Polydactyly, Feathered feet, etc., when mated repeatedly back to wild stock.

The results from 1927 to 1933 led these authors to think that the modifying factors affected only the heterozygotes. Two further generations of selection, however, showed that some of the homozygotes also were beginning to show "intermediate" features. Thus, in a few generations of selection, Dunn and Landauer have not only demonstrated the modificability of dominance by selection, but have gone far towards verifying also the further inference of my 1928 paper (p. 123):

> It is clear, however, that a persistent mutation in which even the homozygote has not too bad a chance of survival, the homozygote may follow in the footsteps of the heterozygote, and become indistinguishable from the wild form.

Dunn and Landauer do not, in their report, call attention to the circumstance to which the rapid success of their experiment in selection is doubtless due, namely, that the gene complex, in which the mutant for Rumpless shows no dominance, is that normally present in other breeds; so that the condition of dominance found in their original stock is to be regarded as a human artifact produced by the selection of breeders for the complete expression of rumplessness. Since the complete expression of rumplessness induces much sterility, this selection must have been chiefly exerted on heterozygotes. In selecting for Mild expression Dunn and Landauer were merely undoing the work by which the completely rumpless heterozygote had been produced. It is, therefore, unnecessary to postulate, as Dunn and Landauer do, that the modifiers they have selected "would be retained in the normal type because of their obviously favourable effect on development". On the contrary, they admit that "No apparent effect of these genes on the normal type has been observed". The favourable effect on development seems only to occur in the presence of the gene for rumplessness; the simplest view is that they have been established in the wild species in response to the continual recurrence of that gene as a mutant over a very long period.

4. The supposition that dominance has been modified by selection of the non-mutant

Hutchinson's results with Crinkled Dwarf

A second case in which dominance modification has been demonstrated, but in which it has been thought that the modification should be ascribed to the selective action of modifiers in the non-mutant homozygote, is one

to which I alluded in 1930 on the basis of information supplied by Mr J. B. Hutchinson ("Genetical Theory of Natural Selection", p. 59):

An extremely interesting case showing the modification of the heterozygote so far as to be indistinguishable from the non-mutant, that is of the acquisition of complete dominance by the wild type gene, has been brought to my notice by Mr J. B. Hutchinson from the work of Dr C. S. Harland on the genetics of the cotton plant. The several species of new-world cottons can be freely intercrossed and yield fertile offspring. One of these, the Sea Island cotton, has repeatedly produced a mutant form known as Crinkled Dwarf, which in that species is completely recessive. It appears to be identical with a similar mutant known as Wrinkled Leaf, appearing in some nearly related forms grown in Egypt, but so far as is known none of the other American species throw this mutant. In the course of Dr Harland's experiments the Crinkled Dwarf mutation of Sea Island was crossed with two other new-world species, Upland and Peruvian. The outstanding results of the cross were the same in both cases. The heterozygote was found to be slightly affected by the mutant character, thus indicating, even at this stage, some incompleteness of dominance. The most remarkable effects, however, were produced in the second generation, derived from the heterozygote by self fertilization. In this we should expect a quarter of the offspring to be Crinkled Dwarf, a half to be heterozygote, and a quarter to be non-mutant. The homozygous forms appeared as expected, but were connected by a practically continuous series of intermediate types. The heterozygotes in fact showed dominance of all grades. It is evident that the Sea Island cotton differed from the other new-world species in a number of modifying factors affecting the development and appearance of the heterozygote, the combined effect of which, in the Sea Island species, is to render the heterozygote normal in appearance. In this case the complete modification in the reaction of the organism to the mutant gene must have been brought about since the separation of this species from its new-world congeners; the whole process of evolution from the first appearance of the mutation, at least with appreciable frequency, must therefore have been comparatively rapid. When the mutation rate has been determined this case should afford a useful guide to the extent of the analogous events which we should expect to have taken place in other species.

Harland later showed that in two cases repeated back-crosses to Upland strains, namely *Triumph* and *Virescent Yellow*, resulted in the re-establishment of dominance. Since Harland believed that the mutations did not spontaneously occur in the Upland cottons (*Gossypium hirsutum*), the fact that this species contained a "modifier complex" producing complete dominance led him to suppose that these modifiers must have been selected for their effects on the non-mutant homozygote. Such effects are, indeed, hypothetical, but would seem to be a fair inference from the facts when complete absence of this mutation from the Upland species is postulated. In 1933, however, Hutchinson discovered a mutation occurring spontaneously in selections of Upland cotton grown at Indore, and later proved that this Indore Crinkled was identical with the Crinkled Dwarf previously discovered, as well as with the Wrinkled Leaf known in Egypt.

