

STUDIES OF MULTIPLE ALLELOMORPHIC SERIES IN THE HOUSE-MOUSE¹

I. DESCRIPTION OF AGOUTI AND ALBINO SERIES OF ALLELOMORPHS

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THE discovery of series of multiple allelomorphs in a large number of animals and plants has raised questions of considerable interest regarding the manner in which the genes influence development. The evidence shows in many cases that these series have arisen through repeated mutations at the same locus in the chromosome, and that the members of such a series represent different alternative conditions of the gene. The phenotypic effects of the allelomorphs of the same series have been found to be frequently similar in kind, affecting the same characters in similar ways, and these effects often appear to differ from each other chiefly in degree or quantity. The evidence for these statements has been collated and critically reviewed by Stern (1930), who has also called attention to certain significant exceptions to the simple rule of qualitatively similar effects of multiple allelomorphs.

As part of a general physiological theory of heredity, Goldschmidt (1927, and previous papers) has assumed that, since the effects of allelomorphs differ in general only quantitatively, these effects are due to quantitative variations in the gene, the effect of a gene on development being in proportion to its quantity. The latter and more general assumption is based in part on the proportionality which exists in many cases between the numbers of one allelomorph present in the individual and the quantity of effect produced. The assumption that genes vary quantitatively cannot be tested directly by evidence from phenotypic effects; but the special case which should follow from the general principle, namely, that the *effects* of changes in the same gene bear a purely quantitative relation to each other, is a question of fact and is susceptible of direct test.

Critical evidence on the phenotypic effects of multiple allelomorphs should of course include quantitative measurements of the characters

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affected, and these are generally difficult to obtain. A second requirement is that the individuals containing different members of the allelomorphic series should be comparable in respect to other genes and to other conditions.

The results of the few analyses in which these requirements have been at least partially met are not entirely conclusive in respect to the question at issue. Wright's (1925) measurements of the intensities of black and yellow pigment in the hairs of guinea-pigs with different combinations of the albino series of allelomorphs showed a general reduction from the intense colour of the wild type (**C**) through intermediate stages, brought about by combinations of three intermediate allelomorphs (**c^k**, **c^d**, **c^r**), to the nearly white coloration of the albino (**c^a**). The order of effect of these genes was slightly different for black and for yellow. Wright assumed that the genes of this series determined different rates of one process fundamental to pigment production, the irregularities in the order of effect on different pigments being due to threshold differences brought about by other genes. The gross effects of the genes appeared to differ quantitatively, but the nature of the changes in the pigments could not be described by the methods used.

Dobzhansky (1930) compared the effects of three allelomorphs in *Drosophila melanogaster* (stubble, stubbloid and wild type) on bristle number and length, wing length and leg length. The order of quantitative effect of the three allelomorphs on these different structures was found not to be the same, from which Dobzhansky concluded that the effects of the allelomorphs do not differ only quantitatively. Goldschmidt (1932), however, has pointed out that such differences in order of effect do not constitute evidence against the quantitative hypothesis, since they may be consequences of differences in the rate and order of differentiation of the different characters affected, processes which may occur independently of the allelomorphs in question.

The effects on eye size of the Bar allelomorphs in *D. melanogaster* have been analysed by Sturtevant (1928). Although the effects of each allelomorph bear a quantitative relation to the numbers of that allelomorph present (e.g. 0 to 4 Bar genes), one allelomorph (Bar) is fully dominant to another (Infrabar) in all combinations in which the two allelomorphs have been found, as has been pointed out by Wright (1929). Since in combinations with infrabar, one, two or three bar genes give the same quantitative effects on eye size, it seems impossible to conclude that the relations between the effects of these genes are purely quantitative. Whether relations of "allelomorphs" at the bar locus may be regarded

as typical of allelomorphs in general is doubtful in view of the unequal crossing-over known to occur in this region.

Other cases have been discussed by Stern, who has concluded that the evidence at present does not permit of a decision between the alternative hypotheses of qualitative and purely quantitative differences in the effects of multiple allelomorphs.

