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REVERSION IN GUINEA-PIGS AND ITS EXPLANATION.

By W. E. CASTLE,

Professor of Zoology in Harvard University,
Research Associate of the Carnegie Institution of Washington.

Paper No. 18, Station for Experimental Evolution at Cold Spring Harbor, New York.

REVERSION IN GUINEA-PIGS AND ITS EXPLANATIO

In 1905 I showed that when black-coated guinea-pigs of pure race mated with red-coated ones only black-coated young are ordinarily produc and that if such young are in turn mated with reds, both black young and ones are obtained. In other words, black is a mendelian dominant to The fact was, however, noted that occasionally the cross of black with causes reversion to the agouti or wild type. But this may be regarded a modified condition of black, since the hairs of the agouti animal contain bl pigment, but disposed in a definite pattern with red, the entire hair being bl except a terminal or subterminal band of red (or yellow).

An examination of the tables of matings published at that time shows t all the agouti animals so produced were the progeny of a single red anin ♂2054. This animal produced black young as well as agouti ones in cros with black, so it was not clear to what the reversion was due. By a study the progeny of this animal the matter was later cleared up. The black you were found never to produce agouti young in crosses with any red anim unless such reds were descended from ♂2054. The agoutis, however, produ a mixture of agoutis, blacks, and reds, when mated with ordinary red anim

These and other corroborating experiments, reported briefly in 19 showed that the agouti reversion in crosses of black with red is due to a fac transmitted by the red parent, never by the black one. For, as I then show (1) a red animal which produces the reversion to agouti in crosses with black animal will produce it in crosses with *any* black animal; but (2) no bl animal will produce agouti young unless crossed with a red animal which a produces agouti young in crosses with *other* black animals.

For simplicity, the something possessed by red animals which indu reversion, I have called the agouti or *A* factor. It is invisible in the red anim since the hairs of such animals are red throughout their length. Its only coverable function is to exclude black from the terminal portion of the h and this function plainly can not be exercised unless black pigment is prese Now this agouti factor is transmitted like any other simple independent m delian factor. Some reds are homozygous in *A* and so transmit it in all th gametes. A very fine female of this sort, kindly loaned me in the summe 1906 by Mr. B. B. Horton, was mated with two different black males (♂4 and ♂9538), by each of which she bore five young, all agouti-marked. Th same males when mated to other red females produced only black young.

Most of the agouti-producing reds which I have had, including the origi ♂2054 (received in June, 1903) and some of his descendants, have been hete zygous in the agouti factor, so that when mated with black animals they duced in approximately equal numbers agouti young and black ones.

reds which I have had, derived from other sources than these two, have failed to produce agouti young in crosses with black animals; see the summary in table 1, p. 8. They may therefore be considered to lack altogether the agouti factor in which wild species of cavy are regularly homozygous.

The agouti factor is transmitted through albinos exactly as are other color factors. Accordingly an albino may or may not possess and transmit the agouti factor; if it does possess this factor, it will produce agouti offspring when crossed with a black animal. Several examples of this have been observed among the albino descendants of ♂2054. Thus red ♂3496, table 1, which when mated with heterozygous black females produced red young and black ones but no agoutis, when later mated with the albino females 4270 and 4262 produced 4 red and 4 agouti young. The father of these albinos, it should be said, was an agouti animal.

Agouti animals produced by crossing black with red do not breed true. They produce three classes of young if bred with each other or with ordinary reds. The latter form of test has been more commonly employed in my experiments because I had more red animals than agoutis and it was easier to ascertain their gametic composition. Fourteen young, however, were obtained from the mating of F_1 agoutis *inter se;* they were 2 red, 2 black, and 10 agouti; see table 2, p. 9. The mating with reds produced 111 red, 45 black, and 40 agouti; expected, 98 : 49 : 49. This expectation is calculated as follows: It is expected that half the young will be red because the agouti parent is known to be heterozygous for red. It is also expected that half the young will receive the agouti character, which those possessing black pigment will show, but which those possessing only red pigment will not show. Hence all the reds should look alike, but half the others should be agouti. In the mating *inter se* of agoutis of this generation the expectation is 4 red : 3 black : 9 agouti; the observed numbers, as stated, are 2 : 2 : 10, in a slightly smaller total, 14. The tests summarized above relate to five different F_1 reversionary agouti males. Three of them were descendants of my original red male, 2054; the other two (9150 and 9152) were sons of Horton's red female. All gave similar results.

Agouti young produced by the mating already described of an F_1 reversionary agouti with an ordinary red produced the same kinds of young as did the F_1 agoutis, viz, red, black, and agouti; see the second division of table 2. The tests applied in this case were identical in character with those applied to the previous generation, viz, matings *inter se* and with ordinary reds (lacking A). Twenty-four different male animals were tested in one or both of these ways, while several females were tested in the first-mentioned way. The data for these are recorded for convenience in connection with the male involved in the same experiment. Only two of the various animals tested failed to produce all three classes of young. In the case of these two, 9602 and 9685, there can be little doubt that a more extended test would have produced the missing class. Male 9602 produced 2 black young and 1 agouti. A further test would almost certainly have given red young, since his mother was red. Male 9685 produced 4 red young and 2 black ones. That he could also have produced agouti young can scarcely be questioned, since he was himself an agouti. The total progeny of the 24 males by red females is 133 red, 66 black, and 69 agouti, the expectation being 134 : 67 : 67. By agouti mates they produced 25 red, 21 black, and 63 agouti young, the expectation being 27 : 21 : 61. These are remarkably close agreements. One of the 24 males, 7932, was also mated with a black female, producing 2 black and 2 agouti young, the expected equality; no red young were to be expected.

Agouti animals produced by mating agouti animals *inter se* are not so uniform in behavior as those thus far discussed. Experiment shows that they fall into four groups:

I. Agoutis producing red, black, and agouti young.
II. Agoutis producing only red and agouti young.
III. Agoutis producing only black young and agouti young.
IV. Agoutis producing only agouti young.

Group I is represented by nine agouti males, whose parents were both agoutis; they were enumerated in the third division of table 2. Together they have produced (*a*) by red mates, 34 red, 20 black, and 19 agouti young; expected 36 : 18 : 18; (*b*) by agouti mates, 3 red, 5 black, and 14 agouti young; expected 5 : 4 : 12, if the females were of the same character as the males, as most of them doubtless were; (*c*) by black mates, 3 black and 3 agouti young, the expected equality, no reds being expected.

Group II is represented by the ten animals enumerated in table 3. They proved to be incapable of producing black young in any sort of mating. Manifestly they were homogyzous in agouti. By red mates they produced 53 red and 52 agouti young. They were accordingly heterozygous in red, and equality of red and agouti young was to be expected. By agouti mates they produced 13 red and 62 agouti young. The expectation in this case varies with the character of the agouti mate employed, which was not in every case definitely determined. If the agouti mate belongs in Group I or II, then the expectation is 1 red : 3 agouti; but if the mate belongs in Group III or IV, the expectation is all agouti young. If the mates are a mixture of the two sorts, as a random group of F_2 agoutis should be, then the expectation lies between 75 and 100 per cent agoutis; the percentage obtained is 82.66. By black mates, the Group II agoutis produced 18 young, all agouti, as expected. These were sired by two animals, both of which by red mates had produced red young as well as agouti young.

Group III is represented by the 16 tested animals enumerated in table 4. They were incapable of producing red young, and hence were homozygous in black. But since they produced black young as well as agouti, it is evident that they were not homozygous in agouti. Three females (374, 437, and 462) are included only provisionally in this group, since they were not tested by matings with red animals, but only with black ones. They are known to have produced black young, but it is not certain that they could not also have produced red young, in which case they would fall in Group I. The test in the case of several other animals (as 5, 68, and 314) rests upon too small numbers to be conclusive, but suffices to show that the animals in question were not in *all* respects homozygous, the condition it was desired to obtain in the experiment. These animals were therefore promptly discarded as soon as evidence was obtained that they produced other than agouti young. In the case of animals 191, 6197, 7894, 8020, and 9939, the numbers of young are sufficiently large to establish beyond question their position in Group III.

The animals included in table 4 together have produced by red mates 51 black and 91 agouti young. If all the red mates used lacked the agouti factor, we should expect equality of black and agouti young; but from this expectation we observe a considerable divergence. It is quite possible that in some of these tests red animals were used which were descended from ♂2054 and had inherited from him an unseen agouti factor, for in making the later tests some such animals were employed, but it is doubtful whether this accounts for the whole discrepancy, amounting to about 14 per cent. This doubt is strengthened by the similar discrepancy observed in the tests with black mates, where we expect equality of black and agouti, but obtain 5 and 12 respectively. The case of animal 191 looks suspicious; he produced only one black young one in a total of 22, yet the record is certainly accurate. We had provisionally pronounced him a pure agouti, when the single black young one came which places him in Group III. It seems doubtful whether the theoretical 50 per cent of his gametes were entirely free from the agouti character. If so, such gametes would seem to have been deficient in vitality. The deviation is, however, not an impossible chance result, though it seems improbable. I regret that this animal was not more extensively tested. The matings of animals of Group III with other agouti animals produced 9 black and 46 agouti young, or 84 per cent agouti, where we expect between 75 and 100 per cent.

Agouti animals of Group IV are included in table 5. They represent the "fully fixed" agouti type breeding exactly like a pure wild species as regards color. Two thoroughly tested animals belong here beyond question, ♂145 and ♂316; two others less fully tested belong here in all probability, viz, ♂160 and ♂181, while ♀473 is included as a possibly pure animal. She was fully tested qualitatively (by a mating with a brown-eyed yellow animal known to lack both black and agouti), but the number of young obtained is not large enough to make the test conclusive. Similar tests of other females might be included in the table, but they would add nothing to the demonstrative case of ♂145, which shows that the reversionary character obtained by crossing can be obtained in a homozygous, pure condition, as it occurs in wild species. The five animals enumerated in table 5 have produced only agouti young: (*a*) by red mates, 52; (*b*) by agouti mates, 135; (*c*) by black mates, 26.

The occurrence of four different types of F_2 agoutis indicates that the F_1 agoutis, their parents, were heterozygous as regards two independent mendelian unit-characters, in agreement with the interpretation already given. These two characters are: (1) black-pigmented fur; (2) the agouti pattern (visible only in black-pigmented animals). Designating these two units as B and A respectively, the F_1 agoutis are all of the formula AB (heterozygous in both units). Their gametes are AB, A, B, O. If an animal producing such gametes is mated with a red animal lacking both units, the zygotes formed would be, as regards these units, AB, A, B, and O, or agouti, red, black and red respectively, or collectively 2 reds : 1 black : 1 agouti, as obtained (table 2). Further, such agoutis as came from this cross would be identical in character with the F_1 agoutis. This expectation is confirmed by table 2, second division.

But if the F_1 agoutis are mated *inter se,* then we expect to get zygotes corresponding with the product of two sets of gametes, each $AB + A + B + O$, that is A_2B_2[*] $+ 2A_2B + 2AB_2 + 4AB + 2A + 2B + A_2 + B_2 + O$. In appearance these zygotes would fall into three classes, agouti, black, and red, as shown in the accompanying table.

The agoutis in this (F_2) generation, it will be noticed, should be of four different types, as actually observed. The AB group should produce all three sorts of young, agouti, black, and red, being heterozygous in both characters, A and B. The group designated by A_2B would be pure for A but heterozygous for B. All their young would be potentially agoutis, but since part of them would lack black pigment, such would be red. Hence they would produce only the two sorts of young, agouti and red; see table 3. The group designated by AB_2 would transmit black pigment to all their young, but only part of these would receive A. Hence they would produce agouti young and black ones, but no reds; compare table 4.

Agouti.	Black.	Red.
4 AB	$2B$	$2A$
2 A_2B	B_2	A_2
2 AB_2		O
A_2B_2		
9	3	4

The group A_2B_2 would transmit both black and agouti to all their young; hence they would produce nothing but agouti young, however mated; compare table 5. The expected proportions of these four groups of agouti animals are obviously 4 : 2 : 2 : 1. The numbers shown in the tables are 9 : 10 : 16 : 5. The apparent deficiency of individuals in Group I and excess in Groups II and III is readily accounted for. Not all the agoutis recorded as derived from an agouti × agouti cross were *second*-generation agoutis; many of them were *third*-generation agoutis, having been obtained from two successive matings of agouti with agouti. In that case one or both of their parents may have been of Groups II or III, in which case the expectation for young of those groups is increased, while that for Group I is correspondingly diminished. Therefore both the kinds of agoutis obtained in the experiment and their numerical proportions are in harmony with the hypothesis presented in this paper.

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[*] The subscript 2 is used (instead of the algebraic exponent 2) to indicate double representation of a factor, *i. e.*, a homozygous condition as regards it. (See Castle, 1909.)

SUMMARY.

1. The agouti coat characteristic of wild cavies and of most other wild rodents is dependent upon the presence in the fur of black pigment disposed in a definite pattern with red (or yellow).

2. The factors which control, respectively, the development of black pigment and the production of the agouti pattern are independent of each other.

3. The agouti coat is obtained only when both these factors are possessed by an individual.

4. Only such agouti individuals as are homozygous in both factors breed true under all circumstances.

5. An agouti animal which is homozygous in *A* (the agouti factor), but heterozygous in *B* (black pigmentation), may produce agouti young and red ones, but not black.

6. An agouti animal which is homozygous in *B* but heterozygous in *A* may produce agouti young and black ones, but not red.

7. An agouti animal heterozygous in both *A* and *B* may produce three sorts of young, agouti, red, and black. All F_1 (reversionary) agoutis produced by crossing black with red are of this sort. Agoutis of the other three sorts are obtained only in the second or later generations of agouti young.

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Table 1.—*Differences among red guinea-pigs as regards the transmission of agouti.*

	Young by red mates.			Young by heterozygous black mates.			Young by homozygous black mates.			Young by agouti mates.		
	R	*B*	*Ag*	*R*	*B*	*Ag*	*R*	*B*	*Ag*	*R*	*B*	*Ag*
I. Homozygous in *A*.												
♀ Horton's red							0	0	10			
II. Heterozygous in *A*.												
♂2054	10	0	0	3	1	2	0	3	1	0	1	9
♀1278, daughter of ♂2054				2	0	1						
♀1280, ♀1281, daughters of ♂2054				10	5	6						
III. Lacking *A*.												
♂9347				18	8	0						
♂2004	44	0	0	20	12	0						
♂3496				19	17	0						

TABLE 2.—*Agouti parents producing red young, black young, and agouti young.*

	Young by red mothers.			Young by agouti mothers.			Young by black mothers.		
	R	*B*	*Ag*	*R*	*B*	*Ag*	*R*	*B*	*Ag*
From red × black cross:									
♂1178	39	16	16	....	....	....	....	....	....
♂3019	28	17	7	....	....	....	....	....	....
♂4812	9	1	2	....	....	....	....	....	....
♂9150	21	8	7	2	2	10	....	....	....
♂9152	14	3	8	....	....	....	....	....	....
Totals	111	45	40	2	2	10	....	....	....
From red × agouti cross:									
♂2797	13	6	11	....	....	....	....	....	....
♂2944	....	....	....	9	7	14	....	....	....
♂3982	7	4	7	....	....	....	....	....	....
♂4881	6	2	0	2	3	3	....	....	....
♂4882	8	2	4	4	2	16	....	....	....
♂4934	11	6	5	....	....	....	....	....	....
♂4935	7	3	4	....	....	....	....	....	....
♂7916	13	2	6	....	....	....	....	....	....
♂7932	5	6	2	....	....	....	0	2	2
♂7978	5	2	3	....	....	....	....	....	....
♂7979	8	5	4	....	....	....	....	....	....
♂9190	....	....	....	4	5	17	....	....	....
♂9511	7	3	4	....	....	....	....	....	....
♂9528	3	2	2	....	....	....	....	....	....
♂9583	7	4	1	....	....	....	....	....	....
♂9602	0	2	1	....	....	....	....	....	....
♂9620	5	2	3	....	....	....	....	....	....
♂9657	3	1	1	....	....	....	....	....	....
♂9684	....	....	....	6	3	9	....	....	....
♂9685	4	2	0	....	....	....	....	....	....
♂9687	4	1	3	0	0	2	....	....	....
♂9698	9	6	5	....	....	....	....	....	....
♂9734	2	3	1	0	1	2	....	....	....
♂9747	6	2	2	....	....	....	....	....	....
Totals	133	66	69	25	21	63	0	2	2
From agouti × agouti cross:									
♂59	3	3	2	....	....	....	....	....	....
♂179	2	1	1	....	....	....	0	1	2
♂318	3	0	0	....	....	....	0	2	1
♂6220	5	3	1	....	....	....	....	....	....
♂9258	1	1	0	1	4	4	....	....	....
♂9259	9	4	9	....	....	....	....	....	....
♂9411	1	2	3	0	0	2	....	....	....
♂9753	8	5	2	2	1	8	....	....	....
♂9993	2	1	1	....	....	....	....	....	....
Totals	34	20	19	3	5	14	0	3	3
Grand totals	278	131	128	30	28	87	0	5	5

TABLE 3.—*Agouti parents producing only red young and agouti young.*

	Young by red mates.			Young by agouti mates.			Young by black mates.		
	R	*B*	*Ag*	*R*	*B*	*Ag*	*R*	*B*	*Ag*
From agouti × agouti cross:									
♂26	4	0	10	2	0	14	0	0	15
♂31	2	0	2	0	0	5	....	....	....
♂137	4	0	4	0	0	3	....	....	....
♂147	5	0	0	....	....	....	0	0	3
♂180	5	0	3	1	0	5	....	....	....
♂309	1	0	1	....	....	....	....	....	....
♂429	2	0	2	....	....	....	....	....	....
♂6219	17	0	18	5	0	18	....	....	....
♂7887	7	0	6	5	0	17	....	....	....
♂7926	6	0	6	....	....	....	....	....	....
Totals	53	0	52	13	0	62	0	0	18

TABLE 4.—*Agouti parents producing only black young and agouti young.*

	Young by red mates.			Young by agouti mates.			Young by black mates.		
	R	*B*	*Ag*	*R*	*B*	*Ag*	*R*	*B*	*Ag*
From agouti × agouti cross:									
♂5	0	1	3	....	....	....	....	....	....
♂68	0	1	4	0	0	2	....	....	....
♂191	0	0	14	0	0	2	0	1	5
♂314	0	2	2	....	....	....	....	....	....
♀374	....	....	....	....	....	....	0	1	0
♂434	0	2	4	....	....	....	....	....	....
♀437	....	....	....	....	....	....	0	1	2
♀462	....	....	....	....	....	....	0	1	1
♂6197	0	17	16	0	6	11	....	....	....
♂7819	0	5	11	0	0	1	....	....	....
♂7894	0	2	2	0	3	17	....	....	....
♂8020	0	9	7	....	....	....	....	....	....
♂9810	0	2	4	0	0	7	....	....	....
♂9906	0	4	6	....	....	....	0	0	3
♂9939	0	5	16	0	0	3	0	1	1
♂9941	0	1	2	0	0	3	....	....	....
Totals	0	51	91	0	9	46	0	5	12

TABLE 5.—*Agouti parents producing only agouti young.*

	Young by red mates.			Young by agouti mates.			Young by black mates.		
	R	*B*	*Ag*	*R*	*B*	*Ag*	*R*	*B*	*Ag*
From agouti × agouti cross:									
♂145	0	0	21	0	0	68	0	0	16
♂160	0	0	6	0	0	4	....	....	....
♂181	0	0	8	0	0	6	....	....	....
♂316	0	0	14	0	0	57	0	0	10
♀473	0	0	3	....	....	....	....	....	....
Totals	0	0	52	0	0	135	0	0	26

EXPERIMENTAL STUDIES OF THE INHERITANCE OF COLOR IN MICE.

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Paper No. 19, Station for Experimental Evolution at Cold Spring Harbor, New York.

PREFATORY NOTE.

The experiments on which the following paper is based were begun in the Zoological Laboratory of Harvard University at Cambridge, Massachusetts, in November 1907. Since that time more than 10,500 young have been recorded. In 1909 the animals were moved to the Laboratory of Genetics at the Bussey Institution, Forest Hills, Massachusetts, at which place the experiments are still in progress.

Throughout the course of the experiments the writer has been encouraged, aided, and advised by Dr. William E. Castle, to whom any merit that this paper may possess is chiefly due.

The skillful and accurate representations of the various color varieties are from water-color paintings from life, by Mr. Eugene N. Fischer, whose interest has shown itself in the excellent work that he has done.

The experiments have been supported in part by an annual grant from the Carnegie Institution of Washington made to Dr. Castle "for the continuation of the study of heredity in small mammals."

CLARENCE C. LITTLE.

MAY 1912.

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EXPERIMENTAL STUDIES OF THE INHERITANCE OF COLOR IN MICE.

PART 1.

THE FACTORS PRODUCING COLOR IN MICE.

In the coat of the common house mouse (*Mus musculus*) three pigments are recognizable, yellow, brown, and black. No connecting intergradations of color between these three types are visible. The inheritance of these colors and of their distribution, both qualitatively and quantitatively, has been the object of many investigations and is the principal feature of the present paper.

All mammalian color has been found due to melanin pigment. Riddle (1909) has discussed the process of the formation of melanin pigment and states that all chemical evidence supports the idea that melanin pigment is the product of an oxidation process. The substances (chromogens) on which the oxidizing agents (enzymes) act were found to be tyrosin and certain related aromatic compounds. It has been further shown that tyrosinase-like ferments, which occur widely distributed in the organism, act as oxidizing agents, thus producing melanin compounds. Furthermore, it has been proved that at least artificial melanins may pass through a series of colors before arriving at the final stage of oxidation. In such series the earlier stages of oxidation give lighter colors than the later ones.

Cuénot (1903) advanced an hypothesis to explain the formation of color by the interaction of a chromogen substance and an enzyme. He called the chromogen the general factor for the production of color, *C*, and supposed that in albinos this chromogen substance is lacking, thus making it impossible for color to be formed. Riddle, however, states that the nature of the chromogen, it being very widely distributed throughout the organism, is such that any theory postulating the absence of this substance would be chemically absurd. Gortner (1912), however, finds evidence that chromogens in insects may be of *restricted distribution,* thus forming color patterns.

At present it is impossible to decide finally between the explanation offered by Cuénot and that suggested by Riddle. We shall have to await further chemical evidence to determine whether the albino does or does not lack the oxidizable substance or substances necessary for pigment production.*

If we assume that there is only one enzyme present to act as an oxidizing agent, we must assume for it as many different degrees of activity as are required to explain the occurrence of the various colors known to mendelize (three in mice, yellow, brown, and black). If we assume that a different enzyme or

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*A recent paper by Keeble and Armstrong (1912) has shown that in *Primula sinensis* lack of chromogen seems to be the cause of albinism, thus favoring the original hypothesis of Cuénot.

group of enzymes is responsible for the production of each pigment we must suppose that in mice at least three such enzymes or groups of enzymes exist. To determine which of these conditions occurs in mice is not a problem for the biologist, but for the chemist. The biologist must confine his attention to determining the number of distinct agencies at work in pigment formation irrespective of their chemical nature. These agencies, because of their physiological behavior, the biologist chooses to call "factors," and attempts to learn what he can about their functions in the evolution of color varieties.

FORMATIVE AND DISTRIBUTIVE COLOR FACTORS.

As has already been stated, three pigments (yellow, brown, and black) are observable in mice. Yellow has been found, by Riddle, to be the lowest in the scale of mammalian pigments. Nevertheless, in mice no case has been recorded where yellow alone is present. The eye always has, in addition, brown or black pigment granules, while in many cases both are present. The same fact holds good for the coat, so far as observation goes.

These three pigments—yellow, brown, and black—are, however, discontinuous stages. If they are not the products of *distinct enzymes* they are the result of *distinct grades of activity of a single enzyme.* Which of these conditions holds makes no difference at present, so we may, for purposes of discussion, refer their causation to three distinct factors, *Y* for yellow, *Br* for brown, and *B* for black.

Certain animals possess yellow and brown pigment to the exclusion of black. In such animals, with no evidence of variation in the total amount of pigmentation, there occur varieties in which the proportion of brown to yellow in the coat varies greatly. As the brown increases in amount the yellow decreases. It is fair, then, to assume that something is acting to convert the lower-grade pigment (yellow) into the higher grade (brown). This, we suppose, is the factor *Br* already mentioned.

The activity of such a factor may, however, be affected by other factors which determine *the amount of brown formed and its location.* Experiment shows that these assumed factors governing the development of brown are independent of the *brown-forming factor Br,* for they can be transferred without visible alteration to animals with black, and *vice versa.* Such factors we may call *distributive.*

Black is the highest grade of mammalian pigment and doubtless, as Riddle states, is a higher oxidation stage of brown; for brown pigment is often, if not always, seen in black animals, but never the reverse. We may, therefore, assume a distinct agency for the conversion of brown into black and call this factor *B*. If by a given cross this factor *B* is added to a certain distributional stage of brown, the corresponding distributional stage of black is obtained, showing that the factor *B* is independent of the distributive factors.

Such factors as *Y*, *Br*, and *B*, indicating as they do distinct qualitative steps in pigment formation, we may call *formative factors,* in somewhat the same way as the factors controlling the distribution and amount of pigment have been considered *distributive factors.*

LOCATION OF PIGMENT.

In wild mammals all three pigments (yellow, brown, and black) commonly occur in the same hair. In many domesticated or "fancy" varieties, one or the other pigment prevails almost, if not quite, to the exclusion of the others; thus yellow, brown, and black varieties arise. Brown varieties (completely lacking black) occur in certain mammals (*e. g.*, mice, rabbits, guinea-pigs, and dogs). Theoretically they would seem to be possible in all.

Pigment appears in mice in three general regions. These are the eyes, the skin, and the hair. The pigment occurs in granules.

In the eyes microscopic examination has shown that the pigment granules are located in both the retina and the iris. Of these two localities the iris seems the more permanent pigment-producing center; for when reduction in the amount of pigment occurs the retina seems the more easily and extensively affected.

In the skin the pigment is located only a short distance from the surface in the malpighian layer. In contradistinction to the eyes, which are visibly pigmented at birth, the skin apparently becomes pigmented only after the animal is several days old; this is largely because the hairs, in which much of the pigment lies, are not formed at birth. The pigment granules of the hair may be clearly observed under the microscope. Bateson (1903), among other investigators, has determined their location with considerable accuracy and finds that they are situated in the cortex or outer sheath of the hair, and also in the interior of the hair in the proximal walls of the medullary spaces.

To recapitulate, we find three general pigment-producing regions in mice: the eye, the skin, and the hair. The pigments (melanins) produced are limited to three: yellow, brown, and black—which we consider to be caused by the action (jointly or severally) of the factors Y, Br, and B. Domesticated or "fancy" varieties of mice appear to differ from the wild in the partial or complete exclusion of one or more of the pigments. Such exclusion may be the result of (1) the action of a distributive factor, or (2) the loss of the formative factor necessary to the production of a particular pigment.

FORMATIVE COLOR FACTORS.

1. THE GENERAL COLOR FACTOR, Y.

It has long been recognized by investigators that, in mice, pigmented varieties differ from albinos by a single mendelian unit-character. Thus in crosses between homozygous self-pigmented and albino animals we find that the first generation (F_1) consists entirely of pigmented animals. If these first-generation hybrids be then crossed *inter se* we should expect in F_2 that the ratio 3 pigmented young to 1 albino would be approximated. The experimental results agree well with this expectation and we have as a result of crossing F_1 *inter se:*

	Pigmented.	Albino.
Observed..	598	206
Expected..	603	201

If we consider, in addition to the above result, those obtained in a similar cross by other investigators, we may construct the following table:

	Pigmented.	Albino.
Allen	240	97
Crampe	164	57
Cuénot	269	93
Darbishire	418	137
Durham	808	255
von Guaita	232	77
Parsons-Copeman*	49	14
Little	598	206
Total observed	2,778	936
Expected	2,785.5	928.5

*See Bateson (1903).

In the cross between the heterozygous pigmented animals obtained in F_1 and pure albinos, where equality of pigmented and albino young is expected, the following result has been obtained:

	Pigmented.	Albino.
Observed	21	16
Expected	18.5	18.5

As this cross has been largely neglected in my experiments the numbers are extremely small. If, however, a table is made showing the work of other investigators, larger and more valuable results are obtained:

	Pigmented.	Albino.
Allen	84	64
Darbishire	106	119
Durham	31	33
von Guaita	24	20
Parsons-Copeman	59	59
Little	21	16
Total observed	325	311
Expected	318	318

All investigators have found that when albino mice are crossed *inter se*, only albino young are produced. Albinism is, then, a recessive character. Cuénot (1903) considered albinism due to the loss of the general color factor *C* (chromogen), but for the reasons given by Riddle this interpretation seems of doubtful validity.

As before stated, mammalian pigment results from the action of an enzyme or enzymes upon a chromogen substance. Albinos are formed from colored varieties by the loss or restriction of one of these substances. Present chemical evidence discredits the possible loss of the chromogen; the enzyme or enzymes remain to be considered. Albinos probably lack one or more of these. If further chemical investigation should show that what albinos lack is really chromogen, as Cuénot supposed, no change in the gametic formulæ here used will be necessary, beyond the addition of a symbol C (chromogen) in the case of colored animals.