It thus appears that both the Sea Island cotton (*G. barbadense*) and the Upland cottons (*G. hirsutum*) are subject to this mutation, and that, in

both, the mutation has become completely recessive. In *G. hirsutum*, indeed, Hutchinson shows that the homozygous mutant has been modified somewhat further towards normality than in *G. barbadense*. The modifiers by which dominance is produced in the two species are, however, largely different. Hutchinson therefore concludes that the occurrence of the mutation antedates the separation of the two species, but that, owing to the low initial viability of the heterozygote, the development of dominance was for long extremely slow, becoming progressively more rapid as the differences in viability between heterozygote and normal decreased. He suggests further that the rate of improvement must have been accelerated in recent times by changes in the method of cultivation. The cultivation of the primitive perennial forms of *G. barbadense* by the South American Indians was very crude, and reproduction was usually from a cluster of seeds. With intense competition among seedlings the survival of the Crinkled heterozygote would be very rare, and its rate of improvement correspondingly slow. Under modern cultivation, with a low seed rate and early thinning of seedlings, there is a much greater chance of a slightly Crinkled heterozygote yielding seed. In addition, the development of the annual habit must have increased the rate of improvement by allowing four or five generations in the period formerly occupied by one. Since Upland cottons have longer been cultivated as annual types, modification towards normality is more advanced in this species.

Hutchinson concludes that all the available evidence agrees strikingly with expectation on the selection theory, and, while not inconsistent with Harland's theory of selection of modifiers on their own account, provides no support for it.

5. Rose comb

The case of Rose comb is one of the most interesting of those found among the seven factors studied. The breeding data summarized in Table III are, indeed, inconclusive, since the one homozygote, proved to be such by breeding test, did not appear to differ in any clear characteristic from his heterozygous brethren. Nevertheless, the chance observation, made late in the experiment, that the gene for Rose comb also produces very noticeable changes in the bones of the head, will, it may be anticipated, enable workers with domesticated breeds to determine the degree of dominance exhibited in this case with a metrical precision far beyond what could be obtained from such scanty numbers as I have been able to breed.

Apart from this effect on the skull, Rose comb would be a most difficult

structural feature in which to study dominance, especially in the wild jungle fowl. In the adult male the comb is much depressed vertically, though expanded laterally. The expanded upper surface presents a complicated pattern of ridges and tubercles, showing no constancy from bird to bird. The posterior end may be single, though not prolonged as in most of the fancy breeds, but rather shaped like a rudder, or it may be trifid, as it was with the one male proved to be homozygous. Whereas, with the adult males, it is the complex inconstancy of the organ which makes classification difficult, in the females and in immature birds of both sexes, the Rose comb is so slightly developed that variations in its structure would be likely to be imperceptible without a minute examination. Although the character can be diagnosed at hatching by the absence of the lamina of a single comb, the lack of development in young birds and females has reduced the material available for the study of the range of normal variability among heterozygotes to numbers really trifling in comparison with those of the other characters studied in this experiment.

It was in the preparation of heads for the examination of the hernia, found to accompany homozygosis in Crested birds, that it was noticed that birds with Rose comb had not the comb only widened, but also the frontal bone between the orbits. The extent of this widening may be gauged by measurements on the prepared skull, and, in the case of adult males, the width is increased, on the average, from 12 to 15 mm., or by about 25%. The lateral distance between the outer branches of the nasal bones is also materially increased, but the intra-orbital width of the frontal bone affords an entirely convenient measurement for metrical study. This measurement also is accessible on the living bird. The completeness or incompleteness of dominance in the case of Rose comb may therefore be satisfactorily determined from the average measurements of suitably large samples of the three genotypes, Single comb, heterozygous Rose, and homozygous Rose. Since many strains of popular breeds, such as the Rhode Island Red, have both single and rose combs, such material should be available to many workers in poultry genetics without special breeding experiments. I understand that Dr A. E. Brandt, of the State College of Agriculture of Ames, Iowa, has already material of this kind in view, and its examination will, I hope, establish the status of the Rose-comb factor as a complete or partial dominant far more decisively than could be hoped from any discussion of variations in the external structure.

The examination of domesticated material should not, in my opinion, be in any way inferior to that of the wild jungle fowl for such a metrical study. Whereas fanciers have been infinitely solicitous with regard to the external

form of the comb, the simultaneous widening of the frontal bone seems to have escaped the notice even of poultry geneticists, and there appear to be no strong grounds for fearing that dominance in this character has been appreciably modified by human selection.

It is a matter of some general interest that, of the four structural characters tested in this experiment, all, without exception, should affect the development of the skeleton. In my previous communication it was shown, as further breeding has confirmed, that the gene responsible for Crest causes, when homozygous, an opening of the frontal bone leading to cerebral hernia. In the present paper it has appeared that the gene responsible for Feathered feet caused, when homozygous, a pronounced brachydactyly, with the suppression of the terminal phalanx of the outermost toe. This is also partially brought about, in some genic combinations, in the heterozygote. The fourth structural character studied has been polydactyly, the skeletal nature of which has never been in doubt. In view of these examples the remarkable conservatism of the skeleton in phylogeny should certainly not be ascribed to any lack of abundance of mutations affecting its structure, but rather to the persistent success of selection in preventing such mutations, as must constantly be occurring, from having any evolutionary effect, save in favourable and most exceptional circumstances.

