STUDIES OF

INHERITANCE IN GUINEA-PIGS AND RATS

BY

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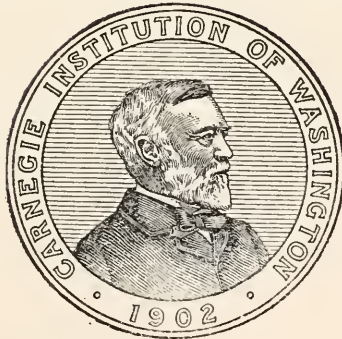
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PART I

AN EXPEDITION TO THE HOME OF THE GUINEA-PIG AND SOME BREEDING EXPERIMENTS WITH MATERIAL THERE OBTAINED

By W. E. CASTLE

INTRODUCTION.

For several years I have been engaged in studies of heredity in guinea-pigs. In the course of these studies all the common varieties of guinea-pigs have been investigated by the method of experimental breeding and something has been learned concerning their inter-relationships and probable mode of origin. The actual origin of most of these varieties is, however, unknown, as is true also concerning most varieties of domesticated animals. One or two varieties have, however, been made synthetically in the laboratory and it is conceivable that, if we had the original wild stock to work with, from which the domesticated guinea-pig has arisen, some or all of the existing varieties might be synthesized anew and perhaps still others might be obtained, and that in this way something might be learned of the method by which new varieties arise. From considerations such as these I have for several years been seeking to obtain living specimens of the wild species which most closely resemble guinea-pigs. In 1903 I received from Campinas, Brazil, 3 wild-caught individuals referred at the time to the species *Cavia aperea*, but since found to agree better with the description of *C. rufescens*. From two of these animals young were obtained, and crosses, the results of which have been described in detail by Dr. Detlefsen (1914), were made with domesticated guinea-pigs. It may be noted that all male F_1 hybrids were sterile, but that the F_1 females were fertile, and that upon repeated crossing of these with male guinea-pigs, a race of fertile hybrids was at last obtained, these being, in the language of breeders, about $\frac{7}{8}$ guinea-pig, $\frac{1}{8}$ *rufescens*. From this result it seems doubtful whether *C. rufescens* has any close genetic relationship to the domesticated guinea-pig, although by hybridization it has been found possible to produce races ($\frac{7}{8}$ or more guinea-pig) which have derived certain characters from a *rufescens* ancestor.

Cavia aperea from Argentina has been crossed with the guinea-pig by Nehring (1893, 1894) in Berlin, with the production of fully fertile hybrids. This result indicates a closer relationship with the guinea-pig than *C. rufescens* manifests. Darwin (1876), however, did not regard *aperea* as the ancestor of the guinea-pig, because he found it to be infested with a different species of louse. I have not myself been able as yet to obtain specimens of *C. aperea*. Nehring (1889) has argued with much plausibility that *Cavia cutleri* of Peru is more probably the ancestor of the guinea-pig, for (1) it agrees closely with the guinea-pig in cranial characters and it occurs in a region where guinea-pigs have been for a long time kept in domestication, as is shown by the occurrence of mummified guinea-pigs which had been buried with the dead. Natu-rally I formed a strong desire to secure living specimens of *C. cutleri* for

experimental study, but for several years I was unable to do so. Through correspondence with Professor S. I. Bailey, who was at the time director of the Harvard Astronomical Observatory at Arequipa, Peru, I ascertained that a wild species of cavy occurred in that locality. Professor Bailey kindly captured some of the cavies and attempted repeatedly to forward them to me, but without success. The steamship companies refused to accept them for transportation on the ground that they might lead to detention or quarantining of their vessels, since all rodents were suspected of being carriers of bubonic plague. After several years of waiting and fruitless negotiation with every chance traveler to Peru with whom I came in contact, I resolved to go to Peru myself and get the desired specimens. Through a grant made by the Carnegie Institution of Washington I was enabled, in the fall of 1911, to carry this resolution into effect.

The Carnegie Institution of Washington and the Bussey Institution have together provided means for carrying out the breeding experiments described in this paper. I wish to express my gratitude to both institutions and to thank the director and other officers of the Harvard College Observatory for hospitality and generous assistance given me at the Arequipa station. I am indebted also to Professor C. J. Brues for kindly bringing me a stock of guinea-pigs obtained by him near Lima, Peru, in 1912.

SOME OBSERVATIONS ON GUINEA-PIGS IN PERU.

On a midsummer day in December 1911 I arrived as a guest at the Harvard College Observatory in Arequipa, Peru, where I went in search of guinea-pigs, wild and domesticated, to be used in breeding experiments.

The day after my arrival at the observatory I walked a short distance up the highway through a group of adobe cabins, straw-thatched and without chimney or windows, and with a single door. On looking in at the open door of one of the cabins, I was pleased to see a domesticated guinea-pig of the common spotted black-and-white sort familiar to lovers of pet-stock throughout the world. In other near-by cabins I found considerable numbers of guinea-pigs were kept, in one as many as 40. They were fed on fresh-cut alfalfa or the green leaves of maize, receiving apparently no other food and no water. At the back or sides of the cabin was a sort of shelf or bench of stone used as a seat or couch, underneath which the guinea-pigs had their home. Their escape through the open door was prevented by a high lintel of stone, perhaps 15 inches (38 cm.) high, over which one has to step in entering. In these cabins were seen most of the common color varieties of guinea-pigs known to us, agouti, black, yellow, and white (albino). None of the colored individuals which I saw was self-colored; all were spotted with white or with yellow or in both ways. The same predilection for spotting is seen in the other important native domesticated animal, the llama. I saw no llamas except such as were spotted; some were black spotted with white, but the majority were of a soft shade of buff or fawn spotted with white. The common spotted condition of our guinea-pigs is undoubtedly one of long standing; indeed it would seem that the Peruvian natives breed no other variety except such as are either white spotted or all white. The unspotted or "self-colored" varieties now kept by fanciers in Europe and America have probably been produced by selection from stock originally spotted. This is indicated by the great difficulty in securing a self-colored race entirely free from spotted individuals. Most self-colored races, even when bred for many generations from self-colored ancestors exclusively, will produce an occasional individual bearing a few hairs or a patch of hairs of some other color, or of white.

Among the guinea-pigs kept by the natives near Arequipa, I observed an occasional animal having a rough or rosetted coat. This variety is known to fanciers in Europe and the United States under the name Abyssinian. (See Castle, 1905.) It is said, on the authority of Geoffroy Saint-Hilaire, to have been introduced from Peru into Europe about the year 1872 in a rough-coated, long-haired individual received at the Jardin d'Acclimatation, Paris. In conformity with this account

it may be said that the rough-coated long-haired variety has ever since its introduction been called by fanciers "Peruvian." I saw no long-haired individuals, either rough-coated or smooth, among the guinea-pigs kept by the natives at Arequipa, and the short-haired rough-coated ones observed had imperfectly developed rosettes, much inferior to the best standard-bred rosetted Abyssinians of fanciers in Europe and the United States. For this reason I infer that no particular attention was given to this character in the breeding of the guinea-pigs which I saw, though this may very likely have been done in other parts of the country. But the unit-character variation which is responsible for the rosetted condition of the coat in Abyssinian guinea-pigs was plainly represented in the stocks kept by the natives in Arequipa and needed only selection to bring it up to the standards of fanciers.

Eight independent mendelizing unit-character variations had been recognized as affecting the coat characters of guinea-pigs up to this time. Six of these were represented among the four or five dozen guinea-pigs which I actually saw in the cabins of natives, the other two unit characters being (1) the long-haired variation which, as already noted, is said to have been brought originally from Peru to Europe; and (2) the brown variation which first came to the notice of fanciers in England about 1900 and was certainly in existence before that time in the United States, as I can state from personal knowledge. It is uncertain whether or not this last variation had already occurred in Peru and was thence transferred to Europe, but it is certain that all the other 7 had done so, and it is very probable that this also originated in Peru. Further, a ninth wholly independent unit-character variation (presently to be described, viz, the pink-eyed variation) has made its appearance in stocks of domesticated guinea-pigs obtained by me at Arequipa in 1911 and by my colleague, Professor C. T. Brues, at Lima, in 1912. So it is clear that this variation also is widely disseminated among domesticated guinea-pigs kept by the natives in Peru and which have never been in the hands of European fanciers at all.

It can be stated, therefore, with probable correctness, that the guinea-pig has undergone in domestication more extensive variation in color and coat characters than any other mammal, and that this variation has occurred almost if not quite exclusively under the tutelage of the natives of Peru. This conclusion points either to a great antiquity of the guinea-pig as a domesticated animal or to more rapid evolution by unit character variation than by other natural processes.

That the natives do give careful attention to the selection of animals for breeding is shown by the following incident: In the cabin near the observatory, where I first saw guinea-pigs in Peru, and where I ultimately secured two pairs of animals, one of which I brought back with me, I observed a very large individual which I desired to purchase, and though other individuals were offered me at a very reasonable price,

this particular one could not be had because, I was assured, he was the "padre" (sire) of the entire family. Size seemed to be the point especially emphasized in the breeding of guinea-pigs in this cabin, as would naturally be the case when the animals formed the meat-supply of the family, as they do now among the native poor of Peru and doubtless have done since ancient times.

But the chief object of my journey to Peru was the study not of the domesticated guinea-pigs of the country, but of their wild progenitors. Accordingly special efforts were made to secure specimens of the wild cavy, which Professor Bailey had found to be abundant in the locality. Once or twice, when riding along a road between irrigated fields, I had seen a cavy scurry to cover in a pile of rocks; further, I had observed droppings of the animals in the rocky wall of a cattle corral in an alfalfa field. But how to capture the animals alive was a problem which baffled immediate solution. It seemed likely that the natives would know better how to go about this than I did. Accordingly word was passed around among the near-by villages that a good price would be paid at the observatory for wild cavies, either alive or dead. Within a few hours boys began to arrive with the coveted specimens and for the next week I was kept busy preparing skins and saving bones of the animals which were received dead, or making cages and caring for such as arrived alive. In this way 11 cavies (all I could hope to transport safely) and about a dozen skins were soon secured, and preparations were made for the return journey. In due time the journey was accomplished, and with such success that three new races of guinea-pigs were added to our experimental stocks, viz, (1) a wild species, the probable ancestor of the domesticated guinea-pig, identified as *Cavia cutleri* Bennett; (2) a feral race from Ica, probably identical with that described by Von Tschudi; (3) domesticated guinea-pigs, such as are at present kept by the natives of Peru.

HYBRIDIZATION EXPERIMENTS WITH CAVIA CUTLERI.

LIFE HISTORY OF CAVIA CUTLERI.

The primary object of my journey to Peru was to secure representatives of the wild species of cavy, *Cavia cutleri* Bennett, known to exist there. Four pairs of these animals captured at Arequipa were successfully installed in cages at the Bussey Institution in January 1913.

One of the males soon died without leaving descendants; the other 7 animals (4 females and 3 males) produced offspring in captivity, which have continued to breed succesfully, though the stock has at times been seriously reduced by disease in cold weather. Three generations of descendants have been reared from the original stock of 7 animals. Together they number 100 individuals, of which 47 are males and 53 females. All are very uniform in color, size, general appearance, and behavior.

Their color is a dull leaden gray-brown, well adapted to escape notice amid the arid surroundings of their native habitat. The fur is agouti-ticked and the belly light, but the yellow of the ticking and belly is so pale as to resemble a dirty white or very light cream shade. The color is much paler than that of the Brazilian species, *Cavia rufescens*, studied by Detlefsen. The fur is also finer and softer, in which respect it resembles the guinea-pig. The size of *C. cutleri* is about the same as that of *C. rufescens*, and between one-third and one-half that of the guinea-pig. The maximum weight of an adult male is about 525 grams; that of a domesticated male guinea-pig obtained in Arequipa ($\male$ 1002) is nearly three times this amount.

In wildness *Cavia cutleri* is very much like *C. rufescens*. The animals live contentedly in small cages, 2 feet 6 inches square, but invariably retreat under their box or conceal themselves in the hay if anyone approaches.

The extreme savageness toward each other of individuals of *Cavia cutleri* makes it difficult to rear large numbers of them in captivity. It is seldom possible to keep more than a single pair in a cage together for any length of time. Two adult males will not live together peaceably under any circumstances, and if two females are placed together in a cage with one male persecution of one female by the other usually follows. Even when the young are allowed to grow up in the same cage with their parents, family dissensions are likely to arise as soon as the young become mature.

The period of gestation (minimum interval between litters) averages 3 or 4 days shorter than in guinea-pigs, being 60 to 70 days, and the number of young to a litter varies from 1 to 4. Fifty-three litters born in captivity include exactly 100 young, an average of 1.89 young to a litter. The size of litter occurring most frequently is 2, which has been recorded

TABLE 1.—*Number and size of litters produced by each mother, Cavia cutleri.*

Mother and date of her birth.	Date of litter.	Size of litter.	Mother's age at birth of young.	Days since last litter.
			months	
♀ 2 (caught wild); born March 1911 (?)........	Mar. 5, 1913	2	24	..
	June 28, 1913	2	27	..
	Aug. 29, 1913	2	29	62
	Nov. 4, 1913	2	31	67
♀ 3 (caught wild); born May 1911 (?).........	May 29, 1912	3	12	..
	Oct. 3, 1912	3	17	..
	Dec. 26, 1912	1	20	..
	July 5, 1913	3	26	..
	Dec. 15, 1913	1	32	..
♀ 5 (caught wild); born Jan. 1910 (?)..........	July 12, 1912	3	18	..
	Sept. 12, 1912	3	20	62
	Nov. 15, 1912	3	22	64
	Jan. 22, 1913	2	24	68
♀ 6 (caught wild); born Jan. 1910 (?)..........	Sept. 6, 1912	3	20	..
♀ 11; May 29, 1912.........................	Sept. 26, 1912	1	4	..
♀ 15; July 12, 1912........................	Dec. 10, 1912	2	5	..
	Feb. 17, 1913	1	7	69
	June 30, 1913	3	12	..
	Oct. 1, 1913	2	15	..
	Aug. 15, 1914	2	25	..
	Dec. 2, 1914	1	29	..
♀ 26; Sept. 6, 1912........................	July 5, 1912	1	10	..
	Sept. 4, 1912	2	12	61
	Nov. 4, 1912	2	14	61
♀ 27; Sept. 6, 1912........................	Apr. 25, 1913	1	7	..
	June 25, 1913	1	9	61
	Aug. 25, 1913	1	11	61
♀ 36; Oct. 3, 1912.........................	June 17, 1913	1	8	..
	Oct. 16, 1913	4	12	..
	Aug. 3, 1914	2	22	..
	Nov. 2, 1914	2	25	..
♀ 42; Nov. 15, 1912........................	July 26, 1913	2	8	..
	Sept. 20, 1913	2	10	56
	Aug. 25, 1914	2	21	..
	Nov. 2, 1914	2	24	69
♀ 65; Jan. 22, 1913........................	July 26, 1913	2	6	..
	Nov. 1, 1913	2	9	..
	Dec. 27, 1913	3	11	56
♀ 66; Jan. 22, 1913........................	June 25, 1913	2	5	..
	Aug. 29, 1913	2	7	65
♀ 79; March 5, 1913........................	June 28, 1913	1	$3\frac{2}{3}$!	..
	Sept. 4, 1913	2	6	68
♀ 118; June 28, 1913.......................	Nov. 4, 1913	1	4	..
	Jan. 5, 1914	1	6	62
♀ 124; June 30, 1913.......................	Nov. 1, 1913	3	4	..
♀ 129; July 5, 1913........................	Dec. 27, 1913	2	6	..
	Mar. 1, 1914	1	8	64
♀ 184; Sept. 4, 1913........................	Mar. 15, 1914	1	6	..
	May 18, 1914	1	8	64
	July 20, 1914	2	10	63
♀ 224; Oct. 16, 1913.......................	July 30, 1913	1	9	..
	Dec. 8, 1913	1	14	..
♀ 241; Nov. 4, 1913........................	Jan. 12, 1915	2	14	..

24 times; litters of 1 have been recorded 18 times, litters of 3, 10 times, and a litter of 4 once.   Factors which influence size of litter are evidently age and state of nourishment of the mother.   Table 2 shows the relation of age of mother to size of litter.   Very young mothers (age 4 months or less) have only 1 young at a birth.   The females become sexually mature at a very early age, as do female guinea-pigs.   Well-nourished females may breed at 2 months of age, when they are less than half-grown, full growth not being attained until they are 12 or 13 months old.   Females over 4 months but under 12 months of age produce usually 1 or 2 young at a birth, rarely 3; those which are 1 or 2 years old produce the maximum number of young, usually 2 or 3, rarely 1 or 4.   After the age of 2 years the number of young again

TABLE 2.—*Relation between age of mother and size of litter, Cavia cutleri.*

Age of mother in months.	Size of litters and number of each size.				Age of mother in months.	Size of litters and number of each size.			
	1 in litter.	2 in litter.	3 in litter.	4 in litter.		1 in litter.	2 in litter.	3 in litter.	4 in litter.
4..........	3	..	..	..	12 to 15.......	1	3	2	1
5..........	..	2	1	..	16 to 19.......	..	1	2	..
6..........	1	3	..	..	20 to 23.......	1	2	3	..
7..........	3	1	..	..	24 to 27.......	..	6	1	..
8..........	3	1	..	..	28 to 31.......	1	2	..	..
9..........	2	1	..	..	32............	1	..	..	..
10..........	1	2	..	..					
11..........	1	..	1	..	Total litters...	18	24	10	1

decreases to 1 or 2.   The oldest female known to have borne young (one of the original stock) had at the time been in captivity over 2 years and her estimated age was 32 months.   None of the females born in captivity has given birth to young at a more advanced age than 29 months.   Our records accordingly indicate that females rarely breed after they have attained the age of $2\frac{1}{2}$ years.   The duration of the breeding period in the case of males is more extended.   It is probable that males do not attain sexual maturity quite so early as females, for females may breed when less than 2 months old, but we have no evidence that males can breed before they are 3 months old.[1]   But the capacity to breed once attained continues indefinitely.   One male ($\male$4) caught wild in December 1911 and estimated then to have been 6 months old is still siring young, more than 3 years after his capture, being, it is estimated, nearly 4 years old.

Females are capable of breeding again immediately after the birth of a litter, but if they do so the number of young at the next birth is

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[1]Mr. Wright has called my attention to a record from his experiments which shows that a male guinea-pig containing a slight infusion of *rufescens* blood must have been sexually mature at $2\frac{1}{2}$ months of age.   This is the only record known to me of a guinea-pig male breeding when less than 3 months old.

apt to be less, or the young will be born smaller and less fully developed (with smaller bodies and shorter hair), and the period of gestation will be shortened, even to 56 days in extreme cases, the normal period being, as in the guinea-pig, between 60 and 70 days. (See table 4.) If the mother is well nourished and has not borne a litter recently, she is more likely to have a large litter of young. The largest litter recorded (4) was borne by a female 1 year old, which had previously had only 1 young, born 4 months earlier. The recorded date of the birth of each litter of young is given in table 1, together with the interval in days between successive litters by the same mother, except in cases where the interval is obviously greater than the ordinary period of gestation, and it is to

TABLE 3.—*Relation of size of litter and number of litters to time of year.*

Born in—	Size of litters and number of each size.				Total litters.	Total young.
	1 in litter.	2 in litter.	3 in litter.	4 in litter.		
January.........	1	2	..	..	3	5
February........	1	..	..	..	1	1
March..........	2	1	..	..	3	4
April...........	1	..	..	..	1	1
May...........	1	..	1	..	2	4
June...........	3	2	..	..	5	7
Total born in first 6 months[1]......	9	5	1	0	15	22
July...........	2	3	3	..	8	17
August.........	1	5	..	..	6	11
September......	1	3	2	..	6	13
October.........	..	1	1	1	3	9
November.......	1	5	2	..	8	17
December.......	4	2	1	..	7	11
Total born in second 6 months[2]..	9	19	9	1	38	78

[1]Average, 1.47 young per litter.   [2]Average, 2.05 young per litter.

be supposed that the mother did not breed again immediately. The variation in these day intervals between litters is shown in table 4, from which it appears that the gestation period ordinarily continues from 61 to 69 days, with 63.3 days as an average. However, the periods as recorded can not be relied upon as accurate, except within limits of about 2 days, for the cages were not inspected daily, but only once or twice a week, and when young more than 24 hours old were found in a cage, the estimated age of the young may differ from the true age by 1 or 2 days. Young less than a day old are readily recognized as such by the condition of the umbilical cord.

The 4 original wild-caught females have a somewhat better record of productiveness than their descendants reared in captivity, which indi-

cates that laboratory conditions of close captivity are not as favorable for full growth and vigor as the freer life and better air of the original habitat. The 4 wild-caught females produced 33 young in 14 litters, an average of 2.36 young to a litter. Their daughters or granddaughters, reared in captivity, when of like age, have produced 27 young in 13 litters, an average of 2.07 young to a litter.

Too much emphasis must not be laid, however, on this difference, because productiveness depends largely on food, care, and weather conditions, and it is not certain that these were equally favorable for the original females and for their descendants, respectively.

Table 1 shows for each mother how many litters of young she has borne, at what age she bore them, and how many young were contained in each litter. In the case of the 4 females caught wild, the age given for the mother is of course not known; the age recorded is an estimate based on the size of the mother when captured.

Table 3 shows in what month each litter of young was born and what its size was. This table brings out rather strikingly the effect of the seasons and consequent character of food available upon the size and number of the litters.

TABLE 4.—*Variation in period of gestation (interval since previous litter) in Cavia cutleri. Average, 63.3 days.*

Days between litters.	Cases.	Days between litters.	Cases.
56	2	65	1
61	4	67	1
62	3	68	2
63	1	69	2
64	3		

In the 6 months from July to December inclusive, litters were born which were conceived under summer conditions, with an abundance of green food available. It will be observed that in this half of the year the litters are numerous (38) and large (average 2.05 young to a litter). The young born in the 6 months January to June inclusive were conceived under winter conditions, when the mothers were subsisting largely on a diet of dried or concentrated foods, with a limited amount of green food available. In this half of the year the litters are less numerous (15) and smaller (average size 1.47 young).

Temperature probably does not directly affect the result, as the animals were kept in a heated house, but purity of the air may possibly do so, as the house is much better ventilated in the warmer months. But food is probably the most important factor, as the condition of the animals changes promptly with change of food, even when other conditions show no change.

CROSSES OF CAVIA CUTLERI MALES WITH GUINEA-PIG FEMALES.

Crosses have been made only between male *Cavia cutleri* and female guinea-pigs. The reciprocal cross was not undertaken, because the number of *cutleri* females on hand at any one time has been insufficient and because it seemed probable that a cross with the much larger guinea-pig would be fatal to the *cutleri* females because of the probable large size of the hybrid offspring. Two races of guinea-pigs were employed in the crosses, these being the purest races available, the genetic properties of which had been long and thoroughly tested.

The race most extensively used may be called race C. It consisted of "brown-eyed cream" individuals or of albinos borne by brown-eyed cream parents. The results of crosses of colored and albino individuals of race C will be described separately. The other race may be called race B. It consisted of intensely black-pigmented individuals or of albinos produced by such black individuals. The results of crosses with the two sorts of individuals will be described separately. A *cutleri* male bred in captivity (σ78) was mated with black females of race B, and produced 9 F_1 young, all colored like *C. cutleri*, but darker, the ticking of the fur being brick red or yellow instead of creamy white as in *cutleri*.

Albino females of race B were mated with the same *cutleri* male (σ78) or with σ114, another *cutleri* male reared in captivity, or else with σ4 or σ8, which were original *cutleri* males caught wild. Such matings produced 39 F_1 young, all with the same (golden agouti) type of coloration as the young produced by the black mothers.

Females of race C were mated only with the two wild-caught *cutleri* males (σ4 and σ8). The cream-colored mothers of race C produced 34 young, all golden agouti in color like the young derived from race B crosses, but much lighter. They were, however, darker in color than *C. cutleri*, the agouti ticking being yellow or reddish, not creamy white as in *cutleri*. (See plate 3.) Albino females of race C produced by the *cutleri* males 14 young, indistinguishable in appearance from the young produced by their cream-colored sisters.

The F_1 hybrids, whose total number was 96, were all vigorous and large, their adult size nearly or quite equaling that of guinea-pigs. They grew with great rapidity and have proved fully fertile *inter se*. In wildness and ferocity they are intermediate between the parent races.

COLOR INHERITANCE AMONG THE F_2 HYBRIDS.

(a) CROSS ♀ ALBINO (RACE B) × ♂ CUTLERI.

By breeding *inter se* certain of the F_1 hybrids, from the cross ♀ albino, race B, × ♂ *cutleri* there has been produced a second (or F_2) generation of hybrids, which number 75 individuals. As regards color, disregarding minor differences of intensity of pigmentation, these hybrids fall into three classes: golden agouti, black, and albino. Of the

agoutis there are 43, of the blacks 15, and of the albinos **17**. **The** numerical relations of the classes suggest a dihybrid Mendelian ratio of $9:3:4$, which is in entire agreement with existing knowledge of color inheritance in guinea-pigs (Castle, 1905; Sollas, 1909). *C. cutleri* is evidently homozygous for all Mendelian color factors, since it breeds very true to color. Albino guinea-pigs from a black race are known to possess two independent recessive modifications from this condition, lacking both the agouti factor and the so-called color factor. As regards these factors, then, the wild race, *cutleri*, forms gametes AC, the albino forms gametes ac, and the F_1 hybrids form gametes of the four types AC, Ac, aC, and ac. From recombination of such gametes should arise in F_2 zygotes as in table 5.

TABLE 5.

1 AACC	1 aaCC	1 AAcc	1 aacc
2 AaCC	2 aaCc	2 Aacc	
2 AACc			
4 AaCc			
9 agouti	3 black	3 albino	1 albino

The several kinds of albinos being similar in appearance, the expected result is 9 agouti, 3 black, 4 albino. The agreement with this expectation is fairly close (see table 6).

TABLE 6.

	Agouti.	Black.	Albino.
Observed......	43	15	17
Expected......	42.19	14.06	18.75

(b) CROSS ♀ ALBINO (RACE C) × ♂ CUTLERI.

F_1 animals from the cross between an albino of race C and a *cutleri* male have produced 44 F_2 young, which fall into 7 color classes, disregarding differences of intensity of pigmentation. These classes and their numerical representation among the 44 young are as follows: golden agouti, 10; black, 1; cinnamon, 8; black-eyed cream, 4; brown-eyed cream, 3; chocolate, 4; albino, 14. (See plate 4.) The occurrence of these several classes of F_2 young is what previously existing knowledge of color inheritance among guinea-pigs would have led us to expect, for it was known that albinos of race C differed from agoutis in the same two factors as the albinos of race B, viz, the agouti factor and the color factor. In addition, the albinos of race C were known to differ from agoutis in two other factors, seen respectively in chocolate and yellow races. The chocolate race may be considered to have arisen by a recessive modification of the black factor B, and the yellow race by a similar modification of the extension factor E. Accordingly this cross

was supposed in advance to involve 4 independent Mendelian factors, a supposition which the observed result justifies. The factor differences in the two races are: gametes of *cutleri*, ABCE; of albino (race C), abce. On this hypothesis the F_1 hybrids should form 16 different kinds of gametes, the color potentialities of which are indicated in parentheses:

1 ABCE (agouti).	7 AbcE (albino).	12 Abce (albino).
2 aBCE (black).	8 abCE (chocolate).	13 aBce (albino).
3 AbCE (cinnamon).	9 aBCe (black-eyed yellow).	14 abCe (brown-eyed yellow).
4 ABcE (albino).	10 aBcE (albino).	15 abcE (albino).
5 ABCe (black-eyed yellow).	11 AbCe (brown-eyed yellow).	16 abce (albino).
6 ABce (albino).		

From this list it will be observed that 2 different gametic factorial combinations are capable of producing black-eyed yellow, and that the same is true concerning brown-eyed yellow, while 8 different combinations contain the potentialities of albinos. From these considerations it follows that the F_2 ratio will be peculiar, since each of the yellow classes that can be distinguished from each other (black-eyed and brown-eyed) will itself be composite, and the same will be true of the albino class. The expected classes and their proportional frequencies will accordingly be:

Golden agouti	81	Yellow (brown-eyed)	12
Black	27	Chocolate	9
Cinnamon	27	Albino	64
Yellow (black-eyed)	36		

A cross involving the formation of so many classes of individuals can not be expected to show very satisfactory Mendelian ratios in so small a number of offspring as 44. All the expected classes are represented, although black is represented in a single individual only.

The colored individuals of race C were known in many cases to carry albinism as a recessive character. The albino gametes of such individuals would, in crosses with *cutleri* mates, form the same kind of zygotes as the albinos of race C, which were used in the cross just described. In considering the results of such crosses, it is therefore proper to include in one category F_1 animals derived from both sources. If this is done the F_2 young are increased to 108, distributed as shown in table 7, the expected theoretical number in each class being shown in a parallel column.

TABLE 7.

	Observed.	Expected.		Observed.	Expected.
Golden agouti	33	34.17	Chocolate	7	3.80
Black	7	11.39	Albino	27	27.00
Cinnamon	13	11.39			
Black-eyed yellow	13	15.08		108	108.00
Brown-eyed yellow	8	5.07			

(c) CROSS ♀ BROWN-EYED CREAM (RACE C) × ♂ CUTLERI.

The F_1 animals produced by crossing brown-eyed cream females of race C with *cutleri* males themselves produced 132 F_2 young, distributed among the same 7 classes as the albino cross had produced (table 8).

TABLE 8.

	Observed.	Expected.		Observed.	Expected.
Golden agouti........	57	48.94	Chocolate..........	5	5.44
Black...............	17	16.31	Albino.............	16	.....
Cinnamon..........	10	16.31			
Black-eyed yellow....	19	21.75		132	116.00
Brown-eyed yellow....	8	7.25			

Except in regard to albinos, the result expected from this cross is the same as that expected from crossing albinos of race C. Accordingly the albinos may be for the moment disregarded. The expectation as regards the colored classes of young may then be stated as shown in the column of "observed" results.

The occurrence of 16 albinos in this F_2 generation shows that certain of the F_1 pairs were heterozygous for this character, which they obviously derived from the brown-eyed cream parent, not from the *cutleri* parent; for the brown-eyed cream animals of race C were known in many cases to be capable of producing albinos, whereas the *cutleri* stock bred true. Accordingly such pairs of F_1 animals from this cross as produced albino young should be tabulated with the hybrids produced by crossing albinos of race C with *cutleri* males. If this is done there remain 68 instead of 116 F_2 young to be considered. Among these are 3 albinos which it is impossible to transfer to table 7, because it is not known what colored individuals were born in the same litters with them. They were born in a pen containing 2 females which had young simultaneously, one of which was known to produce albino young, though the other did not. Omitting the 3 albinos, there remain 65 colored young, distributed as shown in table 9.

TABLE 9.

	Observed.	Expected.		Observed.	Expected.
Golden agouti........	34	27.42	Brown-eyed yellow....	3	4.06
Black...............	11	9.14	Chocolate..........	2	3.05
Cinnamon..........	5	9.14			
Black-eyed yellow....	10	12.19		65	65.00

(d) RESULTS FROM (b) AND (c) COMBINED.

Since the expectation is the same as regards the relative proportions of the several colored classes in all crosses of race C females (whether albino or colored) with *cutleri* males, we may legitimately combine all

the F_2 results, omitting only albinos (which have been dealt with already). When this is done we get the results shown in table 10. No class deviates from expectation enough to suggest "linkage" or "coherence" of characters involved in the cross.

TABLE 10.

	Observed.	Expected.		Observed.	Expected.
Golden agouti........	67	61.59	Brown-eyed yellow....	11	9.13
Black..............	18	20.53	Chocolate...........	9	6.85
Cinnamon..........	18	20.53			
Black-eyed yellow....	23	27.37		146	146.00

(e) INTENSITY AND DILUTION AMONG THE HYBRIDS.

It has been stated that the F_1 young produced by the cross of female albinos of race B with male *cutleri* were dark golden agouti in color, much darker than the *cutleri* parent. This darkening of the color persisted undiminished into the following generation (F_2). Of the 58 colored F_1 young derived from this cross none was as light in coloration as the *cutleri* grandparent. Hence it would appear that the darker coloration introduced by the cross, apparently through the albino parent, does not behave as a simple Mendelian character either dominant or recessive; otherwise pale-colored F_2 young should have been produced. Whatever factors, Mendelian or otherwise, are responsible for the darkening of the pigmentation are evidently unconnected with the so-called color factor, since they are transmitted by albinos, which lack this factor.

A very different result was observed in crosses of the same *cutleri* males with females of race C. The colored animals of race C are very pale cream-colored. The F_1 young which they produced showed a more intense yellow than either parent, but were much lighter than the hybrids produced in the cross with race B albinos. (See plate 3.)

Among their F_2 young appeared some very light-colored individuals, 16 being recorded in a total of 56 young produced by pairs which produced no albinos. The pale-colored young were not confined to any one colored class, but were recorded among the agoutis, blacks, cinnamons, and yellows. (See table 11.) The proportion recorded is close to one-fourth, from which it would seem that dilution had been introduced as a recessive character by the cream guinea-pig grandparents. Since, however, *C. cutleri* is relatively pale in pigmentation, it is probable that some of the animals classified as pale were not "dilute," owing to a factor derived from the guinea-pig ancestor, but because of conditions derived from the *cutleri* ancestor. This statement applies to the young of matings which produced albinos as well as to those which did not. The significant thing is that *more* pale-pigmented young and those which excelled in paleness were obtained from those matings which did not involve albinsim.

TABLE 11.—*Distribution of intensity and dilution among the F₂ young derived from the cross ♀ race C × ♂ cutleri.*

Color variety of young.	From pairs producing no albinos.		From pairs producing albinos.	
	Intense.	Dilute.	Intense.	Dilute.
Agouti.................	25	8	28	4
Black.................	5	3	6	1
Cinnamon.............	2	3	13	..
Black-eyed yellow.......	5	2	10	4
Brown-eyed yellow......	2	..	6	2
Chocolate.............	1	..	7	..
Total.............	40	16	70	11

It was expected that albinos of race C would produce a much larger proportion of pale-colored grandchildren, but strange to say this expectation was not realized; 81 F₂ colored young produced in matings which yielded albinos (showing that the guinea-pig characters had been received through albino gametes) included only 11 pale-colored young, and none of these is recorded as being paler in color than the *cutleri* grandparent. It would appear, therefore, that the albino gametes of race C mothers do not transmit the dilution seen in the cream-colored animals of race C. This would be a puzzling state of affairs had not Wright (1915) already discovered an easy explanation for it, viz, that the dilution of the cream race is an allelomorph of albinism, and so can not be transmitted in the same gamete with albinism.

Comparing the F₂ hybrids derived from race C crosses with those derived from race B crosses, it is certain that the pigmentation of both is darker than that of wild *C. cutleri*, but the intensity of the race B hybrids much exceeds that of the race C hybrids. Among the race B hybrids no evidence can be discovered of segregating Mendelian intensity factors; among the race C hybrids dilution segregates as a simple Mendelian recessive, precisely as does albinism, but apparently no gamete transmits both dilution and albinism, for the reason that they are alternative conditions of the same factor. Aside from the factorial difference in dilution, how does race B differ from race C? Apparently in no simple factorial way, but in a general way as regards energy of pigment production, in which hybrids of both races surpass *C. cutleri* but differ quantitatively from each other. No Mendelian explanation of this difference is at present justified by the observations made.

(f) SIGNIFICANCE OF THE RESULTS OBSERVED.

The complete fertility of the hybrids produced by crossing wild *Cavia cutleri* with the guinea-pig is in striking contrast with the sterility of hybrids between *C. rufescens* and the guinea-pig, as observed by Det-

lefsen. This indicates that *C. cutleri* from Peru is the actual wild ancestor of the guinea-pig or closely related to that ancestor. Since, however, Nehring has reported that *C. aperea* (from Argentina) also produces fertile hybrids with the guinea-pig, it seems likely that these two species are closely related to each other and might interbreed freely if their respective ranges were not completely separated. It seems possible also that both species have contributed to the production of the domesticated form, or that still other species have shared in producing it. Further observations are needed to clear up this matter.

It is evident that the mendelizing unit-character differences, which distinguish one variety of domesticated guinea-pig from another, also exist between guinea-pigs and the wild *Cavia cutleri*. They are inherited in precisely the same way among the hybrids produced by crossing guinea-pigs with *C. cutleri* as in crosses of one variety of guinea-pig with another—that is, they mendelize. It is evident that these variations have arisen by a process of retrogressive or loss variation. For example, in the matter of color varieties such as black, brown, yellow, and white, which (in relation to the parent form) are known to breed true without exception, it is evident that these have arisen by loss (or retrogressive modification) of physiological processes which occur in the wild species, since crosses with the wild form bring them back in a heterozygous state, after which they continue to form all possible permutations and recombinations with each other. Thus albinos of race C (which breed true *inter se* and without crossing with some other variety could produce no other sort) if crossed with *C. cutleri* (which also breeds true) produce in F_2 a definite series of color varieties. This series includes all the color varieties of guinea-pigs more commonly known, such as (1) golden agouti, (2) black, (3) cinnamon, (4) chocolate, (5) black-eyed yellow, (6) brown-eyed yellow, and (7) albino.

The mode of origin of the color varieties of guinea-pigs (and by inference of other domesticated animals also) is therefore clear. These varieties have originated by loss variations or loss "mutations." Is this the means by which species themselves originate? Many biologists have recently advocated this view, as, for example, Lotsy, Baur, and Bateson, but the present case affords rather strong evidence against it. The color varieties of guinea-pigs differ from *Cavia rufescens* and *C. cutleri* (undoubtedly distinct species) by the same mendelizing color-factors, but there is no evidence that these two species differ from each other by *any* color-factor. The two wild species are probably distinct enough to show interspecific sterility, since one is known to form sterile hybrids, the other fertile hybrids, in crosses with the guinea-pig. Their specific distinctness accordingly can not be due to such mendelizing factors as distinguish one domesticated variety from another, but to something more fundamental in character, though less striking in appearance.

HYBRIDIZATION EXPERIMENTS WITH A RACE OF FERAL GUINEA-PIGS FROM ICA, PERU.

ORIGIN AND CHARACTERISTICS OF THE ICA RACE.

Von Tschudi in 1844, in his Fauna of Peru, described, under the name of *Cavia cutleri*, a wild cavy found occurring in great numbers in the state of Ica. He says that the natives call it "cuy del monte," the mountain cavy, and regard it as the original of *C. cobaye*, the guinea-pig. Subsequent writers carefully distinguish the *C. cutleri* of Von Tschudi from that of Bennett, with which my wild cavies from Arequipa agree. One of the objects which I hoped to accomplish by the trip to Peru was to learn more about the cavy which Von Tschudi reported as occurring at Ica, and, if possible, to determine its relation to *C. cutleri* Bennett and to the guinea-pig.

Through the kindly interest of Messrs. W. R. Grace & Co. I was able to secure 3 wild-caught cavies (a male and 2 females) from Ica and to bring them back with me to the Bussey Institution, where they have produced a numerous progeny.

These animals were about the size of domesticated guinea-pigs, were very timid, and were self-colored golden agouti, in every respect similar in appearance to tame guinea-pigs of the color variety named.

The 3 animals brought from Ica produced 7 golden-agouti young, all similar to the parents in color, except that one bore a spot of red, the first observed indication of contamination of the stock with characters found in domesticated guinea-pigs. That other indications were not observed in this first mating of the animals was probably due to the fact that the male was homozygous for all other color factors, as subsequent matings of the females with a son of one of them by the original male proved that both mother and son were heterozygous in that variation of the color factor which is seen in "red-eyed" guinea-pigs (Castle, 1914; Wright, 1915). The same matings with the son (♂505, table 12) proved that one of the two original females (♀503) was also heterozygous in the agouti factor and transmitted white-spotting, since she produced a black daughter which had one white foot. Three other inbred descendants of the original trio of Ica animals have also borne spots of white; two of them in addition bore spots of red, and so were tricolors. One of the original trio of animals from Ica (♀502), when mated with ♂505, produced a son (♂575) which was imperfectly rough-coated. Accordingly we have clear evidence that the stock derived from Ica was contaminated with at least 5 of the supposedly independent unit-factor variations which occur among domesticated guinea-pigs and there can be little doubt that it really has been derived wholly or in part from domesticated guinea-pig ancestors.

TABLE 12.—*Young produced by the three original Ica guinea-pigs or their inbred descendants.*

A. Both parents golden agouti, one only heterozygous for red-eye (indicated by *).

Father.	Mother.	Golden agouti young.	Black young.	
501	*502 and *503	7	..	One young with spot of red.
*505	509	4	..	
*505	510	1	1	
*505	530	3	..	
*533	509	7	..	One young spotted with red and with white.
*533	625	2	..	
Total............		24	1	

B. Both parents golden agouti and heterozygous for red-eye.

Father.	Mother.	Golden agouti young.	Silver agouti young.	Black young.	
505	502	10	4	..	One slightly rough.
505	503	9	2	2	One black with white foot.
505	504	1	4	..	
505	507	8	5	..	One spotted with red and with white.
505	605	1	1	..	
533	529	5	1	..	
533	540	4	1	..	One spotted with white.
Total........		38	18	2	

C. Both parents silver agouti (red-eyed).

Father.	Mother.	Silver agouti young.	Father.	Mother.	Silver agouti young.
565	527	5	569	587 and 588	8
565	528	8	602	608	1
565	573	1	798	701	1
565	593	2	798	872	1
565	601 and 604	3			
565	607	1	Total............		31

The question at once arises whether the stock obtained by me from Ica was really a feral stock, in origin like the animals described by Von Tschudi, or whether they were present-day domesticated animals concerning whose origin I was deceived. Since I did not myself see the animals captured or see similar animals running at large and did not even visit Ica, I can make no positive statement as to their feral origin, but I believe the report made to me by the agents of W. R. Grace & Co., that they were caught feral in the neighborhood of Ica, to be correct for the following reasons: (1) The animals were placed

on board our steamer during a stop made in the night at Pisco, the terminus of the short line of railway which leads down from Ica to the coast.   I found them the next morning in the "butcher-shop," consigned from Ica to W. R. Grace & Co. in Callao.   I conclude that they really did come from the neighborhood of Ica.   (2) I saw no domesticated guinea-pigs in Peru which were self-colored like these animals. All domesticated ones which I saw in Peru, except albinos, were spotted with white, or with yellow, or both.   Self varieties are not fancied in Peru.   Varieties of this sort are not uncommon among the guinea-pigs kept by European and American fanciers, but apparently they have been established only by careful and long-continued selection from the pied stock originally introduced from South America.   (3) The spotting and the rough character which have cropped out as recessives among the descendants of the three Ica animals are *feebly expressed characters* which appear to have been almost obliterated, but which still come to expression feebly under inbreeding.   This is what we should expect to find in a feral race acted upon by natural selection, conspicuous variations like spotting tending to disappear.

TABLE 13.—*Parentage of pure Ica animals whose matings are recorded in table 12.*

Individual.	Father.	Mother.	Individual.	Father.	Mother.	Individual.	Father.	Mother.
♂501[1]	...	......	♀527	505	507	♀601	565	527
♀502[1]	...	......	♀528	505	503	♂602	565	527
♀503[1]	...	......	♀529	505	503	♀604	505	503
♀504	501	502 or 503	♀530	505	503	♀605	505	503
♂505	501	502 or 503	♂533	505	544	♀607	565	528
♀507	501	502	♀540	505	509	♀608	565	528
♀509	501	503	♂565	505	507	♀625	533	509
♀510	501	503	♂569	505	504	♀701	565	601 or 604
			♀573	505	502	♂798	569	587 or 588
			♀587	505	507	♀827	798	701
			♀588	505	507			
			♀593	505	504			

[1]Original stock.

The 3 original Ica animals or their inbred descendants mated *inter se* have produced 114 young, of which 62 have been golden agoutis, 49 silver agoutis, and 3 blacks; 4 of the 114 have shown a small amount of white spotting, 3 have shown yellow spotting, and 1 has shown a small amount of roughness of the coat.

The various matings which have produced these young are classified in three groups in table 12, and the parentage of each animal which took part in a mating is shown in table 13, from which pedigrees may readily be drawn tracing back to the original trio.   It will be observed from table 12 that silver agouti was derived from golden agouti as a recessive and has bred true without exception (31 silver agouti young being produced by silver agouti parents).

CROSSES BETWEEN THE ICA RACE AND GUINEA-PIGS OF RACE C.

An albino male guinea-pig ($\male$54) of race C was mated with 5 golden agouti females of the Ica stock. It was hoped from this cross to learn as promptly as possible the gametic composition of the Ica race, since race C contained a larger number of recessive Mendelian factors than any other race in the laboratory. In this hope we were not disappointed. Race C has already been described. It contains two different recessive variations of the color factor, dilution and albinism, which are allelomorphic with each other and with ordinary color, thus forming a system of triple allelomorphs, C, C_d, and C_a, with dominance in the order named (see Wright, 1915). It lacks agouti, black, and extension factors. Visibly the animals of this race are either brown-eyed cream or albino. Male 54 was an albino, bearing the color allelomorph C_a, which is recessive to the color allelomorph C_d found in brown-eyed cream individuals of race C. The mating between $\male$54 and the 5 golden agouti females of the Ica race produced 13 young, 7 of which were

TABLE 14.—*F_1 result of mating the albino $\male$54 of race C with golden agouti females of the Ica race.*

Mother.	Dark-eyed young. Golden agouti.	Red-eyed young.	
		Silver agouti.	Sepia.
502	3	1	..
503	1	1	1
504	..	..	2
507	1	1	..
509	2	..	..
Total...	7	3	3

golden agouti (like the mothers), 3 silver agouti, and 3 a dull black or slate color, which will be called *sepia*. The silver agouti young were like those produced by Ica animals bred *inter se*. The sepia young represented a new class not previously observed. In common with the silver agoutis they had no yellow in their fur. The ticking and spotting of silver agoutis was of white, as was also the spotting of the sepias, which had no ticking. It seemed probable, therefore, as proved to be the case, that the silver agouti and the sepia young differed from each other only in the presence or absence of the agouti factor. But these two classes of young taken together differ from golden agoutis in lacking yellow pigmentation with which the golden agouti fur is ticked. They also differ from golden agoutis in the intensity of the eye pigmentation, which is very great in golden agoutis and blacks, but ordinarily shows such reduction in silver agoutis and sepias that the eye by reflected light has a deep red glow. It will be convenient to distinguish them as red-

eyed, it being understood that the red eye is invariably associated with no-yellow in the coat.

Four of the five Ica mothers which were mated with ♂54 had produced silver agouti (red-eyed) young by Ica mates. Each of them produced red-eyed young by ♂54; together they produced 5 dark-eyed young (golden agouti) and 6 red-eyed (silver agouti or sepia). The fifth Ica mother (♀509) had produced 11 golden agouti young when mated with Ica males known to be heterozygous for silver agouti. (See table 12.) This is good evidence that she did not carry red-eye as a recessive character and was accordingly homozygous for dark-eye. By ♂54 she produced 2 golden agouti young.

From these several facts it appears that dark-eyed Ica animals capable of producing red-eyed young when mated *inter se*, produce equal numbers of dark-eyed and red-eyed young when mated to albinos, but produce no albinos. This indicates that albinism is recessive both to red-eye and dark-eye, an indication which the F_2 result confirms. It will be shown further that the three conditions are mutually allelomorphic, so that a zygote may contain any two of the three, but not more. Red-eye is in fact a fourth member of the albino series of allelomorphs, which includes the following conditions in order of dominance: (1) ordinary dark-eye and colored coat, such as is seen in *Cavia cutleri* and in golden agouti animals of the Ica race; (2) dark-eye with dilute coat, seen in colored animals of race C; (3) red-eye and non-yellow coat; (4) albino. (See Wright, 1915.) For convenience these allelomorphs may be designated by C, C_d, C_r, and C_a. The cross of Ica females with the albino ♂54 involves animals of the formulæ CC or CC_r mated with an animal of the formula C_aC_a. The 7 golden agouti young are expected to be of the formula CC_a; the 6 red-eyed young of the formula C_rC_a. We may now compare the experimental with the expected results of breeding such animals in various ways.

THE F_2 GENERATION.

One of the F_1 silver agouti males (♂517) was known from his pedigree to be heterozygous in four characters, viz, red-eye *vs*. albinism, agouti *vs*. non-agouti, black *vs*. brown, and extension *vs*. restriction. His formula was accordingly $C_rC_aAaBbEe$, and we should expect him to form gametes of 16 different sorts, all equally numerous. This animal was mated with all three kinds of F_1 females, with the results shown in table 15. The golden agouti females produced 25 young, distributed among 10 classes very distinctly different in appearance. These golden agouti females were known from pedigree to be heterozygous for the same 4 factors as ♂517, but to contain a different allelomorph for albinism. Both he and they carried albinism as a recessive character, but whereas he carried red-eye (C_r) as its dominant allelomorph, they carried dark-eye (the ordinary condition of the color

factor, viz, C). His gametes accordingly could transmit either C_r or C_a, but theirs would transmit either C or C_a. Accordingly their young should be in the ratio 2 dark-eyed to 1 red-eyed to 1 albino. The observed numbers were 13: 8: 4. Each of these three groups might theoretically contain 8 different kinds of individuals, but certain of these would be visibly indistinguishable. The classes visibly different which might themselves be expected to be composite are black-eyed reds and brown-

TABLE 15.—*F_2 young from the cross ♂54 albino (race C) × golden agouti females of Ica race.*

Parents.	Dark-eyed young.					
	Golden agouti.	Black.	Cinnamon.	Chocolate.	Black-eyed red.	Brown-eyed red.
♂517 silver agouti × ♀ golden agouti....	6	1	2	0	2	2
Expected........................	5.3	1.8	1.8	0.6	2.3	0.8
♂517 silver agouti × ♀ silver agouti.....	...	...	...	...	...	...
Expected............................	...	...	...	...	...	...
♂517 silver agouti × ♀ sepia...........	...	...	...	...	...	...
Expected.............................	...	...	...	...	...	...
Total observed......................	6	1	2	0	2	2
Total expected......................	5.3	1.8	1.8	0.6	2.3	0.8

Parents.	Red-eyed young.					Albino young.	Total.
	Silver agouti.	Sepia.	Silver cinnamon.	Red-eyed chocolate.	Red-eyed white.		
♂517 silver agouti × ♀ golden agouti....	3	2	2	1	0	4	25
Expected.........................	2.6	0.9	0.9	0.3	1.5	6.3	..
♂517 silver agouti × ♀ silver agouti.....	0	1	1	0	4	3	9
Expected.........................	2.8	0.9	0.9	0.3	1.7	2.3	..
♂517 silver agouti × ♀ sepia...........	5	5	1	1	8	15	35
Expected.........................	7.4	7.4	2.4	2.4	6.5	8.7	..
Total observed......................	8	8	4	2	12	22	69
Total expected......................	12.8	9.2	4.2	3.0	9.7	17.3	..

eyed reds, each of which might include both agouti and non-agouti animals; also red-eyed whites, which might have either black or brown pigment in the reddish eye, and might transmit either agouti or non-agouti; and finally, the albinos, which might be of as many different sorts as the colored classes, viz, 16.

All except 2 of the 12 visibly different classes expected from this mating were obtained in as small a total number of young as 25. In the two missing classes, chocolate and red-eyed white, the theoretical

numbers were only 0.6 and 1.5 individuals respectively, so that their absence was not surprising.

By silver agouti F_1 females, $\male 517$ had 9 young of 4 different color varieties, the maximum number of classes expected being 6.

By sepia F_1 females, $\male 517$ had 35 young, distributed among 6 different color classes, as expected. Summarizing the results from all three kinds of matings, we find that the F_2 young of $\male 517$ number 69, distributed among 11 of the 12 expected classes of young, the missing class being one in which the expectation is for 0.6 of an individual, scarcely more than an even chance for the production of such an individual in the number of young recorded. (See table 15.)

TABLE 16.—*Young produced by red-eyed white parents mated inter se.*

Father.	Mother.	Red-eyed white young.	Albino young.
567	571	2	1
576	726	10	0
774	747	5	2
774	758	3	3
774	775	8	0
842	571	2	0
849	851	2	0
Total		32	6

A word as to the number of classes expected may not be out of place. The dark-eyed classes expected are 6, identical with those expected from the cross of race C animals with wild *Cavia cutleri.* (Compare p. 16.) The number of classes expected among the red-eyed young is 1 less, namely 5, because red-eyed whites which have brown pigment in the eye can not be distinguished (except by breeding-test or *post mortem*) from those which have black pigment in the eye, the quantity of pigment present being too small, and the coat in both cases white.

On the whole the agreement between expected and observed in this experiment is so good as to preclude the idea that any coupling or association occurs among the 4 unit factors involved in the cross.

This experiment produced 4 color varieties of guinea-pig previously unknown to me, viz, the 4 red-eyed classes other than silver agoutis, which had already been obtained from the uncrossed Ica race. (See plates 1, 2, and 5.) The eye has a similar appearance in all the red-eyed classes, showing a deep-red glow by reflected light. The silver agouti variety, as already explained, differs from golden agouti in the ticking of the fur, which is white in silver agouti, instead of red or yellow as in golden agouti. Sepia as compared with black has a more faded appearance, approaching chocolate on the sides of the body and belly, but always darker and unmistakably black above. Silver cinna-

mon (or "red-eyed cinnamon," plate 5, fig. 31) differs from silver agouti in having brown hairs ticked with white instead of black hairs ticked with white. It is one of the handsomest of guinea-pig varieties. Red-eyed chocolate is indistinguishable from dark-eyed chocolate, except in eye color. The red-eyed whites all look alike, though they may differ considerably in factorial composition. Their production in this experiment was a complete surprise to us and very puzzling until the suggestion was made (I think by Mr. Wright) that an essential feature of the red-eyed variation was the absence of yellow color from the fur. It was then realized that a "yellow" animal with red eyes and "non-yellow" fur must of necessity have white fur. This suggestion was immediately put to the test by mating the red-eyed white ♂576 with 3 dark-eyed cream females. They produced 12 young, of which 5 were brown-eyed cream, 2 black-eyed cream, 3 red-eyed white, and 2 albino. No young were produced which had coats of any other color than yellow! Hence it is clear that red-eyed whites do not transmit the extension factor.[1]

TABLE 17.—*Results of mating red-eyed white individuals with albinos.*

Father, red-eyed.	Mother, albino.	Red-eyed young.					Albino young.
		Silver agouti.	Sepia.	Silver cinnamon.	Choco-late.	White.	
567	564	..	..	..	..	4	4
567	568	..	..	..	1	..	2
567	572	..	..	1	1	1	2
567	177	..	1	..	..	..	..
567	711	..	2	..	..	..	7
576	1430	1	..	..	..	..	1
576	1439	1	..	..	..	..	1
576	1446	1	..	..	..	..	2
Total......		3	3	1	2	5	19

This same red-eyed white ♂576 was also mated with 3 albino females of race B, which carry the extension factor. Both parents, it will be observed, were white, one having red eyes, the other pink eyes. This mating produced 7 young, of which 3 were red-eyed with silver-agouti-colored coats and 4 were albinos. The production of colored young in this case shows that red-eyed white animals may transmit all that is necessary for the production of a colored coat except the extension factor, which the albino parents supplied.

The red-eyed white ♂576 was evidently heterozygous for the black factor, since, when he was mated with brown-eyed cream females, he produced both black-eyed and brown-eyed cream young. Another

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[1]As a further test of red-eyed whites, two other red-eyed white males (615 and 616) were mated with several different red or yellow coated females. They produced 9 red or yellow young, 5 red-eyed young, and 5 albino young, a result completely in accord with that given by ♂ 576.

red-eyed white male, 567, an F_3 descendant of the albino $\male$ 54, race C, was found to be homozygous for brown (table 17). What pigment his eyes contained was undoubtedly brown, for when he was mated with 3 albino females descended from the albino $\male$ 54, race C, he produced 1 silver cinnamon and 2 red-eyed chocolate young, besides 5 red-eyed white and 8 albino young. The entire absence of black-colored young indicates that this male, as well as his albino mates, transmitted the capacity to form brown but not black pigmentation. When, however, this same male (567) was mated with an albino derived from race B, which never produces brown individuals, there were obtained 3 sepia-colored young with red eyes, besides 7 albinos, showing that when the mother transmitted black, this male produced black-pigmented young, black being dominant over brown which he himself transmitted.