In the writer's opinion the only enzyme which all albinos in common lack is that which acting alone produces the lowest grade of melanin pigment, namely, yellow. To this supposed factor I have given the designation Y. The factor B may or may not be present in an albino, but Br apparently is never lost. Y then forms the step between color and no color, producing yellow when present, no color being produced in its absence. This yellow is converted to brown pigment by the ever-present factor Br, whose action, however, is locally inhibited wherever yellow pigment appears as the final oxidation stage.

2. The Brown-Producing Color Factor, *Br*.

This factor, in my experience, is never wanting, though its presence is often at least partly concealed by the factor B, which carries forward the process of pigment formation from the brown to the black stage. In albinos, also, when Y (the factor for producing yellow) is absent the factor Br, lacking the material on which to act, does not function visibly. Thus it is not to be wondered at that this factor Br has been omitted from the zygotic formulæ of most investigators and that brown is considered commonly the result of the *absence of black*. The chemical evidence already given, however, together with the fact that brown pigment is often, if not always, to be found in black animals, seems to justify the use of a distinct term to designate the factor that forms brown. This factor is not to be confused with the *absence* of the factor for black formation, which is a pure negation and can not be considered as an active agent in the formation of anything.

3. The Black-Producing Color Factor, *B*.

As before stated, this factor is necessary for the production of the highest stage of mammalian pigment, viz, black. In its absence, the final oxidation stage is brown, so that we may speak of "animals lacking black" as brown, but it is conceivable that animals might be found which also lack Br, in which case the final oxidation stage would be yellow, not brown, and mere absence of black would not in that case be equivalent to brown.

If we cross, then, animals homozygous for the factor B with animals entirely lacking that factor, we should expect F_1 to consist entirely of heterozygous black animals. By experiment, 589 animals have been produced in this way, all of which possessed black pigment. We should expect, now, that if such black animals are crossed *inter se*, the next generation will consist of three animals possessing black pigment to one lacking it completely. When this cross was made the following result was obtained:

	Black.	Brown.
Observed.....	591	216
Expected......	605.25	201.75

In the cross between heterozygous black animals and the extracted brown recessives, where equality of black young and young lacking black are expected, the following result has been obtained:

	Black.	Brown.
Observed.....	198	187
Expected......	192.5	192.5

If brown animals are crossed *inter se*, only brown young are expected. The observed facts coincide with the expectation, 822 brown young having been thus obtained.

It is, then, clear that the presence of the factor for the production of black pigment and its absence result in a pair of allelomorphic unit characters. In all the cases above mentioned the heterozygous black animals were indistinguishable from the homozygous blacks, so far as external appearances go. The dominance of black is thus apparently complete. Miss Durham (1911), however, has recorded the occurrence of a distinct heterozygous form ("chocolate lilac") in crosses between pink-eyed black ("blue lilac") and pink-eyed brown ("champagne") mice. The writer has made similar crosses with animals of these color varieties, but is unable to confirm Miss Durham's results.

Pink-eyed black mice vary in depth and intensity of pigmentation, which fact will be discussed more fully under the head of distributive factors, but the writer has been unable to detect any greater degree of brownness in the pink-eyed blacks which are heterozygous ("chocolate lilacs") than in those which are homozygous. While it is possible that microscopic examination of the hair of such heterozygous pink-eyed black animals may reveal a greater relative amount of brown than occurs in the homozygous form of the same color variety, it seems of doubtful propriety to call the heterozygous form a distinct color variety. Furthermore, if the distinction between homozygous and heterozygous pink-eyed blacks were a good one, it should be recognizable in the heterozygotes produced by crossing pink-eyed black agouti with pink-eyed brown agouti types. Miss Durham, however, mentions no such difference between homozygous and heterozygous pink-eyed black agoutis, and I have been unable to find any such difference in my own experiments.

Black, in its method of inheritance, forms one of the best examples of a mendelian unit character. It is, moreover, clearly a positive character which is dominant over its absence, or chemically expressed it is a higher oxidation stage epistatic to a lower stage and independent of the latter in inheritance.

DISTRIBUTIVE COLOR FACTORS.

We have seen that three factors act as agents in the formation of the pigments of mice. We may now consider the factors concerned in controlling the distribution of pigments thus formed. It is obvious that theoretically the distribution of pigment may be controlled in two general ways: (1) by the ability to form either a greater or less total amount of pigment; or (2) by the restriction or loss of one or more pigments from certain portions of the pelage, thus producing "coat patterns." The existence of two distinct factors of each of these types has been proved by experiment. These will be presently described.

For a basis from which to calculate increase or diminution in the total amount of pigmentation (the first category of modifications mentioned), it is desirable to have, as a standard, some known stock of as nearly constant pigmentation as possible. For this purpose none seems better than the wild house-mouse, *Mus musculus*. There is, to be sure, variation among the wild individuals of this species, but on the whole it forms as satisfactory and constant a basis as can be obtained. To the factor producing the degree of pigmentation observed in the common house-mouse we may give the designation *D* (density of pigmentation).

This factor *D* affects the distribution of pigment granules of the three sorts, yellow, brown, and black, but there is experimental evidence that *another* factor exists which determines the amount of brown and black granules present without affecting the number of yellow granules in the coat. To this factor we may give the designation *P* (plenitude or fulness of brown and black pigmentation). There is a complete series of color varieties as described by Castle and the writer (1909), in which simultaneous modifications of both these factors exist, as well as two other series in each of which one only of the two factors is modified.

Of the second category of distributive factors, those which cause local restriction or loss of certain pigments, there are two clear examples in mice. The first of these is seen in the case of the wild type, where the so-called "agouti" pattern exists. This pattern results from the activity of a factor determining the order in which pigments are laid down in the individual hair, and also producing a differentiation between hairs of the dorsal and ventral surfaces. This factor we may designate *A* (agouti). A factor of this sort produces the "ticked" coat characteristic of almost all wild rodents. In the absence of *A*, animals are self-colored.*

The second factor of this category is a restrictive factor which almost excludes black and brown pigment from the hair and skin, thus leaving a preponderance of yellow granules in those localities and producing the so-called "yellow" varieties of mice. This factor we may call *R* (restriction). In its absence colored animals are either agouti if *A* is present, or self-colored if *A* is absent.*

From this very brief description it may be seen that the presence of certain distributive factors, or modifications of them, determines what color varieties of mice shall be formed. These distributive factors determine either the total amount of pigmentation or the relative amounts of yellow, brown, and black that are visible. It is, then, obvious that they are factors dealing with "quantity" of pigment, not with "quality" of pigment, as do the formative factors *Y*, *Br*, and *B*. Since the "distributive" factors *D*, *P*, *A*, and *R* deal with

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*This ignores spotted forms, which will be considered separately.

quantity of pigment, we might expect that they would show more fluctuations than do the formative or qualitative factors *Y*, *Br*, and *B;* and such is the case, as will presently be more fully described.

4. The Distributive Factor, *D*.

We have stated that this factor is responsible for the degree of *density* of yellow, brown, and black pigmentation seen in the common wild house-mouse. The presence of this factor is allelomorphic to a modification of density of pigmentation which we may call "*dilute*" pigmentation and designate by *d*. This dilute type of pigmentation was recognized by Bateson (1903) in mice. At that time he stated that it consisted of a reduced number of pigment granules, affecting both the cortex and medulla of the hair. To this the writer may add that the pigmentation of the skin is visibly lessened in "dilute" forms, and that the eyes are also affected. When the eye of a "dilute" mouse is examined under the microscope, reduction in the amount of pigment, as compared with the densely pigmented forms, is seen to exist. This reduction occurs in both retina and iris, but is more extensive in the former locality than in the latter.

The dilute forms of rabbits, as compared with the intense forms, show, on microscopic examination of the hair, a reduction in number of the pigment granules in the cortex of the hair. The dilution in this case seems transferable to hair of any color and is therefore comparable to dilution in mice, as it is also in superficial resemblance, having a streaky and washed-out appearance to the unaided eye.

In guinea-pigs the condition seems somewhat different. The problem there does not appear to have been worked out with especial reference to dilution. There dilute forms do *not* appear streaky, although the cream type of reduction seems either directly or indirectly transferable to black and brown. It seems, however, doubtful whether a true *dilution* exists in guinea-pigs. There is no evidence showing a modification of the intense colors, which modification behaves as a unit character; and it seems probable, from the recent occurrence of a pink-eyed colored guinea-pig (Castle, 1912*b*), that the reduction of pigment seen in guinea-pigs is due to a modification approaching that seen in pink-eyed mice, rather than the dilute modification.

The "dilute" modification affects all three pigments (yellow, brown, and black), wherever they may occur. Castle and the writer (1909) recognized this in mice in the "non-yellow" varieties, including those possessing the agouti factor. Plate (1910) recognizes a dilute series of color varieties, though using a slightly different nomenclature to designate them. Morgan (1911*a*) independently puts on record the occurrence of dilute animals with the agouti pattern. Miss Durham (1911) also recognizes the existence of a dilute type of every color variety. Previous to that time, however, she had not recognized the relation of the dilute agouti animals to the dilute "non-agouti" forms.

Entirely distinct from this modification of the factor for density of pigmentation, which produces dilute forms, is the fluctuation of the degree of density itself. Though "density" and "dilution" act as a pair of allelomorphic characters, "density" is subject to considerable fluctuation. Thus we may have a gradual series of yellow mice, all possessing the factor *D*, but varying in depth of pigmentation from an extremely light cream-color to a deep rich orange. Microscopic examination of the hair of these various forms shows in "cream" animals a distinctly smaller amount of pigment than in the hairs of the darker grades of "dilute" yellow animals. Dilute animals also vary in depth of color. For example, certain dilute browns may be of a distinctly lighter color than others. We know from the behavior of "density" and "dilution" in crosses that they are allelomorphic to each other, but we must admit that they are fluctuating characters and not stable in the sense of the formative qualitative factors *Y*, *Br*, and *B*. The differences in depth of color in the case of any color variety, either intense or dilute, are more easily discerned in those animals which have a preponderance of light pigment, such as yellows, or in those possessing reduction in amount of pigment due to some modification, such as dilute dark-eyed and intense pink-eyed mice.

In this connection it is interesting to note the occurrence of certain "coat patterns" on mice, reported by Morgan (1911*a*). He describes, among others, patterns consisting of distinct regions of lighter and darker color. He further states that when the light hairs are examined under the microscope they show a lessening of pigment granules in different regions, "a lessening that is a characteristic feature of the so-called dilute condition." But as reduction in the amount of pigment occurs in the case of the "light" densely pigmented and the "pink-eyed" forms, as well as in the dilute forms, evidences of the sort offered by Morgan can not be considered to establish his conclusion.

Is it not possible that these cases are those of intensely pigmented animals showing on their coat somatic segregation of certain of the fluctuations that are seen in dense pigmentation? Such "lightness" would not be in any way correlated with *dilution*, and would appear in homozygous animals as well as in heterozygous ones.

The writer suggested (1911*b*) that such patterns as were described might not be a criterion of the heterozygosity of their possessor, but due entirely to the physiological condition of the animal at moulting. Morgan in reply (1911*c*) stated that the cases he described were not "moulting" patterns, which were, as he stated, "too familiar to * * * call for comment." Yet in his first paper (1911*a*) he mentions certain "gray" animals, and figures two, which, as he states, "show areas of lighter and darker color, and these *may come and go at each moult.*"

The writer has obtained in a homozygous dilute brown animal (♂317) regions of clearly lighter hair than the predominant body color of the individual. These lighter hairs are apparently full-grown, and remained clearly distinguishable in this animal for nearly a year, after which the animal died. If this individual was heterozygous he might, as Morgan states, be considered as giving "evidence of his dual nature," but his gametic composition is "single;" so perhaps the "evidence" in the case of the heterozygous animals reported by Morgan is a matter of coincidence.

The above-described fluctuations in the density of pigmentation are to a certain extent hereditary. Thus cream-colored mice crossed *inter se* have a greater number of cream-colored than of deep-yellow young. So, too, from deep-yellows crossed together the deep-yellow young preponderate, but cream-colored young may occur as well.

We may now consider the result of crosses between intense animals possessing the factor D and animals with the modified or "dilute" condition d. If homozygous intensely pigmented animals (DD) are crossed wtih dilute animals (dd) only intense young (Dd) are formed in F_1. In my experiments 424 young have been thus produced, all intense, manifesting D. If these heterozygotes are crossed together we should expect in F_2 the ratio 3 intense to 1 dilute young. The experimental results are as follows:

	Intense.	Dilute.
Observed.....	610	205
Expected......	608.25	203.75

When the heterozygous intense animals are crossed back with the dilute type the following results have been obtained:

	Intense.	Dilute.
Observed.....	301	197
Expected......	249	249

Here there is a marked deficiency of dilute animals, which is in all probability partly due to failure on my part to recognize as dilute certain of the pink-eyed *dilute* animals produced during the years 1907–08. During these years many matings of this type were made. In classifying the young obtained from these I may have been in error. Thus if we consider the matings made since 1908, which should theoretically produce both dilute and intense young, we should have the following results:

	Cross of heterozygous F_1 intense animals *inter se*.		Cross of heterozygous F_1 intense animals with recessive.	
	Intense.	Dilute.	Intense.	Dilute.
Observed...	345	140	146	166
Expected...	363.75	121.25	156	156

Here there is an excess of *dilute* animals, which makes it seem probable that in the matings previous to 1909, of the two types given above, I confused the dilute and intense pink-eyed forms, often failing to distinguish them correctly. However, I feel sure that errors of this sort have not occurred since 1909, and the figures given above may be considered as a correct representation of the observed facts. For the most part the behavior of density and dilution is clearly that of a pair of allelomorphic unit characters, and they may therefore be treated as such. Thus dilute animals crossed *inter se* give, as expected, only *dilute* young, 603 such animals having been produced.

5. The Distributive Factor, P.

As before stated, this factor affects brown and black pigment, but does not affect the amount of yellow present. The modification of this factor giving rise to the "pink-eyed" series of colored mice, reduces the amount of black and brown pigment to a very great extent. The reduction affects hair, skin, and eyes. Miss Durham (1908) has pointed out the fact that the eyes, as the hair, are not entirely devoid of pigment. In examining with the microscope sections of the eye of a "pink-eyed" colored mouse, she found traces of pigment present, but in such minute quantities as to make any qualitative analysis impossible. The writer has examined under the microscope crushed eyes of the brown, dilute brown, pink-eyed brown, and pink-eyed dilute brown varieties and has thus been able to trace the steps in the reduction of pigment in these four varieties with fair success. The eyes were prepared by dehydrating and clearing in xylol. The lens was then removed and the iris and retina spread on the slide and mounted in balsam. When thus prepared, the following conditions were observed:

(1) In *intense-brown* animals, the iris is more heavily pigmented than the retina, but both are thickly pigmented with *brown only, no yellow.*

(2) In *dilute-brown* animals, there is reduction of the total amount of pigment, but the retina shows the effects of the reduction more than does the iris. The pigment is *brown only, no yellow.*

(3) In *pink-eyed intense-brown animals* there is very little pigment in the retina. The iris is moderately pigmented, but much less so than in the dilute-brown form. The pigment is *brown only.*

(4) In *pink-eyed dilute-brown animals* the retina is apparently unpigmented, but the iris still contains a small amount of brown pigment. *No yellow pigment is present.*

We may now turn to the experimental results obtained in crosses between dark-eyed animals (PP) and pink-eyed animals (pp). In this case F_1 consists entirely of dark-eyed animals (Pp), 1,085 individuals having been thus obtained, all dark-eyed and to external appearances indistinguishable from homogyzous dark-eyed animals. These F_1 heterozygotes crossed *inter se* have given the following result:

	Dark-eyed.	Pink-eyed.
Observed....	1,673	457
Expected....	1,597.5	532.5

If these results are added to those obtained by Miss Durham in similar matings we have:

	Dark-eyed.	Pink-eyed.
Durham	876	303
Little	1.673	457
Total observed	2,549	760
Expected	2,481.6	827.4

The result is not strikingly close to the expected numbers. There is in my experiments a deficiency of pink-eyed animals too extensive to be overcome by the excess of pink-eyed obtained by Miss Durham. The difference in result in the two cases may be considered as probably too great to be due entirely to chance.* Furthermore, in the following cross the result is still more aberrant and again there is a lack of pink-eyed animals. The cross is that of heterozygous dark-eyed animals (*Pp*) with pink-eyed animals (*pp*). Equality of dark-eyed and pink-eyed young is expected.

	Dark-eyed.	Pink-eyed.
Observed	370	284
Expected	327	327

Here, if the higher numbers (gained by adding Miss Durham's results) are considered, the numbers are closer to equality, though still widely unequal:

	Dark-eyed.	Pink-eyed.
Durham	105	113
Little	370	284
Total observed	475	397
Expected	436	436

It is possible that in the "pink-eyed" animals of my strain some constitutional weakness exists, either directly connected with the "pink-eyed" modification or to a marked degree correlated with it, which tends to cause a higher degree of mortality among the pink-eyed than among the dark-eyed young. I have tried, so far as possible, to record the eye-color of young *at birth,* but have failed in many cases. Even if it had been possible, it would not be safe to state that animals with apparently unpigmented eyes were all pink-eyed *colored* forms, for albinos at birth are indistinguishable from the pink-eyed colored series.

When "pink-eyed colored animals are crossed *inter se,* only "pink-eyed" animals have been produced; 496 young have been thus obtained.

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*Using the method described by East & Hayes (1911) p.37, we find that the deviation from the expected ratio is 0.0810, while the probable error is ±0.0752.

"Pink-eyed" colored varieties are much "yellower" in appearance than their corresponding dark-eyed intense and dilute forms. This is due to two facts:

(1) That in such forms as the pink-eyed black agouti and pink-eyed brown agouti (both intense and dilute) *the yellow band of the agouti pattern is left fully pigmented, while the black and brown pigment in the same hairs is much reduced in amount.* Similarly pink-eyed yellow animals possess fully pigmented yellow hair and thus have as heavily pigmented coats as do the dark-eyed yellow types.

(2) In the pink-eyed black and pink-eyed brown varieties (intense and dilute) there are *no yellow pigment granules in the hair,* but the extremely small amount of black or brown pigment present *gives the optical effect of an animal with yellow pigment.* This is especially marked in the case of the pink-eyed brown variety.

The mutual independence of the factors D and P, and of their modifications d and p, was recognized by Castle and the writer (1909) and found to hold good in all the color varieties, whether possessing the agouti pattern or not. At that time we reported the cross of a dilute "dark-eyed" animal with an intense "pink-eyed" animal, resulting in the production of a "dark-eyed intense" F_1. We had then only a small number of F_2 animals from such crosses, but those showed that the four theoretical classes of offspring were produced. In similar crosses we have now obtained the following result:

	Dark-eyed intense.	Dark-eyed dilute.	Pink-eyed intense.	Pink-eyed dilute.
Observed...	71	32	28	6
Expected...	77	25.7	25.7	8.6

Other crosses showing the independence of D and P have been made, and the results all follow the expectations with reasonable accuracy. Miss Durham (1911) has also recognized the independence of D and P, but without giving numerical results showing the occurrence of the intense and dilute types of the various pink-eyed color varieties. She, however, recognizes the independence of pink-eye and dilution only in those mice "in which yellow is absent." The fact that their independence has been observed and experimentally proved in animals (agouti) in which yellow is present seems to remove this restriction. Thus, for example, the cross reported in 1909, and already referred to, shows that their independence is clear-cut, even in the individual hair, and that the presence of yellow in the hair aids in showing their independence; for in the *dilute* agoutis (brown or black) all the pigment in the hair is reduced in amount, while in the *pink-eyed* agoutis (brown or black), the yellow band in the hair is as heavily pigmented as in dark-eyed agouti forms.

We may now consider, in order, the two factors which have to do with the relative distribution of the three pigments, yellow, brown, and black, in the hair and skin. These factors A (agouti) and R (restriction), already briefly described, have certain characteristics in common, and evidence exists (as will be discussed later) that they may be closely related. Their sphere of action is limited to the hair and skin, to the exclusion of the eye. In this respect they differ fundamentally from the distributive factors D and P, already described.

6. The Distributive Factor, A.

This factor was first recognized by Cuénot (1902) under the designation of G (*gris*), as producing the pattern seen on the coat of the wild house-mouse; but he erred in considering the factor G as allelomorphic to the factor N (*noir*) for the production of black pigment. Castle (1907*a*) proved that in guinea-pigs the agouti pattern is a unit character allelomorphic to its absence. Guided by this hypothesis he formed a new color variety of guinea-pig (cinnamon). Furthermore, he proved (1907*a*) that the agouti pattern might be carried by certain red animals, which when crossed with blacks produced agouti young in the first generation. By experimental test it was proved that all black animals behaved the same in the crosses made *and that the reds differed.* Morgan (1911*a*) quotes Castle as stating that in the above-mentioned crosses *both* the blacks and reds were able to transmit the agouti type of coat. Having thus misquoted Castle, Morgan offers as a suggestion the explanation which Castle proved was correct in 1907.

The agouti pattern consists in mice (Allen, 1904) of two chief types of dorsal hairs: (1) *Those having a fine black tip,* a sub-apical band of light ochraceous color (occupying about one-fifth of the hair) and a dark plumbeous basal portion. (2) Others, less numerous, are black throughout.

The ventral hairs Allen describes as possessing a distal half, which is dirty white to pale ochraceous buff, and a basal half which is plumbeous. Castle (1907*b*), in describing the agouti pattern in guinea-pigs, states that *the tips are black* in hairs showing the ticking; then follows a yellow or red band, and then the hair is black to the base. Both of these investigators find that the "ticked" hairs have *black tips,* as does Hurst (1905) in the case of rabbits.

Morgan (1911*a*) states that he has obtained black animals which have certain of their hairs *brown-tipped.* These he characterizes as agoutis without the yellow band and further states that the ticked hairs in the coat of "agouti" animals are *brown-tipped.* It is obvious that he is dealing with a color pattern in his "gray" (agouti) animals *which is not identical with the agouti pattern as described by other investigators.* It tends, therefore, to confusion to treat the pattern that he is dealing with as *agouti.* Furthermore, it seems probable that the blacks, which he reports as having ticked (*brown-tipped*) hairs, do not possess a factor in the least comparable with the "agouti" pattern. Morgan himself states that these *brown-tipped* hairs occur *only in heterozygous black mice.* The question suggests itself, how can mice possess, as a result or necessary concomitant of heterozygosis, a pattern which is the characteristic of a homozygous wild race?

Bateson (1903) stated that in black mice the tips of the large contour hairs are often brown. Ticked hairs in non-agouti (black) mice are not, then, a new development, and as black mice have been long used in experiments and have never been found to transmit the agouti pattern, it seems that Morgan has been misled by the superficial appearance of "ticking" in the hair.

That superficial ticking is not identical with the agouti pattern is observable in the case of "sable" mice, as will be more fully discussed later. It is also observable in certain "dingy" or "smoky" young produced by Himalayan rabbits. In this case there may be as many as two light bands in the "ticked" hairs, the dark portions of which seem to contain a small amount of black pigment producing the dingy appearance alluded to. In such cases it is known that neither parent carries the agouti pattern, yet here are hairs with an *apparently* similar ticking; therefore not all ticking of rodent hairs is due to the same factor.

We may now consider crosses in which the "agouti" pattern is involved. In the cross between homozygous agouti and non-agouti forms, F_1 consists entirely of agouti (black agouti or brown agouti) animals, 344 young having been thus obtained. When certain of these heterozygous F_1 animals were crossed *inter se* there were obtained:

	Agouti.	Non-agouti.
Observed....	257	74
Expected.....	243.75	81.25

If the heterozygous F_1 agoutis are crossed with non-agouti mice we should expect equality of agouti and non-agouti young. In this cross I have obtained:

	Agouti.	Non-agouti.
Observed....	194	170
Expected.....	182	182

When non-agouti animals are crossed *inter se* only non-agouti young are produced, the numbers in this case being 1,812.

From the result of these crosses it may be stated that the agouti pattern, though it may or may not *be* a single unit character, certainly behaves like one. Until it has been shown to be complex, the only safe course seems to be to consider it simple and allelomorphic to its absence.

7. THE DISTRIBUTIVE FACTOR, *R*.

This factor produces the true yellow varieties of mice by an almost complete exclusion of brown and black from the skin and hair. In those localities, therefore, the process of pigment formation is carried only as far as the "yellow" stage. The chief point of importance in connection with the appearance of yellow in the coat is this: Yellow-pigment granules, so far as experimental evidence goes, never appear in the skin and hair of mice unless certain distributive factors (*A* or *R*) are present to exclude part or all of the brown and black from those localities. In such regions oxidation beyond the yellow stage is impossible. In the absence of factors *A* and *R* the oxidation proceeds, over the whole coat, to the stage determined by the presence of the formative factors, *Br* or *B*.

"Yellow" mice are *not* produced by a factor comparable to the factors *Br* and *B*, but by a factor having an entirely different function, namely, that of restriction or inhibition. The nature of the agouti factor *A* is also restrictive, though in a much more limited degree. Thus the factors *A* and *R* have functions which are roughly comparable, in that they both "restrict" the formation of black and brown, allowing yellow to take their place.

In studying the relation of "yellow" to black agouti mice, Miss Durham (1911) has obtained extremely interesting and valuable results. Thus she has in two cases obtained a "yellow" animal from agouti parents, which is a reversal of the ordinary conditions. The fact that such a reversal of dominance can exist is of extreme importance and adds one more peculiarity to the genetic behavior of "yellow" mice. In all crosses made by the writer, however, yellow has proved epistatic to black agouti. When the black agouti young obtained from yellows were crossed *inter se*, 71 young were obtained, none of which were yellow.

When cream (fig. 18) is crossed with *wild black agouti* the yellow young obtained are *cream;* thus 3 cream and 2 *light-black agouti* young have been obtained. The wild black agouti possesses potentially a "cream" degree of pigmentation. If creams are crossed with black agouti animals produced by synthesis in experiments with other varieties, the yellow young produced are *yellow, not cream,* thus 12 *yellows* and 6 intense non-yellow young have been produced. These synthesized agoutis, then, are not potentially cream, but are darker-colored members of the series which fluctuates between cream and deep orange.

Cuénot (1905) reported the fact that homozygous yellow mice were not obtainable in his extensive experiments. This fact has been corroborated by other investigators. Cuénot (1911) has stated that the factor *R*, which restricts brown and black from the pelage, is the same in function as the factor *Y*, which forms the "yellow" degree of oxidation, and that there is no need of including both in the gametic formulæ of mice. But chemical evidence indicates that all brown or black *pigmented* mice *must* possess the ability to form yellow pigment in order to form the higher stages, viz, brown and black. Furthermore, they *must* possess this at times in all their gametes, otherwise a homozygous brown or black animal would be impossible. *Y*, therefore, which produces the yellow degree of oxidation is *not* comparable to *R*, which can occur in only one of the gametes of a zygote and which restricts brown and black forming material, thus producing visibly yellow mice.

Mice homozygous in *Y* are represented by wild black agoutis, but mice homozygous in *R* need not occur, by any present theory, nor *do they* occur in actual experiment.

Yellow varieties of mice exist, as Cuénot (1911) recognizes, in all the color varieties in which non-yellow mice exist. Their external appearance, however, leads one to identify only six types, namely: (1) black-eyed yellows, brown-eyed yellows, black-eyed dilute yellows, and brown-eyed dilute yellows in the "dark-eyed" series; (2) pink-eyed yellows and pink-eyed dilute yellows in the pale series. The experimenter can not distinguish by external appearances the black eyed and brown-eyed forms of the pink-eyed yellow series, and so must class them together unless breeding tests be applied.

The "yellow" coat of mice is due to as true a *pattern* factor as is the agouti coat, and the investigator errs when he considers the "yellow *coat*" a lower stage of development of a black or brown *coat*. Yellow pigment appears in the ticked or agouti coat by the action of a factor whose function is of a *restrictive* or inhibitive nature. In a very similar fashion yellow pigment appears on a greater scale in the coat of the "yellow" mouse.

"Yellow" in mice is no more allelomorphic to gray than is gray allelomorphic to black. Castle, as already stated, has shown that the factor which produces the ticked or gray coat is allelomorphic to its absence, not to black or any other pigment. It is an excellent thing to simplify gametic formulæ when this can be done with the support of experimental evidence, but the experimental work should precede the "simplification" unless a false impression is to be produced.