TABLE III. MATINGS INVOLVING ROSE COMB

	Back-crosses	Normal	Rose	Total
1929	Purchased Silkies by Wild ♂	19	15	34
1930	9 Rose (1929) ♀♀ × Wild ♂♂	65	78	143
1931	Mixed pens of 1930 ♀♀ × Wild ♂♂; no segregation obtainable			
1932	Wild ♀♀ × (1931) Rose ♂	2	8	10
1933	4 Rose ♀♀ × Wild ♂	4	4	8
	Total of four generations back-cross	90	105	195
	Intercrosses			
1934	2 Rose (1933) ♀♀ × Rose (1933) ♂	6	11	17
1935	Idem adding 1 (1934) ♀	5	9	14
		11	20	31
	Test matings			
1935	Single ♀♀ × Rose ♂ (1934A)	—	11	11
1936	Idem	—	9	9
		—	20	20
1935	Single ♀♀ × Rose ♂ (1934B)	3	7	10
1935	Single ♀♀ × Rose ♂ (1934C)	3	7	10

The first matings (1929) shows that the Silky hens were probably all heterozygous for Rose. The ratio 90 : 105 does not differ significantly from unity.

If the 1934 female bred in 1935 she was apparently heterozygous, since there is an excess of normals from the intercross matings in both years; the numbers differ widely from the 1 : 5 expectation, but not greatly from an expectation of 1 : 3.

Of the three males from 1934 successfully tested, one is clearly homozygous, and two heterozygous. Of the two other Rose males from this year one died in 1935 without breeding, while the other failed to breed both in 1935 and 1936. This was, unfortunately, the only other male of this year with a trifid comb.

6. Black internal pigment

The factor for black internal pigment produces an intense black pigmentation on many internal membranes. It was doubtless this factor which led Darwin to describe the Japanese Silky as the "black-boned Silk fowl". Externally, it may be easily recognized at hatching by the feet being a deep green instead of yellow. Throughout life the comb and wattles and bare skin of the face are usually somewhat darkened, the effect being more striking and regular on the underside of the wing. It has been propounded that the pigmentation caused by this factor is characteristically mesodermal, and, if it is exclusively so, the peculiar down plumage, mentioned below, must be ascribed to some other factor. For, although it will be shown that in this factor, as in others, dominance is irregular, and controlled in its degree by other genetic factors, the few birds which it has been possible to breed in this line do not suffice to demonstrate that the characteristic down plumage observed is really a manifestation of homozygosis.

Of the thirty-four chicks bred from the first cross (1929) of Silky hens with a wild *Gallus* cock, thirty-two were pigmented and two unpigmented. This aberrant ratio might perhaps be due to one of the four bought hens being heterozygous and the remainder homozygous for the mutant gene. However this may be, manifestation of the pigmentation was notably variable in this first cross, and it was thought at the time that the factor might have to be abandoned as too difficult for the study of dominance. The variability, however, diminished greatly in later generations.

Nine pigmented hens, bred to wild cocks in 1930, gave a regular segregation of seventy-eight pigmented to sixty-six unpigmented. Pigmented birds were bred in two pens along with other factors in 1931, and two

pigmented females were available for a fourth cross to the wild in 1932. These, constituting now a separate line, gave ten chicks, six of which were pigmented, while only two, a male and a female, survived for breeding.

In order to follow the original plan for making five crosses to wild it would have been better at this point to have mated the cock to wild hens. The wild line had, however, bred so badly that likely pullets were not available, and, rather than abandon the factor, the two surviving birds were intercrossed in 1933. They gave six pigmented to one normal, of which again a pigmented pair survived. The parental cross could not, unfortunately, be repeated, owing to the death of the female. The male used in 1934 was proved later to be homozygous, and it is a most unfortunate omission, in view of his progeny, that his down characters were not noted.

Of the ten chicks, hatched in 1934, one, a female, showed much additional pigmentation in the down of the head. The normal eye to ear stripes were extended backward (see fig. 1) to meet the median band at the back

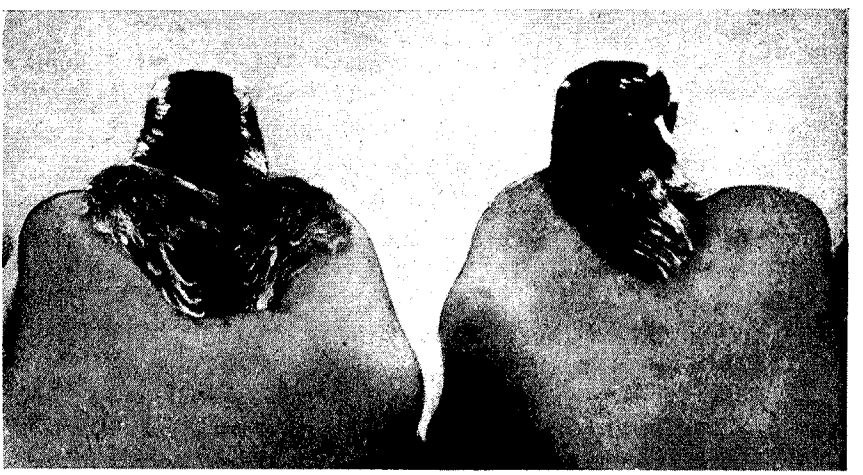

FIG. 1. Photographs of chickens showing: right, abnormal extension of brown pigment on the sides and back of the head; left, chick from the same brood classified as normal.

of the head, and there were additional spots above and in front of the eyes. This extension of the dark brown pigment seemed associated, in many of the chicks that showed it in later years, with a lightening of the area to a less dark brown. The probability that it is an effect of the factor for internal pigment, rather than that it is due to some other factor happening to segregate when the line was inbred, is suggested by the observation, which was carefully confirmed in later years, that the feet, at about a week, were

so much darkened as to appear black rather than dark green. This observation, combined with the fact that the new down pattern only appeared in this line, and in broods which should have contained some homozygotes, give probability to the view that black internal pigment, like Crest, Barred, Polydactyly and Feathered feet, has a special homozygous manifestation. The experiments yield no evidence contrary to this view, but are insufficient to establish it with confidence. The numbers showing normal and extended down plumage have regularly departed from the 1 : 1 ratio which, in the absence of genetic complications, would be expected.