TABLE 18.—*Results of mating a red-eyed white male with brown-eyed cream females.*

Father.	Mother.	Young.			
		Black-eyed cream.	Brown-eyed cream.	Red-eyed white.	Albino.
576	−46	..	2	1	2
576	M250	1	1	..	..
576	762	1	2	2	..
842	870	..	1	..	1
Total........		2	6	3	3

Both the males whose matings have just been described, viz, 567 and 576, were heterozygous in albinism, since when mated with albinos they produced about 50 per cent of albino young. They were evidently of the formula C_rC_a. If red-eyed white animals of this formula should be mated with each other we should expect individuals to be produced which are homozygous for red-eye, i. e., are of formula C_rC_r. Two probably homozygous red-eyed females of this sort have been discovered in mating red-eyed white animals *inter se*. One of them ($\female$ 726, table 16) produced 10 young, all red-eyed white, in matings with $\male$ 576, known to be heterozygous for albinism. Had this female formed albino gametes she should have produced 25 per cent of albino young in the matings mentioned. It seems probable, therefore, that she did not form such gametes. The F_3 $\female$ 775 (table 16) was probably likewise homozygous, since her mate is known to have been heterozygous for albinism, but she produced no albinos in a total of 8 young.

In the foregoing account nothing has been said concerning spotting with white or with yellow; nevertheless spotting of both sorts occurred among certain of the F_1 and F_2 young obtained from the Ica crosses. Since the uncrossed Ica race contained spotted animals of both sorts, it is not surprising that the cross-bred descendants of this race should

do the same. Race C, like the Ica race, contains only an occasional individual sparingly spotted with white; yellow spotting is of course not visible in a race like C, which contains only yellow or albino individuals. It will suffice to say that the cross-breds, like the parent races, consisted principally of self-colored individuals, and that only an occasional dark-eyed individual bore white markings, which in no case were extensive, but were usually limited to a white foot. Among the red-eyed individuals, white spotting was commoner and more extensive, which might seem surprising, unless one remembers that in red-eyed individuals it is impossible to distinguish true white spotting from yellow spotting, since both produce uncolored areas in the coat. Complications of this nature make this cross unfavorable for the study of the inheritance of spotting.

SUMMARY ON THE ICA RACE.

1. The "Ica race" of guinea-pigs consists of descendants of 1 male and 2 female golden agoutis obtained from the vicinity of Ica, Peru, in 1911, and reported to have been caught wild. These animals are supposed to have been descendants of guinea-pigs long since escaped from domestication.

2. This explanation is supported by the observation that within the Ica race have cropped out 5 Mendelian variations which are common among domesticated guinea-pigs, viz, (1) the "red-eye" variation, one of the four allelomorphic forms of the color factor in guinea-pigs; (2) the "non-agouti" allelomorph of the agouti factor; (3) the factor which produces rough coat; (4) the factor for white spotting; and (5) the factor for yellow spotting.

3. An albino guinea-pig of race C differing from wild guinea-pigs by 4 recessive Mendelian characters was crossed with golden agouti females of the Ica race. From this cross were obtained in F_2 all except one of the expected recombinations of the 4 unit-factor differences between the races crossed. Leaving out of consideration spotting with white and with red, which occurred among some of the hybrids as well as in the uncrossed Ica race, there occurred 5 easily distinguishable classes of dark-eyed young and 5 classes of red-eyed young, besides albinos. Only one "expected" class of F_2 young was missing, the occurrence of which among other races is well known. There is almost an even chance for its failure to appear in this experiment in the number of young recorded.

4. The four color factors involved in the cross and their allelomorphs are:

A, a = agouti, non-agouti;
B, b = black, brown;
C, C_r = full color, red-eye;
E, e = extension (of black or brown), restriction.

These are capable theoretically of forming 16 different combinations, as follows, heterozygous combinations being omitted. The appearance of zygotes containing each of these several combinations is indicated opposite the respective combinations.

ABCE, golden agouti = wild type.

Single mutations.

ABCe,	black-eyed red.	AbCE,	cinnamon.
ABC_rE,	silver agouti.	aBCE,	black.

Double mutations.

ABC_re,	red-eyed white.	AbCe,	brown-eyed red.
AbC_rE,	silver cinnamon.	aBC_rE,	red-eyed sepia.
abCE,	chocolate.	aBCe,	black-eyed red

Triple mutations.

AbC_re,	red-eyed white.	abCe,	brown-eyed red.
aBC_re,	red-eyed white.	abC_rE,	red-eyed chocolate.

Quadruple mutation.

abC_re, red-eyed white.

Of the 16 different combinations, 2 produce black-eyed red individuals indistinguishable except by breeding test; the same is true regarding brown-eyed reds. Four other combinations identical with these, except for the substitution of C_r for C, produce red-eyed whites, which visibly are all alike but which breed differently. Three of the four kinds of red-eyed whites have been identified by breeding test; no doubt the fourth can easily be obtained. The fact that the several classes of red-eyed whites look alike, and that the two kinds of black-eyed reds look alike, and further, that the two kinds of brown-eyed reds look alike, reduces the number of visibly distinguishable classes from 16 to 11, all except one of which have been recorded from this single experiment. The experiment also produced albinos which theoretically should be of 8 different formulæ, if in the formula C_a is everywhere substituted for its allelomorphs C or C_r. No attempt has been made to distinguish the several expected classes of albinos by breeding tests, the only certain means of identifying them.

5. The close agreement observed between theoretical and recorded numbers of F_2 offspring in this cross lends no support to the idea that any association or linkage occurs among the 4 factorial variations involved.

HYBRIDIZATION EXPERIMENTS WITH A DOMESTICATED GUINEA-PIG FROM AREQUIPA.

While in Arequipa, in December 1911, I purchased in the cabin of a native living near the observatory a pair of domesticated guinea-pigs about one-third grown and perhaps 2 or 3 months old.   These animals resembled the ordinary pied guinea-pigs kept for pets or laboratory use in Europe and North America.   The female was a tricolor, red, white, and black, and was rough-coated of grade B (Castle, 1905, p. 57).   The male was a dilute-pigmented, agouti-marked tricolor (yellow agouti,[1] cream, and white), and smooth-coated.   This pair of animals was successfully transported to the Bussey Institution, where they produced 3 litters, of 1, 3, and 2 young respectively.   The young of the first 2 litters died at birth; the third litter consisted of 2 males, and as the mother died soon afterward it was impossible to propagate the family farther for lack of females.   Of the 6 young produced, 3 were rough-coated and 3 smooth, showing the mother to have been heterozygous for rough coat, a dominant character (Castle, 1905).   Three were golden agouti and white and three tricolor, one being golden agouti red and white, the other two silver agouti yellow and white.

MALE 1002 AND HIS F₁ OFFSPRING.

The father of this family of guinea-pigs ($\male$1002) proved to be an animal of great vigor and vitality.   Although born in Peru (about September 1911) and brought to North America in mid-winter, he has successfully escaped the ravages of disease among our guinea-pigs throughout the rigors of four New England winters and is still vigorous and active.   In crosses with other races of guinea-pigs he has sired several hundred young and is now being mated with females which are simultaneously his daughters, his granddaughters, and his great-granddaughters!   By repeated back-crosses such as these a race has been established which derives its inherited characters largely from this one animal.   This race will be designated the "Arequipa" race.

Crosses of $\male$1002 and repeated back-crosses with his female descendants have permitted a very full analysis of the factorial constitution of this animal.   He possesses either as dominant or as recessive characters a majority of the Mendelian variations of guinea-pigs, including one not previously known to occur in any animal other than mice, viz,

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[1]It should be noted that "silver agoutis" may be of two different sorts: (1) dark-eyed silver agouti with *cream-colored* hair-tips, and (2) red-eyed silver agouti with *white* hair-tips.   The two varieties resemble each other somewhat and it often requires close observation to discriminate between them, but genetically they are quite distinct.   Only the former sort was known to me previous to the Peruvian expedition, and the term "silver agouti" as used in my 1905 paper and by fanciers generally refers to this.   It would be better, I think, to use the term *cream agouti* or *yellow agouti* for such agouti animals as develop pale yellow in the fur and to restrict the term silver agouti to those which are non-yellow.

the pink-eye variation with colored coat, first brought to the attention of scientists in the case of mice through the experiments of Darbishire (1902). A similar variation has, however, since been found to occur in rats (Castle, 1914). The number of factors in which ♂1002 is heterozygous is surprisingly large and implies doubtless considerable crossbreeding in the guinea-pig colonies kept by the natives of Arequipa, a fact perhaps connected with the great size and vigor of their animals. The factorial constitution of ♂1002, as at present understood, is as follows:

(1) Agouti factor, Aa, agouti-marked but transmitting non-agouti as a recessive character.
(2) Black factor, BB, homozygous.
(3) Color factor, C_dC_r, two different recessive variations, dilution (C_d) being dominant over red-eye (C_r). Both are recessive to ordinary intense color (C) and dominant over albinism (C_a), the four forming a series of quadruple allelomorphs, as shown by Wright (1915).
(4) Extension factor, EE, homozygous.
(5) Dark-eye factor, Pp, heterozygous for the recessive pink-eye (p) variation, with which goes dilution of black or brown pigments, but not of yellow.
(6) As regards the rough variation, this animal is smooth, but nevertheless transmits occasionally a trace of the rough character, but the character does not crop out among his descendants in any as yet recognizable Mendelian proportions.
(7) White spotting, homozygous.
(8) Yellow spotting, homozygous.

TABLE 19.—*Classification of young obtained from matings of ♂1002 with unrelated guinea-pigs.*

Mothers.	Intense dark-eyed.		Dilute dark-eyed.		Red-eyed.	
	Golden agouti.	Black.	Yellow agouti.	Sepia.	Silver agouti.	Sepia.
5 dark-eyed non-agoutis........	4	7	2	2	..	..
15 dark-eyed non-agoutis, heterozygous for albinism......	16	8	6	2	17	6
6 albinos....................	..	..	2	5	9	2
Total....................	20	15	10	9	26	8

Male 1002 was mated with 20 dark-eyed guinea-pigs and 6 albinos derived either from race B, from a 4-toed race (see Castle, 1906), or from crosses between the two. Both these races contain only non-agouti animals. The dark-eyed mothers produced 70 F_1 young, the albino mothers produced 18 F_1 young. Disregarding spotting with yellow and with white, the young of the dark-eyed mothers fall into three classes—dark-eyed intense, dark-eyed dilute, and red-eyed—and each class may be further subdivided into agouti and non-agouti. (See table 19.)

The albino mothers, though derived from the same races as the dark-eyed mother, produced only two of the three main classes of young, viz, dark-eyed dilute and red-eyed, which fact confirms Wright's (1915)

conclusion that albinos, even when derived from intense dark-eyed parents, do not transmit intensity to their young in crosses, for the reason that albinism is an allelomorph of dilution as well as of intensity. The fact that σ1002 produced no albino young, even when mated with albinos, shows that he did not produce albino gametes. The fact that he produced red-eyed young when mated with albinos shows that he transmitted red-eye as a recessive character and that this is dominant over albinism. The fact that he produced no intense dark-eyed young by the albino mothers shows that he lacks intensity and forms only gametes which transmit either dilution or red-eye. All these facts are in harmony with the hypothesis suggested by Wright (1915) that intensity, dilution, red-eye, and albinism are allelomorphs of each other, so that a gamete can transmit only one of the four allelomorphs, and a zygote can contain only two of them. Male 1002 is evidently a heterozygote of dilution and red-eye ($C_d C_r$), both of which are recessive to intensity (C) and dominant over albinism (C_a). Consequently, when he is crossed with albinos, zygotes of two sorts are expected in equal numbers, viz, $C_d C_a$ and $C_r C_a$ (dilute and red-eyed), as observed (table 19); and when he is crossed with intense dark-eyed animals carrying albinism as a recessive character (as 15 of the 20 dark-eyed mothers of table 19 did), zygotes of four sorts are expected in equal numbers, viz, CC_d, CC_r, $C_d C_a$, and $C_r C_a$, the first two being dark-eyed intense, the third dark-eyed dilute, and the fourth red-eyed. The observed result is in perfect accord with this expectation as regards the classes of young produced, and agrees with expectation sufficiently well as regards the proportions of the classes.

It is expected further that each of the three main classes will be subdivided about equally into agoutis and non-agoutis. The 6 expected subclasses appear in the experimental results, but there is a considerable excess of agoutis, viz, 56 agoutis to 32 non-agoutis. Whether this departure from the expected equality has any probable significance will be considered further in connection with the F_2 generation.

F_2 OFFSPRING OF σ1002.

For the production of an F_2 generation a golden agouti and 4 silver agouti males were selected. The golden agouti male was mated only with a black female, his sister, but the silver agouti males were mated with practically all classes of the F_1 females. (See table 20.) They produced altogether 190 F_2 young, which, being classified as regards intensity and eye color alone, fall into 6 main classes, viz, (1) dark-eyed intense, (2) dark-eyed dilute, (3) red-eyed, (4) pink-eyed, (5) red-and-pink-eyed,[1] and (6) albino. Each of these main groups falls into two

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[1]Animals called red-and-pink-eyed are in reality *pink-eyed*, but *lack* yellow in the coat. They transmit in every gamete both the factor for pink-eye and the factor for red-eye.

subclasses (agouti and non-agouti), readily distinguishable, except in the case of albinos.

Matings in which both parents were agoutis produced 44 agouti to 13 non-agouti young, expected 43 to 14, which is good agreement. Matings of an agouti with a non-agouti animal produced a considerable excess of agoutis, viz, 58 agouti to 42 non-agouti, where 50 to 50 is the expected distribution. The departure from the expected equality of agouti and non-agouti young is, however, not probably significant.

TABLE 20.—*Classification of the F_2 young of $\male 1002$, obtained from F_1 animals classified in table 19.*

Nature of F₁ mating.	Dark-eyed intense.		Dark-eyed dilute.		Red-eyed.	
	Golden agouti.	Black.	Yellow agouti.	Sepia.	Silver agouti.	Sepia.
Golden agouti × black..........	12	4	3	1	..	..
Golden agouti × silver agouti....	2	..	2	..	1	1
Black × silver agouti...........	4	4	4	3	3	2
Yellow agouti × silver agouti....	..	..	5	2	2	..
Dark-eyed sepia × silver agouti..	..	..	11	10	12	6
Silver agouti × silver agouti.....	..	..	..	..	28	7
Silver agouti × sepia (red-eyed)..	..	..	..	..	7	12
Total....................	18	8	25	16	53	28
Dark-eye × red-eye...........	6	4	22	15	18	9
Red-eye × red-eye............	..	..	..	..	35	19

Nature of F₁ mating.	Pink-eyed.		Red-and-pink-eyed.		Albino.
	Agouti.	Non-agouti.	Agouti.	Non-agouti.	
Golden agouti × black..........	..	..	..	..	..
Golden agouti × silver agouti....	1	1	..	..	..
Black × silver agouti...........	..	..	..	..	..
Yellow agouti × silver agouti.....	..	..	..	..	4
Dark-eyed sepia × silver agouti..	..	..	..	..	11
Silver agouti × silver agouti......	..	..	3	2	7
Silver agouti × sepia (red-eyed)..	..	..	2	..	11
Total....................	1	1	5	2	33
Dark-eye × red-eye...........	1	1	..	..	15
Red-eye × red-eye............	..	..	5	2	18

If we summarize the matings in which every mother and father is known to have been capable of producing albinos, we have 96 colored to 28 albino young; expected 93 to 31—a very good agreement with expectation.

Summarizing the matings between a red-eyed male and a dark-eyed female known to have been capable of producing red-eyed young, we get 40 dark-eyed and 27 red-eyed; expected 33.5 and 33.5. This

apparent deficiency of red-eyed young may have been due to our failure at first to distinguish dark-eyed sepias from red-eyed sepias, which look very much alike when first born. In the summary all sepias are treated as dark-eyed unless a specific record in the ledger indicates that they were red-eyed.

Matings yielding pink-eyed young produced 17 non-pink-eyed and 6 pink-eyed young, which is good agreement with the expected 3 to 1 ratio.

BACK-CROSS AND OTHER OFFSPRING OF ♂1002.

Male 1002 was mated with certain of his F_1 daughters, producing 90 young of 10 different color classes, as indicated in table 21. He was later mated with certain of the female young produced by the matings last described, these females being both his daughters and his grand-daughters and so "$\frac{3}{4}$-blood" Arequipa tracing back to himself. (See

TABLE 21.—*Classification of young of ♂1002 by his F_1 daughters (table 19).*

Mothers.	Intense dark-eyed.		Dilute dark-eyed.		Red-eyed.		Pink-eyed.		Red-and-pink-eyed.	
	Golden agouti.	Black.	Yellow agouti.	Sepia.	Silver agouti.	Sepia.	Agouti.	Non-agouti.	Agouti.	Non-agouti.
4 black...........	1	6	3	3	..	3	2	1	..	1
1 sepia (dark-eyed).	..	..	2	1	..	1	..	..	..	..
6 silver agouti.....	..	..	13	3	11	7	3	..	1	..
3 sepia (red-eyed)..	..	..	8	7	5	2	2	2	2	..
Total.......	1	6	26	14	16	13	7	3	3	1

table 22.) The table 22 matings have produced to date (April 1915) 61 young, distributed in 9 of the 10 classes represented among the table 21 young. The classes of young recorded in tables 21 and 22 are the same as those represented among the F_2 young (table 20), with the exception of albinos, which are never produced by ♂1002, since he does not transmit albinism, which is recessive to both of its allelomorphs. As regards the characters in which ♂1002 is heterozygous, there is evidence from tables 20 to 22 that in the case of each he forms equal numbers of gametes bearing the dominant and the recessive allelo-morphs respectively. By agouti daughters he has had 50 agouti and 15 non-agouti young; expected, 49 and 16. By non-agouti daughters he has had 45 agouti and 41 non-agouti young; expected, 43 of each. Combining these totals with those recorded in table 19, we find that in all matings with non-agouti animals he has sired 101 agouti and 73 non-agouti young, a not improbable chance deviation from the ex-pected equality of the two classes.

By red-eyed daughters ♂1002 has had 51 dark-eyed and 40 red-eyed young. Adding to this result that recorded in table 19 (last category

of matings), which has the same expectation of red-eyed young (50 per cent), we get a total of 58 dark-eyed and 51 red-eyed, fairly good agreement with the expected equality.

By dark-eyed daughters which have produced red-eyed young and so have shown that they transmit either red-eye or albinism, σ1002 has produced 18 dark-eyed and 16 red-eyed young; expected 25.5 and 8.5. Doubtless other daughters which have not chanced to produce red-eyed young in the litters recorded are also heterozygous for red-eye, in which case their recorded litters should be added to the foregoing. If this were done, the observed departure in this case from the expected 3 to 1 ratio would doubtless disappear.

TABLE 22.—*Classification of young of σ1002 by his granddaughters which were also his daughters (table 21).*

Mother.	Intense dark-eyed.		Dilute dark-eyed.		Red-eyed.		Pink-eyed.		Red-and-pink-eyed.	
	Golden agouti.	Black.	Yellow agouti.	Sepia.	Silver agouti.	Sepia.	Agouti.	Non-agouti.	Agouti.	Non-agouti.
2 golden agouti....	4	..	1	..	1	1	..	1	1	..
1 black...........	..	1	2	..	..	..	..	..	..	..
1 yellow agouti....	..	..	2	..	..	..	..	..	..	..
3 sepia (dark-eyed).	..	..	4	2	1	2	1	3	2	..
2 silver agouti.....	..	..	4	1	2	..	1	..	..	..
2 sepia (red-eyed)..	..	..	3	1	1	4	..	..	..	..
2 non-agouti (pink-eyed)..........	..	..	..	1	2	..	3	..	1	..
2 agouti (red-and-pink-eyed)......	..	..	..	1	3	1	2	..	1	..
Total.......	4	1	16	6	10	8	7	4	5	0

By pink-eyed daughters, σ1002 has produced 7 pink-eyed young and 8 with eyes not pink—complete agreement with the expected equality. By daughters not pink-eyed, but which nevertheless are clearly heterozygous in pink-eye, he has produced 23 pink-eyed and 58 not-pink-eyed young; expected, 20 and 61—an excess of pinks capable of explanation on the same ground as the excess of red-eyed young.

By dilute-colored daughters σ1002 has produced 52 dilute-colored young, but no intense-colored ones, as expected, since dilution is recessive to intensity. By intense-colored daughters heterozygous for dilution he produced 10 intense and 9 dilute young, equality being expected.

MISCELLANEOUS MATINGS OF THE DESCENDANTS OF σ1002.

Matings of the descendants of σ1002 beyond the F_2 generation were made chiefly with a view to test further the genetic character of the new varieties. Their results are presented in tables 23 to 28 and serve to confirm the interpretations already offered.

Matings of red-eyed animals *inter se* have in most cases produced only red-eyed or albino young, but two matings have also produced pink-and-red-eyed young, *i. e.*, animals which are pink-eyed but develop no yellow in their fur, in which last respect they differ from ordinary pink-eyed and agree with ordinary red-eyed. (See tables 24 and 27.)

TABLE 23.—*Young produced by matings of red-eyed males, descended from ♂1002, with dark-eyed females of race B.*

Nature of mating.	Dark-eyed.		Red-eyed.		Albino.
	Golden agouti.	Black.	Silver agouti.	Sepia.	
Silver agouti × black (homozygous)	1	5	..	..	..
Silver agouti × black (heterozygous in albinism)......................	20	7	9	7	10
Sepia (red-eyed)× black (homozygous)..	..	6	..	..	..
Total........................	21	18	9	7	10

Most of the red-eyed animals, when bred *inter se*, produce albino as well as red-eyed young, showing themselves to be heterozygous for albinism and so of the formula C_rC_a. This is not surprising when we recall that all the F_1 red-eyed animals must by hypothesis be of this formula, and that two-thirds of the F_2 red-eyed should be of the same sort. In a few matings of red-eyed with red-eyed, which failed to produce albino young (table 24), it is probable that one or both parents

TABLE 24.—*Young produced by matings inter se of red-eyed descendants of ♂1002. (See also table 27).*

Nature of mating.	Red-eyed young.		Albino young.
	Silver agouti.	Sepia.	
Both parents agouti............	56	19	22
Only one parent agouti.........	18	6	11
Neither parent agouti..........	..	9	..
Total....................	74	34	33

were homozygous for red-eye. Matings of red-eyed with albino animals (table 25), which failed to produce albinos in 6 or more young, afford clear criteria for red-eyed animals free from albinism and so of formula C_rC_r. Only one mating of a red-eyed animal with an albino has produced pink-eyed young. (See table 27.) The red-eyed parent in this case (♂48) was mated with 4 other albinos (all of race B) without producing pink-eyed young, but only red-eyed (13) and albinos (17). The female which produced pink-eyed young was his sister, derived like

himself from parents known to transmit pink-eye. This indicates that the character pink-eye in guinea-pigs (as in mice) may be transmitted by albinos. The fact should be emphasized that the pink-eyed young

TABLE 25.—*Young produced by red-eyed descendants of ♂1002 mated with albinos. (See also table 27.)*

Nature of red-eyed parent.	Red-eyed young.		Albino young.
	Silver agouti.	Sepia.	
Silver agouti, heterozygous for albinism...........	21	11	17
Sepia, heterozygous for albinism.................	..	31	34
Silver agouti (homozygous for red-eye)	18	11	..
Sepia (homozygous for red-eye).................	..	20	..
Total..................................	39	73	51

produced in this mating were also red-eyed, *i. e.*, were non-yellow, for red-eyed animals may carry pink-eye as a recessive character, and conversely pink-eyed may carry red-eye as a recessive character. However, if these recessive characters crop out as recessive *individuals* from a mating of two like parents with each other, it can in either case occur only in the form of the double recessive, *both* pink- and red-eyed.

TABLE 26.—*Young produced by pink-eyed descendants of ♂1002, mated inter se.*

Nature of mating.	Pink-eyed.		Pink-and-red-eyed.		Albino.
	Agouti.	Non-agouti.	Agouti.	Non-agouti.	
Both parents agouti................	15	2	..	..	1
One parent agouti, one non-agouti...	4	4	1	..	7
Total......................	19	6	1	0	8

Pink-eyed animals (with yellow in their fur) have made their appearance as recessives produced by mating dark-eyed animals *inter se.* (See tables 20, 22, and 27.) In some cases red-eyed young have been produced by the same matings, or pink-and-red-eyed or albinos, for pink-eye seems to be quite independent of the color factor in its inheritance. Pink-eyed animals mated *inter se* have produced only pink-eyed, pink-and-red-eyed, and albino young. (See table 26.) Any of these three forms so derived will doubtless be found to transmit pink-eye in every gamete.

Pink-and-red-eyed animals of whatever origin have been found to produce (when mated with each other) only pink-and-red-eyed young or albinos. But the record as regards albinos is doubtful. Two

albino young have been recorded as produced by ♂88 mated with his daughters, ♀204 and ♀205; but this same male mated with albino females of race B produced 11 red-eyed young but no albinos, for which reason it seems very doubtful whether he transmits albinism. More probably the two young by pink-and-red-eyed mothers were not albinos, but very pale-colored non-yellow young, possibly lacking the extension factor, in which case their fur would be pure white, their eyes being uncolored because of the pink-eye factor. If so, they would be in appearance indistinguishable from albinos, though behaving very differently in crosses.

TABLE 27.—*Matings of descendants of ♂1002 which have produced pink-eyed young.*

Nature of mating as regards—		Dark-eyed young.		Red-eyed young.	
Color factor.	Agouti factor.	Golden agouti.	Black.	Silver agouti.	Sepia.
Dark-eye × dark-eye...	Agouti × agouti..........	4	..	..	..
Dark-eye × red-eye....	.....Do................	..	..	..	..
Do..............	Agouti × non-agouti......	3	2	1	2
Red-eye × red-eye.....	Agouti × agouti..........	..	..	8	4
Red-eye × albino......	Non-agouti × non-agouti..	..	..	..	5
Total...................		7	2	9	11

Nature of mating as regards—		Pink-eyed young.		Pink-and-red-eyed young.		Albino young.
Color factor.	Agouti factor.	Agouti.	Non-agouti.	Agouti.	Non-agouti.	
Dark-eye × dark-eye.	Agouti × agouti.........	..	1	1	..	..
Dark-eye × red-eye...	.....Do...............	2	..	..	..	..
Do............	Agouti × non-agouti.....	1	1	..	..	..
Red-eye × red-eye....	Agouti × agouti.........	..	..	3	..	7
Red-eye × albino.....	Non-agouti × non-agouti.	..	..	..	2	5
Total...................		3	2	4	2	12

Nevertheless, it is to be expected that pink-and-red-eyed animals can be produced which are heterozygous for albinism. Such animals necessarily would be heterozygous for red-eye also, which is an allelomorph of albinism, and so would be of the formula C_rC_app, for it is known (1) that pink-eyed animals may transmit albinism; (2) that red-eyed animals may transmit albinism; and (3) that pink-eye and red-eye are independent of each other in transmission. Consequently, there is every reason to suppose that albinism may exist as a recessive allelomorph of red-eye in animals which are both pink-eyed and red-eyed.

A pink-eyed animal mated with a dark-eyed one produced 3 dark-eyed young and 1 albino, which adds to the evidence that pink-eye is recessive to dark-eye and may be present in the same zygote as albinism. A pink-eyed animal (♀307) mated with a pink-and-red-eyed

male (σ140) produced 2 pink-and-red-eyed young. A pink-and-red-eyed male mated with 2 dark-eyed females of race B, which were heterozygous in albinism, produced 4 dark-eyed and 4 red-eyed young. Another pink-and-red-eyed male (140) mated with a dark-eyed female descended from σ1002 produced 1 pink-eyed young, in which red-eye was undoubtedly recessive. Most of the foregoing matings are tabulated in table 28.

TABLE 28.—*Character of young produced in matings of pink-and-red-eyed descendants of σ1002.*

Character of mate.	Character of mating as regards agouti.	Dark-eyed young.		Red-eyed young.	
		Golden agouti.	Black.	Silver agouti.	Sepia.
Dark-eyed...........	Agouti × agouti...........	..	..	..	..
Do..............	Agouti × non-agouti.......	2	2	2	2
Red-eyed............	Agouti × agouti...........	..	..	4	2
Do..............	Agouti × non-agouti.......	..	..	5	10
Pink-eyed.............	.....Do...................	..	..	..	..
Albino................	.....Do...................	..	..	8	7
Pink-and-red-eyed....	Agouti × agouti...........	..	..	..	..
Do..............	Agouti × non-agouti.......	..	..	..	..
Do..............	Non-agouti × non-agouti...	..	..	..	..
Total...................................		2	2	19	21

Character of mate.	Character of mating as regards agouti.	Pink-eyed young.		Pink-and-red-eyed young.		Albino young.
		Agouti.	Non-agouti.	Agouti.	Non-agouti.	
Dark-eyed.........	Agouti × agouti.........	1	..	..	..	....
Do...........	Agouti × non-agouti.....	..	..	..	..	....
Red-eyed..........	Agouti × agouti.........	..	..	..	..	....
Do...........	Agouti × non-agouti	..	..	4	3	2 (?)
Pink-eyed.........	.....Do.................	..	..	1	1	....
Albino............	.....Do.................	..	..	..	..	1
Pink-and-red-eyed..	Agouti × agouti.........	..	..	1	2	2 (?)
Do...........	Agouti × non-agouti.....	..	..	15	18	....
Do...........	Non-agouti × non-agouti.	..	..	..	6	....
Total...................................		1	0	21	30	1+4 (?)

Pink-and-red-eyed males mated with albinos of races free from pink-eye produce red-eyed or albino young, but not pink-eyed young, since pink-eye also is a recessive character and becomes visible only when doubly represented in the zygote.

It is clear, accordingly, that when pink-and-red-eyed animals are mated with red-eyed animals (or albinos), young are produced which are red-eyed, but in which pink-eye is recessive; and when the same pink-and-red-eyed animals are mated with pink-eyed animals, young are produced which are pink-eyed, but in which red-eye is recessive. Hence the two characters, pink-eye and red-eye, are independent of each other, though red-eye is the dominant allelomorph of albinism, with which pink-eye is wholly unrelated.

SUMMARY ON THE AREQUIPA DOMESTICATED RACE.

1. A domesticated male guinea-pig obtained from the cabin of a native in Arequipa, Peru, has proved to be of great interest because of the large number of color mutations which it either possesses or transmits without itself manifesting them. Two wholly new variations (red-eye and pink-eye) were obtained from this animal as recessive characters. The former has been obtained subsequently from the Ica race and the latter from a race of guinea-pigs brought from Lima by Professor Brues. Both are probably variations of long standing among the guinea-pigs kept by the natives in Peru, but seem not previously to have been observed among guinea-pigs in Europe or North America.

2. Red-eye is a Mendelian allelomorph of albinism, of dilute pigmentation, and of intense pigmentation, the four being quadruple allelomorphs (Wright, 1915). A gamete may transmit one of the four, but not more; a zygote may contain and transmit (separately) two of the four, but not more. Dominance is in the order of decreasing intensity, viz, (1) intensity, (2) dilution, (3) red-eye, (4) albinism. Intensity and dilution affect all pigments similarly; red-eye and albinism inhibit yellow completely, but affect black in very different degrees, the inhibition of black being nearly complete in albinism, but being partial only in red-eye. Red-eye is a variation unknown as yet in any other animal, but the sooty coat of young Himalayan rabbits possibly is a parallel variation, and the same may be true of Siamese cats.

3. Pink-eye is a variation wholly independent genetically of albinism. It affects only black (or brown) pigments, the intensity of yellow pigment being unimpaired in its presence. A similar variation (genetically and physiologically) occurs in mice and also in rats.

4. The new variations (red-eye and pink-eye) have formed, with the previously known unit-character variations of guinea-pigs, many new unit-character combinations, which are here described.

5. From the crosses of the Arequipa domesticated guinea-pig with other guinea-pigs, involving a maximum number of color factors, no evidence is forthcoming that any two of the factors are "coupled" or "linked."

SIZE INHERITANCE IN GUINEA-PIG CROSSES.

PREVIOUS WORK ON SIZE INHERITANCE.

For several years my pupils and I have been engaged in studying the inheritance of size among tame or domesticated animals, a subject deserving of careful investigation both because of its economic importance and because of the light which it may throw on general theories of heredity. A preliminary study based on skeletal measurements of rabbits was published in 1909 (Castle *et al.*), which seemed to show that size inheritance is "blending" and does not involve the segregation and recombination of distinct Mendelian size-factors. MacDowell (1914), at my suggestion, repeated this work on a larger scale and with similar observational results, establishing, however, the additional fact that an F_2, or a back-cross generation, usually shows greater variability in size than an F_1 generation, following a cross between animals of unlike sizes, though the general result in both cases is the production of intermediates. On theoretical grounds MacDowell favored the Nilsson-Ehle view that all variation, even when continuous, is caused by genetic factors themselves discontinuous, and that blending inheritance involves multiple segregating factors. But MacDowell points out that this interpretation is not the only one of which his observations are capable. The genetic purity of his material also, while sufficient to establish the general blending character of the inheritance, is not sufficient to meet the extreme demands of the multiple-factor hypothesis.

At the same time that MacDowell was making his observations on size inheritance in rabbits, Detlefsen (also in my laboratory) made observations on size inheritance in crosses between *Cavia rufescens* and the guinea-pig. He was unable to rear an F_2 generation, because of the complete sterility of the male hybrids, but from a study of repeated back-crosses concluded that "there were no great differences in variability in the back-crosses of hybrids to guinea-pigs which would indicate segregation and recombination of factors for size." This conclusion he reached without theoretical bias, for he adds: "The results in no way controvert the possibility that size may be due to factors which are inherited in Mendelian fashion; but segregation was not apparent in these classes of matings in this species cross."

My colleague, Dr. John C. Phillips, at about the same time (1912, 1914), undertook crosses of very pure races of ducks, which differed widely in size, viz, Rouens and Mallards. The two parent races did not overlap in variability in size. The F_1 offspring were of intermediate weight, as were also the F_2 offspring. The F_2 generation of 63 individuals included only 1 individual which fell outside the range of the 70 F_1 individuals, though the standard deviation of the F_2 generation was somewhat larger than that of the F_1 generation. Four body-

dimensions of the F_1 and F_2 ducks were also studied by Phillips, viz, length of bill, tarsus, neck, and total length.   Length of bill and length of neck were slightly more variable in F_2 than in F_1; length of tarsus was slightly less variable in F_2 than in F_1, while total length was more variable in males but less variable in females in F_2 than in F_1.   It thus appears that F_2 is not even uniformly more variable than F_1 in size characters in this the purest material that had thus far been investigated as to size inheritance among animals.   Yet this supposed increase of variability is the only criterion of segregation in size crosses which has been discovered or even suggested.   Surely this is a wholly inadequate basis on which to rest a theory that all inheritance is based on discontinuous Mendelian factors.

While the several investigations of size inheritance in rabbits, guinea-pigs, and ducks were in progress, but before their outcome had become apparent, the Peruvian expedition brought to the laboratory material which seemed very favorable for such studies, and I have constantly kept in mind its use in this way.   *Cavia cutleri* from Peru gave us a small race of undoubted purity, less than half the size of the guinea-pig, but which has been found to produce fertile hybrids with it, which permits obtaining an F_2 generation, a thing impossible with the *rufescens* hybrids.   The Ica race and the Arequipa race have also afforded valuable material for size crosses with our own long-inbred and standardized races of guinea-pigs.

The results which have been obtained, so far as the demonstration of mendelizing size-factors is concerned, are negative, like those previously obtained, though in some respects the material is more satisfactory.   But from their bearing on the question whether or not size inheritance depends upon discontinuous Mendelian factors, these observations have, it is believed, several interesting features which will become apparent as the description progresses.

WEIGHTS AND GROWTH CURVES OF CAVIA CUTLERI, OF VARIOUS GUINEA-PIG RACES, AND OF THEIR HYBRIDS.

It will be recalled, from the description of the color inheritance crosses, that *cutleri* males were crossed with females of two inbred races of guinea-pigs, which we have designated races B and C respectively. Many observations have been made on the weight of race B covering the period from birth to old age.   These afford an accurate knowledge of the variability in weight of race B, and of the normal growth rate of animals of this race.   Our knowledge of the weight of race C is less complete, though this race is equally inbred and appears not to be more variable in size than race B.   Its average size is probably a little greater than that of race B, but the difference is negligible in comparison with the difference of both from the size of *C. cutleri*.   In the hybridization experiments, race C hybrids were bred *inter se*, as were also the race

B hybrids, and in no case were hybrids from the two races bred with each other. Nevertheless, the results obtained in the two cases were so similar that for statistical purposes it was thought best to combine them. Race B is taken as the standard guinea-pig race with which the hybrids are compared.

For a period of about a year and a half all *cutleri* individuals in the laboratory, whether of pure race or hybrids, were weighed two or three times a month. In this way records were obtained from which growth curves, averages of weight, etc., can be deduced. The repeated and frequent weighings allow the detection of periods of depression due to illness or poor feeding. Due allowance has been made for all such observations, as well as for increase in weight of females through pregnancy. Nevertheless, observations on weight are at best not
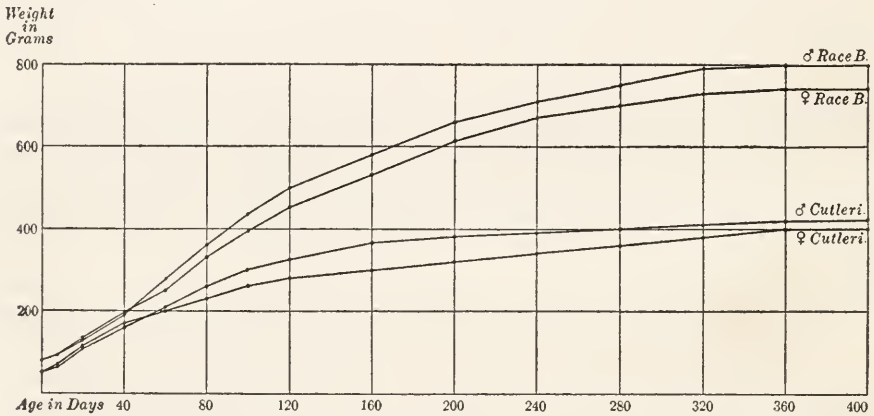
FIG. 1.—Growth-curves of *C. cutleri* and of race B guinea-pigs, the growth-curve of each sex being shown separately.

altogether satisfactory, since they are subject to fluctuation through conditions of food, accumulations of fat when maturity has been reached, etc. Greater value attaches to the bone measurements of fully adult individuals (over 1 year old) so far as individual variability is concerned. But the observations on weight afford a basis entirely satisfactory for the determination of *average* sizes and *average* growth curves in different classes of hybrids. Incidentally they afford a control on the bone measurements, for they indicate cases of abnormal growth (through disease, fighting, or other cause) and allow of either remedying conditions or rejecting suspicious material.

Pure *cutleri* young of both sexes are of about the same average weight at birth, viz, 50 grams (see fig. 1). The females at first grow a little faster than the males, a fact perhaps correlated with their earlier sexual maturity. At about 50 days of age the two sexes are of practically the same weight, the males having again caught up with the females, and

subsequently the males are heavier. The average adult weight of a female is about 400 grams, that of a male about 420 grams.

Race B animals of both sexes weigh on the average about 80 grams at birth (see fig. 1), but females grow at first a little faster than males, so that between 10 and 50 days of age females are slightly heavier. But the males soon catch up with the females and from 50 days on are heavier. The same difference between the growth curves of the two sexes is observable here, as in *Cavia cutleri*. The phenomenon is possibly a general one among mammals. Earlier maturity of the female is attended by more rapid growth, but the ultimate weight attained by males is greater. There is no indication in our observations that the attainment of sexual maturity is followed by any slowing-up of the growth rate in either sex.

In the growth of both *C. cutleri* and of race B, as in other growth-curves to be described, the curve is at first concave upward, but later becomes convex upward. This agrees with observations on rabbits, fowls, and other organisms, and its significance has been discussed elsewhere (Castle *et al.*, 1909).
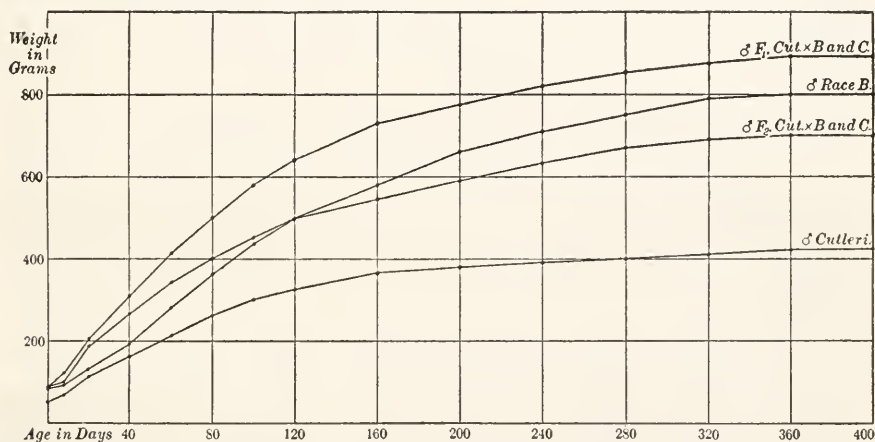
FIG. 2—Growth curves of race B and *cutleri* males and of their male hybrids, both F_1 and F_2.

F_1 hybrid males (from the cross ♂*cutleri* × ♀ race B or C, fig. 2) weigh about 85 grams at birth, *i. e.*, they are slightly heavier than the young of either pure race, a lead which they retain throughout subsequent life. At maturity they weigh about 890 grams, as compared with 800 grams, the average adult weight of race B males, and 420 grams, the average adult weight of pure *cutleri* males. The females (fig. 3) weigh about the same as the males at birth, or are even a little heavier, but soon begin to grow less rapidly, weighing about 750 grams when 1 year old. The F_2 hybrids of both sexes are smaller than the F_1 hybrids from birth on, a fact of undoubted significance. (See figs. 2 and 3.) The superior growth impetus which was produced by

hybridization has not been retained in the second-generation offspring, which sink as regards weight to a position intermediate between the parent races. Nevertheless the F_2 hybrids are nearer to race B than to *cutleri* in adult size, which fact suggests that not all the growth impetus furnished by hybridization has yet been dissipated. In *form* of growth curve the F_2 hybrids are also intermediate. The growth curve at first rises rapidly, due in part perhaps to the good milk-giving qualities of their vigorous F_1 hybrid mothers, but in part probably to inheritance of *cutleri* qualities, since the *cutleri* growth curve is a relatively steep but low one, indicating rapid growth at first and early maturity. The F_2 hybrids also grow rapidly at first, being considerably heavier than race B animals until an age of 120 to 150 days has been reached. Then they fall below and stay below the weight of race B animals, running a course nearly parallel with that of pure *cutleri* animals, whereas the growth curve of the F_1 animals more nearly approached that of race B animals.
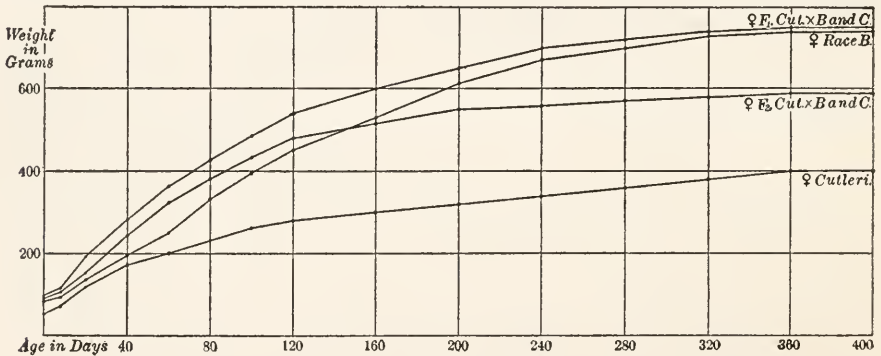
FIG. 3.—Growth curves of race B and *cutleri* females and of their female hybrids, both F_1 and F_2.

While we are on this subject it may be well to refer to the growth curves observed in the cross between the Arequipa male, 1002, and females of race B (or of similar character). (See fig. 4.) The data for the growth curves of males are more complete in this case than the data for females and accordingly only the former will be considered. The F_1 animals are of great size and vigor, attaining an average adult weight of over 1,200 grams. The F_2 animals are even larger at birth than the F_1 animals, a fact which indicates that the size of the mother has something to do, other than through heredity, with the size of the young at birth, for the F_2 young rapidly lose the lead which they had in weight at birth over their F_1 parents, and subsequent to 40 days of age fall below them in weight. At maturity they weigh less than 1,000 grams, having lost more than half of the gain which the F_1 animals showed over race B animals. This difference, it should be stated emphatically, is not due to environmental conditions of any sort, such

as season of the year, food, or the like, for it exists between lots of F_1 and F_2 animals reared simultaneously and treated exactly alike. It is clear, therefore, that a cross of distinct races, whether wild or domesticated, brings a stimulus to growth which leads to the attainment of size considerably beyond that which truly inherited size factors would produce. This stimulus, however, lasts unimpaired for only a single generation. But if it lasts at all into a second generation, and if its persistence is not uniform in amount in all cases, it is evident that it would *increase the variability of F_2* as compared with F_1. This is a matter requiring careful consideration when the significance of increased variability in F_2 is considered.
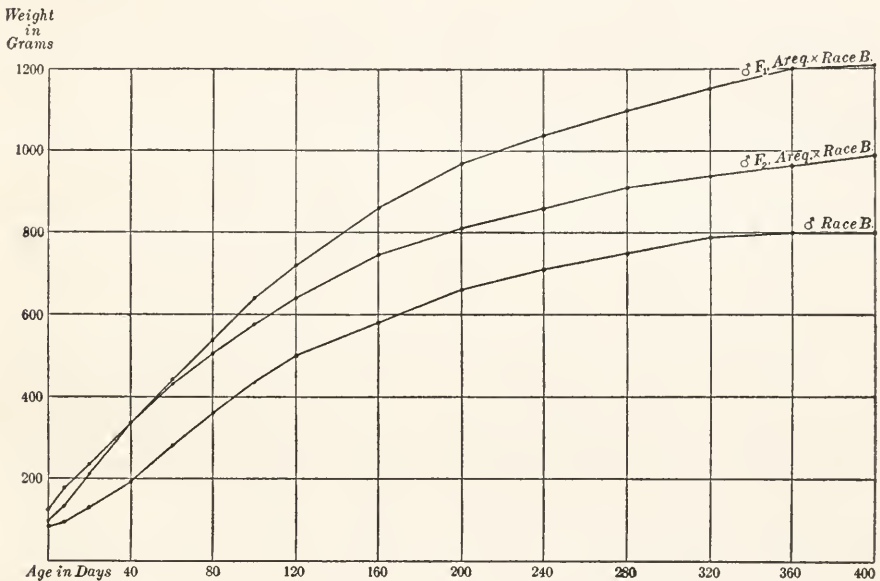
Fig. 4.—Growth curves of race B males and of the male hybrids, both F_1 and F_2, between the Arequipa male 1002 and females of race B or similar races.

SKELETAL MEASUREMENTS OF CAVIA CUTLERI, OF VARIOUS RACES OF GUINEA-PIGS, AND OF THEIR HYBRIDS.

It has been stated that skeletal measurements of adult animals are considered more reliable criteria of size than total body-weight. For this reason we have carefully preserved for study the skull and the long bones of the right fore leg and right hind leg of each adult animal which died a natural death or was killed, in the races whose size was under investigation. Observations made by MacDowell, Detlefsen, Wright, and Fish (see MacDowell, 1914, appendix) have shown the various long bones of the legs to be closely correlated in length, so that it seems sufficient for our purpose to measure a single one of these, and we have chosen for this purpose the femur. On this we have taken the

length measurement as indicated on MacDowell's figure 5, *F*. Two observations have also been made of skull dimensions, one of basilar skull length as indicated in MacDowell's figure 1, *O. M.*, and the other of maximum zygomatic width (Z). The measurements here dealt with are found upon repeated measurement to be accurate within 0.1 mm. The observations are combined in classes of 5 mm. range in tables 29 to 31 for the several races and hybrids studied. We may consider first the observations on skull length.

THE CUTLERI HYBRIDS.

Ten adult *cutleri* females have skull lengths distributed as shown in table 29. The range extends over 10 classes; the mean is 51.55 mm., and the standard deviation 13.50 mm. Twenty-eight adult females of race B have a range in skull length of 15 classes; their mean is 58.14 mm., and the standard deviation 19.75 mm. F_1 hybrid females between *cutleri* males and females of races B and C available for study number 24, with a range of 13 classes, a mean skull length of 57.70 mm., and a standard deviation of 16.85 mm. These figures indicate (like the weight observations) that the F_1 hybrids are practically as large as the larger parent race and not more variable. The 33 F_2 hybrids studied show a range of 18 classes, with a mean at 54.35 mm. and a standard deviation of 17.20 mm. The F_1 mean was about 3 mm. greater than the intermediate between the races crossed, but the F_2 mean practically coincides with it. Judged by the standard deviation, F_2 is not more variable than pure race B and is only slightly more variable than F_1. The means show in F_1 an increase in size over that we should expect through inheritance, but a loss of this increase in F_2.

Observations on the male hybrids from the same cross are recorded in the next four rows of table 29. The mean of the F_1 hybrids is again greater than that of either pure race and surpasses the intermediate point by nearly 4.5 mm. The mean of the F_2 hybrids is close to the intermediate, which it exceeds by about 0.6 mm. The variability (standard deviation) of F_2, however, is considerably greater than that of F_1 and even exceeds that of pure race B. Particularly noteworthy is the occurrence of one very large F_2 individual, nearly as large as the largest F_1 individual. Compare this with the occurrence of a single very small F_2 female, as small as the smallest pure *cutleri* female.

The *cutleri* hybrids with races B and C show similar results in regard to the other measurements studied—zygomatic width and femur length. (See tables 30 and 31 and plate 6.) In every case F_1 exceeds the means of both parent races, but F_2 approximates the intermediate between them, which it exceeds by a fraction of a millimeter only. In no case is the F_2 mean as great as the race B mean—that of the larger parent race. These facts, like the weight curves, indicate (1) that, so far as heredity is concerned, an exact intermediate between the parent races would

TABLE 29.—*A tabulation of skull length measurements of Cavia cutleri and of certain races of guinea-pigs and of their hybrids.*

Classes (in millimeters) and frequencies.

Race	48.5–48.9	49.0–49.4	49.5–49.9	50.0–50.4	50.5–50.9	51.0–51.4	51.5–51.9	52.0–52.4	52.5–52.9	53.0–53.4	53.5–53.9	54.0–54.4	54.5–54.9	55.0–55.4	55.5–55.9	56.0–56.4	56.5–56.9	57.0–57.4	57.5–57.9	58.0–58.4	58.5–58.9	59.0–59.4	59.5–59.9	60.0–60.4	60.5–60.9	61.0–61.4	61.5–61.9	62.0–62.4	62.5–62.9	63.0–63.4	63.5–63.9	64.0–64.4	64.5–64.9	65.0–65.4	65.5–65.9	66.0–66.4	66.5–66.9	67.0–67.4	Total	Mean	Standard deviation
♀ cutleri	1			2			2	2	2	1																													10	51.55	13.50
♀ race B											1	1	1	4		2	3	1	3	4	2	4	3	1	3														28	58.14	19.75
♀ F₁ cut. × race B or C												1		4	1	2		1		1	2	1	3	9	7	4	7	4	1	1	1	1	1	1					24	57.70	16.85
♀ F₂ cut. × race B or C	1					6	1	3		1	2	6	7	4	1	2	3					1	1																33	54.35	17.20
♂ cutleri							2		2		2																												7	52.91	9.45
♂ race B																		2		3	6	7	9	9	7	4	7	4			1	1							63	60.35	15.05
♂ F₁ cut. × race B or C												1	1	1	2	2	3	1	3	1		1	3			3			1	1									26	61.20	12.15
♂ F₂ cut. × race B or C						1				1	1	1	1				3		3	4	4	1							4	1	1	1							24	57.26	20.00
♀ F₁ Areq. × race B										1						1		1			3	4	1		3	3	3		2	2	3	1						2	18	61.92	12.10
♀ F₂ Areq. × race B																			2	4	3	4	4	2	3	9	5	2	4	3	1	1	1	1					41	60.44	20.65
♂ F₁ Areq. × race B																	1	1		1		1			2	1	1		3	2	3	5	4	4	4		1		27	64.40	15.15
♂ F₂ Areq. × race B																				1	3	1	7	5	3	9	9	5	5	5	4	2	1	1					56	61.86	17.75
♀ Ica														1			1	2	2	1			2	2	2	2													8	57.45	10.00
♂ F₁ Ica × race B or C															1					1	3	1	2	2	1	1													7	60.20	10.00
♀ F₂ Ica × race B or C															1				1	1		1	2	2	1	1							1						14	58.84	11.20
♂ Ica														1	1			2				1	3		1	1		1		1	1								10	58.10	22.65
♂ F₁ Ica × race B or C														1				1						1	1	1				1		3		1					8	62.20	23.55
♂ F₂ Ica × race B or C																			1			1	1	1	3	1	2				3	3					1		17	62.17	24.55

TABLE 30.—A tabulation of skull width measurements of Cavia cutleri and of certain races of guinea-pigs and of their hybrids.

Classes (in millimeters) and frequencies.

Race.	29.5–29.9	30.0–30.4	30.5–30.9	31.0–31.4	31.5–31.9	32.0–32.4	32.5–32.9	33.0–33.4	33.5–33.9	34.0–34.4	34.5–34.9	35.0–35.4	35.5–35.9	36.0–36.4	36.5–36.9	37.0–37.4	37.5–37.9	38.0–38.4	38.5–38.9	39.0–39.4	39.5–39.9	40.0–40.4	40.5–40.9	41.0–41.4	41.5–41.9	42.0–42.4	42.5–42.9	Total.	Mean.	Standard deviation.
♀ cutleri	2	2	2	1	2		1																					10	30.84	9.35
♀ race B							1	3	4	4	3			2														28	34.68	10.56
♀ F₁ cut. × race B or C			1	1	1				3	1	5	8	1	1	2	1	1											24	35.24	11.60
♀ F₂ cut. × race B or C					1	1	8	9	5	2	3	3		2	2													33	33.26	11.45
♂ cutleri			2		3	1	1																					7	31.63	6.80
♂ race B									1	2	4	6	11	13	11	2	8	1	2	2								63	36.33	11.90
♂ F₁ cut. × race B or C							1		2	1	9		1	4	2	2	5	5	2	3	1							26	37.79	11.70
♂ F₂ cut. × race B or C												1	5	1	1	1	2				1	1						24	35.24	12.05
♀ F₁ Areq. × race B															2	2	1	3	6	1	3	3	3	2				18	38.37	9.40
♀ F₂ Areq. × race B												2	2	10	7	5	1	5	1	3	4	4	3	2	1		1	41	37.35	14.05
♂ F₁ Areq. × race B																	5	1	5	2	5		3					27	39.40	11.95
♂ F₂ Areq. × race B											5					3	10	7	17	5	4		3					56	38.87	11.40
♀ Ica												2	2	1	1	1		1										8	36.28	9.80
♀ F₁ Ica × race B or C														1	2	2	1	1										7	37.13	6.30
♀ F₂ Ica × race B or C											5	2	1	3	2	1												14	35.63	8.70
♂ Ica													1	3					2	2	1	1						10	38.00	16.40
♂ F₁ Ica × race B or C																1		1	2		1	2		1				8	39.26	12.10
♂ F₂ Ica × race B or C													1			1	2	2	3	3	3	1	1					17	38.73	11.80

TABLE 31.—A tabulation of femur length measurements of Cavia cutleri and of certain races of guinea-pigs and of their hybrids.