If yellow animals are crossed with non-yellow, equality of yellow and non-yellow young is approximated. The following numbers have been obtained:

	Yellow.	Non-yellow.
Observed....	864	872
Expected.....	868	868

Several litters of young have been produced by yellows mated *inter se* since the publication in 1910 of figures showing approximately a 2 to 1 ratio. The additional observations are:

	Yellow.	Non-yellow.
Observed...............	48	20
Expected, 2 to 1..........	45.2	22.6
Expected, 3 to 1..........	51	17

If these figures be added to those obtained by Miss Durham (1911), by Cuénot (1903), and by Castle and the writer (1910), the following result is obtained:

	Yellow.	Non-yellow.
Miss Durham (1911)......	448	232
Cuénot (1903)............	263	100
Castle & Little (1910)....	1,024	538
Little (1910 and 1911).....	48	20
Total.............	1,783	890
Expected, 2 to 1....	1,782.2	891
Expected, 3 to 1....	2,004.75	668.25

The relation of the restriction factor *R* to the factors *P* and *D* has been considered briefly under the head of those factors. The occurrence of dilute yellow mice, clearly distinguishable from "creams" or "light yellows," was reported by the writer (1911) in the dark-eyed color series. Since that time a few crosses have been made with *pink-eyed* dilute yellows and they have been found to conform in their general behavior with other yellow varieties. They apparently can not be obtained in a homozygous state, and when crossed *inter se* give *pink-eyed dilute* yellow and *pink-eyed dilute non-yellow,* as 2 to 1.

Dilute yellow animals, whether clear, sooty, or sable, are in appearance more heavily pigmented than are the lightest creams; but they, as the intense yellows, are found in shades of yellow that vary between cream and deep orange. Any and all *dilute* yellows have, however, the characteristic streaky, washed-out look of the dilute black or dilute brown forms. In crosses, dilute yellows bred *inter se* have given:

	Dilute yellow.	Dilute non-yellow.
Observed........	100	54
Expected, 2 to 1..	102.67	51.33
Expected, 3 to 1..	115.5	38.5

It will, then, be seen that dilute yellows, like intense yellows, give a 2 to 1 ratio, the homozygous type being apparently unable to develop.

Dilute yellows crossed with dilute non-yellows have given the following:

	Dilute yellow.	Dilute non-yellow.
Observed........	61	56
Expected.........	58.5	58.5

8. SOOTY YELLOWS AND SABLES.

It is well-known that varieties of yellow mice exist which have a varying amount of dark pigment (brown or black) in the hairs on their dorsal and lateral surfaces; this produces types of yellow known as "sooty yellows" or "sables." The amount of dark pigment varies from a few dark hairs, scattered along the mid-dorsal line, to a condition in which the whole dorsal and nearly all the lateral surfaces are dark, leaving yellow confined to the more ventral portions of the sides and to the belly. A series of arbitrary grades indicating the degree of sootiness has been constructed within the past year. By this means it is hoped to get more accurate ideas as to the nature of sooty yellows. The grades are based upon skins of "sooty" animals and these skins are used as the types by which the living animals are graded. Several experiments have been attempted with the sooty yellows, but all these are still in a preliminary state. Higher numbers of individuals from experiments now in progress may tend to change the conclusions to be drawn from work with this variety.

The sooty yellows in my stock are most of them homozygous for black, *i. e.*, *BB*. The question arose, how would such sooty forms behave if crossed with clear yellow lacking *B*. Experimental evidence shows that sooty yellows having only one dose of *B* are not as dark as those with two doses.

Thus 7451 sooty (grade $+1\frac{1}{4}$) when crossed with sooty yellow female 7452 ($+1\frac{1}{4}$) gave sooty yellow young, the average grade of which was +1. The same male when crossed with a brown (♀ 7730) gave yellow young, the grades of which averaged +.31. The writer has never obtained a sooty yellow or sable that did not carry the factor for the production of black pigment (*B*) in at least half its gametes. Several hundred sooty yellows or sables have been obtained.

Yellows having one dose of *B* when crossed *inter se* should give (besides yellows of their own type) those lacking *B* entirely as well as those having two doses of *B*. If the "sooty" character segregates, 25 per cent of the yellow animals should approximate the grade of their "sooty" grandparent, 50 per cent should resemble their parents, and 25 per cent should be clear yellow like their other grandparent. A table follows, showing the results of two families in this experiment. The numbers of young are as yet small.

Sooty yellow × brown.

Grade of sooty grand-parent.	No. of F_1 yellow young.	Average grade of F_1 yellows.	No. of F_2 yellow young.	Grades of F_2 yellow young.					Average of F_2 yellow young.
				0	.25	.50	.75	1.00	
+ .25....	12	+.06	7	7	..	..	..	..	+.00
+1.25....	4	+.31	6	1	2	2	..	1	+.42

It will, then, be seen that when the sooty grandparent is of low grade, $+\frac{1}{4}$, nearly clear yellow, his "sooty" character is to all intents and purposes lost in the cross with brown. It fails to reappear in F_2, so far as the animals obtained are concerned. When the grade of the sooty grandparent is 5 times as great, that is, +1.25, it will be seen that the average grade of F_1 is also about 5 times as great (that is, 0.31 as compared with 0.06). Also in F_2 darker forms are obtained which may approach the degree of sootiness seen in the grandparent.

Miss Durham (1911) is able to distinguish clearly between "sooty yellows" and "sables." In this connection she characterizes "sables" as produced in crossing yellows with blacks or browns. They have a dark black or brown streak down the middle of the back, while the rest of the mouse is yellow. Generally the hairs in the dark streak show a ticked pattern independent of whether the animal carries agouti or not. She has had certain animals (sables) which were dark-pigmented except for a yellow belly. Such animals always molted out sables. She says "sables" are not to be confused with sooty yellows, which result from mating yellow with black, and are dirty color all over with no pattern. She finds that yellows crossed *inter se* may give "sables," and that "sables" crossed *inter se* may give yellows, and that matters are further complicated by the occurrence of so-called "reversed sables," in which the dark hairs had yellow tips and bases, with a dark subapical band.

The writer must confess that he is unable to draw a clear line between "sables" and "sooty yellows" in all cases. The term sooty yellow is therefore intended in this paper to cover both varieties.

It is possible to explain the appearance of sooty yellows on the basis of fluctuation in activity of the factor *R*, restriction. Thus, when *R* is present in full strength the animal is clear yellow; if *R* is slightly weaker, some dark pigment shows itself.

The amount of dark pigment visible becomes progressively greater as the factor *R* becomes weaker or takes on a rhythmical activity. Thus, if *R* is hampered in activity during the growth of the first part of the hair, we have a dark tip formed. But if *R* comes into full activity again, a yellow band results, followed by a second weakening of *R*, resulting in a dark base to the hair. This would account for the superficial similarity to the agouti pattern. "Reversed sables" may possibly result from a reversal of the order in which the strong and weak periods of *R* occur. So, too, those very dark sooty yellows that lack the ticked-hair pattern may be considered due to continued weakness of the factor *R* during development of the hair of the first coat. When the second coat is formed, however, the factor *R* makes its appearance felt more strongly and an ordinary type of sable results, with less dark pigment than was present on the first coat.

In all such cases the idea is present that there is quantitative variation in the activity of the restriction factor *R*, showing itself in the varying amount of black or dark pigment present. If such weakness is due to any interchange of substance between gametes or any quantitative inexactitude in the process of segregation, we should expect that repeated crosses of sooty yellows with blacks would tend to produce much weakened yellows (*i. e.*, very dark sooty) with much black pigment, as well as *modified blacks* with some yellow pigment present. While this experiment has not yet been carried to large numbers it may be of interest to record the pedigree of one family:

Generation.	Parents.	Progeny.
I.........	♂4347 sooty yel. × ♀4346 black	9 sooty, av. + .78, and 2 blk.
II........	♂7451 sooty yel. × ♀7729 black	4 sooty, av. + 1.25, and 2 blk.
III.......	♂1029 sooty yel. × {♀1027 ♀1033} black.	6* sooty, av. + 1.50, and 7* blk.

*Among these sooties was ♂1318 (fig. 20) graded +3, darker by four "one-quarter" grades than any sooty previously obtained. The best previous was +2. Among the blacks in the same litter was ♂1316, *the first visibly modified black known to be homozygous* in hundreds of black animals that I have seen. His coat is distinctly tawny.

"Sooty yellows" and "sables" have not been reported in the pink-eyed series. This accords with the results expected by theory, for the modification of the factor *P*, which produces pink-eyed forms, reduces the brown and black pigment granules in the hair to such a degree that we should expect the dark pigment in the hairs of dark-eyed "sooty," yellows, and "sables" to be entirely lost in corresponding pink-eyed forms.

We have seen that the factor which produces "yellow" mice is dominant to its absence and is (in function) an inhibitor or restrictor of brown and black. It is interesting to compare with this condition the conditions observed in rabbits and guinea-pigs.

In rabbits Castle (1907*b*) has shown the occurrence of two types of "yellow" animals, both of which are hypostatic to non-yellow forms. The process of restriction, if it be such, that produces the yellow type of coat in rabbits is not as extensive as that which produces the clear yellow of mice. Thus all yellow rabbits which lack the factor *A* are, as Castle has shown, *sooty;* that is, they have considerable black pigment in the hair, which produces not a clear yellow, but a dull or dingy yellow coat. Such a condition, varying or fluctuating as it does in sooty yellows of the same gametic composition, may be called due to an *imperfectly recessive* character; that is to say, a condition which shows varying amounts of a dominant character on extracted recessive individuals, may be considered as showing *imperfect recessiveness.* Such a condition would be more explicable on the grounds that "yellow" in rabbits appeared as a *restriction* of *black and brown* than *as a loss* of those substances. Yellow in rabbits would then be, according to a nomenclature and system suggested by Dr. Castle, due to a *semi-potent restrictive factor.* By *semi-potent* is meant a positive character which must be present *in all the gametes* of an individual, for its manifestation in the zygote.

With such *semi-potent* characters may be contrasted *uni-potent* characters, which cause visible effect in the zygote when present in *one-half its gametes.* An example of this category of factors is seen in the factor *R*, in mice, which we have been discussing.

In guinea-pigs, however, we seem to have a different condition, in that sooty-yellow animals are *very rarely* formed. Thus yellow guinea-pigs extracted as recessive from a black race are, in a great majority of cases, *clear* yellows, whether they are "reds" or light "creams." The occurrence of such clear yellows is more explicable on a theory demanding *loss* of brown and black pigment from the skin and hair than from a process of *restriction,* for it has been seen that restriction is at times an extremely imperfect process, subject to frequent fluctuations in degree of activity, while *loss* is or should be a *clear-cut* process, removing the possibility of frequent fluctuations by *completely* removing the materials from which such fluctuations arise.

In studying "yellow" color varieties *similarity of color* should not have sufficient value in analysis to argue a common origin of all yellow forms. Discussion of such a question as the origin and physiological significance of different types of yellow must, at least for the present, be based on generalities, since definite evidence is wanting. On the evidence given by such general facts, the writer has above outlined a possible explanation of the observed conditions, fully realizing, however, that at best such an explanation is incomplete and unsatisfactory.

THE INHERITANCE OF SPOTTING.

Spotted forms exist in all the various color varieties of mice. Such spotted or piebald animals possess an amount of white varying from a few white hairs to a condition in which pigment occurs in the eye alone, all the coat being white. Spotting is at present one of the least-understood color phenomena, and further research is necessary before the correctness of any hypothesis concerning it can be proved. Nevertheless, it seems advisable to consider the physiological nature of spotting and to attempt to eliminate such theories as may be shown, even with our present imperfect knowledge, to be incorrect. As stated in the first part of this paper, present chemical knowledge leads us to the belief that all mammalian pigments are melanins.

Superficially, spotting appears to be partial albinism, and the question naturally arises as to whether it really is due to the same cause or causes that produce albinism, such cause or causes manifesting their presence in a lesser degree or in a mosaic condition.

Experimental evidence does not support a theory which postulates the common origin of white produced by spotting and that produced by albinism. If spotting is partial albinism we should expect, when spotted animals are crossed with albinos, that only spotted or albino animals would be obtained. Among the results observed by various investigators, none show better the fallacy of this point of view than the classic experiments of Darbishire (1902) with crosses of spotted waltzing mice and albinos of gray (black agouti) ancestry. The appearance of uniformly pigmented animals in the first generation of this cross proved conclusively that the processes producing the white of spotted coats and the white of albinos are not only non-identical, but are fundamentally different.

Since a difference in origin of these two types of white exists, the next matter of interest is to find out whether the difference lies in the qualitative chemical make-up of the two whites or in the nature of the distributive processes which allow them to appear in the hair.

Experiments bearing upon the qualitative nature of the two types of white have been made by Mudge (1909*a*) on piebald (spotted) and albino rats. He treated the pelage of animals of both these varieties with chemical agents calculated to provide an oxidizing substance which might act upon the chromogen in the white portions of the coat, if such a chromogen were present there. He found that the white hairs in both categories of animals became yellow, both reacting equally to the agent provided. A few months after the publication of his work on rats he obtained similar results in piebald and albino mice, by slightly varying the composition of the agent used.

The writer does not possess sufficient knowledge of chemistry to comment upon the ultimate value of the work done by Mudge, but in absence of contrary evidence it seems that his work, especially as it deals with the very types that we are considering, is worthy of confidence and forms a suitable base from which to draw conclusions.

If, as Riddle states, it seems absurd to postulate the *complete loss of chromogens in albinos,* we must suppose that *an enzyme or enzymes have been lost,* in order to prevent the formation of pigment. If, now, the work of Mudge shows that the white of spotting lacks the same class of substance as the white of albinism we must say that here also the enzyme or enzymes are absent from the white areas. But by the work of Darbishire, already alluded to, and that of later investigators as well, it is shown that the processes concerned in the origin of the two types of whites are *not identical.* We must then, by elimination, come to the conclusion that the nature of the *processes which control the distribution of the enzyme or enzymes* differs in the two categories.

We have seen that the amount of pigment in the hair of intense pigmented animals is dependent upon the cooperation of two factors, D and P. In the wild *Mus musculus* the pigment occurs distributed over the entire coat, and the animal is said to be *self or uniformly pigmented.*

We have supposed that the distribution of pigment is controlled by certain factors. Thus we have supposed that *density* of pigmentation is controlled by a factor D, by the activity of which a certain amount of pigment is formed in eyes and skin and hair. We have recognized a quantitative modification of this factor in the case of dilute varieties, possessing *less* pigment. Since this modification affects all three pigments (yellow, brown, and black) and since we have supposed brown and black to be higher oxidation stages of yellow, it seems logical to consider D a factor modifying Y, and in this way also modifying Br and B, which are, so to speak, converted Y. When D is modified in amount, less Y is converted to the brown or black stage. This is the condition seen in dilute animals. Logically we should expect another type of modification of Y. In *self* animals Y is distributed over the whole coat. We should expect some forms in which Y was distributed only to certain portions of the body. This modification is seen in the forms in which white spots occur. Such white areas may be considered as those from which the Y-forming substance is absent. Thus the relation of these factors to one another may be roughly shown as follows:

Color producing substance Y	Distributed in a certain degree of density $= D$	Modified in amount to form dilute varieties $= d$
	Distributed to a certain extent (self) $= S$	Modified in amount to form spotted varieties $= s$

If we designate the spotted (piebald) forms by the letter s, we may logically consider the unmodified self forms as being of the constitution S. We would expect, then, that in crosses between a spotted race of known gametic formula (s) and a self race of formula (S) a mendelian monohybrid ratio would be observed. That such is the case has been recorded by Doncaster (1906) and by Castle and MacCurdy (1907) in the case of "hooded" and self rats. Such a type of spotting as that seen in the hooded rats is, then, a unit character so far as its behavior in crosses is concerned.

Cuénot, working with mice, has found that spotted forms exist, varying greatly in proportion of white to colored areas. This series of spotted forms he accounts for by supposing that there are present a number of small factors for the production of spotting (*panachure*). These he designates p_1, p_2, p_3, p_4, ... etc. Cuénot is by no means alone in favoring multiple factors as an explanation for spotting. It is easy and attractive to imagine a factor for every observed degree of spotting. The various types of spotted animals seem clear-cut, the colored and white areas seem to form a marked contrast, and the presence of many factors to produce these many forms gives an air of finality to an hypothesis which is alluring.

The advantages of a multiple-factor hypothesis, however, are rendered dubious by the observed occurrence of strains which show that a certain amount of fluctuation exists in the manifestation of even these assumed multiple units. It is questionable whether it would be possible to distinguish between a result produced by multiple factors of the number necessary to explain the occurrence of the various spotted forms and a continuous series formed by fluctuation of of the original modification which produces spotting.

Observed experimental facts, however, do not favor a multiple-factor hypothesis. Thus, if multiple factors for spotting existed, the black-eyed white variety would possess the greatest number of these spotting factors. Cuénot in mice and Castle in guinea-pigs found that spotting was recessive to self in crosses. Therefore the black-eyed white forms would possess a great number of recessive spotting factors, p_1, p_2, p_3, p_4, p_5, p_6, etc. How, then, could two such animals when crossed *inter se* give in their young practically the whole gamut of spotted forms, as Castle (1905, p. 45), found was the case.

In a somewhat similar way the presence-and-absence hypothesis meets with trouble in the same cross, *i. e.*, black-eyed white × black-eyed white. The spotting from which the black-eyed whites are derived is recessive. It is, therefore, according to the presence-and-absence hypothesis, as advanced by Bateson and Punnett, due to the *loss* or *absence* of a factor or factors for uniformity of pigmentation. Yet two animals having, according to this theory, lost the factors for pigment production in the coat, give young which often have a large amount of pigment on the coat. The presence-and-absence hypothesis, in order to explain this case, must imagine a degree of fluctuation in the manifestation of the spotting character which makes proof of the *multiple-factor hypothesis* difficult if not impossible.

In the writer's opinion, present knowledge of spotted forms is too scanty to decide whether spotting is due to a process of *loss* of the factor for uniformity of pigmentation, or to a hypostatic restrictive factor. It seems, however, that such spotting as one encounters in guinea-pigs, hooded rats, and in many mice is a unit character subject to enormous quantitative fluctuation, and that it may be considered due to a modification of the factor *Y* or *U* which is hypostatic to unmodified or "self" forms.

In view of the fact that the same substance *Y* is distributed in two different ways to produce spotting and dilution, we may consider it as consisting of an amount of pigment (*D*) distributed over the entire animal (*S*); therefore we may consider the pigment of the wild mouse as being designated by the letters *DS*. An animal may then be of one of the following formulæ:

DS intense self. *Ds* intense spotted. *dS* dilute self. *ds* dilute spotted.

We have previously discussed the observable fluctuations in amount of pigment in animals possessing D, for example in yellows. The fluctuations observed in the case of spotted animals are little if any greater in extent than the fluctuations from deep orange to cream already noted in the case of yellow mice. If there are two ways (d and s) in which the factors D and S may respectively be modified, we should expect that the same might hold in the case of the factor P. The quantitative modification of this factor (p), acting upon brown and black pigment to the exclusion of yellow, produces the pink-eyed colored series.

If a regional modification of black and brown forming substances (Br and B) existed, we should expect a spotted condition to be formed. Here, however, the spots would be *black or brown on a yellow ground.* To such a class as this we may say that the tortoise varieties of guinea-pigs belong. This condition is in a measure *hypostatic* to self-pigmented forms, as are the (s) spotted forms. We have supposed that the factor P produced a certain amount of black or brown substance typified by the wild *Mus musculus.* This factor, then, appears to bear the same relation to the factors Br and B that the factor D does to the factor Y. We may, therefore, logically construct a rough diagram to show the relations of the distributive factors to Br and B, as we did in the case of Y:

$$\begin{array}{r}\text{Factors for the}\\ \text{production of}\\ \text{brown and}\\ \text{black pigment}\end{array}\left\{\begin{array}{l} Br\left\{\begin{array}{l}\text{Distributed in a certain}\\ \quad\text{degree of depth} = P\end{array}\right.\left\{\begin{array}{l}\text{Modified in amount to form}\\ \quad\text{pink-eyed varieties} = p\end{array}\right.\\ Br\left\{\begin{array}{l}\text{Distributed to certain}\\ \quad\text{extent (total)} = T\end{array}\right.\left\{\begin{array}{l}\text{Modified in amount to form}\\ \quad\text{tortoise varieties} = t\end{array}\right.\end{array}\right.$$

If we designate the tortoise spotting by t, we may consider its epistatic allelomorph as T, total or self pigmentation. In this case the factor P becomes complicated, as did the factor D, becoming PT. As in the case of the factor DS, animals may be of any one of the following formulæ:

PT dark-eyed self. pT pink-eyed self.
Pt dark-eyed tortoise. pt pink-eyed tortoise.

In mice we find that the p modification has taken place, while in guinea-pigs the t modification is well known, and Castle (1912*b*) has described the origin of a pink-eyed form of guinea-pig which may turn out to be the p modification.

It may be seen from the foregoing description that the two forms of spotting (piebald and tortoise) are entirely independent, and it is thus entirely conceivable that they should occur in the same individual. This appears to be the case in the well-known tri-colored breeds of domesticated animals.

One of the best-known cases of inheritance in tri-colored races is found in the case of "basset" hounds, on which Galton based his "law" of heredity. The character considered was the presence or absence of black in addition to yellow and white. When black was present the tri-color condition was produced. Though there is no direct evidence at hand, Bateson (1909), in discussing these experiments, states that yellow is not usually dominant to black. If this is the case the observed facts may be explained as follows:

In guinea-pigs the presence of black and yellow spots on any individual depends upon the presence of a spotting character which acts upon a *totally* *black* pigmented animal to produce a blotched black-and-yellow appearance. For the sake of convenience we may call animals possessing this "tortoise" marking *t*. All self-black animals lacking this modification, and therefore having no red blotches, are of the formula *T*. Experiments with guinea-pigs (at present being carried on by Dr. Castle) shows that *self-black* is epistatic to tortoise. This pair of characters is, however, independent from the factors, *E* =*extended black pigmentation, necessary for the production of any* black hairs on the coat, and its allelomorph *e* =the loss of black pigment from the coat, producing yellow animals.

Thus, if a race of tortoise animals existed, formula *EEtt,* we should have a homozygous race of tortoise animals (which in fact exist). If, however, the tortoise animals were of the formula *Eett* we should expect young of three kinds:

(*a*) *EEtt* tortoise. (*b*) *Eett* tortoise. (*c*) *eett* yellow.*

Types (*a*) and (*b*) having *E* present would be able to form black pigment on the coat; but type (*c*), lacking *E*, would be *yellow* in appearance, though it would be potentially tortoise.

If the factor for spotting with white (*s*) be added to the formula of a tortoise animal (*Eett*), we should have, if these animals were bred together, three kinds of young.

(*a*) *EEttss* tri-color (tortoise and white).
(*b*) *Eettss* tri-color (tortoise and white).
(*c*) *eettss* yellow and white.*

Types (*a*) and (*b*) would be tri-color, that is, tortoise and white; type (*c*) would be yellow and white. This might account for the appearance of yellow and white individuals in a race of tri-colored animals.

If, however, yellow were epistatic to black, as in mice, we should have to explain things differently. Tortoise animals could then be of only one formula and would breed true, being recessives, whereas self yellows might also produce tortoise young.

rrtt =tortoise.
Rrtt =yellow (heterozygous in tortoise).
RRtt =yellow (homozygous).

If, now, the modification *s* were added to such hypothetical tortoise animals, we should have

rrttss =tri-color (tortoise and white) homozygous.

If such animals were crossed *inter se*, we should, on genetic grounds, have to suppose a change of dominance to explain the occurrence of yellow-and-white young. This does not seem likely. A simple mechanical fact is, however, able to account for the occurrence of yellow-and-white animals in an homozygous or heterozygous race of tortoise-and-white (tri-color) animals. Both forms of spotting are independent as to the regions of the coat which they affect. If the *white* regions should, by chance, coincide with the black regions

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*Castle (1905), p. 34, has described such animals.

of a tortoise animal we should have an animal yellow-and-white in appearance, though gametically a pure tri-color (tortoise and white). This condition is found in guinea-pigs where two yellow (red) and white animals when crossed together have given young with black on the coat (Castle, 1912), and we know that one of these animals at least must have the gametic composition of a tri-color. In a case of this sort the yellow-and-white animals would occur in ratios entirely free from any mendelian principle, and would give a *spurious reversal of dominance.*

Perhaps one of the two foregoing suggestions may serve to throw some light on the results upon which Galton's "law" of heredity was based. It must be remembered that tortoise-shell animals are in their gametic composition no more intermediates between black (extended) and yellow (restricted) animals than forms spotted with white are intermediate between colored forms and albinos.

CROSSES WITH JAPANESE WALTZING MICE.

Morgan (1911*a*) has mentioned the fact that in crosses between self and spotted forms, in mice, the spotting seemed modified or contaminated by the cross. He gives no figures, however, in support of this statement and fails to mention that the modification of spotted forms by crossing with self was reported by MacCurdy and Castle (1907).

Dr. Castle and the writer have examined carefully the degree of pigmentation of a race of pure Japanese spotted mice and have estimated the percentage of colored area on the dorsal surface; 72 animals were thus examined. The average pigmentation was 32 per cent. The range of pigmentation was from 20 to 55 per cent. Animals of this pure Japanese race were crossed with a uniform self-pigmented race of homozygous dilute brown animals, known to *produce no spotted or albino young.* F_1 from these animals consisted of all *self* pigmented young showing no spots of white. Certain of these F_1 animals were crossed *inter se* to obtain F_2, others were crossed back with females of the pure Japanese race.

In the first case F_2 was found to consist of 45 self animals (no spots) and 21 animals having some white hairs or spots on the dorsal surface. The 3 to 1 ratio is here approximated, the exact theoretical expectation being 49.5 self to 16.5 spotted. The extracted spotted animals differ widely from the original Japanese race from which they inherited the spotted-coat character. A comparison of the two categories of spotted forms (together with the back cross, which will be treated later) will be seen in the following table:

	No. of spotted individuals.	Average percentage of dorsal surface pigmented.	Range of individuals in percentage of dorsal surface pigmented.
(1) Japanese........	72	32	20 to 55
(2) F_2..............	21	85.3	50 to 99
(3) Back cross......	47	60.2	40 to 99
(4) Back cross F_2...	19	70.4	47 to 85

From this table it will be seen that the spotted individuals of F_2 have been contaminated by the cross, having their dorsal pigmentation increased on the average more than 50 per cent over the average of the pure Japanese race. The range of the spotted forms in F_2 is also very different from that in the Japanese race. There are no F_2 animals within 18 per cent of the average grade of the Japanese mice (32 per cent); also there is only one F_2 animal out of 21 that is as lightly pigmented as the darkest of the Japanese race.

The back cross, between F_1 animals and individuals from the pure Japanese race, we should expect to give *spotted* and self animals in a 1 : 1 ratio. The spotted animals, on a basis of contamination, should not be so extensively modified as in the F_2 animals; that is, their degree of dorsal pigmentation should be less. There have been 96 animals produced in this back cross, of which 49 are self and 47 spotted, showing that "spotting" and "self" are still behaving as a pair of allelomorphic characters. The spotted animals from this cross—see above table, (3)—show an average of 60.2 per cent of the dorsal surface pigmented; their range is from 40 to 99 per cent. This coincides qualitatively with the expectation.

One more cross may be recorded. Certain of the 49 selfs produced by the back cross were bred *inter se*, thus producing a generation which may be designated as "back cross F_2." Spotted animals resulting from this cross, on the theory of contamination, should show a degree of dorsal pigmentation between that of the first F_2 (85.3 per cent) and of the back cross (60.2 per cent). As a matter of fact the results show that their average pigmentation is 70.4 per cent.

ASSOCIATION OF CHARACTERS.

The question naturally arises as to whether the various characters are completely independent of each other or whether coupling or gametic association of any sort exists between some of them. Morgan (1911*b*) has observed in *Drosophila* certain results best explained on an hypothesis of "association" of certain characters in the gamete. It remains to be seen whether any such "association" of characters exists in mice. For this purpose the writer has tabulated the results of four crosses:

I. Cross 10A. Wild Black Agouti (Mus musculus) Crossed with Dilute Brown.

The black-agouti parent possesses factors B = black, A = agouti, and D = density. The dilute-brown parent lacks the factors B, A, and D. F_1 resembles the wild parent. In F_2 we expect 8 classes, as follows:

(1) Black agouti = $BrBAD$[*]
(2) Black = $BrBD$
(3) Brown agouti = $BrAD$
(4) Dilute black agouti = $BrBAd$
(5) Brown = BrD
(6) Dilute brown agouti = $BrAd$
(7) Dilute black = $BrBd$
(8) Dilute brown = Brd

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[*] All animals in this cross possess the general color factor Y, and the factor for *fullness* of black and brown pigmentation, P. They are therefore omitted from the formulæ for purpose of simplification.

On an hypothesis of association we should expect types (1) and (8) to be in excess of the numbers called for by random segregation. The experimental results are:

	(1) *BAg.*	(2) *Blk.*	(3) *BrAg.*	(4) Dilute *BAg.*	(5) Brown.	(6) Dilute *BrAg.*	(7) Dilute *Blk.*	(8) Dilute *Br.*
Observed.............	20	9	7	9	0	4	4	2
Expected on a basis of random segregation.	23	7.7	.77	7.7	2.6	2.6	2.6	1.0

The sum of classes (1) and (8) on a basis of random segregation is 24. The observed number is *less* by 2, showing no signs of association of the characters *A*, *B*, and *D*.