In 1935 the same male, mated with the same hen as before, together with two 1934 daughters having normal down, bred thirty-three chicks, of which eleven had extended pigmentation in the down. In 1936 the same pen gave two with extended pigmentation out of five. On the total of 3 years, only fourteen out of forty-eight showed the down character, a proportion more nearly a quarter than a half.

The attempt to test the abnormal female of 1934 by outcrossing failed in both of the following years. One female with abnormal down from 1935 was successfully outcrossed in 1936, and gave five pigmented young. She was, therefore, probably homozygous, and this test, so far as it goes, supports the view that the extended down pigmentation is an indication of homozygosity.

It may be noted that the homozygous male possessed, when adult, a brown, instead of a black breast, and that the adult plumage of the two females reared from abnormally marked chicks both differed from wild females in the lighter buffish tone of their plumage.

7. Variable dominance shown by early experiments with Black Internal pigment

Proof that the dominance of the factor for Black Internal pigment, whatever its status in the wild fowl, is subject to modification in breed crosses, is afforded by an extensive experiment reported by Bateson and Punnett (1911).

Reciprocal crosses between Silky fowls and Brown Leghorns showed that the latter breed contained a factor, referred to as an inhibitor (I), which reduced the visible pigmentation due to the factor from the Silky. This inhibitor was sex-linked.

Although the experiment was prolonged, and many different crosses were made, it was not carried out in such a way as to exhibit the manifestation in all the genotypes, six in number for females, and nine for males,

produced by combining an autosomal with a sex-linked factor. Most of the broods were classified in three classes, deeply pigmented, slightly pigmented, and unpigmented. It is, however, not clear whether all parts of the body, or perhaps only the feet were referred to in this classification.

The fifteen genotypes are shown in the following plan, in which **G** is used for the gene for black internal pigment, and **I** for the inhibitor.

	Females		Males		
	I–	**i–**	**II**	**Ii**	**ii**
GG	—	Deep	—	—	Deep
Gg	Slight	Usually deep	Slight	Slight	Deep
gg	Unpigmented	Unpigmented	Unpigmented	Unpigmented	Unpigmented

The whole of the data are consistent with the following statements:

(*a*) All **gg** genotypes are unpigmented.

(*b*) **GGi–** females, and **GGii** males are deeply pigmented.

(*c*) **GgI–** females and **GgII** males are slightly pigmented.

(*d*) **GgIi** males are slightly pigmented, with one exception classified as deeply pigmented out of more than 100 (Table XI).

(*e*) **Ggi–** females are nearly always deeply pigmented, but nearly 4% are classified as slightly pigmented.

(*f*) **Ggii** males are apparently always deeply pigmented.

The evidence of the data bearing on statement (*e*) may be summarized by comparing the numbers of deeply and slightly pigmented females with the numbers expected, on the supposition that 3·9% of the genotype **Ggi–** were classified as slightly pigmented.

TABLE IV. BROODS SHOWING THE CLASSIFICATION OF **Ggi–** FEMALES

Reference	Deeply pigmented		Total females
	Expected	Observed	
Table II	38·44	39	40
V	86·97	82	362
VII	58·83	56	60
VIII, IX	59·81	61	61
X	10·09	9	21
XI	100·90	101	105
XII(*a*)	2·88	3	6
XII(*b*)	24·99	26	26
Total	382·91	377	681

produced by combining an autosomal with a sex-linked factor. Most of the broods were classified in three classes, deeply pigmented, slightly pigmented, and unpigmented. It is, however, not clear whether all parts of the body, or perhaps only the feet were referred to in this classification.

The fifteen genotypes are shown in the following plan, in which **G** is used for the gene for black internal pigment, and **I** for the inhibitor.

	Females		Males		
	I–	**i–**	**II**	**Ii**	**ii**
GG	—	Deep	—	—	Deep
Gg	Slight	Usually deep	Slight	Slight	Deep
gg	Unpigmented	Unpigmented	Unpigmented	Unpigmented	Unpigmented

The whole of the data are consistent with the following statements:

(*a*) All **gg** genotypes are unpigmented.

(*b*) **GGi–** females, and **GGii** males are deeply pigmented.

(*c*) **GgI–** females and **GgII** males are slightly pigmented.

(*d*) **GgIi** males are slightly pigmented, with one exception classified as deeply pigmented out of more than 100 (Table XI).

(*e*) **Ggi–** females are nearly always deeply pigmented, but nearly 4% are classified as slightly pigmented.

(*f*) **Ggii** males are apparently always deeply pigmented.

The evidence of the data bearing on statement (*e*) may be summarized by comparing the numbers of deeply and slightly pigmented females with the numbers expected, on the supposition that 3·9% of the genotype **Ggi–** were classified as slightly pigmented.