It should, however, be possible to throw some additional light on this question by comparing the actual products affected by the allelomorphs. If these are found to differ only in quantity in the different compounds of an allelomorphic series, the assumption of qualitative differences is unnecessary. If differences in kind also appear, then the need for further analysis is indicated, which must determine whether such differences could have arisen by quantitative variations in other preceding products or reactions.

As materials for studying the nature of the relationships between the effects of allelomorphs, two series of multiple allelomorphs in mice affecting the melanin pigments of the hair seemed favourable. In studying such colour effects there is at once the possibility of making objective measurements of the quantity and of the quality of pigment present, and of eventually making direct observations of some of the chemical steps by which pigments are produced, since the processes involved in the formation of melanin are known in outline.

THE AGOUTI SERIES

Both series of allelomorphs have been known for several years, although neither has been thoroughly described (cf. Dunn, 1928 and Keeler, 1931). One of these, known as the "Agouti" series, affects chiefly the relative distribution of black (or brown) and yellow pigments over the body and in the individual hairs. It consists of the following members (the effects on wild type only are described):

- A^Y**: all hairs yellow with occasional dark granules. Dominant to all other members of the series and lethal when homozygous. Shows tendency to become fat and sterile with age and acts as a modifier of white spotting, these effects not being shared by other members of the series.
- A^L**: agouti with light belly. Hairs on back with narrow yellow band near the tip. Belly hairs light yellow for most of their length. Sometimes referred to as agouti white belly, **A^w**, but known now not to affect intensity of yellow. Dominant to **A**, **a^t** and **a**.

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- A** or + : agouti with grey belly, the wild type of *Mus musculus*. Hairs on both back and belly black with yellow band near tip. Dominant to **a**; compound **Aa^t** is agouti with yellow belly.
- a^t**: black-and-tan; back black; belly yellow with dark patch on throat. Dominant to **a** (Dunn, 1928).
- a**: non-agouti, black.

Although extensive evidence shows that these genes segregate as allelomorphs, their relations to each other are in some respects unusual. The peculiar effects of **A^y** on pigment, viability and spotting suggest that this at least may not be an allelomorph but possibly a deficiency so near to the agouti locus that it shows no crossing-over with it. **a^t** seems to bear the same relation to black which **A^l** bears to wild-type agouti, that is each allelomorph changes the belly colour to yellow or lighter shade, and it has been suggested by Pincus (1930) that a mutation closely linked to the agouti locus has occurred in an agouti stock resulting in light-bellied agouti and in a black stock resulting in light-bellied black (black-and-tan). No evidence for this exists, since crossing-over between the assumed light-belly mutation and the agouti locus has not been observed.

For the objects we have had in mind, the agouti series does not provide the most favourable material, and we have used it chiefly to provide different backgrounds against which to observe the action of another series of allelomorphs. For present purposes it is immaterial whether the agouti members are "good" allelomorphs or not. We shall present later some evidence on the quantities of pigment found in various members and shall then discuss this series in more detail.

THE ALBINO SERIES

A second series of four allelomorphs is known in mice, affecting the intensities of both black and yellow pigments in the hairs. It consists of the following members (the effects described are those of homozygotes on wild-type agouti):

- C** or + : wild type—full intensity of black, brown and yellow. Completely dominant to other members. Eyes dark.
- c^{ch}**: ruby or chinchilla dilution. Sometimes referred to as **c^r**.¹ Black reduced to dull black or very dark slate; yellow reduced to

¹ The original symbols **c^r** and **c^d** have been replaced here by **c^{ch}** and **c^h** in order to avoid confusion with albino allelomorphs **c^r** and **c^d** in the guinea-pig (Wright, 1925), which were discovered earlier and in which **c^r** represents the lighter condition.

- light yellow or cream. Eyes dark. First described by Feldman (1922).
- c^h : Himalayan dilution. Sometimes called extreme dilution c^d . Black reduced to pale brownish grey; yellow reduced to white. Eyes dark. First described by Detlefsen (1921).
- c^a : complete albinism; no pigment in either hair or eyes.