II. Cross 10. Pink-Eyed Black Agouti Crossed with Dilute Brown Agouti.

The pink-eyed black agouti parent possesses *B* (black), *D* (density), and lacks *P* (fullness of black and brown pigmentation, dark eye). The dilute brown agouti parent is of the formula *dP*, lacking the factor for density but possessing that for dark eye. F_1 is indistinguishable from the wild black agouti (*Mus musculus*).

Pink-eyed black agouti BrpBD × *dilute-brown agouti BrPd.*

F_1 Black agouti, BBr_2PpDd
F_2 (1) Black agouti, *BrBPDA*
(2) Brown agouti, *BrPDA*
(3) Pink-eyed black agouti, *BBrpDA*
(4) Dilute black agouti, *BrBPdA*
F_2 (5) Pink-eyed brown agouti, *BrpDA*
(6) Pink-eyed dilute-black agouti, *BrBpdA*
(7) Dilute-brown agouti, *BrPdA*
(8) Pink-eyed dilute-brown agouti, *BrpdA*

Classes (3) and (7) should be in excess if there is any association. The experimental results follow:

	(1) *BAg.*	(2) *BrAg.*	(3) *pBag.*	(4) *dBag.*	(5) *pBrAg.*	(6) *pdBag.*	(7) *dBrag.*	(8) *pdBrag.*
Observed.............	40	13	12	18	3	3	5	2
Expected on a basis of random segregation.	40.5	13.5	13.5	13.5	4.5	4.5	4.5	1.5

The sum of classes (3) and (7) on a basis of random segregation is 18, the observed number in the classes is 17; again no evidence of association.

III. Cross 66. Pink-eyed Black Crossed with Brown.

The pink-eyed black parent possesses the factor *B* but lacks *P* and is therefore *Bp;* the brown parent lacks *B* but possesses *P*.

Parents black Bp × *brown P.*

F_1 Black *BPp*. F_2 (1) Black *BP*,
(2) Pink-eyed black *Bp*, (3) Brown *P*, (4) Pink-eyed brown *p*.

On a basis of association of characters both classes (2) and (3) should be in excess. The observed result follows:

Classes.	(1) Black.	(2) Pink-eyed black.	(3) Brown.	(4) Pink-eyed brown.
Observed	199	75	61	19
Expected on basis of random segregation	199	66.3	66.3	22.1

It will be seen that while type (2), pink-eyed black, is slightly in excess, the browns (which must also on the association hypothesis be in excess) are not. The sum of classes (2) and (3) is 136, while on the supposition of random segregation we should expect 132.6.

IV. CROSS 96. BROWN CROSSED WITH PINK-EYED DILUTE-BROWN.

Brown possesses both factors *D* and *P;* pink-eyed dilute brown has neither of them and is *dp* in formula.

Brown DP × *Pink-eyed dilute brown dp.*

F_1 Brown, *DdPp*. F_2 (1) Brown, *DP*, (2) Dilute brown, *dP*,
(3) Pink-eyed brown, *Dp*, (4) Pink-eyed dilute brown, *dp*.

On an association hypothesis both classes (1) and (4) should be in excess.

Classes.	(1) Brown.	(2) Dilute brown.	(3) Pink-eyed brown.	(4) Pink-eyed dilute brown.	Sum of classes (1) and (4).
Observed	49	21	3	1	50
Expected on a basis of random segregation	41.4	13.8	13.8	4.6	46

The sum of classes (1) and (4) is only 4 in excess of the expectation on a basis of random segregation. This may be considered as showing no association, because class (4) is not in excess of the expectation. If now we add together the numbers of individuals observed in the classes that should show "association," if it exists, we have 225, while the number called for by the mendelian hypothesis of random segregation is 220.6, a striking approximation to the observed numbers. We may then conclude that these experiments show no sign of association in the gametes between the factors *D, P, A,* or *B* or between the four conditions characteristic of their absence.

PART II. EXPERIMENTAL DATA.

EXPLANATION OF SYMBOLS.

Before giving in detail the matings made, a few general facts may be stated. In the course of the experiments noted here, more than 10,500 animals have been raised. The independence of all the factors given in this paper has been made certain from breeding tests. The results may first be considered in a general way which may serve, for the present, to show that the factors included in this paper exist as units in inheritance. We may best consider the yellow and non-yellow forms under different headings. For non-yellow mice, the results given here are largely corroborative of evidence previously given by Cuénot, Bateson, Durham, and other investigators.

In expressing the gametic or zygotic formulæ of the various types we employ a slight modification of the two systems most frequently used. Thus, when a given factor is known to be *absent,* its symbol is *omitted* from the formula. For example, the gametic formula of homozygous brown-pigmented animals is given as $YBrDP$, the zygotic formula $Y_2Br_2D_2P_2$. Albinos, which are gametically homozygous brown animals, would differ merely in that the color producer Y is absent; they would, therefore, have the gametic formula $BrDP$ and the zygotic formula $Br_2D_2P_2$. If the original brown race had been heterozygous in the color factor Y, its zygotic formula would be $YBr_2D_2P_2$ and the gametes that could be formed would be obviously $YBrDP$ and $BrDP$.

If, however, we are dealing with such a pair of characters as "dark-eye" P and "pink-eye" p, we are not justified in supposing an *absence of* P in the pink-eyed forms. We merely know that an hypostatic modification of P has occurred, and this is best designated by p. If now we have a homozygous brown animal, with the zygotic formula $Y_2Br_2D_2P_2$, we may designate the homozygous *pink-eyed* brown as $Y_2Br_2D_2p_2$. The dark-eyed brown heterozygous in P would then be $Y_2Br_2D_2Pp$ and would form two sorts of gametes $YBrDP$ and $YBrDp$.

It is interesting to note that the system employed by the foremost exponents of the presence-and-absence hypothesis really hints at the *presence of two conditions, the one* (B) *epistatic to the other* (b). On the other hand, Castle, who does not follow so implicitly the limits of the presence-and-absence hypothesis, adopts a system of notation which, in the case of certain characters, indicates the hypostatic condition by *the absence of any symbol to designate it.*

The excellent comparative study by Cuénot (1911) has served to make clear many debated points due to variations in systems of notation, and it is therefore with some doubt as to its advisability that the writer advances still a different one. It seems, however, exceeding present knowledge to denote by the same system characters which may obviously be absent and those whose absence is far from proved.

There should exist, according to the hypothesis advanced above, 81 types of zygotes in the non-yellow self-colored races. A similar number of types of albinos should also be formed. In the experiments here recorded no effort has been made to obtain a large number of types of zygotes, yet 58 of the 81 pure colored types have been met with. The occurrence of these 58 types is assured by breeding tests, but it is almost certain that all 81 types have occurred many times in the writer's experiments, since only a very small part of the animals raised has been used for breeding.

A table follows showing the numbers of possible zygotic types, and the number of the observed types in the 16 self-pigmented non-yellow color varieties which are homozygous in the color-producer (*Y*).

Gametic formula.	Description.	Possible.	Observed.
YBrBDPA	Black agouti	16	8
YBrBdPA	Dilute black agouti	8	5
YBrBDpA	Pink-eyed black agouti	8	8
YBrBDP	Black	8	5
YBrDPA	Brown agouti	8	5
YBrBdpA	Pink-eyed dilute black agouti	4	2
YBrDpA	Pink-eyed brown agouti	4	3
YBrBDp	Pink-eyed black	4	3
YBrdPA	Dilute brown agouti	4	2
YBrDP	Brown	4	4
YBrBdP	Dilute black	4	4
YBrdP	Dilute brown	2	2
YBrDp	Pink-eyed brown	2	2
YBrdpA	Pink-eyed dilute brown agouti	2	2
YBrBdp	Pink-eyed dilute black	2	2
YBrdp	Pink-eyed dilute brown	1	1
		81	58

If yellow animals differ from the non-yellow by the presence of an epistatic restriction factor, *R*, we should expect that the 81 zygotic types of non-yellow mice would have their counterpart in the yellow series. Cuénot (1911) recognizes this fact, but explains it in a slightly different way, which need not be discussed here.

Yellow animals corresponding with 14 of the 16 non-yellow color varieties have been recognized in breeding tests. The yellows which are potentially dilute brown and those which are potentially pink-eyed dilute-brown agouti are the only forms not as yet demonstrated by breeding tests. There is no reason to suppose that these can not be produced, and it is almost certain that they have occurred among my animals but have not happened to be chosen for breeding.

The gametic and zygotic formulæ used in this part of the paper will be identical with those employed in the first part. A set of abbreviations, given on p. 50, will be used in tables. The results here tabulated follow the various experiments through April 15, 1912.

COLOR VARIETIES OF MICE.*

A. EXTENDED SERIES (RESTRICTION FACTOR ABSENT).

1. *With the agouti pattern.*

Color variety.		
1. Black agouti, fig. 1	*YBrBDPA*	Black agouti series
2. Dilute black agouti, fig. 2	*YBrBdPA*	
3. Pink-eyed black agouti, fig. 3	*YBrBDpA*	
4. Pink-eyed dilute black agouti, fig. 4	*YBrBdpA*	
5. Brown agouti, fig. 5	*YBrDPA*	Brown agouti series
6. Dilute brown agouti, fig. 6	*YBrdPA*	
7. Pink-eyed brown agouti, fig. 7	*YBrDpA*	
8. Pink-eyed dilute brown agouti, fig. 8	*YBrdpA*	

2. *Without the agouti pattern.*

9. Black, fig. 9	*YBrBDP*	Black series
10. Dilute black, fig. 10	*YBrBdP*	
11. Pink-eyed black, fig. 11	*YBrBDp*	
12. Pink-eyed dilute black, fig. 12	*YBrBdp*	
13. Brown, fig. 13	*YBrDP*	Brown series
14. Dilute brown, fig. 14	*YBrdP*	
15. Pink-eyed brown, fig. 15	*YBrDp*	
16. Pink-eyed dilute brown, fig. 16	*YBrdp*	

B. RESTRICTED SERIES. ANIMALS IN THIS SERIES ALWAYS HETEROZYGOUS IN *R*.

Color variety.			
17. Black-eyed yellow	*YBrBDPAR*		Dark-eyed intense yellow series
18. Black-eyed yellow, fig. 17	*YBrBDPR*		
19. Brown-eyed yellow, fig. 18	*YBrDPAR*		
20. Brown-eyed yellow	*YBrDPR*		
21. Dilute black-eyed yellow	*YBrBdPAR*		Dark-eyed dilute yellow series
22. Dilute black-eyed yellow	*YBrBdPR*		
23. Dilute brown-eyed yellow	*YBrdPAR*		
24. Dilute brown-eyed yellow, fig. 19	*YBrdPR*		
25. Pink-eyed yellow	*YBrBDpAR*	Black, brown and yellow pigment.	Pink-eyed intense yellow series
26. Pink-eyed yellow	*YBrBDpR*		
27. Pink-eyed yellow	*YBrDpAR*	Brown and yellow pigment only	
28. Pink-eyed yellow	*YBrDpR*		
29. Pink-eyed dilute yellow	*YBrBdpAR*	Black, brown and yellow pigment	Pink-eyed dilute yellow series
30. Pink-eyed dilute yellow	*YBrBdpR*		
31. Pink-eyed dilute yellow	*YBrdpAR*	Brown and yellow pigment only	
32. Pink-eyed dilute yellow	*YBrdpR*		

There are 32 pigmented varieties of mice which may be obtained in pure races. The "restricted series," however, may be obtained pure in the sense only that animals may be obtained which give merely the type of yellow written before their gametic formula, and the single variety of the "extended" series which the rest of their gametic constitution demands. Albino varieties corresponding with these 32 colored forms are expected to occur and may be produced at will. These albinos are distinguishable from one another only by breeding tests, and it is therefore doubtful whether all the 32 varieties have as yet been isolated.

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* The factors T (total pigmentation) and S (self-pigmentation) are not included in these formulæ.

In the following pages will be found a brief description of the various color varieties, as they appear to the unaided eye, followed by a list of crosses made with each color variety. In the tables it has been found expedient to use the following abbreviations to designate in simpler form the color varieties, a list of which has already been given:

B = black,
Br = brown,
d = dilute,
p = pink-eyed,
Ag = agouti,
W = white (albino),
Y = yellow,
sY = sooty yellow,
cY = cream yellow.

Thus, for example, $pdBAg$ is equivalent to pink-eyed dilute black agouti, color variety No. 4 of the extended series.

Unfortunately, in many of the crosses the numbers of animals recorded are small. Aberrations from the expected mendelian ratios of the color classes may also be found in some cases; but an examination of these seems to indicate that they would diminish with an increase in the number of animals recorded.

EXTENDED SERIES.

I. BLACK AGOUTI, $YBrBDPA$ (FIG. 1).

The common coloration seen in the house-mouse (*Mus musculus*). Eyes black, ears darkly pigmented, hairs on ventral surface tipped with dull-yellowish, then dark slaty to the base. Tail dark-pigmented. Dorsal hairs tipped with black, then having a yellow band and below that being slaty to their base. Such an arrangement produces the "ticked" or "agouti" coat pattern. Tuft of hairs at the base of the ears yellowish—a few light hairs on sides, flanks, and feet. Hairs around anus are light.

Black agouti × black agouti.

CROSS 1. Giving only BAg young; therefore one of the parents, at least, may be considered homozygous black agouti, type 1 (extended series). The animals used in this cross were descended from yellows.

Mating.	Parents.	BAg.
74	166 or 131 × 135.......	6
64	166 × 135.............	2
82	164 or 131 × unmarked.	9
44	139 × 530.04B........	11
48	509.4B × 530.07B.....	8
		36

CROSS 2. Parents heterozygous in black. $Y_2Br_2BD_2P_2A_2 \times Y_2Br_2BD_2P_2A_2$. Expectation, 3 BAg to 1 $BrAg$.

Mating.	Parents.	BAg.	$BrAg$.
561	4914 or 4915 × 4913...	7	2

Cross 3. Parents heterozygous in color factor and in black. $YBr_2BD_2P_2A_2 \times YBr_2BD_2P_2A_2$. Expectation, 9 *BAg*, 3 *BrAg*, to 4 *W*. The parents in this cross were derived from yellows.

Mating.	Parents.	*BAg.*	*BrAg.*	*W.*
45	530.02*B* × 176.....	5	5	2

Cross 4. Parents heterozygous in black and density. $Y_2Br_2BDdP_2A_2 \times Y_2Br_2BDdP_2A_2$. Expectation, 9 *BAg*, 3 *BrAg*, 3 *dBAg*, 1 *dBrAg*.

Mating.	Parents.	*BAg.*	*BrAg.*	*dBAg.*	*dBrAg.*
25	530.6*A* × 530.5*A* ...	9	4	1	1

Cross 5. Parents heterozygous in dark eye. $Y_2Br_2B_2D_2PpA_2 \times Y_2Br_2B_2D_2PpA_2$. Expectation, 3 *BAg* to 1 *pBAg*.

Mating.	Parents.	*BAg.*	*pBAg.*
134	673 × 671 ...	8	2
138	672 × 671 ...	10	1
		18	3

Cross 6. Parents heterozygous in color factor, dark eye, and agouti. $YBr_2B_2D_2PpA \times YBr_2B_2D_2PpA$. Expectation, 27 *BAg*, 9 *B*, 9 *pBAg*, 3 *pB*, 16 *W*.

Mating.	Parents.	*BAg.*	*pB.*	*W.*
404	2889 × unmarked....	2	1	1

Cross 7. Parents heterozygous in black, dark eye, and agouti. $Y_2Br_2BD_2PpA \times YBr_2BD_2PpA$. Expectation, 27 *BAg*, 9 *pBAg*, 9 *BrAg*, 9 *B*, 3 *pBrAg*, 3 *Br*, 3 *pB*, 1 *pBr*.

Mating.	Parents.	*BAg.*	*BrAg.*	*B.*	*pBAg.*	*pBrAg.*	*Br.*	*pB*	*pBr.*
163	545 × 546	5	5	3	3	..	1	..	..
119	547 × 546	5	1	2	1	..	2	..	..
175	548 × 546	7	3	2	3	..	1	1	..
116	545 or 548 × 546 ...	6	3	2	..	..	2	..	..
140	545–547–548 × 546..	16	6	1	2	3	1	1	..
162	672–673 × 918	5	..	1	..	..	2	1	..
169	917 × 918	4	..	..	..	..	..	1	..
		48	18	11	9	3	9	4	..

Cross 8. Parents heterozygous in color factor, density, and dark eye. $YBr_2B_2DdPpA_2 \times YBr_2B_2DdPpA_2$. Should give 27 *BAg*, 9 *dBAg*, 9 *pBAg*, 3 *pdBAg*, 16 *W*.

Mating.	Parents.	*BAg.*	*dBAg.*	*pBAg.*	*pdBAg.*	*W.*
340	2756, 2760 × 2757	2	2	1	1	1
462	3120 × unmarked	3	2	..	..	..
		5	4	1	1	1

Cross 9. Parents heterozygous in density, dark eye, and agouti. $Y_2Br_2B_2DdPpA \times Y_2Br_2B_2DdPpA$. Expectation, 27 *BAg*, 9 *pBAg*, 9 *B*, 9 *dBAg*, 3 *pdBAg*, 3 *dB*, 3 *pB*, 1 *pdB*.

Mating.	Parents.	*BAg.*	*dBAg.*	*B.*	*pBAg.*	*pB.*	*pdBAg.*	*dB.*	*pdB.*
403	Unmarked × unmarked ..	9	5	9	1	2	..	..	..

Cross 10. Parents heterozygous in black, density, and dark eye. $Y_2Br_2BDdPpA_2 \times Y_2Br_2BDdPpA_2$. Expectation, 27 *BAg*, 9 *pBAg*, 9 *BrAg*, 9 *dBAg*, 3 *pdBAg*, 3 *pBrAg*, 3 *dBrAg*, 1 *pdBrAg*.

Mating.	Parents.	*BAg.*	*dBAg.*	*pBAg.*	*BrAg.*	*dBrAg.*	*pdBAg.*	*pBrAg.*	*pdBrAg.*	*p*–?	?
338	1290 × 1289	9	1	..	2	2	..	..	1	1	..
199	1291 × 1289	5	7	3	4	1	1	1	..	..	..
203	1293 × 1289	2	1	3	2	..	..	..	..	..	..
241	1291 – 1293 × 1289 ..	3	3	..	1	1	..	1	..	..	..
275	1290–1291, 1293 × 1289	17	4	5	2	1	2	1	1	1	..
260	1539 × 1289	4	2	1	2	..	..	..	..	2	3
		40	18	12	13	5	3	3	2	4	3

Cross 10a. Parents heterozygous in black, density, and agouti $Y_2Br_2BDdP_2A \times Y_2Br_2BDdP_2A$. Expectation, 27 *BAg*, 9 *dBAg*, 9 *BrAg*, 9 *B*, 3 *dBrAg*, 3 *dB*, 3 *Br*, 1 *dBr*.

Mating.	Parents.	*BAg.*	*dBAg.*	*BrAg.*	*B.*	*dBrAg.*	*dB*	*Br.*	*dBr.*
A 2	*S*6 × *S*5 × *S*8.	7	3	4	3	..	..	..	..
A 7	*S*19 × *S*8	10	6	2	4	2	2	..	1
A 8	*S*18 × *S*8	3	..	1	1	1	..	..	..
*A*10	*S*98 × *S*5	..	..	..	1	1	2	..	1
		20	9	7	9	4	4	0	2

Black agouti × dilute black agouti.

Cross 11. Giving only *BAg* young, both parents homozygous. $Y_2Br_2B_2D_2P_2A_2 \times Y_2Br_2B_2d_2P_2A_2$.

Mating.	Parents.	*BAg.*
67	131 × 135. .	8

Cross 11a. Black agouti heterozygous in black, density, and agouti crossed with dilute black agouti heterozygous in black and agouti. $Y_2Br_2BDdP_2A \times Y_2Br_2Bd_2P_2A$. Expectation, 9 *BAg*, 9 *dBAg*, 3 *BrAg*, 3 *dBrAg*, 3 *B*, 3 *dB*, *1 Br*, *1 dBr*.

Mating.	Parents.	*BAg.*	*dBAg.*	*BrAg.*	*B.*
All	*S*105 × *S*5.	3	1	1	1

Cross 12. Black agouti, heterozygous in color factor, black, dark eye, and agouti, crossed with dilute black agouti heterozygous in color factor, black, dark eye, and agouti. $YBr_2BD_2PpA \times YBr_2Bd_2PpA$. Expectation, 81 *BAg*, 27 *B*, 27 *pBAg*, 27 *BrAg*, 9 *Br*, 9 *pB*, 9 *pBrAg*, 3 *pBr*, 64 *W*.

Mating.	Parents.	*BAg.*	*BrAg.*	*B.*	*pBAg.*	*pB.*	*Br.*	*pBrAg.*	*pBr.*	*W.*
422	3405 × 3404.....	7	3	5	5	1	..	..	..	5

Black agouti × brown agouti.

Cross 13. Black agouti, heterozygous in black and density, crossed with brown agouti heterozygous in density. $Y_2Br_2BDdP_2A_2 \times Y_2Br_2DdP_2A_2$. Expectation, 3 *BAg*, 3 *BrAg*, 1 *dBAg*, 1 *dBrAg*.

Mating.	Parents.	*BAg.*	*BrAg.*	*dBAg.*	*dBrAg.*
507	Unmarked × 3114........	1	3	1	2
374	3116 × unmarked........	3	1	1	..
464	Unmarked × 3114–3115...	6	7	1	1
		10	11	3	3

Black agouti × black.

Cross 14. Black agouti heterozygous in the color factor crossed with black heterozygous in the color factor. $YBr_2B_2D_2P_2A_2 \times YBr_2B_2D_2P_2$. Expectation, 3 *BAg*, 1 *W*.

Mating.	Parents.	*BAg.*	*W.*
410	Unmarked × unmarked....	5	1

Cross 15. Black agouti heterozygous in agouti crossed with homozygous black. $Y_2Br_2B_2D_2P_2A \times Y_2Br_2B_2D_2P_2$. Expectation, 1 *BAg*, 1 *B*.

Mating.	Parents.	*BAg.*	*B.*
576	7215 × 7216....	2	5
*A*5	*S*59 × *S*54.....	8	4
*A*13	*S*59 × *S*5......	1	1
		11	10

Cross 16. Black agouti heterozygous in dark eye and agouti crossed with black heterozygous in dark eye. $Y_2Br_2B_2D_2PpA \times Y_2Br_2B_2D_2Pp$. Expectation, 3 *BAg*, 3 *B*, 1 *pBAg*, 1 *pB*.

Mating.	Parents.	*BAg.*	*B.*	*pBAg.*	*pB.*
132	447 × 454	1	1	2	2
128	449 × 454	3	3	. .	1
129	452 × 454	. .	4	. .	1
97	447, 449 × 454	3	. .	. .	1
179	447–449–452 × 454	2	5	. .	. .
165	447 × 919	8	5	. .	1
177	452 × 919	2	2	. .	. .
		19	20	2	6

Cross 17. Black agouti heterozygous in black, dark eye, and agouti, crossed with black heterozygous in black and dark eye. $Y_2Br_2BD_2PpA \times Y_2Br_2BD_2Pp$. Expectation, 9 *BAg*, 9 *B*, 3 *pBAg*, 3 *pB*, 3 *BrAg*, 3 *Br*, 1 *pBrAg*, 1 *pBr*.

Mating.	Parents.	*BAg.*	*B.*	*pBAg.*	*BrAg.*	*Br.*	*pBrAg.*	*pB.*	*pBr.*
130	551 × 553	1	. .	. .	. .	1	. .	. .	. .
107	551 × 671	. .	3	6	. .	. .	. .	1	. .
335	2461 × 2122	3	4	1	1	3	1	. .	2
324	2460 × 2122	5	4	2	. .	1	1	. .	. .
		9	11	9	1	5	2	1	2

Cross 17A. Black agouti heterozygous in black, density, and agouti, crossed with black heterozygous in density and black. $Y_2Br_2BDdP_2A \times Y_2Br_2BDdP_2$. Expectation, 9 *BAg*, 9 *B*, 3 *dBAg*, 3 *dB*, 3 *BrAg*, 3 *Br*, 1 *dBrAg*, 1 *dBr*.

Mating.	Parents.	*BAg.*	*B.*	*BrAg.*	*Br.*	*dBAg.*	*dBrAg.*	*dB.*	*dBr.*
*A*6	*S*6 × *S*35 . . .	2	5	3	2	1	. .	1	1

Black agouti × brown.

Cross 18. Black agouti heterozygous in black crossed with homozygous brown. $Y_2Br_2BD_2P_2A_2 \times Y_2Br_2D_2P_2$. Expectation, 1 *BAg*, 1 *BrAg*.

Mating.	Parents.	*BAg.*	*BrAg.*
526	5943 × 4920	3	3

Cross 18A. Black agouti heterozygous in black and agouti crossed with homozygous brown. $Y_2Br_2BD_2P_2A \times Y_2Br_2D_2P_2$. Expectation, 1 *BAg*, 1 *BrAg*, 1 *B*, 1 *Br*.

Mating.	Parents.	*BAg.*	*BrAg.*	*B.*	*Br.*
*A*14	*S*6 × *Blz*—3001	. .	2	1	2

Cross 19. Black agouti heterozygous in color factor, black, and agouti crossed with brown heterozygous in the color factor. $YBr_2BD_2P_2A \times YBr_2D_2P_2$. Expectation, 3 *BAg*, 3 *B*, 3 *BrAg*, 3 *Br*, 4 *W*.

Mating.	Parents.	*BAg.*	*BrAg.*	*B.*	*Br.*	*W.*
401	3306 × 3307	7	1	2	1	5

Black agouti × dilute brown.

Cross 20. Black agouti heterozygous in color factor, black, and density crossed with dilute brown heterozygous in color factor. $YBr_2BDdP_2A_2 \times YBr_2d_2P_2$. Expectation, 3 *BAg*, 3 *dBAg*, 3 *BrAg*, 3 *dBrAg*, 4 *W*.

Mating.	Parents.	*BAg.*	*dBAg.*	*BrAg.*	*dBrAg.*	*W.*
559	–25 × –89.	1	2	2	1	1

Cross 20A. Homozygous black agouti × homozygous dilute brown. $Y_2Br_2B_2D_2P_2A_2 \times Y_2Br_2d_2P_2$. Expectation, all *BAg*.

Mating.	Parents.	*BAg.*
*A*1	*S*2 × *S*1. . .	8

Cross 20B. Black agouti heterozygous in black and density crossed with homozygous dilute brown. $Y_2Br_2BDdP_2A_2 \times Y_2Br_2d_2P_2$. Expectation, 1 *BAg*, 1 *dBAg*, 1 *BrAg*, 1 *dBrAg*.

Mating.	Parents.	*BAg.*	*BrAg.*	*dBAg.*	*dBrAg.*
*A*12	309 × *Blz* × 3012.	2	. .	2	2
*A*15	381 × *Blz* × 3012.	1	. .	. .	2
		3	. .	2	4

Cross 20C. Black agouti heterozygous in black, density, and agouti crossed with homozygous dilute brown. $Y_2Br_2BDdP_2A \times Y_2Br_2d_2P_2$. Expectation, 1 *BAg*, 1 *BrAg*, 1 *dBAg*, 1 *B*, 1 *dBrAg*, 1 *Br*, 1 *dB*, 1 *dBr*.

Mating.	Parents.	*BAg.*	*BrAg.*	*B.*	*dBAg.*	*dBrAg.*	*Br.*	*dB.*	*dBr.*
A–	373–374 × *S*5. . .	2	2	. .	1	1	. .	1	2
*A*4	*S*6 × dil. *Br*.	1	1	4	1	3	1	. .	. .
*A*9	*S*62 × *S*5.	1	1	1	1	1	2	. .	1
		4	4	5	3	5	3	1	3

Black agouti × pink-eyed brown.

Cross 21. Black agouti heterozygous in dark eye and agouti, crossed with homozygous pink-eyed brown. $Y_2Br_2B_2D_2PpA \times Y_2Br_2D_2p_2$. Expectation, 1 *BAg*, 1 *pBAg*, 1 *B*, 1 *pB*.

Mating.	Parents.	*BAg.*	*pBAg.*	*B.*	*pB.*
398	3305 × *p*3309...	3	7	3	6

Black agouti × pink-eyed dilute brown.

Cross 21A. Homozygous black agouti crossed with homozygous pink-eyed dilute brown. $Y_2Br_2B_2D_2P_2A_2 \times Y_2Br_2d_2p_2$. Expectation, all *BAg*.

Mating.	Parents.	*BAg.*
626	p. dil. *Br.* × Vermont *BAg* .	26
630	7854 × Vermont *BAg* .	9
633	7855 × Vermont *BAg* .	7
		42

Cross 21B. Black agouti heterozygous in black, density, and agouti crossed with homozygous pink-eyed dilute brown. $Y_2Br_2BDdP_2A \times Y_2Br_2d_2p_2$. Expectation, 1 *BAg*, 1 *BrAg*, 1 *B*, 1 *dBAg*, 1 *dBrAg*, 1 *Br*, 1 *dB*, 1 *dBr*.