TABLE IV. BROODS SHOWING THE CLASSIFICATION OF **Ggi–** FEMALES

Reference	Deeply pigmented		Total females
	Expected	Observed	
Table II	38·44	39	40
V	86·97	82	362
VII	58·83	56	60
VIII, IX	59·81	61	61
X	10·09	9	21
XI	100·90	101	105
XII(*a*)	2·88	3	6
XII(*b*)	24·99	26	26
Total	382·91	377	681

The agreement with expectation is seen to be excellent throughout. The forty birds of Table II, the 105 of Table XI and the twenty-six of Table XII (*b*) were all of genotype **GgIi**. From these alone an estimate of five cases out of 171, or 2·92%, slightly pigmented could have been made. The sixty birds of Table VII should have been **GGi-** and **Ggi-** in equal numbers; the four slightly pigmented were presumably all **Ggi-** birds. The similar matings of Tables VIII and IX gave no exceptions. The three types of mating of Tables V, X and XII (*a*) all show genotypes **Ggi-** mixed with other genotypes showing slight or no pigmentation; they all agree with expectation when most of the **GGi-** birds are expected to be deeply pigmented.

The consistent results for the heterozygote in the absence of the inhibitor (**Ggi-**) enable us to investigate the homozygote in the presence of the inhibitor (**GGI-**), for which only indirect data are available. These show some discrepancy, though not to the extreme extent shown by the males.

Table III shows seventy-four deeply to fifty-five slightly pigmented from a mating **GgI-** × **GgIi** which should give among the pigmented birds

$$2\mathbf{GgI-} + 2\mathbf{Ggi-} + 1\mathbf{GGI-} + 1\mathbf{GGi-}.$$

We may estimate the behaviour of the homozygotes containing the inhibitor by differences (Table V):

TABLE V. ALLOCATION OF **GGI-** FEMALES IN TABLE III

	Deeply	Slightly
GgI-	—	43·00
Ggi-	41·32	1·68
GGi-	21·50	—
GGI-	11·18	10·32
Observed total	74	55

Apparently more than half the homozygotes containing the inhibitor show full pigmentation.

The reciprocal cross has the same expectation in the females (Table VI).

TABLE VI. ALLOCATION OF **GGI-** FEMALES IN TABLE IV

	Deeply	Slightly
GgI-	—	18·67
Ggi-	17·94	0·73
GGi-	9·33	—
GGI-	0·73	8·60
Observed total	28	28

In this case the homozygotes appear to be almost completely inhibited.

The mating of Table VI should give the same four genotypes now in equal numbers; there are, however, only forty-nine females classified.

TABLE VII. ALLOCATION OF GGI– FEMALES IN TABLE VI

	Deeply	Slightly
GgI–	—	12·25
Ggi–	11·77	0·48
GGi–	12·25	—
GGI–	−2·02	14·27
Observed total	22	27

There is again in this experiment no evidence of the homozygotes being deeply pigmented. The view that no appreciable fraction show deep pigmentation is, however, scarcely compatible with the data of Table III, for which it would give:

TABLE VIII. TEST OF SIGNIFICANCE FOR TABLE III

	Expected (m)	Observed (a)	$a-m$	$\frac{(a-m)^2}{m}$
Deeply	62·82	74	11·18	1·990
Slightly	66·18	55	−11·18	1·889
Total	129	129		3·879

The value of 3·879 exceeds its 5 % value for one degree of freedom, so that it is probable, though not certain, that even in the female an appreciable fraction of homozygotes carrying the inhibitor were yet classified as deeply pigmented. Since deep pigmentation does not occur among the heterozygotes **GgI–**, this would show that in the presence of **I** the factor **G** was not completely dominant. If the whole of the data for females is used to estimate the proportion of those homozygotes deeply pigmented it appears that this is most probably as high as 17·5 %. With this value the expectations are as follows:

TABLE IX. TEST OF HETEROGENEITY OF DIFFERENT TABLES

		Expected	Observed	Deviation
Table III:	Deeply	66·59	74	−7·41
	Slightly	62·41	55	+7·41
Table IV:	Deeply	28·91	28	+0·91
	Slightly	27·09	28	−0·91
Table VI:	Deeply	26·17	22	+4·17
	Slightly	22·83	27	−4·17

The observed values do not differ significantly from expectation. $\chi^2 = 3{\cdot}188$ for 2 degrees of freedom is exceeded by chance more than once in five times. It is a possible view that the proportion deeply pigmented was uniformly at about $17\frac{1}{2}\%$. More probably perhaps it was higher in the larger experiment, and negligible in the two smaller ones.

The evidence for the males is more decisive. We will first show that the heterozygotes without the inhibitor (**Ggii**) were uniformly classified as deeply pigmented. The relevant types of mating were as follows:

TABLE X. BROODS SHOWING CLASSIFICATION OF **Ggii** MALES

	Deeply pigmented		Total
	Expected	Observed	birds
Table VIII	42	42	42
IX	21	21	21
X	14·5	14	29
XII(*a*)	2·5	1	5
XII(*b*)	18	18	18
Total	98	96	115

So far as the published classification of pigmentation goes, the factor for black internal pigment was completely dominant in the absence of the inhibitor.