Classes (in millimeters) and frequencies.

Race.	35.5–35.9	36.0–36.4	36.5–36.9	37.0–37.4	37.5–37.9	38.0–38.4	38.5–38.9	39.0–39.4	39.5–39.9	40.0–40.4	40.5–40.9	41.0–41.4	41.5–41.9	42.0–42.4	42.5–42.9	43.0–43.4	43.5–43.9	44.0–44.4	44.5–44.9	45.0–45.4	45.5–45.9	46.0–46.4	46.5–46.9	47.0–47.4	Total	Mean.	Standard deviation.
♀ cutleri		1	1	1	1	1	1	3	3																12	38.45	12.05
♀ race B							3		2	3	2	6	5	5	1	1	1								29	41.16	12.50
♀ F₁ cut. × race B or C											2	2	2	4	2	4	6		1						23	42.63	10.35
♀ F₂ cut. × race B or C	1									6	2	6	3		3		1	1	4	1					33	40.38	15.60
♂ cutleri					2	1	1	1	1	1															7	38.77	8.20
♂ race B											2	6	9	10	12	4	3	3		1	2				52	42.39	10.70
♂ F₁ cut. × race B or C											1				4	2	5	3	3	1					19	43.57	9.80
♂ F₂ cut. × race B or C											5	4	4	3	2	1	2	3							24	41.32	14.20
♀ F₁ Areq. × race B														3	3	3	1	4	5	1			2	1	23	44.07	13.35
♀ F₂ Areq. × race B										2	1	4	6	6	4	5	3	5		1		1			41	42.95	15.30
♂ F₁ Areq. × race B																2	1	5	5	5	4	2	1		25	45.16	10.05
♂ F₂ Areq. × race B											1	5	3	9	8	7	10	6		1			1		54	43.15	11.80
♀ Ica														2	2	3		1							8	42.64	10.75
♀ F₁ Ica × race B or C															3	1	1	1		1					7	43.49	9.05
♀ F₂ Ica × race B or C										1	1	1	4	1	6										14	42.06	10.85
♂ Ica									1		1	1	2			2	2		1						10	42.90	16.10
♂ F₁ Ica × race B or C													1			1	1		1		1		1	1	7	44.63	17.60
♂ F₂ Ica × race B or C												1	1	4	2	2			3	2	1	1			17	43.44	17.80

result from the cross, but (2) that a physiological growth stimulus (not hereditary) results in F_1 from the fact that the zygotes produced are formed by the union of gametes from very dissimilar races, and (3) that the increased F_1 vigor is largely, but not entirely, lost in F_2. No evidence is found that it persists in full force in any F_2 zygote (with one possible exception), since the upper half of the range of the F_1 zygotes is almost completely wanting in F_2, while the absence of any appreciable increase of variability in F_2 shows that any increased vigor due to the cross which persists into F_2 persists also very generally among the zygotes of that generation, so that practically all are changed in the same sense and in like amount; otherwise increased variability must result, irrespective of whether size inheritance occurs other than by complete blending.

HYBRIDS OF THE AREQUIPA ♂ 1002.

Crosses between the Arequipa ♂ 1002 and females similar to those of race B, but averaging a little larger, have yielded an extensive and vigorous race for the study of size inheritance. Among the animals of this crossed race the mortality has been comparatively small, so that good numbers are available. The male 1002, sole male ancestor of this race, is still alive, so that his bone measurements are not available; but a female, 1001, secured in the same cabin in Arequipa in 1911, lived until fully grown and her bones are available for comparison. Further, a son of ♂ 1002 and ♀ 1001 lived until fully grown and his bones also are available. From the measurements of these two and a comparison of the empirical ratio of female to male measurements in the other races studied, it is possible to arrive at estimates of the racial size of the Arequipa stock which it is believed are fairly reliable. These are given in table 32, where it is further assumed that the racial size of the animals mated with ♂ 1002 was substantially that of race B, measurements of the latter being given for comparison. But whether these assumptions are sound or not does not affect the validity of the observations on the F_1 and F_2 hybrids from this cross, which are valuable as regards their interrelations, for the numbers of adult individuals are considerable (43 F_1 and 77 F_2 animals) and the mortality among them is small. F_1 in this experiment (tables 29 to 31, rows 9–12) regularly exceeds the assumed mid-parental measurement, as in the crosses previously considered; F_2 is in all cases close to the mid-parental, being slightly greater in three cases and slightly less in three cases. As regards the relative variability of the two generations, the standard deviations indicate that the F_2 females (as compared with those of F_1) are considerably more variable in skull length (though scarcely more so than race B) and are slightly more variable in skull width and femur length. The male F_2 hybrids differ very little in variability from the F_1 hybrids, the standard deviations being slightly greater in skull measurements but less in femur length.

THE ICA HYBRIDS.

Crosses with the Ica race were made principally by a male of race C whose measurements are known and which slightly exceed the averages for race B males; but a few crosses with the Ica race were also made with race B females (mated with Ica males). The measurements given in table 32 for the mates of the Ica race are a mean between the measurements of races B and C. The standard deviation of the mixed parents should of course exceed that of race B alone, which should increase the variability of F_1 and F_2, but should not alter the *relative* variability of these two, since the race B and race C hybrids were bred

TABLE 32.—*Statistical constants derived from tables 23 to 25.*

Races.	No. of indi-vid-uals.	Skull-length.		Skull-width.		Femur-length.	
		Mean.	Standard deviation.	Mean.	Standard deviation.	Mean.	Standard deviation.
♀ cutleri...............	10	51.55	13.50	30.84	9.35	38.45	12.05
♀ race B...............	28	58.14	19.75	34.68	10.56	41.16	12.50
♀ F_1, cutleri × B or C...	24	57.70	16.85	35.24	11.60	42.63	10.35
♀ F_2, cutleri × B or C...	33	54.35	17.20	33.26	11.45	40.38	15.60
♂ cutleri...............	7	52.91	9.45	31.63	6.80	38.77	8.20
♂ race B...............	63	60.35	15.05	36.33	11.90	42.39	10.70
♂ F_1, cutleri × B or C...	26	61.20	12.15	37.79	11.70	43.57	9.80
♂ F_2, cutleri × B or C...	24	57.26	20.00	35.24	12.05	41.32	14.20
♀ 1001, Arequipa........	..	61.10	.....	39.70	.....	45.50	.....
♀ race B...............	28	58.14	19.75	34.68	10.56	41.16	12.50
♀ F_1, Arequipa × race B .	18	61.92	12.10	38.37	9.40	44.07	13.35
♀ F_2, Arequipa × race B .	41	60.44	20.65	37.35	14.05	42.95	15.30
♂ Arequipa (estimated) ..	..	63.11	.....	41.20	.....	46.50	.....
♂ race B...............	63	60.35	15.05	36.33	11.90	42.39	10.70
♂ F_1, Arequipa × race B .	27	64.40	15.15	39.40	11.95	45.16	10.05
♂ F_2, Arequipa × race B .	56	61.86	17.75	38.87	11.40	43.15	11.80
♀ Ica.................	8	57.45	10.00	36.28	9.80	42.64	10.75
♀ races B and C.........	..	59.00	.....	35.00	.....	42.00	.....
♀ F_1, Ica × race B or C...	7	60.20	10.00	37.13	6.30	43.49	9.05
♀ F_2, Ica × race B or C...	14	58.84	11.20	35.63	8.70	42.06	10.85
♂ Ica.................	10	58.10	22.65	38.00	16.40	42.90	16.10
♂ races B and C.........	..	62.00	.....	38.00	.....	42.50	.....
♂ F_1, Ica × race B or C...	8	62.20	23.55	39.26	12.10	44.63	17.60
♂ F_2, Ica × race B or C...	17	62.17	24.55	38.73	11.80	43.44	17.80

entirely distinct from each other and are only tabulated together to secure greater numbers. Again in this cross we are confronted with the same phenomena as regards the skeletal measurements: (1) in F_1 a substantial increase in size (least in skull length of F_1 male hybrids); (2) while in F_2 a return is made toward the mid-parental (mean of the races crossed), in 4 of the 6 measurements it is closely approximated; (3) the standard deviation meanwhile alters little, not enough to have significance; the Ica crosses are of particular interest because the races mated are of nearly the same size. The phenomenon of increased size in F_1 followed by a prompt loss of the increase in F_2 is here observed

exactly as in the crosses between races of widely different and heritably different sizes, but without indication in either case that the size inheritance is other than a simple and permanent blend.

THEORETICAL EXPLANATIONS OF SIZE INHERITANCE AND OF BLENDING INHERITANCE IN GENERAL.

We conclude therefore that, so far as present knowledge goes, the statement made in 1909 that size inheritance is blending and does not mendelize still holds. This does not preclude the possibility that in special cases mendelizing factors may exist which affect size. For example, in man brachydactyly is due to such a factor, a simple Mendelian dominant, as was first shown by Farabee (1905), and has been confirmed by Drinkwater in the case of three separate English families. This character involves a shortening of the skeleton generally, but of the digits in particular. It is transmitted only through affected individuals, the normal offspring of affected individuals producing only normals. Professor James Wilson has stated that the Dexter-Kerry cattle of Ireland differ from ordinary Kerry cattle by a similar mendelizing factor. If one were to restrict his study of size inheritance to cases such as these, he would reach the conclusion that size inheritance in general is Mendelian, a wholly mistaken idea. (See Castle, 1914.) Such cases among animals are distinctly rare. Among cultivated plants they seem to be somewhat commoner, so that many of the inherited size differences studied by botanists involve such factors. One of the commonest of these is involved in the difference between normal (tall) and dwarf habit of growth, a case demonstrated by Mendel for peas in his original experiments; but it is more than doubtful whether Mendelian factors produce the differences in height observed among different races of tall or of dwarf peas respectively. The same is true concerning differences in size or shape of seeds and fruits, as described by Emerson and Gross. It seems almost certain that Mendelian factors are involved in many of the cases studied, but associated with other factors not Mendelian, possibly merely physiological, which render the results extremely complex and the variation seemingly continuous in character. To have shown that size inheritance is occasionally affected by Mendelian factors is not by any means to have demonstrated that all size inheritance is due to Mendelian factors. The physiological increase of size due to the crossing of unrelated races is a fact of far greater economic importance to the animal breeder than the existence of any Mendelian factor affecting size that has thus far been demonstrated.

The question may be raised, how are we to account for the increased variability of F_2 as compared with F_1, if this is not due to segregation and recombination of multiple factors, as assumed under the Nilsson-Ehle principle. (1) This would be sufficiently accounted for in the

case under discussion by an unequal persistence, among the F_2 zygotes, of the increased growth stimulus observed in F_1 and due evidently to the act of crossing, not to inheritance. (2) Increased variability in F_2 would also result if a blending occurs in F_1, which is imperfect, so that the gametes formed by the F_1 individuals are not all the exact mean of the parental gametes, but fluctuate around that mean.

What may we imagine the germinal basis of a blending character to be? Perhaps some substance or ferment which varies in amount, larger amounts producing larger results. If a 5 per cent solution of cane sugar were poured into the same dish with a 10 per cent solution and then samples were dipped from this before the two solutions had been thoroughly stirred together, it might very well happen that the samples would not be of uniform strength. Any other result would be surprising. A character genuinely blending in heredity might be expected to behave in this same way, the quantitatively different conditions found in parent races not blending perfectly in a single generation of association together in an F_1 zygote, which therefore would produce gametes less uniform in character than those of the respective inbred parent races.

The multiple factor interpretation of size inheritance, besides being superfluous, meets with this serious logical difficulty: If we suppose the difference between two races to depend upon a certain number of independent factors whose action is cumulative, then a less difference must be due to fewer factors, and the fewer factors concerned in a cross, the more obvious is the segregation. But we do not find it easy to detect segregation when races are crossed which differ little in size; the general result is the same as when races are crossed which differ widely from each other. It is difficult to detect any evidences of segregation unless the parent races differ widely from each other, under which condition, if multiple factors are involved, complete segregation should occur least often.

On the whole, the hypothesis of quantitative variations in a blending character presents fewer difficulties as an explanation of size inheritance than the hypothesis of multiple unvarying segregating factors. It is to be preferred on the ground of simplicity alone, but it also accords better with the results obtained in other fields. Jennings now finds, contrary to his earlier observations on paramecium, which Calkins and Gregory were unable to confirm, that size is a character varying even in asexual reproduction, within what would be a "pure line" if the theory of factorial constancy were true. My own observations of rats and other rodents (Castle, 1915) may be cited to show that even single Mendelian unit characters are quantitatively variable. If this is so, the hypothesis of multiple factors as a general explanation of variability is quite unnecessary and so should be discarded.

PART II

AN INTENSIVE STUDY OF THE INHERITANCE OF COLOR
AND OF OTHER COAT CHARACTERS IN GUINEA-
PIGS, WITH ESPECIAL REFERENCE TO
GRADED VARIATIONS.

By Sewall Wright, S. D.

COLOR AND ITS INHERITANCE IN GUINEA-PIGS.

The experiments described in the following paper were carried on at the Bussey Institution of Harvard University, between September 1912 and August 1915, under the direction of Professor W. E. Castle. A large number of stocks of guinea-pigs and wild cavies, containing an extensive assortment of variations, were available throughout the experiments, and furnished excellent material for studies on inheritance. The writer wishes here to express his gratitude for the privilege of using freely this material and for the constant encouragement and assistance which Professor Castle has given.

SKIN, FUR, AND EYE COLORS OF GUINEA-PIGS.

COLOR OF CAVIA CUTLERI.

The fur color of *Cavia cutleri*, the probable ancestor of the guinea-pig, is of the agouti type found in most wild rodents, as well as in many other wild mammals. (See plate 3.) The back and sides are slaty black, ticked with yellow (more accurately, cinnamon buff). An isolated hair is of a dull slate color at the base, becoming blacker toward the tip. Near the tip there is a yellow band some 2 or 3 mm. long. The extreme tip for 1 to 2 mm. is black. The belly is cream-colored (more accurately cartridge buff) and is sharply separated from the ticked sides. An isolated hair is pale neutral gray throughout its basal half and cream-colored in the remaining portion. *Cavia rufescens* of Brazil has a similar ticked coat, but differs in showing less ticking on the back and sides and often in having a ticked belly not sharply separated from the sides. The general appearance is darker. Tame guinea-pigs show a great variety of colors and color patterns and also deviations from the dark skin and black eye color of the wild species.

MELANIN PIGMENT.

The coat colors of mammals are largely due to granular pigments of a kind known chemically as melanin. The pigment in the hair is found principally in the walls of air-spaces in the medulla, but to some extent in the cortex, as described by Bateson (1903) in mice. Melanin pigments are also found in the skin (principally in the epidermis) and in the iris and retina of the eye. A deficiency of pigment in the retina is revealed by a red reflection through the pupil.

PRIMARY CLASSIFICATION OF FUR COLORS.

Three qualitatively distinct melanin pigments are generally recognized in mammals, viz, black, brown, and yellow (Bateson, 1903). There are reasons, however, for regarding black and brown as more closely related to each other than either is to yellow. Black and brown granules are acted upon similarly by most hereditary factors which act

on either.   Yellow pigment, on the other hand, is acted upon very differently from black and brown by many factors.   Accordingly it will be convenient to use a term to include both black and brown pigments, as dark pigments.   The fur colors fall naturally into two groups, the dark and yellow colors, characterized by the predominant presence of dark and yellow pigments respectively.

YELLOW GROUP OF COLORS.

In the yellow group of colors the one of highest intensity is a rich yellow-orange, which matches quite well with ochraceous tawny in Ridgway's color charts (1912).   There are all gradations from this ochraceous tawny through cinnamon buff and cartridge buff to white. In this paper it will be more convenient to use the conventional names, red, yellow, and cream, for these grades.   In grading the guinea-pigs, three samples of hair have been used as standards of grades called red_0, $yellow_3$, and $cream_6$, respectively.   White is considered to be $cream_8$.   All of the yellow colors in guinea-pigs fall into this series, as far as known.   In mice, however, Little (1911) has shown that two dilution series between red and white can be distinguished.   There is a series from red to cream resembling in appearance (though not genetically) the guinea-pig series.   Another series (the "dilute" reds, yellows, and creams) has a peculiar streaky appearance.   The physical relation between these two series is probably similar to that between the sepia and blue types of dilution among the dark colors, which is discussed below.

DARK GROUP OF COLORS.

Among the dark colors there are at least three distinct series:

(1) There is the series of neutral grays, passing from black to white. Such colors are shown by the blue rabbits, blue mice, and maltese cats. There are no tame guinea-pigs known whose colors fall distinctly into this series; but the dull black of the wild *Cavia cutleri*, especially on the belly, is a neutral gray quite free from any brown.   Examination of the hair of the blue rabbit under the microscope shows dense black pigment masses alternating with colorless spaces, a condition described by Miss Sollas (1909) in the hair of the blue mouse and apparently comparable to the clumped condition of the black pigment in the feathers of blue pigeons, described by Cole (1914).

(2) There is a series of grades from black through dull brown and tow-color to white.   This series is shown by dilute black guinea-pigs. The various shades of human hair, from black through brown to tow-color, match samples from this guinea-pig series very closely.   The increase in quantity of pigment in this series in passing up from the lower grades is accompanied by a change in quality.   Yellowish-brown pigment gives way to black.   Dilution of this sort is produced inde-

pendently by different factors, the combination of which gives doubly dilute colors, which may still be classed in the same series. Dilute guinea-pigs of this series have been called blue in the literature, but the name is as inappropriate as it would be applied to human brown hair, and, moreover, tends to confusion with the very distinct type of dilution of the blue rabbit. In this paper the colors of this series will be called sepia. Grades of dilution have been represented by numbers, as in the yellow series. White is considered as grade 16. Grading has been done by comparison with standard samples of hair, the colors of which are defined in terms of Ridgway's colors at the end of this section.

(3) The most intense grade of this series is a rich dark brown, such as is found in chocolate guinea-pigs, mice, and rabbits and in liver-colored dogs. This color is not very different from sepia$_4$, but is somewhat warmer and less dull. As noted by Miss Durham in the case of brown mice, there seems to be a complete absence of black granules, but a large quantity of brown granules. No intergrades between this brown and black are known. There are dilute browns, each corresponding closely to a color in the sepia series. They are often difficult to distinguish from grades of sepia in isolated samples of hair. On the animals, however, the browns seem conspicuously richer than the sepias. There are, further, correlated differences in skin and eye color which are even more conspicuous.

Most guinea-pig colors can be matched fairly well in the sepia, brown, or yellow series, but one other class of variations must be noted. The animals have been graded by the color near the tip of the hair, but while in some blacks, sepias, browns, and yellows the hair is nearly uniform, in most cases the base is much duller than the tip. This gives a somewhat streaky effect to the fur. In the case of dull blacks of this kind, the color at the base of the fur is usually between a neutral slaty black and a dark sepia.

SKIN COLORS.

The color of the skin usually corresponds roughly to the color of the hair which comes from it. Where the fur is thick there is very little pigment in the skin, while exposed places (as ears and feet) are often very strongly pigmented.

Where the fur is yellow the skin in exposed places shows an orange-yellow color, usually with considerable admixture of black. On most of the body the skin is white, with occasional orange-yellow spots. The dilution of fur color is accompanied by dilution of the skin color.

Where the fur is black the exposed parts of the skin are very black, while the rest of the skin is dull black. Where the fur is of the sepia series the color of the ears and feet depends much on the genetic factors responsible for the dilution of the black. In the sepias of the albino

series the ears and feet are quite black, often with intense black blotches. Even in albinos, where the fur is nearly pure white, the ears and feet may be black. In the pink-eyed sepias, on the other hand, there is very little pigment anywhere in the skin.

Brown fur goes with a uniform brown color of ears and feet very different from the dull black of sepias of corresponding intensity of fur color. Dilution in the skin accompanies dilution in the fur.

The different skin colors are very conspicuous in animals with spotted fur. In these it is easy to find places where the skin spots do not correspond exactly to the fur spots. White fur may arise from colored skin and yellow fur from black skin, but the reverse cases do not seem to occur.

EYE COLORS.

The iris and retina usually contain black and brown pigment. Where there is reduction of pigment in the iris, the pigment tends to disappear first next to the pupil, leaving a dark outside ring. Decreasing grades of retinal pigment are most easily recognized by the apparent color of the pupil. In black eyes the pupil appears black. Occasionally a red reflection can be obtained in strong light. In brown eyes a dark-red reflection is easily obtained by holding the guinea-pig away from the light. In the red eye the pupil looks red most of the time and the inner ring of the iris often transmits red light. A pink eye has a transparent iris and a pink reflection is visible through both iris and pupil in all lights.

The following summary shows the color terms to be used in this paper, with their nearest equivalent on Ridgway's color charts (1912). The numbers $15'i$, etc., refer to the position in Ridgway's system. For purposes of convenience in defining the color factors, white is included as a member of each color series as well as in a class by itself. In some cases white may be shown to represent extreme dilution of a particular color; in other cases it stands in no relation to particular colors.

DEFINITION OF FUR COLORS BY RIDGWAY'S CHARTS.

1. Pigment absent because of factors not belonging to a dilution series.
    White.
2. Pigment present, or absent only because of factors demonstrably belonging to a dilution series.
    a. *Yellow group.*
        $Red_0 = 15'i$, ochraceous tawny.
        $Yellow_3 = 16''b$, redder than cinnamon buff, $17''b$.
        $Cream_6 = 19''f$, cartridge buff.
        White.
    b. *Dark group.*
        (1) Black.
        Slaty black = dark neutral gray.
        Blue = neutral gray.
        White.

b. Dark group—Continued.
  (2) Black.
  Sepia$_3$ = 16'''n, warmer and darker than clove brown, 17''' m.
  Sepia$_6$ = 16'''l, warmer and lighter than clove brown, 17''' m.
  Sepia$_9$ = 17''''i, hair brown, slightly purer, however.
  Sepia$_{12}$ = 17''''b, light drab, somewhat purer.
  Sepia$_{15}$ = 17''''f, pale drab gray, somewhat purer.
  White.
  (3) Brown = 15'' m, bister, 15''m, but somewhat warmer and duller.
  Brown$_3$ = 15'''i, between army brown, 13'''i, and buffy brown, 17'''i.
  Brown$_6$ = 17'''b, somewhat duller than avellaneous, 17'''b.
  Brown$_9$ = 17''''f ?
  White.

DEFINITIONS OF EYE COLORS.

(1) Black: black iris and pupil.
  Dark red: black iris, dark-red pupil in favorable lights.
  Red: partially transparent iris, red pupil in most lights.
  Pink: transparent iris, pink reflection through both iris and pupil.
(2) Brown: brown iris, dark-red pupil.
  Brown-red: partially transparent brown iris, red pupil.
  Pink: as above.

HEREDITY OF FUR AND EYE COLOR.

COLOR FACTORS OF GUINEA-PIGS.

Considerable work has been done on the inheritance of color variations in guinea-pigs. The numerous colors which have been listed and several patterns in which these colors may be arranged have been found to be due in the main to relatively few hereditary factors. Some of these factors determine effects which are very easily defined. Thus, any guinea-pig which is homozygous for factor C_a is an albino with pink eyes and white fur, regardless of the presence of any combination of other known factors. On the other hand, certain factors determine nothing except in combination with other factors. Factor E may be present in guinea-pigs of any known color variety whatever. It can only be said that its presence is a necessary condition for the development of more than a trace of dark pigmentation in the fur. The color which results from a given combination of factors can be made clear most easily by classifying the factors into a series of groups. The following classification is based upon the factors in the rodents which have been most studied, viz, guinea-pigs, mice, rats, and rabbits.

CLASSIFICATION OF COLOR FACTORS.

1. Factors which affect the distribution and intensity of color largely irrespective of the kind of color.
  A. Factors which govern the distribution of color as opposed to no color (white) in patterns in the fur, in individual hairs, and in the eyes.
  B. Factors which govern the intensity of general color development within colored areas of fur and eyes.
2. Factors which govern the differentiation between yellow and dark colors in colored areas of the fur.
3. Factors which determine the kind of dark color in the areas with dark pigmentation in fur and eyes, without influence on yellow areas.

COLOR VS. WHITE (1 A).

Probably dilution of the type of the blue and dilute yellow mice and rabbits and maltese cats belongs here, rather than in 1 B, since the effect seems to be due to the distribution of pigment within the individual hairs rather than to any effect on the actual pigment granules. Most of the factors which belong in this class, however, are those which determine patterns of white as opposed to areas which are colored under most combinations of other factors. In this class are such factors as on the one hand determine a self-colored coat, and on the other black-eyed whites, as in mice; white patterns, as in hooded rats, Dutch and English rabbits; or scattered white hairs, as in silvered guinea-pigs. In cases where several independently inherited white patterns have arisen it is evident that there can be no single factor which alone determines self. The "self" allelomorphs of the white-pattern factors can merely be defined as conditions for self. Where more than one white-pattern factor is present in an animal, combination patterns are produced.

Clear-cut Mendelian factors which belong to this group are known in mice, rats, and rabbits, but none have been isolated in guinea-pigs, although irregular blotching and silvering with white are common. The symbol Σ will be used to represent an assemblage of unanalyzed factors.

Σw, an assemblage of unanalyzed factors which determine white spotting.

INTENSITY OF GENERAL COLOR DEVELOPMENT (1 B).

In this group fall albinism and its variations. These factors affect all color, but not wholly irrespective of the kind of color. There are several peculiarities which are discussed more fully in a later section (page 70). The most important is the fact that the level of intensity of the color factor at which yellow can develop at all is higher than the threshold for black or brown. This does not affect the differentiation of the fur into yellow and dark pigmentation areas by factors of group 2, but involves the result that with certain albino series factors, yellow areas appear white, while dark areas are quite strongly colored. Indeed, in albinism itself, dark pigmentation areas can often be distinguished from yellow areas by a slight sootiness in the former, absent in the latter.

C. Determines the highest intensity of color of skin, fur, and eye which is to be found with a given array of other factors; dominant over C_d, C_r, and C_a, where distinguishable in its effects. In the following table, and in the similar tables under C_d, C_r, and C_a, are given the ranges of intensity in the yellow, black, and brown series to which these colors develop when the factor under consideration is present. In the case of black and brown, factor P is assumed to be present. When p is present, black and brown undergo a two-fold dilution. P is also considered present in the case of eye-color.

Yellow series—red_0 to $yellow_2$ in guinea-pigs; $yellow_3$ to $cream_6$ in *Cavia cutleri*.

Black series—$black_0$ to $black_2$.

Brown series—$brown_0$ to $brown_2$.

Eye color—black, brown.

C_d. Determines an intensity of yellow distinctly lower than does C, an intensity of dark pigmentation usually, but not always lower than does C, and an intensity of eye color rarely distinguishable from that determined by C. More or less dominant over C_r and C_a where distinguishable. (Wright, 1915.)

> Yellow series—yellow$_2$ to cream$_7$.
> Black series—black$_0$ to sepia$_7$.
> Brown series—brown$_0$ (?) to brown$_7$.
> Eye color—black, brown.

C_r. Determines the complete absence of yellow, an intensity of dark pigmentation indistinguishable from that determined by C_d and an intensity of eye color lower than that determined by C or C_d. More or less dominant over C_a where distinguishable. (Castle, 1914a; Wright, 1915.)

> Yellow series—white.
> Black series—black$_0$ to sepia$_3$.
> Brown series—brown$_0$ (?) to brown$_7$.
> Eye color—red, brown-red.

C_a. Determines an absence of pigment, complete with yellow, not quite complete with dark pigments of the fur and skin, but complete in the eyes. (Castle and Allen, 1903; Castle, 1905; Sollas, 1909; Detlefsen, 1914; Wright, 1915.)

> Yellow series—white.
> Black series—white, dark smudges on nose, ears, and feet.
> Brown series—white, brown smudges on nose, ears, and feet.
> Eye color—pink.

DARK VS. YELLOW COLOR (2).

Factors of this group affect skin and fur color, but not eye color. In this group come the factors responsible for self yellows, tortoise-shells, and brindles, on the one hand, and self blacks or browns on the other, as contrasted with the ticked or agouti patterns of the wild rodents. Where more than one factor is present which determines a yellow pattern, combination effects are produced, such as in yellow-spotted agoutis among guinea-pigs. The following factors are known in guinea-pigs:

E. A condition for more than a trace of dark pigmentation in the fur; determines dark pigmentation wherever yellow is not determined by other factors; dominant over e, found in the wild species, all agoutis, blacks, browns, etc., but very rarely in self yellows.

e. Determines the presence of one of the yellow colors in all colored areas of the fur, aside from a slight sootiness; responsible for the yellow in most self yellows, for the white in red-eyed whites, etc. (Castle, 1905, 1907, 1907a; Sollas, 1909; Detlefsen, 1914.)

A. Determines the presence of a yellow color in the light-bellied agouti pattern wherever there is dark pigmentation in which the yellow group ticking may show; dominant over A′ and a, found in *Cavia cutleri* and light-bellied agouti guinea-pigs, including the red-eyed silver agoutis, in which the agouti pattern is in white.

A′. Determines the presence of yellow colors in a more restricted agouti pattern than does A, a pattern usually characterized by a ticked belly not sharply distinct from the sides in color; dominant over a, found in *Cavia rufescens* and in ticked-bellied agouti hybrids which have *rufescens* ancestry. (Detlefsen, 1914.)

a. Determines the absence of yellow group ticking in hairs of dark pigmentation; found in blacks, browns, etc. (Castle, 1905, 1907, 1907a, 1913; Sollas, 1909; Detlefsen, 1914.)

Σy. An assemblage of unanalyzed factors which determine the presence of spots of a yellow color, conditional on factors of group (1); found in black and yellow tortoise-shells, black, yellow, and white tricolors, and in some red-eyed black and white bicolors; probably responsible for an occasional self yellow, though never in the writer's experience.

VARIATIONS OF DARK COLOR (3)

Factors of this group are responsible for browns and pink-eyed sepias, as compared with blacks, in guinea-pigs; for browns and pink-eyed sepias in mice, and for the new pink-eyed and red-eyed dilute variations in rats. Where more than one factor of this group or of group 1B determines dilution, combination effects are produced. Thus we have very pale sepias resulting from the combined effects of two independent dilution factors (C_dC_dpp).

B. Determines a color of the black-sepia series wherever dark pigmentation develops, including the eyes; has no influence where yellow pigmentation develops; dominant over b, present in the wild species and in blacks, sepias, albinos with black points, black-eyed yellows, etc.

b. Determines a color of the brown series wherever dark pigmentation develops, including the eyes; has no influence where yellow pigmentation develops; present in browns, brown-eyed yellows, etc. (Castle, 1907a, 1908; Sollas, 1909; Detlefsen, 1914.)

P. A condition for intense development of dark pigmentation in the fur and for eye colors more intense than pink; not necessary for intense development of yellow; dominant over p.

p. Determines a low development of dark colors, *i. e.*, below sepias; has no influence where yellow develops; determines pink eye color. (Castle, 1914a.)

TABLE OF FACTOR COMBINATIONS.

In determining the color which corresponds to a given array of factors the groups of factors must be considered in the order given. Table 33 gives a list of the color varieties corresponding to the combinations of Mendelian factors. At the top and left of the table are indicated, by symbols, the factors present in each of the varieties named in the body of the table. The color of spots produced by Σw and Σy are given below. Only the varieties marked with an asterisk have not yet been synthesized. These include the pink-eyed yellows and creams and a kind of pink-eyed white which is expected to be indistinguishable from an albino in appearance, though breeding wholly differently. The pink-eyed brown series (bbpp) has not yet been produced and is not included. Some of the varieties have names given by fanciers which have been used in the literature. In this table, however, it seemed best to use a consistent scheme of naming, indicating at once the color and pattern. Agouti is used as the name for a pattern, the banding of hairs of predominantly a dark color with a yellow color. The names preceding agouti give the two colors in each hair. The following table of synonyms may be useful:

Black-red agouti = golden agouti.
Sepia-yellow agouti = yellow agouti.
Sepia-cream agouti = silver agouti.
Brown-red agouti = cinnamon.
Brown-cream agouti = light cinnamon.
Sepia = blue.
Brown = chocolate.
Brown eye = brown eye (Castle), ruby eye (Sollas).

TABLE 33.

Factors present.	Fur.			Eye.
	EA (agouti light-belly). EA' (agouti ticked-belly).	Eaa.	ee (A, A' or aa).	
B P C.....	Black-red agouti............	Black.........	Red.............	Black.
CdCd..	Dark sepia-yellow agouti.....	Dark sepia.....	Yellow..........	Do.
CdCr...	Dark sepia-cream agouti.....	....Do........	Cream..........	Do.
CdCa..	Light sepia-cream agouti.....	Light sepia.....	....Do..........	Do.
CrCr...	Dark sepia-white agouti.....	Dark sepia.....	White (light points).	Red.
CrCa...	Light sepia-white agouti.....	Light sepia.....	....Do..........	Do.
CaCa..	White (dark points).........	White (dark points).	....Do..........	Pink.
Bpp C....	Pale sepia-red agouti........	Pale sepia......	Red.............	Pink.
CdCd..	Very pale sepia-yellow agouti.	Very pale sepia.	*Yellow.........	Do.
CdCr...	Very pale sepia-cream agouti..	....Do........	*Cream.........	Do.
CdCa..	....Do....................	....Do........	...*Do..........	Do.
CrCr...	Very pale sepia-white agouti..	....Do.	*White..........	Do.
CrCa...	....Do....................	....Do........	...*Do..........	Do.
CaCa..	White (light points).........	White (light points).	...*Do..........	Do.
bbP C....	Brown-red agouti...........	Brown.........	Red.............	Brown.
CdCd..	Medium brown-yellow agouti.	Medium brown.	Yellow..........	Do.
CaCr...	Medium brown-cream agouti.	....Do........	Cream..........	Do.
CdCa..	Light brown-cream agouti....	Light brown....	....Do..........	Do.
CrCr...	Medium brown-white agouti..	Medium brown.	White..........	Brown-red.
CrCa...	Light brown-white agouti....	Light brown....	....Do..........	Do.
CaCa...	White (lt. br. points)........	White (lt. br. points).	....Do..........	Pink.

Factors present.	Σw.	Σy.	ΣwΣy.	Eye.
C......	White spots (clear)..........	Red spots......	Red and white tri-color.	
CdCd..	....Do....................	Yellow spots...	Yellow and white.	
CdCr...	....Do....................	Cream spots....	Cream and white tricolor.	
CdCa..	....Do....................	....Do........	....Do..........	
CrCr...	....Do....................	}White spots,	Sooty and clear,	
CrCa...	....Do....................	} often sooty.	white spots.	
CaCa...	(Albino)..................	(Albino).......	(Albino)........	

HEREDITARY FACTORS AND THE PHYSIOLOGY OF PIGMENT.

The definitions which have been given for the hereditary factors are based largely on the colors as seen without a microscope. It would be very desirable, however, to correlate color factors accurately with the variations in quality and quantity of the actual pigments and ultimately with the physiology and chemistry of pigment formation.

Considerable progress has been made in recent years in the study of the chemistry of melanin pigments. The melanins are amorphous granular pigments found throughout the animal kingdom. A large number of researches have established the fact that substances which closely resemble the natural melanins can be produced by the action of

certain oxidizing enzymes on tyrosin and related aromatic compounds. Tyrosin is an important constituent of protein molecules and there is much reason to believe that tyrosin and related substances are the chromogens from which the natural melanins are formed.   Tyrosinase, an enzyme, which can oxidize tyrosin to dark substances resembling melanins, has been found very widely among animals, including the skins of mammals, as will be discussed later.

There have been many theories on the mode of origin of pigment in the cells.   Early observations indicated that melanin was directly extruded from the nucleus.   Recent studies by Hooker (1915) on *in vitro* cultures of mesenchyme and epithelium of the frog indicate that melanin granules form in the cytoplasm but at the point of known greatest efficiency of the nucleus as an oxidizing agent.   Thus, probably chromogen (tyrosin or derivatives) is in the cytoplasm, while oxidizing enzymes are given off by the nucleus.

The color white in the fur of mammals is due to the absence of pigment.   The theory of a white melanin seems effectively disproved (Gortner, 1910).   *A priori*, the presence or absence of pigment might be conceived as due either to a deficiency of chromogen or of enzyme. In line with the first view, Gortner (1911) found that the pattern in the elytra of potato beetles is due to a deficiency of chromogen.   Further, Cuénot (1903, 1904), in the first attempt to correlate the facts of Mendelian inheritance with the physiology of pigment, suggested provisionally that albinos lack the power of producing chromogen, while the different colors which he demonstrated could be transmitted through albinos depend on specific enzymes.   On the other hand, recent observations by Onslow (1915) demonstrate that absence of pigment in widely different cases in mammals depends on enzyme differences.   He found peroxidases in the skins of gray, black, blue, and brown rabbits, which produce a black pigment from tyrosin in the presence of hydrogen peroxide.   In the skins of albino rabbits and mice and in the white part of the Dutch pattern in rabbits, all recessive whites, he was unable to demonstrate a peroxidase, although there was nothing present which prevented the oxidation of tyrosin to a black pigment when tyrosinase was added.   In the white of the English rabbit, a dominant white, he did find an anti-tyrosinase.

Finally, there is strong genetic evidence that albinism in guinea-pigs is not due to absence of chromogen.   A diminution in quantity of chromogen should bring about the same diminution in quantity of all pigments, regardless of quality.   But in red-eyed guinea-pigs (which we may consider as incomplete albinos, as they have an allelomorph of albinism C_r) no yellow develops, leaving white areas where factors of group 2 determine yellow differentiation, but there may be nearly as much black as in normal guinea-pigs.   Indeed, in the albino guinea-pigs and Himalayan rabbits, there is no yellow, but some black.

The physical or chemical differences between the pigments of the different fur colors are not wholly clear. According to Onslow (1915) the pigments of black, brown, and yellow rabbits can not be distinguished, physically or chemically, when isolated. At first sight this seems hardly possible with such apparently different colors. A result thoroughly in line with this view, however, followed the matching of fur colors with Ridgway's charts, much to the writer's surprise at the time. Ridgway distinguishes 72 hues passing from red through orange, yellow, green, blue, and purple, back to red. The yellows, sepias, and browns of guinea-pigs and human brown and red hair all matched colors near hue 17, "orange yellow," in the classification. The differences depended merely on differing amounts of black and white. Bateson (1903), indeed, found that yellow pigment is dissolved from hair by potassium hydroxide very much more rapidly than brown pigment, which dissolved more rapidly than black. This, however, might be due merely to size or density of granules.

This apparent qualitative difference in pigments has been attributed to several causes: (1) to variations in the chromogen acted on by a given enzyme, (2) to interruptions at different stages in the process of oxidation of a given chromogen, (3) to specific enzymes which in each case can only produce a certain result once the action on the chromogen is begun.

Observations of Onslow indicate that for qualitative differences, as well as for the absence of pigment, enzyme and not chromogen differences are responsible. He could find no peroxidase in self yellows, a recessive variation. There must of course have been some peroxidase at some time to produce pigment at all. Perhaps the apparent absence indicates a very low degree of stability in the yellow-producing enzyme. Again, grays differ from blacks by a dominant factor which causes yellow to appear in ticking over the back but white to appear on the belly. Onslow found a tyrosinase inhibitor in the belly and compared the case with that of the dominant white of the English rabbit. As grays differ from self blacks by only one Mendelian factor, it would seem likely that all of the changes in appearance—dorsal yellow ticking, ventral white—are to be ascribed to one physiological cause. If black is absent from the belly because of an enzyme inhibitor, it would seem likely that black is replaced by yellow in the dorsal ticking by the presence, for a certain period in the development of a hair, of the same enzyme inhibitor, which, however, is in this case merely an inhibitor of the black-producing reaction, not of the yellow. Reasons for which yellow can appear on the back of rabbits, but not on the belly, when black is inhibited will be discussed later. Thus, a recessive yellow and a dominant yellow-pattern factor are both due to enzyme, not chromogen, differences.

The second hypothesis—that yellow, brown, and black are due to interruptions of the normal process of oxidation at different stages is difficult to reconcile satisfactorily with the genetic facts in guinea-pigs. If brown and black pigments pass through a yellow stage, identical with the final stage of the pigment in yellow guinea-pigs, any factor which inhibits the development of yellow must *a fortiori* inhibit the development of brown and black. We have seen that with factor C_r there is complete absence of yellow pigment, but nearly full development of brown and black. We find nearly the converse of this in the effect of factor p. When factor p is present, the development of brown and black is very greatly reduced without the slightest dilution of yellow. This indicates that neither is yellow a stage in the development of black nor black a stage in the development of yellow. The most satisfactory hypothesis is the third—that there are distinct enzymes which produce yellow and dark pigment.

There are a number of curious facts in connection with the albino series of factors in guinea-pigs which perhaps warrant further speculation. As has been mentioned, Onslow has shown that albinism is due to the absence of tyrosinase in the skin (and presumably the eye). It seems reasonable to suppose that the higher allelomorphs are quantitative variations in a factor which determines the power of producing tyrosinase. If this is so, we would expect to find that the different zygotic formulæ could be arranged in a linear series with respect to their effects on pigments of all sorts. Following are the series with respect to black pigment of eye and fur, and yellow of the fur. (See plates 1 and 2.)

Formula.	Black eye.	Black fur.	Yellow fur.
CC	Black....	Black..........	Red.
CC_d........	...Do....	.....Do........	Do.
CC_r........	...Do....	.....Do........	Do.
CC_a.......	...Do....	.....Do........	Do.
C_dC_d.......	...Do....	Dark sepia.....	Yellow.
C_dC_r.......	...Do....	.....Do........	Cream.
C_dC_a.......	...Do....	Light sepia.....	Do.
C_rC_r........	Red.....	Dark sepia.....	White.
C_rC_a.......	...Do....	Light sepia.....	Do.
C_aC_a.......	Pink.....	White (sooty)...	Do.

The yellow series and the less accurately known eye-color series can be arranged in the same sequence. There is the striking difference, however, that the level of no pigment production is much higher in yellow than eye color. The black of the fur agrees with eye color in the level at which pigmentation becomes evident—between C_aC_a and

C_rC_a—but the sequence can not be made to agree with either the eye-color or yellow series. C_dC_a is distinctly lighter than C_rC_r in black fur but distinctly more intense in eye color while, in yellow fur C_dC_a is above, C_rC_r below the threshold of any color. The effects could be explained by a complicated linkage hypothesis. We would need to suppose that there are separate series of allelomorphs acting on yellow, black of fur, and black of eye, respectively, and that C_r and C_a are complexes identical in the yellow-dilution factor, C_d and C_r identical in the black-fur-dilution factor and perhaps C and C_d in the black-eye-dilution factor. But an hypothesis according to which it is a mere accident that the factors which dilute yellow, black of fur, and black of eye are perfectly linked in inheritance can hardly be taken seriously. Another escape would be to suppose that our four factors, C_a, C_r, C_d, and C, are, indeed, variations of the same thing but not linear quantitative variations. However, it seems most satisfactory to the writer to attempt to explain the results on the basis of four quantitative gradations of one factor, which determines the amount of the basic color-producing enzyme, if it is in any way possible. Let us see what assumptions must be made to do this. First, it will be convenient to assume with Little (1913) that the basic color-producing enzyme (I) acting by itself on chromogen, produces yellow pigment. The addition of a second substance (II) makes it a black-producing enzyme (I-II). We will further assume that I is relatively unstable and must be produced above a certain rate (that determined by C_rC_r) in order to reach and oxidize the chromogen in the cytoplasm. United with II it becomes more stable and even produces some effect at the rate of production determined by C_aC_a. The next assumption is that above the threshold for yellow, I-II and the excess of I compete for the chromogen. As a result of partial displacement by the paler color, the intensity of black decreases just above the yellow threshold. C_dC_a seems paler (and somewhat browner) than C_rC_r. In the eye, no factor ever brings out a yellow color. There is perhaps never an excess of I here and the intensity of black follows the normal sequence.

Summarizing, the hypothesis to which consideration of the physiological and genetic seems to lead is as follows:

(1) There is a basic color-producing enzyme (I) which acting alone on chromogen produces a diffuse or finely granular pigment which appears yellow. It is relatively unstable. Intensity of production and absence or inhibition in parts of fur and eye are determined by the various factors of group 1—the albino series, "blue"-dilution factors, and recessive and dominant white-pattern factors.

(2) There is a second substance (II) which may unite with I to produce a more stable enzyme, which reacts with chromogen to produce a coarsely granular pigment which appears sepia, brown, or black. When II is present, I is stabilized to such an extent that pigment is

produced at a lower rate of production of I than is the case of I alone. Above the level at which I alone produces yellow, the two kinds of enzymes, yellow- and black-producing, compete with each other for chromogen, producing a mixture of black and yellow, the relative importance depending on the rate at which II is produced. Because of the competition the intensity of black shows two maxima as production increases—one just below the yellow threshold and the other at maximal production of I. Intensity of production or inhibition of II in patterns in the fur are determined by various factors (group 2) which produce self yellow, yellow spotting, agouti, etc.

(3) There is a third group of substances which, added to the dark-pigment-producing enzyme (II), affect the intensity of dark color produced but not the power of fixing chromogen in competition with the yellow-producing enzyme. They have no effect on the intensity of yellow. In this group are the brown factors of mice and guinea-pigs, and perhaps rabbits and dogs, the pink-eye factor of rats, mice, and guinea-pigs and the new red-eye factor of rats, i. e., the factors of group 3.

While based to a larger extent on the genetic facts in the albino series in guinea-pigs, the hypothesis explains many cases in other mammals in the sense that apparently complex variations are reduced to a single physiological cause.

In rabbits, single Mendelian factors produce some rather complex variations. A single factor changes a self black to the gray color with a yellow-ticked back but a pure white belly. Another variation changes a self black to a sooty yellow with a black belly. These variations combined in one animal give a white-bellied clear yellow. How can each of these apparently complex color changes be determined by a simple physiological change? Let us suppose that in *all* rabbits I is produced strongly on the back, but so feebly on the belly that it is below the yellow threshold, but not so feebly that black is greatly affected. Let us suppose that II is likewise more strongly produced on back than on belly. A factor which tends to produce an inhibitor of II is added. On the back II (the black-producing enzyme) is inhibited in only a portion of the development of the hair, leaving yellow ticking. On the belly all II is inhibited, leaving white. The result is a gray rabbit. The other factor causes a general slowing up in the production of II. On the back this enables the yellow-producing enzyme to predominate in competition and sooty yellow results. On the belly—below the yellow threshold—what little black-producing enzyme does develop has no competition and only black can result. We get a black-bellied sooty yellow. The combination pattern can only be a white-bellied yellow. In many other mammals color phases are found which can be explained as due either to variations in production of II or I. The red phase of the red fox has a white chest. The level of production of I is below the yellow threshold

but above the black threshold on the chest. Increase in production of II produces the silver phase, nearly self sepia in color, including the chest. The colors of the varying hare seem to be due to variations in production of I determined by environmental causes. The white winter pelage gives way in blotches to a white-ticked sepia; this gives way to yellow-ticked sepia as the intensity of production of the basic enzyme rises above the yellow threshold and in some varieties the full summer pelage is almost self red.

Many other cases could be given in which two color phases of an individual animal or the color patterns of closely allied varieties seem to differ in many respects and yet can be explained on the basis outlined as due to a single physiological change.

In the case of very complex color patterns, it is necessary to suppose that the power of producing the hypothetical enzymes I, II, or III may be distributed in quite complex patterns. But the hypothesis often gives a simple explanation for certain peculiarities in a pattern. In the tiger, the stripes on the back are quite intense yellow and black. The yellow stripes grow paler down the sides, becoming white on the lower sides and belly. The black stripes likewise grow lighter down the sides but at the point at which the yellow becomes white, the black stripes suddenly grow more intense, at least in some individuals, to become paler again on the belly. Again, on the legs, which are white on the inside, yellow on the outside, black stripes are visible on the white part, but either disappear completely or leave merely a streak of sooty red on the yellow part. All of this becomes intelligible if we assume that the basic enzyme (I) is produced at decreasing rates from back to belly and from outside to inside of leg, while the black-producing supplement (II) is distributed in vertical stripes (horizontal on the legs). Two parallel stripes give a remarkable reproduction of the variation in black and yellow in the albino series in guinea-pigs. We have the same change from black and intense yellow to sepia and cream, then to *darker* sepia and white, and finally light sepia and white, illustrating the different thresholds for the appearance of black and yellow and the reduction in intensity of black above the yellow threshold due to the entrance of competition at this point.

DISCUSSION OF EXPERIMENTS.

MATERIAL.

SYSTEMATIC POSITION.

Guinea-pigs belong to the family Caviidæ of the hystricomorph division of rodents. There are three living genera of Caviidæ: *Dolichotis* Desm., which contains the large Patagonian cavies; *Hydrochœrus* Brisson, to which belongs the capybara; and *Cavia* Pallas, containing the small cavies. Genus *Cavia* is divided into two subgenera, *Cavia* proper and *Cerodon* F. Cuv., distinguished most conspicuously by the greater complexity of the molars in the former. Seven living species are listed under *Cavia* proper by Trouessart (1904):

> *C. rufescens* Lund, a small dark Brazilian cavy with subspecies in Guiana and Argentina.
> *C. fulgida* Wagler, a Brazilian cavy probably closely allied to *rufescens* (Thomas, 1901).
> *C. aperea* Erxl., a large pale-colored Brazilian cavy.
> *C. azaræ* Wagner, a cavy of Paraguay probably closely allied to *aperea* (Thomas, 1901).
> *C. cutleri* Bennett, a small pale-colored cavy of Peru.
> *C. tschudii* Fitzinger, a large, richly colored cavy described from Ica, Peru.
> *C. porcellus* Linn., the tame guinea-pig, much larger than at least *rufescens* and *cutleri*.

DESCRIPTION OF STOCKS.

Four of these species are dealt with in the experiments to be described, viz, *Cavia rufescens*, *C. cutleri*, *C. porcellus*, and a type which is quite certainly that described as *C. tschudii*, although it is also quite certain that it is simply feral *porcellus*. Breeding experiments have been carried on with a fifth species, *C. aperea*, by Nehring (1894).

The *C. rufescens* stock was derived from 3 individuals received from Mr. Adolph Hempel, of Campinas, Brazil, in 1903. The history of this stock is fully described by Detlefsen (1914). When received by the writer, most of the stock consisted of hybrids containing only from $\frac{1}{16}$ to $\frac{1}{64}$ *rufescens* blood. There were a few $\frac{1}{8}$ and $\frac{1}{4}$ bloods and one $\frac{1}{2}$ blood, ♀ A68, which is still alive (August 1915) at the remarkable age of 8 years 1 month,[1] a good illustration of the vigor of the first-generation hybrids. All of the pure *rufescens* stock has died out. The *rufescens* hybrids have been crossed with nearly all of the guinea-pig stocks to be described, and most of the color varieties may be found among them. The ticked-bellied type of agouti has been found only among them and in pure *rufescens*. *C. rufescens* was not completely fertile with the guinea-pigs (Detlefsen, 1914). Detlefsen found that while the female hybrids were fertile, all of the male hybrids obtained were sterile. In the $\frac{1}{4}$ *rufescens*, derived by crossing the females with guinea-pigs, the males were again all sterile. Not until the $\frac{1}{8}$ bloods were obtained did

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[1] Died October 1915, aged 8 years, 3 months.—*W. E. C.*

a few fertile males appear. The percentage of fertile males gradually increased in later generations.

The *Cavia cutleri* stock was derived from animals captured by Professor Castle in Peru in 1911. Like *C. rufescens*, these are much smaller than the guinea-pig. All show the agouti pattern. The color is described on page 59. Unlike *C. rufescens*, *C. cutleri* breeds freely in captivity and crosses readily with the guinea-pig. The male and female hybrids are fertile.

The Ica stock of guinea-pigs was derived from 3 guinea-pigs which were obtained by Castle near Ica, Peru, in 1911. They were as large as or larger than average guinea-pigs, and of a rich golden agouti color, very different from *C. cutleri*. Two independent color variations appeared at once in the pure stock, viz, black (aa) and red-eye (C_rC_r). Such variations are very uncommon among wild species of animals; *e. g.*, none has occurred within the pure *rufescens* or *cutleri* stocks. Both of these variations are found in domesticated guinea-pigs in Peru (Arequipa stock). From the description of *Cavia tschudii*, quoted in Waterhouse (1848) under the name *C. cutleri* Tschudi, it seems clear that our Ica stock is the same as the former, which was likewise described from Ica. In view, however, of the size, color, and possession of recessive color varieties found among tame guinea-pigs of Peru, there can be little doubt that they are feral *porcellus*.

The Arequipa stock comes from a pair of guinea-pigs brought from Arequipa, Peru, by Castle in 1911. He obtained them from Indians who had them under domestication. Owing to the early death of the only female, no pure stock could be developed, but numerous descendants have been derived from the original male 1002, a sepia-cream agouti with white and cream spots, demonstrated to be of constitution $EEAaBBPpC_dC_r$, and from a son of the original pair, male 1007, a yellow agouti with white and yellow spots, demonstrated to be of constitution $EeAaBBPPC_dC_d$. These were crossed mainly with the 4-toe and BW stocks, which are described below. For a full discussion of the origin and nature of the pure *cutleri*, Ica, and Arequipa stocks, see Part I.

The Lima stock comes from 8 guinea-pigs obtained from Indians near Lima, Peru, by Professor Brues in 1913. These guinea-pigs and their descendants have only recently been crossed with other stocks. There have been no agoutis in this stock. The pink-eye and yellow variations, as well as white spotting (but not yellow spotting), have occurred in this stock. A pink-eyed red, the lowest recessive, of this stock is of constitution eeaaBBppCC. There were both rough-furred and smooth-furred individuals in the original stock.

The following stocks come from guinea-pigs obtained from fanciers by Professor Castle and have been maintained for several years at the Bussey Institution.

BB stock.—A stock consisting exclusively of very intense blacks. No red or white spotting has been observed among them. Unfortunately it is a stock of low fertility, and could not be used much to advantage.

BW stock.—This stock has for years consisted exclusively of very intense blacks and very sooty albinos. The blacks occasionally show a few red hairs or a small red patch. This has been an extremely useful stock, among other things, furnishing albinos known to be genetically identical with blacks, except for the albino factor. (Race B of Part I.)

Four-toe stock.—This is a much-inbred stock, practically all the individuals of which show four good toes on the hind feet instead of the normal three. This stock was developed by selection and inbreeding by Professor Castle (Castle, 1906). Most of the individuals are a dull black with dull red blotching and brindling and often with white spots. Albinos appear quite frequently and reds much more rarely.

TABLE 34.—*Genetic formulæ of stocks.*

Stock.	Color. Mendelian.					Color. Unanalyzed.		Roughness. Mendelian.	Roughness. Unanalyzed.	
Cavia cutleri	E	A	B	P	C	....	Σint −	r S	Σ −	....
Cavia rufescens	E	A′	B	P	C	....	......	r S	Σ −	....
Ica	E	A,a	B	P	C,C_r	(ΣwΣy)	Σint +	r S	....	ΣR
Arequipa	E,e	A,a	B	P,p	C,C_d,C_r	ΣwΣy	Σint +	R,r s	....	ΣR
Lima	E,e	a	B	P,p	C	Σw	......	R,r (S)s	Σ −	....
BB	E	a	B	P	C	....	Σint +	r s	Σ −	....
BW	E	a	B	P	C,C_a	(Σy)	Σint +	r s	....	ΣR
4-toe	E(e)	a	B	P	C,C_a	ΣwΣy	Σint −	R,r s	Σ +	....
Tricolor	E	a	B,b	P	C	ΣwΣy	......	R,r S,s	....	....
Sepia + cream	E,e	a	B	P	C_d,C_a	(ΣwΣy)	Σint −	r s	....	....
Brown-eyed cream	e	a	b	P	C_d,C_a	....	Σint −	r s	....	....
C. rufescens hybrids	E,e	A,A′,aB,b	P		C,C_d,C_r,C_a	ΣwΣy	Σint ±	R,r S,s	....	....