Mating.	Parents.	*BAg.*	*BrAg.*	*B.*	*dBAg.*	*dBrAg.*	*Br.*	*dB.*	*dBr.*
*A*3	Unmarked × *S*5..........	3	..	2	3	1	3	..	1
599	Unmarked × unmarked...	1	1	1	1	3	1	2	..
		4	1	3	4	4	4	2	1

II. Dilute Black Agouti, *YBrBdPA* (Fig. 2).

Eyes black, ears moderately pigmented, ventral hairs light slate colored with a yellowish tinge. Tail moderately pigmented. Dorsal hairs showing the "agouti" pattern distinctly but somewhat faded, or washed out in appearance. Tuft of light hairs present at base of the ears and around the anus.

Dilute black agouti × dilute black agouti.

Cross 22. Both parents homozygous. $Y_2Br_2B_2d_2P_2A_2$. Expectation, all *dBAg*.

Mating.	Parents.	*dBAg.*
621	7477 × unmarked...	12

Cross 22A. Both parents heterozygous in black, dark eye, and agouti. $Y_2Br_2Bd_2PpA$. Expectation, 27 *dBAg*, 9 *dB*, 9 *pdBAg*, 9 *dBrAg*, 3 *dBr*, 3 *pdB*, 3 *pdBrAg*, 1 *pdBr*.

Mating.	Parents.	*dBAg.*	*dBrAg.*	*dB.*	*pdBAg.*	*pdBrAg.*	*pdB.*	*dBr.*	*pBr.*
629	7695 × 7690–91–92..	9	2	1	1	1	1	1	..
642	7694 × 7690........	..	..	1	2	1	1	..	..
		9	2	2	3	2	1	1	0

Dilute black agouti × black.

Cross 22B. Dilute black agouti heterozygous in agouti crossed with homozygous black. $Y_2Br_2B_2d_2P_2A \times Y_2Br_2B_2D_2P_2$. Expectation, 1 *BAg*, 1 *B*.

Mating.	Parents.	*BAg.*	*B.*
562	6406 × 5881	5	6

Dilute black agouti × pink-eyed black.

Cross 23. Both parents homozygous. $Y_2Br_2B_2d_2P_2A_2 \times Y_2Br_2B_2D_2p_2$. Expectation, all *BAg*.

Mating.	Parents.	*BAg.*
323	*p*845 × 1871	8

Cross 24. Dilute black agouti heterozygous in black, dark eye, and agouti crossed with pink-eyed black heterozygous in black. $Y_2Br_2Bd_2PpA \times Y_2Br_2BD_2p_2$. Expectation, 3 *BAg*, 3 *B*, 3 *pBAg*, 3 *pB*, 1 *BrAg*, 1 *Br*, 1 *pBrAg*, 1 *pBr*.

Mating.	Parents.	*BAg.*	*B.*	*BrAg.*	*Br.*	*pBAg.*	*pB.*	*pBrAg.*	*pBr.*
372	*p*2688 × 2488	1	3	1	1	..	..	4	..

Dilute black agouti × pink-eyed dilute black.

Cross 25. Both parents homozygous. $Y_2Br_2B_2d_2P_2A_2 \times Y_2Br_2B_2d_2p_2$. Expectation, all *dBAg*.

Mating.	Parents.	*dBAg.*
416	*p*3627 × unmarked	5

Dilute black agouti × pink-eyed black agouti.

Cross 26. Dilute black agouti heterozygous in dark eye, crossed with pink-eyed black agouti heterozygous in density. $Y_2Br_2B_2d_2PpA_2 \times Y_2Br_2B_2Ddp_2A_2$. Expectation, 1 *BAg*, 1 *pBAg*, 1 *dBAg*, 1 *pdBAg*.

Mating.	Parents.	*BAg.*	*pBAg.*	*dBAg.*	*pdBAg.*
368	2255 × *p*1775	..	1	1	..

Dilute black agouti × pink-eyed dilute black agouti.

Cross 27. Dilute black agouti heterozygous in dark eye crossed with homozygous pink-eyed dilute black agouti. $Y_2Br_2B_2d_2PpA_2 \times Y_2Br_2B_2d_2p_2A_2$. Expectation, 1 *dBAg*, 1 *pdBAg*.

Mating.	Parents.	*dBAg.*	*pdBAg.*
522	*p* unmarked × unmarked	3	2
386	2254 × *p*2339	1	4
560	*p*4060 × 4244	2	..
		6	6

Dilute black agouti × brown.

CROSS 28. Dilute black agouti heterozygous in agouti crossed with homozygous brown. $Y_2Br_2B_2d_2P_2A \times Y_2Br_2D_2P_2$. Expectation, 1 *BAg*, 1 *B*.

Mating.	Parents.	*BAg.*	*B.*
227	Unmarked × unmarked ..	3	1

Dilute black agouti × pink-eyed dilute brown.

CROSS 28A. Both parents homozygous. $Y_2Br_2B_2d_2P_2A_2 \times Y_2Br_2d_2p_2$. Expectation, all *dBAg*.

Mating.	Parents.	*dBAg.*
586	Unmarked × unmarked..	7
610	7477 × 7476.............	8
615	7545 × 7503	8
613	Unmarked × unmarked..	11
		34

CROSS 28B. Dilute black agouti heterozygous in agouti crossed with homozygous pink-eyed dilute brown. $Y_2Br_2B_2d_2P_2A \times Y_2Br_2d_2p_2$. Expectation, 1 *dBAg*, 1 *dB*.

Mating.	Parents.	*dBAg.*	*dB.*
598	Unmarked × unmarked ...	4	3
617	Unmarked × unmarked ...	4	2
		8	5

CROSS 28C. Dilute black agouti heterozygous in black crossed with homozygous pink-eyed dilute brown. $Y_2Br_2Bd_2P_2A_2 \times Y_2Br_2d_2p_2$. Expectation, 1 *dBAg*, 1 *dBrAg*.

Mating.	Parents.	*dBAg.*	*dBrAg.*
585	Unmarked × unmarked ...	4	4

CROSS 28D. Dilute black agouti heterozygous in black and agouti, crossed with homozygous pink-eyed dilute brown. $Y_2Br_2Bd_2P_2A \times Y_2Br_2d_2p_2$. Expectation, 1 *dBAg*, 1 *dB*, 1 *dBrAg*, 1 *dBr*.

Mating.	Parents.	*dBAg.*	*dB.*	*dBrAg.*	*dBr.*
591	Unmarked × unmarked....	..	3	..	1

III. Pink-eyed Black Agouti, *YBBrDpA* (Fig. 3).

Eyes very deep pink. Ears apparently unpigmented. Hairs on ventral surface dull yellow with bluish base, showing the presence of the agouti pattern. Dorsal hair closely resembling that of the dark-eyed brown agouti form to the unaided eye. More yellow, however, seems to be present in the coat, though it has been seen that this is not because of an increased amount of yellow pigment. There is a tuft of light hairs at the base of the ears. The hairs directly around the anus, however, resemble the other ventral hairs so closely as to be indistinguishable from them.

Pink-eyed black agouti × pink-eyed black agouti.

Cross 29. One or both parents homozygous. $Y_2Br_2B_2D_2p_2A_2 \times Y_2Br_2B_2D_2p_2A_2$. Expectation, all *pBAg*.

Mating.	Parents.	*pBAg.*
112	560 × 559	15
136	690 × 691	7
153	689 × 691	5
139	692 × 691	16
190	690-692 × 691	15
		58

Cross 30. Both parents heterozygous in black. $Y_2Br_2BD_2p_2A_2 \times Y_2Br_2BD_2p_2A_2$. Expectation, 3 *pBAg*, 1 *pBrAg*.

Mating.	Parents.	*pBAg.*	*pBrAg.*
120	558 × 559	19	1
101	558 or 560 × 559	3	4
		22	5

Cross 31. Both parents heterozygous in black, density, and agouti. $Y_2Br_2BDdp_2A \times Y_2Br_2BDdp_2A$. Expectation, 27 *pBAg*, 9 *pdBAg*, 9 *pBrAg*, 9 *pB*, 3 *pdB*, 3 *pdBrAg*, 3 *pBr*, 1 *pdBr*.

Mating.	Parents.	*pBAg.*	*pdBAg.*	*pBrAg.*	*pB.*	*pdBrAg.*	*pdB.*	*pBr.*	*pdBr.*
300	2018 × 2017	17	2	6	3	..	..	..	..

Pink-eyed black agouti × black.

Cross 32. Pink-eyed black agouti heterozygous in agouti crossed with homozygous black. $Y_2Br_2B_2D_2p_2A \times Y_2Br_2B_2D_2P_2$. Expectation, 1 *BAg*, 1 *B*.

Mating.	Parents.	*BAg.*	*B.*
152	416 × *p*409	1	2
83	163 × *p*412	2	3
		3	5

Pink-eyed black agouti × pink-eyed black.

Cross 33. Both parents homozygous. $Y_2Br_2B_2D_2p_2A_2 \times Y_2Br_2B_2D_2p_2$. Expectation, all *pBAg*.

Mating.	Parents.	*pBAg.*
171	*p*1049 × *p*898.....	4
174	*p*985 × *p*898......	4
		8

Cross 34. Pink-eyed black agouti heterozygous in black and agouti crossed with pink-eyed black heterozygous in black. $Y_2Br_2BD_2p_2A \times Y_2Br_2BD_2p_2$. Expectation, 3 *pBAg*, 3 *pBrAg*, 1 *pB*, 1 *pBr*.

Mating.	Parents.	*pBAg.*	*pB.*	*pBrAg.*	*pBr.*
84	*p*408 × *p*412...	2	2	1	..

Pink-eyed black agouti × dilute black.

Cross 35. Pink-eyed black agouti heterozygous in density crossed with dilute black heterozygous in dark eye. $Y_2Br_2B_2Ddp_2A_2 \times Y_2Br_2B_2d_2Pp$. Expectation, 1 *BAg*, 1 *dBAg*, 1 *pBAg*, 1 *pdBAg*.

Mating.	Parents.	*BAg.*	*dBAg.*	*pBAg.*	*pdBAg.*
413	3062 × *p*1922....	4	7	..	7

Pink-eyed black agouti × dilute brown agouti.

Cross 36. Both parents homozygous. $Y_2Br_2B_2D_2p_2A_2 \times Y_2Br_2d_2P_2A_2$. Expectation, *BAg* only.

Mating.	Parents.	*BAg.*
148	682 × *p*691...	15

Cross 37. Homozygous pink-eyed black agouti crossed with dilute brown agouti heterozygous in dark eye. $Y_2Br_2B_2D_2p_2A_2 \times Y_2Br_2d_2PpA_2$. Expectation, 1 *BAg*, 1 *pBAg*.

Mating.	Parents.	*BAg.*	*pBAg.*
387	*p* unmarked × 1873.....	4	2

Cross 38. Pink-eyed black agouti heterozygous in density and agouti crossed with dilute brown agouti heterozygous in agouti. $Y_2Br_2B_2Ddp_2A \times Y_2Br_2d_2P_2A$. Expectation, 3 *BAg*, 3 *dBAg*, 1 *B*, 1 *dB*.

Mating.	Parents.	*BAg.*	*dBAg.*	*B.*	*dB.*
506	*p*1441 × 4608..	6	3	1	1

CROSS 39. Pink-eyed black agouti heterozygous in black and density crossed with dilute brown agouti heterozygous in dark eye. $Y_2Br_2BDdp_2A_2 \times Y_2Br_2d_2PpA_2$. Expectation, 1 *BAg*, 1 *pBAg*, 1 *dBAg*, 1 *BrAg*, 1 *pBrAg*, 1 *dBrAg*, 1 *pdBAg*, 1 *pdBrAg*.

Mating.	Parents.	*BAg.*	*pBAg.*	*dBAg.*	*BrAg.*	*pBrAg.*	*dBrAg.*	*pdBAg.*	*pdBrAg.*
369	*p*unmarked × 1873...	10	..	..	5	..	..	..	..
302	*p*1923–*p*1874 × 1873..	13	15	1	2	..	..	..	..
344	*p*1875 × 1873........	1	..	4	2	..	5	4	1
		24	15	5	9	..	5	4	1

Pink-eyed black agouti × brown.

CROSS 40. Both parents homozygous. $Y_2Br_2B_2D_2p_2A_2 \times Y_2Br_2D_2P_2$. Expectation, only *BAg*.

Mating.	Parents.	*BAg.*
252	*p*1416 × 1561.......	5
187	*p*1125 × 1527.......	4
286	*p*1533 × 1405.......	8
202	*p*1396 × unmarked..	8
223	*p*1368 × unmarked..	5
198	*p*1297 × unmarked..	5
207	1403 × *p*1099......	2
206	572 × *p*1099......	6
235	1403 × *p*691.......	16
		59

CROSS 41. Pink-eyed black agouti heterozygous in agouti crossed with homozygous brown. $Y_2Br_2B_2D_2p_2A \times Y_2Br_2D_2P_2$. Expectation, 1 *BAg*, 1 *B*.

Mating.	Parents.	*BAg.*	*B.*
249	*p*1326 × 1674............	2	1
228	*p*1062 × 1674............	14	10
219	*p*1060 × 1674............	8	3
279	*p*1328 × 1561............	3	1
193	*p*1148 × 1527............	1	2
209	*p*1330 × 1404............	2	2
213	1570 × *p*1120...........	3	2
161	646 × *p*1061...........	1	3
239	1488 × *p*844............	4	3
227	Unmarked × unmarked..	3	1
		41	28

CROSS 42. Pink-eyed black agouti heterozygous in black and agouti crossed with homozygous brown. $Y_2Br_2BD_2p_2A \times Y_2Br_2D_2P_2$. Expectation, 1 *BAg*, 1 *B*, 1 *BrAg*, 1 *Br*.

Mating.	Parents.	*BAg.*	*B.*	*BrAg.*	*Br.*
253	*p*1443 × 1405..	..	1	1	2
332	*p*1972 × 2071..	4	2	2	..
		4	3	3	2

Cross 43. Pink-eyed black agouti heterozygous in agouti crossed with brown heterozygous in dark eye. $Y_2Br_2B_2D_2p_2A \times Y_2Br_2D_2Pp$. Expectation, 1 *BAg*, 1 *B*, 1 *pBAg*, 1 *pB*.

Mating.	Parents.	*BAg.*	*pBAg.*	*B.*	*pB.*
182	1097 × 1526...	1	..	..	1
181	1098 × 1526...	14	11	1	1
231	1125 × 1526...	2	1	..	..
		17	12	1	2

Cross 44. Pink-eyed black agouti heterozygous in density crossed with brown heterozygous in density. $Y_2Br_2B_2Ddp_2A_2 \times Y_2Br_2DdP_2$. Expectation, 3 *BAg*, 1 *dBAg*.

Mating.	Parents.	*BAg.*	*dBAg.*
298	2179 × 1922...	4	2

Cross 45. Pink-eyed black agouti heterozygous in black, density, and agouti crossed with brown heterozygous in density. $Y_2Br_2BDdp_2A \times Y_2Br_2DdP_2$. Expectation, 3 *BAg*, 3 *BrAg*, 3 *B*, 3 *Br*, 1 *dBAg*, 1 *dBrAg*, 1 *dB*, 1 *dBr*.

Mating.	Parents.	*BAg.*	*BrAg.*	*B.*	*Br.*	*dBAg.*	*dBrAg.*	*dB.*	*dBr.*
229	1710 × 1405...	..	6	4	1	1	..	..	..

Cross 46. Pink-eyed black agouti heterozygous in density and agouti, crossed with brown heterozygous in density. $Y_2Br_2B_2Ddp_2A \times Y_2Br_2DdP_2$. Expectation, 3 *BAg*, 3 *B*, 1 *dBAg*, 1 *dB*.

Mating.	Parents.	*BAg.*	*dBAg.*	*B.*	*dB.*
317	1326 × 1404.....	5	2	4	2
221	1332 × 1404.....	3	..	..	1
291	1326–32 × 1404..	1	2	4	..
		9	4	8	3

IV. Pink-eyed Dilute Black Agouti, *YBBrdpA* (Fig. 4).

Eyes pink; ears, feet, and tail apparently unpigmented. The color of the coat is markedly washed-out in quality. The agouti pattern is distinguishable, but not easily so, because of the "streaky" due to the absence of intense pigmentation. The whole coat resembles a little that of a very light dilute dark-eyed brown agouti. The ear tufts of yellowish hair are prominent. There are no crosses to be included under this variety, though some in which one parent is pink-eyed dilute black agouti have been recorded under the preceding varieties.

V. Brown Agouti, *YBrDPA* (Fig. 5).

Eyes a deep rich brown, ears brown pigmented. Hairs on ventral surface yellowish on tip, dull brown at base. Tail brown pigmented. Dorsal hairs brown at the tip, then a yellow band, and finally dull brown to the base, giving the unmistakable "ticked" or "agouti" coat. Whiskers and feet are brown. Light hairs around the anus and at the base of the ears.

Brown agouti × brown agouti.

Cross 47. One or both parents homozygous. $Y_2Br_2D_2P_2A_2 \times Y_2Br_2D_2P_2A_2$. Expectation, all brown agouti.

Mating.	Parents.	*BrAg.*
124	651 × 272.................	6
86	367 × 272.................	18
143	281 × 272.................	6
414	Unmarked × unmarked....	7
		37

Cross 48. Both parents heterozygous in agouti. $Y_2Br_2D_2P_2A \times Y_2Br_2D_2P_2A$. Expectation, 3 *BrAg*, 1 *Br*.

Mating.	Parents.	*BrAg.*	*Br.*
104	586 × 588.....	3	1

Cross 49. Both parents heterozygous in density and the color factor. $YBr_2DdP_2A_2 \times YBr_2DdP_2A_2$. Expectation, 9 *BrAg*, 3 *dBrAg*, 4 *W*.

Mating.	Parents.	*BrAg.*	*dBrAg.*	*W.*
89	511.1*A* × 411.	3	2	2

Cross 49a. Both parents heterozygous in density, dark eye, and agouti. Y_2Br_2DdPpA. Expectation, 27 *BrAg*, 9 *dBrAg*, 9 *pBrAg*, 9 *Br*, 3 *pBr*, 3 *pdBrAg*, 3 *dBr*, 1 *pdBr*.

Mating.	Parents.	*BrAg.*	*dBrAg.*	*pBrAg.*	*Br.*	*dBr.*	*pBr.*	*pdBrAg.*	*pdBr.*
631	7679 × 7678–80....	6	1	1	3	..	..	..	..
643	7663 × 7660.......	2	1	1	..	..	..	..	..
644	7664 × 7662.......	2	2	1	..	..	..	..	..
		10	4	3	3	..	..	..	..

Brown agouti × pink-eyed brown agouti.

Cross 50. Brown agouti heterozygous in dark-eye, color factor, and agouti crossed with pink-eyed brown agouti heterozygous in the color factor and agouti. $YBr_2D_2PpA \times YBr_2D_2p_2A$. Expectation, 9 *BrAg*, 9 *pBrAg*, 3 *Br*, 3 *pBr*, 8 *W*.

Mating.	Parents.	*BrAg.*	*Br.*	*pBrAg.*	*pBr.*	*W.*
407	*p* unmarked × 2735....	8	4	2	2	3
365	*p*2137 × 2735..........	..	1	2	..	1
350	*p*2138 × 2735..........	..	1	2	..	1
		8	6	6	2	5

Brown agouti × brown.

CROSS 51. Homozygous brown agouti crossed with homozygous brown. $Y_2Br_2D_2P_2A_2 \times Y_2Br_2D_2P_2$. Expectation, all *BrAg*.

Mating.	Parents.	*BrAg.*
96	488 × 162 . . .	6

CROSS 52. Brown agouti heterozygous in dark eye and agouti crossed with brown heterozygous in dark eye. $Y_2Br_2D_2PpA \times Y_2Br_2D_2Pp$. Expectation, 3 *BrAg*, 3 *Br*, 1 *pBrAg*, 1 *pBr*.

Mating.	Parents.	*BrAg.*	*Br.*	*pBrAg.*	*pBr.*
405	Unmarked × unmarked.	. .	3	1	. .
305	2129 × 2130.	6	9	5	2
347	Unmarked × 2130.	4	6	4	3
		10	18	10	5

Brown agouti × pink-eyed brown.

CROSS 53. Both parents homozygous. $Y_2Br_2D_2P_2A_2 \times Y_2Br_2D_2p_2$. Expectation, all *BrAg*.

Mating.	Parents.	*BrAg.*
359	*p*2309 × 2131. .	4

Brown agouti × dilute black.

CROSS 54. Brown agouti heterozygous in density and agouti, crossed with dilute black heterozygous in black. $Y_2Br_2DdP_2A \times Y_2Br_2Bd_2P_2$. Expectation, 1 *BAg*, 1 *dBAg*, 1 *B*, 1 *dB*, 1 *BrAg*, 1 *dBrAg*, 1 *Br*, 1 *dBr*.

Mating.	Parents.	*BAg.*	*dBAg.*	*BrAg.*	*dBrAg.*	*B.*	*Br.*	*dB.*	*dBr.*
527	5381 × 5203. . .	6	3	1	. .	1	1	. .	. .

Brown agouti × pink-eyed dilute brown.

CROSS 54A. Both parents homozygous, $Y_2Br_2D_2P_2A_2 \times Y_2Br_2d_2p_2$. Expectation, all *BrAg*.

Mating.	Parents.	*BrAg.*
595	Unmarked × unmarked. . . .	19
603	7505 × 7501.	7
		26

VI. DILUTE BROWN AGOUTI, *YBrdPA* (FIG. 6).

Eyes brown; ears, feet, and tail lightly pigmented with brown. Ventral hairs dull fawn Dorsal hairs showing the agouti pattern. The whole appearance is that of a dull, faded, intense brown agouti.

Dilute brown agouti × pink-eyed dilute brown agouti.

Cross 55. Dilute brown agouti heterozygous in dark eye crossed with homozygous pink-eyed dilute brown agouti, or pink-eyed dilute brown. $Y_2Br_2D_2PpA_2 \times Y_2Br_2d_2p_2(A_2)$. Expectation, 1 *dBrAg*, 1 *pdBrAg*.

Mating.	Parents.	*dBrAg.*	*pdBrAg.*
510	3439 × *p*4519....	12	10
642*a*	7650 × 8023.....	1	2
		13	12

Dilute brown agouti × brown.

Cross 56. Dilute brown agouti heterozygous in dark eye and agouti crossed with brown heterozygous in dark eye. $Y_2Br_2d_2PpA \times Y_2Br_2D_2Pp$. Expectation, 3 *BrAg*, 3 *Br*, 1 *pBrAg*, 1 *pBr*.

Mating.	Parents.	*BrAg.*	*Br.*	*pBrAg.*	*pBr.*
428	3439 × 3739....	12	7	1	2

VII. Pink-Eyed Brown Agouti, *YBrDpA* (Fig. 7).

Eyes clear pink; ears apparently unpigmented, as are also feet and tail. Hairs on ventral surface indistinguishable superficially from a deep pink-eyed yellow. When examined more closely they are found to be darker at the base than at the tip, showing the presence of the agouti pattern. Dorsal hair a very rich brownish yellow and deeper colored at the base with dull brownish pigment. Because of the reduction of brown pigment at the tips of the hairs the appearance of banding or "ticking" is almost entirely wanting. Whiskers, hairs at base of ears, and around the anus are yellow.

Pink-eyed brown agouti × pink-eyed brown agouti.

Cross 57. Both parents heterozygous in agouti. $Y_2Br_2D_2p_2A \times Y_2Br_2D_2p_2A$. Expectation, 3 *pBrAg*, 1 *pBr*.

Mating.	Parents.	*pBrAg.*	*pBr.*
419	*p* unmarked × *p*2903....	6	1
399	*p*3109 × *p*2903.........	4	1
		10	2

Cross 58. Both parents heterozygous in density and agouti. $Y_2Br_2Ddp_2A \times Y_2Br_2Ddp_2A$. Expectation, 9 *pBrAg*, 3 *pBr*, 3 *pdBrAg*, 1 *pdBr*.

Mating.	Parents.	*pBrAg.*	*pBr.*	*pdBrAg.*	*pdBr.*
400	*p*2904 × *p*2903 . .	2	2	1	. .

Pink-eyed brown agouti × brown.

Cross 59. Both parents homozygous. $Y_2Br_2D_2p_2A_2 \times Y_2Br_2D_2P_2$. Expectation, *BrAg* only.

Mating.	Parents.	*BrAg.*
360	*p* unmarked × 2393....	1

Cross 60. Homozygous pink-eyed brown agouti crossed with brown heterozygous in dark eye. $Y_2Br_2D_2p_2A_2 \times Y_2Br_2D_2Pp$. Expectation, 1 *BrAg*, 1 *pBrAg*.

Mating.	Parents.	*BrAg.*	*pBrAg.*
261	*p*1395 × 1526..........	9	4

VIII. Pink-eyed Dilute Brown Agouti, *YBrdpA* (Fig. 8).

Eyes pink; ears, tail, and feet very lightly pigmented with brown. In both ventral and dorsal hairs this form resembles a dull intense pink-eyed brown agouti, differing chiefly in the comparative lack of bright yellow pigment and in the mealy, washed-out look. The agouti pattern is very weak indeed.

Pink-eyed dilute brown agouti × pink-eyed dilute brown agouti.

Cross 61. Both parents heterozygous in agouti. $Y_2Br_2d_2p_2A \times Y_2Br_2d_2p_2A$. Expectation, 3 *pdBrAg*, 1 *pdBr*.

Mating.	Parents.	*pdBrAg.*	*pdBr.*	*p?*
479	Unmarked × *p*4519..	1	2	..
535	*p*4213 × *p*4519.......	1	..	3
		2	2	3

Pink-eyed dilute brown agouti × dilute brown.

Cross 61a. Pink-eyed dilute brown agouti heterozygous in agouti crossed with dilute brown heterozygous in dark eye. $Y_2Br_2d_2p_2A \times Y_2Br_2d_2Pp$. Expectation, 1 *dBrAg*, 1 *dBr*, 1 *pdBrAg*, 1 *pdBr*.

Mating.	Parents.	*dBrAg.*	*dBr.*	*pdBrAg.*	*pdBr.*
596	Unmarked × unmarked..	1	3	1	2
605	7471 × 7468.............	2	..	2	1
		3	3	3	3

Cross 61b. Both parents homozygous. $Y_2Br_2d_2p_2A_2 \times Y_2Br_2d_2P_2$. Expectation, all *dBrAg*.

Mating.	Parents.	*dBrAg.*
609	Unmarked × unmarked..	2

IX. Black, *YBrBDP* (Fig. 9).

Hairs on ventral surface not so heavily pigmented as the dorsal hairs, and of a dull slaty black. Tail dark. Dorsal hairs deep, glossy black. Tuft of yellowish hairs at base of ears. A few yellowish hairs scattered along the flanks, sides and feet. The hairs around the anus are light yellowish. The feet are dark.

Black × black.

Cross 62. One or both of the parents homozygous. $Y_2Br_2B_2D_2P_2 \times Y_2Br_2B_2D_2P_2$. Expectation, all *B*.

Mating.	Parents.	*B*.
3	401 × 400...	2
6	200 × 201...	2
		4

Cross 63. Both parents heterozygous in black. $Y_2Br_2BD_2P_2 \times Y_2Br_2BD_2P_2$. Expectation, 3*B*, 1 *Br*.

Mating.	Parents.	*B*.	*Br*.
1	1 × 400..	6	2

Cross 64. Both parents heterozygous in density. $Y_2Br_2B_2DdP_2 \times Y_2Br_2B_2DdP_2$. Expectation, 3 *B*, 1 *dB*.

Mating.	Parents.	*B*.	*dB*.
577	7214 × 7217...	3	3

Cross 65. Both parents heterozygous in dark eye. $Y_2Br_2B_2D_2Pp \times Y_2Br_2B_2D_2Pp$. Expectation, 3 *B*, 1 *pB*.

Mating.	Parents.	*B*.	*pB*.
492	Unmarked × 2948.........	3	1
168	455 × 919................	12	1
189	450 × 540................	6	2
114	Unmarked × 454..........	12	1
131	543 × 444................	2	1
135	450 × 444................	7	4
379	Unmarked × unmarked...	60	20
		102	30

CROSS 66. Both parents heterozygous in dark eye and black. $Y_2Br_2BD_2Pp \times Y_2Br_2BD_2Pp$. Expectation, 9 *B*, 3 *pB*, 3 *Br*, 1 *pBr*.

Mating.	Parents.	*B.*	*pB.*	*Br.*	*pBr.*	*p ?*
361	2596 × 2593	2	1	..	..	..
376*a*	Unmarked × unmarked	78	26	23	5	1
376*b*	Unmarked × unmarked	13	7	5	2	..
247	1706 × 541	2	1	..	1	..
318	2031 × 1942	8	2	4	..	..
316	1948 × 1950	5	4	2	1	..
267	1948 × 1949–1950	3	..	1	..	..
364	2084 × 2086	2	..	2	..	..
303	2084–2085 × 2086	11	3	3	1	..
295	2186-87-88-89 × 2184	31	16	6	4	..
349	2212 × 2213	7	4	2	..	..
334	2218 × 2213	6	5	2	..	..
358	2210 × 2219	4	..	1	1	..
333	2210–14 × 2219	15	2	6	..	..
444	2216 × 2219	4	2	..	1	..
336	Unmarked × 2593	7	1	3	3	..
447	2945 × unmarked	1	1	1	..	..
		199	75	61	19	1

CROSS 66A. Both parents heterozygous in black, dark eye, and density. Y_2Br_2BDdPp. Expectation, 27 *B*, 9 *dB*, 9 *pB*, 9 *Br*, 3 *pBr*, 3 *dBr*, 3 *pdB*, 1 *pdBr*.