The experiments of Detlefsen and of Feldman indicated that the dilute mutant forms (c^{eh} and c^h) were probably allelomorphs of the long-known albino mutation (c^a). Each was completely recessive to the normal condition (C) and formed compounds intermediate in colour when crossed with c^a and with each other. The dominance order appeared to be $C \gg c^{eh} > c^h > c^a$.¹ Extensive experiments were not made to test this relationship and to exclude the possibility that the differences in density of pigment found might be due to other genes (modifiers). The effects of these genes in all the compounds and in combinations with other genes have not been described previously.

In preparing material for the present study it was thus necessary (1) to confirm the fact of allelomorphism of the four factors involved, (2) to study the effects of these on coat colour in various combinations, and (3) to prepare the combinations on as nearly comparable genetic backgrounds as possible, so that the effects of genes outside of the albino series might be minimized. Combinations of C , c^{eh} , c^h , and c^a in homozygous condition, and in the compounds $c^{eh}c^h$, $c^{eh}c^a$, c^hc^a , a total of seven genotypes, were made with the five agouti allelomorphs, other colour genes being of the wild type (B , black; D , dense; P , dark eyes, etc.). This yielded thirty-five combinations, in which the effects of the albino allelomorphs could be observed on backgrounds varying in pattern from yellow to black. The gene brown (b) was then substituted for black (B) in the seven albino combinations with A^L and a of the agouti series, which yielded fourteen combinations in which the effects of the albino allelomorphs on brown and yellow could be observed. A few combinations of c^{eh} and c^h with other colour-dilution genes (d , maltese dilution and p , pink-eyed dilution) have been made, but all of the possible combinations have not yet been prepared.

SOURCES OF MATERIAL

The c^{eh} gene was obtained from two white-bellied agouti animals kindly supplied by Prof. W. E. Castle in June 1928. These were descendants of the original c^{eh} animals described by Dr Feldman and con-

¹ \gg indicates complete dominance, $>$ indicates incomplete dominance.

formed to his description. They proved to be $A^L A^L B B c^{ch} c^{ch}$. These were crossed with inbred stocks of black-and-tan, yellow, agouti, and black obtained in 1927 from English fanciers and maintained in our laboratory.

The c^h gene was obtained from three extreme dilute animals kindly supplied by Dr H. W. Feldman in March 1930. These proved to be $A A b b c^h c^h$ and gave rise to a line of this genotype which was inbred for two years and was crossed with other stocks in preparing the various combinations with c^h .

The c^a gene was obtained from albinos which appeared in a stock of English blacks. In making combinations involving brown, the Bagg strain of albinos was used, since this is known to be $A A b b c^a c^a$.

Thus a number of different stocks were used in making the first combinations, and these may have differed in minor modifying factors affecting colour intensity, although the results show that the effects of such other genes, except in two cases, were relatively unimportant. The relations between the albino allelomorphs were studied chiefly in combinations with A^L and were extracted after successive back-crosses to an inbred stock of $A^L A^L B B C C$ (our line 101 yellow-bellied agouti), which constitutes also the chief hereditary background of the other combinations. This standard stock has been brother-sister inbred in our laboratory for fifteen generations and has shown no hereditary variation in depth of colour.

From the breeding experiments required to produce these combinations were obtained data confirming the allelomorphism of C , c^{ch} , c^h , and c^a , and a preliminary gross description of the effects of these genes on yellow, black and brown pigments.

ALLELOMORPHISM OF THE c GENES

The ratios resulting from crosses involving members of this series need not be quoted in detail, since no exceptions to the expectations based on the assumption of allelomorphism have been found.