In the tricolor stock the fur is typically a patchwork of red, white, and black. Full-roughs, partial-roughs, and smooths occur among them. The writer has used many guinea-pigs of very mongrel ancestry, which, however, owe their partial rough coat to this stock.

The sepia-and-cream and *brown-eyed cream* stocks have been selected for years for extreme dilution. The former stock consists exclusively of sepias, black-eyed yellows and creams, and albinos. The latter consists exclusively of brown-eyed yellows and creams and albinos. (Race C of Part I.) In the tables, these together are called dilute-selection stock.

Table 34 shows the Mendelian factors affecting color and roughness of fur which occur in each stock. Unanalyzed hereditary conditions which affect color and roughness are also included, prefixed by the symbol Σ. Σw and Σy, as has already been stated, mean hereditary

white and yellow spotting respectively. Σ int+ and Σ int− mean hereditary constitutions which intensify or dilute, respectively, the color associated with a given array of Mendelian factors. $\Sigma +$ and $\Sigma -$ in the rough column have a similar meaning with respect to the rough character. ΣR means the presence of roughness of a different kind from that analyzed. Where a factor occurs only rarely in a stock, it is inclosed in parentheses.

PROBLEMS.

The inheritance of the discontinuous color variations which are known in guinea-pigs has been solved by previous work. After each factor variation from the wild type (*Cavia cutleri*) in the definitions of the factors the principal papers on the subject are given. The writer has been concerned mainly with an analysis of inheritance in the continuous series of variations by which each of the intense colors—red, brown, and black—grade into dilute colors and ultimately white. A second group of problems concerns the variations in the amount of yellow ticking in agoutis. The writer has worked with the agouti patterns of *Cavia cutleri*, *C. rufescens* hybrids, and tame guinea-pigs. The inheritance of variations in the rough coat occasionally found in guinea-pigs is discussed in a later section.

INHERITANCE OF DILUTION.

THE RED-EYE FACTOR.

The experiments with dilution have become closely associated with experiments with certain imported South American stocks (Ica, Arequipa) which are discussed in detail in Part I. A number of hitherto unknown color varieties appeared in these stocks, the inheritance of which could be explained by assuming the existence of a new allelomorph of albinism intermediate in effect and dominance between albinism and its normal allelomorph. More specifically, this new factor is characterized by the production of red eyes, slight dilution of black in the fur, and complete inhibition of yellow pigment development.

The writer has used animals of both the Ica and Arequipa stocks in experiments, with results in full agreement with those given in Part I. Crosses 20–1 and 21 to 25 involve red-eye (from Ica stock) without also involving dilution. In cross 20–1 a pure Ica male, a red-eyed agouti, is crossed with intense guinea-pigs, giving young all intense. This illustrates the dominance of intensity over red-eye.

In cross 21 a pure Ica intense male crossed with albinos of intense stock gives both intense and red-eye young. The Ica male no doubt was heterozygous for red-eye, but the albinos could not possibly transmit red-eye, as they come from a stock in which red-eye has never appeared. This illustrates the apparent reversal of dominance of red-eye whenever albinism is introduced into a cross. A further illustration is given in cross 23, in which red-eye by albino of intense

stock gives red-eyes, but no intense young. In cross 25, red-eyes crossed with albinos from various sources give no intense young, but only red-eyes and albinos. One possible explanation of these results would be the supposition that red-eye becomes dominant over its normal allelomorph in the presence of heterozygous albinism. In this case intense young should appear when such heterozygous red-eyes are crossed together; but, as is shown in cross 24, none such appears. Here red-eyes from cross 21, mated *inter se*, gave 17 red-eyes, 6 albinos, no intense. Numerous results of this kind have made it clear that intensity can never be recovered in any generation after a cross of red-eye with albino. This means that neither red-eye nor albino can transmit the normal allelomorph of the other. Now, the one thing which a recessive variation, of necessity, can not transmit, is its own normal allelomorph. Therefore the normal allelomorphs of red-eye and albino must be identical.

This does not yet demonstrate that albinism, red-eye, and intensity form a series of three allelomorphs. There is still the possibility that red-eye and albinism involve the same recessive allelomorph (C_a) of normal color (C), but differ by an independent modifying factor. Symbolically we could suppose albinos to be C_aC_arr, red-eyes to be C_aC_aRR (or C_aC_aRr), intense guinea-pigs of ordinary stocks to be CCrr (or CC_arr), and intense guinea-pigs of Ica stock to be CCRR (or CC_aRR). We must suppose the Ica stock to be homozygous for the modifier R, to account for the absence of albinos. R must be a unit factor to account for the simple 3 to 1 ratio in cross 24. This hypothesis fits all of the facts given so far. The critical test of its truth is the possibility (as it turns out, impossibility) of producing intense animals (CC_aRr) which will give both red-eyes and albinos when crossed with albinos. If intensity, red-eye, and albinism are triple allelomorphs, it should be impossible to obtain such animals. Crosses 21 and 22 are interesting as furnishing just this test. Cross 21 may be represented symbolically as follows, according to the two hypotheses:

> *Albino* (BW) × *intense* (Ica) = 9 *intense* + 4 *red-eye.*
> (1) C_aC_arr × CC_aRR = CC_aRr C_aC_aRr.
> (2) C_aC_a × CCr = CC_a CrC_a.

In either case the F_1 red-eyes crossed *inter se* should give 3 red-eyes to 1 albino. The result obtained in cross 24 (17 red-eyes to 6 albinos) is in nearly perfect agreement. But the cross of F_1 intense with albinos gives very different results under the two hypotheses (cross 22):

> *Albino*   × *intense* (F_1) = 16 *intense*   + (0 *red-eye*) + 25 *albinos.*
> (1) C_aC_arr × CC_aRr = CC_aRr + CC_arr + C_aC_aRr + C_aC_arr.
> (2) C_aC_a × CC_a = CC_a + C_aC_a.

The complete absence of red-eyes among the 41 young, as well as the excess of albinos where an excess of intense is expected, thoroughly eliminates the first hypothesis. The results agree reasonably well with

the hypothesis of triple allelomorphs, which we have found to agree with the results of all the other crosses. The only possibility which has not been eliminated is a linkage so close as to simulate a system of triple allelomorphs. Unless exceptions occur which require it, such an hypothesis need not be considered.

Thus the data obtained by the writer are not only in harmony with the theory that albinism, red-eye, and intensity form a series of triple allelomorphs, but can be explained on no other basis, barring the possibility just noted.

<center>DILUTION.</center>

Such color varieties as agouti, black, brown, yellow, etc., are sharply distinct from each other. They segregate from crosses without producing intergrades and in unforced agreement with Mendelian expectation. In contrast with these discontinuous variations are the continuous variations in the intensity of color of each main color variety. Thus, among the yellows, there are all gradations from a pale cream to an intense red. Among the agoutis, there are the pale silver agoutis, the intense golden agoutis, and the intermediate yellow agoutis. There are all grades of dilute blacks known to the fanciers as blues, for which term, as has been explained, sepia is substituted in this paper. Finally, there are all grades of dilute browns and cinnamons. (See plates 1 and 2.)

The existence of these dilute types was noted by Castle (1905) and Sollas (1909), both of whom also recognized that dilution could be transferred from one series to another, e. g., from creams to blacks, giving rise to sepias. They did not, however, suggest any factorial explanation, finding the results of crosses highly irregular. Detlefsen (1914) considered dilution to be recessive, but found the inheritance of dilution very irregular among C. rufescens hybrids. He obtained dilutes in F_1 after crossing dilute hybrids with a race of guinea-pigs (brindle or 4-toe), among which dilution had never occurred and which therefore should not carry it as a recessive. It may be remarked in passing that the 4-toe race does contain albinism, which, with present knowledge, satisfactorily accounts for these F_1 dilutes.

Thus the difficulties in the way of an understanding of the heredity of dilution have been due (1) to the intergrading of dilute with intense; (2) to data which seemed to indicate that dilution could be due neither to a recessive nor to a dominant unit factor, without complications. Cross 39 gives many examples in which intense by intense has given very dilute young, which seems to indicate that dilution must be recessive if simple Mendelian at all. On the other hand, such cases as that given by Detlefsen are difficult to interpret on this basis. Further, dilute by dilute has often given young much more intense than either parent. Thus, in cross 42–8, we have two medium sepias producing a black. In cross 37 are many cases in which cream by cream

has produced yellow.   Apparently intense by intense may give any intensity whatever, and almost the same can be said of dilute by dilute.

Amid this confusion, however, one cross has been found which consistently gives a very definite, although unexpected, result.   It is found that a dilute crossed with an albino, even of intense stock, never gives intense young, but only well-defined dilutes and albinos.   There are only a few possible ways in which this result can be explained and, from the results of other crosses, all but one of these explanations have been definitely eliminated, namely, that dilution is an allelomorph of albinism.   An allelomorph of albinism was already known to be responsible for the red-eyed condition in certain South American stocks (Castle, 1914a).   It could now be shown that albinism, red-eye, dilution, and intensity are due to a series of four allelomorphs with dominance in the order of increasing pigmentation.   A preliminary account of this demonstration has been given in a previous paper (Wright, 1915).   In the present paper the demonstration is given in more detail and further steps are taken in the analysis of the variations.

THE DILUTION FACTOR.

The dilute varieties have some resemblance to the red-eyed varieties. The fact that red-eye is due to an allelomorph of albinism suggested that dilution might also be due to a member of the same series of allelomorphs.   A stock was chosen which was known to carry no dilution. This was the BW stock, which for years has consisted exclusively of the most intense blacks and sooty albinos.   The following crosses were designed to eliminate the hypothesis of allelomorphism if incorrect:

(1) Albinos from intense stock were crossed with dilutes:
$$C_aC_aII \times CCii = CC_aIi.$$
(2) Albinos from dilute stock were crossed with blacks of intense stock:
$$C_aC_aii \times CCII = CC_aIi.$$

If intensity and dilution form a pair of allelomorphs (I, i) which segregate independently of the pair color and albinism (C, C_a), as is the case in mice and rabbits, these two crosses *must* give identical results. In each case, color is introduced by one parent, albinism by the other; intensity by one parent, dilution by the other.   In fact, identical results should be obtained regardless of whether dilution is due to a unit factor or to multiple factors, or even whether its inheritance is Mendelian or not, provided only that it is inherited independently of albinism. Crosses 16 and 17 and table 35 give the actual results.   All cases are included, which involve an intense stock known to carry no dilution.

Among those called dilute below (among the young), none was more intense than $sepia_2$ or $yellow_4$.   Among the intense, none was more dilute than a dull black comparable in grade but not in color with $sepia_2$, or a red in very few if any cases as dilute as $yellow_2$.   There was therefore no difficulty in drawing a natural line between intense and dilute in these crosses.

It is evident that the two sets of crosses give consistently different results. This difference demonstrates that dilution does not segregate independently of albinism.

An even more striking result follows from a portion of the above data. F_1 dilutes, one of whose parents was of intense stock, were back-crossed with albinos of intense stock. They gave 9 dilute, 20 albino young, no intense, although these young were at least three-quarters of intense stock. On the other hand, F_1 intense, one of whose parents was an albino of dilute stock, were back-crossed with albinos of dilute stock. They gave 5 intense, 7 albinos, no dilutes, although these young were at least three-quarters of dilute stock. It is clear that the hereditary difference between a dilute and an intense can not be transmitted through an albino.

TABLE 35.

	Intense.	Dilute.	Red-eyed.	White.
♂ albino (intense stock) ✕ ♀ dilute...............	..	56	5	39
♀ albino (intense stock) ✕ ♂ dilute...............	..	29	10	21
Total......................................	..	85	15	60
♂ albino (dilute stock) ✕ ♀ intense (intense stock)..	47	..	..	10
♀ albino (dilute stock) ✕ ♂ intense (intense stock)..	9	..	..	2
	56	..	..	12

It was emphasized above that all the intense animals used in cross **17** came from stocks which have never given dilutes. This was necessary because in other crosses (18, 34, 41) intense by albino has given many dilute young. No such precaution was taken with the dilutes used in cross 16. Any available dilutes were used regardless of ancestry. In fact, 11 of them, with 38 young, had one or both parents intense. In none of the other crosses in which dilute has been crossed with albino (19, 27, 38, 44) has any intense young appeared. Thus in crosses with albinos an intense may transmit dilution, but a dilute never transmits intensity. From these crosses it seems clear that intensity is dominant over dilution. Other crosses on the whole bear this out. The apparent exceptions will be ignored for the present but discussed later.

We have reached the definite conclusion that dilute by albino can never give intense, regardless of ancestry on either side. Since the only thing which a variety of necessity can not transmit is a dominant allelomorph of its essential factor, it follows that dilution and albinism must have the same dominant allelomorph, which we will call intensity.

There are only a few hypotheses which will satisfy this condition. We already know two recessive allelomorphs of intensity, viz, red-eye and albinism. It is conceivable that dilution may be due to the cooperation of an independent factor (or factors) with one or more of the known combinations C_rC_r, C_rC_a, and C_aC_a. If this is not the case,

dilution must be due to a new allelomorph in the albino series, let us say C_d. A modifying factor which shows partial coupling would give intermediate results.

(1) Since dilution and red-eye show considerable resemblance, it would be a plausible hypothesis to assume that they are due to the same allelomorph in the albino series (C_r) but differ by an independent modifying factor (D). With this hypothesis, all stocks used (except the Ica and Arequipa) must needs be homozygous for the modifier in order that no red-eyes should appear. Dilutes would be C_rC_rDD or C_rC_aDD albinos C_aC_aDD in these stocks. Thus albinos of these stocks should transmit the modifier and in crosses with red-eyes (C_rC_rdd) should produce diluted at least in F_2. But in crosses 23 and 25, red-eyes mated with such albinos have given no dilutes, nor have dilutes appeared in F_2 in cross 24, among 23 young. Thus an albino can not transmit the hereditary difference between a dilute and a red-eye and the hypothesis is untenable.

(2) Next to be considered is the hypothesis that there is a modifier which converts into a dilute an animal which would otherwise be an albino. Diluted of ordinary stock would be C_aC_aDD or C_aC_aDd. In cross 20, dilutes of ordinary stock crossed with a pure Ica male No. 724, a homozygous red-eye (C_rC_rdd), produced 5 dilute young which must be of formula C_rC_aDd. This shows that if the hypothesis is to stand at all, it must be extended, so that the factor which converts an albino into a dilute also converts a red-eye into a dilute. The fact that a dilute may transmit red-eye (crosses 19 and 27) is further evidence that this extension is necessary. In this form most of the results can be explained satisfactorily.

(3) The only other hypothesis which remains is that dilution is due to a new allelomorph in the albino series making a series of four—C, C_d, C_r, and C_a. The results cited above (crosses 20, 19, and 27) make it evident that dilution is dominant over red-eye. The meaning of a series of four allelomorphs can be made clear by considering all of the possible zygotic formulæ. Every zygote must have two representatives from the series, but never more than two. Intense guinea-pigs may be homozygous (CC), or carry dilution (CC_d), or red-eye (CC_r), or albinism (CC_a), but can never transmit more than one of the recessive conditions. Diluted may be homozygous (C_dC_d) or carry red-eye (C_dC_r) or albinism (C_dC_a), never both. Red-eyes may be homozygous (C_rC_r) or carry albinism (C_rC_a), while albinos can only be homozygous (C_aC_a) and can never transmit any of the higher conditions.

The critical test between this hypothesis of four allelomorphs and the preceding one (that dilute is a modified red-eye or albino), lies in the possibility or impossibility of producing animals which in crosses with albinos will transmit more than one recessive condition. If an intense animal can be obtained which transmits both dilution and red-eye

(CC_rDd) or dilution and albinism (CC_aDd), or if a dilute can be obtained which transmits both red-eye and albinism (C_rC_aDd), the hypothesis of modifiers must be adopted. But all attempts to obtain these double heterozygotes have failed. All of the results substantiate the hypothesis of quadruple allelomorphs.

Arequipa male No. 1007 was of formula C_rC_rDD or C_dC_d, depending on the hypothesis chosen (see crosses 28 to 34). He was crossed with intense guinea-pigs of BW or 4-toe stock, known to transmit no dilution $(CC_add$ or $CC_a)$. The intense young could only be CC_rDd or CC_d under the two hypotheses. Five of them were crossed with albinos and gave 13 intense, 20 dilute young, no others (cross 34). Expectation on the hypothesis of a modifier is 16 intense, 8 dilute, 8 red-eye. On the hypothesis of allelomorphs it is 16 intense to 16 dilute. Both the excess of dilutes and the absence of red-eyes point conclusively to the latter.

In cross 18, intense guinea-pigs, each of which had a dilute parent known to transmit albinism and with no Ica or Arequipa blood, are crossed with albinos or red-eyes. Under the modifier hypothesis we would expect about half of them to be CC_aDd. Under the allelomorph hypothesis, they should be CC_d or CC_a. As it turned out, there were 6 which gave only intense and dilute (30 intense, 35 dilute) and 8 which gave no dilute young (57 intense to 61 red-eye or albino). Thus there was no intense which had dilute young and also red-eyes or albinos. This result distinctly favors the hypothesis of allelomorphs.

In crosses 19 and 27 dilutes, each from the cross of a red-eye with a stock guinea-pig free from South American ancestry, are crossed with albinos. Under the modifier hypothesis, those which transmit red-eye at all are necessarily C_rC_aDd, for they must be $C_{ra}C_{ra}D$ in order to appear dilute; they could get C_a, but not C_r, from the stock guinea-pig parent, and they would necessarily get d from the red-eye parent. Under the allelomorph hypothesis, they should be C_dC_r, the rest C_dC_a; 9 gave only dilutes and red-eyes (18 dilutes, 24 red-eyes); 9 others gave only dilutes and albinos (20 dilutes, 16 albinos). There were 3 which had had only 8 dilute young when tabulated. The fact that none of the 9 which had red-eye young also had albinos among 42 young gives a third body of evidence pointing toward the allelomorph hypothesis.

These results make it reasonably certain that the allelomorph hypothesis is correct. The only other possibility would involve coupling so close as to simulate multiple allelomorphs. The hypothesis of allelomorphs has been reached by a method of elimination. It remains to show that all of the data are in harmony with it. In the next section, definite conclusions are reached as to the inheritance of variations in intensity and dilution which make it possible to distinguish intense animals from dilute in all but very exceptional cases.

INHERITANCE IN GUINEA-PIGS.

The following table gives a summary of the data bearing on the inheritance of the albino series of allelomorphs based on these conclusions. It will be noticed that animals of every possible formula have been tested by crosses with albinos, the lowest recessives. No attempt has been made to make all other possible crosses, and several (especially

TABLE 36.—*Summary of albino series crosses (crosses 16 to 44).*

Parents.	Formulæ.		Int.	Dil.	R.E.	W.	From crosses—
Intense × albino.......	CC	$\times$ C_aC_a...	40	....	....	....	17a, b.
	CC_d	C_aC_a...	31	36	....	....?	18b, 34, 41
	CC_r	C_aC_a...	9	....	4	....	21
	CC_a	C_aC_a...	64	....	....	71	17c, 17d, 18c, 22
Dilute × albino........	$C_dC_d\times$	C_aC_a...	....	26	....	....	16a, 38a, 44
	C_dC_r	C_aC_a...	....	18	24	....	19, 27
	C_dC_a	C_aC_a...	....	98	....	79	16b, 16c, 19, 27, 33, 38b, 44
Red-eye × albino.......	$C_rC_r\times$	C_aC_a...	....	....	30	....	25
	C_rC_a	C_aC_a...	....	....	6	3	23, 25
Albino × albino........	$C_aC_a\times$	C_aC_a...	....	....	....	×	Long established.
Intense × red-eye......	CC	$\times \begin{cases} C_rC_r \\ C_rC_a \end{cases}$..	9	....	....	....	20
	CC_d	$\begin{cases} C_rC_r \\ C_rC_a \end{cases}$..	28	31	....	....	18a, 20
	CC_a	$\begin{cases} C_rC_r \\ C_rC_a \end{cases}$..	25	....	20	7	18c
Dilute × red-eye.......	$C_dC_d\times$	$\begin{cases} C_rC_r \\ C_rC_a \end{cases}$..	....	15	....	....	20, 26, 43
	C_dC_a	C_rC_r...	....	1	1	....	20
		C_rC_a...	....	13	5	8	26, 43
Red-eye × red-eye......	C_rC_a	$\times$ C_rC_a...	....	....	17	6	24
Intense × dilute........	CC	$\times$ C_dC_d..	14	....	....	....	28
	CC	C_dC_a..	12	....	....	....	35
	CC_d	C_dC_d..	10	7	....	....	29, 40a
	CC_d	C_dC_a...	32	40	....	....	32, 36, 40a
	CC_a	C_dC_d..	12	10	....	....	28, 40a
	CC_a	C_dC_a..	28	22	....	15	36, 40b
Dilute × dilute.........	$C_dC_d\times$	C_dC_a...	....	15	....	....	30, 37, 42
	C_dC_a	C_dC_a...	....	82	....	24	37, 42
Intense × intense.......	CC_d	$\times$ CC_d...	57	19	....	....	31, 39
	CC_d	CC_a...	75	35	....	....	39
	CC	CC....	×	....	....	....	See rough and Lima crosses.

ones involving red-eye) have not yet been made by the writer. The last column refers to the crosses tabulated at the end of the paper. The ratios expected are obvious from the nature of the matings, except that 39 to 44 were not random crosses of their kind. The appearance of recessive young was used as a criterion of the nature of the parents in these cases. This causes an excess of recessives to be expected.

INHERITANCE OF MINOR VARIATIONS IN INTENSITY.

METHODS AND ACCURACY OF GRADING.

The method of grading has been described on page 60. Every guinea-pig which showed dilute black or yellow in the fur was compared with standard samples of hair within a week of birth. These samples were $black_0$, $sepia_3$, $sepia_6$, and $sepia_9$, in the black series, and red_0, $yellow_3$, and $cream_6$ in the yellow series. Intermediate grades were given by estimate. Grades were taken later in life in many cases in order to determine the relation of age to intensity of pigmentation.

In interpreting the results, it is important to know the accuracy with which the grading could be done and the difficulties met. In some cases the back and belly are fairly uniform in intensity, but usually the belly is considerably the lighter. Tufts of hair for grading have always been taken as near the middle of the back as possible.

In some cases the hair is of fairly uniform intensity from base to tip. In most cases, however, the base is very much lighter than the tip. The color at the tip has been used in grading, although extreme variations in the intensity at the base have also been noted. The color at the tip has most to do with the general appearance of the animal.

The attempt has been made to get both a yellow and a sepia grade for every animal, so that the correlation between the intensities in these series could be determined. This is easy in the sepia and yellow-spotted animals, but in agoutis (where the yellow band of the agouti pattern displaces the sepia near the tip of the hair) determination of the intensity of sepia has not been so satisfactory. Several independent determinations have been taken in many of these cases. In most cases the same grade was assigned the second time and rarely did the second grade differ from the first by more than one point.

VARIATIONS IN INTENSE GUINEA-PIGS AND ALBINOS.

Before discussing the inheritance of variations among dilutes, it will be well to note briefly the range of variation among guinea-pigs which have the intensity factors (CP). In the BW race the blacks are a very intense black. The base of the hair is only slightly lighter than the tip. In other races, especially the 4-toe stock, the tip of the hair is a dull slaty black and the base a very dull color, often with less pigment than many typical dilutes. The animals have a dull streaky black appearance very different usually from the uniform dark sepia of the darker dilutes. This dull color is not associated with heterozygous albinism. Male M330 was undoubtedly homozygous (CC), having had 9 intense young by albino females and no others; yet he was one of the dullest blacks in stock. On the other hand, nearly all of the intense blacks of the BW race are heterozygous for albinism.

This dull black can not be due to an allelomorph of albinism between intensity (C) and dilution (C_d), since it is a condition which can be transmitted by albinos. Indeed, the albinos themselves of the BW and 4-toe stocks differ conspicuously in appearance. The BW albinos have jet black ears and feet, dark smudges on the nose, and usually some sootiness on the back. The 4-toe and most other albinos (at the Bussey Institution) have very much less black on ears, nose, and feet, and the rest of the fur is pure white.

There are parallel variations in the intensity of red in these stocks. The occasional red spots in the BW race are of a very intense red (standard red_0). In the 4-toe and other dull stocks the red is considerably less intense, especially at the base of the hair. The most dilute grade found in tame guinea-pigs known to have factor C is $yellow_2$ (D12 cross 35–1).

The wild *Cavia cutleri* is quite light in color. The black of the fur is a dull slaty color, more like the dull black of the 4-toes than any other color in tame guinea-pigs. The yellow on the back is about $yellow_3$, on the belly $cream_6$. In spite of the resemblance to tame yellow agoutis, *Cavia cutleri* has the intensity and not the dilution factor. When crossed with animals of the BW race, whether blacks or albinos, the young are intermediate in intensity and would be called intense (Part I). Crossed with black animals of the 4-toe race, the young are but little more intense than *Cavia cutleri*. (See plate 3.)

Summing up: All variations may be found among intense guinea-pigs, from uniform $black_0$ to a dull slaty $black_2$ and from red_0 to $yellow_2$. In the dull grades the hair is especially dull at the base. These variations are hereditary, but have not been analyzed. The hereditary factors for these variations in intense guinea-pigs are responsible for visible differences among albinos. It is to be expected, as indeed is the case, that variations will be found among dilutes, for which these same unanalyzed hereditary differences of different stocks are responsible. Finally, the residual heredity of all tame guinea-pigs has more intensifying effect than that of *Cavia cutleri*, the wild species.

MULTIPLE ALLELOMORPHS.

The presence of at least four allelomorphs in the albino series suggests the hypothesis that other allelomorphs in the series may be responsible for the intermediate grades in intensity. It is a tempting hypothesis to suppose that the continuous series of variations is correlated with a continuous series of allelomorphs, such that each grade of intensity is dominant over all lower grades. If this were the case a stock of dilutes, in which all derive their dilution from a single gamete of one animal, should be fairly constant in their degree of dilution. Again, the cross of dilute by dilute should never give young more intense than the darker parent.

However, both of these tests fail. No single gamete stock of dilutes has been found which will not give the entire range of variation when tested. Thus, male D30 red$_0$, an intense which carried dilution as a recessive (CC$_d$), was crossed with red-eyes. His dilute young must all owe their dilution to the same single gamete. They ranged from D340 black$_1$ to D152 sepia$_5$. Yellows which owe their dilution to this same single gamete (derived from male 00 cream$_6$ C$_d$C$_a$, the father of D30) range from D391 yellow$_2$ to 00 cream$_6$. Dilution from a single gamete of A674 sepia$_6$ (C$_d$C$_a$) has given rise to D652 black$_1$ and M306 sepia$_7$, D409 yellow$_3$, and M199 cream$_7$. This last case involves no admixture of South American blood. Inspection of the tables will yield many similar cases. Evidently dilution from a single gamete may appear in dilutes of any grade of intensity. The extreme variations may occur within a single litter (offspring of D30). Again, many examples can be given in which the offspring are much darker than either parent. D652 black$_1$ was the offspring of D215 sepia$_3$ and D106 sepia$_4$. In cross 37 there are 6 cases in which cream$_6$ × cream$_6$ has produced yellow$_3$, with other less extreme cases of this kind. These results do not demonstrate that no more than four allelomorphs in the albino series are present in our stock. They do show that there are other causes producing variation of much more importance than any other allelomorphs which may be present.

THE RELATIONS OF IMPERFECT DOMINANCE, STOCK, AND AGE TO GRADES OF INTENSITY.

In tables 37 and 38, and diagrammatically in figure 5 and figure 6, all records of grades of dilution at birth are analyzed with respect to genetic constitution and stock. All of those whose genetic constitution was known with complete or nearly complete certainty, either from parentage or from offspring, are put after the proper formula, C$_d$C$_d$, C$_d$C$_r$, etc. All from litters containing two classes are listed separately with the numerical expectation of the classes as (20 C$_d$C$_d$: 32 C$_d$C$_a$), etc. Those in the litters whose formulæ were later determined by a test mating are given below in parentheses. These tested individuals are included both among those of certain constitution and in the litters containing two classes. No very close analysis of the influence of stock was possible from the data obtained. However, the following stocks were recognized:

Dil., Dilute selection stock.
Misc., Miscellaneous stocks with but little BW blood and no Ica or Arequipa blood. These contained much dilute selection and 4-toe blood and some *C. rufescens* ancestry.
½BW, F$_1$ from the cross of miscellaneous with BW stock.
¾BW, Back-cross of ½BW with BW stock.
S. Am., All animals with Ica or Arequipa blood, in most cases about ¼ South American, ¼ BW, and ½ miscellaneous, but including pure Ica, Ica × BW, etc.

In each array of animals of known constitution and stock the number of animals involved, the mean grade of dilution, and the standard deviation of the frequency polygon are given. It will be noticed that the standard deviations decrease as the analysis is made closer. For
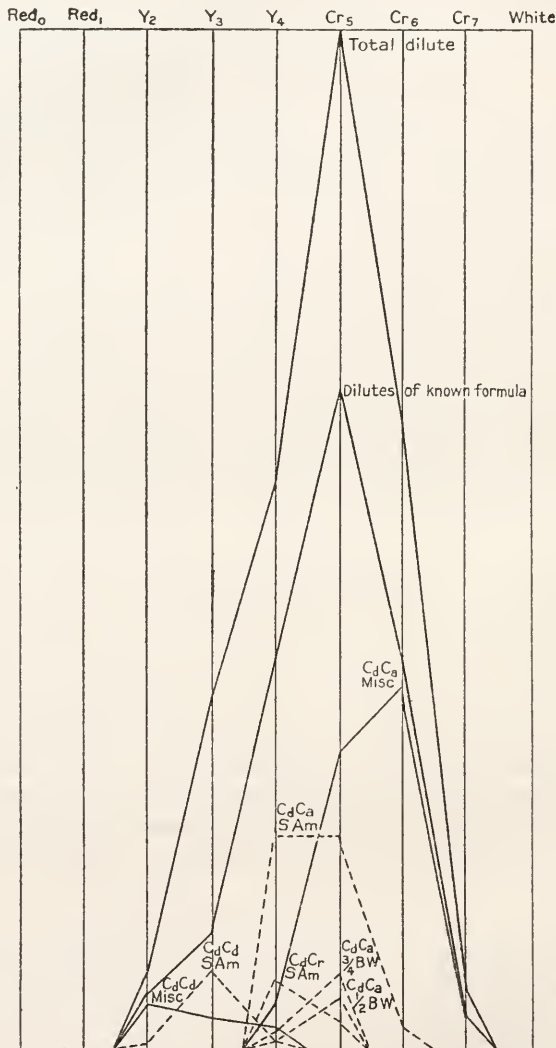
FIG. 5.—Variations in intensity of yellow. Formula and stock printed near mode of each distribution.

example, the standard deviation for all dilute blacks is 1.53, for dilute blacks of formula C_dC_a is 1.13, and for those of formula C_dC_a and of South American stock is 1.02. The corresponding numbers for dilute yellows are 1.10, 0.76, and 0.59, respectively.

In tables 39 and 40 are given the mean grades at birth and when more than 4 months old for all guinea-pigs which were graded these two times. These data are arranged by constitution and stock. In most cases the mean grade at birth of the sample graded twice agrees well with the mean grade at birth of the whole array of the same constitution and stock.
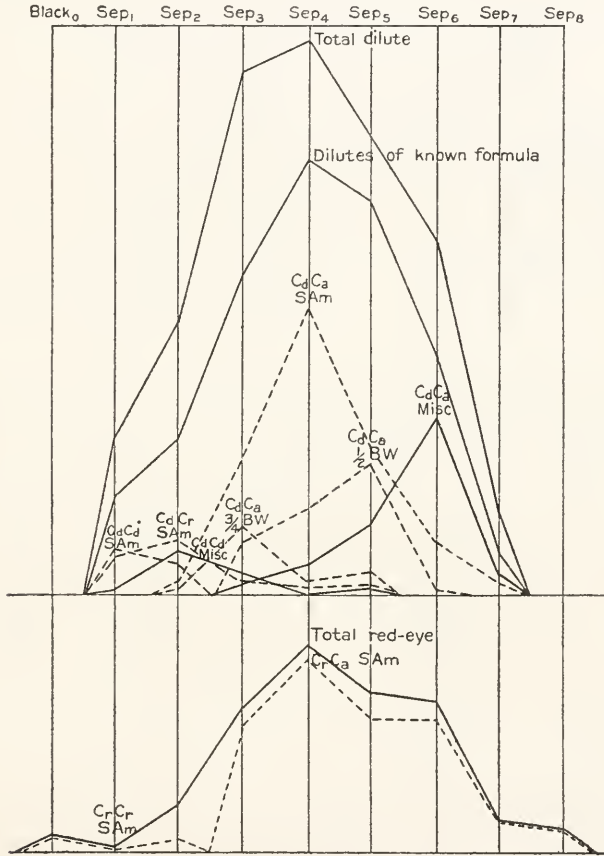
FIG. 6.—Variations in intensity of dilute blacks. Formula and stock printed near mode of each distribution.

VARIATIONS OF YELLOW.

I owe the suggestion that heterozygous albinism may be correlated with extreme dilution of yellow to Professor Castle, who found that attempts to select for a cream stock of maximum dilution led to stocks which invariably gave numerous albinos. The tables and figures confirm this suggestion in a very striking way. Animals known to be homozygous dilute (C_dC_d) vary between yellow$_2$ and yellow$_4$ with the mean at yellow$_{2.9}$. Those known to transmit albinism vary between

TABLE 37.—*Effects of stock and imperfect dominance on intensity of yellow.*

Constitution.	Stock.	Red₀	Red₁	Y₂	Y₃	Y₄	Cr₅	Cr₆	Cr₇	No.	Mean	σ	Y	Cr
CdCd	Dil	...	...	...	1	1	...	...	...	2	3.50	0.50	...	...
Do	Misc	...	...	6	3	2	...	...	...	11	2.64	.77	6	...
Do	S.Am	...	...	1	10	1	...	...	...	12	3.00	.41	...	...
CdCr	...Do	...	...	...	...	9	4	...	...	13	4.31	.46	...	...
CdCa	Dil	...	...	...	...	2	14	21	...	37	5.51	.60	...	...
Do	Misc	...	...	...	...	3	23	25	4	55	5.54	.71	1	33
Do	½BW	...	...	...	...	1	7	...	...	8	4.88	.33	...	...
Do,	¾BW	...	...	...	...	3	9	...	...	12	4.75	.43	...	...
Do	S.Am	...	...	...	...	27	27	3	...	57	4.58	.59	...	1
⎧ 25 CdCr: 15 CdCa	...Do	...	...	...	...	19	20	1	...	...	...	...	...	4
⎨ CdCr by test	...Do	...	...	...	...	(3)	(3)	...	...	...	...	...	...	...
⎩ CdCa by test	...Do	...	...	...	...	(2)	(4)	...	...	...	...	...	...	...
12 CdCd: 23 CdCa	Dil	...	...	...	9	1	13	12	...	...	...	...	...	...
⎧ 29 CdCd: 43 CdCa	Misc	...	...	3	20	7	19	18	5	...	...	...	4	5
⎨ CdCd by test	...Do	...	...	(1)	(2)	(1)	...	...	...	...	...	...	(1)	...
⎩ CdCa by test	...Do	...	...	...	...	...	(4)	(3)	(2)	...	...	...	...	(2)
2.5 CdCd:3.5 CdCa	S.Am,BW	...	...	...	3	...	3	...	...	...	...	...	...	...
CdCd	Total	...	...	7	14	4	...	...	...	25	2.88	.65	6	...
CdCr	...Do	...	...	...	...	9	4	...	...	13	4.31	.46	...	...
CdCa	...Do	...	...	...	...	36	80	49	4	169	5.12	.76	1	34
Dil	...Do	...	...	9	44	70	128	77	7	335	4.72	1.10	10	41

TABLE 38.—*Effects of stock and imperfect dominance on intensity of black.*

Constitution.	Stock.	B₀	S₁	S₂	S₃	S₄	S₅	S₆	S₇	S₈	No.	Mean.	σ
CdCd	Misc	...	1	6	3	...	1	...	...	...	11	2.45	0.99
Do	S.Am	...	6	4	...	...	...	...	...	...	10	1.40	.50
CdCr	..Do	...	6	7	2	1	1	...	...	...	17	2.06	.94
CrCr	..Do	2	...	2	...	...	...	...	...	...	4	1.00	1.00
CdCa	Misc	...	...	...	2	4	9	23	3	...	41	5.51	1.05
Do	½BW	...	...	...	7	11	17	1	...	...	36	4.33	.82
Do	¾BW	...	...	1	9	2	3	...	...	...	15	3.47	.88
Do	S.Am	...	...	2	18	37	19	7	2	...	85	4.20	1.02
CrCa	..Do	...	...	...	16	24	17	17	4	3	81	4.73	1.32
⎧ 20 CdCd: 32 CdCa	Misc	...	...	...	9	9	6	8	13	7	...	...	...
⎨ CdCd by test	..Do	...	...	(2)	...	...	...	...	...	...	...	...	...
⎩ CdCa by test	..Do	...	...	...	...	(1)	(1)	(3)	(2)	...	...	...	...
4 CdCd: 8 CdCa	½BW	...	1	1	9	1	...	...	...	...	...	...	...
⎧ 1.5 CdCd: 1.5 CdCa	S.Am	...	1	1	...	1	...	...	...	...	...	...	...
⎩ CdCa by test	..Do	...	...	...	...	(1)	...	...	...	...	...	...	...
⎧ 29 CdCr: 20 CdCa	..Do	...	10	6	9	12	4	6	2	...	...	...	...
⎨ CdCr by test	..Do	...	(5)	(1)	(2)	(1)	(1)	...	...	...	...	...	...
⎩ CdCa by test	..Do	...	...	...	...	(2)	(2)	(2)	(2)	...	...	...	...
⎧ 6 CrCr: 11 CrCa	..Do	2	...	5	2	3	3	2	...	...	...	...	...
⎨ CrCr by test	..Do	(2)	...	(1)	...	...	...	...	...	...	...	...	...
⎩ CrCa by test	..Do	...	...	...	...	(1)	...	...	...	...	...	...	...
CdCd	Total	...	7	10	3	...	1	...	...	...	21	1.95	.95
CdCr	..Do	...	6	7	2	1	1	...	...	...	17	2.06	.94
CrCr	..Do	2	...	2	...	...	...	...	...	...	4	1.00	1.00
CdCa	..Do	...	...	3	36	54	48	31	5	...	177	4.47	1.13
CrCa	..Do	...	...	...	16	24	17	17	4	3	81	4.73	1.32
CdrCdr	..Do	2	13	19	5	1	2	...	...	...	42	1.90	1.06
CdrCa	..Do	...	...	3	52	78	65	48	9	3	258	4.55	1.20
Dilute	..Do	...	20	34	66	70	58	45	10	...	303	3.95	1.53
Red-eye	..Do	2	...	6	18	26	20	19	4	3	98	4.45	1.54
Dil + RE	..Do	2	20	40	84	96	78	64	14	3	401	4.07	1.53

yellow$_4$ and cream$_7$, mean at cream$_{5.1}$ very distinctly paler. Litters which should give both have given the entire range with two modes, at yellow$_3$ and cream$_5$, respectively. It is especially to be noted that among 13 of these, which were given grades before their constitution was known, 4 ranging from yellow$_2$ to yellow$_4$ proved to be homozygotes, while 9 ranging from cream$_5$ to cream$_7$ proved to be heterozygotes. Dilutes known to transmit red-eye (C_dC_r) have been either yellow$_4$ or cream$_5$, mean at yellow$_{4.3}$. These should be compared with those of

TABLE 39.—*Effect of age on intensity of yellow.*

Constitution.	Stock.	Mean.	No. in sample.	Mean at birth.	Mean adult.	Darkening.
C$_d$C$_d$.....	Misc-Dil	2.8	9	3.1	2.9	0.2
C$_d$C$_a$.....	Misc....	5.5	17	5.1	5.0	.1
Do.....	Dil	5.5	9	5.2	6.0	− .8
Do.....	$\frac{1}{2}$-$\frac{3}{4}$BW .	4.8	11	5.0	4.7	.3
Do.....	S.Am ...	4.6	9	4.4	4.7	− .3
C$_d$C$_r$.....	..Do....	4.3	5	4.8	4.2	.6

TABLE 40.—*Effect of age on intensity of black.*

Constitution.	Stock.	Mean.	No. in sample.	Mean at birth.	Mean adult.	Darkening.
C$_d$C$_d$.....	Misc....	2.5	8	3.0	2.4	0.6
C$_d$C$_a$.....	..Do....	5.5	14	5.6	4.6	1.0
Do.....	$\frac{1}{2}$BW....	4.3	20	4.3	3.2	1.1
Do.....	$\frac{3}{4}$BW....	3.5	6	3.3	2.5	.8
Do.....	S.Am...	4.2	15	4.8	3.3	1.5
C$_r$C$_a$......	..Do....	4.7	8	4.9	2.0	2.9
C$_d$C$_r$.....	..Do....	2.1	16	2.2	1.1	1.1
C$_r$C$_r$......	..Do....	1.0	4	1.0	1.0	0

the same stock (S. Am.) which transmit albinism. The difference, yellow$_{4.3}$ compared with yellow$_{4.6}$, is too small to be relied on. Litters which should give both C_dC_r and C_dC_a have given a range of yellow$_4$ to cream$_6$, as expected. Thus grade yellow$_4$ may be any sort of a dilute; one more intense is quite certain to be homozygous (C_dC_d); one more dilute is quite certain to transmit either red-eye or albinism.

The influence of stock can only be recognized surely in the case of those known to be C_dC_a. The numbers are too small among the homozygotes. Among the heterozygotes (C_dC_a) it is clear that those of dilute and miscellaneous stocks, both with a mean of cream$_{5.5}$, are distinctly paler than those with an admixture of BW or S.Am. blood with means from cream$_{4.6}$ to cream$_{4.9}$.

The data in table 39 indicate that yellow undergoes no appreciable change in intensity during the life of an animal, except in the dilute selection stock. In this case there is a change from cream$_{5.2}$ at birth to cream$_{6.0}$ when adult, among those carrying albinism.

VARIATIONS OF SEPIA.

We find rather more overlapping of distributions among the sepias than among the yellows when different genetic constitutions are compared. Nevertheless there are significant differences in the means. The groups C_dC_d, C_dC_r, and C_rC_r with means from sepia$_1$ to sepia$_{2.1}$, nearly black, average distinctly darker than groups C_dC_a and C_rC_a with means of sepia$_{4.5}$ and sepia$_{4.7}$, respectively. The case is quite different from yellow dilution in which C_dC_r and C_dC_a have the same effect (or nearly so) contrasting with C_dC_d. C_r seems to be essentially identical with C_d in effect on black, but like C_a in effect on yellow.

For further analysis we must compare stocks. In the miscellaneous stock the average for C_dC_a is sepia$_{5.5}$. When this stock is crossed with albinos of BW stock the average of the young—again C_dC_a—is sepia$_{4.3}$. When these are crossed again with BW albinos the average becomes sepia$_{3.5}$. The darkening influence of the BW stock is apparent. The South American stock also has a darkening influence with an average of sepia$_{4.2}$. We find a similar difference between the miscellaneous and South American stocks among the homozygotes.

The comparison of C_dC_a with C_rC_a within the same stock (South American) yields a slight but probably significant difference (C_dC_a, sepia$_{4.2}$; C_rC_a, sepia$_{4.7}$). Thus there is a difference of 0.5 with a probable error of 0.12. It is certain that some of the red-eyed sepias have been paler than any black-eyed sepia.

If there is a real difference here, we would expect C_rC_r to be lighter than C_dC_d or C_dC_r, but the 4 individuals known to be C_rC_r give the darkest average of any array. They were not, however, a random sample and, further, were either pure Ica or F$_2$ Ica$\times$BW and hardly to be compared in stock with those known to be C_dC_d or C_dC_r. For the present C_dC_d, C_dC_r, and C_rC_r may be considered identical in effect on black fur.

As in the case of yellows, the most critical test of the hypothesis of imperfect dominance is the success of prophecy. In litters which should give both C_dC_d and C_dC_a, the 2 darkest tested (sepia$_2$) both proved to be homozygous, while 8 others (sepia$_4$ to sepia$_7$) proved to transmit albinism. Among those which when graded might be either C_dC_r or C_dC_a, 18 were tested. There is some overlapping of ranges, but those which were found to transmit red-eye average very distinctly darker than those which transmitted albinism. Four were tested in an F$_2$ from red-eye by albino. The 3 dark ones, including 2 which were actually as black as blacks of the BW race, proved to be C_rC_r, while the other, sepia$_4$, had albino young and was therefore C_rC_a.

Table 40 shows that in the case of the sepias there is a very perceptible darkening with age. This is shown in all groups except the homozygous red-eyes, which were practically jet black to begin with. Another interesting point brought out is a race difference in the amount of

darkening. The darkening was about 1.0 among 40 animals C_dC_a without South American blood, although with considerable BW blood in most cases; among 23 animals C_dC_a or C_rC_a, with South American blood, the average darkening is 2.0—twice as much. One case among the latter was very striking. Male D238, a red-eyed sepia, C_rC_a, was the palest sepia recorded. The tip of the hair was called sepia$_3$; the base was nearly white. When 2 months old, most of the hair was still of this pale color, but there were sharply contrasting areas which were nearly black (sepia$_2$) on the nose, in spectacles around the eyes, in front of the ears, on the feet, and in an asymmetrical patch on the back. At the age of 4 months, most of the fur on the back was sepia$_2$, although the belly remained fairly light. In the Ica and Arequipa stocks the dark color always appears first on the nose, feet, and ears. These are the darkest regions generally in all dilutes, a fact which recalls the location of the dark smudges in sooty albino guinea-pigs and Himalayan rabbits. In adult animals with a large amount of South American blood, the darkening with age is so great that $C_{dr}C_{dr}$ can seldom be distinguished from $C_{dr}C_a$, although quite reliable predictions could be made at birth as to the nature of the same animals.

VARIATIONS OF EYE COLOR.

The variations of eye color have not been studied as carefully as those of yellow and sepia fur colors. In intense guinea-pigs (C–) the eye ordinarily appears black (factors B and P of course assumed to be present as throughout the discussion of dilution); in many cases, however, it is possible in the proper light to obtain a red reflection through the pupil. In dilute guinea-pigs C_dC_d, C_dC_r, or C_dC_a, the eye also appears black ordinarily, but a red reflection seems to be obtained more easily as a rule than in intense guinea-pigs. The difference is not great enough to be of value as a criterion. In guinea-pigs which are C_rC_r or C_rC_a the pupil appears red in most lights and usually the inner ring of the iris is transparent and also appears red. In very few, if any, cases is the eye so dark that confusion with a dilute or intense is possible. There is much variation in the amount of pigment present. These variations are probably connected with differences in stock and possibly imperfect dominance of C_r over C_a. No pigment has been noted in the pink eyes of albinos. A red-eye can never be confused with a pink-eyed type, unless, of course, factor p is present.

SUMMARY.

1. First-order effects in the dilution of yellow are due to the presence of various combinations of factors of the albino series of allelomorphs. The red-eye and albino factors (C_r and C_a respectively), produce nearly if not quite identical effects. In the case of black, first-order effects may be due either to different combinations in the albino series or to

independent factors (p). In the albino series, the dilution and red-eye factors (C_d and C_r respectively) produce nearly if not quite identical effects. In eye pigmentation, as in the black pigmentation of the fur, first-order effects may be due either to different combinations in the albino series or to other factors (p); but there is a sharp difference from the effects on black fur, in that the dilution and red-eye factors produce very different effects. In this case the intensity and dilution factors apparently produce nearly identical effects.

TABLE 41.

Yellow fur.		Black fur.		Black eye.	
Formula.	Color.	Formula.	Color.	Formula.	Color.
$C-$......	Red.....	$C-$	Black......	$C-$	Black.
C_dC_d...	Yellow...	$C_{dr}C_{dr}$...	Dark sepia .	C_d.......	Nearly black.
C_dC_{ra}...	Cream...	$C_{dr}C_a$....	Light sepia .	C_r.......	Red.
$C_{ra}C_{ra}$..	White....	C_aC_a....	White......	C_aC_a....	Pink.

2. Second-order effects in dilution of yellow, black, and probably eye-color, are due to the unanalyzed residual heredity of different stocks. In the stock at the Bussey Institution BW and South American blood intensify as compared with dilute selection or 4-toe blood. This residual heredity seems to be more important in the case of black than yellow, producing more overlapping of the ranges of the different albino series combinations.

3. In only one stock has the intensity of yellow at birth been observed to change appreciably in the lifetime of the animal. In this case, the dilute selection stock, the creams grow *paler* as they grow older. Sepia, on the other hand, grows distinctly darker as the animals grow older in all stocks. In the imported South American stocks this darkening is so pronounced that adults of any albino series combination, except albinism itself (C_aC_a), are practically black.

INHERITANCE OF VARIATIONS IN THE AGOUTI PATTERN.

Most wild rodents and many other mammals have a coat color of the agouti type, viz, a predominantly black fur in which each hair has a subterminal yellow band. In many cases, as in the mouse and rat, the entire coat is fairly uniform in appearance. This is not true in all cases, however. The color of *Cavia cutleri* has been described at the beginning of this paper. It will be recalled that the color of the belly is sharply distinct from that of the back, appearing wholly yellow instead of ticked. Tame guinea-pigs of the agouti variety likewise have this so-called light-bellied type of agouti.

The agouti pattern of mice was shown by Cuénot in 1903 to be a unit Mendelian character dominant over its absence as found in blacks. In this and later papers (1903, 1904, 1907) he demonstrated that a white-bellied type of agouti and self yellow are due to members of the same series of allelomorphs. Castle, 1905, demonstrated that guinea-pig agouti is a simple dominant over non-agouti.

This agouti pattern of guinea-pigs is subject to considerable variation. In some cases the belly hairs are entirely yellow, a condition correlated with very broad yellow ticking in the dorsal fur. At the other extreme, the base of the hairs on the belly is black for about half the length, and the dorsal ticking is markedly decreased. This dark type has been produced by repeated crossing with intense blacks (BB race). Although distinctly darker than usual, all of the agoutis from such crosses are distinctly yellow-bellied.

PREVIOUS WORK.

Detlefsen (1914) made experiments with the wild species *Cavia rufescens* of Brazil. This has the agouti pattern, but is somewhat darker than *C. cutleri* or the tame guinea-pig. The yellow bands in the dorsal fur are narrower and there is usually more black on the belly, which indeed is usually slightly ticked with black. The difference in appearance is not very great. Detlefsen found, as he expected, that *C. rufescens* was homozygous for the agouti factor. In the hybrids between *C. rufescens* and black guinea-pigs, the agouti behaved as a simple Mendelian dominant. What was not expected was a marked darkening of the agoutis which occurred among the hybrids in many cases. The yellow subterminal bands became so reduced on the back that many of the agoutis appeared more like blacks than guinea-pig agoutis at birth. Black appeared at the ends of the hairs on the belly, and the appearance changed from yellow to ticked. In the early generations the variations in the agouti were exceedingly erratic in their hereditary behavior. Light-bellied hybrids crossed with blacks often gave ticked-bellied young, and ticked-bellied hybrids gave light-bellied young. Nevertheless, as more guinea-pig blood was introduced by repeated back-crosses, the trend was constantly toward the ticked-bellied type. In lines in which the ticked-bellied type had become constant, crosses were made with typical light-bellied agouti guinea-pigs. The ticked-bellied type was found to be recessive and segregated out in later crosses in regular fashion. Detlefsen found that the results in these lines were adequately explained by assuming that the ticked-bellied type is due to an allelomorph of both the light-bellied agouti factor and the non-agouti factor, recessive to the former, dominant to the latter. He used the nomenclature A, A', and a for the tame agouti, wild agouti, and non-agouti factors, respectively.

THE INHERITANCE OF THE AGOUTI OF CAVIA RUFESCENS.

The writer has had the opportunity of experimenting with the hybrid *rufescens* stock developed by Dr. Detlefsen. As the mode of inheritance of the type of agouti is of special interest in being a character in which two wild species differ, it seemed worth while to obtain additional data. New crosses were made to test out the hypothesis of triple allelomorphs as thoroughly as possible. It may be said at once that the results obtained completely confirm Detlefsen's hypothesis.

When received by the writer, there were only 2 light-bellied agouti hybrids in the stock which had derived their agouti from *C. rufescens*. These were A606 and A450, $\frac{1}{4}$ and $\frac{1}{8}$ blood hybrids, respectively. They were crossed with black guinea-pigs and one litter was obtained from each—2 blacks from A606 and 1 light-bellied agouti and 1 black from A450. This light-bellied agouti son unfortunately proved to be sterile, so that experiments with light-bellied *rufescens* agouti came to an end. Only one light-bellied agouti—born dead—has appeared since then which seemed to derive its agouti from *C. rufescens*, and in this case the parentage was doubtful. Thus in the following experiments, *rufescens* agouti and ticked-bellied agouti are practically equivalent. It must be emphasized that this was not the case in Detlefsen's experiments, so that the following results are simpler than those which he encountered in the earlier generations.

Let us consider first the relations of *rufescens* agouti and guinea-pig non-agouti. Cross 1 gives matings of non-agoutis with ticked-bellies known to be heterozygous because of a non-agouti parent (table 42).

TABLE 42.

	Female.	Male.	Agouti light-belly.	Agouti ticked-belly.	Non-agouti.
1a	Non-agouti (g. p.)	✕ agouti ticked-belly...............	..	62	62
1b	Non-agouti (hybrid)	✕ agouti ticked-belly...............	..	17	13
1c	Non-agouti	✕ A'a (red or white)...............	..	11	12
1d	Agouti ticked-belly	✕ non-agouti (g. p.)...............	1	61	63
1e	Agouti ticked-belly	✕ non-agouti (hybrid)...............	..	10	5
			1	161	155

The single agouti light-belly was the son of A450, mentioned above, which, though agouti light-belly, is included under agouti ticked-belly as a *rufescens* agouti. The cross shows that ticked-belly is a simple dominant over non-agouti. The ratio of agouti ticked-belly to non-agouti is sufficiently close to a 1 to 1 ratio. If ticked-bellied agouti were due to independent modifying factors or to the residual heredity of *C. rufescens*, acting with the same agouti factor as found in *C. cutleri* and *C. porcellus*, non-agouti guinea-pigs should possess factors tending

to change ticked-bellied agouti to the typical light-bellied type. The crosses show conclusively that they possess no such tendency. Indeed when it is recalled that, in the early hybrids and *C. rufescens* itself, light-belly was common, it seems necessary to suppose that guinea-pigs possess a residual heredity which tends to darken agouti.

Ticked-bellied agoutis, known to be heterozygous because of parentage, were crossed *inter se.* The results are given in cross 2.

	Aglb.	Agtb.	Non-ag.
Agtb. × Agtb......	0	66	19

This result is sufficiently close to the expected 3 to 1 ratio. One-third of the ticked-bellied young from this cross should be homozygous (A'A') and two-thirds heterozygous (A'a). Several of them have been tested by crosses with blacks (cross 3, table 43).

TABLE 43.

	Female.	Male.	Agouti light-belly.	Agouti ticked-belly.	Non-agouti.
3a	7 agouti ticked-belly	× Non-agouti.....................	..	10	11
3c	Non-agouti	× 9 agouti ticked-belly...........	1	40	38
3b	5 agouti ticked-belly	× Non-agouti.....	..	25	..
3d	Non-agouti	× 1 agouti ticked-belly...........	..	12	..