Mating.	Parents.	*B.*	*dB.*	*pB.*	*Br.*	*pdB.*	*pBr.*	*dBr.*	*pdBr.*
619	7515 × 7513–14–16	4	2	6	2	1	..	..	..
645	7431 × 7514	3	..	..	2	1	..	..	..
646	7733 × 7734	3	..	..	..	..	..	..	..
		10	2	6	4	2	..	..	..

CROSS 66B. Both parents heterozygous in color factor, black, dark eye, and density. YBr_2BDdPp. Expectation, 81 *B*, 27 *dB*, 27 *pB*, 27 *Br*, 9 *pBr*, 9 *dBr*, 9 *pdB*, 3 *pdBr*, 64 *W*.

Mating.	Parents.	*B.*	*Br.*	*W.*
625	7430 × 7428	5	5	3

Black × dilute black.

CROSS 67. Both parents homozygous, $Y_2Br_2B_2D_2P_2 \times Y_2Br_2B_2d_2P_2$. Expectation, all *B*.

Mating.	Parents.	*B.*
552	4865 × 5789	2

Cross 68. Both parents heterozygous in dark eye. $Y_2Br_2B_2D_2Pp \times Y_2Br_2B_2d_2Pp$. Expectation, 3 *B*, 1 *pB*.

Mating.	Parents.	*B.*	*pB.*
197	1363 × 1435..	4	1

Black × pink-eyed black.

Cross 69. Both parents homozygous. $Y_2Br_2B_2D_2P_2 \times Y_2Br_2B_2D_2p_2$. Expectation, all *B*.

Mating.	Parents.	*B.*
306	1695 × *p*1510...	16

Cross 70. Black heterozygous in dark eye crossed with homozygous pink-eyed black. $Y_2Br_2B_2D_2Pp \times Y_2Br_2B_2D_2p_2$. Expectation, 1 *B*, 1 *pB*.

Mating.	Parents.	*B.*	*pB.*
548	Unmarked × *p*5575.....	13	1
571	3290–96 × *p*5575........	6	1
220	1363 × *p*763............	7	8
		26	10

Black × brown.

Cross 71. Both parents homozygous. $Y_2Br_2B_2D_2P_2 \times Y_2Br_2D_2P_2$. Expectation, all *B*.

Mating.	Parents.	*B.*
474	Unmarked × 68..	4

Cross 72. Black heterozygous in black crossed with homozygous brown. $Y_2Br_2BD_2P_2 \times Y_2Br_2D_2P_2$. Expectation, 1 *B*, 1 *Br*.

Mating.	Parents.	*B.*	*Br.*
308	1631 × 1950......	20	15
383	1931 × 1950......	7	5
262	1931 × 1949–50...	10	5
396	2523 × 2122......	14	10
		51	35

Cross 73. Black, heterozygous in black, dark eye, and the color factor crossed with pink-eyed black heterozygous in the color factor and black. $YBr_2BD_2Pp \times YBr_2BD_2p_2$. Expectation, 9 *B*, 9 *pB*, 3 *Br*, 3 *pBr*, 8 *W*.

Mating.	Parents.	*B.*	*pB.*	*Br.*	*pBr.*	*W.*
420	Unmarked × 3307...	3	2	5	4	9

Black × pink-eyed brown.

CROSS 74. Black heterozygous in dark eye crossed with homozygous pink-eyed brown. $Y_2Br_2B_2D_2Pp \times Y_2Br_2D_2p_2$. Expectation, 1 *B*, 1 *pB*.

Mating.	Parents.	*B.*	*pB.*
475	*p* unmarked × 68...	1	4

CROSS 75. Black heterozygous in dark eye and black crossed with homozygous pink-eyed brown. $Y_2Br_2BD_2Pp \times Y_2Br_2D_2p_2$. Expectation, 1 *B*, 1 *pB*, 1 *Br*, 1 *pBr*.

Mating.	Parents.	*B.*	*pB.*	*Br.*	*pBr.*
493	140 × 77...	2	..	1	2

Black × pink-eyed dilute brown.

CROSS 75A. Both parents homozygous. $Y_2Br_2B_2D_2P_2 \times Y_2Br_2d_2p_2$. Expectation, all *B*.

Mating.	Parents.	*B.*
582	7340 × 7341..............	18
589	Unmarked × unmarked...	4
		22

CROSS 75B. Black heterozygous in dark eye, crossed with homozygous pink-eyed dilute brown. $Y_2Br_2B_2D_2Pp \times Y_2Br_2d_2p_2$. Expectation, 1 *B*, 1 *pB*.

Mating.	Parents.	*B.*	*pB.*
620	7472 × 7475...	5	11

X. DILUTE BLACK, *YBrBdP* (FIG. 10).

Eyes black; ears, tail, and feet moderately pigmented. Ventral hairs slate-colored. Dorsal hairs are deep blue slate, somewhat washed-out, and at times resembling a very deep-colored dilute black agouti. There is a small tuft of light hairs at the base of the ears. Light yellowish hairs scattered on sides and feet, and around the anus. Unlike the pink-eyed black form next to be described, one would not hesitate in calling the dilute black animal, black pigmented.

Dilute black × dilute black.

CROSS 76. Both parents homozygous. $Y_2Br_2B_2d_2P_2 \times Y_2Br_2B_2d_2P_2$. Expectation, all *dB*.

Mating.	Parents.	*dB.*
549	Unmarked × 4980..	15
457	4502–03 × 4497.....	10
442	4502 × 4497........	5
		30

Cross 77. Both parents heterozygous in the color factor, black and dark eye. $YBr_2Bd_2Pp \times YBr_2Bd_2Pp$. Expectation, 27 *dB*, 9 *dBr*, 9 *pdB*, 3 *pdBr*, 16 *W*.

Mating.	Parents.	*dB.*	*dBr.*	*pdB.*	*pdBr.*	*W.*
542	5698 × 5699..............	2	1	1	1	..
511	Unmarked × unmarked...	3	1	..	..	..
550	Unmarked × 5699........	6	2	4	1	2
		11	4	5	2	2

Dilute black × pink-eyed black.

Cross 78. Dilute black heterozygous in dark eye crossed with homozygous pink-eyed black. $Y_2Br_2B_2d_2Pp \times Y_2Br_2B_2D_2p_2$. Expectation, 1*B*, 1 *pB*.

Mating.	Parents.	*B.*	*pB.*
337	*p*1049 × 1435.......	..	3
...	Unmarked × 1435..	2	1
		2	4

Cross 79. Dilute black heterozygous in black crossed with pink-eyed black heterozygous in density and black. $Y_2Br_2Bd_2P_2 \times Y_2Br_2BDdp_2$. Expectation, 3 *B*, 3 *dB*, 1 *Br*, 1*dBr*.

Mating.	Parents.	*B.*	*Br.*	*dB.*	*dBr.*
528	*p*4520 × 4523....	1	2	2	..

Dilute black × brown.

Cross 80. Dilute black heterozygous in black, crossed with homozygous brown. $Y_2Br_2Bd_2P_2 \times Y_2Br_2D_2P_2$. Expectation, 1 *B*, 1 *Br*.

Mating.	Parents.	*B.*	*Br.*
441	2563–64–89 × 4495..	18	17

Cross 81. Dilute black heterozygous in black crossed with brown heterozygous in density. $Y_2Br_2Bd_2P_2 \times Y_2Br_2DdP_2$. Expectation, 1 *B*, 1 *Br*, 1 *dB*, 1 *dBr*.

Mating.	Parents.	*B.*	*Br.*	*dB.*	*dBr.*
451	4501 × 4857.....	1	..	..	..
437	4501 × 1404.....	3	2	1	2
		4	2	1	2

Dilute black × pink-eyed brown.

Cross 82. Dilute black heterozygous in black crossed with homozygous pink-eyed brown. $Y_2Br_2Bd_2P_2 \times Y_2Br_2D_2p_2$. Expectation, 1 *B*, 1 *Br*.

Mating.	Parents.	*B*.	*Br*.
557	Unmarked × *p*5806.....	3	2

Cross 82a. Homozygous dilute black crossed with pink-eyed brown, heterozygous in density. $Y_2Br_2B_2d_2P_2 \times Y_2Br_2Ddp_2$. Expectation, 1*B*, 1*dB*.

Mating.	Parents.	*B*.	*dB*.
593	Unmarked × –7.......	7	5
612	–8 × unmarked.......	1	3
		8	8

Cross 83. Dilute black heterozygous in dark eye crossed with pink-eyed brown heterozygous in density. $Y_2Br_2B_2d_2Pp \times Y_2Br_2Ddp_2$. Expectation, 1 *B*, 1 *pB*, 1 *dB*, 1 *pdB*.

Mating.	Parents.	*B*.	*pB*.	*dB*.	*pdB*.
503	4078 × *p*4298...	..	2	..	4

XI. Pink-eyed Black, *YBrBDp* (Fig. 11).

Eyes deep pink; ears very lightly pigmented. Hairs on ventral surface light yellowish-gray. Tail lightly pigmented. Dorsal hairs varying from a very light yellowish slate color to a deep lilac. The tufts of light hairs back of the ears are present. No appearance of black pigment in the dorsal hairs, to the unaided eye. The nose whiskers are light. almost yellow. The whole appearance resembles somewhat the dark-eyed dilute brown, The feet are slightly pigmented and the hairs around the anus are light.

Pink-eyed black × pink-eyed black.

Cross 84. Both parents heterozygous in black. $Y_2Br_2BD_2p_2 \times Y_2Br_2BD_2p_2$. Expectation, 3 *pB*, 1 *pBr*.

Mating.	Parents.	*pB*.	*pBr*.
172	*p*845 × *p*763......	2	2
342	*p*1812 × 1764......	6	1
313	1421–1812 × 1764..	10	6
		18	9

Pink-eyed black × brown.

Cross 85. Both parents heterozygous in the color factor. $YBr_2B_2D_2p_2 \times YBr_2D_2P_2$. Expectation, 3 *B*, 1 *W*.

Mating.	Parents.	*B*.	*W*.
356	2178 × 2175..	4	1

CROSS 86. Both parents homozygous. $Y_2Br_2B_2D_2p_2 \times Y_2Br_2D_2P_2$. Expectation, all *B*.

Mating.	Parents.	*B*.
224	1717 × 1512.......	13
211	1049 × 1630.......	2
230	1042 × 1630.......	4
215	985 × 1630.......	14
234	1638–40 × 1610....	12
270	1721 × 1609.......	9
296	1765 × 1603.......	3
282	1608 × 1603.......	3
281	845 × 1603.......	6
196	Unmarked × 1603.	7
243	1641 × 1194.......	4
236	1520 × 1194.......	9
246	Unmarked × 1194.	14
205	1524 × 1192.......	12
381	1524 × 2175.......	3
		115

CROSS 87. Pink-eyed black heterozygous in black crossed with homozygous brown. $Y_2Br_2BD_2p_2 \times Y_2Br_2D_2P_2$. Expectation, 1 *B*, 1 *Br*.

Mating.	Parents.	*B*.	*Br*.
274	Unmarked × 1764....	3	3
258	1642 × 1764..........	2	5
245	572 × 1394..........	2	1
266	–16 × 1394..........	2	3
280	1421 × unmarked....	2	3
		11	15

CROSS 88. Pink-eyed black heterozygous in the color factor and black crossed with brown heterozygous in color factor. $YBr_2BD_2p_2 \times YBr_2D_2P_2$. Expectation, 3*B*, 3 *Br*, 2 *W*.

Mating.	Parents.	*B*.	*Br*.	*W*.
269	1812 × 1661.......	1	4	2

CROSS 89. Pink-eyed black heterozygous in black crossed with brown heterozygous in dark eye. $Y_2Br_2BD_2p_2 \times Y_2Br_2D_2Pp$. Expectation, 1 *B*, 1 *pB*, 1 *Br*, 1 *pBr*.

Mating.	Parents.	*B*.	*pB*.	*Br*.	*pBr*.
257	1714 × 1526....	2	4	2	4

Pink-eyed black × dilute brown.

CROSS 89A. Both parents homozygous. $Y_2Br_2B_2D_2p_2 \times Y_2Br_2d_2P_2$. Expectation, all *B*.

Mating.	Parents.	*B*.
648	Unmarked × 318...	19

Pink-eyed black × pink-eyed brown.

CROSS 90. Both parents homozygous. $Y_2Br_2B_2D_2p_2 \times Y_2Br_2D_2p_2$. Expectation, all *pB*.

Mating.	Parents.	*pB*.
634	7804 × 7806...	4

CROSS 90A. Pink-eyed black heterozygous in black, crossed with homozygous pink-eyed brown. $Y_2Br_2BD_2p_2 \times Y_2Br_2D_2p_2$. Expectation, 1 *pB*, 1 *pBr*.

Mating.	Parents.	*pB*.	*pBr*.
558	5721 × 5806...	1	2
638	7807 × 7803...	4	5
640	7809 × 7803...	4	5
		9	12

XII. PINK-EYED DILUTE BLACK, *YBrBdp* (FIG. 12).

Eyes pink; ears, tail and feet extremely lightly pigmented. Coat clearly washed out in appearance, and a real bluish lilac, at times almost silvery. This variety is very characteristic, and is one which, when obtained, is easy to recognize. No one would, without breeding tests, class this form as possessing black pigment.

Pink-eyed dilute black × brown.

CROSS 91. Homozygous pink-eyed dilute black crossed with brown, heterozygous in density. $Y_2Br_2B_2d_2p_2 \times Y_2Br_2DdP_2$. Expectation, 1 *B*, 1 *dB*.

Mating.	Parents.	*B*.	*dB*.
449	3627 × 1404..	11	9
594	19 × 17....	1	4
		12	13

Pink-eyed dilute black × dilute brown.

CROSS 91A. Pink-eyed dilute black heterozygous in black crossed with dilute brown heterozygous in dark eye. $Y_2Br_2Bd_2p_2 \times Y_2Br_2d_2Pp$. Expectation, 1 *dB*, 1 *dBr*, 1 *pdB*, 1 *pdBr*.

Mating.	Parents.	*dB*.	*dBr*.	*pdB*.	*pdBr*.
604	7462 × 7461.....	2	3	..	2

XIII. Brown, *YBrDP* (Fig. 13).

Eyes deep brown; ears and tail brown pigmented. Hairs on the ventral surface are lighter than those on the dorsal surface, and are dull dirty brown. Dorsal hairs deep, glossy brown; lighter yellowish hairs occur, as in the black variety, at the base of the ears, scattered on the flanks, sides, and feet, as well as around the anus. The skin is brown pigmented.

Brown × brown.

Cross 92. One or both parents homozygous. $Y_2Br_2D_2P_2 \times Y_2Br_2D_2P_2$. Expectation, only *Br*.

Mating.	Parents.	*Br.*
348	Unmarked × 2291	5
345	Unmarked × 2386	16
525	5942 × 5340	5
		26

Cross 93. Both parents heterozygous for the color factor. $YBr_2D_2P_2 \times YBr_2D_2P_2$. Expectation, 3 *Br*, 1 *W*.

Mating.	Parents.	*Br.*	*W.*
551	Unmarked × 32	4	2
388	2365 × 2374	4	2
504	4859 × 4298	11	2
575	6225–27 × 6226	11	3
		30	9

Cross 94. Both parents heterozygous in dark eye. $Y_2Br_2D_2Pp \times Y_2Br_2D_2Pp$. Expectation, 3 *Br*, 1 *pBr*.

Mating.	Parents.	*Br.*	*pBr.*
406	Unmarked × unmarked	9	3
408	Unmarked × unmarked	22	7
		31	10

Cross 95. Both parents heterozygous in dark eye and the color factor. $YBr_2D_2Pp \times YBr_2D_2Pp$. Expectation, 9 *Br*, 3 *pBr*, 4 *W*.

Mating.	Parents.	*Br.*	*pBr.*	*W.*
408	Unmarked × unmarked	22	7	2
366	Unmarked × 2392	15	4	3
		37	11	5

CROSS 96. Both parents heterozygous in density and dark eye. $Y_2Br_2DdPp \times Y_2Br_2DdPp$. Expectation, 9 *Br*, 3 *dBr*, 3 *pBr*, 1 *pdBr*.

Mating.	Parents.	*Br.*	*dBr.*	*pBr.*	*pdBr.*
496	Unmarked × unmarked..	40	16	2	1
569	Unmarked × 4736.......	3	3	..	..
521	4735 × 4736............	6	2	1	..
581	Unmarked × unmarked..	15	8	4	1
632	7597 × 7601–02..........	11	2	..	..
635	7439 × 7437*a*–38.........	6	4	1	1
		81	35	8	3

Brown × pink-eyed brown.

CROSS 97. Brown heterozygous in density, dark eye and the color factor, crossed with pink-eyed brown heterozygous in density and the color factor. $YBr_2DdPp \times YBr_2Ddp_2$. Expectation, 9 *Br*, 9 *pBr*, 3 *dBr*, 3 *pdBr*, 8 *W*.

Mating.	Parents.	*Br.*	*dBr.*	*pBr.*	*pdBr.*	*W.*
538	–35 × 32...	3	..	1	1	3

Brown × pink-eyed dilute brown.

CROSS 97A. Both parents homozygous. $Y_2Br_2D_2P_2 \times Y_2Br_2d_2p_2$. Expectation, all *Br*.

Mating.	Parents.	*Br.*
583	Unmarked × unmarked.....	13

CROSS 97B. Brown heterozygous in density crossed with homozygous pink-eyed dilute brown. $Y_2Br_2DdP_2 \times Y_2Br_2d_2p_2$. Expectation, 1 *Br*, 1 *dBr*.

Mating.	Parents.	*Br.*	*dBr.*
584	Unmarked × unmarked.......	3	2

XIV. DILUTE BROWN, *YBrdP* (FIG. 14).

Eyes brown; ears, tail and feet, as in the dilute brown agouti, are lightly pigmented with brown. Ventral hairs pale fawn. Dorsal hairs dull, washed-out brown, at times resembling a dark, pink-eyed black in general superficial coloration. Ear tufts barely distinguishable from the rest of the coat. The skin is moderately pigmented with brown.

Dilute brown × pink-eyed brown.

CROSS 98. Both parents homozygous. $Y_2Br_2d_2P_2 \times Y_2Br_2D_2p_2$. Expectation, all *Br*.

Mating.	Parents.	*Br.*
495	4446 × –77..	13
504	4859 × 4298..	11
		24

CROSS 98A. Dilute brown heterozygous in dark eye, crossed with pink-eyed brown heterozygous in density. $Y_2Br_2d_2Pp \times Y_2Br_2Ddp_2$. Expectation, 1 *Br*, 1 *dBr*, 1 *pBr*, 1 *pdBr*.

Mating.	Parents.	*Br.*	*dBr.*	*pBr.*	*pdBr.*
608	7479 × 7478...	3	1	1	3

XV. PINK-EYED BROWN, *YBrDp* (FIG. 15).

Eyes clear pink. Ears, tail, and feet unpigmented. Hairs on ventral surface dull yellowish throughout their length. The yellow hairs at the base of the ears and around the anus are very similar to the rest of the coat, but are, nevertheless, distinguishable from it. The dorsal hairs are rich fawn colored, lighter than the coat of the pink-eyed brown agouti.

Pink-eyed brown × pink-eyed brown.

CROSS 99. One or both of the parents homozygous. $Y_2Br_2D_2p_2 \times Y_2Br_2D_2p_2$. Expectation, only *pBr*.

Mating.	Parents.	*pBr.*
391	Unmarked × 3002..	24
390	Unmarked × 2821..	10
377	2799 × 3002........	3
426	3310 × 3309........	7
524	5805 × 5945........	11
		55

Pink-eyed brown × albino.

(Test matings to determine the gametic constitution of the albinos.)

CROSS 100. Pink-eyed brown heterozygous in the color factor crossed with an albino, potentially a homozygous brown agouti. $YBr_2D_2p_2 \times Br_2D_2P_2A_2$. Expectation, 1 *BrAg*, 1 *W*

Mating.	Parents.	*BrAg.*	*W.*
487	5245 × 4984..	4	6

CROSS 101. Pink-eyed brown heterozygous in the color factor, crossed with an albino, potentially a homozygous brown. $YBr_2D_2p_2 \times Br_2D_2P_2$. Expectation, 1 *Br*, 1 *W*.

Mating.	Parents.	*Br.*	*W.*	?
509	4082 × 4286....	13	2	4

XVI. PINK-EYED DILUTE BROWN, *YBrdp* (FIG. 16).

Eyes clear pink. Very pale pigmentation throughout hairs and skin, a close approximation to a dirty brownish cream but still preserving the streaky washed-out appearance clearly. This form is as characteristic and easily distinguished as the pink-eyed dilute black. The ear tufts are indistinguishable from the rest of the coat. Pink-eyed dilute browns crossed *inter se* have given 120 recorded young, all pink-eyed dilute brown.

It must be remembered that all these descriptions of color varieties are intended to be merely as they appear to the unaided eye. Many of the regions here spoken of as pink or unpigmented have, upon microscopic examination, yielded a small amount of pigment.

RESTRICTED SERIES.

All animals in this series, that is to say, all *yellow* animals, are of the zygotic formula ***Rr***. The combination *RR*, if formed, fails to develop.

(a) *Dark-eyed intense series.*

This series consists of four types of yellows:

XVII. Black-eyed Yellow Carrying Agouti, *YBrBDPAR* (Fig. 20).
XVIII. Black-eyed Yellow Without Agouti, *YBrBDPR* (Fig. 17).
XIX. Brown-eyed Yellow Carrying Agouti, *YBrDPAR*.
XX. Brown-eyed Yellow Without Agouti, *YBrDPR* (Fig. 18).

Types XVII and XVII are similar in appearance, and are indistinguishable save by breeding tests. Types XIX and XX also are only to be distinguished from each other by suitable test matings.

(b) *Pink-eyed intense series.*

This series consists of four types of yellow which are indistinguishable in external appearance:

XXI. Pink-eyed Yellow Carrying Black Agouti, *YBrBDpAR*.
XXII. Pink-eyed Yellow Carrying Black, *YBrBDpR*.
XXIII. Pink-eyed Yellow Carrying Brown Agouti, *YBrDpAR*.
XXIV. Pink-eyed Yellow Carrying Brown, *YBrDpR*.

Test matings are necessary before these forms can be distinguished from each other.

(c) *Dark-eyed dilute series.*

In this series also there are four types:

XXV. Black-eyed Dilute Yellow Carrying Agouti, *YBrBdPAR*.
XXVI. Black-eyed Dilute Yellow Without Agouti, *YBrBdPR*.
XXVII. Brown-eyed Dilute Yellow Carrying Agouti, *YBrdPAR*.
XXVIII. Brown-eyed Dilute Yellow Without Agouti, *YBrdPR* (Fig. 19).

In this series types XXV and XXVI are distinguishable from types XXVII and XXVIII by a careful examination of the eyes. Such a test, however, is not certain enough to be considered final, and a breeding test forms the only sure basis for a permanent classification.

(d) *Pink-eyed dilute series.*

As in the pink-eyed intense series the four forms of this series are indistinguishable save by breeding tests. This is because of the fact that the total amount of pigment in the eye is so small that it is impossible to determine whether it is brown or black by anything short of a microscopic examination. The gametic formulæ follow:

XXIX. Pink-eyed Dilute Yellow Carrying Black Agouti, *YBrBdpAR*.
XXX. Pink-eyed Dilute Yellow Carrying Black, *YBrBdpR*.
XXXI. Pink-eyed Dilute Yellow Carrying Brown Agouti, *YBrdpAR*.
XXXII. Pink-eyed Dilute Yellow Carrying Brown, *YBrdpR*.

Each of these series may now be considered separately.

Up to a certain point there were no pink-eyed or dilute mice, yellow or non-yellow in my stock. All the yellows were therefore intense dark-eyed yellows and would group themselves under one of the first four types (XVII, XVIII, XIX, or XX). To test them a *cross with any type of brown animal lacking the agouti factor would suffice.*

A list of such crosses follows. Yellows which proved to be of type XVII are included in the following table:

Mating.	Parents.	*Y.*	*BAg.*	Zygotic formula of yellow parent.
29	700–702 br. × 508 yel. .	2	5	$Y_2Br_2B_2D_2P_2A_2R$.
34	707 br. × 502.4A yel. . .	6	2	$Y_2Br_2B_2D_2P_2A_2R$.
36	502.2A yel. × br.	1	3	$Y_2Br_2B_2D_2P_2A_2R$.
		9	10	

All these yellows seem to have been homozygous in the factors for black and for agouti. Yellows of type XIX follow:

Mating.	Parents.	*Y.*	*BrAg.*	*Br.*	Zygotic formula of yellow parent.
15–111–85	146 yel. × brown. .	12	8	1	$Y_2Br_2D_2P_2AR$.
18–19	br. × 571 yel.	1	5	. .	$Y_2Br_2D_2P_2A_2R$.
56	br. × 148 yel.	2	1	. .	$Y_2Br_2D_2P_2A_2R$.
82	502.1B yel. × br. . .	2	3	2	$Y_2Br_2D_2P_2AR$.
		17	17	3	

There are two types of zygotes here, those homozygous in the agouti pattern (A) and those heterozygous, the latter giving non-agouti, as well as agouti young.

The yellows of type XVIII are also of two sorts, those homozygous in the factor for the production of black (B) and those heterozygous in this factor. Thus in the following table 502.21*A* yellow is known to be an animal homozygous in the factor B, while all the other yellow animals are heterozygous, producing browns as well as blacks.

Mating.	Parents.	*Y.*	*B.*	*Br.*	Zygotic formula of yellow parent.
63	502.21A yel. × br. . . .	2	1	1	$Y_2Br_2B_2D_2P_2R$.
11	br. × 505 yel.	1	1	2	$Y_2Br_2BD_2P_2R$.
37	502.22A yel. × br. . . .	1	2	1	$Y_2Br_2BD_2P_2R$.
92	br. × 228 yel.	1	2	1	$Y_2Br_2BD_2P_2R$.
100	326 yel. × br.	1	1	1	$Y_2Br_2BD_2P_2R$.
320	2320 yel. × br.	4	2	1	$Y_2Br_2BD_2P_2R$.
		10	9	6	

Type XX, yellows which give browns only, are seen in the following table:

Yellow × brown.

Mating.	Parents.	*Y.*	*Br.*	Zygotic formula of yellow parent.
62	502.23A yel. × br. . . .	2	1	$Y_2Br_2D_2P_2R$.
232	br. × 1316 yel.	1	7	$Y_2Br_2D_2P_2R$.
293	br. × 988 yel.	3	2	$Y_2Br_2D_2P_2R$.
329	2319 yel. × br.	3	4	$Y_2Br_2D_2P_2R$.
331	2109–2110 yel. × br. .	1	. .	$Y_2Br_2D_2P_2R$.
304–314	2109 yel. × br.	13	3	$Y_2Br_2D_2P_2R$.
327–222	br. × 1601 yel.	5	4	$Y_2Br_2D_2P_2R$.
141–142	br. × 580 yel.	11	5	$Y_2Br_2D_2P_2R$.
151–170	br. × 881–883 yel. . . .	4	9	$Y_2Br_2D_2P_2R$.
597	yel. × br.	6	4	$Y_2Br_2D_2P_2R$.
601	yel. × br.	6	3	$Y_2Br_2D_2P_2R$.
602	br. × 7488 yel.	1	6	$Y_2Br_2D_2P_2R$.
		56	48	

It has been shown, then, that yellows of the four dark-eyed intense pigmented types exist.

The pink-eyed yellows (types XXI–XXIV inclusive) have been crossed only *inter se* or with black pigmented forms, but it is certain that they also can occur in the four types comparable to the dark-eyed intense series.

The dark-eyed dilute yellows have been crossed with brown only in a few cases. Chiefly they have been bred *inter se* to determine whether the 2 : 1 ratio holds good in their case as in the intense forms. Of those tested, one, ♀7298, is of the zygotic formula $Y_2Br_2Bd_2PpA_2R$ and when crossed with a pink-eyed brown has given 1 *yel,* 1 *pdyel,* 1 *BAg,* 2 *BrAg,* 1 *pBAg.* This shows that types XXV and XXVII can exist. The other animal, also a female, gave by a pink-eyed brown male, 7 *yel,* 2 *pyel,* 2 *Blk,* 2 *Br,* 3 *pB.* This animal was of the formula $Y_2Br_2Bd_2PpR$, and argues strongly in favor of the existence of types XXVI and XXVIII.

Of the pink-eyed dilute yellows few have been tested, but I have, at present, a race of animals which give only two sorts of young, viz, pink-eyed dilute yellows and pink-eyed dilute browns; such pink-eyed dilute yellows are the ultimate recessives of the yellow series belonging to type XXXII, formula $Y_2Br_2d_2p_2R$.