With the inhibitor heterozygous (**Ii**) we must consider the classification of the homozygotes (**GGIi**). Table VI gives the classification of the mating **GGi**– × **GgIi** yielding the four genotypes

GGii, **GGIi**, **Ggii** and **GgIi**,

in equal numbers; if ν is the proportion deeply pigmented among the homozygotes (**GGIi**) the expectations are $2+\nu$ deeply to $2-\nu$ slightly pigmented. The observed frequencies are 25 : 20, giving the estimate 22·2 % for ν.

In contrast, Table VII gives the classification for the mating **GgI**– × **GGii** yielding the genotypes

GGIi and **GgIi**.

The expectations are $\nu : 2-\nu$ which with the observed frequencies 24 : 31 gives an estimate $\nu = 87{\cdot}3\%$.

The pigmented birds from Table III **Ggi**–♀♀ × **GgIi** ♂♂ should be of the genotypes

2GgIi + 2Ggii + GGIi + GGii

giving an expected ratio $3+\nu : 3-\nu$ with observed frequencies 51 : 55. Here clearly ν is zero or negligible.

Finally, Table IV gives the result of the mating **GgI**–♀♀ × **GgIi** ♂♂, of which the pigmented young should be

$$2\mathbf{GgII} + 2\mathbf{GgIi} + \mathbf{GGII} + \mathbf{GGIi}.$$

We may assume that **II** genotypes are not more strongly pigmented than the corresponding **Ii** genotype. If in the homozygotes the inhibitor was completely recessive the expectation is still only $\nu : 3-\nu$. With observed values 12 : 42 this gives the estimate $\nu = 66{\cdot}7\,\%$; while if it is supposed that **II** birds are never deeply pigmented, the expectation is $\nu : 6-\nu$ which with $\nu = 100\,\%$, is only 9 : 45 against 12 : 42 observed.

It is evident that the proportion of homozygotes heterozygous for the inhibitor varies in these experiments nearly from 0 to 100 %; i.e. that **G** varies from a dominant to an almost complete recessive. For thoroughness I have worked out the best fitting frequency (*a*) on the supposition that **II** birds are never deeply pigmented, and also (*b*) on the supposition that they are as frequently deeply pigmented as are **Ii** birds. In both cases it appears that an appreciable fraction of **GG** birds must be deeply pigmented, when the corresponding **Gg** birds are not so, so that the "inhibitor" itself acts powerfully as a dominance modifier; and that the data are significantly heterogeneous in respect of the degree of dominance shown in different matings. Probably many other factors affecting dominance were segregating in the second inbred generation.

TABLE XI. DISCREPANCIES AND AMOUNTS OF INFORMATION FROM DIFFERENT EXPERIMENTS

GGIi ♂♂ 72·82 deeply pigmented.			**GGII** ♂♂ all slightly pigmented.		
Table VI	$25/(2+\nu)$	9·16355	Table VII	$24/\nu$	32·95798
	$20/(2-\nu)$	15·72574		$31/(2-\nu)$	24·37490
Discrepancy		−6·56219	Discrepancy		+8·58308
Information	$45/(4-\nu^2)$	12·969	Information	$55/\nu(2-\nu)$	59·387
Table III	$51/(3+\nu)$	13·67952	Table IV	$12/\nu$	16·47899
	$55/(3-\nu)$	24·20988		$42/(6-\nu)$	7·96692
Discrepancy		−10·53036	Discrepancy		+8·51207
Information	$106/(9-\nu^2)$	12·515	Information	$54/\nu(6-\nu)$	14·066

Summary of four experiments ($\nu = 72{\cdot}82\,\%$)

	Discrepancy D	Information I	D^2/I
Table VI	−6·56219	12·969	3·3204
Table VII	+8·58308	59·387	1·2405
Table III	−10·53036	12·515	8·8604
Table IV	+8·51207	14·066	5·1511
Total	+0·00260	98·937	−0·0000
$\chi^2(n=3)$			18·5724

TABLE XII. DISCREPANCIES AND AMOUNTS OF INFORMATION FROM DIFFERENT EXPERIMENTS

GGIi ♂♂ and GGII ♂♂ both 64·81 deeply pigmented.

Table VI	$25/(2+\nu)$	9·44073	Table VII	$24/\nu$	37·03132
	$20/(2-\nu)$	14·79399		$31/(2-\nu)$	22·93069
Discrepancy		−5·35326	Discrepancy		+14·10063
Information	$45/(4-\nu^2)$	12·570	Information	$55/\nu(2-\nu)$	62·630
Table III	$51/(3+\nu)$	13·97988	Table IV	$12/\nu$	18·51566
	$55/(3-\nu)$	23·38535		$42/(3-\nu)$	17·85790
Discrepancy		−9·40547	Discrepancy		+0·65776
Information	$106/(9-\nu^2)$	12·354	Information	$54/\nu(3-\nu)$	35·427

Summary of four experiments ($\nu = 64{\cdot}81\,\%$)

	Discrepancy D	Information I	D^2/I
Table VI	−5·35326	12·570	2·2798
Table VII	+14·10063	62·630	3·1746
Table III	−9·40547	12·354	7·1607
Table IV	+0·65776	35·427	0·0122
Total	−0·00034	122·981	−0·0000
$\chi^2(n=3)$			12·6273

For 3 degrees of freedom the 1 % value of χ^2 is only 11·341, so that on both hypotheses heterogeneity in dominance is strongly significant.