The single agouti light-belly was the one of doubtful parentage mentioned above. Sixteen heterozygotes were obtained which gave agouti ticked-belly and non-agouti in approximately equal numbers; 6 possible homozygotes were obtained, rather fewer than is to be expected. The male AA253 with 12 agouti ticked-belly young and 2 females, AA213 and AA217, with 8 agouti ticked-belly young each, were quite certainly homozygous and were used to establish a homozygous ticked-bellied stock. They and their progeny crossed *inter se* have given only ticked-bellies, 26 in number (cross 4). These homozygous ticked-bellies are indistinguishable from heterozygotes in appearance.

Cross 6 gives matings of homozygous light-bellied agouti guinea-pigs with non-agouti hybrids. The young, 29 in number, are all light-bellied. There is no tendency toward ticked-belly introduced by the hybrids.

Cross 7 gives matings of light-bellied hybrids (agouti derived from guinea-pigs) with non-agoutis. All of these light-bellies were known to be heterozygous from their parentage. The result, 18 light-bellies, 21 non-agoutis, no ticked-bellies, is in harmony with expectation (19.5 : 19.5).

Crosses 8 and 9 give data on the relation of light-belly to ticked-belly. Homozygous light-bellied guinea-pig by ticked-bellied hybrid gives exclusively light-bellies, 50 in number. Light-belly is thus clearly

dominant. Heterozygous light-belly (with a non-agouti parent) by heterozygous ticked-belly (also with a non-agouti parent) gave 16 light-bellied, 6 ticked-bellied, and 10 non-agouti young where expectation is 16 : 8 : 8.

The results given so far show that light-belly is dominant or at least epistatic over ticked-belly, that ticked-belly is a simple Mendelian dominant over non-agouti, and that the difference between *rufescens* and *porcellus* agouti is not a question of residual heredity.   The fact that crossing with guinea-pig non-agouti increases the difference between *rufescens* and *porcellus* agouti, instead of destroying it, shows that *rufescens* agouti does not contain the same agouti factor as is found in guinea-pig agoutis. *Rufescens* agouti must have an allelomorph of guinea-pig agouti, recessive to the latter.   This leaves two possibilities. This allelomorph may be (I) the non-agouti factor or (II) a new allelomorph recessive to the *porcellus* agouti factor, dominant to non-agouti (Detlefsen's hypothesis).   Both of these explanations fit equally well all of the data given so far.   Under (I) a guinea-pig light-belly is AAa′a′, a non-agouti aaa′a′, and a *rufescens* agouti aaA′A′.   Under (II) these three varieties are AA, aa, and A′A′, respectively.   The critical test is whether it is possible to produce light-bellies which are double heterozygotes AaA′a′, capable of having both ticked-bellied and non-agouti young, as well as light-bellies when crossed with non-agoutis. Detlefsen obtained 5 light-bellied agoutis from the cross light-belly by heterozygous ticked-belly which bear on this point.   Each of these had ticked-bellied young, but no non-agoutis.   They, therefore, point toward hypothesis (II), which is also more probable *a priori*.   They had, however, only from 3 to 6 young, 21 in all, so that it is not wholly certain that they would have had no non-agouti young if tested further. This point, therefore, seemed to the writer to be one on which additional data would be desirable, and special attention has been paid to it.

The cross heterozygous ticked-belly by heterozygous light-bellies known from their parentage to be free from ticked-belly can be represented as follows under the two hypotheses:

$$\begin{array}{cccccc} Agtb. & Aglb. & Aglb. & Aglb. & Agtb. & Non\text{-}ag. \\ \text{(1) } aaA'a' \times Aaa'a' & = AaA'a' & + Aaa'a' & + aaA'a' & + aaa'a'. \\ \text{(II) } A'a \quad\quad \times Aa & = AA' & + Aa & + A'a & + aa \end{array}$$

In both cases we expect 2 light-bellies to 1 ticked-belly to 1 non-agouti.   Under (I) the light-bellied young which can transmit ticked-belly (AaA′a) must also have the power of transmitting non-agouti. Under (II) such light-bellies (AA′) should not transmit non-agouti. Under (II) half of the light bellies should be of this type and the other half should transmit non-agouti but not ticked-belly (Aa).   Thus, if a large number of young can be obtained from a light-belly from such a cross, which has had ticked-bellied young in crosses with non-agoutis, the presence or absence of non-agouti young is decisive between the

two hypotheses. Cross 10 gives the results of the tests of light-bellied young from such a cross as described (table 44).

TABLE 44.

	Females.	Males.	Aglb.	Agtb.	Non-ag.
10a	7 aglb....	Non-ag ..	17	..	20
10c	Non-ag ..	4 aglb....	26	..	33
10b	10 aglb...	Non-ag ..	18	30	..
10d	Non-ag ..	5 aglb....	45	50	..

In no case has the same animal had both ticked-bellied and non-agouti young. Some of those which have had ticked-bellied young have been quite thoroughly tested. Male M138 had 20 light-bellied and 19 ticked-bellied young. Male B121 had 13 light-bellied and 13 ticked-bellied young. Male M91 had 5 light-bellied and 11 ticked-bellied young. The chance that these can represent 2 : 1 : 1 ratios is negligible. Thus hypothesis (I) may be dismissed.

Light-bellied agoutis demonstrated to carry ticked-belly have been crossed *inter se* (cross 11). They have given 25 light-bellies and 9 ticked-bellies, no non-agoutis. This agrees reasonably well with the expected 3 to 1 ratio. The remaining tables give the results of miscellaneous crosses. All of them are in harmony with the hypothesis of triple allelomorphs.

MINOR VARIATIONS.

Thus there seems no doubt that the light-bellied agouti of *Cavia porcellus*, the ticked-bellied agouti of *C. rufescens* hybrids, and non-agouti form a series of triple allelomorphs. The question remains whether *light*-bellied *Cavia rufescens* hybrids possess a different allelomorph from the ticked-bellied ones, or whether the difference lies simply in the residual heredity. There are no wholly satisfactory data bearing on this point. Nevertheless the fact that the darkening seems associated especially with certain stocks of guinea-pigs seems to favor the second view. The writer has crossed ticked-bellied agoutis repeatedly with the intense blacks of BB or BW stock. Young have been obtained which were self black, except for a few ticked hairs in the chest and whiskers. One ignorant of their history would probably have classified several of them as blacks. Before they became adult, however, these black ticked-bellies acquired a uniform though very slight yellow ticking throughout the entire fur. On crossing such black ticked-bellies with a dull black stock (4-toe) there is a return to a more strongly developed agouti pattern. The young are uniformly ticked when born. Thus these variations in the agouti pattern seem related to the residual heredity of the stocks, possibly with the same residual heredity which determines the very intense development of pigment,

especially black, in the BB and BW races, the feebler development in the 4-toe race, and the much feebler development in the wild species. If this is correct, the resemblance of light-bellied *rufescens* to light-bellied agoutis, like that of the pale color of *C. cutleri* to dilute guinea-pigs, is secondary. In both cases the wild species possess a different allelomorph from the guinea-pig in the principal series of factors involved, but owing to different residual heredity, have a superficial resemblance.

THE INHERITANCE OF THE AGOUTI OF CAVIA CUTLERI.

The writer has had the opportunity of working with the agouti of *Cavia cutleri*. Repeated crosses have been made with blacks of the BW race of guinea-pigs to see whether a ticked-bellied agouti could be obtained. While some ventral ticking has been observed in some cases, the $\frac{1}{8}$-blood *cutleri* hybrids are still on the whole good light-bellied agoutis. The *cutleri* agouti is unquestionably more resistant to darkening influences than was *rufescens* agouti. No results have been obtained yet which serve to differentiate it from the guinea-pig agouti. This is additional evidence that *C. cutleri* was ancestral to *porcellus*. The experimental results are given in crosses 68 to 78.

Only one cross has been made between a *cutleri* and ticked-bellied *rufescens* hybrids. Male K56, a black $\frac{1}{4}$ *cutleri* ($\frac{3}{4}$ 4-toe), was crossed with two ticked-bellied agoutis, which of course had some *rufescens* ancestry. There were 6 young (3 blacks and 3 ticked-bellies) of which one was quite light and one was black, except for a few ticked hairs on the chest and whiskers. There was thus no very conspicuous tendency toward light-belly introduced by the *cutleri* hybrid. It seems safe to assume that *C. cutleri* has a different member of the agouti series of allelomorphs from *C. rufescens*, but the same or nearly the same as *C. porcellus*.

Wild species of the same genus seldom differ as much superficially in any one character as do many varieties of domesticated animals. Yet while very large variations in the latter have been shown in many cases to behave as simple Mendelian units in inheritance, the characters by which wild species differ usually seem to be highly complex in heredity. Few well-defined Mendelian factors are recorded in the literature of hybridization. It is, therefore, interesting to find that the darker agouti of *Cavia rufescens* differs from the lighter agouti of *C. cutleri* by a clear-cut Mendelian factor.

INHERITANCE OF ROUGH FUR.

In the wild species of cavy, and in the ordinary smooth guinea-pigs, the hair shows a definite direction of growth, which is always away from the snout on the body and toward the toes on the legs. This is at least the general tendency of the hair in most mammals, and it is

obviously the most advantageous; the hair lying thus is not ruffled or caught by obstacles when the animal is moving.   This direction is not directly imposed on the hair by outside agencies, as might be supposed, but is due to the direction of growth of the hair follicles (Wilder, 1909).

Certain fancy varieties among guinea-pigs, as the long-haired rough "Peruvians" and the short-haired rough "Abyssinians," show a striking deviation from the normal hair direction.   In these varieties the coat can be divided into a number of areas, within each of which all hair directions radiate from a definite center.   The boundaries of these areas, where contrary hair-currents meet, are marked by crests.   The centers with their radiating hair-currents are called rosettes.   Many mammals, including man, naturally show rosettes, crests, or other peculiarities of hair direction, but less conspicuously than the rough guinea-pigs.   (See plate 7.)

The positions in which rosettes may occur in guinea-pigs are quite definite.   Following are the rosettes and irregularities given by Castle (1905), with the addition of L, irregular roughness on the chest.

A. Forehead, unpaired.	E. Sides, between shoulder and hip.	I. Navel, unpaired.
B. Eyes.	F. Hips.	J. Front toes.
C. Ears.	G. Above the groin.	K. Hind toes.
D. Shoulders.	H. Mammæ.	L. Irregular roughness of chest.

In the grading of the young guinea-pigs, large letters, as above, have been used for well-defined rosettes and small letters for feeble rosettes or slight deviations from normal hair direction in an area, indicated only by crests at a boundary.   Thus a mid-dorsal crest or mane (e) without any side or hip rosettes is characteristic of a certain grade of partial roughs.   The ear rosettes (C) are usually only revealed by a crest between the ears. The shoulder rosettes are seldom well developed. The side rosettes are sometimes doubled in the roughest animals (E,E_2).

The number of rosettes present varies from the full set described above, through a continuous series of intermediate grades, to one pair. The variations are not merely haphazard, but may easily be classified. In the first place, it is necessary to distinguish two series.   A slight roughness found in certain stocks (the BW, Ica, and Arequipa stocks) does not fit into the usual series of variations and will be discussed separately as series II.   The roughness of the remaining stocks and also of the fanciers' "Peruvians" and "Abyssinians" we may call series I.   In series I all the variations found may be arranged with considerable accuracy in a single linear series.   Thus Castle (1905) used six grades, passing from rough A with the maximum number of rosettes to rough F, smooth except for the hind toes.   These grades will be used in this discussion, with the exception that it has been found convenient to combine grades C and D, leaving five grades, A to E.   These letters used for grades must not be confused with those used to name the rosettes.

Reversal of hair direction on the hind toes is the most constant feature of the roughness of series I and has been found in all rough guinea-pigs of series I without exception.   Following is the usual order of succession of the additional rosettes and irregularities found in passing from a smooth to a full-rough:

Hind toes.......................	K	Forehead, hip, ventral rosettes...	A,F,H,I,L
Front toes......................	J	Eye rosettes..................	B
Dorsal crest....................	e	Groin, shoulder, second side ro-	
Side rosettes, crest between ears.....	E,C	settes....................	G,D,E$_2$

There is seldom more than a slight amount of asymmetry.   As a rule the paired rosettes are present or absent as pairs.   The most common exception is in the side rosettes in low-grade partial-roughs. Among these it is not uncommon to find a good rosette on one side and merely a slight change in hair direction on the other.   In classifying, six of the most distinct sets of rosettes have been used as the principal criteria, viz, forehead, eyes, sides, hips, front toes, and hind toes.

CLASSIFICATION.

Rough A.—The forehead and five critical pairs of rosettes must be well developed.   In addition, there is always some ventral roughness and a crest between the ears.

Rough B.—This includes various conditions intermediate between rough A and rough C.

Rough C.—There is only one pair (or half pair) of well-developed rosettes, usually the side rosettes.   There is always, in addition, roughness on at least the hind toes and usually a crest between the ears.

Rough D.—A mid-dorsal crest is present and roughness of at least the hind toes, but no well-marked rosettes.

Rough E.—Roughness is confined exclusively to the toes, usually to the hind toes.

The following list shows the variations which have been met with in each grade; the letters represent the rosettes:

Rough A. ABcEFHIJK to ABCDE$_1$E$_2$FGHIJKL.
Rough B. AcEJK, AcEHJK, abFGJK, ABcFHIJKl, ABcDEHIJKl.
Rough C. EK, EJK, cEK, cEJK.
Rough D. eK, cK, eJK, cJK.
Rough E. K, JK.

PREVIOUS WORK.

Nehring (1894) made crosses between rough guinea-pigs and the wild species *Cavia aperea*. He described the young as smooth, but noted that a mane developed along the middle line of the back.   Castle (1905) demonstrated that rough fur behaves as a Mendelian unit

character, dominant over smooth, and is thus an example of the comparatively rare class of dominant mutations. He found that the grade of roughness, while fairly constant in some stocks, could be reduced by crossing with smooth guinea-pigs of a particular stock (tricolor), which he described as prepotent smooth. Detlefsen (1914) found that rough fur in hybrids between rough guinea-pigs and the wild species *Cavia rufescens* continued to be inherited in Mendelian fashion, but that dominance ceased to be complete. The writer began experiments in 1913 at Professor Castle's suggestion, to investigate further the heredity of variations in the rough character.

<div align="center">MATERIAL.</div>

Several stocks have been used as material:

(1) *4-toe stock.*—A full-rough was crossed with members of the 4-toe stock, and by repeated back-crosses into the latter a stock has been produced which is practically pure 4-toe. No partial-roughs have ever appeared in these crosses. Pure 4-toe smooth animals have been very useful in the experiments, since it has been amply proved that when crossed with full-roughs they never reduce the grade of rough.

(2) *Tricolor stock.*—Most of the partial-roughs experimented with are of very mongrel stock, with, however, more or less tricolor ancestry. In this section on rough fur the term tricolor stock will be used for convenience for these animals, without implying that all of them actually were tricolors.

(3) *Lima stock.*—This stock as has been described was derived entirely from 8 guinea-pigs (2 nearly full-rough (rough B) and 6 smooth) brought from Peru in 1913.

(4) *Rufescens hybrids.*—The writer has worked with a few rough animals descended from Detlefsen's hybrids and containing from $\frac{1}{4}$ to $\frac{1}{64}$ *Cavia rufescens* ancestry.

(5) *Cutleri hybrids.*—Crossing with *Cavia cutleri* has been found by the writer to have a similar effect on the rough character to that described by Nehring (1894) for *C. aperea* and by Detlefsen (1914) for *C. rufescens.* The behavior of the roughness in these *cutleri* hybrids has been investigated.

(6) *Miscellaneous smooth guinea-pig* stocks have been used in some of the experiments. All used resemble the 4-toe smooths in giving no partial-roughs when crossed with full-roughs.

(7) *BW, Ica, and Arequipa stock* occasionally have shown a slight roughness which is distinct from the usual type and is discussed later under series II. The BW stock has been used in a few cases as a source of smooth guinea-pigs. Aside from the slight roughness of series II all of those used have behaved like 4-toe smooths. Smooth

Icas, on the other hand, behaved like the wild cavies in reducing the
roughness.

<div align="center">PROBLEMS.</div>

The following figures show the kinds of roughs which have appeared
in the experiments with the four principal stocks and the nature of
the variability in the rough character, the inheritance of which it is
desired to analyze. All roughs are included, but only such smooths
as had at least one rough parent.

Inspection of figure 7 at once shows striking differences in the
variability of the rough character in the different stocks. In the 4-toe
stock there is a wide gap between the lowest rough and the smooths
which come from the same parents. Only one individual in the 4-toe
stock was graded rough B and this
was close to rough A (lacked only
groin and hip rosettes). Most of
the individuals were strong rough
A. In the Lima stock most of
the individuals which were rough
at all were rough B or a weak
rough A, but 5 were rough C or D.
Among the tricolor and *cutleri*
hybrids a continuous series can
be formed passing from the best
roughs to the smooths. Both
show a distinctly bimodal distri-
bution of the roughs, the modes
being at rough A and rough C.
Such a distribution would of
course be purely artificial if rough
B were a more limited category
than rough A or rough C, but the
definitions show that rough B in-
cludes perhaps the widest range

Fig. 7.—Distribution of grades of roughness of the
fur in four stocks of guinea-pigs.

of possible variation. Further, the large number of rough B's in the
Lima stock shows that this class may be practically as numerous as
rough A under the right hereditary conditions. Thus there are strong
intimations that in the tricolor and *cutleri* stocks, rough A and rough
C differ by a unit hereditary difference.

The problem of the inheritance of the variations in the rough char-
acter thus seems to resolve itself into three phases: (1) The inheritance
of roughness of any sort as opposed to smoothness; (2) the inheritance
of a more or less full-rough type averaging about rough A as opposed
to a partial-rough type averaging between rough C and D; (3) the
inheritance of the variations within the full-rough and partial-rough
types.

INHERITANCE OF ROUGH AS OPPOSED TO SMOOTH.

Castle (1905) demonstrated that all roughs differ from smooths by a Mendelian unit-factor and that rough is dominant over smooth. The writer's experience fully confirms this conclusion.

In nearly 3,000 young recorded, smooth by smooth has never given rise to rough (of series I) in spite of much rough ancestry, with one possible exception. This exception was of a kind which was expected and was being tested for when found. One of the smooth parents was undoubtedly like rough E genetically. The case will be discussed later.

TABLE 45.

Rough × rough.			Rough × smooth.		
Formula and stock.	Rough.	Smooth.	Formula and stock.	Rough.	Smooth.
RR × Rr:			RR × rr:		
4003 (tri)..........	6	0	4003 (tri)..........	11	0
Rr × Rr:			Rr × rr:		
4-toe..............	10	3	4-toe..............	29	32
Tricolor...........	88	28	Tricolor...........	104	125
Lima..............	18	7	Lima..............	56	55
Cutleri hybrid......	17	2	Cutleri hybrid......	60	63
			Miscellaneous........	54	48
Total...........	133	40	Total...........	303	323
Expectation	(130)	(43)	Expectation.......	(313)	(313)
Largely Rr × Rr:					
Miscellaneous.......	46	12	Largely Rr × rr.........	16	12

On the other hand, rough by rough has often given smooth. In the cross of rough by smooths from stocks in which roughs have never occurred, all or half of the young are rough. All wild cavies, for example, are smooth and have only smooth descendants when crossed with smooth guinea-pigs. They have numerous rough young in F_1 when crossed with rough guinea-pigs. Thus it is clear that rough is dominant. Table 45 is a summary of the rough crosses made by the writer. Grades of roughness are ignored. No special attempt has been made to obtain homozygous roughs. Male 4003, rough E, is the only one which has been adequately proved homozygous. Male R197, rough A (cross 46), is another which is probably homozygous. In the cross Rr × Rr above, only matings are included in which both animals are known to be heterozygous, either because of a smooth parent, or, having had 12 or more young, because of smooth young. Tabulated in this way, the expectation is not appreciably different from 3 rough to 1 smooth. Other litters of rough by rough are tabulated above. Probably most of these are of the type Rr × Rr, although in some cases there were no smooth young. In crosses Rr × rr, the only cases tab-

ulated are those in which the rough is known to be Rr because of a smooth parent, or because of a smooth young one in 6 or more. Expectation is here 1 to 1. The remaining cases of rough by smooth, in which expectation is still probably not far from 1 to 1, are also given.

These results are in harmony with the view that rough differs from smooth by a dominant unit factor.

INHERITANCE OF MAJOR VARIATIONS.

Before giving any hypotheses, it will be well to present the experimental results with the immediate deductions which can be drawn from them (tables 46 to 55).

(1) In some stocks there is very little variation in the rough character and there is a wide gap between the lowest rough and smooth. The 4-toe stock is an excellent example of such a stock. It is worthy of note that we get a similar result in the Lima stock if we exclude the litters of L6, L24, L56, and L99. Female L6, smooth, was one of the original 8 in the Lima stock. Female L24, smooth, was her daughter. Female L56, rough C, was the daughter of L24, and male L99, rough C, was the son of L56. Most of the tame guinea-pig stocks (BW, dilute selection) seemed to be like the 4-toe stock in the above respect whenever rough was introduced into them in a cross.

TABLE 46.

Cross.	Stock and grade.	A	B	C	D	E	Sm
	Four-toe stock:						
(45)	A × A....................	10	..	..	..	..	3
(49)	A × Sm.................	28	1	..	..	..	32
	Lima stock, except L6, L24, L56, and L99:						
(58)	B × B....................	7	5	..	..	..	3
(59)	A × Sm.................	21	5	..	..	..	17
(60)	B × Sm..................	5	9	..	..	..	21
	Miscellaneous stock:						
(63)	A, B (Lima) × Sm (4-toe)..	4	4	..	..	..	4
(65, 66)	A × Sm.................	31	1	..	..	..	36

Most of those graded rough A or rough B above must be heterozygous. As nothing higher than rough A appeared in the crosses A × A and B × B, it seems clear that the homozygotes in these stocks at least are no more rough than the heterozygotes, i. e., dominance is complete.

(2) When a wild species of *Cavia* (smooth), or a smooth of certain tame stocks is crossed with a full-rough, the rough young are of low grade—rough C or D.

As has been mentioned before, Nehring (1894) crossed a rough male guinea-pig with *Cavia aperea* of Argentina. He described the young as smooth at first, but developing a mane along the back later. This was evidently the dorsal crest of rough D. The reversal of hair direction on the hind toes might easily have been overlooked. Detlefsen (1914) described crosses of *C. rufescens* of Brazil with full-rough guinea-pigs. His *rufescens* was undoubtedly a different species from the *aperea* used by Nehring, since the latter found complete fertility among the hybrids of both sexes, whereas Detlefsen found sterility among all the male hybrids. The rough young were rough D. The skin of one of them (A10) shows roughness on all the toes and a very slight dorsal crest. The writer has crossed rough A guinea-pigs with *C. cutleri* of Peru with similar results. Nine rough young have been obtained, of which 3 show good side rosettes and are rough C, while the others merely show a dorsal crest (and rough toes) and are rough D. A male of pure Ica stock, which being from feral stock probably had considerable wild ancestry, was tested by crosses with full roughs and also gave only partial-roughs—5 all rough C. Castle (1905) obtained partial-roughs, C or D, on crossing full-roughs with smooths of tricolor stock. The writer has made further crosses of this kind with similar results. One smooth guinea-pig of the Lima stock, L24, had some partial-rough young when crossed with full-roughs of her stock.

TABLE 47.

Cross.	Stock and grade.	A	B	C	D	E	Sm	
	Smooth, of wild or feral stock:							
	A × Sm (C. aperia)......	..	..	..	1	..	..	Nehring (1894).
	A × Sm (C. rufescens)....	..	..	..	4	..	7	Detlefsen (1914).
(68)	A × Sm (C. cutleri)......	..	..	3	6	..	15	
(67)	A × Sm (Ica)...........	..	..	5	..	..	4	
	Certain tame stocks and wild hybrids:							
(71, 74)	A × Sm (½ cutleri).......	10	3	10	1	..	23	
(65)	A × Sm (¼, 3/2 rufescens) .	1	1	2	..	..	..	
(59, 60)	A × Sm (L6, L24).......	4	1	3	..	..	6	
(51)	A × Sm (Tricolor)	6	..	3	3	..	19	

The results given in table 47 show that in partial-roughs from a great variety of sources, the low grade of the roughness is not due to a variation of the rough factor, *i. e.*, to an allelomorph, nor is it due to an independent duplicate rough factor which produces somewhat similar effects to the factor of full-roughs. These partial-roughs have the identical rough factor present in full-roughs derived directly from the latter.

(3) When a wild cavy is crossed with a partial-rough guinea-pig, rough young of the lowest grade (rough E) are produced.

No rough E young were produced in the crosses under (2) where one parent was full-rough.

TABLE 48.

Cross.	Stock and grade.	A	B	C	D	E	Sm
(69)	C, D × Sm (C. cutleri).....	..	..	1	1	9	12

(4) Partial-roughs crossed together may give all grades of roughness from full-rough (A) to the lowest partial-rough (E).

TABLE 49.

Cross.	Stock and grade.	A	B	C	D	E	Sm
(76)	cutleri hybrids: C × C.........	..	..	1	3	1	..
(52)	Tricolor: C, D × C......	18	6	19	7	12	17
(53)	C, D × E......	..	..	4	1	6	1
(55)	E × E.........	..	..	..	..	4	3

(5) Full-roughs crossed together have never given partial-roughs. Crosses in the 4-toe and Lima stock have already been given. Below are crosses of rough A by rough A in the tricolor and *cutleri* stocks in which each rough A parent had one or both of its parents partial-rough (C, D) or in the case of the *cutleri* hybrids, an F_1 hybrid.

TABLE 50.

Cross.	Stock and grade.	A	B	C	D	E	Sm
(46)	Tricolor A × A.....	17	2	..	..	..	7
(75)	¼ cutleri A × A.....	3	..	..	..	..	..

(6) Full-roughs, one or both of whose parents were partial-roughs, have given no partial-rough young in crossing with smooths of 4-toe stock.

TABLE 51.

Cross.	Stock and grade.	A	B	C	D	E	Sm
(50)	A (Tri) × Sm (4-toe)	19	..	..	..	..	20
(73)	A (¼ cut) × Sm (4-toe).....	2	..	..	..	..	2

In (73) two of the ¼ *cutleri* rough A did not come from a partial-rough parent, but from smooth ½ *cutleri* hybrids.

(7) Partial-roughs crossed with smooths of 4-toe or a similar stock give partial-rough young, and also, in most cases, full-rough and smooth young.

TABLE 52.

Cross.	Stock and grade.	A	B	C	D	E	Sm
(54)	C, D (Tri) × Sm (4-toe, etc.)	34	..	29	13	1	79
(64)	C ($\frac{1}{4}$, $\frac{1}{8}$, $\frac{1}{64}$ rufescens) × Sm (4-toe, etc.)..	3	..	2	..	..	5
(72)	C, D ($\frac{1}{2}$, $\frac{1}{4}$ cutleri) × Sm (4-toe, etc.)....	12	..	6	6	..	21
(61)	L 56 C × Sm (Lima).................	2	1	1	..	..	2
(56)	E (Tri) × Sm (4-toe)	..	..	13	..	..	8

Crosses (3) to (7) show that full-rough can be recovered from partial-rough usually without trouble, but that partial-rough can not be recovered from full-rough, either in crossing full-roughs together or with ordinary smooth guinea-pigs (4-toe, etc.). Cross (7) is more significant than appears at first sight. We know that 4-toe smooths transmit nothing which can reduce the grade of roughness. Thus, when we find partial-rough by 4-toe smooth giving partial-rough young, we see that the rough factor and the factor or factors responsible for the low grade of roughness can be transmitted in the same gamete.

(8) Most partial-roughs crossed with full-roughs give a very similar result to the cross partial-rough by 4-toe smooth, except that fewer smooths are produced.

TABLE 53.

Cross.	Stock and grade.	A	B	C	D	E	Sm
(47)	A × C (Tri)	10	1	5	1	..	10
(58)	B (Lima) × C (Lima)...............	..	1	..	1	..	..
(70)	A (4-toe, etc.) × C, D ($\frac{1}{2}$, $\frac{1}{4}$ cutleri)	8	3	8	2	2	4
(48)	A (Tri) × E (Tri)	..	..	2	1	..	..

(9) The lowest grade of roughs (E) very rarely have either a full-rough parent or full-rough young. They also very rarely have a smooth parent of such a stock as 4-toe.

Of the rough young, 507 have been recorded (excluding 8 from mixed bimaternal litters); 413 of these had a full-rough (A, B) or a 4-toe smooth parent; yet these include only 3 rough E young. On the other hand, 13 rough E are included in the 67 rough young from C or D × C; 6 are included in the 11 from C or D × E, 9 are included in the 11 rough young from C × smooth *Cavia cutleri* and *all* of the 4 rough young from E × E were rough E. Table 54 shows the matings in which one or both of the parents were rough E. These are repeated from other crosses.

The offspring of male 4003 rough E are of special interest. He was undoubtedly homozygous rough; the chance that he was heterozygous is $(\frac{1}{2})^{11}(\frac{3}{4})^6 = 0.0001$. As he was the lowest grade of rough, he very emphatically disproves any necessary relation between homozygosis and high development of the rough character, or between heterozygosis and partial roughness.

TABLE 54.

Cross.	Stock and grade.	A	B	C	D	E	Sm
(56)	E × Sm (4-toe).......	..	..	13	..	..	8
(48)	E × A...............	..	..	2	1	..	..
(53)	E × C, D............	..	..	4	1	6	1
(55)	E × E...............	..	..	..	..	4	3

(10) Occasionally a smooth from a cross which produces rough E will transmit the rough factor, breeding like a rough E. Rough E grades into smooth. From a cross which can produce rough E, 8 smooth animals were tested by crossing with 4-toe smooths to determine whether a smooth can ever be like rough E genetically. One such animal, female R201, was found.

TABLE 55.

Cross.	Stock and grade.	A	B	C	D	E	Sm
(57)	7 Sm (C × C) × Sm (4-toe)...	..	..	..	..	..	32
	R 201 Sm (C × C) × Sm (4-toe)...	..	..	1	..	..	1

The case is not quite as clear as could be desired, since R201 seemed to show a trace of irregularity on one hind toe when first graded. As an adult she is indistinguishable from a smooth.

These experiments are sufficient, it is believed, to establish the mode of inheritance of the major variations of the rough character.

First, it is clear that partial-roughs do not owe their roughness to an allelomorph of the rough factor or to an independent duplicate rough factor, but to the same factor found in full-roughs. Reasons were given under (2).

Next, any hypothesis is untenable according to which partial-roughs are due to imperfect dominance and hence are necessarily heterozygous either with the ordinary smooth factor of guinea-pigs or with a more potent allelomorph of the latter present in wild cavies and special stocks of tame guinea-pigs. The latter hypothesis was suggested by Detlefsen (1914), in the case of the partial-roughs among the *rufescens* hybrids. He represented the rough factor by Rf, the ordinary smooth factor by rf, and the smooth factor of *Cavia rufescens* by rf'. He supposed that Rf is completely dominant over rf, but incompletely dominant over rf'. Thus Rfrf would be a full-rough, but Rfrf' a partia-

rough. This hypothesis explains very satisfactorily all of the crosses given except those under (7), repeated under (9) and (10). It can not explain the case of male 4003 rough E, who was undoubtedly homozygous for the rough factor (RfRf) and yet was the lowest grade of partial-rough. Further, it can not explain the occurrence of partial-rough young coming from the cross partial-rough by 4-toe smooth. The latter are necessarily rfrf under the above hypothesis.

$$\text{Rfrf}' \times \text{rfrf} \qquad = \text{Rfrf} + \text{rfrf}'.$$
$$\text{Rough C, D, E} \times \text{smooth} = \text{rough A} + \text{smooth}.$$

Under this hypothesis, the rough factor Rf and the factor which reduces the grade of rough rf' can not be present in the same gamete. But this cross actually gave 70 partial-rough young, 56 from tricolor partial-roughs, 12 from partial-rough *cutleri* hybrids, and at least 1, probably 2, where the partial-rough parent owed its low grade to *Cavia rufescens*. Female A606 rough C was $\frac{1}{4}$ *rufescens*. Her parents were 2193, a full-rough guinea-pig, and A63, a smooth *rufescens* hybrid. The hypothetical factor rf' could only have come from the latter. The parents of A63 were A55, a pure *Cavia rufescens*, and 9586 of BW stock, a stock which has shown no tendency to reduce the grade of full-roughs on crossing with them. It thus seems clear that A606 owes her low grade of rough to her *Cavia rufescens* grandfather. She was crossed with a 4-toe smooth male, 166, and had two rough young, whose grades unfortunately were not recorded at birth. One, however, A1687, is still living (August 1915), and is a typical rough C. There is reason for believing the other to have been of the same grade. Thus in tricolors, *Cavia cutleri* and *Cavia rufescens* hybrids, the same gamete can transmit the rough factor and the factor or factors which limit the full development of the rough character. The formula Rfrf' can not, therefore, be used for partial-roughs.

There remains only one line of explanation. Partial-roughs must differ from full-roughs by possessing an independently inherited modifying factor (or factors). An incompletely dominant unit modifying factor will explain all of the results satisfactorily. Let us represent the wild condition (*aperea, rufescens, cutleri*) by rrSS. Let us suppose that the dominant mutation R is necessary for any roughness [of series I] and produces with rare exceptions at least reversal of hair direction on the hind toes (rough E). The second mutation, s, when heterozygous, may permit roughness to extend to grades D or C; when homozygous it permits roughness to reach grades B or A.

rrSS smooth..................... Wild species, Ica stock.
rrSs smooth..................... Most tricolor smooths.
rrss smooth..................... 4-toe, BW, BB, dilute stock, most Lima smooths.
RrSS rough E (rarely smooth)...... R 140, etc.
RRSS rough E (rarely smooth)..... 4003.
RrSs rough C or D (rarely E or B)... Most tricolor partial-roughs.
RRSs rough C or D.
RrSS rough A (less frequently B).... 4-toe, most Lima roughs.
RRss rough A.

This explanation fits very well the results which have been given qualitatively. As the numbers are rather small, and as it is necessary besides to assume some overlapping of class ranges, much emphasis can not be laid on the quantitative results. Nevertheless, the fit is in all cases reasonably close. Let us take up the qualitative results in order.

(1) In some stocks there is very little variation in the rough character and there is a wide gap between the lowest rough and smooth. Evidently if the 4-toe and similar stocks are pure for factor s, only full-roughs and smooths can appear (RRss, Rrss, rrss). Apparently 7 of the original 8 in the Lima stock were ss, while one, L6, was rrSs.

(2) When a wild species of cavy (smooth) or a smooth of certain tame stocks is crossed with a full-rough, the rough young are of low grade, rough C or D. This result necessarily follows from a cross of the type rrSS (wild, Ica, tricolor) by Rrss (rough A). The rough young RrSs should be rough C or D.

(3) When a wild cavy is crossed with a partial-rough guinea-pig, rough young of the lowest grade, rough E, are produced.

$$\text{rrSS} \times \text{RrSs} = \text{RrSs} + \text{RrSS} + 2\text{rr}$$
$$\text{Sm} \qquad \text{C} \qquad \text{C} \qquad \text{E} \qquad 2\text{ Sm}$$

(4) Partial-roughs crossed together may give all grades of roughness from full-rough (A) to the lowest partial-rough (E). Most of the partial-roughs handled should be RrSs.

$$\text{RrSs} \times \text{RrSs} = 3\text{ Rss} + 6\text{ RSs} + 3\text{ RSS} + 4\text{ rr}$$
$$\text{C} \qquad \text{C} \qquad 3\text{ A} \qquad 6\text{ C, D} \quad 3\text{ E} \qquad 4\text{ Sm}$$

(5) Full-roughs crossed together have never given partial-roughs. A full-rough, whatever its parentage, must be RRss or Rrss. There is no way in which factor S, necessary for partial-roughs, can be transmitted by full-roughs.

(6) Full-roughs, one or both of whose parents were partial-roughs, have given no partial-rough young on crossing with smooths of 4-toe stock. Smooths of 4-toe stock are all necessarily rrss and can not transmit factor S.

(7) Partial-roughs crossed with smooths of 4-toe or a similar stock give partial-rough young and also, in most cases, full-rough and smooth young.

$$\text{RrSs} \times \text{rrss} \qquad = \text{Rrss} + \text{RrSs} + 2\text{ rr}$$
$$\text{C} \qquad \text{Sm (4-toe)} \quad \text{A} \qquad \text{C} \qquad 2\text{ Sm}$$

(8) Most partial-roughs crossed with full-roughs give a very similar result to the cross partial-rough by 4-toe smooth, except that fewer smooths are produced.

$$\text{RrSs} \times \text{Rrss} = 3\text{ Rss} + 3\text{ RSs} + 2\text{ rr}$$
$$\text{C} \qquad \text{A} \qquad 3\text{ A} \qquad 3\text{ C} \qquad 2\text{ Sm}$$

(9) The lowest grade of roughs (E) very rarely have either a full-rough parent or full-rough young. They also very rarely have a

smooth parent of such a stock as 4-toe. The parents and offspring of rough E (SS) must necessarily have at least one S (SS or Ss), while full-roughs and 4-toe smooths are ss. The three exceptional rough E's can only be interpreted as extreme minus fluctuations of type RrSs.

(10) Occasionally a smooth from a cross which produces rough E will transmit the rough factor, breeding like a rough E. The discovery of a smooth (RrSS) which had a rough C young one (RrSs) when crossed with a 4-toe smooth (rrss), apparently violating the dominance of roughness, is the kind of exception that proves the rule, coming as it did where predicted.

The descendants of male 4003 illustrate the theory very well. He was of constitution RRSS by theory.

TABLE 56.

		A	B	C	D	E	Sm
P_1	RRSS × rrss.....................	..	..	..	..	4003	4-toe
F_1	RrSs.............................	..	..	11	..	....	....
F_2	7 Rss + 13 RSs + 7 RSS + 9 rr...	8	5	8	3	5	7
	7 A, B 13 C, D 7 E 9 Sm						

Of those called rough B, 2 were close to rough A and 3 were close to rough C.

POSSIBILITIES OF LINKAGE AMONG ROUGH AND COLOR FACTORS.

In the mating just cited, factors R and S enter the cross from the same individual. The excess of full-roughs (Rss), probably 10 where 7 are expected, makes any linkage between R and S very unlikely. Another test is furnished by the cross of double heterozygotes, RrSs with 4-toe smooths, rrss, where it is definitely known whether R and S enter the cross together or apart. Cases which should show coupling if there is linkage are cross 54–1, 2, 4, 5, 6, 12, 15, 16, 17, and cross 72–5, 6, 7. Cases which should show repulsion are cross 61–1, cross 64–1, 3, and cross 72–1, 2, 8, 9, 10.

TABLE 57.

	A, B Rsrs.	C, D RSrs.	Sm rr—	Cross-overs.	Link-ages.
Coupling—RSrs × rsrs..... (C, D Sm)	26	29	60	26	29
Repulsion—RsrS × rsrs.....	14	6	16	6	14
	..	..	..	32	43

The indication of linkage is too slight to be considered significant, especially in view of the excess of cross-overs in the F_2 data.

Thus there is probably no linkage between R and S. It is interesting to analyze the data with regard to possible linkages of these factors with

any of the 5 known sets of color factors. Four of the sets of color factors, those in which non-agouti (a), yellow (e), brown (b), and albinism (C_a) are the lowest recessives, are known to be independent of each other (Part I). As regards the pink-eye factor (p), it is merely known that cross-overs occur between it and non-agouti, albinism, and yellow, and that it is not an allelomorph of brown (*i. e.*, pink-eye × brown gives black-eyed intense young).

Data on the possible repulsion of R and A are furnished by cross 72–1, 2, 5, 6, 8, 9, 10 and cross 64–1. Coupling data are to be found in 64–3 and 66–1, 3.

<div align="center">TABLE 58.</div>

	Ag–Rf ARar	Ag–Sm Arar	B–Rf aRar	B–Sm arar	Cross- overs.	Link- ages.
Ag–Rf B–Sm Coupling —ARar × arar.....	4	7	11	3	18	7
Repulsion—AraR × arar.....	7	5	7	9	16	12
	..	..	..	..	34	19

There is an excess of cross-overs. The most probable interpretation is that there is no linkage.

Data on the coupling of A and S are to be found in crosses 70–1 to 9, 71–1 to 6, 72–1, 2, 3, 4, 5, 6, 8, 9, 10, 64–1, and 74–1. Repulsion data is to be found in 64–3 and 72–5.

<div align="center">TABLE 59.</div>

	Ag–C ASas	Ag–A Asas	B–C aSas	B–A asas	Cross- overs.	Link- ages.
Ag–C, D B–Sm (4-toe) Ag–Sm (¼ cut) B–RfA Coupling— ASas × asas	12	16	16	16	32	28
Repulsion— AsaS × asas	..	1	..	3	3	1
	..	..	..	..	35	29

A and S are quite clearly independent of each other.

Crosses 72–5 to 7 give a few data on the relation of R and S to C. We find in the case of R and C, 4 linkages to 4 cross-overs and in the case of S and C no linkages and 3 cross-overs, indicating probably independence in both cases.

From cross 72–7 we find that cross-overs can occur between R and E, R and B, and S and B. From 61–1 we find that cross-overs can occur between P and R, and P and S.

Summing up: R is quite certainly independent of S and A and cross-overs are known between it and all of the other known factors E, B, C, and P. S is quite certainly independent of A and cross-overs are known between it and B, C, and P, but not as yet E. It is hoped that more definite statements can soon be made on these points.

SUMMARY OF ROUGH TABLES.

Table 60, in which smooths are omitted, shows the closeness of fit of the hypothesis to the data as regards the inheritance of variations of the rough character.

TABLE 60.

Cross.	ss × ss			A	B	C	D	E
45	A	4-toe...........	A	4-toe............	10	..	..	..	..
46	A	Tri............	A	Tri	27	2	..	..	..
49	A	4-toe...........	Sm	4-toe............	28	1	..	..	..
50	A	Tri............	Sm	4-toe	19	..	..	..	..
58	B	Lima..........	B	Lima............	7	5	..	..	..
[1]59	A	Lima..........	Sm	Lima............	21	5	..	..	..
[2]60	B	Lima..........	Sm	Lima...........	5	9	..	..	..
63	A, B	Lima...........	Sm	4-toe, etc........	4	4	..	..	..
[3]65	A	Misc...........	Sm	Misc	17	..	..	..	..
66	A	Misc...........	Sm	Misc	14	1	..	..	..
73	A	¼ cut...........	Sm	4-toe............	2	..	..	..	..
75	A	¼ cut...........	A	¼ cut............	3	..	..	..	..
	Total................................			157	27	..	..	..
	Expectation ss........................			184		0		0

Cross.	Ss × ss			A	B	C	D	E
47	C	Tri............	A	Tri, 4-toe	10	1	5	1	..
[4]51	Sm	Tri............	A	....	6	..	3	3	..
54	C, D	Tri............	Sm	4-toe, etc........	34	..	29	13	1
58	C	Lima..........	B	Lima...........	...	1	..	1	..
[5]59, 60	Sm	Lima..........	A, B	Lima...........	4	1	3	..	..
61	C	Lima..........	Sm	Lima...........	2	1	1	..	..
64	C	ruf. hybrid.....	Sm	4-toe, etc........	3	..	2	..	..
[6]65	Sm	ruf. hybrid.....	A	....	1	1	2	..	..
[7]70	C, D	½ cut..........	A	G. p	8	3	8	2	2
[7]71	Sm	½ cut..........	A	G. p	10	3	9	1	..
72	C, D	½, ¼ cut........	Sm	G. p	12	..	6	6	..
74	Sm	½ cut	A	¼ cut	...	..	1	..	..
	Total................................			90	11	69	27	3
	Expectation ss + Ss....................			100		100		0

Cross.	Ss × Ss			A	B	C	D	E
52	C Tri.............		C Tri		18	6	19	7	12
76	C ⅜ cut.............		C ¼ cut.............		...	..	1	3	1
	Total................................			18	6	20	10	13
	Expectation ss + 2 Ss + SS............			17		33		17

[1]Omitting young of L24.
[2]Omitting young of L6, L24.
[3]Omitting young of A702, A605.
[4]Some of mothers may be ss or SS.
[5]Mothers L24, L6.
[6]Mothers A702, A605.
[7]Including also one ¼ cut.

<div align="center">TABLE 60—Continued.</div>

Cross.	ss × SS	A	B	C	D	E
48	A Tri.............. E Tri..............	...	..	2	1	..
56	Sm 4-toe............ E Tri..............	...	..	13	..	..
67	A 4-toe, tri......... Sm pure Ica..........	...	..	5	..	..
68	A .... Sm pure cut..........	...	..	3	6	..
	Total.........................	...	..	23	7	..
	Expectation Ss......................	0		30		0

Cross.	Ss × SS	A	B	C	D	E
53	C, D Tri........... E Tri..............	...	..	4	1	6
69	C, D Tri........... Sm pure cut..........	...	..	1	1	9
	Total................................	...	..	5	2	15
	Expectation Ss + SS..................	0		11		11

Cross.	SS × SS	A	B	C	D	E
55	E Tri.............. E Tri.................	...	..	..	..	4
	Expectation SS.......................	0		0		4

The interpretation given is no doubt open to objections. In some cases the ratios seem rather aberrant. This is in part due to the small numbers, but also to the overlapping of class ranges. In most cases rough B must be considered as full-rough genetically (Rss), but in some cases it is probably partial-rough (RSs). Rough E usually seems to be RSS, but in some cases must be heterozygous (RSs). It has not been demonstrated that factor S of the wild species is identical with the similar factor of the tricolor stock. If not identical, however, the latter stock differs from the wild by two mutations which neutralize each other, while if identical we can consider that the original tricolor stock had simply persisted in the primitive condition, never having had the rough intensifying mutation, s, of the fancier's roughs.

<div align="center">MINOR VARIATIONS.</div>

Probably part of the minor variations in roughness are due to chance irregularities in development which are not hereditary. This is indicated by the slight asymmetry not uncommonly present. This asymmetry seldom amounts to more than the absence of a member of one pair of rosettes.

No Mendelian analysis has yet been attempted for minor variations, but certain hereditary differences between different stocks are quite

clear.   The Lima stock shows a distinctly lower level of development
of roughness than is found in the 4-toe stock or even among the full-
roughs of tricolor stock.   A large part of the variation and overlapping
in the remaining experiments in which various stocks have been mixed
is made intelligible by assuming that the residual heredity is unfavor-
able for roughness in the wild species and especially favorable in the
4-toe stock.   If we let $\Sigma +$ stand for favorable and $\Sigma -$ for unfavorable
residual heredity, the wild species and presumably the primitive
guinea-pigs are $rrSS\Sigma -$, while the good fancier's roughs, $RRss\Sigma +$
differ by at least three independent sets of factors, all favorable for
roughness.

ROUGHNESS OF SERIES II.

It has been mentioned that irregularities in hair direction have been
found in certain stocks which can not be classified by the grades which
have been defined.   The BW race is a highly inbred race.   No indi-
viduals of the pure stock have ever been observed to have roughness
on the face, back, or toes, but many of them show irregular partings
and crests along the chest and belly.   It will be remembered that in
series I ventral roughness appears only in high-grade roughs—grades
A or B.   Thus the characteristic roughness of the BW stock is nearly
the least characteristic feature of series I.

The only distinction which has been made in these BW roughs is
between strong-rough with two or more ridges and poor-rough with
only one ridge or a mere trace of roughness.   Table 61 shows the
principal results.

TABLE 61.

	Smooth.	Poor rough.	Strong rough.
Smooth × smooth.....	11	6	6
Poor × poor.......	14	1	1
Strong × strong......	5	5	16

It is clear that this roughness is due neither to a simple dominant
nor to a simple recessive.   Aside from this, the results are exceedingly
difficult to interpret, since poor × poor gives more smooth than does
smooth by smooth.   Probably the results will become more harmonious
when more data are obtained.   It seems safe to conclude at present that
this roughness is wholly independent of ordinary roughness in its
causation.

Irregularity in hair direction on the back, not resembling anything
in series I and not correlated with roughness of the hind toes, has
been observed in a few individuals of Arequipa and Ica stock.   It does
not seem to be like the BW roughness, but resembles the latter in the
irregularity of its inheritance.

SUMMARY.

The principal results which have been reached may be summarized as follows:

1. A classification of guinea-pig fur, skin, and eye colors is given with definitions of fur colors in terms of Ridgway's charts (1912).

2. Rodent color factors are conveniently classified as follows:

 a. Factors which affect the distribution and intensity of color largely irrespective of the kind of color.

 b. Factors which govern the differentiation between yellow and dark colors in colored areas of the fur.

 c. Factors which determine the kind of dark color in the areas with dark pigmentation in fur and eyes, without influence on yellow areas.

Definitions of all known guinea-pig color factors are given on this basis and a table of the color varieties arising from combinations of these factors is given.

3. Genetic and biochemical evidence on the physiology of pigment formation suggests the hypothesis that the three groups of factors determine respectively the distribution and rate of production by the nucleus of the following substances:

 a. A peroxidase which, acting alone, oxidizes chromogen in the cytoplasm to a yellow pigment but is so unstable that it must be produced at a relatively high rate to give any pigment at all.

 b. A supplementary substance which, united with the first, makes it a dark-pigment-producing enzyme and of such stability that color develops at a much lower level of production of peroxidase than when the supplement is absent. Above the level at which both produce effects, the dark and yellow-producing enzymes compete in the oxidation of chromogen.

 c. Additions to the second substance which cause variations in dark color but not in yellow or in the competition between dark color and yellow.

4. There is a continuous series of variations in intensity of pigmentation in the yellow, brown, and black series and in eye color. The ordinary dilute guinea-pigs are found to be imperfect albinos in the sense that dilution is due primarily to a member of the series of allelomorphs—intensity, dark-eyed dilution, red-eyed dilution, and albinism, with dominance in the order of increasing intensity.

5. A further step in the analysis of the continuous series of variations of intensity is taken in the demonstration that dilution is imperfectly dominant over red-eye and albinism as regards the yellow series of colors, and that dilution and red-eye are imperfectly dominant over albinism, as regards the black series. Smaller effects are due to the residual heredity of different stocks and to age.

6. Evidence is presented which confirms the hypothesis of Detlefsen (1914) that the light-bellied agouti pattern of tame guinea-pigs, the ticked-bellied agouti of hybrids between the tame guinea-pig and *Cavia rufescens,* and non-agouti (as seen in self blacks or browns) form a series of triple allelomorphs in which light-belly is the highest dominant and non-agouti the lowest recessive. Evidence is presented which

indicates that *Cavia cutleri* possesses the same agouti factor as tame agouti guinea-pigs. Light agouti of *Cavia cutleri* and dark agouti of *Cavia rufescens* are thus variations in a character in two wild species which differ in heredity by a clear-cut Mendelian factor.[1]

7. There is a continuous series of variations between smooth fur and very rough or rosetted fur in guinea-pigs. The primary effects in this series are due to two independent pairs of allelomorphs. One factor, discovered by Castle (1905), is essential to any roughness of the common type, and is completely dominant over its allelomorph found in wild cavies and smooth guinea-pigs; the other, an incomplete recessive to its allelomorph in the wild cavies and some tame guinea-pigs, is necessary for the higher grades of roughness. Second-order effects seem to be due to the residual heredity of different stocks, and probably to non-hereditary irregularities in development. There is a roughness of a different type from the usual which is inherited independently.

GENERAL CONCLUSION.

Most of the successful earlier attempts at Mendelian analysis of heredity naturally dealt with variations which were obviously discontinuous. But in nature such variations are much less common than apparently continuous series of variations. It was thus a common reproach against the Mendelian analysis that it dealt only with exceptional conditions. The work of Nilsson-Ehle, East, and others has shown how quantitative variation may be brought under a Mendelian explanation. MacDowell (1914) presents data on size inheritance from this standpoint and discusses the literature up to that time. Recently two very interesting papers have been published (Dexter, 1914, Hoge, 1915) which analyze the heredity of certain very variable characters in *Drosophila* by means of linkage relations.

Several of the studies in this paper deal with inheritance in continuous series of variations. The only general statement which can be made about the results is that there is no general rule for such cases. Intermediates between varieties which mendelize regularly have been found to follow very definite modes of inheritance, which, however, are very different in different cases and could not possibly be predicted *a priori*. On the other hand, each mode of inheritance is exactly paralleled by cases among the most diverse groups of animals and plants. It may be interesting to summarize the modes of inheritance of intermediates which have been found.

An intermediate condition is sometimes found to be due to an intermediate variation of the essential hereditary factor involved, *i. e.*, to an allelomorph. Thus yellows are intermediate between red and albino

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[1] It should be pointed out, however, that the original stock of *Cavia rufescens* used in these experiments included individuals of the light-agouti character as well as those classed as dark agouti. It seems quite likely that dark agouti arose as a recessive mutation in *C. rufescens.*—W. E. C.

guinea-pigs in appearance, and we find an allelomorph intermediate in dominance between the intensity and albino factor to be responsible for their condition. Sepias are similarly intermediate between blacks and albinos and are due to the same allelomorph of intensity and albinism. The series, light agouti of *Cavia cutleri*, dark agouti of *C. rufescens*, and black, furnishes another example due to triple allelomorphs.

In other cases, the intermediate type is an unfixable one, due to imperfect dominance. Thus cream is the heterozygote between yellow and albino. A "razor back" rough (rough C or D) is the heterozygote between a type smooth except for the hind toes (rough E) and a full-rough (rough A).

A series of deviations from the original type may depend on the presence of a certain factor necessary for any deviation whose effect is modified to different extents by independently inherited factors. Rough A contains the same rough factor (R) as does rough E, but differs in possessing an independent factor variation (s) favorable for roughness. Most of the variation which we have ascribed to residual heredity probably comes under this head.

Deviations from type, which apparently form a natural series, may be due to wholly independent factors whose effects are merely superficially similar. A pink-eyed pale sepia superficially seems as good an intermediate between an intense black and an albino as does a black-eyed sepia, yet the former is due to a variation which is wholly independent of albinism; the latter is due to an allelomorph of albinism. White-spotted animals are sometimes called partial albinos and considered as natural intermediates between the self-colored type and albinos, but genetically they are wholly distinct. Black, agouti, and self yellow form a series which is due to three allelomorphs in mice, but in guinea-pigs two wholly independent sets of factors are involved.

Finally, we must recognize series of variations in which no Mendelian factors have yet been isolated. The series of white-spotted and yellow-spotted types and the series of polydactylous types are examples in guinea-pigs. Further, in all series of variations, to whatever extent analysis has been carried, there always remains some unanalyzed variation. In many cases such variations are known to be hereditary and can be assigned to the residual heredity of particular stocks. Such unanalyzed variations, however, are probably in general complicated by variation which is not hereditary, due apparently to irregularities in development. If we can measure the importance of such non-hereditary variation by the extent of irregular asymmetry met with, it is very important in white and yellow spotting, in the variations in the development of extra toes on the hind feet, and is noticeable in variations in roughness.

In the continuous series of variations several of these phenomena have generally been found together. In the series from smooth to full-

rough we find a primary unit difference, a modifying factor, imperfect dominance in the effects of the latter, effects of residual heredity, and probably some non-heritable variation.   In the series from red through yellow and cream to white we find multiple allelomorphs, imperfect dominance, and small effects due to residual heredity.   In the series black through sepia to white, we find independent factors, multiple allelomorphs which show imperfect dominance, and rather prominent effects due to residual heredity and to age.   This last series is interesting as at least a close parallel in appearance to the series of variations in human hair—black, brown, tow-color, to white.   Thus in each case a complex of the most varied causes underlies an apparently simple continuous series of variations.

EXPERIMENTAL DATA.

EXPLANATION OF TABLES 62 TO 137.