From the few matings given above, together with the larger number of yellow matings which follow, it is easy to see that yellows may be obtained of the various zygotic compositions found in the non-yellow varieties, differing from them only by the addition of the restriction factor, R.

We shall first consider the crosses between yellow animals of these four varieties, which form the intense dark-eyed series.

Yellow × yellow, giving only dark-eyed intense young.

CROSS 102. Giving *Y* and *Br*.

Mating.	Parents.	*Y.*	*Br.*
127	425 × 424	4	3
38	502.23A × 502.5B	..	3
39	Unmarked × 505.1A	4	3
255	1410 × 1667	5	1
301	1747 × 49–1746	4	2
297	1723 × 1827	2	1
574	7180 × 7181	6	1
166	893 × 895	12	7
		37	21

CROSS 103. Giving *Y*, *Br*, and *W* (and in one case *BrAg*).

Mating.	Parents.	*Y.*	*BrAg.*	*Br.*	*W.*
384	Unmarked × unmarked	22	..	7	6
118	578 × 580	1	..	4	1
145	146 × 895	5	..	8	7
178	146–894 × 895	3	..	..	..
185	894 × 895	1	1	5	2
183	146–893–94 × 895	3	..	..	..
326	1247 × 2311	8	..	1	1
352	726–1247 × 2311	3	..	1	1
		46	1	26	18

Cross 104. Giving *Y*, *BAg*, *B*, and *W*.

Mating.	Parents.	*Y*.	*BAg*.	*B*.	*W*.
8	502.1A × 502.5A....	3	..	..	3
9	502.2A × 502.5A....	10	2	1	3
10	502 × 511..........	7	..	..	2
15	509 × 511..........	2	2	..	1
248	1247 × 1316........	5	..	..	3
570	Unmarked × 3297..	2	..	..	1
		29	4	1	13

Cross 105. Miscellaneous yellows giving *Y*, *BAg*, and *B*.

Mating.	Parents.	*Y*.	*BAg*.	*B*.	*BAg* or *B*.
529	Unmarked × 1938.	38	1	11	4
283	1723 × unmarked..	..	..	1	..
264	1666 × 1667.......	1	..	..	..
27	509.1A × 511......	3	1	..	..
14	509 × 510.........	3	1	..	..
7	502 × 503.........	5	..	..	..
22	514.6A × 505.1A...	1	..	..	..
28	514.4A × 505.1A...	4	..	..	..
		55	3	12	4

Sooty yellow × sooty yellow, giving only dark-eyed intense young.

Cross 106. Giving *Y*, *sY*, *B*, and *BAg*.

Mating.	Parents.	*Y*.	*sY*.	*BAg*.	*B*.	*B* or *BAg*.
440	3196 × 3777.........	3	1	..	2	..
471	Unmarked × 3957...	1	8	3	..	..
502	Unmarked × 3777...	15	13	4	10	1
		19	22	7	12	1

Cream × cream, giving nothing but dark-eyed intense young.

Cross 107. Giving cream, or light yellow, *B* and *Br*.

Mating.	Parents.	Cream *Y*.	*B*.	*Br*.
284	1248 × 1414.....	4	..	..
445	3907 × 875......	2	1	2
122	648 × 647.......	..	2	..
285	1750 × 1745–46..	2	..	2
		8	3	4

Cross 108. Giving cream, *BAg*, *B*, *Br*, and *W*.

Mating.	Parents.	Cream *Y*.	*BAg*.	*B*.	*Br*.	*W*.
397	3908 × 875.........	4	2	2	. .	1
469	4068 × 4796........	1	1	. .	. .	1
325	2050 × 875.........	7	. .	2	4	1
188	1248 × 580.........	. .	. .	. .	1	1
418	Unmarked × 875...	3	. .	2	2	1
		15	3	6	7	5

Yellow × cream, giving nothing but dark-eyed intense young.

Cross 109. Giving *Y*, *B*, *BrAg*, and *Br*.

Mating.	Parents.	*Y*.	*B*.	*BrAg*.	*Br*.
450	Unmarked × 3906...	36	10	3	5
233	882 × 601...........	1	. .	. .	1
		37	10	3	6

Cross 110. Giving *Y*, *B*, *BrAg*, *Br ?*, and *W*.

Mating.	Parents.	*Y*.	*B*.	*BrAg*.	*B* or *Br*.	*W*.
273	2049 × 875...	5	. .	1	1	. .
272	2048 × 875...	4	1	. .	. .	4
		9	1	1	1	4

Cross 111. Giving *Y*, cream, *B*, *Br*, and *W*.

Mating.	Parents.	*Y*.	Cream *Y*.	*B*.	*Br*.	*W*.
146	284 × 875...	1	5	2	. .	. .
123	284 × 647...	. .	5	1	3	. .
154	882 × 881...	10	2	1	8	3
		11	12	4	11	3

Yellow × yellow, giving intense and dilute dark-eyed young.

Cross 112. Giving *Y*, *BAg*, *BrAg*, *Br*, *dY*, *dBAg*.

Mating.	Parents.	*Y*.	*dY*.	*BAg*.	*dBAg*.	*BrAg*.	*Br*.
164	620 × 621.....	2	. .	2	1	1	. .
250	1658 × 1660....	10	3	. .	. .	. .	1
		12	3	2	1	1	1

Cross 113. Giving *Y*, *BAg*, *dBAg*, and *W*.

Mating.	Parents.	*Y.*	*BAg.*	*dBAg.*	*W.*
23	530 × 511...	5	3	1	5

Yellow × yellow, giving intense dark-eyed and intense pink-eyed young.

Cross 114. Giving *Y*, *pY*, *B*, *pB*, *Br*, and *pBr*.

Mating.	Parents.	*Y.*	*pY.*	*B.*	*Br.*	*pB.*	*pBr.*
321	2198 × 2197..............	7	..	5	2	2	..
311	1947 × 1877..............	4	2	6	..	2	1
393	Unmarked × unmarked..	3	2	1	..	..	..
		14	4	12	2	4	1

Cross 114a. Giving *Y*, *sY*, *pY*, *BAg*, *B*, *BrAg*, *Br*, *pBAg*, *pB*, *pBr*, and *p?*.

Mating.	Parents.	*Y.*	*sY.*	*pY.*	*BAg.*	*B.*	*BrAg.*	*Br.*	*pBAg.*	*pB.*	*pBr.*	*p?*
477	Unmarked × 5228..	45	3	2	..	11	..	6	1	..	1	..
459	Unmarked ×4631..	7	1	2	11	..	4	..	..	..	..	..
256	1722 × 1827........	7	1	2	..	2	..	1	..	..	..	..
244	1724 × 1827........	4	1	5	..	1	..	..	..	..	..	..
287	1722–24 × 1827.....	4	..	2	..	2	..	2	..	3	..	1
		67	6	13	11	16	4	9	1	3	1	1

Cross 115. Giving *Y*, *pY*, *BAg*, *BrAg*, *B*, *Br*, *pB*, and *W*.

Mating.	Parents.	*Y.*	*pY.*	*BAg.*	*BrAg.*	*B.*	*Br.*	*pB.*	*W.*
430	3299 × 3297....	5	1	..	..	4	..	1	3
159	786 × 784.....	4	1	1	2	..	1	..	1
		9	2	1	2	4	1	1	4

Sooty yellow × yellow, giving intense dark-eyed and intense pink-eyed young.

Cross 116.

Mating.	Parents.	*Y.*	*SY.*	*pY.*	*BAg.*	*BrAg.*	*B.*	*Br.*	*pBAg.*	*pB.*	*pBr.*
251	1826 × 1829.............	2	..	1	..	..	1	1	..	..	..
240	1828 × 1829.............	5	1	4	..	..	1	1	1	2	..
278	1826–28 × 1829..........	3	..	3	..	..	..	..	..	1	..
328	2666–67 × 1829..........	6	1	..	..	..	2	3	..	..	..
362	2666 × 1829.............	1	1	..	..	..	1	1	..	1	..
367	Unmarked × 1829.......	38	10	13	..	..	18	5	..	6	1
339	2668 × 1829.............	6	..	..	..	..	..	1	..	..	..
353	2667 × 1829.............	1	..	..	..	..	1	1	..	..	..
354	2665 × 1829.............	5	2	..	..	..	3	2	..	..	..
460	Unmarked × unmarked.	4	..	..	..	..	2	..	1	..	..
415	Unmarked × 3460.......	10	3	1	..	..	..	..	..	..	..
411	Unmarked × 3640.......	3	1	..	..	..	..	..	..	..	..
485	Unmarked × 3777.......	4	4	..	1	..	3	..	..	..	..
472	Unmarked × 3957.......	24	9	..	14	6	2	2	..	..	..
		112	32	22	15	6	34	17	2	10	1

Yellow × yellow, giving intense and dilute dark-eyed and pink-eyed young.

CROSS 117.

Mating.	Parents.	*Y.*	*pY.*	*BAg.*	*dBAg.*	*pBAg.*	*pdBAg.*	*pdB.*	*pdBr.*	*W.*
446	Unmarked × 4054..	6	2	2	2	1	1	1	1	1

Yellow × yellow, miscellaneous.

CROSS 118. No color varieties recorded.

Mating.	Parents.	*Y.*	*non Y.*	*W.*
556	Unmarked × 4334........	4	2	..
555	Unmarked × 4523........	9	3	..
579	Unmarked × 4631........	11	9	..
544	Unmarked × 4712........	5	..	..
568	Unmarked × 4891........	5	2	..
543	Unmarked × 4905........	2	4	..
565	Unmarked × 4149........	3	..	..
572	Unmarked × unmarked..	77	38	2
		116	58	2

Yellow × dilute yellow, giving nothing but intense dark-eyed young.

CROSS 119. Giving *Y*, *BAg ?*, *B*, *BrAg*, and *Br*.

Mating.	Parents.	*Y.*	*BAg* or *B.*	*B.*	*BrAg.*	*Br.*
546	Unmarked × 5155.....	14	1	2	..	2
564	Unmarked × 4710.....	2	..	..	3	..
520	Unmarked × 4334.....	1	..	..	..	1
		17	1	2	3	3

Yellow × dilute yellow, giving intense and dilute dark-eyed young.

CROSS 120. Giving *Y*, *dY*, *dBAg*, *BrAg*, and *dBrAg*.

Mating.	Parents.	*Y.*	*dY.*	*dBAg.*	*BrAg.*	*dBrAg.*
567	Unmarked × 4146.....	2	..	..	..	1
566	Unmarked × 4712.....	6	..	..	..	1
553	Unmarked × 4905.....	2	6	1	1	1
		10	6	1	1	3

Yellow × dilute yellow, giving only intense dark-eyed and pink-eyed young.

CROSS 121. Giving *Y*, *pY*, *BAg*, *BrAg*, *B*, and *W*.

Mating.	Parents.	*Y.*	*pY.*	*BAg.*	*BrAg.*	*B.*	*W.*
476	Unmarked × 4710...	10	1	2	2	1	1

Yellow × dilute yellow, giving intense and dilute dark-eyed and pink-eyed young.

CROSS 122. Giving *Y*, *pY*, *dY*, *pdY*, *BAg*, *dBrAg*, *dB*, or *dBAg*.

Mating.	Parents.	*Y.*	*dY.*	*pY.*	*pdY.*	*BAg.*	*dBrAg.*	*dB* or *dBAg.*
563	Unmarked × 4631....	1	1	..	1	..	1	..
533	Unmarked × 5008....	11	5	1	..	1	..	2
		12	6	1	1	1	1	2

Yellow × dilute sooty yellow, giving intense and dilute dark-eyed young.

CROSS 123. Giving *Y*, *sY*, *dY*, *dsY*, *BAg*, *BrAg*, *dBAg*, and *dBrAg*.

Mating.	Parents.	*Y.*	*sY.*	*dY.*	*dsY.*	*BAg.*	*BrAg.*	*BAg* or *BrAg.*	*dBAg.*	*dBrAg.*
463	Unmarked × 4346.	9	2	1	3	6	4	3	1	1
514	Unmarked × 2348.	5	1	5	4	2	1	..	1	..
		14	3	6	7	8	5	3	2	1

Yellow × pink-eyed yellow, giving only intense dark-eyed young.

CROSS 124. Giving *Y* and *BAg*.

Mating.	Parents.	*Y.*	*BAg.*
554	Unmarked × 4149....	3	..
99	227 × 413............	4	1
		7	1

Yellow × pink-eyed yellow, giving intense and dilute dark-eyed young.

CROSS 125. Giving *Y*, *B*, and *dB*.

Mating.	Parents.	*Y.*	*B.*	*dB.*
125	326 × 563.....	4	1	2

Yellow × pink-eyed yellow, giving intense pink-eyed and dark-eyed young.

CROSS 126. Giving *Y*, *pY*, *B* or *BAg*, *B*, *Br*, *pBrAg*, and *pB*.

Mating.	Parents.	*Y.*	*pY.*	*BAg* or *B.*	*B.*	*Br.*	*pBrAg.*	*pB.*	*p?*
200	1282 × 1389............	1	1	2	..	..	..	..	1
216	1283 × 1389............	1	2	..	3	..	..	..	..
514	Unmarked × 4523......	2	2	..	1	..	..	3	..
473	Unmarked × unmarked.	2	..	..	..	1	1	..	..
		6	5	2	4	1	1	3	1

CROSS 127. Giving *Y*, *pY*, *BAg*, *B*, *Br*, *pB*, and *W*.

Mating.	Parents.	*Y.*	*pY.*	*BAg.*	*B.*	*Br.*	*pB.*	*W.*
501	(*a*) unmarked × 3297...	1	1	..	..	..	..	2
532	(*b*) unmarked × 3297...	4	2	1	1	1	1	2
		5	3	1	1	1	1	4

Yellow × pink-eyed yellow, giving intense and dilute dark-eyed and pink-eyed young.

CROSS 128. Giving *Y*, *pY*, *dBAg*, and *pdBAg*.

Mating.	Parents.	*Y.*	*pY.*	*dBAg.*	*pdBAg.*
530	Unmarked × 4152..	1	2	1	1

Cream × pink-eyed yellow, giving nothing but dark-eyed intense young.

CROSS 129. Giving *Y* and *BAg*.

Mating.	Parents.	*Y.*	*BAg.*
184	1223 × 1074..	3	..
210	1223 × 1064..	14	1
		17	1

In the following crosses, between yellow and non-yellow animals, equality of yellow and non-yellow young is to be expected. These matings, like the yellow × yellow matings just cited are planned chiefly to test the relation of yellow to non-yellow forms, not with an eye to producing any certain color variety.

Yellow × black agouti, giving only dark-eyed intense young.

CROSS 130. Giving *Y* and *BAg*.

Mating.	Parents.	*Y.*	*BAg.*
12	506 × 530.5A.....	3	4
24	530.1A × 630.....	1	7
		4	11

CROSS 131. Giving *Y*, *BAg*, and *W*.

Mating.	Parents.	*Y.*	*BAg.*	*W.*
16	608 × 570....	2	1	1

Cross 132. Giving *Y*, *BAg*, *BrAg*, and *W*.

Mating.	Parents.	*Y.*	*BAg.*	*BrAg.*	*W.*
95	622 × 624...	2	1	1	1

Yellow × black agouti, giving intense and dilute dark-eyed young.

Cross 133. Giving *Y*, *BAg*, and *dBAg*.

Mating.	Parents.	*Y.*	*BAg.*	*dBAg.*
26	530.1A × 530.5A.....	1	5	1

Yellow × black agouti, giving intense and dilute dark-eyed and pink-eyed young.

Cross 134. Giving *Y*, *dY*, *pY*, *BAg*, *dBAg*, *BrAg*, *dBrAg*, *B*, *pB*, and *Br*.

Mating.	Parents.	*Y.*	*dY.*	*pY.*	*pdY.*	*BAg.*	*dBAg.*	*BrAg.*	*dBrAg.*	*B.*	*pB.*	*Br.*
489	Unmarked × 3114....	11	1	2	..	4	3	2	1	2	1	2
375	Unmarked × 3114–15.	24	8	..	..	10	5	8	1	1	..	1
		35	9	2	..	14	8	10	2	3	1	3

Cream × black agouti, giving intense dark-eyed young only.

Cross 135. Giving cream and *BAg*.*

Mating.	Parents.	Cream *Y.*	*BAg.*
443	Unmarked × unmarked....	1	1
434	2108–09 × 3947.............	2	1
		3	2

*The black agoutis used in this cross were wild.

Cross 136. Giving *Y*, *BAg*, and *B*.

Mating.	Parent.	*Y.*	*BAg.*	*B.*
265	917 × 1550......	3	2	1

Cross 137. Giving *Y*, *BAg*, and *BrAg*.

Mating.	Parents.	*Y.*	*BAg.*	*BrAg.*
534	4798 × 4796...	2	1	1

Yellow × dilute black agouti, giving only intense dark-eyed young.

Cross 138. Giving *Y*, *BAg*, and *BrAg*.

Mating.	Parents.	*Y.*	*BAg.*	*BrAg.*
322	2154 × 1871...............	4	2	2
412	Unmarked × unmarked...	2	..	..
		6	2	2

Yellow × dilute black agouti, giving intense and dilute dark-eyed young.

Cross 139. Giving *Y*, *dY*, *BAg*, *dBAg*, *B*, *dB*, *BrAg*, and *Br*.

Mating.	Parents.	*Y.*	*dY.*	*BAg.*	*dBAg.*	*B.*	*dB.*	*BrAg.*	*Br.*
438	4435 × 2829..............	4	1	..	..	..	..	..	..
432	4434–35 × 2829...........	4	1	..	..	..	..	..	1
409	Unmarked × 2829........	10	8	3	..	1	3	3	1
421	2352 × 2859..............	2	..	..	1	..	..	1	..
		20	10	3	1	1	3	4	2

Cream × dilute black agouti, giving intense and dilute dark-eyed young.

Cross 140. Giving *Y*, *dY*, *dsY*, and *Br*.

Mating.	Parents.	*Y.*	*dY.*	*dsY.*	*Br.*
373	2348 × 2829..	4	2	1	1

Cross 141. Giving *Y*, *BAg*, *dBrAg*, and *W*.

Mating.	Parents.	*Y.*	*BAg.*	*dBrAg.*	*W.*
402	2255 × 1938...	4	3	1	3

Sooty yellow × dilute black agouti, giving intense dark-eyed and pink-eyed young.

Cross 142. Giving *Y*, *sY*, *pY*, *BAg*, and *pBAg*.

Mating.	Parents.	*Y.*	*sY.*	*pY.*	*BAg.*	*B* or *BAg.*	*pBAg.*
346	2411 × 2609.....	11	7	3	17	6	2

Yellow × pink-eyed black agouti, giving only intense dark-eyed young.

Cross 143. Giving *Y*, *BAg*, and *B*.

Mating.	Parents.	*Y.*	*BAg.*	*B.*
76	509.2B × 409...	..	9	6
78	227 × 412.......	9	8	5
		9	17	11

Yellow × pink-eyed black agouti, giving intense and dilute dark-eyed young.

Cross 144. Giving *Y*, *BAg*, *dBAg*, and *BrAg*.

Mating.	Parents.	*Y.*	*BAg.*	*dBAg.*	*BrAg.*
330	1667 × 1876...	9	2	1	3

Yellow × pink-eyed black agouti, giving intense and dilute dark-eyed and pink-eyed young.

Cross 145. Giving *Y*, *BAg*, *dBAg*, *pBAg*, *B*, and *pB*.

Mating.	Parents.	*Y.*	*BAg.*	*pBAg.*	*dBAg.*	*B.*	*pB.*
371	1806 × 2339.....	8	1	1	1	2	1

Cross 146. Giving *Y*, *pY*, *dY*, *pdY*, *B*, *dB*, and *W*.

Mating.	Parents.	*Y.*	*pY.*	*dY.*	*pdY.*	*B.*	*dB.*	*W.*
433	4051 × unmarked...	5	4	1	1	2	2	4

Yellow × black, giving only dark-eyed intense young.

Cross 147. Giving *Y* and *BAg*.

Mating.	Parents.	*Y.*	*BAg.*
54	502 × 177............	5	2
49	185 × 315............	4	3
90	Unmarked × 502.5B..	2	5
61	502.3B × unmarked..	3	2
		14	12

Cross 148. Giving only *Y* and *B*.

Mating.	Parents.	*Y.*	*B.*
370	1977 × 2046..........	3	2
52	502.22B × 182........	2	3
53	509 × 182............	2	4
88	Unmarked × 321.....	..	2
137	224 × 347............	4	1
40	Unmarked × 505.1A..	..	2
		11	14

Cross 149. Giving *Y*, *BAg*, and *B*.

Mating.	Parents.	*Y.*	*BAg.*	*B.*
35	207 × 502.6B......	3	2	2
103	225 × 347..........	2	1	5
		5	3	7

Cross 150. Giving *Y*, *B*, and *Br*.

Mating.	Parents.	*Y.*	*B.*	*Br.*
117	328 × 323..........	2	5	1
292	1662 × 1660........	7	3	1
238	1662–63 × 1660.....	7	3	1
		16	11	3

Cross 151. Giving *Y*, *BAg*, and *W*.

Mating.	Parents.	*Y.*	*BAg.*	*W.*
46	178 × 530.01B.....	3	1	1
47	509.3B × 177......	3	1	3
17	206 × 510..........	2	3	2
42	201.1A × 511......	2	1	3
43	201.2A × 511......	1	1	3
		11	7	12

Cross 152. Giving *Y*, *B*, and *W*.

Mating.	Parents.	*Y.*	*B.*	*W.*
59	Unmarked × 141...	4	1	1
21	206 × 514..........	3	2	3
72	178 × 320..........	6	8	3
58	168–170–171 × 185..	3	1	2
51	206 × 172..........	1	2	2
		17	14	11

Cross 153. Giving *Y*, cream, *BAg*, *BrAg*, *B*, and *Br*.

Mating.	Parents.	*Y.*	Cream *Y.*	*BAg.*	*BrAg.*	*B.*	*Br.*
73	–67 × unmarked...	5	..	5	1	..	..
71	284 × 182.........	15	1	..	..	4	4
108	Unmarked × 323..	7	..	1	1	..	3
357	1978 × 2406.......	3	..	..	1	1	..
91	328 × 502.5B......	5	..	3	2	..	..
		35	1	9	5	5	7

CROSS 154. Giving *Y*, cream, *BAg?*, *B*, *Br*, and *W*.

Mating.	Parents.	*Y.*	Cream *Y.*	*BAg* or *B.*	*B.*	*Br.*	*W.*
57	152 × 1.1A....	4	..	..	3	1	1
80	185 × 319.....	4	..	..	5	1	1
94	185 × 348.....	9	3	1	9	2	10
		17	3	1	17	4	12

CROSS 155. Giving *Y*, *BAg*, *BrAg*, *B*, and *W*.

Mating.	Parents.	*Y.*	*BAg.*	*BAg* or *B.*	*B.*	*BrAg.*	*W.*
41	206 × 510.2A.........	6	5	5	4	..	2
55	184 × 148*a*...........	6	1	..	..	2	2
70	Unmarked × 319.....	2	2	..	1	1	5
133	325 × unmarked......	6	..	5	..	2	5
66	502.2B × unmarked...	..	..	1	..	3	2
		20	8	11	5	8	16

Yellow × black, giving intense and dilute dark-eyed young.

CROSS 156. Giving *Y*, *B*, *Br*, and *dB*.

Mating.	Parents.	*Y.*	*B.*	*Br.*	*dB.*
276	1663 × 1660.....	2	5	2	1

Yellow × black, giving intense dark-eyed and pink-eyed young.

CROSS 157. Giving *Y*, *pY*, *B*, and *pB*.

Mating.	Parents.	*Y.*	*pY.*	*B.*	*pB.*
341	2195 × 2197.........	2	..	3	1
491	Unmarked × 2948...	5	1	6	1
456	2803 × 2948.........	3	1	2	1
		10	2	11	3

CROSS 158. Giving *Y*, cream, *pY*, *B*, *Br*, *pB*, and *pBr*.

Mating.	Parents.	*Y.*	Cream *Y.*	*pY.*	*B.*	*Br.*	*pB.*	*pBr.*	*p?*
424	2803 × unmarked.....	3	..	..	9	1	1	..	..
319	1941 × 1942..........	6	..	3	9	5	2	1	..
290	1882 × 1877..........	2	..	1	4	1	2	..	..
121	549 × 540–41–42–44...	14	..	..	6	5	3	3	2
214	549 × 541............	14	1	3	13	2	6	1	..
		39	1	7	41	14	14	5	2

Cream × black, giving only intense dark-eyed young.

CROSS 159. Giving *Y*, *B*, and *Br*.

Mating.	Parents.	*Y.*	*B.*	*Br.*
217	Unmarked × 988....	3	1	1
288	2092 × 989..........	3	2	2
		6	3	3

CROSS 160. Giving *Y*, *B*, *Br*, and *W*.

Mating.	Parents.	*Y.*	*B.*	*Br.*	*W.*
156	328 × 988...	11	3	10	7

Cream × dilute black, giving only intense dark-eyed young.

CROSS 161. Giving *Y* and ?

Mating.	Parents.	*Y.*
312	1751 × 1435.....	2

Yellow × dilute black, giving intense and dilute dark-eyed young.

CROSS 162. Giving *Y*, *dY*, *dB*, and *dBr*.

Mating.	Parents.	*Y.*	*dY.*	*dB.*	*dBr.*
448	4499 × 4496...	1	2	3	1

Yellow × pink-eyed black, giving only dark-eyed intense young.

CROSS 163. Giving *Y* and *B*.

Mating.	Parents.	*Y.*	*B.*
271	1639 × 1587...	2	1
289	1666 × 1610...	5	7
307	2049 × 1610...	1	5
		8	13

Yellow × pink-eyed black, giving intense dark-eyed and pink-eyed young.

CROSS 164. Giving *Y*, *Br*, and *pB*.

Mating.	Parents.	*Y.*	*Br.*	*pB.*
309	2050 × 2062...........	4	1	1

Cream × pink-eyed black, giving only dark-eyed intense young.

CROSS 165. Giving *Y*, cream, and *B*.

Mating.	Parents.	*Y.*	Cream *Y.*	*B.*
299	1105 × 1414	2	. .	3
180	1256 × 1192	10	. .	15
204	1195 × 989	1	3	5
225	1193 × 989	7	. .	4
. . .	Unmarked × unmarked	8	2	10
		28	5	37

CROSS 166. Giving *Y*, *sY*, *B*, and *Br*.

Mating.	Parents.	*Y.*	*sY.*	*B.*	*Br.*
208	1411 × 1394	4	1	4	2

CROSS 166A. Giving *Y*, cream, *Br*, and *W*.

Mating.	Parents.	*Y.*	Cream *Y.*	*Br.*	*W.*
226	1105 × 580	2	1	2	2

Yellow × brown agouti, giving only intense dark-eyed young.

CROSS 167. Giving *Y* and *BAg*.

Mating.	Parents.	*BAg.*
30	511.2B × 502.4A	4

CROSS 168. Giving *Y* and *BrAg*.

Mating.	Parents.	*Y.*	*BrAg.*
32	575 × 502.5A	. .	1
110	427 × 424	3	5
461	4340 × unmarked	2	4
		5	10

CROSS 169. Giving *Y*, *BAg*, and *B*.

Mating.	Parents.	*Y.*	*BAg.*	*B.*
50	511.1A × 140	5	1	2

CROSS 170. Giving *Y*, *BrAg*, and *Br*.

Mating.	Parents.	*Y.*	*BrAg.*	*Br.*
191	892 × 895.......	2	3	1

CROSS 171. Giving *Y*, *BrAg*, and *W*.

Mating.	Parents.	*Y.*	*BrAg.*	*W.*
75	170 × 410.......	1	5	2

CROSS 172. Giving *Y*, *BrAg*, *Br*, and *W*.

Mating.	Parents.	*Y.*	*BrAg.*	*Br.*	*W.*
176	891 × 895.....	9	2	5	6

Yellow × brown agouti, giving intense and dilute dark-eyed young.

CROSS 173. Giving *Y*, *BAg*, *BrAg*, and *dBrAg*.

Mating.	Parents.	*Y.*	*BAg.*	*BrAg.*	*dBrAg.*
69	171 × 411....	7	5	5	1

CROSS 174. Giving *Y*, *dY*, and *dBrAg*.

Mating.	Parents.	*Y.*	*dY.*	*dBrAg.*
423	3414 × 3413....	1	2	4

In the following matings the yellow parents were dilute, and of four different sorts, viz:

Dilute black-eyed yellow, $Y_2Br_2B_2d_2P_2A_2R$;
Dilute black-eyed yellow, $Y_2Br_2B_2d_2P_2R$;
Dilute brown-eyed yellow, $Y_2Br_2d_2P_2A_2R$;
Dilute brown-eyed yellow, $Y_2Br_2d_2P_2R$.