On the one extreme view the proportion of homozygotes (heterozygous for the inhibitor) classified as deeply pigmented is 72·82 %. Since scarcely any double heterozygotes are so classified the factor **G** is certainly not here acting as a dominant. Moreover the heterogeneity of the different sets ($\chi^2 = 18{\cdot}57$, for 3 degrees of freedom) shows that the degree of dominance varies very much in the different cases observed. At the other extreme, when **GGII** and **GGIi** birds are supposed to be equally frequently deeply pigmented, the percentage for those two genotypes comes to 64·81 %, with, in this case, somewhat less evidence of heterogeneity $\chi^2 = 12{\cdot}63$. On any view, therefore, the evidence of the males is decisive in showing that dominance of the factor for black internal pigment is greatly affected by the "inhibitor", and probably much affected also by other factors segregating in the same cross.

8. PILE (DOMINANT WHITE)

The factor commonly known in the literature of poultry genetics as "Dominant White", I propose to refer to as Pile (**Pi**), since it is not a

dominant. Moreover, when acting alone on the wild constitution, it does not produce a completely white bird; but rather the pattern known by fanciers as "Pile", in which, though the large feathers are white, the wings of the males are a deep chestnut, while yellow and brown coloration is distributed on the heads and necks, and especially the breasts of females.

Some difficulty was encountered in introducing Pile into wild stock, since all the domestic birds available carrying this factor were somewhat large. However, in 1930, broods were obtained by reciprocal crosses using a small White Leghorn female, and a male of the same breed which was sexually mature at less than six months old. As has often been observed in Leghorn crosses the young were not wholly white, but irregularly suffused with yellow, and marked with black spots. One pen of pullets from this cross mated in 1931 to a wild cock gave twenty-one Pile to fifteen normal, counting as normal all young without the Pile factor, irrespective of the black and barred, which were also segregating in this cross. Seven more Pile young were bred in this year from a mixed pen in which both white and coloured mothers were used.

In 1932 again eight Pile females were crossed with a wild male. Although many eggs were laid only twenty-eight chicks were hatched, fifteen Pile to thirteen normal, and of these only two Pile females survived to lay in 1933. These gave a single brood of six Pile to three normal. Of these one Pile male and three Pile females were available for interbreeding in 1934. In this factor, therefore, as with Feathered feet and Black Internal pigment, the intercross was made after only four generations crossing with wild.

The intercross mating gave, in five broods, twenty-one chickens, of which only three lacked the Pile factor. Of the eighteen Piles, however, only two males and two females attained adult plumage. Of these two, one male and one female attracted attention by having less yellow on the head and neck than was usual, and were judged to be possibly homozygous. In the following year the male was mated with normal females, giving a brood of six Pile chicks. Unfortunately, he died before the chicks were hatched, and before it was realized that homozygotes lack the small coloured specks on the large feathers of the wings and tail, found regularly in heterozygotes. In consequence this important indication was not noted. His brother proved to be heterozygous by a similar test mating, and in this case the feathers were speckled in the usual manner.

The significance of these small spots on the feathers was first noted by A. E. Brandt, who was kindly assisting the author in 1935. They do not appear on the first true plumage, so that at this stage both heterozygotes and homozygotes have clean, or unspecked feathers. In the second plumage,

however, heterozygotes invariably show speckling on almost every feather in the tail and wing primaries, while they are completely absent from homozygotes. Brandt has already published the evidence, based on the examination of numerous purebred and crossbred White Leghorns, on which this conclusion was based.

The interbreeding was repeated in 1935 with the addition of two 1934 pullets to the original pen, but only gave eleven Pile and four normal young. Although one of the five hens in the pen this year was a homozygote it is probable that she did not breed, as the attempt to breed from her in 1936 failed completely. A third homozygote did appear, however, among the 1935 birds, though she also failed to breed in 1936. Had these two years been favourable, as judged by success in other pens, the failure of these two hens to breed would give a presumption that homozygosity in this factor was associated with infertility. In reality, however, all the strains having a high proportion of wild blood were extremely disappointing in these two years, and many other individual birds, besides these two, failed to provide the test broods.

The most definite diagnostic of homozygosity in this factor is undoubtedly supplied by the small pigmented areas on the larger feathers. This indication is the more valuable as it is available in ordinary breed crosses, and will make linkage tests materially easier. In birds of nearly wild ancestry, also, the homozygote is distinguishable by the paler coloration of the head and neck, and, in the case of the females, by a very striking difference in the depth of pigment on the breast.* Pile is not, like barred and feathered feet, more nearly recessive than dominant, on the contrary the heterozygote differs more strikingly from the wild type than from the homozygote; but it differs so decidedly from the latter in adult birds that dominance must be regarded as definitely incomplete.