Crosses 1 to 15 include all matings recorded by the writer which involve the inheritance of agouti and in which at least one of the parents had *Cavia rufescens* ancestry.   A large part of the remaining crosses are non-agouti by non-agouti, producing only non-agouti young.   All the young in which the agouti factor should produce a recognizable effect, if present, are classified under the heads Lb, Tb, and Non, which mean light-bellied agouti, ticked-bellied agouti, and non-agouti, respectively. Most of these are the typical (black-red) light-bellied or ticked-bellied agouti or black.   Those which are not typical, *e. g.*, brown-red agouti light-belly, red-eyed sepia, etc., are described further under the column "Remarks."   Those young in which the agouti factor can produce no visible effect, even though present (albinos, reds, yellows, and creams), are described under the column "Unclassified."   Thus the exact color of every one of the young from each mating can be found from the tables, with the exception that white and red spotting are not noted. The matings in each cross are numbered in the first column.   The number, description, and descent of the mother and father are given in the second and third columns, respectively.   As in the case of the young, black-red agouti light-belly or ticked-belly or black, depending on the heading of the column, are understood where no description is given.   The descent is indicated in most cases by a reference to the mating from which the animal was derived.   Thus 3*b*–4 means mating 4 of cross 3*b*.   In other cases the stock is indicated as BB or BW.   The symbol ArF_2 means F_2 from crosses of Arequipa ♂ 1002 with guinea-pigs.   In some cases merely the amount of *Cavia rufescens* blood is given.   Thus M49, in the first cross given, was an ordinary ticked-bellied agouti from mating 9 of cross 1*a*.   Referring to this mating, we see that his parents were female 84, a black of BB stock, and male A1121, a ticked-bellied agouti with $\frac{1}{32}$ *Cavia rufescens* blood.

Crosses 16 to 44 include all matings recorded by the writer in which there was dilution or red-eye in either parents or offspring, except for a few cases among the *Cavia cutleri* hybrids and cases of intense by dilute with only intense young. Some other crosses are included for special reasons bearing on the inheritance in the albino series. There is some repetition from matings outside of 16 to 44, but most of those outside are intense by intense, with only intense and, in some cases, albino young. As in the agouti crosses, all matings are numbered in column 1. The number, description, and descent of the mother and father are given in columns 2 and 3, respectively. All the offspring are classified under the heads Int, Dil, RE, or W, which stand for intense, dilute, red-eye, and white (albino), respectively. A further description of all except the albinos is given under the column "Remarks." The attempt has been made to give the grade of dilution at birth for every dilute or red-eyed animal where known.

Crosses 45 to 57 give the data on the inheritance of rough fur in the 4-toe and tricolor stocks. As before, the matings are numbered. The young are classified under the heads A, B, C, D, E, and Sm, which refer to the grades of roughness defined in the paper and to smooth.

The parents and offspring were black (usually with red and white blotches) except for a few cases which are all noted. Such a symbol as red-B means a red of grade rough B.

Crosses 58 to 62 give the results in the pure Lima stock and 63 the results in the cross of Lima with other stocks. Where no color is given black is always to be understood.

Crosses 64 to 66 give the matings involving rough fur among *Cavia rufescens* hybrids which were recorded by the writer.

Cross 67 gives crosses of pure Ica with rough A stock.

Crosses 68 to 78 give all the data in matings involving *Cavia cutleri* ancestry made by the writer.

The following symbols are used:

AgLb or Ag	= Black-red agouti, light-belly.	BrYAgLb	= Brown-yellow agouti, light-belly.
AgTb	= Black-red agouti, ticked-belly.		
B	= Black.	BrYAgTb	= Brown-yellow agouti, ticked-belly.
BrAgLb	= Brown-red agouti, light-belly.		
BrAgTb	= Brown-red agouti, ticked belly.	LBr	= Light brown.
		Y	= Yellow (black-eye).
Br	= Brown.	Y(Br)	= Yellow (brown-eye).
R	= Red (black-eye).	Cr	= Cream, used in compounds like Y.
R(Br)	= Red (brown-eye).		
SYAgLb	= Sepia-yellow agouti, light-belly.	SAg(R)	= Sepia-white agouti (red-eye).
		Sep(R)	= Sepia (red-eye).
SYAgTb	= Sepia-yellow agouti, ticked-belly.	W	= White or albino.
		Red (p)	= Red (pink-eye).
Sep, S	= Sepia.	Sep (p)	= Sepia (pink-eye).

In such expressions as S_3Y_3Ag the numerals stand for the grades defined in the text.

In crosses 1–15, Lb and Tb are used at the heads of the columns to include any light-bellied or ticked-bellied agouti. Non means non-agouti.

A, B, C, D, E, and Sm are used for grades of roughness and for smooth.

TABLE 62.

Cross 1.—Matings of non-agouti (aa) with ticked-bellied agouti (A′a).

Each of the latter known to be heterozygous because of a non-agouti parent.
Expectation: A′a × aa = A′a + aa (1 AgTb : 1 Non-Ag).

1a. Mother non-agouti, without *rufescens* ancestry.

No.	♀ Non-Ag.	♂AgTb.	Lb.	Tb	Non	Remarks.	Unclassified.
1	3 ♀ ♀ BW...	M49 $\quad$ 1a–9..	...	9	9	....	6 W
2	4 ♀ ♀ 4-toe..	.....Do.............	...	5	8		1 W
3	3 ♀ ♀ BW...	B5 $\quad$ 1d–16.	...	3	9		5 W
4	3 ♀ ♀ 4-toe..	.....Do............	...	2	2		1 W
5	2 ♀ ♀ BW...	B27 $\quad$ 1d–14.	...	4	3		2 W
6	65 $\quad$ BB...	B30 $\quad$ 1a–1..	...	1	2		......
7	2 ♀ ♀ BW...	B69 $\quad$ 1a–1..	...	6	4		2 W
8	3 ♀ ♀ BW...	B191 $\quad$ 1a–5..	...	9	4		4 W
9	84 $\quad$ BB...	A1121 $\quad$ $\frac{1}{32}$....	...	1	2		
10	C22 $\quad$ Misc..	A1474 $\quad$ $\frac{1}{16}$....	...	....	5		
11	C35 $\quad$ Misc..	.....Do.............	...	2	....		
12	3 ♀ ♀ 4-toe..	B171 $\quad$ 1a–4.	...	8	6		1 W
13	3 W $\quad$ BW...	B117 SCrAgTb 1d–11.	...	3	2	3 SCrAgTb, 2 Sep.....	5 W
14	3 W $\quad$ Misc..	.....Do.............	...	2	3	SCrAgTb, BrCrAgTb, 3 Sep.	1 W
15	D44 Sep $\quad$ 16a–3.	.....Do.............	...	1	....	SCrAgTb...........	2 W
16	AA244 Sep 2–12..	.....Do.............	...	1	....	SCrAgTb...........	......
17	BW 43 W $\quad$ BW...	D113 BCrAgTb 3a–7.	...	1	1	SCrAgTb, Sep......	......
18	Sep (R) $\quad$ S.Am.	AA433a $\quad$ 3b–4.	...	4	2	3 AgTb, SAgTb(R), 2 Sep(R).	1 W
	Total.....................		...	62	62		

1b. Mother non-agouti, with *rufescens* ancestry.

No.	♀ Non-Ag.	♂AgTb.	Lb	Tb	Non	Remarks.	Unclassified.
1	A443 $\quad$ $\frac{1}{8}$......	A469 $\quad$ $\frac{1}{8}$.........	...	....	1	LBr.........	....
2	A1390 $\quad$ $\frac{1}{32}$.....	A1050 $\quad$ $\frac{1}{32}$.......	...	....	1		
3	A1227 W $\quad$ $\frac{1}{64}$.....	A781 $\quad$ $\frac{1}{64}$.......	...	3	....	SCrAgTb......	
4	A1413 $\quad$ $\frac{1}{32}$.... / A1291 W $\quad$ $\frac{3}{32}$....	A1449 $\quad$ $\frac{1}{32}$.........	...	1	2	....	W
5	A1309 W $\quad$ $\frac{1}{32}$....	A1513 $\quad$ $\frac{1}{32}$.......	...	1	1	BrAgTb.......	R, R(Br), Cr(Br)
6	A1407 $\quad$ $\frac{3}{32}$.....	A1449 $\quad$ $\frac{3}{32}$.......	...	3	2	Br...........	
7	A1413 $\quad$ $\frac{3}{32}$.....	.....Do..........	...	3	1	....	
8	M115 W $\quad$ $\frac{1}{16}$.....	M189 $\quad$ 1c–3......	...	1	....		
9	M114 1b–7... / M90 Br	....Do.............	...	4	4	SCrAgTb, Sep..	....
10	M90 Br $\quad$ $\frac{1}{16}$.....	.....Do..........	...	1	1	BrCrAgTb, Sep	Cr
11	A1330 $\quad$ $\frac{1}{128}$....	A1331 $\quad$ $\frac{1}{128}$.......	...	....	....	....	W
	Total.....................		...	17	13		

TABLE 62—Continued.

1c. Male genetically, but not visibly ticked-bellied agouti.

No.	♀ Non-Ag.		♂ AgTb.		Lb	Tb	Non	Remarks.	Unclassified.
1	131 W	G. p..	A412 R(Br) $\frac{1}{16}$....		...	....	2	Sep....................	......
2	13a	G. p..	....Do		...	....	3	....	......
3	20	G. p..	....Do		...	3	1	SCrAgTb.............	......
4	58 Sep	Dil ..	B42 W	1a–3 ..	...	3	....	3 SCrAgTb...........	......
5	17, 30 Cr(B)	Dil ..	....Do		...	....	1	Sep....................	2 W
6	55 Cr(Br)	Dil ..	....Do		...	1	....	SCrAgTb.............	W
7	M292	$\frac{3}{32}$...	D18 W	1c–5 ..	...	2	3	SCrAgTb, 2 Sep......	......
8	M326	$\frac{1}{16}$...	....Do		...	1	1	....	4 W
9	M353	$\frac{3}{64}$..	....Do		...	1	1	Sep....................	......
	Total........................				...	11	12		

1d. Male non-agouti, without *rufescens* ancestry.

No.	♀ AgTb.		♂ Non-Ag.	Lb	Tb	Non	Remarks.	Unclassified.
1	[1]A606 AgLb	$\frac{1}{4}$..........	166 4-toe......	...	....	2	....	....
2	[1]A450 AgLb	$\frac{1}{4}$..........	2966 BB........	[1]1	....	1	....	....
3	A340	$\frac{1}{16}$.........	3013 BB........	...	4	3	....	....
4	A341	$\frac{1}{16}$.........	....Do	...	6	5	....	....
5	A357	$\frac{1}{16}$.........	....Do	...	1	2	....	....
6	A1146	$\frac{1}{16}$.........	....Do	...	7	6	....	....
7	A1058	$\frac{1}{32}$.........	....Do	...	1	1	....	....
8	A1171	$\frac{1}{32}$.........	....Do	...	....	2	....	....
9	A1058, A1171	$\frac{1}{32}$.........	2996 BB........	...	3	2	....	....
10	Do..............		1357 BW........	...	5	5	....	2 W
11	A1117	$\frac{1}{32}$.........	....Do..........	...	2	1	SCrAgTb....	....
12	Do..............		2996 BB........	...	1	....	....	....
13	Do..............		3013 BB........	...	2	4	....	....
14	A1450	$\frac{1}{32}$.........	1357 BW........	...	2	1	....	....
15	A1117, A1450	$\frac{3}{32}$.........	....Do..........	...	3	1	....	W
16	A1582	$\frac{1}{64}$.........	2966 BB........	...	1	1	....	....
17	A1583	$\frac{1}{64}$.........	....Do	...	1	2	....	....
18	A1677	$\frac{1}{64}$.........	....Do	...	9	11	....	....
19	A1678	$\frac{1}{64}$.........	....Do	...	1	....	....	....
20	B8	1d–7......	....Do	...	3	2	....	....
21	B23	1d–12......	....Do	...	5	7	....	....
22	B26	1d–14......	....Do	...	2	1	....	....
23	M113	1b–7......	C20 Misc	...	2	1	....	....
24	M442 BrCrAgTb 1b–10.....		86 W BW........	...	....	2	2 Sep.......	....
	Total..............................			[1]1	61	63		

TABLE 62—Continued.

	1e. Male non-agouti (genetically) with *rufescens* ancestry.						
No.	♀ AgTb.	♂ Non-Ag.	Lb	Tb	Non	Remarks.	Unclassified.
1	A1146 $\frac{1}{16}$	A504 W $\frac{1}{16}$	...	...	2	2 Sep.	....
2	B132 1d–3	M293 Y 42–14	...	2	....	SCrAgTb	....
3	B95 1d–4	......Do	...	1			
4	B24 1d–4	......Do	...	...	1		
5	B52 1d–3	M201 W 42–13	...	2	....		
6	B33 1d–18	......Do	...	2	....		W
7	B110 1a–1	......Do	...	...			W
8	B111 1a–1	......Do	...	1	2		W
9	B128 1a–1	......Do	...	1	....		
10	B23 1d–12	......Do	...	1	....		
	Total		...	10	5		

[1] AgLb, but agouti known to be derived from *C. rufescens*.

SUMMARY OF CROSS 1.

No.	aa	A'a	Lb	Tb	Non
1a	♀ ♀ Non-Ag (g.p.)	♂ ♂ AgTb	...	62	62
1b	♀ ♀ Non-Ag (hybrid)	♂ ♂ AgTb	...	17	13
1c	♀ ♀ Non-Ag	♂ ♂ A'a (R or W)	...	11	12
1d	♂ ♂ Non-Ag (g.p.)	♀ ♀ AgTb	1	61	63
1e	♂ ♂ aa (Y or W) hybrid	♀ ♀ AgTb	...	10	5
	Total		1	161	155

TABLE 63.

Cross 2.—Matings of ticked-bellied agouti (A'a) with ticked-bellied agouti (A'a), in which both are known to be heterozygous because of the parentage in each case.

Expectation: A'a × A'a = A'A' + 2A'a + aa (3AgTb : 1 Non-Ag).

No.	♀ AgTb.	♂ AgTb.	Lb	Tb	Non	Remarks.	Unclassified.
1	B15 1d–6	B118 1d–6	....	1	2	....	......
2	B58 1d–15	.....Do		9	2	3 BrAgTb, SYAgTb,Sep	......
3	B59 1d–15	.....Do		6	4	2 BrAgTb	......
4	B68 1a–1	.....Do		5	2	SCrAgTb	......
5	A529 BrAgTb $\frac{1}{32}$	AA15 $\frac{1}{32}$		6	1	BrAgTb, SCr AgTb, BrCr AgTb	......
6	A913 $\frac{1}{32}$	.....Do		5	....	BrAgTb	......
7	A1273 SCrAgTb $\frac{1}{32}$	AA16 $\frac{1}{32}$		4	2	3 SCrAgTb	3W
8	Do	A1121 $\frac{1}{32}$		1	....		
9	A780 $\frac{1}{64}$	A781 $\frac{1}{64}$		5	....	BrYAgTb	3R,Y
10	A1306 $\frac{1}{128}$	A1307 $\frac{1}{128}$		1	....		2W
11	A1561 $\frac{1}{32}$	A1050 $\frac{1}{32}$		3	....		4W
12	A1566 $\frac{1}{32}$	.....Do		5	1	BrAgTb, SCr AgTb, Sep	......
12a	A1566	AA15 $\frac{1}{32}$		2	1	SCrAgTb	......
13	A702 $\frac{1}{32}$	AA16 $\frac{1}{32}$		2	2	Br	......
14	A1450 $\frac{1}{32}$	AA433a 3b–4		1	....		
15	A1058 $\frac{1}{32}$	.....Do		...	...		W
16	A1523 $\frac{1}{32}$	A1449 $\frac{1}{32}$		2	1	BrAgTb	W
17	AA176 41–4	AA177 SCrAgTb 41–4		5	1	SCrAgTb	W
18	AA175 41–4	.....Do		...	...		W
19	M78 9–5	A1161 $\frac{1}{32}$		2	....		
20	M110 1b–6	A1170 $\frac{1}{32}$		1	....		
21	D26 SCrAgTb 1c–4	D33 SCrAgTb 1c–6		....	....		W
	Total		...	66	19		

TABLE 64.

Cross 3.—Matings of ticked-bellied agouti from cross 2 or 12 (A′A′, 2A′a) with non-agouti (aa) made in order to test for the presence of homozygotes.

Expectation: A′A′ × aa = A′a (all AgTb)
   or A′a × aa = A′a + aa (1 AgTb : 1 Non-Ag).

No.	♀ AgTb.		♂ Non-Ag.		Lb	Tb	Non	Remarks.	Unclassified.
	3a. Heterozygous females.								
1	M19	2–16..	393	4-toe....	...	2	1	....	......
2	M203	2–19..	M116 Sep	42–11...	...	....	1	....	......
3	AA211	2–6...	C20	Misc. ...	...	....	2	....	......
[1]4	AA240	12–8..	A1040	$\frac{1}{16}$......	...	2	1	....	......
5	AA257	12–2..	A1040, 356 $\frac{1}{16}$, 4-toe.		...	2	2	....	......
[1]6	AA285 SCrAgTb	12–7..	393	4-toe....	...	1	1	....	......
[1]7	AA242 SYAgTb	12–8..	I5 Sep(R)	21–1....	...	1	2	BCrAgTb, 2 Sep.	......
[1]8	AA240, AA242	12–8..	A1040	$\frac{1}{16}$......	...	2	1	....	......
	7 females............................				...	10	11		
	3b. Possible homozygous females.								
1	AA209	2–11..	C21 Misc.		...	4	....	....	......
2	AA212 BrAgTb	2–6...	C20 Misc.		...	2	....	....	......
3	AA213	2–12..	C21 Misc.		...	8	....	....	......
4	AA217	2–7...	.....Do............		...	8	....	....	......
5	AA298	2–13..	356 4-toe.........		...	3	....	....	......
	5 females............................				...	25	....	....	......

[1]Not certain that both parents were heterozygous (A′a).

TABLE 64.—Continued.

3c. Heterozygous males.

No.	♀ Non-Ag.	♂AgTb.	Lb	Tb	Non	Remarks.	Unclassified.
1	M79 W $\frac{1}{32}$.....	M77 BrAgTb 2–16...	...	1	1	BrAgTb, Br...	3 W
2	{M72 1c–2... / M86 9–1 ...}	....Do.......	...	2	2	BrAgTb, Br...	......
3	M42 LBr 42–12..	AA197 2–10...	...	....	1	....	......
4	M44 Cr 42–12..	.....Do....	...	3	....	SCrAgTb....	......
5	M99 42–13?.	.....Do....	...	1	....	....	......
6	M101 42–13?.	.....Do....	...	2	1	....	......
7	{A1407 $\frac{1}{32}$..... / A1413 $\frac{1}{32}$.....}	AA199 SCrAgTb 2–12...	...	5	3	....	......
8	S6 $\frac{1}{256}$....	AA223 BrYAgTb 2–9....	...	1	....	....	......
9	S15 $\frac{1}{256}$....	.....Do....	...	....	2	Br....	......
10	A1659 $\frac{1}{256}$....	.....Do....	...	2	2	....	......
11	B♀ Misc...	.....Do....	...	2	....	BrAgTb....	......
12	S2 Misc...	AA226 2–13...	...	....	1	....	......
13	A1665 Misc...	.....Do....	...	1	2	....	R
14	S22, A1674 {$\frac{1}{256}$.... / $\frac{1}{128}$....}	.....Do....	...	3	1	....	......
15	B7 1d–7...	AA235 12–1...	[1]1	....	[1]3	....	......
16	B21 1d–9...	.....Do....	...	2	....	....	......
17	B28 1d–14..	.....Do....	...	....	1	....	W
18	M168 $\frac{1}{32}$....	.....Do....	...	....	....	....	W
19	M169 $\frac{1}{32}$....	.....Do....	...	....	1	....	W
20	M177 1c–2...	.....Do....	...	2	3	BrAgTb, LBr .	......
21	4♀♀ Misc...	[2]AA241 SYAgTb 12–8...	...	2	6	SCrAgTb, Sep, LBr.	......
22	B28 1d–14..	[2]AA284 12–7...	...	3	4	Br....	......
23	M183 $\frac{1}{16}$.....	[2]AA299 12–8...	...	4	....	SCrAgTb....	......
24	M261 Sep 7–7....	.....Do....	...	....	1	Sep....	......
25	AA58 $\frac{1}{16}$....	.....Do....	...	2	1	....	......
26	M261, AA58	.....Do....	...	2	2	....	......
	9 males...........................		1	40	38		

3d. Homozygous male.

No.	♀ Non-Ag.	♂AgTb.	Lb	Tb	Non	Remarks.	Unclassified.
1	S6 $\frac{1}{256}$.....	AA253 SCrAgTb 2–7......	...	6	....	2 BrAgTb....	......
2	S15 $\frac{1}{256}$.....	....Do....	...	4	....	....	......
3	A1659 $\frac{1}{256}$.....	....Do....	...	2	....	2 SCrAgTb...	......
	1 male...........................		...	12	....		

[1]A litter with an unexpected AgLb. Paternity not wholly certain.
[2]Not certain that one of parents was heterozygous (A'a).

SUMMARY OF CROSS 3.

	AgTb, from cross A'a×A'a, tested by cross with Non-Ag.	Lb.	Tb.	Non
3a	7♀♀ .... A'a..........	...	10	11
3b	5♀♀ .... A'A'(?)......	...	25	..
3c	9♂♂ .... A'a..........	1	40	38
3d	1♂ .... A'A'........	...	12	..

TABLE 65.

Cross 4.—Ticked-bellied agoutis, known to be homozygous because of test (cross 3), or parentage (cross 4), crossed together.

Expectation: A'A' × A'A' = A'A' (all AgTb).

No.	♀ AgTb.		♂ AgTb.		Lb	Tb	Non	Remarks.	Unclassified.
1	AA213	2–12..	AA253 SCrAgTb 2–7...	...	...	9	....	2 SYAgTb, SCrAgTb, BrAgTb, BrYAgTb, BrCrAgTb	....
2	AA217	2–7...	.....Do..............	...	...	11	....	3 SYAgTb, SCrAgTb	....
3	AA613	4–1...	.....Do..............	...	...	3	....	3 SCrAgTb...	....
4	AA671	4–1...	.....Do..............	...	...	....	....	....	W
5	AA577	4–2...	AA573 BrAgTb 4–1....	...	...	1	....	BrAgTb......	....
6	AA606 SYAgTb 4–2...		.....Do..............	...	...	2	....	SCrAgTb.....	....
	Total........................				...	26	....		

TABLE 66.

Cross 5.—Homozygous ticked-bellied agouti (A'A') crossed with heterozygous ticked-bellied agouti (A'a) or with non-agouti (aa).

Expectation: All AgTb (A'A' or A'a).

No.	♀ AgTb or Non-Ag.		♂ AgTb.		Lb	Tb	Non	Remarks.	Unclassified.
1	M181 BrCrAgTb 15–15..		AA253 SCrAgTb 2–7...	...	...	1	....	SYAgTb.....	W
2	Do..............		AA573 BrAgTb 4–1...	...	...	5	....	3 BrAgTb, 2 BrCrAgTb	2 W
3	M442 BrCrAgTb 1b–10..		AA573 BrAgTb 4–1...	...	...	1	....	BrCrAgTb...	....
4	M296 SAgTb 14–4...		M116 Sep 42–11...	...	...	3	....	3 SYAgTb...	....
5	D194 Sep(R) 26–2...		AA670 SCrAgTb 4–1...	...	...	3	....	2 SCrAgTb, SAgTb(R)	2 W
	Total........................				...	13	....		

TABLE 67.

Cross 6.—Matings of non-agouti hybrid (aa) with homozygous light-bellied agouti (AA).
Expectation: AA × aa = Aa (all AgLb).

No.	♀ Non-Ag.	♂ AgLb.	Lb	Tb	Non	Remarks.	Unclassified.
		6a. Female non-agouti.					
1	A605 $\frac{1}{4}$.........	2597 G.p....	2	...	....	....	....
2	A642 $\frac{1}{4}$.........	.....Do.....	2	...	....	....	....
3	A842 $\frac{1}{4}$.........	.....Do.....	5	...	....	....	....
	Total..................		9	...	....		

No.	♀ AgLb.	♂ Non-Ag.	Lb	Tb	Non	Remarks.	Unclassified.
		6b. Male non-agouti hybrid.					
1	15a G.p..	A674 Sep $\frac{1}{4}$....	6	...	....	....	....
2	3520 Cr(Br) G.p..	.....Do.....	3	...	....	2 SCrAg, BrCrAg.	Y(Br), 2 Cr(Br), W
3	3a G.p..	1040 $\frac{1}{16}$..	7	...	....	....	....
4	11a G.p..	A504 W $\frac{1}{16}$..	3	...	....	....	....
5	3392 G p..	A1539 $\frac{1}{16}$..	1	...	....	SCrAgLb........	....
	Total..................		20	...	....		

SUMMARY OF CROSS 6.

No.	aa (hybrid).	AA (g.p.).	Lb	Tb	Non
6a	♀ ♀ Non-Ag....	♂ ♂ Ag Lb.......	9	....	....
6b	♂ ♂ Non-Ag....	♀ ♀ Ag Lb.......	20	....	....
	Total......................		29	....	....

TABLE 68.

Cross 7.—Matings of non-agouti (aa) with light-bellied agouti (Aa) of *rufescens* ancestry, known to transmit non-agouti, because of a non-agouti parent.

Expectation: Aa × aa = Aa + aa (1 AgLb : Non-Ag).

7a. Female AgLb.							
No.	♀ AgLb.	♂ Non-Ag.	Lb	Tb	Non	Remarks.	Unclassified.
1	A601 $\frac{1}{16}$	103 4-toe	1	....	1	....	W
2	A614 $\frac{1}{16}$	224 4-toe	....	....	2	....	......
3	A953 $\frac{1}{32}$	A718 $\frac{1}{32}$	2	....	3	....	......
4	A1310 $\frac{1}{32}$	166 4-toe	....	....	2	....	......
5	A1311 $\frac{1}{32}$	....Do	1	....	1	....	......
6	A1324 $\frac{1}{32}$	A719 W $\frac{1}{32}$	....	....	....	Sep	3 W
7	M102 6b–1	A462 W $\frac{1}{16}$	....	....	2	Sep..........	......
8	Do............	M2 $\frac{1}{16}$	3	....	2	SCrAgLb......	......
9	{ M357 SCrAgLb 10b–7.... / D95 SCrAgLb 10b–8.... }	} 20W BW....	3	....	2	3 SCrAg, 2 Sep.	7 W
10	D61 SCrAgLb 13–5....	BW 36 W BW....	....	....	....	....	W
11	D63 SCrAgLb 13–5....	....Do..........	2	....	2	2 SAg(R), Sep, Sep(R)	......
12	{ D69 SCrAgLb 18–5.... / M425 SCrAgLb 13–7.... }	} ....Do..........	2	....	1	2 SCrAg, Sep,..	W
	Total........................		14	....	18		

7b. Male AgLb.							
No.	♂♀ Non-Ag.	♂ AgLb.	Lb	Tb	Non	Remarks.	Unclassified.
1	67 G.p ..	M123 13–2..	2	....	1	....	......
2	D43 Sep 16a–3.	D94 SCrAgLb 10b–8.	1	....	1	SCrAg, Sep...	......
3	M236 Sep(R) ArF₂..	M331 BrCrAgLb 42–10.	....	....	....	....	W
4	D45 Sep 16a–3.	D94 SCrAgLb 10b–8.	1	....	1	SCrAg, Ag....	W
	Total........................		4	....	3		

SUMMARY OF CROSS 7.

No.	Aa (hybrid).	aa	Lb	Tb	Non
7a	♀♀ AgLb....	♂♂ Non-Ag..	14	..	18
7b	♂♂ AgLb....	♀♀ Non-Ag..	4	..	3
	Total...............		18	..	21

TABLE 69.

Cross 8.—Matings of ticked-bellied agouti (A′a) with homozygous light-bellied agouti (AA).

Expectation: AA × A′a = AA′ + Aa (all AgLb).

No.	♀ AgLb.	♂ AgTb.	Lb	Tb	Non	Remarks.	Unclas-sified.
		8a. Female AgLb.					
1	03 G.p..............	B5 1*d*–16........	5	...	...	....	......
2	3392 G.p..............	.....Do............	4	...	...	SCrAg......	......
3	02, 03 G.p..............	A1155 $\frac{1}{16}$...........	4	...	...	....	......
4	5*a* G.p..............	A1474 $\frac{1}{16}$...........	8	...	...	....	......
5	20*a* G.p.................	.....Do............	4	...	...	SCrAg......	......
	Total.............................		25	...	...		

No.	♀ AgTb.	♂ AgLb.	Lb	Tb	Non	Remarks.	Unclas-sified.
		8b. Male AgLb.					
1	B33 1*d*–18.....	2597 G.p.....	3	...	...	....	......
2	B36 1*d*–18.....	.....Do...........	5	...	...	....	......
3	B37 1*d*–20.....	.....Do...........	2	...	...	....	......
4	B52 1*a*–3......	.....Do...........	3	...	...	....	......
5	{B40 W 1*a*–3...... / B37, B33 above.... }	.....Do...........	6	...	...	....	......
6	A702 $\frac{1}{32}$........	.....Do...........	2	...	...	....	......
7	A913 $\frac{1}{32}$........	.....Do...........	2	...	...	....	......
8	[1]AA606 SYAgTb 4–2......	724 SAg(R) (Ica)....	2	...	...	2 SYAgLb..	......
	Total.............................		25	...	...		
	Total cross 8.............................		50	...	...		

[1]AA606 was A′A′

TABLE 70.

Cross 9.—Matings of light-bellied agouti (Aa) with ticked-bellied agouti (A′a), both known to be heterozygous with non-agouti.

Expectation: Aa × A′a = AA′ + Aa + A′a + aa (2 AgLb : 1 AgTb : 1 Non-Ag).

No.	♀ AgLb.	♂ AgTb.	Lb	Tb	Non	Remarks.	Unclas-sified.
1	3015 G.p........	A1474 $\frac{1}{16}$........	6	2	5	....	3R
2	M46 BrCrAg 13–3.......	A1170 $\frac{1}{32}$........	2	...	...	BrAgLb.....	W
3	M57 13–1.......	.....Do..........	...	1	1	....	...
4	A1310 $\frac{1}{32}$........	A1449 $\frac{1}{32}$........	...	1	1	....	Cr
5	Do............	A1513 $\frac{1}{32}$........	...	1	...	....	...
6	A1311 $\frac{1}{32}$........	A1449 $\frac{1}{32}$........	1	...	...	....	...
7	Do............	A1513 $\frac{1}{32}$........	5	1	2	....	...
8	A1026 $\frac{1}{32}$........	A1050 $\frac{1}{32}$........	2	...	1	....	...
	Total.............................		16	6	10		

<div align="center">TABLE 71.</div>

Cross 10.—Matings of light-bellied agouti from such crosses as 8 and 9 (AA', Aa) with non-agouti, made in order to test whether light-bellied agouti can transmit both ticked-bellied agouti and non-agouti.

Expectation: AA' × aa = Aa + A'a (1 AgLb : 1 AgTb).
  or Aa × aa = Aa + aa (1 AgLb : 1 Non-Ag).

10a. Females Aa.

No.	♀ AgLb.		♂ Non-Ag.		Lb	Tb	Non	Remarks.	Unclassified.
1	B120	8b–2	C20	G.p.	2	....	3	....	......
2	B140	8a–2	M328 B–Y	42–17	3	....	1	....	......
3	Do		20 W	BW	3	....	2	....	......
4	M195	9–7	M116 Sep	42–11	....	....	2	2 Br	......
5	M217	8a–3	356	4-toe	1	....	2	....	......
6	M282	15–12	M116 Sep	42–11	2	....	2	Sep	......
7	A1562 W	$\frac{1}{32}$	AA83	$\frac{1}{64}$	....	....	2	....	......
8	A1691	8b–7	.....Do		6	....	6	....	......
	7 females				17	....	20		

10b. Females AA'.

No.	♀ AgLb.		♂ Non-Ag.		Lb	Tb	Non	Remarks.	Unclassified.
1	A389 BrAgLb	$\frac{1}{16}$	A511 W	$\frac{1}{16}$	1	....	....	....	2 W,R
2	A499 BrAgLb	$\frac{1}{16}$	AA83	$\frac{1}{64}$	1	2	....	BrAgLb,BrAgTb	R
3	A1688	8b–6	.....Do		2	3	....	BrAgTb	......
4	A1690	8b–7	.....Do		1	5	....	....	3 R
5	B139	8a–2	M328 B–Y	42–17	3	2	....	3 SYAgLb	......
6	Do		20 W	BW	....	2	....	SCrAgTb	......
7	B141 SCrAgLb	8a–2	M328 B–Y	42–17	1	3	....	SCrAgLb, 3 SY AgTb	......
8	Do		20 W	BW	2	1	....	2 SCrAgLb, SCr AgTb	6 W
9	M25	9–1	356	4-toe	2	3	....	....	......
10	M27a	9–1	393	4-toe	2	5	....	....	......
11	M82	9–7	M116 Sep	42–11	2	3	....	SCrAgLb, BrY AgLb, SYAgTb	......
12	M92	8a–4	.....Do		1	1	....	....	......
	10 females				18	30	....		

TABLE 71—Continued.

10c. Males Aa.

No.	♀ Non-Ag.	♂ AgLb.	Lb	Tb	Non	Remarks.	Unclassified.
1	75 BB....	A581 $\frac{1}{16}$ ...	2	....	2	....	....
2	08 W 4-toe...	....Do	2	....	3	BrAgLb..........	4 R,Y?
3	09 W 4-toe...	....Do	2	....	4	....	....
4	M7 $\frac{1}{16}$	M133 8a-4...	3	....	3	SCrAgLb, Sep.....	....
5	{M7 $\frac{1}{16}$ / AA58 $\frac{1}{16}$}	....Do	2	....	2	....	....
6	M183 $\frac{1}{16}$	....Do .....,	1	....	1	....	....
7	M261 Sep 7a-7..	....Do	1	....	....	....	....
8	S7 $\frac{1}{256}$	M205 8a-4...	2	....	1	....	....
9	S2 $\frac{1}{256}$	....Do	4	....	3	....	R
10	A1665 $\frac{1}{256}$	....Do	1	....	2	....	....
11	S7, A1665 $\frac{1}{256}$	....Do	3	....	2	....	2 R
12	B137 1a-1...	B155 8a-1...	1	....	2	....	....
13	{B133 1d-3.. / B98 1a-3..}	....Do	1	....	7	....	....
14	D148 W 1c-8...	D240 BCrAgLb14-5..	1	....	1	SCrAg, Sep......	....
	5 males........................		26	....	33		

10d. Males AA'.

No.	♀ Non-Ag.	♂ AgLb.	Lb	Tb	Non	Remarks.	Unclassified.
1	31 Misc.....	M138 9-1....	....	2	....	....	....
2	M255 1a-10....	....Do	4	5	....	....	....
3	M253 1a-10....	....Do	4	3	....	....	....
4	M256 1a-10....	....Do	1	1	....	....	....
5	M254, M256 1a-10....	....Do	1	2	....	....	....
6	AA279 3a-3....	....Do	1	1	....	....	....
7	C22, AA278 G.p., 3a-3	....Do	4	....	....	....	....
8	B♀♀ (above)..	....Do	5	5	....	....	....
9	M168 $\frac{1}{32}$	M91 8a-4...	3	2	....	SCrAgLb..........	....
10	{M169 $\frac{1}{32}$ / M171 $\frac{1}{32}$}	....Do	1	5	....	{BrYAgLb, 2 BrCr AgTb}	....
11	M177 1c-2.....	....Do	1	4	....	SYAgTb..........	....
12	M86 9-1......	M210 15-14..	....	1	....	....	....
13	M79 W $\frac{1}{32}$	....Do......	3	1	....	BrAgLb..........	....
14	B31 1a-1....	B121 8b-2...	2	3	....	....	....
15	B53 1a-3....	....Do	1	2	....	....	....
16	B54 1a-1....	....Do	4	2	....	....	....
17	C29 G.p	....Do	1	2	....	....	....
18	B♀♀ (above)..	....Do	5	4	....	....	....
19	M119 $\frac{1}{32}$	B130 8a-1...	3	2	....	....	....
20	AA174 14-1.....	....Do	1	3	....	....	....
	5 males........................		45	50	....		

SUMMARY OF CROSS 10.

No.	AgLb (Aa or AA') tested by cross with Non-Ag (aa).		Lb	Tb	Non
10a	7 females Aa........	....	17	..	20
10c	5 males Aa........	....	26	..	33
	Total...........	....	43	..	53
10b	10 females AA'.......	....	18	30	..
10d	5 males AA'........	....	45	50	..
	Total...........	....	63	80	..

<center>TABLE 72.</center>

Cross 11.—Light-bellied agoutis (AA') crossed together.

Both parents known to carry recessive ticked-belly by test (except in the case of AA533 with one young).

Expectation: AA' × AA' = AA + 2AA' + A'A' (3 AgLb : 1 AgTb).

No.	♀ AgLb.		♂ AgLb.	Lb	Tb	Non	Remarks.	Unclassified.
1	A1690	8b–7.....	M91 8a–4......	4	2	....	....	....
2	M25	9–1......	.....Do........	7	3	....	4 SYAgLb....	....
3	M27a	9–1......	.....Do........	5	....	....	....	....
4	M25, M27a	9–1......	.....Do........	4	....	....	....	....
5	B139	8a–2.....	.....Do........	1	....	....	....	....
6	M25, M27, B139	....	.....Do........	1	3	....	BYAgTb....	....
7	AA533	11–1.....	.....Do........	1	....	....	....	....
8	AA588	11–2.....	.....Do........	2	1	....	SYAgTb....	....
	Total....................			25	9	....		

<center>TABLE 73.</center>

Cross 12.—Miscellaneous matings of ticked-bellied agouti with ticked-bellied agouti.

No.	♀ AgTb.		♂ AgTb.		Lb	Tb	Non	Remarks.	Unclassified.
1	AA203 BrCrAgTb	2–5....	AA16	$\frac{1}{32}$......	...	3	1	SCrAgTb, LBr	W
2	M19	2–16...	.....Do..............		...	3	....	LBr.......	W
3	AA497 SYAgTb	10d–11.	AA284	12–7...	...	1	1	LBr.......	R
4	AA598	3c–22..	.....Do..............		...	2	....	BrAgTb...	W
5	A1523	$\frac{1}{32}$.....	AA199 SCrAgTb	2–12...	...	3	....	SCrAgTb..	....
6	M203	2–19...	AA284	12–7...	...	3	2	Sep.......	....
7	AA202	2–7....	AA15	$\frac{1}{32}$.....	...	4	....	2 SCrAgTb	....
8	AA206	2–9....	AA177 SCrAgTb	1b–3...	...	7	....	4 SCrAgTb	....
9	Do.................		AA507	3c–22..	...	1	....	....	....
10	AA342	12–8...	.....Do..............		...	4	....	....	....
11	A1058	$\frac{1}{32}$.....	M298	15–16..	...	2	....	BrAgTb...	....
12	AA242 SCrAgTb	12–8...	B117 SCrAgTb	1d–11..	...	1	....	SCrAgTb..	....

<center>TABLE 74.</center>

Cross 13.—Miscellaneous matings of light-bellied agouti guinea-pig with non-agouti hybrid.

No.	♀ AgLb.		♂ Non-Ag.		Lb	Tb	Non	Remarks.	Unclassified.
1	⎰3392 ⎱3444	G.p.... G.p....	⎱A1539	$\frac{1}{16}$.....	3	...	1	SCrAgLb.........	....
2	⎰01 ⎱02	G.p.... G.p....	⎱A426 R(Br)	$\frac{1}{16}$.....	5	...	1	....	3 R
3	3256 BrYAgLb	G.p....	A678 W	$\frac{1}{16}$.....	7	...	2	7 BrCrAgLb, 2 LBr	......
4	3220 BrAgLb	G.p....	.....Do........		2	...	....	2 BrAgLb.........	......
5	271 SAg(R)	G.p....	M333 Y	$\frac{1}{16}$.....	4	...	....	4 SCrAgLb........	......
6	3a	G.p....	M34 Sep	16c–1..	...	...	2	2 Sep...........	......
7	241 SAg(R)	ArF₂...	M328 B–Y	42–17..	3	...	....	3 SCrAgLb........	......
8	2♀♀ SAg(R)	ArF₂..	M156 R	$\frac{1}{16}$.....	4	...	3	2 SAg(R).........	4 W
9	I2, I6 SAg(R)	21–1 ..	M34 Sep	16c–1..	1	...	2	SCrAg, Sep.......	......

TABLE 75.

Cross 14.—Miscellaneous matings of light-bellied with ticked-bellied agouti.

No.	♀ AgLb.	♂ AgTb.	Lb	Tb	Non	Remarks.	Unclassified.
1	{20a, 5a G.p.... ; 3015, 3014 G.p....}	A412 R(Br) $\frac{1}{16}$.....	3	...	1	....	3 R
2	20a, 5a, 3014 G.p....	A1474 $\frac{1}{16}$.....	3	1	....	....	....
3	AA173 14–1...	AA199 SCrAgTb 2–12...	1	1	....		....
4	M82 9–7....	A1161 $\frac{1}{32}$.....	....	2	....	SCrAgTb....	....
5	4♀♀ SAg(R) ArF₂...	AA508 3d–2...	13	1	4	9 SCrAg, BY AgTb	....

TABLE 76.

Cross 15.—Miscellaneous crosses involving the inheritance of agouti in *rufescens* hybrids.

No.	♀ Misc.	♂ Misc.	Lb	Tb	Non	Remarks.	Unclassified.
1	AA171 R 14–1..	AA1161 AgTb $\frac{3}{32}$....	...	1	....	....	R, Cr
2	M137 R 9–1...	AA286 AgTb 3c–4..	...	1	....		....
3	Do.............	M29 Br 1b–6..	...	2	....		....
4	M181 BrCrAgTb 15–15.	C20 B G.p...	...	6	....		....
5	A1472 BrAgLb $\frac{1}{16}$....	163 B 4-toe..	2	...	....		....
6	{A1562 W $\frac{1}{16}$.... ; A1688 AgLb 8b–6..}	AA83 B $\frac{1}{64}$....	4	...	1		....
8	{M27a AgLb 9–1... ; M19 AgTb 2–16..}	393 B 4-toe..	3	6	2		....
9	{M175 AgLb 8a–3... ; AA242 SCrAgTb 12–8..}	A1040 B $\frac{1}{16}$....	1	...	4		....
10	{M195 AgLb 9–7... ; M203 AgTb 2–19..}	M116 Sep 42–11.	1	2	....		....
11	{B122 AgLb 8b–2.. ; AA212 BrAgTb 2–6...}	C20 B G.p...	2	2	2		....
12	{M92 AgLb 8a–4.. ; M106 Y 10c–2..}	A1513 $\frac{3}{32}$....	1	2	1	BrAgTb........	2 R
13	{M85 R 1b–5.. ; M82 AgLb 9–7..}	AA1161 AgTb $\frac{3}{32}$....	1	1	....	BrAgLb........	W
14	{M56 AgLb 13–1.. ; M50 AgTb 1b–7..}	A1170 AgTb $\frac{1}{32}$....	1	...	2		....
15	AA28 W $\frac{1}{32}$....	A1513 AgTb $\frac{3}{32}$....	2	3	....	BrAgLb, SCrAg Tb, BrCrAg Tb	R, 2 Cr
16	A1523 AgTb $\frac{1}{32}$....	M83 AgLb 9–7...	1	1	....		....
17	A1413 B $\frac{3}{32}$....	Do.............	2	...	....		....
18	M84 R(Br) 1b–5..	A1161 AgTb $\frac{1}{32}$....	...	...	....		W
19	{A556 AgLb $\frac{1}{16}$.... ; A587 W $\frac{1}{16}$.... ; A533 Y $\frac{1}{16}$....}	104 B 4-toe..	2	...	3	....	....
20	{A495 AgLb $\frac{1}{16}$.... ; A867 B $\frac{1}{16}$....}	163 B 4-toe..	...	...	1	....	3 R
21	{AA621 SYALb 11–2.. ; AA621 SYALb ......}	BW36 W.....BW... ; 724 SAg(R) Ica...	... ; 3	1	....	SCrAgTb...... ; 3 SYAgTb....	
22	3♀♀ SAg(R) ArF₂..	M224 BrAgLb 9–2...	21	1	....	10 SAg(R), SAg Tb(R)	W
23	198W ArF₂..	M291 B $\frac{3}{32}$....	1	...	....		....
24	2♀♀ W ArF₂..	M2 B $\frac{1}{16}$....	2	...	1		3 W
25	D125 W 1a–13	I33 SAg(R) 24–1..	1	...	1	SAg(R), Sep(R).	....
26	D427 W 1a–14.	I33 SAg(R)	...	1	1	SAgTb(R), Sep (R)	....
27	D86 W 7b–3..	126 BWAg(R) 24–2..	2	...	3	2 SAg(R), 3 Sep (R)	....

<div align="center">

TABLE 77.

Cross 16.—Matings of dilute with albino of intense stock.

</div>

Expectation: $C_dC_d \times C_aC_a = C_dC_a$ (all Dil).
$$C_dC_r \times C_aC_a = C_dC_a + C_rC_a \text{ (1 Dil : 1 RE).}$$
$$C_dC_a \times C_aC_a = C_dC_a + C_aC_a \text{ (1 Dil : 1 W).}$$

16a. Females C_dC_d.

No.	♀ Dil.		♂ W (intense stock).		Int	Dil	RE	W	Remarks.
1	AA621 S₃Y₂Ag	39–4....	BW36 W	BW....	....	1	...	...	S₅Cr₅AgTb
2	58 Sep₅	Dil	75 W	BW....	....	2	...	...	2 Sep₃
3	Do.................		20 W	BW....	...	3	...	...	2 Sep₃, Sep₃–Cr₅
4	Do.................		B42 W	1a–3...	...	3	...	...	3 S₅Cr₅AgTb
	Total..				...	9	...	...	

16b. Females C_dC_a.

No.	♀ Dil.		♂ W (intense stock).		Int	Dil	RE	W	Remarks.
1	15 Sep₆	Dil	75 W	BW....	....	4	...	3	2 Sep₃, 2 Sep₄
2	17 Cr₅	Dil	B42 W	1a–3...	....	1	...	...	Sep₆
3	30 Cr₅	Dil	.....Do		...	...	...	2	....
4	55 Cr₅(Br)	Dil	.....Do		...	1	...	1	S₅Cr₅AgTb
5	{ M42 LBr	42–12...	{ 15 W	BW....	....	8	...	4	8 Sep₅
	{ M44 Cr₅	42–12...							
6	M42 LBr	42–12...	.....Do		...	3	...	...	3 Sep₄
7	AA600 LBr–Cr₅	39–19...	.....Do		...	1	...	...	Sep₄
8	M357 S₄Cr₅Ag	42–1....	20 W	BW....	...	3	...	3	S₃Y₄Ag, S₅Cr₅Ag Sep₄
9	B141 S₄Y₄Ag	39–23...	.....Do		...	3	...	6	S₂Cr₅AgTb, 2 S₃ Y₄Ag
10	D43, D44 Sep₃	16a–3...	.....Do		...	...	...	4	
11	D45 S₃–Cr₅	16a–3...	.....Do		...	1	...	1	Sep₃–Cr₅
12	D95 S₃Y₄Ag	16b–9...	20 W	BW....	...	...	...	2	
12a	D95, M357	....	.....Do		...	2	...	2	Sep₃, S₃Cr₅Ag
13	D67 S₃–Cr₅	16c–4...	.....Do		...	...	...	2	
14	M384 Sep₅	39–12...	86 W	BW....	...	3	...	1	Sep₅, 2 Sep₄
15	M442 BrCr₅AgTb	39–12...	.....Do		...	2	...	...	Sep₄, Sep₅
16	D66 S₃–Cr₅	40b–13..	.....Do		...	1	...	1	Sep₂
	Total..				...	33	...	32	

16c. Males C_dC_a.

No.	♀ W.		♂ Dil.		Int	Dil	RE	W	Remarks.
1	132 W	4-toe....	A674 Sep₆	⅓.......	...	4	...	...	3 Sep₆–Cr₅, Sep
2	12a W	4-toe....	M34 Sep₆–Cr₅	16c–1..	...	3	...	...	3 Sep₆–Cr₆
3	5 W	BW.....	.....Do		...	2	...	1	2 Sep₅
4	82 W	BW.....	B117 S₄Cr₅AgTb	39–14...	...	2	...	5	S₃–Cr₅, S₃Cr₅Ag Tb
5	{ BW11 W	BW.....	} ....Do		...	3	...	...	2 S₅Cr₅AgTb Sep₄
	{ BW15 W	BW.....							
6	I20, 21, 23, 29 W	22–.....	13 Cr₅(Br)	Dil.......	...	8	...	13	2 S₅Y₄Ag, 3 S₄– Y₄, 2 S₄, S₅
	Total..				...	22	...	19	

SIMILAR MATINGS FROM CROSSES 19, 27, AND 33, AND SUMMARY OF CROSS 16.

No.	Dilute.	W (intense stock).	Int	Dil	RE	W
	5 ♀♀ Dil (CdCr)....	W BW....	....	9	10	....
	3 ♂♂ Dil (CdCr)....	...Do.....	....	3	5	....
	7 ♀♀ Dil (CdCa)....	...Do.....	....	5	....	7
	1 ♂ Dil (CdCa)....	...Do.....	....	4	....	2
16a	♀♀ Dil (CdCd)....	W	....	9	....	
16b	♀♀ Dil (CdCa)....	...Do.....	....	33	....	32
16c	♂♂ Dil (CdCa)....	...Do.....	....	22	....	19
	Total..................		....	85	15	60

TABLE 78.

Cross 17.—Matings of intense from intense stock with albinos from dilute stock or from two dilute parents.

Expectation: $CC \times C_aC_a = CC_a$ (all Int).
$CC_a \times C_aC_a = CC_a + C_aC_a$ (1 Int : 1 W).

	17a. Male CC.						
No.	♀ W.	♂ Int.	Int	Dil	RE	W	Remarks
1	M117 W 42–11............	3013 B BB..........	2	....	....	....	2 B
2	M327 W 42–17............	....Do..........	2	....	....	....	2 B
3	D 37 W Dil.............	....Do..........	2	....	....	....	2 B
	Total.................		6	....	....	....	

	17b. Female CC.						
No.	♀ Int.	♂ W.	Int	Dil	RE	W	Remarks.
1	22, 23, 33 Ag Misc..........	11 W Dil..........	11	....	....	....	11 Ag
2	C18, C50 Ag Misc.........	....Do..........	6	....	....	....	6 B
3	{C24 Ag Misc......... / C34 B Misc.........	}....Do..........	4	....	....	....	Ag, 3 B
4	22 Br Misc.........	....Do..........	4	....	....	....	4 Br
5	{S22 B $\frac{1}{256}$........ / A1665 B $\frac{1}{256}$.........	}M313 W 42–16.......	4	....	....	....	4 B
7	3223 B Misc.	....Do..........	2	....	....	....	2 B
8	B232 B 1d–21.........	M201 W 42–13	2	....	....	....	2 B
9	B23 AgTb 1d–12.........	....Do..........	1	....	....	....	AgTb
	Total.................		34	....	....	....	

	17c. Male CC$_a$.						
No.	♀ W.	♀ Int.	Int	Dil	RE	W	Remarks.
1	D37 W Dil.............	06 B BW..........	2	....	....	....	2 B
2	♀ W Dil.............	....Do..........	1	....	....	2	B
	Total.................		3	....	....	2	

TABLE 78—Continued.

					Int	Dil	RE	W	Remarks.
No.	♀ Int.		♂ W.						
1	D48 Ag	17b–1......	11 W Misc.......		....	....	....	2	
2	D49 Ag	17b–1......	..... Do		1	....	....	2	Br.
3	D224 Ag	17b–1......	..... Do		1	....	....	1	R
3a	D224, D226 Ag	17b–1......	..... Do		3	....	....	2	Ag, 2 B
4	B33 AgTb	1d–18......	M201 W 42–13		2	....	....	1	2 AgTb
5	B52 AgTb	1a–3......	..... Do		2	....	....	....	2 AgTb
6	B110 AgTb	1a–1......	..... Do		....	....	....	1	
7	B111 AgTb	1a–1......	..... Do		3	....	....	1	AgTb, 2 B
8	B128 AgTb	1a–1......	..... Do		1	....	....	....	AgTb
	Total.................................				13	....	....	10	

17d. Female CC$_a$. (table title)

SUMMARY OF CROSS 17.

No.	Intense (intense stock).	White (dilute stock).	Int	Dil	RE	W
17a	♂ ♂ Int CC....	W............	6	..	..	..
17b	♀ ♀ Int CC....	..... Do.......	34	..	..	..
17c	♂ ♂ Int CC$_a$..	..... Do.......	3	..	..	2
17d	♀ ♀ Int CC$_a$..	..... Do.......	13	..	..	10
	Total..................		56	..	..	12

TABLE 79.

Cross 18.—Intense guinea-pigs, each of which had a dilute parent known to transmit albinism, mated with albinos or red-eyes to test whether the same intense animal can transmit both dilution and albinism.

Expectation: $CC_d \times C_{ra}C_{ra} = CC_{ra} + C_dC_{ra}$ (1 Int : 1 Dil).

$CC_a \times C_{ra}C_{ra} = CC_{ra} + C_aC_{ra}$ (1 Int : 1 RE or W).

18a. Male CC$_d$ by test.

No.	♀ Red-eye.		♂ Int.		Int	Dil	RE	W	Remarks.
1	515 SAg (R)	ArF$_2$..	D 10 R (Br) 35–1...		3	3	...	...	3 Ag,SCrAg, 2 S$_3$Y$_4$Ag
2	774 SAg (R)	ArF$_2$..	.....Do		1	...	...	...	Ag
3	515, 774 SAg (R)	ArF$_2$..	.....Do		3	3	...	...	3 Ag,2 S$_2$Y$_4$Ag, S$_4$Cr$_5$ Ag
4	514 Sep (R)	ArF$_2$..	.....Do		4	3	...	...	4 B,2 S$_2$–Cr$_5$, S$_4$–Y$_4$
5	281 SAg (R)	ArF$_2$..	D 30 R (Br) 36–1...		3	8	...	...	3 Ag,S$_3$Y$_4$Ag, S$_4$Y$_4$Ag S$_5$Cr$_5$Ag, 2 S$_1$Y$_4$Ag 2 S$_4$Cr$_5$Ag, S$_5$Cr$_6$ Ag
6	741 SAg (R)	ArF$_2$..	.....Do		3	3	...	...	3 Ag,2 S$_3$Y$_4$Ag, S$_5$Y$_4$ Ag
7	241 SAg (R)	ArF$_2$..	AA508 AgTb 3d–2...		2	1	...	...	2 B,S$_3$Cr$_5$Ag
8	413 SAg (R)	ArF$_2$..	.....Do		3	2	...	...	3 Ag,B$_1$Y$_4$AgTb, S$_3$Cr$_5$ Ag
9	759 SAg (R)	ArF$_2$..	.....Do		1	7	...	...	Ag,S$_3$Y$_4$Ag, S$_2$Y$_4$Ag 4 S$_4$Cr$_5$Ag, S$_5$Cr$_5$ Ag
10	M430 SAg (R)	18c–4.	.....Do		2	...	...	...	2B
	Total, 3 males........................				25	30	...	...	

Table 79—Continued.

18b. Female CC$_d$ by test.							
No.	♀ Int.	♂ Red-eye or W.	Int	Dil	RE	W	Remarks.
1	M292 B $\frac{3}{32}$....	D 18 W 16b–3..	2	3	...	...	AgTb, B,S₆Cr₆AgTb, 2 Sep₆
2	M353 B $\frac{3}{64}$....	.....Do.............	1	1	...	...	AgTb,Sep₅
3	D6a R (Br) 35–1..	724 SAg (R) Ica....	2	1	...	...	(Cross 20)
	Total, 3 females......................		5	5	...	...	