These four varieties are extremely difficult, if not impossible, to tell from one another by superficial examination. The two brown-eyed types may, however, be distinguished at times by their eye-color, which is, as in the corresponding intense types, always brown. The following description will apply then to these four varieties:

Eyes black or brown, ears pink. Ventral hairs much the same as in the intense yellow type. Tail unpigmented. Dorsal hairs a dull heavy yellow with the characteristic washed-out appearance of all dilute forms. Hairs at the base of the ears and around the anus are indistinguishable from the rest of the coat.

Dilute yellow × dilute yellow, giving only dilute dark-eyed young.

Cross 175. Giving *dY* and *dBAg*.

Mating.	Parents.	*dY*.	*dBAg*.
499	Unmarked × 3875....	9	2

Cross 176. Giving *dY* and *dB*.

Mating.	Parents.	*dY*.	*dB*.
547	Unmarked × 5155......	6	2

Cross 177. Giving *dY*, *dBAg*, and *dBrAg*.

Mating.	Parents.	*dY*.	*dBAg*.	*dBrAg*.
382	3401 × 2233........	9	2	3
481	Unmarked × 4456..	15	8	4
482	Unmarked × 4712..	25	2	9
		49	12	16

Cross 178. Giving *dY*, *dBAg*, *dBrAg*, and *dBr*.

Mating.	Parents.	*dY*.	*dBAg*.	*dBrAg*.	*dBr*.
484	Unmarked × 4334....	8	1	3	3

Cross 179. Giving *dY*, *dBrAg*, and *W*.

Mating.	Parents.	*dY*.	*dBrAg*.	*W*.
483	4147 × 4146....	4	2	3

Cross 180. Giving *dY*, *dBAg*, *dBrAg*, and *W*.

Mating.	Parents.	*dY*.	*dBAg*.	*dBrAg*.	*W*.
531	Unmarked × 4146.....	9	1	2	4

Dilute yellow × pink-eyed yellow, giving intense and dilute dark-eyed young.

Cross 181. Giving *dY*, *BAg*, *B*, *dBAg*, and *dBrAg*.

Mating.	Parents.	*dY*.	*BAg*.	*B*.	*dBAg*.	*dBrAg*.
500	Unmarked × 4152..	2	1	1	1	1

Dilute yellow × pink-eyed yellow, giving intense and dilute dark-eyed and pink-eyed young.
Cross 182. Giving *Y*, *pY*, *dY*, *pdY*, *BAg*, *dBAg*, *B*, and *pB*.

Mating.	Parents.	*Y.*	*pY.*	*dY.*	*pdY.*	*BAg.*	*dBAg.*	*B.*	*pB.*	*BAg* or *B.*
545	Unmarked × 4152.	2	..	1	2	2	..	1	..	..
480	Unmarked × 3875.	1	2	..	..	..	..	..	..	2
467	4524 × 4523.......	2	3	3	1	..	1	..	1	..
539	Unmarked × 4523.	..	3	1	..	..	..	2	..	..
		5	8	5	3	2	1	3	1	2

Dilute yellow × pink-eyed dilute yellow, giving only dilute dark-eyed young.
Cross 183. Giving *dY*, *dBAg*, and *dB*.

Mating.	Parents.	*dY.*	*dBAg.*	*dB.*
512	Unmarked × 3875....	15	8	2

Dilute yellow × wild black agouti, giving intense dark-eyed young.
Cross 184. Giving *Y* and ?

Mating.	Parents.	*Y.*
523	4345 × 5160 – 5161 ...	1

Dilute yellow × dilute black agouti, giving dilute dark-eyed young.
Cross 185. Giving *dY*, *dsY*, and *dBAg*.

Mating.	Parents.	*dY.*	*dsY.*	*dBAg.*
439	3553 × 3876.......	7	..	5
417	3554 × 3875........	5	1	3
		12	1	8

Dilute yellow × dilute brown agouti, giving only dilute dark-eyed young.
Cross 186. Giving *dY*, *dBAg*, and *dBrAg*.

Mating.	Parents.	*dY.*	*dBAg.*	*dBrAg.*
450	4023–24 × 4021–22....	1	5	5
427	4024 × 4021–22.......	8	..	5
431	4023 × 4021–22.......	6	4	1
343	2259 × 2233..........	6	4	3
		21	13	14

Dilute sooty yellow × dilute brown agouti, giving dilute dark-eyed and pink-eyed young.

Cross 187. Giving *dsY*, *pdY*, *dBAg*, and *dBrAg*.

Mating.	Parents.	*dsY.*	*pdY.*	*dBAg.*	*dBrAg.*
490	4803 × 4573.........	3	1	1	1
465	Unmarked × 4753...	2	1	..	..
		5	2	1	1

In the following crosses, the yellow parents were pink-eyed, and of four different types, viz.:

Pink-eyed yellow, $Y_2Br_2B_2D_2p_2A_2R$;
Pink-eyed yellow, $Y_2Br_2B_2D_2p_2R$;
Pink-eyed yellow, $Y_2Br_2D_2p_2A_2R$;
Pink-eyed yellow, $Y_2Br_2D_2p_2R$.

The eyes of the two varieties last named contain only a small number of granules, all of which are brown. They are indistinguishable from the eyes of the first two varieties, which, however, contain black granules. The following description will serve for all four varieties:

Eyes clear deep pink. Ears pink and unpigmented. In every other way these pink-eyed types resemble closely the dark-eyed yellow types. They occur in all grades from a deep orange to light cream, as do the dark-eyed forms. Because of the reduction of black and brown granules sooty pink-eyed yellows are seldom if ever obtained.

Pink-eyed yellow × pink-eyed yellow, giving only intense pink-eyed young.

Cross 188. Giving *pY*, *pBAg*, and *pB*.

Mating.	Parents.	*pY.*	*pBAg.*	*pB.*	*p?*
155	1066 × 1064..	3	..	..	..
195	801 × 1064..	2	5	..	1
160	1067 × 1064..	2	..	..	..
173	1074 × 563...	2	1	2	2
113	562 × 563...	6	3	2	1
		15	9	4	4

Pink-eyed yellow × pink-eyed yellow, giving intense and dilute pink-eyed young.

Cross 189. Giving *pY*, *pdY*, and *pdB*.

Mating.	Parents.	*pY.*	*pdY.*	*pdB.*
468	Unmarked × 4523.....	1	1	1

Pink-eyed yellow × pink-eyed dilute yellow, giving intense and dilute pink-eyed young.

Cross 190. Giving *pY*, *pdY*, *pB*, and *pdB*.

Mating.	Parents.	*pY.*	*pdY.*	*pB.*	*pdB.*	*pB* or *pdB.*	*p?*
351	2342 × 2343...	13	1	4	2	3	2

Pink-eyed yellow × black agouti, giving intense dark-eyed and pink-eyed young.

CROSS 191. Giving *Y*, *pY*, *BAg*, and *B*.

Mating.	Parents.	*Y*.	*pY*.	*BAg*.	*B*.	Dark-eyed.
126	414 × 563..	8	1	5	5	2

Pink-eyed yellow × dilute black, giving intense and dilute dark-eyed and pink-eyed young.

CROSS 191A. Giving *Y*, *pY*, *B*, *dB* or *dBAg*, *pdBAg*.

Mating.	Parents.	*Y*.	*pY*.	*B*.	*dB* or *dBAg*.	*pdBAg*.	*p?*
254	685 × 1435.....	1	2	3	1	3	1

Pink-eyed yellow × brown, giving intense dark-eyed young.

CROSS 192. Giving *Y* and *BAg*.

Mating.	Parents.	*Y*.	*BAg*.
201	1489 × 1437...	5	3

Pink-eyed yellow × pink-eyed black agouti, giving only pink-eyed intense young.

CROSS 193. Giving *pY* and *pBAg*.

Mating.	Parents.	*pY*.	*pBAg*.	*p?*
79	413 × 412........	16	14	..
167	1062 × 1065.......	..	4	..
157	1060 × 1065.......	3	4	3
		19	22	3

CROSS 194. Giving *pY*, *pBAg*, and *pB*.

Mating.	Parents.	*pY*.	*pBAg*.	*pB*.
102	557 × 563.........	23	8	2

Pink-eyed yellow × pink-eyed brown agouti, giving only pink-eyed intense young.

CROSS 195. Giving *pY* and *pBAg*.

Mating.	Parents.	*pY*.	*pBAg*.
194	1395 × 1441...	3	2

Pink-eyed yellow × pink-eyed black, giving only intense pink-eyed young.

CROSS 196. Giving *pBAg* and *pY?*

Mating.	Parents.	*pBAg*.
237	684 × 763.....	3

In the following crosses the yellow parents would fall into one of the four following classes:

Pink-eyed dilute yellow, $Y_2Br_2B_2d_2p_2A_2R$;
Pink-eyed dilute yellow, $Y_2Br_2B_2d_2p_2R$;
Pink-eyed dilute yellow, $Y_2Br_2d_2p_2A_2R$;
Pink-eyed dilute yellow, $Y_2Br_2d_2p_2R$.

These four types, as in the intense pink-eyed forms, are indistinguishable from one another by superficial examination.

Eyes pink, otherwise indistinguishable from the dark-eyed dilute yellows already described. No case of a pink-eyed dilute sooty yellow has been recorded in these experiments.

Pink-eyed dilute yellow × dilute black agouti, giving dilute dark-eyed and dilute pink-eyed young.

CROSS 197. Giving *dY*, *pdY*, *dBAg*, *pdBAg*, *dB*, *pdB*, *dBrAg*, and *dBr*.

Mating.	Parents.	*dY*.	*pdY*.	*dBAg*.	*pdBAg*.	*dB*.	*pdB*.	*dBrAg*.	*dBr*.	*pd?*
435	Unmarked × 2488.	3	5	2	1	1	4	..	1	..
425	3493 × 2488.......	1	3	1	1	..	..	1	..	..
436	3490 × 2488.......	4	4	1	3	..	3	..	..	1
		8	12	4	5	1	7	1	1	1

Pink-eyed dilute yellow × black, giving intense and dilute dark-eyed and pink-eyed young.

CROSS 198. Giving *Y*, *pY*, *pdY*, *B*, *pB*, and *dB*.

Mating.	Parents.	*Y*.	*pY*.	*pdY*.	*B*.	*pB*.	*dB*.	*p?*
389	2345 × 2343.....	4	5	1	4	3	2	1

We may now consider a few tests of albinos which have been made. All of these seem to show that albinos may be potentially any of the 32 color varieties already mentioned or any of their heterozygous combinations. None of the following albinos were tested for dilution and therefore they are treated as intense in their formulæ, though if the proper test was made they might not turn out so.

Albino × pink-eyed brown.

CROSS 199.

Mating.	Parents.	*Y.*	*B.*	*BrAg.*	*Br.*	*pB.*	*pBrAg.*	*pBr.*	Formula of albino parent.
517	Unmarked × unmarked	..	..	..	8	..	..	..	$Br_2D_2P_2$.
536	4871 × –07	..	..	..	7	..	..	..	$Br_2D_2P_2$.
458	Unmarked × 440	..	..	..	6	..	..	..	$Br_2D_2P_2$.
540	4873 × –07	..	4	..	1	..	..	..	$Br_2BD_2P_2$.
466	4870–73 × –07	..	3	..	9	..	..	..	$Br_2BD_2P_2$.
518	4870 × unmarked	..	4	..	3	..	..	..	$Br_2BD_2P_2$.
498	4870 × –07	..	3	..	1	..	..	..	$Br_2BD_2P_2$.
470	4272 × 5162	..	..	..	6	..	..	3	Br_2D_2Pp.
516	4285–72 × 5162	..	..	..	5	..	2	6	Br_2D_2PpA.
497	4872 × –07	..	2	..	1	2	..	2	Br_2BD_2Pp.
478	4273 × 5163	..	..	..	..	..	8	7	$Br_2D_2p_2A$.
508	4285 × 5162	..	..	..	..	..	3	3	$Br_2D_2p_2A$.
505	4271 × 5163	..	..	..	..	..	5	..	$Br_2D_2p_2A_2$.
429	4408 × 3746	2	..	..	2	..	..	..	$Br_2D_2P_2R$.
578	Unmarked × unmarked	2	1	1	2	..	..	..	$Br_2BD_2P_2AR$.

A small number of more accurate tests of albinos follow:

Albinos × pink-eyed dilute brown.

CROSS 200.

Mating.	Parents.	*dBr.*
614	Unmarked × 7551 albino	4
626	Unmarked × 7868 albino	18
		22

Both 7551 and 7868 albinos turned out potentially homozygous dilute brown animals.

Two crosses between homozygous dilute brown animals carrying albinism, and 7868 albino, together with another albino (7748) of similar constitution, follow:

CROSS 201.

Mating.	Parents.	*dBr.*	*W.*
628	7749 dil. br. × 7748 albino	6	4
637	7677 dil. br. × 7868 albino	2	7
		8	11

The expectation is equality of white and dilute brown young.

The following case may in one sense be considered as unconformable. It seems probable, however, that the animal recorded as yellow was a dilute form, for the experiment occurred early in the series (1907) before I had learned to recognize dilute animals by sight when young. This animal did not live more than two weeks and could not therefore be tested by breeding.

Pink-eyed black agouti × brown.

CROSS 202.

Mating.	Parents.	*Y?*	*BAg.*	*B.*
77	415 × 409	*1	3	1

*Probable incorrect classification.

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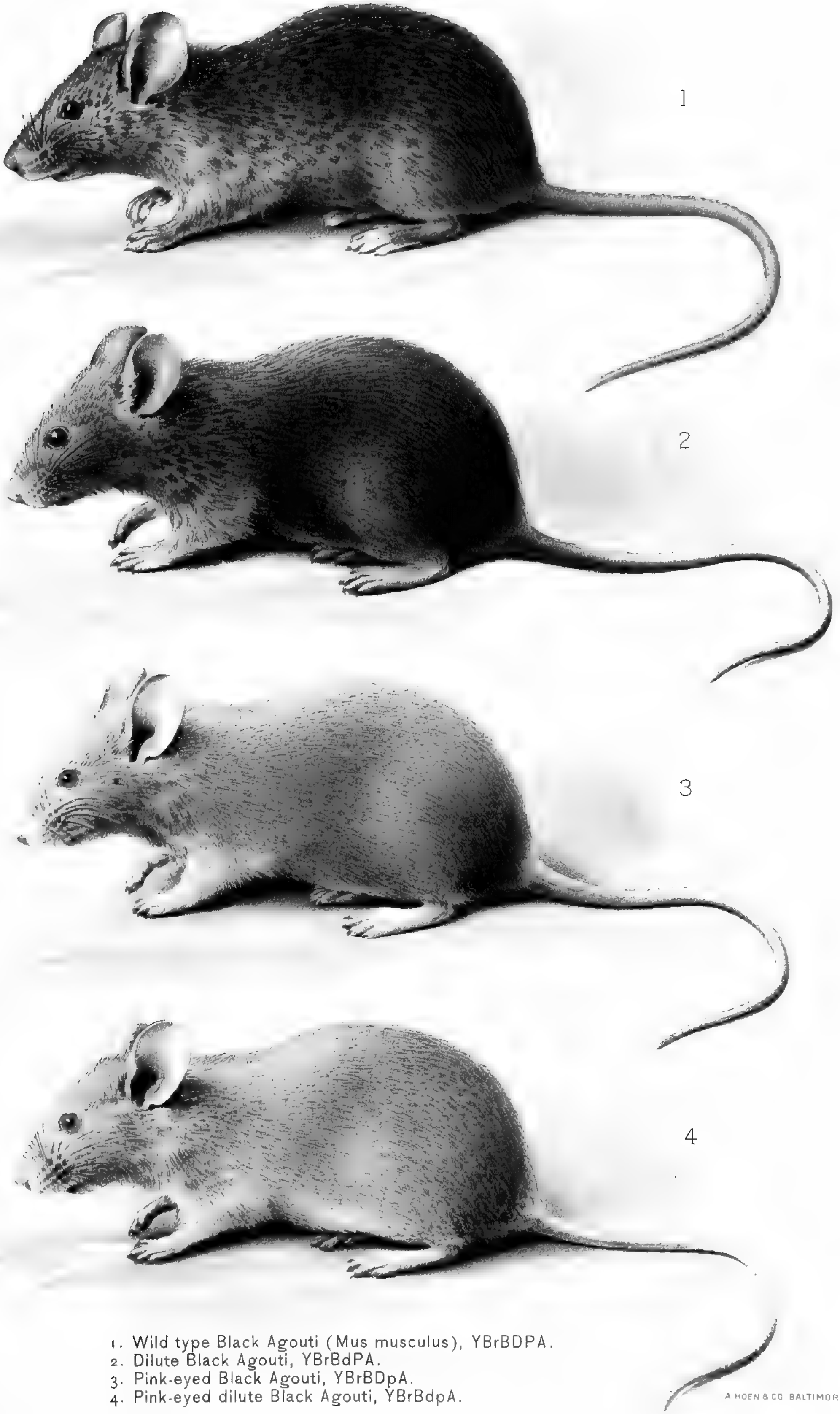

1. Wild type Black Agouti (Mus musculus), YBrBDPA.
2. Dilute Black Agouti, YBrBdPA.
3. Pink-eyed Black Agouti, YBrBDpA.
4. Pink-eyed dilute Black Agouti, YBrBdpA.

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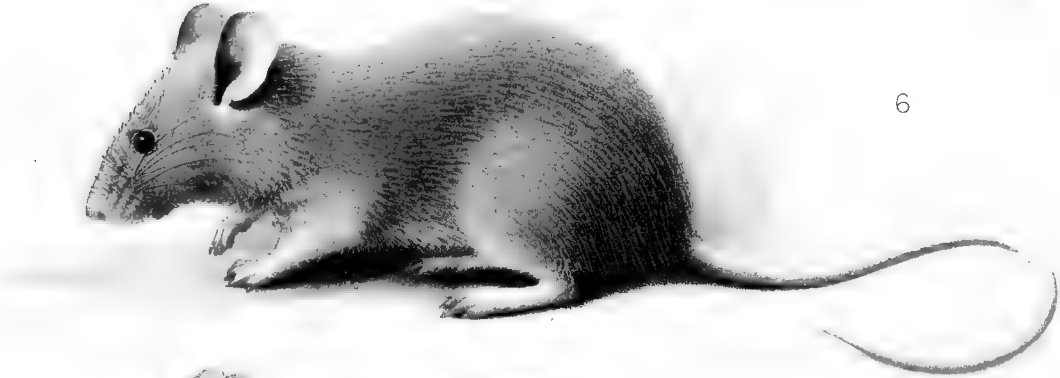

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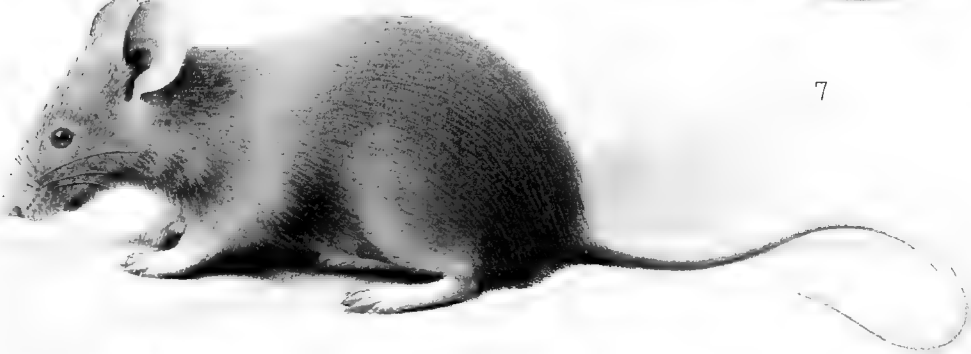

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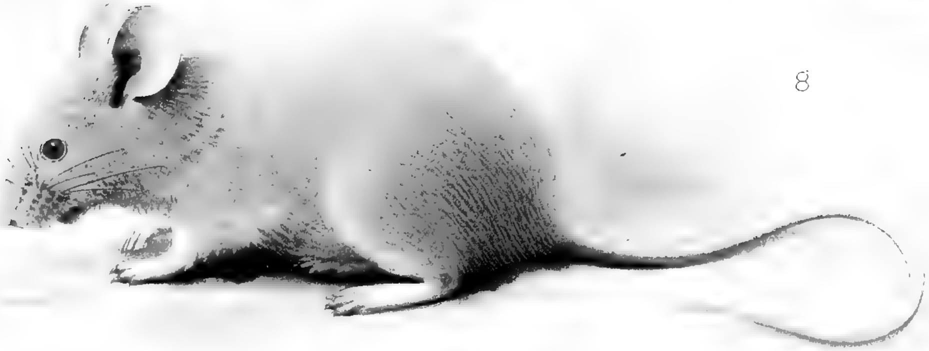

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5. Brown Agouti, YBrDPA.
6. Dilute Brown Agouti, YBrdPA.
7. Pink-eyed Brown Agouti, YBrDpA.
8. Pink-eyed dilute Brown Agouti, YBrdpA

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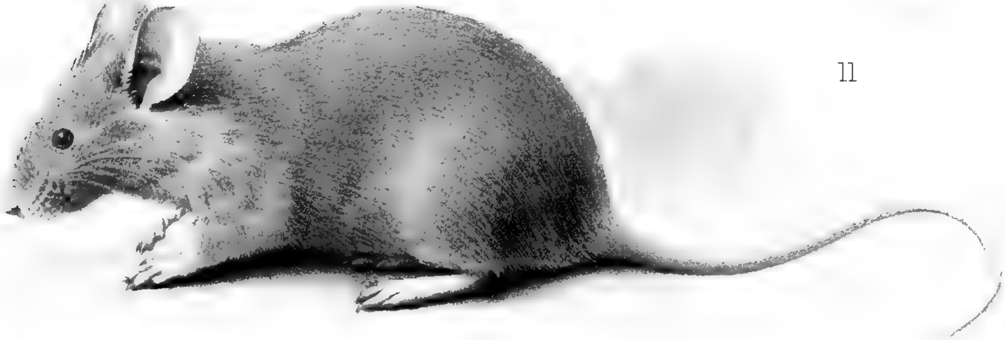

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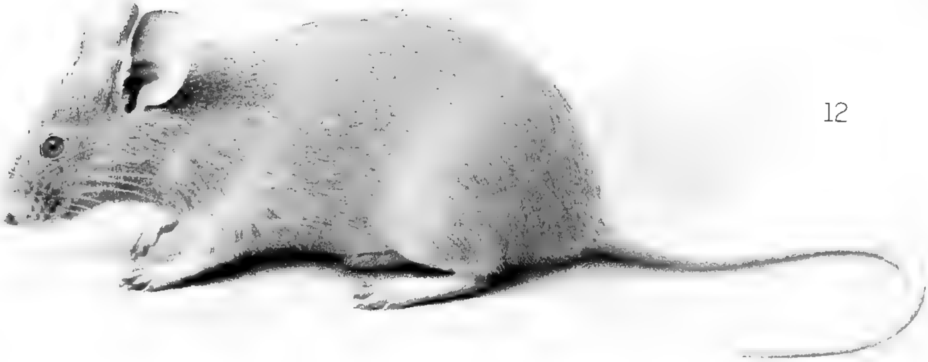

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9. Black, YBrBDP.
10. Dilute Black, YBrBdP.
11. Pink-eyed Black, YBrBDp.
12. Pink-eyed dilute Black, YBrBdp.

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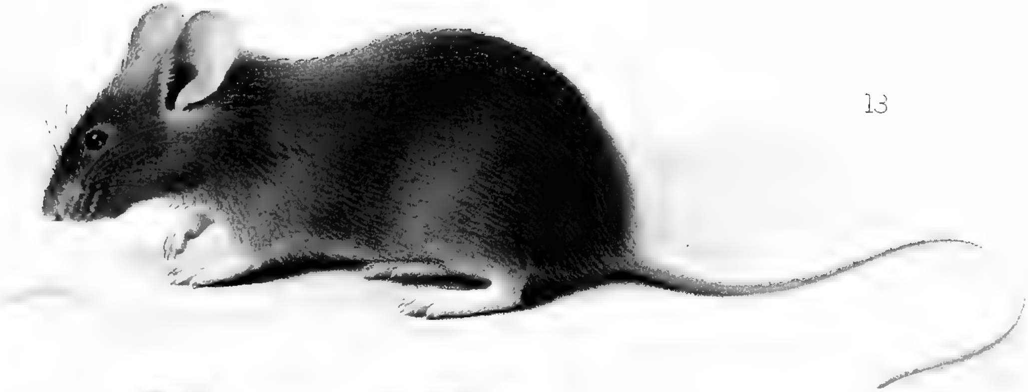

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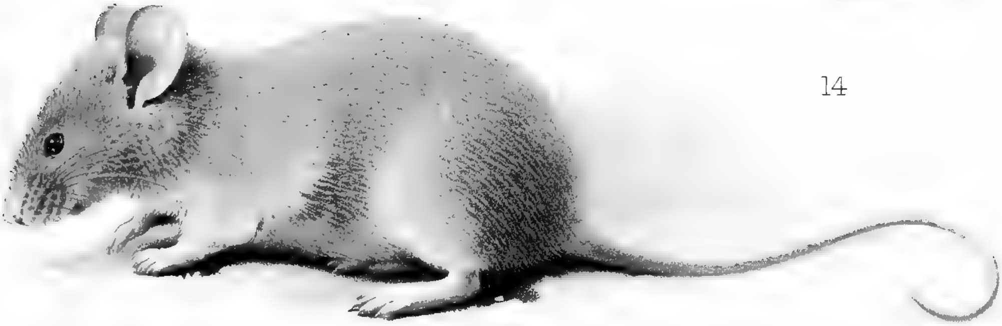

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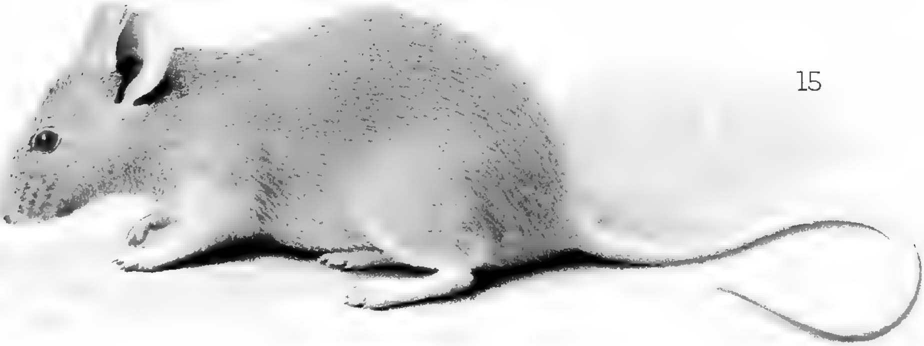

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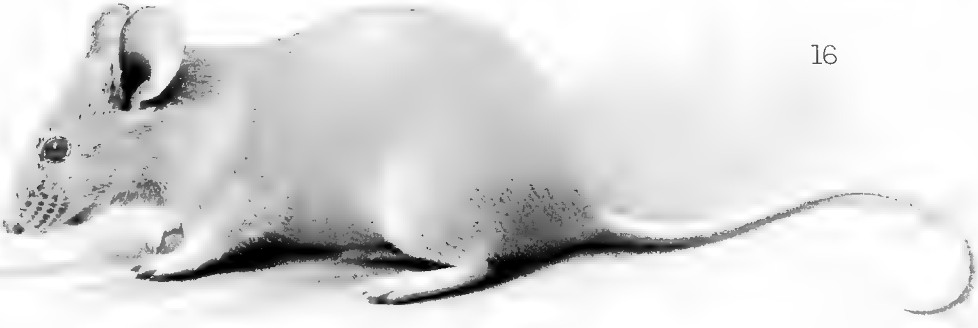

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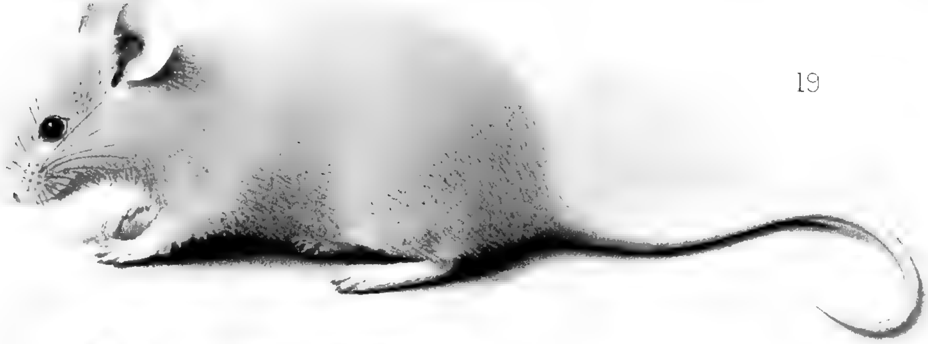
13. Brown, YBrDPr.
14. Dilute Brown, YBrdP.
15. Pink-eyed Brown, YBrDp.
16. Pink-eyed dilute Brown, YBrdp.

17

18



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17. Black-eyed Cream (Yellow), YBrBDPR.
18. Brown-eyed Yellow, YBrDPR.
19. Dilute Brown-eyed Yellow, YBrdPR.
20. Sooty Yellow, YBrDPR.