9. General summary

The experiments with wild *Gallus* have dealt with seven reputed dominants among the mutant genes known in the domestic fowl. They have shown that in six of these cases dominance is far from complete. The seventh case is that of Rose comb, for which the present data are inconclusive, although on the basis of the observations presented a very exact

* Apparently this difference also is sometimes observable in domesticated breeds, for Punnett, p. 142, observes that "Breeders of exhibition piles recommend the cross with the black-red to deepen the colour of the orange markings. Probably this is because the depth of the orange is affected in a bird which is homozygous".

determination of the quantitative degree of dominance should soon be possible in domestic material. In some cases the incompleteness of dominance is clearly demonstrated from my own material alone, in others the demonstration receives material support from the data of others.

Three of the factors concerned affect pigmentation, Barred plumage, Pile, and Black Internal pigment. In all these three dominance is incomplete; in the case of Bar the mutant gene is more nearly recessive than dominant. With Bar and Pile the homozygous manifestation is unmistakable. I have not been able to determine whether the peculiar down pattern observed is a homozygous manifestation of Black Internal pigment, but the data of Bateson and Punnett show that dominance in this factor is certainly much influenced by other genetic factors. The apparent dominance of Bar in domestic breeds appears to be largely due to its association with a factor for black. It is possible that the apparent dominance of Pile may be enhanced by association with Bar and Silver.

The four other factors are structural. These are Rose comb, Crest, Polydactyly and Feathered feet. It is remarkable that all these affect the skeleton. Rose comb widens the frontal bone between the orbits; it is not yet known whether this widening is equal in homozygous and in heterozygous birds, or greater in the homozygote. Rose comb may therefore be a true dominant. Crest, when homozygous, not only enlarges the tuft of feathers on the head, but produces an obvious cerebral hernia. Its apparent dominance in the Silky breed appears to be due to a suppression by modifying factors of this dangerous manifestation. In polydactyly the bones of the foot in wild stock are nearly intermediate in the heterozygote between their structures in the two homozygotes. In breed crosses dominance in this factor appears to be widely variable. In Feathered feet the homozygote differs in many respects from the heterogyzote, notably, in my material, in the brachydactyly or dwarfing of the fourth toe, and in the extent and nature of the feathering. Apparent dominance may have been produced in some breeds by genes capable of mitigating this deformity. In both Feathered feet and Polydactyly the heterozygote is often indistinguishable from the normal, as with complete recessives.

Regarding these factors as a group they appear to be quite analogous to the imperfect "dominant" mutations known as such in *Drosophila*. It must be remembered that they were chosen out of the material available in poultry as the best authenticated dominants known. Earlier work has shown the incompleteness of dominance in many other factors in poultry such as Pea comb, Frizzled plumage, Rumpless, Silver, and Spangled, in which dominance was at first postulated, and in one case, the Andalusian

Blue, in which absence of dominance was recognized from the first. An inevitable conclusion from the results presented is that the wild species from which domestic poultry are derived provides no exception to the genetical situation found in other organisms, in which, while completely recessive mutant genes are common, complete dominance of the mutant is absent or exceptional. The striking point in the genetics of fowls is the frequency of incomplete dominants as compared with complete recessives (a consequence presumably of the conditions on which domestication was initiated), and the frequency with which apparent dominance has been produced, or enhanced, by the introduction of additional factors into the domestic breeds.

References

Bateson, W. 1909 "Mendel's Principles of Heredity." Cambridge.
Bateson, W. and Punnett, R. C. 1911 *J. Genet.* **1**, 185–203.
Bond, C. J. 1920 *J. Genet.* **10**, 87–91.
Brandt, A. E. 1936 *J. Hered.* **27**, 79–82.
Darwin, C. 1868 "Variation of Animals and Plants under Domestication", Chap. 7.
Davenport, C. B. 1906 *Publ. Carneg. Instn*, No. 52.
Dunn, L. C. and Jull, L. H. 1927 *J. Genet.* **19**, 27–63.
Dunn, L. C. and Landauer, W. 1930 *J. Genet.* **22**, 95–101.
— — 1936 *J. Genet.* **33**, 401–5.
Fisher, R. A. 1928 *Amer. Nat.* **62**, 115–26.
— 1928 *Amer. Nat.* **62**, 571–4.
— 1930 *Amer. Nat.* **64**, 385–406.
— 1930*a* "Genetical Theory of Natural Selection." Oxford Univ. Press.
— 1931 *Biol. Rev.* **6**, 345–68.
— 1935 *Philos. Trans.* B, **225**, 195–226.
Ford, E. B. 1930 *Amer. Nat.* **64**, 560–5.
Hutchinson, J. B. 1931 *Amer. Nat.* **65**, 376–9.
Hutchinson, J. B. and Ghose, R. L. M. 1937 *J. Genet.* **34**, 437–46.
Hutt, F. B. 1933 *Genetics*, **18**, 82–94.
Landauer, W. 1932 *Biol. gen.* **8**, 219–26.
Punnett, R. C. 1923 "Heredity in Poultry." London: Macmillan and Co.
Punnett, R. C. and Pease, M. S. 1929 *J. Genet.* **22**, 341–66.
Serebrovsky, A. S. and Petrov, S. G. 1930 *J. exp. Biol.* (Russian), **6**, 157.
Suttle, A. D. and Sipe, G. R. 1932 *J. Hered.* **23**, 135–42.
Timofeeff-Ressovsky, N. W. 1934 *Z. indukt. Abstamm.- u. VererbLehre*, **66**, 319–44.