18c. Male CC$_a$ by test.							
No.	♀ Red-eye or W.	♂ Int.	Int	Dil	RE	W	Remarks.
1	271 SAg (R) ArF₂..	M224 BrAg 40b–12.	5	...	3	1	5 Ag,2 S₄Ag(R), S₇Ag (R)
2	278 SAg (R) ArF₂..	.....Do.............	2	...	5	...	2 Ag,5 SAg(R)
3	716 SAg (R) ArF₂..	.....Do.............	4	...	3	...	4 Ag,S₅Ag(R), SAg(R) S₄AgTb (R)
4	233 SAg (R) ArF₂..	M156 R (B) $\frac{1}{16}$.....	5	...	2	3	2 Ag, 3 B,2 SAg (R)
5	773 SAg (R) ArF₂..	.....Do.............	...	...	...	1	
6	236 Sep (R) ArF₂..	AA433a AgTb 3b–4...	1	...	2	1	AgTb,S₃AgTb (R) Sep₃ (R)
7	264 Sep (R) ArF₂..	.....Do.............	2	...	1	...	2 AgTb,Sep₄ (R)
8	485 Sep (R) ArF₂..	D7 R (Br) 35–1...	4	...	3	...	4 B,Sep₆ (R), 2 Sep(R)
9	235 Sep (R) ArF₂..	D13 R (Br) 35–1...	2	...	1	1	2 Ag,Sep₄ (R)
10	693 W ArF₂..	.....Do.............	2	...	...	2	Ag, B
11	D42 W 16b–1.	.....Do.............	...	...	...	3	
12	AA578 W 3c–18.	.....Do.............	3	...	...	...	2 Br, Ag
13	3 ♀♀ W ArF₂..	M291 B $\frac{3}{32}$.....	6	...	...	9	5 B, Ag
14	4 ♀♀ W Misc..	M339 B 40a–14.	11	...	...	13	11 B
15	3 ♀♀ W ArF₂..	M2 B $\frac{1}{16}$.....	10	...	...	7	2 Ag, 8 B
	Total, 8 males........................		57	...	20	41	

TABLE 80.

Cross 19.—Matings of dilute from cross 18*a* or 43, with albino.

Expectation: $C_dC_r \times C_aC_a = C_dC_a + C_rC_a$ (1 Dil : 1 RE) (1–6).
$C_dC_a \times C_aC_a = C_dC_a + C_aC_a$ (1 Dil : 1 W) (7–13).

No.	♀ Dil (or W).		♂ W (or Dil).		Int	Dil	RE	W	Remarks.
1	D72 S$_3$Y$_4$Ag	18*a*–5..	BW36 W BW....		...	1	2	...	S$_4$–Y$_4$, S$_3$Ag (R), Sep$_3$ (R)
2	D63 S$_4$Y$_4$Ag	43–2...	.....Do.............		...	1	3	...	Sep$_4$, 2 S$_3$Ag (R), Sep$_4$ (R)
3	D121 W	18*c*–9..	D71 S$_5$Cr$_5$Ag 18*a*–5..		...	2	2	...	S$_3$Cr$_5$Ag, S$_4$–Cr$_5$, S$_5$Ag(R) Sep$_3$ (R)
4	I57 W	22–3...	.....Do.............		...	...	2	...	S$_3$Ag(R), Sep$_3$(R)
5	D148 W	1*c*–8...	D240 S$_2$Y$_4$Ag 18*a*–9..		...	2	...	...	S$_4$Cr$_5$Ag, Sep$_4$
6	D239 W	18*c*–6..	.....Do.............		...	3	1	...	2 S$_5$Cr$_5$Ag, S$_5$–Cr$_6$, S$_4$Ag (R)
7	D61 S$_5$Y$_4$Ag	43–2...	BW36 W BW....		...	...	...	1	
8	D241 S$_5$Cr$_5$Ag	18*a*–9..	BW50 W BW....		...	1	...	1	S$_5$Y$_4$Ag
9	D69 S$_4$Cr$_5$Ag 18*a*–5.. / M425 SYAg 43–1...		BW36 W BW....		...	3	...	1	2 S$_4$Cr$_5$Ag, Sep$_4$
10	S772 W	ArF$_2$..	D70 S$_4$Y$_4$Ag 18*a*–5..		...	1	...	...	S$_4$Cr$_5$Ag
11	256 W	ArF$_2$...	.....Do.............		...	3	...	3	3 S$_4$Cr$_5$Ag
12	S781 W	ArF$_2$...	.....Do.............		...	2	...	1	S$_3$Y$_4$Ag, S$_4$–Cr$_5$
13	D69 S$_4$Cr$_5$Ag	18*a*–5..	BW36 W BW....		...	3	...	...	3 S$_4$Y$_4$Ag
14	D206 S$_4$–Y$_4$	18*a*–4..	BW50 W BW....		...	1	...	...	Sep$_6$
	2 females C$_d$C$_r$....................				...	2	5	...	
	2 males C$_d$C$_r$.....................				...	7	5	...	
	3 females C$_d$C$_a$....................				...	2	...	3	
	1 male C$_d$C$_a$.....................				...	6	...	4	
	2 females (?).....................				...	6	...	...	

TABLE 81.

Cross 20.—Matings of pure Ica male 724 C$_r$C$_r$.

Expectation: $CC \times C_rC_r = CC_r$ (all Int) (1).
$CC_d \times C_rC_r = CC_r + C_dC_r$ (1 Int : 1 Dil) (2–3).
$C_dC_d \times C_rC_r = C_dC_r$ (all Dil) (4–5).
$C_dC_a \times C_rC_r = C_dC_r + C_rC_a$ (1 Dil : 1 RE) (6).

No.	♀ Misc.		♂ Red-eye Ica.	Int	Dil	RE	W	Remarks.
1	5 ♀ ♀ B	Tri or 4-toe	724 SAg(R) Ica...	9	...	...	...	9 Ag
2	D6a R(Br)	35–1......	.....Do.........	2	1	...	...	2 Ag, S$_2$Y$_4$Ag
3	D209 R(Br)	36–3......	.....Do.........	1	...	...	...	Ag
4	AA606 S$_2$Y$_3$AgTb	40*a*–8.....	.....Do.........	...	2	...	...	2 S$_2$Y$_4$Ag
5	AA621 S$_3$Y$_2$Ag	39–4......	.....Do.........	...	3	...	...	3 S$_2$Y$_4$Ag
6	SA61 Sep$_4$	32–2......	.....Do.........	...	1	1	...	B$_1$Cr$_5$Ag, S$_5$Ag(R)

TABLE 82.

Cross 21.—Matings of pure Ica male 575 CC$_r$.

Expectation: $CC_r \times C_aC_a = CC_a + C_rC_a$ (1 Int : 1 RE).

No.	♀ W.		♂ Int Ica.	Int	Dil	RE	W	Remarks.
1	5 ♀ ♀ W BW....		575 Ag Ica..	9	...	4	...	4 Ag, 5 B, 2 S$_4$Ag(R), 2 Sep$_4$(R)

TABLE 83.

Cross 22.—Matings of intense F_1 Ica (cross 21) with albinos.
Expectation: $CC_a \times C_aC_a = CC_a + C_aC_a$ (1 Int : 1 W).

No.	♀ W (or Int. F_1 Ica.		♂ Int F_1 Ica (or W).	Int	Dil	RE	W	Remarks.
1	2 ♀ ♀ W	BW.....	I3 Ag 21–1...	4	....	....	3	4 B
2	141 W	ArF₂....	.....Do	....	....	....	4	
3	M79 W	$\frac{1}{3}$2.......	I4 B 21–1...	2	....	....	4	2 B
4	D17 W	16b–3...	.....Do	....	....	....	2	
5	I9 Ag	21–1....	♂ W BW....	2	....	....	2	2 B
6	I11 Ag	21–1....	.....Do	4	....	....	4	Ag, 3 B
7	I7 B	21–1....	.....Do	4	....	....	6	4 B
	Total......................			16	....	....	25	

TABLE 84.

Cross 23.—Matings of red-eye F_1 Ica (cross 21) with albinos of intense stock.
Expectation: $C_rC_a \times C_aC_a = C_rC_a + C_aC_a$ (1 RE : 1 W).

No.	♀ White.	♂ Red-eye F_1 Ica.	Int	Dil	RE	W	Remarks.
1	S W BW....	I5 Sep₄(R) 21–1....	...	...	3	...	3 Sep₃(R)

TABLE 85.

Cross 24.—F_2 from red-eye F_1 Ica (cross 21).
Expectation: $C_rC_a \times C_rC_a = C_rC_r + 2 C_rC_a + C_aC_a$ (3 RE : 1 W).

No.	♀ Red-eye F_1 Ica.	♂ Red-eye F_1 Ica.	Int	Dil	RE	W	Remarks.
1	I2 S₄Ag(R) 21–1..	I5 Sep₄(R) 21–1..	...	...	5	5	(S₂, S₃, S₅) Ag (R), S₄(R), S₅ (R)
2	I6 S₄Ag(R) 21–1..	.....Do	...	...	12	1	(B₀, 3 S₂, S₃, S₆) Ag (R); (B₀, S₂, 2 S₄, S₅, S₆)(R)

TABLE 86.

Cross 25.—Matings of F_2 Ica (cross 24) with albinos.
Expectation: $C_rC_r \times C_aC_a = C_rC_a$ (all RE) (1–7).
$C_rC_a \times C_aC_a = C_rC_a + C_aC_a$ (1 RE : 1 W) (8–9).

No.	♀ White.		♂ Red-eye F_2 Ica.	Int	Dil	RE	W	Remarks.
1	D86 W	43–3....	I26 B₀WAg(R) 24–2..	...	...	5	...	S₄Ag(R), S₅Ag(R), S₃ (R), 2 S₅(R)
2	M431 W	18c–4...	.....Do	...	...	6	...	3 S₄Ag(R), 2 S₆Ag(R), Sep₄(R)
3	D76, D78 W 18c–14..		I37 B₀(R) 24–2..	...	...	5	...	2 S₅(R), 3 S₆(R)
3a	D76 W	18c–14..	.....Do	...	...	4	...	S₃, S₄, S₅, S₆
4	D77 W	18c–14..	.....Do	...	...	5	...	3 S₆(R), 2 S₆(R)
5	D125 W	16c–4...	I33 S₂Ag(R) 24–1..	...	...	2	...	S₆Ag(R), S₆(R)
6	BW48 W	BW....	.....Do	...	...	1	...	S₆(R)
7	D427 W	44–3....	.....Do	...	...	2	...	S₆AgTb(R), S₆(R)
8	D73 W	42–6....	I34 Sep₄(R) 24–1..	...	...	3	2	3 S₄(R)
9	S755 W	ArF₂....	.....Do	...	...	...	1	

TABLE 87.

Cross 26.—Matings of red-eye F_1 Ica (cross 21) with dilute.

Expectation: $C_dC_d \times C_rC_a = C_dC_r + C_dC_a$ (all Dil).
$C_dC_a \times C_rC_a = C_dC_r \times C_dC_a + C_rC_a + C_aC_a$ (2 Dil : 1 RE : 1 W).

No.	♀ Dil (or Red-eye F_1 Ica.		♂ Red-eye F_1 Ica (or Dil).		Int	Dil	RE	W	Remarks.
1	AA242 S_3Y_3AgTb	40a–6..	I5 Sep$_4$(R)	21–1...	....	3	....	....	B_1Cr_5AgTb, B_1–Cr_5, Sep$_5$
2	{AA244 Sep$_4$ M261 Sep$_4$	39–15.. 41–2...	} ....Do..............		...	8	4	5	{5 B_1, S_4, S_5–Cr_5, S_6, S_3(R), 2 S_4(R), S_6(R)
3	I2 S_4Ag(R)	21–1...	M34 Sep$_6$–Cr_5 16c–1..	....	...	1	....	....	S_3
4	I6 S_4Ag(R)	21–1...	.....Do..............		...	2	....	....	S_7Cr_5Ag, S_7–Cr_5

TABLE 88.

Cross 27.—Matings of dilute from cross 26 with albinos.

Expectation: $C_dC_r \times C_aC_a = C_dC_a + C_rC_a$ (1 Dil : 1 RE) (1–6).
$C_dC_a \times C_aC_a = C_dC_a + C_aC_a$ (1 Dil : 1 W) (8–12).

No.	♀ W (or Dil).		♂ Dil (or W).		Int	Dil	RE	W	Remarks.
1	3 ♀ ♀ W	Misc...	D89 Sep$_3$	26–3..	....	4	6	...	2 S_4, S_5–Y_4, S_6–Cr_6, 2 S_5(R), S_6(R), 2 S_7(R), S_8(R)
2	D221 W	$\frac{1}{32}$...	D196 B_1	26–2..	....	1	....	...	S_3
3	G30 W	St	.....Do..............		....	1	3	...	S_5, S_4(R), S_3(R), S_7 (R)
4	D115 B_1–Cr_5	26–1...	BW50	BW ..	....	....	3	...	3 S_3(R)
5	D197 B_1	26–2..	}BW46	BW ..	....	3	2	...	3 S_4, 2 S_5(R)
6	D198 B_1	26–2...							
7	BW43 W	BW....	D113 B_1Cr_5AgTb	26–1..	....	2	....	....	S_4, S_5–Cr_5AgTb
8	482 W	ArF$_2$..	D123 S_1–Cr_5	26–4..	....	3	...	1	S_5, 2 S_5–Y_4
9	D42 W	16b–1...	D55 S_5–Cr_5	26–2..	....	4	...	3	S_5, S_6, S_4, S_6–Cr_6
10	BW56, 57	BW....	D114 Sep$_5$	26–1..	....	4	...	2	2 S_4, 2 S_4–Y_4
11	D122 S_7Cr_5Ag	26–4...	BW50	BW ..	....	....	...	2	
12	D195 Sep$_4$	26–2...	.....Do..............		...	1	...	1	S_4

TABLE 89.

Cross 28.—Matings of pure Arequipa male 1007 C_dC_d with black guinea-pigs.

Expectation: $CC \times C_dC_d = CC_d$ (all Int).
$CC_a \times C_dC_d = CC_d + C_dC_a$ (1 Int : 1 Dil).

No.	♀ Intense.	♂ Dilute (Arequipa).	Int	Dil	RE	W	Remarks.
1	2 ♀ ♀ B 4-toe.......	[1]1007 SYAg.......	4	....	....	....	3 Ag, B
2	4 ♀ ♀ B BW........	.....Do..........	10	....	....	....	5 Ag, 5 B
3	1442 B BW........	.....Do..........	3	2	....	....	2 Ag, B, SCrAg, Sep$_3$

[1]1007 SYAg C_dC_d from 1001 BRAg CC_d and 1002 SCrAg C_dC_r pure Arequipa stock.

TABLE 90.

Cross 29.—Matings of intense F_1 (cross 28) with $\male$ 1007.

Expectation: $CC_d \times C_dC_d = CC_d + C_dC_d$ (1 Int : 1 Dil).

No.	$\female$ Intense ArF$_1$.	$\male$ Dilute (Arequipa).	Int	Dil	RE	W	Remarks.
1	SA4 Ag 28–3	[1]1007 SYAg	3	. . . .	. . . .	. . . .	2 Ag, R
2	SA8 Ag 28–2	. . . . Do	2	2	. . . .	. . . .	Ag, R, B$_1$–Y$_3$, Y$_3$
3	{SA4, SA8 . . . . {SA10 B 28–2	} . . . . Do	3	2	. . . .	. . . .	2 Ag, B, B$_1$Y$_3$Ag, Y$_3$

[1]1007 SYAg C$_d$C$_d$ from 1001 BRAg CC$_d$ and 1002 SCrAg C$_d$C$_r$ pure Arequipa stock.

TABLE 91.

Cross 30.—Mating of dilute F_1 (cross 28) with $\male$ 1007.

Expectation: $C_dC_a \times C_dC_d + C_dC_d + C_dC_a$ (all Dil).

No.	$\female$ Dilute ArF$_1$.	$\female$ Intense (Arequipa).	Int	Dil	RE	W	Remarks.
1	SA3 Sep$_3$ 28–3	[1]1007 SYAg	. . . .	2	. . . .	. . . .	B$_1$Y$_3$Ag, Y$_3$

[1]1007 SYAg C$_d$C$_d$ from 1001 BRAg CC$_d$ and 1002 SCrAg C$_d$C$_r$ pure Arequipa stock.

TABLE 92.

Cross 31.—F_2 from intense F_1 Arequipa (cross 28).

Expectation: $CC_d \times CC_d = CC + 2 CC_d + C_dC_d$ (3 Int : 1 Dil).

No.	$\female$ Intense ArF$_1$.	$\male$ Intense ArF$_1$.	Int	Dil	RE	W	Remarks.
1	{SA6 B 28–2 . . . . {SA11 B 28–2	} SA2 B 28–2	17	3	. . . .	. . . .	17 B, 2 B–Y$_3$, B$_2$–Y$_4$
2	SA13 B 28–3	SA7 Ag 28–2	1	. . . .	. . . .	. . . .	B
3	{SA8 Ag 28–2 . . . . {SA10 B 28–2	} . . . . Do	3	. . . .	. . . .	. . . .	Ag, 2 B
4	SA8 Ag 28–2	. . . . . Do	1	2	. . . .	. . . .	Ag, B$_2$Y$_3$Ag, B$_2$–Y$_3$
5	SA4 Ag 28–3	. . . . . Do	1	2	. . . .	. . . .	Ag, 2 B$_1$Y$_3$Ag
	Total		23	7	. . . .	. . . .	

TABLE 93.

Cross 32.—F_2 from dilute F_1 × intense F_1 (cross 28).

Expectation: $C_dC_a \times CC_d = CC_d + CC_a + C_dC_d + C_dC_a$ (2 Int : 2 Dil).

No.	$\female$ Dil ArF$_1$.	$\male$ Int ArF$_1$.	Int	Dil	RE	W	Remarks.
1	SA3 Sep$_3$ 28–3	SA7 Ag 28–2	1	1	. . . .	. . . .	B, B$_2$Y$_3$Ag
2	Do	SA12 Ag 28–3	1	1	. . . .	. . . .	B, S$_4$

TABLE 94.

Cross 33.—Mating of dilute F_1 Arequipa with albino.

Expectation: $C_dC_a \times C_aC_a = C_dC_a + C_aC_a$ (1 Dil : 1 W).

No.	♀ Dil ArF₁.	♂White.	Int	Dil	RE	W	Remarks.
1	SA3 Sep₃ 28–3...........	75 W BW..............	....	....	....	1	

TABLE 95.

Cross 34.—Matings of intense F_1 Arequipa with albinos.

Expectation: $CC_d \times C_aC_a = CC_a + C_dC_a$ (1 Int : 1 Dil).

No.	♀ Int ArF₁ (or W).	♂W (or Int ArF₁).	Int	Dil	RE	W	Remarks.
1	SA4 Ag 28–3....	M313 W 42–16..	....	2	...	...	2 Y4
2	SA10, 11, 13 B 28–2, 3..	.....Do........	4	8	...	...	3 B, R, 2 S₃, 4 S₃–Cr₅, 2 Y₄
3	I49 W 22–2....	SA26 Ag 28–1...	3	2	...	...	2 Ag, B, S₃Y₄Ag, S₃Cr₅Ag
4	I61 W 24–1....	.....Do........	3	1	...	...	2 Ag, B, S₂
5	349 W ArF₂....	.....Do........	1	1	...	...	Ag, S₃
6	I49, 349 W	.....Do........	2	6	...	...	Ag, B,S₃ Cr₅Ag, 2 S₅Y₄Ag, 2 S₅Cr₅Ag, S₃–Cr₅
	Total......................		13	20	...	...	

TABLE 96.

Cross 35.—Mating of cream of dilute selection stock with a red stock free from albinism or dilution.

Expectation: $CC \times C_dC_a = CC_d + CC_a$ (all Int).

No.	♀ Intense.	♂Dilute.	Int	Dil	RE	W	Remarks.
1	4♀ ♀ R(B₁) Misc.....	00 Cr₆(Br) Dil......	12	....	....	....	11 R(Br), Y₂(Br)

TABLE 97.

Cross 36.—F_1 (cross 35) mated with father.

Expectation: $CC_d \times C_dC_a = CC_d + CC_a + C_dC_d + C_dC_a$ (2 Int : 2 Dil) (3).
$CC_a \times C_dC_a = CC_d + CC_a + C_dC_a + C_aC_a$ (2 Int : 1 Dil : 1 W) (1–2).

No.	♀ Intense F₁.	♂Dilute.	Int	Dil	RE	W	Remarks.
1	D1 R(Br) 35–1....	00 Cr₆(Br) Dil...	4	6	...	2	4 R(Br), 2 Y₄(Br), 4 Cr₅(Br)
2	D2 R(Br) 35–1....	.....Do.........	...	1	...	1	Cr₆(Br)
3	D6 R(Br) 35–1....	.....Do.........	3	4	...	...	3 R(Br), Y₂(Br), 3 Cr₅(Br)
4	D136 R(Br) 36–1....	.....Do.........	2	1	...	...	2 R(Br), Cr₅(Br)

TABLE 98.

Cross 37.—Matings of dilute with dilute in the dilute-selection stock.

Expectation: $C_dC_d \times C_dC_d = C_dC_d$ (all Dil).
$C_dC_d \times C_dC_a = C_dC_d + C_dC_a$ (all Dil) (1).
$C_dC_d \times C_dC_a = C_dC_d + 2 C_dC_a + C_aC_a$ (3 Dil : 1 W) (2–11).

No.	♀ Dilute.		♂ Dilute.		Int	Dil	RE	W	Remarks.
1	D301 Y$_4$	Dil....	D292 Y$_4$	Dil...	...	3	...	...	Y$_3$, 2 Cr$_5$
2	Do............		D298 Cr$_6$	Dil...	...	2	...	...	Y$_3$, Cr$_5$
3	D300 Cr$_6$	Dil....	.... Do..........		...	3	...	1	Y$_3$, 2 Cr$_5$
4	D299 Cr$_6$	Dil....	.... Do..........		...	5	...	...	Y$_4$, 3 Cr$_5$, Cr$_6$
5	D289 Cr$_6$	Dil....	D290 Cr$_6$	Dil...	...	6	...	1	Y$_3$, 4 Cr$_5$, Cr$_6$
6	D291 Cr$_6$	Dil....	.... Do..........		...	...	...	2	
7	{D260 Y$_3$(Br)	Dil....	}D261 Cr$_6$(Br) Dil...		...	4	...	1	Y$_3$(Br), 3 Cr$_6$(Br)
	D262, D263 Cr$_6$(Br) Dil....								
8	D263 Cr$_6$(Br)	Dil....	.....Do...........		...	3	...	2	Y$_3$(Br), 2 Cr$_6$Br
9	D262 Cr$_6$(Br)	Dil....	.....Do...........		...	3	...	2	Y$_3$(Br), Cr$_6$(Br), Cr$_6$(Br)
10	{D265 Cr$_6$(Br)	37–7..	}....Do...........		...	4	...	...	Y$_3$(Br), 3 Cr$_6$(Br)
	D266 Cr$_6$(Br)	37–7..							
11	D265	37–7..	.....Do...........		...	2	...	1	Y$_3$(Br), Cr$_6$(Br)
	Total (excluding 1)............				...	32	...	10	

TABLE 99.

Cross 38.—Matings of dilute with albino in the dilute-selection stock.

Expectation: $C_dC_d \times C_dC_a = C_dC_a$ (all Dil).
$C_dC_a \times C_aC_a = C_dC_a + C_aC_a$ (1 Dil : 1 W).

No.	♀ White (or Dilute).		♂ Dilute (or W).		Int	Dil	RE	W	Remarks.
	38*a.*								
1	D293 W	Dil	D292 Y$_4$	Dil	....	4	....	....	4 Cr$_5$
2	D294 W	Dil	....Do..........		....	2	....	....	2 Cr$_6$
3	D264 Y$_3$(Br) 37–7......		11 W	Dil	....	2	....	....	2 Cr$_6$(Br)
	2C$_d$C$_d$...............				....	8	....	....	
	38*b,*								
1	D293 W	Dil	D290 Cr$_6$	Dil	....	2	....	....	2 Cr$_5$
2	D302 W	Dil	D298 Cr$_5$	Dil	....	1	....	....	Cr$_5$
3	D303 W	Dil	.....Do..........		....	2	....	....	2 Cr$_5$
4	D 75 W	Dil	D267 Cr$_6$(Br) 37–7.....		....	...	....	4	....
5	Do...............		D274 Cr$_6$(Br) Dil		....	2	....	1	2 Cr$_5$(Br)
6	{D276 W	Dil	}D261 Cr$_6$(Br) Dil		....	3	....	2	3 Cr$_6$(Br)
	D272 W	Dil							
	5 C$_d$C$_a$..............				....	10	....	7	

TABLE 100.

Cross 39.—All matings of intense with intense which have given dilute young, except those given in cross 31.

Expectation: $CC_d \times CC_d = CC + 2\,CC_d + C_dC_d$ (3 Int : 1 Dil) (1–7).
$CC_d \times CC_a = CC + CC_d + CC_a + C_dC_a$ (3 Int : 1 Dil) (8–33).
3, 9, 11, 24, 26, 30, and 32 not wholly certain.

No.	♀ Intense.	♂ Intense.	Int	Dil	RE	W	Remarks.
1	M353 B $\frac{3}{64}$.....	SA26 Ag 28–1...	3	1	...	...	Ag, B, R, S_2–Y_2
2	A780 AgTb $\frac{1}{64}$.....	A781 AgTb $\frac{1}{64}$.....	7	2	...	...	4 AgTb, 3 R, BrYAg Tb, Y
3	B58 AgTb 1d–15..	B118 AgTb 1d–6...	9	2	...	...	5 AgTb, 3 BrAgTb, B, S_3Y_3AgTb, S_2
4	M25 AgLb 9–1....	M91 AgLb 8–4....	6	4	...	...	3 Ag, 3AgTb, 2 SYAg Lb, 2 S_3Y_2AgLb
5	AA588 Ag 39–4...	.....Do...........	2	1	...	...	2 Ag, S_3Y_3AgTb
6	{M25, M27a Ag 9–1.... / B139 Ag 39–23..}	....Do...........	3	1	...	...	{Ag, 2 AgTb, B_1Y_4Ag Tb}
7	M177 B 1c–2...	.....Do...........	4	1	...	...	Ag, 3 AgTb, SYAgTb
8	M168 B $\frac{3}{32}$....	.....Do...........	4	1	...	...	2 Ag, 2 AgTb, SCr_6Ag
9	M169, M171 B $\frac{3}{32}$....	.....Do...........	3	3	...	...	3 AgTb, 2 BrCrAgTb, BrYAg
10	B68 AgTb 1a–1...	B118 AgTb 1d–6...	6	1	...	...	4 AgTb, 2 B, S_3Cr_5 AgTb
11	A443 B $\frac{1}{8}$......	A469 AgTb $\frac{1}{8}$......	....	1	...	...	LBr
12	M90 Br $\frac{1}{16}$....	M189 AgTb 39–30..	....	3	...	...	$BrCr_5$AgTb, S_5, Cr_6
13	{M90 Br $\frac{1}{16}$.... / M114 B 1b–7...}	.....Do...........	6	2	...	...	3 AgTb, 3 B, S_5Cr_6 AgTb, S_5
14	A1117 B $\frac{1}{32}$.....	1357 B BW....	2	1	...	...	AgTb, B, S_4Cr_5AgTb
15	A1566 AgTb $\frac{1}{32}$.....	A1050 AgTb $\frac{1}{32}$.....	4	2	...	...	3 AgTb, BrAgTh, SCr AgTb, S_4
16	Do.............	AA15 AgTb $\frac{1}{32}$.....	2	1	...	...	AgTb, B, SCrAgTb
17	A529 BrAgTb $\frac{1}{32}$.....	.....Do...........	5	2	...	...	3 AgTb, B, BrAgTb, SCrAgTb, BrCrAg Tb
18	AA202 AgTb 40b–8..	.....Do...........	2	2	...	...	2 AgTb, 2 SCrAgTb
19	M177 B 1c–2...	AA235 AgTb 40b–7..	4	1	...	...	AgTb, 2 B, BrAgTb, LBr–Cr_5
20	M102 AgLb 6b–1...	M2 B $\frac{1}{16}$...	4	1	...	...	2 Ag, 2 B, S_5Cr_5Ag
21	3392 AgLb Misc ..	A1539 B $\frac{1}{16}$....	....	1	...	...	SCrAg
22	3392, 3444 Ag Misc ..	.....Do...........	3	1	...	...	2 Ag, B, SCrAg
23	3392 Ag Misc ..	B5 AgTb 1d–16..	3	1	...	...	3 Ag, S_4Y_4Ag
24	20a Ag Misc ..	A1474 AgTb $\frac{1}{16}$....	3	1	...	...	3 Ag, SCrAg
25	A1310 Ag $\frac{1}{32}$....	A1449 AgTb $\frac{1}{32}$....	2	1	...	...	AgTb, B, Cr
26	M203 AgTb 2–19...	AA284 AgTb 39–18..	4	1	...	...	3 AgTb, B, S
27	M82 Ag 9–7....	A1161 AgTb $\frac{1}{32}$.....	1	1	...	...	AgTb, SCrAgTb
28	AA171 R $\frac{1}{32}$.....	......Do...........	2	1	...	...	AgTb, R, Cr
29	M183 B $\frac{1}{16}$....	AA299 AgTb 40–6...	3	1	...	...	3 AgTb, SCrAgTb
30	20 B Misc ..	A412 R(Br) $\frac{1}{16}$....	3	1	...	...	2 AgTb, B, SCrAgTb
31	M7 B $\frac{1}{16}$....	M133 Ag 8–4....	4	2	...	...	2 Ag, 2 B, SCrAg, S_6
32	A1420 B $\frac{1}{32}$.....	A811 Br $\frac{1}{32}$.....	1	1	...	...	Br, LBr
33	A385 B $\frac{1}{32}$.....	12845 B 4–toe...	4	1	...	...	4 B, S
	Total...................		109	[1]47	...	..	

[1]Excess of dilutes expected because the presence of at least one dilute young is used as a criterion for admission to the table.

TABLE 101.

Cross 40.—All matings of intense with dilute which have given dilute or albino young, except those of crosses 28, 29, 32 and 36.

Expectation: $CC_d \times C_dC_d = CC_d + C_dC_d$ (1 Int : 1 Dil), 1.

$CC_a \times C_dC_d = CC_d + C_dC_a$ (Int : 1 Dil), 2–5 (5?).

$CC_d \times C_dC_a = CC_a + CC_a + C_dC_d + C_dC_a$ (1 Int : 1 Dil), 6–19 (9, 10, 12, 14, 15, 16, 17?).

No.	♀ Int (or Dil).		♂ Dil (or Int).		Int	Dil	RE	W	Remarks.
	40a.								
1	B139 Ag	39–23..	M328 B₂–Y₄	42–17.	2	3	...	...	2 AgTb, 3 S₂Y₂ Ag
2	AA606 S₂Y₃AgTb	40a–8..	AA573 BrAgTb	40a–7.	1	1	...	...	AgTb, S₆Cr₅AgTb
3	4 ♀♀ B	Misc...	AA241 SYAgTb	40a–6.	5	3	...	...	AgTb, 4 B, S₆Cr₅AgTb, S₆–Cr₆, LBr
4	169 B	4-toe...	A656 Br–Y	⅛.....	1	3	...	...	B, 3 S–Cr
5	AA497 SYAgTb	39–7...	AA284 AgTb	39–18.	2	1	...	...	AgTb, R, LBr
6	AA206 AgTb	39–2...	AA177 S₆Cr₆AgTb	41–4..	3	4	...	...	3 AgTb, SYAgTb, 2 S₃Y₃AgTb, S₆Cr₅AgTb
7	AA213 AgTb	39–15..	AA253 S₅Cr₆AgTb	40b–8..	4	5	...	...	3 AgTb, BrAgTb, S₂Y₂AgTb, BrY₃AgTb, S₆Cr₅AgTb, S₆Cr₅AgTb, Br Cr₆AgTb
8	AA217 AgTb	40b–8..	.....Do		7	4	...	...	7 AgTb, S₂Y₃AgTb, 2 S₃Y₃AgTb, SCrAgTb
9	AA613 AgTb	40a–7..	.....Do		...	3	...	...	S₂Y₃AgTb, S₃Cr₅AgTb, S₄Cr₅AgTb
10	3a AgLb	Misc...	M34 Sep₆–Cr₅	16c–1.	...	2	...	...	2 S₆–Cr₆
11	M261 Sep₄	41–2...	AA299 AgTb	40a–6.	...	1	...	...	S₃
12	M282 Ag	15–12..	M116 Sep₅–Y₄	42–11.	3	1	...	...	2 AgLb, B, S₆–Cr₆
13	30 Br	Misc...	M34 Sep₆–Cr₅	16c–1.	1	2	...	...	R, B₂, S₅
14	M99 B	42–13?.	.....Do		2	1	...	...	2 B, S₆–Cr₆
15	M101 B, M99 B	42–13?.	.....Do		3	1	...	...	B, 2 R, S₇
16	M99 B	42–13?.	A674 Sep₆	⅛.....	...	1	...	...	S₇–Cr₇
17	M155 B	1/16.....	.....Do		...	3	...	...	2 S₆, S₇
18	M82 Ag	9–7....	M116 Sep₆–Y₄	42–11.	2	3	...	...	2 AgTb, SY₃AgTb, BrY₃AgTb, SCr₆AgTb
19	SA13 B	28–3...	M306 S₇–Cr₇	42–15.	...	2	...	...	S₆–Cr₅, S₇–Cr₇
	Total...............................				36	44¹	...	...	

¹Excess of dilutes expected.

TABLE 101—Continued.

Cross 40—Continued.

No.	♀ Int (or Dil).		♂ Dil (or Int).		Int	Dil	RE	W	Remarks.
	40b.[1]								
1	A1659 B	$\frac{1}{256}$....	AA253 S₅Cr₅AgTb	40b–8.	...	2	...	...	2 SCrAgTb
2	A1523 AgTb	$\frac{1}{32}$.....	AA199 SCrAgTb	39–15.	2	1	...	...	2 AgTb, SCrAgTb
3	B132 AgTb	1d–3...	M293 Y₄	42–14.	1	1	...	...	AgTb, S₆Cr₆AgTb
4	M442 BrCr₅AgTb	39–12..	AA573 BrAgTb	40a–7.	...	1	...	...	BrCr₅AgTb
5	M44 Cr₅	42–12..	AA197 AgTb	2–10..	2	1	...	...	2 AgTb, SCrAgTb
6	M181 BrCr₅AgTb	41–6...	AA573 BrAgTb	40a–7.	3	2	...	2	3 BrAgTb, Br Cr₅AgTb, Br Cr₆AgTb
7	AA203 BrCrAgTb	39–17..	AA16 AgTb	$\frac{1}{32}$....	2	2	...	1	2 AgTb, SCrAgTb, LBr
8	A1273 SCrAgTb	$\frac{1}{32}$.....	.....Do...............		3	3	...	3	AgTb, 2 B, SCrAgTb, S₆Cr₅AgTb, S₃–Y₄
9	AA176 AgTb	41–4...	AA177 S₆Cr₆AgTb	41–4..	5	1	...	1	4 AgTb, B SCrAgTb
10	AA175 AgTb	41–4...	.....Do..............		...	...	...	1	
11	AA671 AgTb	40a–7..	AA253 S₅Cr₅AgTb	40b–8.	...	...	...	1	
12	M46 BrCr₆Ag	44–1...	A1170 AgTb	$\frac{1}{32}$....	2	...	...	1	Ag, BrAg
13	S443 Sep	ArF₂...	M156 R	$\frac{1}{16}$....	4	1	...	2	4 B, S₃–Cr₅
	Total...................................				24	15²	...	12²	

[1]Expectation: CCa × CdCa = CCd + CCa + CdCa + CaCa (2 int : 1 dil : 1W).
[2]Excess of dilutes and albinos expected.

TABLE 102.

Cross 41.—All matings of intense with albino which have given dilute young, except those given in crosses 18 and 34.

Expectation: CCd × CaCa = CCa + CdCa (1 Int : 1 Dil).

No.	♀ Int (or W).		♂ W (or Int).		Int	Dil	RE	W	Remarks.
1	A1146 AgTb	$\frac{1}{16}$....	A504 W	$\frac{1}{16}$...	...	2	...	...	S, S–Y
2	M102 AgLb	6b–1..	A462 W	$\frac{1}{16}$...	1	1	...	...	B, S₄
3	B139 Ag	39–23.	20 W	BW.	1	1	...	...	AgTb, S₃Cr₅AgTb
4	A1227 W	$\frac{1}{64}$...	A781 AgTb	$\frac{1}{64}$...	2	1	...	...	2 AgTb, S₆Cr₆ AgTb
5	A1309 W	$\frac{1}{32}$....	A1513 AgTb	$\frac{1}{32}$...	4	1	...	...	BrAgTb, B, R, R(Br), Cr(Br)
6	AA28 W	$\frac{1}{32}$....	.....Do..........		4	4	...	...	Ag, BrAg, AgTb, R, SCrAgTb, BrCr₅AgTb, 2 Cr
7	131 W	4-toe..	A412 R(Br)	$\frac{1}{16}$...	1	1	...	...	B, S–Cr
	Total........................				13	11¹	...	...	

[1]Excess of dilutes expected though not found.

TABLE 103.

Cross 42.—All matings of dilute with dilute, except those of crosses 30 and 37.

Expectation: $C_dC_d \times C_dC_a = C_dC_d + C_dC_a$ (all Dil) (M328, AA242, M394, C_dC_d).

$C_dC_a \times C_dC_a = C_dC_d + 2 C_dC_a + C_aC_a$ (3 Dil : 1 W).

No.	♀ Dilute.		♂ Dilute.		Int	Dil	RE	W	Remarks.
1	B141 S4Y4Ag	39–23..	M328 B2–Y4	42–17..	...	4	...	...	3 S2Y3AgTb, S4Cr5Ag
2	AA242 S3Y3AgTb	40a–6..	B117 S4Cr5AgTb	39–14..	...	1	...	...	S5Cr6AgTb
3	AA244 Sep4	39–15..	.....Do....		...	1	...	...	S6Cr5AgTb
4	D44 Sep3	16a–3..	.....Do....		...	1	...	2	S4Cr5AgTb
5	D43 Sep3	16a–3..	D94 S3Y4Ag	16b–9..	...	2	...	...	S3Cr6Ag, S3
5a	D45 Sep3–Cr5	16a–3..	.....Do....		...	2	...	1	S2, S3Cr5Ag
6	D26 S6Cr6AgTb	16a–4..	D33 S5Cr5AgTb	16b–4..	...	...	...	1	
7	{D110 Sep5 16c–3.. / D107 Sep4 16b–1..}		}D106 Sep4	16b–1..	...	5	...	1	5 S3
8	D215 Sep3	16a–2..	.....Do....		...	2	...	...	B1, S3
9	M181 BrCr5AgTb	41–6...	AA253 S5Cr5AgTb	40b–8..	...	1	...	1	SY4AgTb
10	3520 Y4(Br)	Dil....	A674 Sep6	⅛....	...	6	...	1	S3Y3Ag, S6Cr5Ag, BrCr6Ag, Y4(Br), 2 Cr6(Br)
11	3417 Cr6	Dil....	.....Do....		...	3	...	2	S5–Y4, Y2, Cr6
12	{3417 Cr6 Dil.... / 3462 Cr6(Br) Dil....}		}....Do....		...	4	...	...	S–Cr, LBr, Y, Cr5
13	O6 LBr–Cr	Misc...	.....Do....		[1]2	4	...	1	2 B, S–Cr, S7–Cr7, Cr6(Br), Cr6
14	M127 Cr5	42–13..	.....Do....		...	1	...	...	Y4
15	M44 Cr5	42–12..	.....Do....		...	1	...	1	S7–Cr7
16	M164 Cr7	44–6...	.....Do....		...	...	...	2	
17	M126 Cr6(Br)	42–13..	.....Do....		...	1	...	1	B2–Y4
18	M164 Cr7	44–6...	M306 Sep7–Cr7	42–15..	...	2	...	1	S7–Cr6, Cr5
19	M44 Cr6	42–12..	.....Do....		...	3	...	...	S6–Cr6, Cr7, Cr6
20	M296 SCrAgTb	39–27..	M116 Sep5–Y4	42–11..	...	3	...	...	SY2AgTb, 2 S Y3AgTb
21	M310 Sep7–Cr7	40a–16..	M335 Sep6	40a–17..	...	1	...	1	S6
22	M336 Sep6	40a–17..	.....Do....		...	3	...	1	S6–Cr6, S5, S4
23	M336 Sep6	....	M34 Sep6–Cr5	16c–1..	...	1	...	...	S4–Y3
24	M394 Sep4	42–22..	.....Do....		...	3	...	...	S4–Y4, Y3, Cr6
25	{M336, Sep6 40a–17.. / M394 Sep4 42–22..}		}....Do....		...	4	...	...	S6, S5, S4, S3
26	M393 Sep5	42–22..	.....Do....		...	...	...	1	
27	D278 Cr5(Br)	38b–5..	D138 Cr5(Br)	36–1..	...	1	...	1	Cr6(Br)
	Total.................				[1]2	60	...	19	
	CdCd × CdCa...........				...	10	...	0	
	CdCa × CdCa...........				...	50	...	19	

[1]Recorded from a mixed pen before the study of dilution was begun, probably an error.

TABLE 104.

Cross 43.—All matings of dilute with red-eye, except those of crosses 20 and 26.

Expectation: $C_dC_d \times C_rC_a = C_dC_r + C_dC_a$ (all Dil) (1–2).

$C_dC_a \times C_rC_a = C_dC_r + C_dC_a + C_rC_a + C_aC_a$ (2 Dil : 1 RE:1W) (3–4).

No.	♀ Red-eye.		♂ Dilute.		Int	Dil	RE	W	Remarks.
1	241 SAg(R)	ArF2..	M328 B2–Y4	42–17..	...	3	...	...	3 SCrAg
2	271 SAg(R)	ArF2..	M333 Y2	42–11..	...	4	...	...	2 S6Y4Ag, 2 S4Y4Ag
3	236 Sep(R)	ArF2..	M331 BrCr6Ag	42–10..	...	...	...	1	
4	D194 Sep4(R)	26–2..	AA670 S6Cr5AgTb	40a–7..	...	2	1	2	S2Cr5AgTb, S6Cr5AgTb, S5AgTb (R)

<div align="center">TABLE 105.</div>

Cross 44.—All matings of dilute with albino, except those of crosses 16, 19, 27, 33, and 38.
Expectation: $C_dC_d \times C_aC_a = C_dC_a$ (all Dil) (1).
$C_dC_a \times C_aC_a = C_dC_a \times C_aC_a$ (1 Dil : 1 W) (2–6).

No.	♀ Dil (or W).	♂ W (or Dil).	Int	Dil	RE	W	Remarks.
1	3256 BrYAgLb Misc..	A678 W $\frac{1}{16}$......	...	9	...	...	7 SCr₆Ag, 2 Br–Cr₅
2	A505 Sep $\frac{1}{16}$....	A868 W $\frac{1}{16}$......	...	1	...	...	S
3	3 ♀ ♀ W Misc..	B117 S₄Cr₅AgTb 39–14..	...	5	...	1	S₄, S₅Cr₆AgTb, Br Cr₆AgTb, 2 S₆
4	S176 S–Cr ArF₂..	11 W Dil	...	2	...	3	2 S₃–Y₄
5	S263 SCr₅Ag ArF₂..	.....Do.................	...	1	...	...	S₄Cr₅Ag
6	O7 W Misc..	A674 Sep₆ $\frac{1}{4}$......	...	2	...	...	S₇Cr₇Ag, Cr₇

<div align="center">TABLE 106.</div>

<div align="center">*Cross 45.*—Rough A (4-toe) × rough A (4-toe).</div>

<div align="center">Rrss × Rrss = 3 Rss + rrss (3 A : 1 Sm).</div>

No.	♀ Rough A.	♂ Rough A.	A	B	C	D	E	Sm
1	3769 4-toe.....	3609 4-toe.....	1	....	....	....	....	....
2	96 4-toe.....	.....Do........	....	....	....	....	....	2
3	{3769 4-toe..... 3770 4-toe.....}	....Do........	5	....	....	....	....	1
4	3769 4-toe.....	3987 4-toe.....	2	....	....	....	....	....
5	3770 4-toe.....	.....Do........	2	....	....	....	....	....
	Total..................		10	....	....	....	....	3

<div align="center">TABLE 107.</div>

Cross 46.—Rough A (tricolor) × rough A (tricolor); one or both of parents of each, rough C or D.

Rrss × Rrss = 3 Rss + rrss (3 A : 1 Sm) (1–8).
or Rrss × RRss = Rss (all A) (9–12?).

No.	♀ Rough A.	♂ Rough A.	A	B	C	D	E	Sm
1	4018 Tri	3775 Tri	....	....	....	....	....	1
2	3941 Tri	3940 Tri	3	....	....	....	....	....
3	3943 Tri	.....Do..........	1	....	....	....	....	....
4	{R65 54–17..... 3943 Tri .....}	....Do..........	7	....	....	....	....	1
5	R65 54–17.....	.....Do..........	2	....	....	....	....	2
6	R171 47–3......	.....Do..........	2	....	....	....	....	2
7	R278 52–14.....	R248 52–10.....	1	1	....	....	....	....
8	R357 Red 52–8.....	.....Do..........	1	1	....	....	....	1
9	R65 54–17.....	R197 52–14.....	2	....	....	....	....	....
10	R171 47–3......	.....Do..........	3	....	....	....	....	....
11	R194 54–1......	.....Do..........	2	....	....	....	....	....
12	R196 52–14.....	.....Do..........	3	....	....	....	....	....
	Total 1 to 8.....................		17	2	....	....	....	7
	Total 9 to 12....................		10	....	....	....	....	....

TABLE 108.

Cross 47.—Rough A × rough C (tri); all mothers of tricolor stock except R175−4-toe.

Rrss × RrSs = 3 Rss + 3 RSs + 2rr (3 A : 3 C : 2 Sm).

No.	♀ Rough A.	♂ Rough C.	A	B	C	D	E	Sm
1	R21 46–2....	R52 56–1.....	1	....	....	....	..	2
2	R23 46–2....	....Do	1	....	....	....	....	1
3	R42 50–1....	....Do	1	....	1	....	....	1
4	R21 46–2....	R99 56–1.....	1	....	...	....	....	2
5	R23 46–2....	....Do	....	....	1	1	....	....
6	R42 50–1....	....Do	3	1	2	....	....	4
7	R175 49–1....	....Do	3	....	1	....	....	....
	Total.................		10	1	5	1	....	10

TABLE 109.

Cross 48.—Rough A (Tri) × rough E (Tri).

Rrss × RRSS = RSs (all C).

No.	♀ Rough A.	♂ Rough E.	A	B	C	D	E	Sm
1	R42 50–1.....	4003 Tri......	....	....	2	1	....	....

TABLE 110.

Cross 49.—Rough A (4-toe) × smooth (4-toe).

Rrss × rrss = Rrss + rrss (1 A : 1 Sm).

No.	♀ Smooth.	♂ Rough A.	A	B	C	D	E	Sm
1	4 ♀ ♀ 4-toe.....	3922 4-toe....	18	....	....	....	....	13
2	5 ♀ ♀ 4-toe.....	3609 4-toe....	10	1	....	....	....	19
	Total.................		28	1	....	....	....	32

TABLE 111.

Cross 50.—Rough A, B (tri) × smooth (4-toe etc.). Rough A, B with one or both of parents partial rough.

Expectation as in cross 49.

No.	♀ Smooth (or rough B).	♂ Rough A (or smooth).	A	B	C	D	E	Sm
1	7 ♀ ♀ Sm 4-toe......	3775 A Tri.......	13	....	....	....	....	14
2	R121 Sm 50–1......	.....Do	....	....	....	....	....	3
3	R62 Sm 50–1......	R22 A 46–2......	3	....	....	....	....	3
4	[1]R163 B 52–13.....	99 Sm 4-toe......	3	....	....	....	....	....
	Total.........................		19	....	.	....	....	20

[1]R163 may be RR.

TABLE 112.

Cross 51.—Rough A × smooth (tri); smooth with one or both parents partial rough.

Rrss × rrSS = RrSs + rrSs (1 C : 1 Sm).
Rrss × rrSs = Rrss + RrSs + 2 rr (1 A : 1 C : 2 Sm).
Rrss × rrss = Rrss + rrss (1 A : 1 Sm).

No.	♀ Smooth.		♂ Rough A.	A	B	C	D	E	Sm
1	R13	52–1......	R22 46–2......	....	....	1	3	....	4
2	R123	54–3......	R76 4-toe......	....	....	2	....	....	4
3	R124	54–3......	.....Do........	1	....	....	....	....	2
4	R133	47–2......	.....Do........	2	....	....	....	....	....
5	R124, R133		.....Do........	2	....	....	....	....	8
6	R142	54–3......	.....Do........	1	....	....	....	....	1
	Total..........................			6	....	3	3	....	19

TABLE 113.

Cross 52.—Rough[1] C, D (tri) × rough C (tri).

RrSs × RrSs = 3 Rss + 6 RSs + 3 RSS + 4 rr (3 A : 6 C : 3 E : 4 Sm).

No.	♀ Rough C, D.		♂ Rough C.	A	B	C	C	E	Sm	Remarks.
1	3013	Tri	3780 Tri	1	...	3	1	1	2	
2	3246	Tri	.....Do........	...	...	...	1	....	2	
3	R11	52–1.....	.....Do........	1	...	...	...	2	3	
4	R54	52–1.....	.....Do........	1	...	...	...	....	1	
5	3245	Tri	4019 Tri	...	...	2	1	....	....	
6	3939	Tri	R58 52–5.....	4	1	1	...	....	....	Red–A
7	3809	Tri	.....Do........	...	...	...	...	2	1	Red–E, Red–Sm
8	3246	Tri	.....Do........	2	...	1	...	1	....	Red–A
9	3724 D	Tri	.....Do........	...	...	...	1	1	....	
10	3724, 3246 Tri		.....Do........	1	...	4	...	....	1	
11	R51	56–1.....	R56 56–1.....	2	1	2	2	1	3	
12	R57	56–1.....	.....Do........	...	...	1	...	1	....	
13	R51, R57 56–1.....		.....Do........	...	1	...	...	....	2	
14	R98	56–1.....	.....Do........	5	2	...	...	3	1	
15	R103	56–1.....	.....Do........	1	1	5	1	....	1	Red–C
	Total......................			18	6	19	7	12	17	

[1]All rough C except 3724.

TABLE 114.

Cross 53.—Rough C, D (tri) × rough E (tri).

RrSs × RRSS = RSs + RSS (1 C : 1 E).
or RRSs × RrSS = RSs + RSS (1 C : 1 E).
or RrSs × RrSS = 3 RSs + 3 RSS + 2 rr (3 C : 3 E : 2 Sm).

No.	♀ Rough C, D.		♂ Rough E.	A	B	C	D	E	Sm
1	R6 D	54–15....	4003	Tri	....	....	....	1	2	....
2	R88 C	52–1.....	R200 Red 52–7.....	....	....	....	....	2	....
3	R286 C 52–6.....		R280	52–14....	....	....	3	....	....	....
4	R222 C 52–12....		.....Do..........	....	....	1	....	2	1
	Total..........................			....	....	4	1	6	1

TABLE 115.

Cross 54.—Rough C, D (tri) × smooth (4-toe, etc.).

RrSs × rrss = Rrss + RrSs + 2 rr (1 A : 1 C : 2 Sm).

No.	♀ Smooth (or rough C,D).		♂ Rough C,D (or smooth).		A	B	C	D	E	Sm
1	3 ♀ ♀ Sm	4-toe........	3780 C	Tri........	1	....	1	....	....	8
2	R62 Sm	50–1..........	.....Do		....	....	....	2	....	2
3	5 ♀ ♀ Sm	4-toe........	R12 C	52–1.......	4	....	12	....	....	17
4	3 ♀ ♀ Sm	4-toe........	R26 D	54–15......	8	....	3	5	....	14
5	4 ♀ ♀ Sm	4-toe........	R52 C	56–1.......	2	....	2	....	....	6
6	5 ♀ ♀ Sm	4-toe........	R102 C	56–1.......	4	....	5	3	....	9
7	B31 Sm	1d–9.........	R105 C	48–1.......	2	....	....	....	....	....
8	M253 Sm	1a–10........	R106 C	48–1.......	2	....	....	....	....	....
9	M255 Sm	1a–10........	.....Do		....	....	1	....	....	....
10	M380 Sm	$\frac{3}{64}$........	.....Do		....	....	1	....	....	....
11	I31, M253, M255 Sm........		.....Do		1	....	....	....	....	3
12	M384 Sep–Sm	1b–9........	R99 C	56–1.......	....	....	2	....	....	2
13	R62 Sm	50–1.........	R112 C	52–11......	....	....	....	....	....	3
14	65 Sm	4-toe........	.....Do		1	....	1	....	....	1
15	3246 C	Tri	2967 Sm BB........		5	....	1	2	....	3
16	3809 C	Tri	.....Do		1	....	....	....	....	3
17	3724 D	Tri	.....Do		3	....	....	1	1	8
	Total.......................................				34	....	29	13	1	79

TABLE 116.

Cross 55.—Rough E (tri) × rough E (tri).

RrSS × RrSS = 3 RSS + rrSS (3 E : 1 Sm).

No.	♀ Rough E.	♂ Rough E.	A	B	C	D	E	Sm
1	R221 52–12......	R140 52–3......	....	....	....	....	2	3
2	[1]R201 Sm 52–7.......	.....Do.	....	....	....	....	2	....
	Total...........................		....	....	....	....	4	3

[1]See note, cross 57.

TABLE 117.

Cross 56.—Rough E (tri) × smooth (4-toe).

RRSS × rrss = RrSs (all C) 1.
RrSS × rrss = RrSs + rrSs (1 C : 1 Sm) 2–5.

No.	♀ Smooth (or rough E).		♂ Rough E (or smooth).		A	B	C	D	E	Sm
1	3 ♀ ♀ Sm	4-toe....	4003 E	Tri......	....	....	11	....	....	....
2	1 ♀ Sm	4-toe....	R140 E	52–3.....	....	....	1	....	....	3
3	B31 Sm	1a–1.....	......Do		....	....	....	....	....	2
4	[1]R201 Sm	52–7.....	13 W–Sm 4-toe....		....	....	1	....	....	1
5	R221 E	52–12....	......Do		....	....	....	....	....	2
	Total (1)...........................				....	....	11	....	....	....
	Total (2–5)........................				....	....	2	....	....	8

[1]See note, cross 57.

TABLE 118.

Cross 57.—Smooth (tri) × smooth (4-toe, etc.); *both* parents of tricolor smooths were *partial* roughs (cross 52).

$$rr \times rr = rr \text{ (all Sm).}$$

If, however, RSS, normally rough E, is ever Sm:

$$RrSS \times rrss = RrSs + rrSs \text{ (1 C : 1 Sm).}$$

No.	♀ Smooth.	♂ Smooth.	A	B	C	D	E	Sm
1	6 ♀ ♀	R131 52–4.....	....	....	....	....	....	14
2	R139 52–3.......	99 4-toe.....	....	....	....	....	....	2
3	R13 52–1.......	.....Do	....	....	....	....	....	6
4	R164 52–13.....	.....Do	....	....	....	....	....	2
5	R199 Red 52–7.......	13 W 4-toe.....	....	....	....	....	....	3
6	R249 52–10.....	.....Do	....	....	....	....	....	3
7	R263 52–11.....	.....Do	....	....	....	....	....	2
8	[1]R201 52–7.......	.....Do	....	....	1	....	....	1

[1]R201 was called rough E? at birth with the note that there seemed to be a trace of roughness on one hind toe. No roughness was apparent when adult and she was called Sm, but nevertheless was tested by mating with a 4-toe smooth. The result shows that she was, genetically at least, like a rough E.

TABLE 119.

Cross 58.—Rough B, C (Lima) × rough B (Lima).