Crosses of $C C$ animals (with B or b , combined with A^Y , A^L , A , a^t or a) with $c^{ch} c^{ch}$, $c^h c^h$ and $c^a c^a$, containing any combination of these other genes, show complete dominance of C in F_1 and regular monohybrid ratios in F_2 and back-crosses. No effects of c^{ch} , c^h or c^a on viability have been noted. Crosses of $c^{ch} c^{ch}$ animals containing the genes for black (B) in combination with A^L , A , a^t or a , with $c^h c^h$ animals containing these combinations produce in F_1 compounds $c^{ch} c^h$ which are intermediate in colour between the $c^{ch} c^{ch}$ and $c^h c^h$ parents,

and in F_2 segregation occurs in the ratio of $1/4$ $c^{ch}c^{ch}$; $1/2$ $c^{ch}c^h$; $1/4$ c^hc^h . In agoutis, A^L or A , the separation of these three types is easily made. The $c^{ch}c^{ch}$ agoutis are somewhat lighter than type, the bases of the hairs being dull black and the tips light cream colour; in $c^{ch}c^h$ the bases of the hairs are medium brown, the tips white; while in c^hc^h , black is reduced to very light brown or tan, and yellow is reduced to white. In black-and-tans ($a^t a^t BB$) separation is also clear. C is shiny black with yellow belly, $c^{ch}c^{ch}$ is dull black with white or nearly white belly; $c^{ch}c^h$ is medium brown with white belly; and c^hc^h is very light brown or tawny with white belly. In blacks (aaB) separation of $c^{ch}c^{ch}$ from C is sometimes difficult, although with practice $c^{ch}c^{ch}$ may be distinguished by the lesser saturation of black which tends to be dull and slate coloured near the base of the fur, and especially by the shade of the hairs lining the ears which in C forms are yellowish, in $c^{ch}c^{ch}$ creamy or nearly white. $c^{ch}c^h$ mice with aaB are brown, c^hc^h black, much like the chocolate coloration of abC mice.

Crosses of $c^{ch}c^{ch}$ animals containing also the gene B in combination with A^L , A , a^t or a with albinos produce in F_1 compounds $c^{ch}c^a$, which are identical in appearance with the $c^{ch}c^h$ animals described above, and in F_2 segregation of $c^{ch}c^{ch}$, $c^{ch}c^a$ and c^ac^a is readily discernible in a $1 : 2 : 1$ ratio. In none of the combinations examined have we been able to find any constant differences in appearance between $c^{ch}c^h$ and $c^{ch}c^a$ animals. As shown in Part III, c^h and c^a have about the same effect in reducing the total quantity of pigment when combined with c^{ch} .

Crosses of c^hc^h animals containing also B together with A^L , A , a^t or a with albinos produce in F_1 compounds c^hc^a which are nearly white, but always show some traces of pigment giving them a slight dusky tone. In F_2 three classes appear as $1/4$ c^hc^h , $1/2$ c^hc^a , $1/4$ c^ac^a . The two latter classes can always be separated by eye colour, c^hc^a having dark eyes and dark pigment ring at birth, c^ac^a having pink eyes and no pigment ring. c^hc^h and c^hc^a are usually easily separable by the greater darkness of c^hc^h , but in some combinations the two may overlap and progeny tests must be made.

These results show that C , c^{ch} , c^h and c behave as allelomorphs, only two of these genes ever being present in any individual and only one in any gamete. No reversion to full colour occurs after crosses between c^{ch} , c^h or c^a forms in any combination. The dominance order of effect on coat colour in combinations with B and either A^L , A , a^t or a is $C \gg c^{ch} > c^h > c^a$.

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COMBINATIONS OF THE **c** SERIES WITH BROWN

When the members of the **c** series are combined with brown (**b**) instead of black (**B**), their relative effects on coat colour are somewhat different. As in the case of the black combinations, **C** appears to be completely dominant to **c^{ch}**, **c^h** and **c^a**. In **A^Lb**, and **Ab** combinations, **c^{ch}c^{ch}** is distinguished from **C** only by the lighter shade of the yellow band on the back hairs and by the lighter shade of the yellow belly hairs. In these parts **C** is yellow, **c^{ch}c^{ch}** is cream. The brown parts of the hair are alike in **C** and **c^{ch}c^{ch}**. The separation of **Abc^{ch}c^{ch}** from **AbC** cannot always be made with certainty. Dilute brown agoutis (**A^Lbhc^hc^h** and **Abbc^hc^h**) are, however, easily distinguished from brown agoutis (**A^L** or **AbbC**). The brown pigment in **c^hc^h** forms is reduced to light brown or tan; and the yellow parts appear white.

Chinchilla dilute brown-and-tan animals (**a^ta^tbbc^{ch}c^{ch}**) resemble full-coloured brown-and-tans (**a^ta^tbbC**) in the colour of the back, which is full brown or chocolate in both forms. In the **C** forms, however, the belly colour is yellow; in **c^{ch}c^{ch}** it is light cream colour or nearly white. Extreme dilute brown-and-tans (**a^ta^tbbc^hc^h**) are very light brown dorsally and clear white ventrally.

In combination with non-agouti (**a**) and brown (**b**) the genotypes **C**, **c^{ch}c^{ch}** and **c^{ch}c^h** are indistinguishable. **c^{ch}** even in compound with **c^h** does not visibly dilute brown. **c^{ch}c^a** is slightly lighter brown than **C** but cannot always be distinguished from it; **c^hc^h** is definitely lighter than **C**, of about the shade of **c^hc^h** black. In all brown combinations **c^hc^a** is generally white with brown eyes, so that as far as coat colour is concerned **c^a** acts as a dominant to **c^h**. However, we found **c^hc^a** browns from one family which did develop some light brown pigment in the coat, in a few cases almost as much as appears in **c^hc^h** browns. From the **c^hc^a** browns, dark **c^hc^h** browns were isolated and inbred and showed a monohybrid difference from the normal light **c^hc^h** browns. There is thus at least one other gene independent of the **c** series which affects the intensity of pigment. This gene is being studied further. Leaving aside the effects of such genes, the dominance order of the **c** genes in their effect on brown is probably about as follows:

$$\mathbf{C} = \mathbf{c}^{\mathbf{ch}} \gg \mathbf{c}^{\mathbf{h}} = \text{or} > \mathbf{c}^{\mathbf{a}}.$$

COMBINATIONS OF THE **c** SERIES WITH YELLOW **A^y**

All combinations of the **c** genes with yellow (**A^y**) have not yet been obtained on comparable genetic backgrounds, due to the difficulty of standardizing the darkening genes which exist in many strains of mice,

and when introduced into yellow produce "sooty" yellow, sable, and similar variations in darkness. Preliminary results from experiments in which combinations of A^y , B and the c genes are being extracted from an inbred agouti stock in which such modifying genes have been standardized show (1) that C is fully dominant to c^{ch} , c^h and c^a ; (2) that c^{ch} has a considerable effect on yellow, reducing it to a pale but still clear yellow shade in $c^{ch}c^{ch}$; (3) that c^h entirely prevents the appearance of yellow, $A^yc^hc^h$ being clear white. The compound $A^yc^{ch}c^a$ appears to be white as is also c^hc^a . $c^{ch}c^h$ has not yet been obtained.

The order of effect on yellow is probably

$$C \gg c^{ch} > c^h = c^a.$$

COMBINATIONS OF c SERIES WITH p

A few combinations of other colour genes with those of the c series have been obtained but not extensively studied as yet. The gene p (pink eye) is known to have a considerable diluting effect on black pigment, somewhat less effect on brown, and apparently none at all on yellow. $AppBC$ (pink-eyed black agouti) is superficially yellow, but the bases of the hairs are light slate colour. $AppBc^{ch}c^{ch}$ is creamy buff colour, much lighter than $APBc^{ch}c^{ch}$, due apparently to the cumulative diluting effect of c^{ch} and p on black and the diluting effect of c^{ch} alone on yellow. In the present stock of $AppBc^{ch}c^{ch}$, the yellow appears to be somewhat more intense than the yellow in $A^yPBc^{ch}c^{ch}$. $AppBc^{ch}c^a$ also shows traces of yellow pigment of a light cream shade, and in $APBc^{ch}c^a$ yellow is also reduced to cream. A^L or A with $ppBc^hc^h$, $aappBc^hc^h$, $aappbbc^hc^h$ and the c^hc^a compounds of these types are all clear white with pink eyes indistinguishable from full albinos. Since the dark-eyed (P) forms of these genotypes develop considerable dark pigment (black or brown) it is apparent that c^h and p have cumulative effects on the dilution of these pigments. c^h appears to inhibit yellow entirely both in combination with P and with pp . From these as yet incomplete observations the order of effect of the c genes when combined with p appears to be:

- (1) on black $C \gg c^{ch} > c^h = c^a$.
- (2) on yellow $C \gg c^{ch} > c^h = c^a$.

COMBINATIONS WITH d

The gene d (maltese or blue dilution) reduces black to blue-grey and yellow to cream. One combination of this gene with c^{ch} has been made up, $A^Ld d c^{ch}c^{ch}$. This is lighter than $A^LBDc^{ch}c^{ch}$. The black parts

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of the agouti pattern are light blue; the yellow parts are white or nearly so; so that c^{ch} and d appear to have cumulative effects on black and possibly on yellow.

SUMMARY

From these observations the genes of the c series in mice appear to dilute both black and yellow pigments in the hair. Yellow is more affected than black, being markedly diluted by c^{ch} , and entirely suppressed by c^h and c^a . Black appears to be but little affected by c^{ch} , considerably diluted by c^h , and eliminated only by c^a . Brown seems not to be affected at all by c^{ch} , and although diluted by c^h is relatively less affected than black by this gene. A rough description of the relative order of visible effects of these genes on these three colours is given below:

	C	Cc^{a1}	$c^{ch}c^{ch}$	$c^{ch}c^h$	$c^{ch}c^a$	c^hc^h	c^hc^a	c^ac^a
Yellow	4	4	2	?	0.5	0	0	0
Black	4	4	3	2	2	1	0.5	0
Brown	4	4	4	4	3	2	0	0

(or 0.5)

¹ $c^a = c^{ch}, c^h$ or c^a .

In this table the density of the pigment in wild type ($C+$) is represented by 4, the apparent relative reduction in density by 3, 2, etc. These are based on gross estimations and not on measurements.

The c genes affect these pigments in the same order, i.e. C , c^{ch} , c^h , c^a ; each effect which is apparent is of the same nature, to reduce the intensity of the pigments.

The effects of these genes are thus essentially similar to those of the albino allelomorphs in the rat and rabbit, and especially in the guinea-pig where they have been intensively studied by Wright (1925, 1927). A more detailed comparison with the other rodent series will be made after the quantitative data on the mouse have been presented.

As one examines the hair colours in the combinations in these several series, the impression is one of a general reduction in *quantity* of pigment from $C \rightarrow c^a$. This appearance raises the question whether all differences brought about by the members of this series of allelomorphs can be adequately described in terms of the quantity of pigment present in each member, or whether mutations at this locus also effect other changes in the pigments.

In order to answer this question it is necessary to *measure* the actual *amounts* of pigment present in different members of the series; and to search for other measurable effects of these genes on pigment. The first

step in such a study was to develop a technique for the extraction, purification and estimation of the amount of melanin pigment which is responsible for the coloration of the hairs. (In the following report only the black and brown pigments will be considered, since we have not yet developed a comparable quantitative technique for measuring the amounts of yellow pigment.) The melanin obtained from each member was then described in two other ways, independently of the amount present. First the form and sizes of the pigment granules in which melanin is organized were measured, and second the characteristics of the melanin from each member were studied in solution. The chief measure found useful in this study was colour density per unit of concentration, as measured by relative light absorption in a colorimeter.

In the following paper of this series these techniques are described in detail, since the methods which we have developed appear to be of general usefulness for quantitative work on pigments. The results obtained to date will be given in a third paper which will also contain a preliminary interpretation of the action of the genes of the c series on hair pigments.

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