No.	♀ Rough B.	♂ Rough B.	A	B	C	D	E	Sm
1	L7 Lima ...	L5 Lima ...	2	2	...	...	...	1
2	L97 60–6....	L26 58–1....	1	...	...	...	...	...
3	L140 60–7....	.....Do	1	1	...	...	...	...
4	{ L97 60–6.... } { L81 Red 59–3.... }	}L98 60–6....	3	2	...	...	...	2
5	L99 Rough C 61–1....	.....Do	...	1	...	1	...	...
6	L81, L97, L99 (above) .	.....Do	1	1	2	...	...	4
	Total....................		8	7	2	1	...	7

TABLE 120.

Cross 59.—Rough A (Lima) × smooth (Lima).

No.	♀ Smooth (or rough A).	♂ Rough A (or smooth).	A	B	C	D	E	Sm	Remarks.
1	L13 Sm 62–2..	L9 A 58–1..	2	...	...	...	...	1	
2	L14 Sm 60–1..	.....Do	7	1	...	...	...	2	
3	L24 Sm 60–2..	.....Do	2	1	3	...	...	5	Red–B
4	L25 Sm 58–1..	.....Do	4	1	...	...	...	3	2 Red–A, 2 Red–Sm
5	L37 Sm 62–3..	.....Do	...	...	...	...	...	1	
6	L57 Sm 59–3..	.....Do	1	2	...	...	...	2	Red–A
7	L24, L57 Sm (above)	.....Do	1	2	...	...	...	1	Red–B
8	L22 A 60–2..	L1 Sm Lima .	4	1	...	...	...	6	2 Sep(p)–Sm
9	L62 A 59–3..	.....Do	1	...	...	...	...	2	
10	L100 Sep(p)–A 61–1..	L82 Sep(p)–Sm 59–8..	2	...	...	...	...	...	2 Sep(p)–A
	Total.........................		24	8	3	...	...	23	

TABLE 121.

Cross 60.—Rough B (Lima) × smooth (Lima).

No.	♀ Smooth.	♂ Rough B.	A	B	C	D	E	Sm	Remarks.
1	L4 Lima .	L5 Lima .	3	2	...	...	...	2	Red–A. 2 Red–B, Red–Sm
2	L6 Sep(p) Lima .	.....Do	2	...	...	...	...	1	
3	L34 62–2..	L26 58–1..	...	2	...	...	...	2	
4	L37 62–3..	.....Do	...	...	...	...	...	1	
5	L43 62–1..	.....Do	...	1	...	...	...	3	
6	L34, L43 (above)	.....Do	...	2	...	...	...	8	
7	L41, L43 62–1..	.....Do	...	2	...	...	...	3	
8	L132 60–3..	.....Do	1	...	...	...	...	1	
9	L75 60–4..	.....Do	1	...	...	...	...	1	
10	L14 60–1.. L24 60–2.. L25 58–1..	L131 60–3..	1	...	...	...	...	8	Red–Sm
	Total....................		8	9	...	...	...	30	

TABLE 122.

Cross 61.—Rough C (Lima) × smooth (Lima).

No.	♀ Rough C.	♂ Smooth.	A	B	C	D	E	Sm	Remarks.
1	L56 59–3....	L1 Lima....	2	1	1	...	...	2	Sep(p)–A

TABLE 123.

Cross 62.—Smooth (Lima) × smooth (Lima).

Offspring all smooth.

No.	♀ Smooth.	♂ Smooth.	B	Red	Sep(p)	Red(p)
1	L3 B Lima ..	L1 B Lima ..	4	2	..	..
2	L2 Red Lima ..	.....Do	3	3	..	..
3	L8 Red Lima ..	.....Do	4	3	2	1
4	L2, L8 Red Lima ..	.....Do	1	3	..	..
5	L12 Red 62–2...	L11 Red 62–2..	..	1	..	..
6	Do	L40 Red 62–1..	..	8	..	..
7	L35 Red 62–3...	.....Do	..	1	..	..
8	L17 Red 62–3...	.....Do	..	7	..	..
9	L8 Red Lima ..	.....Do	..	4	..	..
10	L8, L17 Red (above)	.....Do	..	4	..	..
11	L64 Red 62–13..	L59 Red 62–3...	..	6	..	3
12	L6 Sep(p) Lima ..	L1 B Lima ..	1	..	1	..
13	L19 Sep(p) 62–3...	.....Do	2	4	1	..
14	L6 Sep(p) Lima ..	L18 Sep(p) 62–3...	..	..	1	1
15	L19 Sep(p) 62–3...	.....Do	..	..	..	1
16	Do	L82 Sep(p) 59–8...	..	..	3	..
17	L58 Red(p) 62–3...	L59 (Red) 62–3...	..	..	..	2
18	L121 Red(p) 62–11..	.....Do	..	2	..	..
19	Do	L149 Red(p) 62–11..	..	..	..	2
20	L120 Red(p) 62–11..	.....Do	..	..	..	4

TABLE 124.

Cross 63.—Rough A, B (Lima) × smooth (4-toe, etc.).

No.	♀ Rough A (or smooth).		♂Smooth (or rough A).	A	B	C	D	E	Sm
1	L107 A	59–9....	13W–Sm 4-toe....	2	...	...	...	...	1
2	L108 A	59–7....	.....Do	1	...	...	...	...	...
3	L110 B	59–7....	.....Do	1	...	...	...	...	1
4	D180 W–Sm 18c–14..		L98 B 60–6....	...	2	...	...	...	1
5	D236 W–Sm 17d–7...		.....Do	...	2	...	...	...	1
	Total..........................			4	4	...	...	...	4

TABLE 125.

Cross 64.—Rough C (low grade due to *C. rufescens*) × smooth (4-toe, etc.).

RrSs × rrss = Rrss + RrSs + 2 rr (1 A : 1 C : 2 Sm).

No.	♀ Rough C.		♂Smooth.	A	B	C	D	E	Sm	Remarks.
1	A606 Ag	$\frac{1}{4}$.....	166...4-toe...	...	...	2	...	...	...	2B–C
2	A1687	64–1..	99 4-toe...	...	...	...	...	...	1	B–Sm
3	A1688 Ag	65–1..	AA83 $\frac{1}{64}$.....	3	...	...	...	...	4	BrAgTb–A, 2 AgTb–A, 4 AgSm
	Total...................			3	...	2	...	...	5	

TABLE 126.

Cross 65.—Smooth (some *C. rufescens* blood) × rough A.

rrSs × Rrss = Rrss + RrSs + 2rr (1 A : 1 C : 2 Sm).
rrss × Rrss = Rrss × rrss (1 A : 1 Sm).

No.	♀ Smooth.		♂Rough A.		A	B	C	D	E	Sm
1	A702 AgTb	$\frac{1}{32}$.....	2597 Ag stock		1	...	1	...	...	...
2	A605	$\frac{1}{4}$........	.....Do.		...	1	1	...	...	...
3	A642	$\frac{1}{4}$........	.....Do.		2	...	...	...	...	...
4	A842	$\frac{1}{4}$........	.....Do.		2	...	...	...	...	3
5	A913 AgTb	$\frac{1}{32}$.....	.....Do.		2	...	...	...	...	...
6	6 ♀ ♀ AgTb	$\frac{1}{128}-\frac{1}{256}$	.....Do.		7	...	...	...	...	12
7	B238	1a–5....	R88 52–1..		2	...	...	...	...	4
8	B240 1a–5.... K61, K62 78–6....		.....Do		2	...	...	...	..	5

TABLE 127.

Cross 66.—Rough A × smooth; both parents with a little *C. rufescens* blood.

Rrss × rrss = Rrss + rrss (1 A : 1 Sm).

No.	♀ Rough A.	♂ Smooth.	A	B	C	D	E	Sm	Remarks.
1	A1690 Ag 65–5..	AA83 B–Sm $\frac{1}{64}$...	4	1	...	...	...	4	3 AgTb–A, Red–A, Ag Tb–B, AgLb–Sm, Ag Tb–Sm, 2 Red–Sm
2	Do........	M91 Ag–Sm 8–4..	2	...	...	...	...	4	2 AgLb–A, 2 AgLb–Sm, 2 AgTb–Sm
3	A1691 Ag 65–5..	AA83 B–Sm $\frac{1}{64}$...	8	...	...	...	...	4	4 AgLb–A, 4 B–A, 2 Ag Lb–Sm, 2 B–Sm
	Total........................		14	1	...	...	...	12	

TABLE 128.

Cross 67.—Rough A (4-toe, tri) × smooth (pure Ica).

Rrss × rrSS = RrSs + rrSs (1 C : 1 Sm).
Young all light-bellied agouti.

No.	♀ Rough A.	♂ Smooth.	A	B	C	D	E	Sm
1	R215 49–1.... R252 49–2....	724 SAg(R) Ica....	...	...	3	...	...	...
2	R236 50–3....	.....Do..........	...	...	2	...	...	1
3	R205 46–4....	.....Do..........	...	...	...	...	...	1
4	R213 49–1....	.....Do..........	...	...	...	...	...	2
	Total........................		...	...	5	...	...	4

TABLE 129.

Cross 68.—Rough A × smooth (pure *C. cutleri*).

Rrss × rrSS = RrSs + rrSs (1 C : 1 Sm).
Young all light-bellied agouti.

No.	♀ Rough A.	♂ Smooth.	A	B	C	D	E	Sm
1	3986 4-toe...	C128 Ag.....	...	...	...	1	...	2
2	3988 4-toe...	.....Do.....	...	...	2	...	...	1
3	3986, 3988 4-toe...	.....Do......	...	...	...	2	...	3
4	A1691 Ag 65–5...	.....Do......	...	...	1	2	...	3
5	AA567 Ag 66–3...	.....Do......	...	...	...	1	...	3
6	AA568 66–3... R80 54–15..	....Do......	...	...	...	...	...	3
	Total........................		...	...	3	6	...	15

TABLE 130.

Cross 69.—Rough C (tricolor) × smooth (pure *C. cutleri*).

RrSs × rrSS = RrSs + RrSS + 2 rr (1 C : 1 E : 2 Sm).
Young all light-bellied agouti.

No.	♀ Black rough C. D.		♂ Smooth.	A	B	C	D	E	Sm
1	3245	Tri....	C128Ag.......	...	...	...	...	...	2
2	R54	52–1...	....Do	...	...	...	1	1	1
3	R152	54–4...	....Do	...	...	...	...	1	2
4	3245, R110	....	....Do	...	...	...	...	2	1
5	R110	51–1...	....Do	...	...	...	...	2	1
6	R170	47–3...	....Do	...	...	1	...	...	2
7	R11	52–1...	....Do	...	...	...	...	1	...
8	R101 D	52–5...	....Do	...	...	...	...	...	3
9	R154 D	54–4...	....Do	...	...	...	...	2	...
	Total.................			...	...	1	1	9	12

TABLE 131.

Cross 70.—Rough A (guinea-pig) × rough C, D ($\frac{1}{2}$, $\frac{1}{4}$ *cutleri*).

Rrss × RrSs = Rss + RSs + 2rr (3 A : 3 C : 2 Sm).
All $\frac{1}{2}$ *cutleri* Rough C, D, except K58, $\frac{1}{4}$ blood.
R116 and R137 may be RRss.

No.	♀ Rough A (or C, D).		♂ Rough D (or A).		A	B	C	D	E	Sm	Remarks.
1	R116 B–A	46–4..	K54 Ag–D	68–1..	2	...	1	...	...	...	Ag–A, B–A, Ag–C
2	R117 B–A	46–4..	.....Do		...	...	...	1	...	1	B–D, B–Sm
3	R137 B–A	47–1..	.....Do		...	...	2	...	...	...	2 B–C
4	AA608 B–A 66–3..		.....Do		3	...	...	...	1	...	Ag–A, 2 B–A, Ag–E
5	K12 Ag–D	68–3..	R31 B–A	45–3..	...	...	2	...	...	1	2 B–C, B–Sm
6	K14 Ag–D	68–3..	.....Do		...	2	...	...	...	...	2 Ag–B
7	Do.........		3609 B–A	4-toe..	1	1	...	...	1	...	B–A, Ag–B, Ag–E
8	Do.........		R76 B–A	45–4..	1	...	...	1	...	...	B–A, B–D
9	K12 Ag–D	68–3..	.....Do		1	...	2	...	...	1	Ag–A, 2 Ag–C, B–Sm
10	K58 B–C	70–5..	.....Do		...	...	1	...	...	1	B–C, B–Sm
	Total.................				8	3	8	2	2	4	

TABLE 132.

Cross 71.—Rough A (guinea-pig) × smooth ($\frac{1}{2}$, $\frac{1}{4}$ *cutleri*).

Rrss × rrSs = Rrss + RrSs + 2rr (1 A : 1 C : 2 Sm).
All $\frac{1}{2}$ *cutleri* except K79, $\frac{1}{4}$ *cutleri*.

No.	♀ Smooth.		♂ Rough A.		A	B	C	D	E	Sm	Remarks.
1	K7 Ag	77–1..	R31 B	45–3..	3	2	1	...	...	7	Ag–A, 2 B–A, 2 B–B, B–C, 6 Ag–Sm, B–Sm
2	K15 Ag	68–3..	.....Do		3	...	2	...	...	9	Ag–A, 2 B–A, Ag–C, B–C, 3 Ag–Sm, 6 B–Sm
3	K55 Ag	68–1..	.....Do		...	...	2	...	...	1	2 Ag–C, B–Sm
4	K7, K55 (above)		.....Do		2	...	...	...	...	3	2 Ag–A, 2 Ag–Sm, B–Sm
5	K68 Ag	77–1..	.....Do		1	1	2	1	...	...	B–A, B–B, Ag–D, 2 B–C
6	K116 Ag 68–6..		.....Do		...	...	...	...	...	1	B–Sm
7	K81 Ag	69–1..	3609 B	4-toe.	...	...	1	...	...	1	Ag–C, Ag–Sm
8	K79 B	78–1..	3922 B	4-toe.	1	...	1	...	...	...	B–A, B–C
	Total.................				10	3	9	1	...	22	

TABLE 133.

Cross 72.—Smooth (guinea-pig) × rough C, D ($\frac{1}{2}$, $\frac{1}{4}$ *cutleri*).

rrss × RrSs = Rrss + RrSs + 2rr (1 A : 1 C : 2 Sm).
K71a, K92 may be RR.

No.	♀ Rough C, D (or Sm).		♂ Smooth (or rough C, D).	A	B	C	D	E	Sm	Remarks.
1	K12 Ag–D	68–3...	00 Cr(Br)Sm Dil....	1	...	...	2	...	...	Ag–A, 2 B–D
2	K14 Ag–D	68–3...	.....Do...........	3	...	...	...	...	6	2 Ag–A, B–A, 3 Ag–Sm, 3 B–Sm
3	{K12 Ag–D 68–3 {A71a Ag–C 70–1...}		....Do..........	...	...	1	...	...	3	{B–C, 2 Ag–Sm, { B–Sm
4	K92 Ag–C	70–9...	.....Do...........	1	...	2	...	...	...	Ag–A, 2 Ag–C
5	K157 Ag–C	72–12..	13 Cr(Br)Sm Dil....	1	...	...	...	...	1	Ag–A, Sep–Sm
6	K147 AgTb–D	72–13..	.....Do...........	...	...	...	...	...	3	2 B–Sm, Sep–Sm
7	K142 B–D	72–1...	00 Cr(Br)Sm Dil....	1	...	...	1	...	1	Red–A, W–D, B–Sm
8	D40 Cr(Br)Sm	36–1...	K60 Ag–C 71–2..	1	...	...	...	...	1	B–A, Ag–Sm
9	R173 B–Sm	49–1...	.....Do...........	1	...	...	...	...	1	Ag–A, Ag–Sm
10	20 B–Sm	4-toe ..	K54 Ag–D 68–1..	2	...	1	...	...	2	Ag–A, B–A, Ag–C, 2 B–Sm
11	AA533 Ag–Sm	66–2...	K56 B–C 70–5..	...	...	...	...	...	1	Ag–Sm
12	AA586 Ag–Sm	10b–10..	.....Do...........	...	...	1	1	...	...	Ag–C, B–D
13	{M382 AgTb–Sm 1b–9... {B239 AgTb–Sm 1a–5...}		....Do..........	1	...	1	2	...	1	{B–A, 3 AgTb– { C +D, B–Sm
14	B239 AgTb–Sm	1a–5...	.....Do...........	...	...	...	...	...	1	B–Sm
	Total............			12	...	6	6	...	21	

TABLE 134.

Cross 73.—Smooth (4-toe) × rough A, B ($\frac{1}{4}$ *cutleri*).

rrss × Rrss = Rrss + rrss (1 A : 1 Sm).

No.	♀ Rough A, B.	♂ Smooth.	A	B	C	D	E	Sm	Remarks.
1	K95 B–B 71–1.......	99 B 4-toe........	...	...	...	...	...	1	B–Sm
2	{K101 B–A 70–8....... {K106 B–A 71–2.......}	}13 W 4-toe........	2	...	...	...	...	1	2 B–A, B–Sm
	Total............		2	...	...	...	...	2	

TABLE 135.

Cross 74.—Smooth ($\frac{1}{2}$, $\frac{1}{8}$ *cutleri*) × rough A ($\frac{1}{4}$ *cutleri*).

rrSs × Rrss = Rrss + RrSs + 2rr (1 A : 1 C : 2 Sm).
rrss × Rrss = Rrss + rrss (1 A : 1 Sm).

No.	♀ Smooth.	♂ Rough A.	A	B	C	D	E	Sm	Remarks.
1	K68 Ag 77–1.......	K59 B 71–2.......	...	...	1	...	...	...	B–C
2	K42 B 78–2.......	....Do...........	...	...	...	...	...	1	B–Sm
	Total............		...	...	1	...	...	1	

TABLE 136.

Cross 75.—Rough A, B ($\frac{1}{4}$ *cutleri*) $\times$ rough A ($\frac{1}{4}$ *cutleri*).

Rrss $\times$ Rrss = 3 Rss + rrss (3 A : 1 Sm).

No.	♀ Rough A, B.	♂ Rough A.	A	B	C	D	E	Sm	Remarks.
1	K50 Ag–B　70–6.......	K59 B　71–2.......	1	...	...	...	...	...	B–A
2	K53 B　　71–1.......	....Do............	2	...	...	...	...	...	2 B–A
	Total...............................		3	...	...	...	...	...	

TABLE 137.

Cross 76.—Rough C ($\frac{3}{8}$ *cutleri*) $\times$ rough C ($\frac{1}{4}$ *cutleri*).

RSs $\times$ RSs = Rss + 2 RSs + RSS (1 A : 2 C : 1 E : ? Sm ?).

No.	♀ Rough C.	♂ Rough C.	A	B	C	D	E	Sm	Remarks.
1	K114 B　74–1....	K93 Ag　70–9 ..	...	...	1	3	1	...	{Ag–C, Ag–D, 2 B–D, Ag–E

TABLE 138.

Cross 77.—Black (BB) $\times$ agouti (pure *cutleri*).

Parents and offspring all smooth.

No.	♀ Black.	♂ Agouti.	AgLb	Black	W
1	2 B ♀ ♀　　BB.....	C128 Ag　pure C....	6	......	......

TABLE 139.

Cross 78.—Black (BW) $\times$ agouti ($\frac{1}{2}$, $\frac{1}{4}$, $\frac{1}{8}$ *cutleri*).

Expectation: 1 Ag : 1 black : some white.
Parents and offspring all smooth.

No.	♀ Black (or agouti).	♂ Agouti (or black).	AgLb	Black	W
1	6 B ♀ ♀　　BW.....	C67 Ag　　　($\frac{1}{2}$).....	12	12	6
2	2 B ♀ ♀　　BW.....	K4 Ag ($\frac{1}{4}$)　78–1....	6	9	......
3	3 B ♀ ♀　　BW.....	K24 Ag ($\frac{1}{4}$)　78–1....	9	5	......
4	K20 Ag ($\frac{1}{4}$)　78–1....	39 B BW............	3	......	......
5	K22 Ag ($\frac{1}{4}$)　78–1....	.....Do............	1	......	1
6	K29 Ag ($\frac{1}{4}$)　78–1....	.....Do............	3	3	......
7	K103 Ag ($\frac{1}{8}$)　78–4....	.....Do............	......	2	......
8	K66 Ag ($\frac{1}{8}$)　78–2....	.....Do............	......	4	......
9	K109 Ag ($\frac{1}{8}$)　78–6....	.....Do............	1	1	......
10	3 B ♀ ♀　　BW.....	K104 Ag ($\frac{1}{8}$) 78–4....	......	5	3
	Total...............................		35	41	10

PART III

FURTHER STUDIES OF PIEBALD RATS AND SELECTION, WITH OBSERVATIONS ON GAMETIC COUPLING

By W. E. CASTLE

THE PROGENY OF HOODED RATS TWICE CROSSED WITH WILD RATS.

In 1914 Castle and Phillips published a report on breeding experiments with hooded rats, in which it was shown that the hooded color pattern—itself a Mendelian recessive character in crosses with the entirely colored (or "self") coat of wild rats—is subject to quantitative variation, and that different quantitative conditions of the hooded pattern are heritable. (Compare fig. 36, plate 7.) It was also shown that by repeated selection of the more extreme variations in the hooded pattern (either plus or minus) it is possible gradually to modify the racial mean, mode, and range as regards these fluctuations, without eliminating further fluctuation or greatly reducing its amount. We concluded that the unit character, hooded color pattern, is a quantitatively varying one, but were at that time unable to decide whether the observed variability was due simply and exclusively to variation in a single Mendelian unit factor or partly to independent and subsidiary modifying Mendelian factors.

Since publication of the above I have been engaged in further experiments designed to show which of the alternative explanations is the correct one, and these are now sufficiently advanced to indicate definite conclusions. Previous experiments had shown that when a race of hooded rats, whose character has been modified by selection (either plus or minus), is crossed with wild rats, the extracted hooded animals obtained in F_2 as recessives show regression toward the mean condition of the recessive race before selection began. This result suggested that the regression observed might be due to removal by the cross of modifying factors, which selection had accumulated in the hooded race. If this view was correct, it was thought that further crossing of the extracted hooded animals with the same wild race should result in *further* regression, and that if this further regression was *not* observed a different explanation must be sought for the regression already noted.

The entire experiment has accordingly been repeated from the beginning, with the same result as regards regression in the first F_2 generation, but with *no regression* of the same sort in a second F_2 containing twice-extracted hooded animals. So far from observing further regression as a result of the second cross with wild rats, we have unmistakable evidence that the movement of the mean, mode, and range of the hooded character has been in the *reverse* direction. So the hypothesis of modifying factors to account for the regression and for the progressive changes observed under selection becomes untenable.

In repeating the experiment of crossing hooded rats of our selected races with wild rats, great care has been taken to employ as parents individuals of the greatest racial purity and to inbreed the offspring

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brother with sister, thus precluding the possibility of introducing modifying factors from other sources. In making the second set of crosses, the extracted individual has, wherever possible, been crossed with its own wild grandparent. In the few cases in which this was impossible, wild animals of the same stock have been used. This stock consisted of a colony of wild rats which invaded the basement of the Bussey Institution apparently from a nearby stable. Owing to faulty construction of the building they were able to breed in spots inaccessible to us, and it took many months of continuous and persistent trapping to secure their extermination. During this period we trapped a hundred or more of them, all typical Norway rats, colored all over, without even the white spot occasionally seen on the chest of wild rats. Two generations of rats from this wild stock have been reared in the laboratory, and all have this same self-colored condition.

The hooded animals used in the experiments to be reported on in this connection consisted of 4 individuals of the plus-selected series, a male and 3 females, as follows:

TABLE 140.

Individual.	Grade.[1]	Generation.
♀ 5513....	$+4\frac{1}{4}$	10
♂ 6348....	$+4$	10
♀ 6600....	$+4\frac{1}{4}$	12
♀ 6955....	$+4$	12

[1]See figure 35, plate 7, for significance of the grades.

Each of these animals was mated with a single wild mate, and their children were weaned directly into breeding cages containing a male and two or three females (brother and sisters). In the case of two matings, F_1 males of the same parentage were at the time lacking and males from a different cross were used. The results of such matings are tabulated by themselves and serve a useful purpose as controls. The F_1 animals all closely resembled their wild parents, but many of them had a white spot on the chest. They ranged from grade $+5\frac{1}{4}$ to $+6$ (self).

The F_2 animals are classified in table 141, where it appears that 73 of them were hooded and 219 non-hooded (i. e., like F_1), an exact 1 : 3 ratio. More than half of this F_2 generation consists of the grandchildren of ♀ 5513, produced by breeding her children brother with sister, those children all having been sired by the same wild rat. Her grandchildren include 41 hooded and 107 non-hooded young. The hooded young range in grade from $+1\frac{1}{2}$ to $+4$, their mean grade being $+3.05$, a considerable regression from the grade of the grandmother, which was 4.25.

Hooded rats of the same grade and generation as the grandmother, when bred with each other, produced young of mean grade $+3.84$.

(See table 10, Castle and Phillips.) The mean of the extracted hooded grandchildren in this case (being 3.05) shows a regression of 0.79 from that expected for the uncrossed hooded race. From the extracted hooded grandchildren of ♀ 5513, produced as just described by a cross with a wild male, 7 individuals, 2 males and 5 females, were selected for a second cross with the wild race. They ranged in grade from $+2$ to $+3\frac{1}{4}$. (See table 142.) They produced several litters of young of the same character as the first F_1 young, all being similar to wild rats in appearance, except for the frequent occurrence of a white spot on the belly. These second F_1 young were at weaning time mated, brother with sister, in breeding-pens, precisely as had been done with the first F_1's. They produced 394 second F_2 young, of which 98 were hooded and 296 non-hooded, a perfect 1 : 3 ratio. The hooded young varied in grade from $+2$ to $+4$, as shown in table 142, the data there being given for each family separately as well as for all combined in the totals. One family was very like another as regards the character of the hooded young, except that the higher-grade grandparents had grandchildren of slightly higher grade. Thus the average of all the 98 hooded young was $+3.47$, but the average of those descended from the 3 grandparents of lowest grade was *less* than this, while the average of those descended from the 3 grandparents of highest grade was *greater*. This is just what had been observed throughout the entire selection experiments. (See Castle and Phillips.)

If we weight each of the grandparents in table 142 in proportion to the number of its hooded grandchildren, then the mean grade of all the grandparents is $+2.95$. Since the mean grade of all the 41 first F_2 hooded grandchildren, from which these 7 were chosen, was $+3.05$, it will be seen that these 7 are, so far as grade is concerned, fair representatives of the 41, being in fact of slightly lower mean grade. It is therefore all the more striking that their grandchildren, the second F_2 hooded young (table 142), are of higher grade. They regress in an *opposite* direction to that taken by the first F_2 hooded young. Thus the original hooded ancestor (♀ 5513) was of grade 4.25. The grade of hooded young expected from such animals is 3.84. What she produced in F_2, following a cross with the wild male, was young of mean grade 3.05. Seven of these of mean grade 2.95 produced a second F_2 containing hooded young of mean grade 3.47. This is a *reversed* regression of 0.52 on the grade of their actual hooded grandparents, or of 0.42 on the group from which their grandparents were chosen. Their mean lies about midway[1] between that which would have been expected from the original hooded female (5513) had no crossing with wild rats occurred and that which was observed in the first F_2.

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[1] In *The Scientific Monthly* (Jan. 1916) I have stated that a second cross showed "a return to about what the selected race would have been had no crossing at all occurred." This is obviously inaccurate and should be corrected. It rests on a comparison with the combined average of both the older and the more recent experiments.

Obviously these facts do not harmonize with the assumption that the regression observed in the first F_2 was due to loss of modifying factors accumulated during the ten preceding generations of selection; for no further loss occurs in the second F_2. On the other hand, a partial recovery is made of what was lost in the first F_2. This suggests the idea that that loss may have been due to physiological causes non-genetic in character, such as produce increased size in racial crosses; for among guinea-pigs (as among certain plants) it has been found that F_1 has an increased size due to vigor produced by crossing and not due to heredity at all. This increased size persists *partially* in F_2, but for the most part is not in evidence beyond F_1. I would not suggest that the present case is parallel with this, but it seems quite possible that similar non-genetic agencies are concerned in the striking regression of the first F_2 and the subsequent reversed regression in the second F_2.

Whatever its correct explanation may be, the *fact* of the reversed regression in a second F_2 is very clear, as other cases than those already discussed will show.

A hooded rat of grade +4 and generation 10, $\male 6348$, had by a wild female several young of the character already described for the young of $\female 5513$. These, mated brother with sister, produced a first F_2 (table 141) of 90 rats, 22 of which were hooded, 68 being non-hooded, again a good 1 : 3 ratio. The hooded young ranged from +2 to +4 in grade, their mean being 3.28. Of the 22 hooded individuals, 1 male and 7 females were mated with wild rats to obtain a second F_1, and the second F_1 animals were then mated brother with sister to obtain the desired second F_2. The character of this is shown family by family in table 143. It contained 497 individuals, of which 121 were hooded and 376 non-hooded, a ratio of 1 : 3.1. The weighted mean of the 8 selected grandparents is 2.93, which is 0.35 below the mean of the 22 first F_2 hooded animals which they represent. The mean of the second F_2 hooded young is 3.22, which indicates a *reversed* regression of 0.29 on the grade of the grandparents, but shows no significant difference from the mean of the grandparental group (3.28).

All except one of the 8 families classified in table 143 show unmistakably the reversed regression. This exceptional family consists of the grandchildren of $\female 9747$. They have a mean grade of 2.90, substantially the same as that of the entire group of grandparents but considerably lower than that of their own hooded grandmother. Apparently she did not come up genetically to her phenotypic grade. This the other grandparents of the group did. For those of lowest grade $(2, 2\frac{3}{4})$ produced lower-grade hooded grandchildren than did the grandparents of highest grade $(3\frac{1}{2}, 4)$, as was found to be the case also in table 142.

We may next trace the inheritance of the hooded character through a third but smaller family produced by two successive crosses with wild

rats, the hooded character in this case being derived from ♀6955, grade +4, generation 12. The character of her first F_2 descendants is shown in table 141. They consist of 5 hooded and 27 non-hooded individuals. The mean grade of the hooded young is 3.51, but the number of these young is too small to make this mean of much significance. One of the hooded young (♂9660, +3¾) was mated with a wild female to secure a second F_1 generation and from this in due course was produced the second F_2 generation (table 144). It consisted of 21 hooded and 44 non-hooded young. The hooded young showed the usual range (2 to 4). Their mean grade was 3.50, substantially identical with that of the first F_2 animals, but 0.25 below that of the actual hooded grandparent. This family history is less satisfactory than the two already discussed because of the smaller numbers which it includes. It contains nothing contradictory to the interpretation already given, though reversed regression is not in this case in evidence.

In two cases F_1 females could not be mated with brothers and so mates were taken from other families. Thus "mixed F_1 matings" were made between children of 5513 and 6600 and children of 5513 and 6955. (See table 141.) The former mating produced 3 hooded and 12 non-hooded "first" F_2 young; the latter produced 2 hooded and 5 non-hooded "first" F_2 young. The grade of the hooded young produced by these mixed matings was not different from that of brother-sister matings, so far as the small numbers permit one to judge. One of these mixed matings was carried into a second F_2 generation. The first F_2 hooded ♂9711, +3¼, was mated with a wild female, and the young were bred, brother with sister, producing 16 hooded and 33 non-hooded young. (See table 144.) The mean grade of the 16 hooded young was 3.28, nearly the same as that of the first F_2 hooded grandparent. No additional regression through loss of modifiers (or other agency) is here in evidence. The result is the same as that observed in families wholly unmixed. The attention of my pure-line critics, who think that in our mass-selection experiments insufficient attention has been given to individual pedigrees, is particularly directed to the foregoing case.

Having now discussed each family history separately, we may combine all the second F_2 families in one table, in order to get a clearer impression of the results as a whole. (See table 145.) The second F_2 generation thus combined includes 256 hooded and 749 non-hooded individuals, a ratio of 1 : 2.9, an unmistakable mono-hybrid Mendelian ratio. The mean grade of the hooded individuals is 3.34. The weighted mean grade of their hooded grandparents was 3.02, which indicates a *reversed regression* of 0.32 for the entire second F_2 group of hooded animals.

Classified according to the grade of the (first F_2) grandparent, they show a correlation between grade of grandparent and grade of grand-

child. The lower-grade grandparent has lower-grade hooded grandchildren, and the higher-grade grandparent has higher-grade hooded grandchildren. This shows that the variation in grade is (in part at least) *genotypic*. As the experiment yields no evidence that the variation in the hooded character is due to independent modifying factors, there remains no alternative to the conclusion that the single genetic Mendelian factor concerned fluctuates in genetic value. Fluctuation accordingly is not exclusively phenotypic, as DeVries and Johannsen have thought, but may be genetic also. Hence racial changes may be effected through selection by the isolation of genetic fluctuations, as well as by the isolation of mutations. Moreover, genetic fluctuation makes possible *progressive change* in a particular direction, repeated selection attaining results which it would be quite hopeless to seek by any other means.

A SECOND REPORT ON MASS SELECTION OF THE HOODED PATTERN OF RATS.

The experiments in selection for the modification of the hooded pattern of rats, when reported on by Castle and Phillips in 1914, had been carried through 13 generations. Since then the experiments with the same selected races have been carried through 3 or 4 additional generations, the results of which will now be described. Additional records have also been obtained for certain of the generations reported on by Castle and Phillips, which may now be combined with those previously published. Thus, revised data, based on larger totals, may be given for generations 12 and 13 of the plus-selection series and for generation 13 of the minus-selection series. These do not materially change the results previously obtained, but add to their trustworthiness. The additional generations of selection show a continued progressive movement of the racial character in the direction of the selection and indicate the existence of no natural limit to the progress which selection can make in changing the hooded character.

For details concerning the earlier history of the experiments and the methods of grading the animals the reader is referred to the publication of Castle and Phillips. The grading scale (exclusive of the newer and more extreme grades) is reproduced in figure 35, plate 7. Attention may be called to the fact that the entire selection series, both plus and minus, consist of animals descended from an original stock of less than a dozen individuals. These descendants number more than 33,000. In their ancestry, since the beginning of the selection experiment, not a single cross out of the race has occurred. At the same time no effort has been made to avoid inbreeding. Brother and sister and cousin matings are frequent in our records. Under these circumstances it is inevitable that the selected races should have become much "inbred."

Our critics with a leaning toward the "pure-line" idea have insisted that nothing but brother-sister matings should have been employed in our experiments. We have several times endeavored to carry forward certain high-grade families on this basis, but have been unable to secure large enough numbers of offspring to make this possible; but we have in several cases produced families of considerable size, descended exclusively from a single pair of ancestors—notably in the case of our pure "mutant" race and in a race descended from one hooded and one wild rat, which race was continued through 8 filial generations. (See p. 21, Castle and Phillips.) It would have been impossible, in these and other races, to make as rapid progress as we secured through selection in our two principal races, for when only brother-sister matings are permitted, it often happens that a mate of proper grade can not be secured for an individual among its own brothers and sisters, though such a mate may be found among its cousins or more remote relatives. It being our first object to test the effectiveness of selection, we have made selection of any individual within the group (series or family with which we were dealing) regardless of relationship, making the selection as rigid as the maintenance of a stock of considerable size would permit. More than once we have crossed the danger-line in advancing the standard of selection to such an extent that only small numbers of parents came up to it; more than once we have had to relax our standard temporarily in order to keep the race alive.

That the long-continued inbreeding of our selected races has affected their vigor and fecundity is unquestionable. It is shown by the fact that the plus and minus races, which had a common origin many generations ago and have ever since been bred in the same room and under identical conditions, *if crossed with each other*, produce offspring of much greater vigor and fecundity than either parent strain. In this our observations on the effects of inbreeding are entirely in harmony with those of Darwin, Bos, Weismann, and of breeders of farm animals quite generally. Miss King is credited with the view that inbreeding of rats may *increase* their size, vigor, and fecundity, but this is certainly contrary to common experience with these and other animals. It is probably true that under inbreeding it is possible, in exceptional cases, to isolate a strain relatively immune to ill effects from inbreeding (like Darwin's "Hero" morning-glory) or so inherently vigorous that it succeeds in spite of inbreeding. But it is very doubtful whether inbreeding of itself affects vigor other than disadvantageously. It is a sufficient test to cross-breed an inbred strain, in order to ascertain whether the inbreeding has increased or impaired its vigor.

PLUS AND MINUS–SELECTION SERIES.

The plus-selection experiment, when described by Castle and Phillips, had been carried through 13 generations, but the last 2 generations were incomplete. The number of offspring included in generation 12 (table 146) has now been raised from 590 to 682 and the number of offspring included in generation 13 (table 147) has been raised from 194 to 529. The mean grade of the parents for generation 12 has advanced from 4.09 to 4.10; that of the offspring has fallen from 3.94 to 3.93. Neither of these changes is of significant size. The correlation is now found to be 0.168 instead of 0.161.

In generation 13 (table 147) the changes are greater, as might be expected from the greater change in the number of observations. The mean of the parents is now 4.13 (formerly 4.22); that of the offspring is 3.94 (instead of 3.88). The correlation is 0.117, as compared with 0.132, the value previously obtained.

Generation 14 (table 148) includes 1,359 offspring of mean grade 4.01. They are descended mostly from parents of grade +4 or higher, mean 4.14.

Generation 15 (table 149) includes 3,690 individuals, more than have been produced in any other generation of the series. The mean grade of the parents was in this generation advanced about a quarter grade to 4.38; that of the offspring advanced a little, to 4.07.

Generation 16 (table 150) was also large, including 1,690 offspring. The grade of the parents was again advanced a little to 4.45; that of the offspring followed a similar amount, to 4.13.

In the three generations (14 to 16) which have been added since the last report, the grade of the selected parents has been advanced by 0.32, from 4.13 to 4.45; that of the offspring has advanced 0.19, from 3.94 to 4.13 (the mean grade of the parents three generations earlier).

The upper limit of variation of the offspring has meanwhile advanced from 5.25 to 5.87, the highest grade being found in a rat black all over except for a few white hairs on the chest. This rat has produced a few offspring of almost as high grade, though the most of his young are of much lower grade.

In the minus-selection series, generation 13, in our previous report, contained 571 offspring. This number has now been raised to 1,006 (table 151), the mean grade of both parents and offspring being practically unchanged by the additional young recorded. The parents are of mean grade −2.49, the offspring of mean grade −2.40.

In the next generation (14) the offspring number 717, their mean grade being −2.48, that of the selected parents being −2.64. (See table 152.)

Generation 15 includes 1,438 young of mean grade −2.54. The mean grade of the parents is −2.65. (See table 153.)

Generation 16 is the largest in the minus-selection series. It includes 1,980 young of mean grade −2.63. The grade of the parents is −2.79. (See table 154.)

Generation 17 (table 155) includes 868 young of mean grade −2.70. The grade of their parents is −2.86.

Four generations of selection have thus been added to the minus series as it stood at the last report. The mean grade of the parents has been advanced from −2.49 to −2.86; that of the offspring from −2.40 to −2.70, the former is an advance of 0.37, the latter of 0.30. In the plus series the corresponding changes for one less generation of selection (three), were 0.32 and 0.19, respectively. In both series a change in the mean of the offspring attends that in the parents, coinciding with it in character but not quite equaling it in amount.

The lagging behind of the offspring, as compared with their selected parents, gives a good illustration of regression, the phenomenon made familiar by Galton's researches, but explained away by Johannsen as due to a sorting-out action of selection on mixed races. The extent to which in these experiments the offspring lag behind their parents or "regress on their parents" is indicated in each table in the column headed "regression." Tables 146 and 150 illustrate particularly well how the offspring regress toward the general average of the race for the time being. The offspring of parents substantially the same grade as the general average of the race show *no* regression; the offspring of parents below this average show regression *upward* (indicated in the tables by the minus sign); the offspring of parents above the racial average show regression *downward*, the amount of the regression increasing with the aberrant character of the parents.

If one examines either selection series as a whole (compare Castle and Phillips), he will notice that the point (toward which regression occurs) changes with the progress of the selection. At the beginning of the plus-selection series regression was toward a grade of about +1.75 (see table 1, Castle and Phillips); after about 15 generations of plus selection it has advanced to +4.00. (See tables 148 to 150.) At the beginning of the minus-selection series, regression occurred toward a grade of 0 to −1 (Castle and Phillips, tables 16 and 17); in generation 17 (table 155) regression is apparently toward grade −2.62. These grades toward which regression occurs represent points of racial equilibrium or stability at which the race would tend to remain in the absence of further selection, but these points of equilibrium are capable of being moved either up or down the scale of grades at the will of the breeder, provided he has patience and persistency and will select repeatedly.

Regression indicates that there is not complete agreement between the somatic and the genetic character of the parents selected. But the steady movement (in the direction of the selection) of the point of

equilibrium toward which regression occurs serves to show that genotypic as well as phenotypic fluctuations occur in the material on which selection is brought to bear. DeVries and Johannsen have damned the word *fluctuation* by ascribing to it purely phenotypic significance. Is it not worth while to rescue the term from its present odious position, since it is clear that variation having a genetic basis may in every way resemble somatic fluctuation, except in its behavior under selection? Fluctuation may conceivably be either somatic or genetic or both. No one, in advance of actual experiment, can tell what its nature is in a particular case. In the case under discussion the fluctuation is obviously partly somatic and partly genetic. The somatic fluctuation occasions regression, the genetic fluctuation permits a change (under selection) of the point toward which regression occurs—that is, in the general average of the race.

Tables 156 and 157 show (generation by generation) the progress made by selection in modifying the racial character. It will be observed that as the mean advances in the direction of the selection both the upper and the lower limits of variation move in the same direction. The amount of the variation as measured by the standard deviation is less in the last half of the experiment than in the first half. It is also *steadier*, owing in part doubtless to the fact that the numbers are larger, and in part to a more stable genetic character of the selected races. But the genetic variability is plainly still large enough to permit further racial modification and there is no indication that it will cease until the hooded character has been completely selected out of existence, producing at one extreme of the series all-black rats, and at the other end of the series black-eyed white rats.

FURTHER OBSERVATIONS ON THE "MUTANT" SERIES.

Castle and Phillips described, under the name "mutants," 2 rats of the plus-selection series of very high grade. They proved to be heterozygotes between the average condition of the plus-selected race at that time, about $+3.75$, and a new condition, not previously known in our hooded races, but resembling that seen in "Irish" rats, which are black all over except for a white spot on the belly and would be classed on our grading scale as about $+5\frac{1}{2}$. In later generations we secured animals homozygous for the darker condition just described (that of Irish rats). The homozygous "mutant" race proved to be very stable in color-pattern, varying only from $5\frac{1}{4}$ to $5\frac{3}{4}$, with a majority of animals graded $5\frac{1}{2}$. Attempts to alter the modal condition of the race by selection have thus far proved futile because of our inability to increase the race sufficiently to afford a basis for selection. Its inbredness and its feebleness are perhaps causally related.

The suggestion was made that the change from our plus-selected race, which had occurred in the mutant stock, might be due to some supplementary modifying factor, not to a change in the hooded factor itself. If so, a cross with a race lacking the hooded factor or its "modifiers" might serve to demonstrate their distinctness by separating one from the other. A wild race seemed best suited for a test of this hypothesis, since it would be free from suspicion on the possible ground of harboring either the hooded pattern or its supposed modifier, which had converted the hooded pattern into the mutant. It was to be expected, if the hypothesis were correct, that the mutant character was hooded plus modifier; that then a cross with wild should produce in F_2 *hooded* young (lacking the modifier) as well as mutants and selfs. But if the mutant race had arisen through a change in the hooded factor itself, then the cross should produce only mutants and selfs, without hooded young in F_2. Crosses have now been made on a sufficient scale to show beyond question the correctness of the latter alternative, which is entirely in harmony also with the results described in the preceding parts of this paper.

Six homozygous "mutant" females of grade $+5\frac{1}{2}$ were mated with wild males of the same race described in Part I. They produced 46 young, all gray like wild rats and of grades as follows:

Grade......	$5\frac{1}{2}$	$5\frac{3}{4}$	$5\frac{7}{8}$	6
No........	1	15	7	23

Exactly half of the 46 F_1 rats bore no white spot, *i. e.*, were of grade $+6$. Seven more bore only a few white hairs (grade $5\frac{7}{8}$). The remainder were very similar to the mutant parent in grade.

Several matings were made of the F_1 rats, brother with sister, which produced 212 F_2 young. About a quarter of these were black (non-

agouti), the rest being gray (agouti).   Both sorts included about equal
numbers of individuals with and without white spots.   No difference
was observed in this respect between the progeny of spotted and of
unspotted parents.   Table 158 shows the F_2 young grouped family by
family according to grade.   Three of the four families are descended
from a single mutant grandparent; the fourth family is descended
from two different mutant grandparents which were bred simultane-
ously to the same wild male in the same cage.   The 10 F_2 young of
this family may have been produced either by full brother and sister,
or by half-brother and half-sister; it is uncertain which.   All other
F_2 young were produced by brother-sister matings.

It will be observed that the F_2 young (table 158) which are white-
spotted are in no case hooded.   Their range of variation does not fall
beyond that of the uncrossed mutant race.   It is certain, therefore,
that the "mutant" condition is not *hooded plus an independent Mendel-
ian modifier*.   It is a changed form of white-spotting, alternative to the
form of spotting found in the race from which it was derived (the plus-
selection series, generation 10).   It is, without much doubt, also alter-
native to the self condition of wild rats, though fluctuation in grade ob-
scures the segregation, which may, very likely, be imperfect.   This serves
to confirm the general conclusion that throughout the entire series of
experiments with the hooded pattern of rats we are dealing with quan-
titative variations in one and the same genetic factor.

GAMETIC COUPLING IN YELLOW RATS.

Two yellow-coated varieties of the Norway rat (*Mus norvegicus*) made their appearance as sports or mutations in England a few years since (Castle, 1914) and are now recognized as distinct varieties by fanciers. Both are similar in appearance except for the eye color. In one variety the eye is pink, showing under gross inspection only the color of the blood in the retina. In the other variety the eye is a reddish-black, owing to the combined effect of the red-colored blood and the black-pigmented retina. Since the retinal pigment is much less in this variety than in rats with gray or black coats, the eye is redder. It will be convenient to distinguish the dark-eyed yellow variety as red-eyed, reserving the name *black-eyed* for gray or black rats.

In the coats of both the pink-eyed and the red-eyed varieties of yellow rats black pigment is very feebly developed. It is in fact of a pale cream color. But the true yellow pigment seen on the tips of the hairs of gray rats is retained in full intensity in the yellow varieties. For this reason agouti varieties of yellow rats are much brighter-colored than non-agouti varieties. A non-agouti yellow variety has fur cream-colored throughout its length; the corresponding agouti variety has fur of this same cream color at its base, where the fur of gray rats is black-pigmented, but the hair-tips are of a bright yellow color of exactly the same shade as the hair-tips of gray rats. Hence it is clear that in these yellow varieties of rats a genetic factor for *black* pigmentation has been affected without any apparent change in the genetic apparatus for producing ordinary yellow pigment.

This is quite different from the genesis of yellow coat in most rodents—for example, in guinea-pigs and rabbits—in which black pigment is not apparently changed in character but merely in distribution, being "*restricted*" chiefly to the eye. In the yellow varieties of rats black pigment seems to be affected in the same way as in the pink-eyed variety of guinea-pigs and mice, viz, to be greatly *weakened* without affecting in the least the development of yellow pigment. The genetic behavior as well as the appearance of the pink-eyed yellow variation in rats is in every way parallel with the behavior of the variations known by the same name in mice and guinea-pigs. But red-eyed yellow in rats is a genetically distinct variation, as we shall presently see. In no other mammal does there occur a parallel variation, so far as I know. Both red-eyed yellow and pink-eyed yellow were found to be recessive Mendelian variations in crosses with black-eyed rats. From a cross between black-eyed and red-eyed an F_2 generation of 609 rats was raised, of which 452 were black-eyed and 157 red-eyed; expected, 457 : 152. From a cross between black-eyed and pink-eyed rats, certain F_1 females were back-crossed with a pure pink-eyed male. They produced 46 black-eyed and 39 pink-eyed; expected, 42 of each.

The pink-eyed yellow and red-eyed yellow of rats are complementary loss variations; for when the two varieties are crossed with each other they produce F_1 offspring which are either gray or black pigmented, according as their yellow parents did or did not transmit the agouti factor. These F_1 reversionary grays or blacks are paler in pigmentation than ordinary gray or black rats, indicating that neither character in a heterozygous form is the full complement of the other. But it is evident that in homozygous form each is the full complement of the other, since in F_2 and later generations grays and blacks of full intensity are obtained.

The F_1 black-eyed animals (blacks or grays) obtained by crossing pink-eyed yellows with red-eyed yellows, if mated with each other, produce an F_2 generation containing (1) black-eyed young (black or gray), (2) red-eyed yellow young, and (3) pink-eyed yellow young. We have obtained thus far 324 such F_2 young, of which 162 were of class (1), 90 of class (2), and 72 of class (3).

If, as suggested, red-eyed yellow and pink-eyed yellow are due to mutually independent Mendelian factors, then F_2 should contain four classes instead of the apparent three; wherefore it seemed probable that one of the three classes was really composite and that the three should be as $9 : 3 : 4$. On this basis the F_2 expectation would be $182 : 61 : 81$ instead of the observed $162 : 72 : 90$. Hence there appear to be fewer black-eyed young than are expected. Further, when we came to test the other F_2 classes to discover which of them was composite, we found very few individuals which would fall in the hypothetical fourth class transmitting both pink-eyed and red-eyed yellow in the same gamete. Instead of 1 in 16 as expected, we have been able to discover a much smaller number of double recessives. Both a deficiency in double recessives and a deficiency in double dominants (the black-eyed class), which have been observed among the F_2 rats, would be expected if pink-eyed yellow and red-eyed yellow are due to "linked genes," i. e., to factors located near each other in the germ-plasm. For in the cross under consideration each form of yellow enters the F_1 zygote in a different gamete. Hence, in the gametes arising from such zygotes we should expect the two forms of yellow to show mutual repulsion. If they did so, then the gametes formed by F_1 zygotes, of the four possible combinations, RP, Rp, rP, and rp, would not be equally numerous, but Rp and rP should be more numerous than RP and rp. That this is true is indicated by the facts presently to be stated. To test the gametic composition of the F_2 yellows, those which were red-eyed were mated with pink-eyed yellows of pure race, and those which were pink-eyed were mated with red-eyed yellows of pure race. For it was known that, since red-eyed yellow is a recessive variation, every red-eyed F_2 yellow must be homozygous for red-eye, but conceivably it might be either heterozygous for pink-eye or might lack it altogether. A cross with the pure pink-eyed yellow race would

decide between these possibilities. Further, it was clear that every pink-eyed F_2 yellow must be homozygous for that character, which is also recessive, but might be either homozygous or heterozygous for red-eye without affecting its appearance, or might even lack the gene for red-eye altogether. A cross with pure red-eyed animals would suffice to show in each case which possibility was realized. In accordance with this reasoning the proposed tests have been made in the case of 45 red-eyed and 40 pink-eyed F_2 yellows.

Of the 45 red-eyed yellows tested, 32 have given exclusively black-eyed young (blacks or grays), no test being considered adequate which did not produce 4 or more young; but 13 of the tested animals gave a mixture of black-eyed and of red-eyed young in approximately equal numbers. The former group, numbering 32, evidently lacked the gene for pink-eye, since they always produced atavists in crosses with pink-eyed yellows; the latter group, numbering 13, were evidently heterozygous for pink-eye, since only part of their young were atavistic.

Of the 40 pink-eyed F_2 yellows which were tested, 27 produced only black-eyed young; these evidently lacked the gene for red-eye. Ten others produced both black-eyed and red-eyed young, being evidently heterozygous for red-eye. Three have produced only red-eyed young, which shows them to be homozygous for red-eye as well as for pink-eye. Hence they are the *double recessives*, expected to be one-sixteenth of all F_2 rats if no linkage occurs, but less numerous if linkage occurs.

We are now in a position to estimate the strength of the linkage shown. If we designate by r the recessive gene for red-eye, and by p the recessive gene for pink-eye, then in the current Mendelian terminology the following F_2 classes are to be expected in the frequencies shown, if no linkage occurs:

Black-eyed.	Red-eyed.	Pink-eyed.
1 RRPP...	1 rrPP.....	1 RRpp
2 RrPP...	2 rrPp.....	2 Rrpp
2 RRPp...	....	1 rrpp
4 RrPp		
9	3	4

For the present we may pass by the black-eyed classes, since none of these were individually tested. The individual tests already described have shown the existence of the expected two classes of red-eyed and three classes of pink-eyed young, but in proportions very different from those given in the table. Among the red-eyed, instead of the expected 1 rrPP : 2 rrPp, we observe 32 : 13. Among the pink-eyed, where we expect 1 RRpp : 2 Rrpp : 1 rrpp, we observe 27 : 10 : 3. These are very different frequencies from those expected, and they strongly suggest linkage. How strong is the linkage? We may estimate it

from the actual proportions of the four possible kinds of gametes which the F_1 parents produced. With *no* linkage these gametes should be of four sorts, all equally numerous, viz, RP + Rp + rP + rp. Linkage would tend to increase the proportion of the two middle classes (Rp and rP, the original combinations) at the expense of the extremes (RP and rp, the double dominant and double recessive classes). The latter may be called "cross-over" classes, the former "non-cross-over." In producing the 85 F_2 yellow rats which were tested, twice that number of gametes were concerned, viz, 170. From the demonstrated genetic constitution of the tested animals, we can estimate how many cross-over and how many non-cross-over gametes entered into each.

Zygotes.	Cross-over gametes.	Non-cross-over gametes.
32 rrPP......	....	64
13 rrPp......	13	13
27 RRpp.....	....	54
10 Rrpp......	10	10
3 rrpp.......	6	....
85	29	141

The estimated proportion of cross-over to non-cross-over gametes is seen to be 29 : 141 or 1 : 4.8. In the terminology of Bateson and Punnett this would be a reduplication series lying between 1 : 4 : 4 : 1 and 1 : 5 : 5 : 1; in the terminology of Morgan, 17 per cent of the gametes formed by F_1 individuals are cross-over gametes.

We can test this linkage theory in another way. If linkage exists it should modify the proportions of the apparent classes in F_2 as well as of the real classes, which we have just been considering. The apparent classes are three, viz, black-eyed, red-eyed, and pink-eyed, with observed frequencies of 162 : 90 : 72. If no linkage exists the expected frequencies are 182 : 61 : 81, which deviate considerably from the expected frequencies. But if linkage exists, it will lessen the discrepancies. Linkage of 17 per cent strength will change the expectations to 164 : 79 : 81. This alteration shows agreement almost perfect in the case of the black-eyed class, a much reduced discrepancy in the case of the red-eyed class, and no change in the pink-eyed class—on the whole a much improved agreement between expected and observed frequencies.

Sturtevant has called attention to the fact that double recessives could occur among our F_2 animals only as a result of cross-overs occurring simultaneously in the gametes of *both* parents, a fact which Wright and I considered too obvious to demand comment in our preliminary paper, but recognized in our calculation by counting *two cross-over* gametes for every double recessive zygote. Sturtevant has questioned the adequacy of our tests in the case of these doubly recessive individuals because apparently he had formed the idea, from studies made on insects, that crossing-over could occur only in the gametogenesis of

one sex. I may say, therefore, that the classification of two animals as double recessives made in our preliminary paper was based on tests which had produced 14 and 9 yellow young respectively. The only possible alternative classification would have involved an expected 1 : 1 ratio of black-eyed to red-eyed young. The chances are overwhelmingly great against the observed results being departures due to random sampling from this expectation. The additional case of a double recessive reported in this paper is so classified on tests which, to the present time, have produced all together 28 yellow young. The number of young produced in each of the other tests is indicated below. Tests taken to indicate that the parent was of the formula rrPP produced only dark-eyed young (gray or black-coated), as follows:

No. of young.... 4 5 6 7 8 9 10 11 12 13 16 17 19
Cases........... 2 4 4 5 2 2 1 3 1 2 3 1 2=32

Tests showing the parents to be of the formula rrPp gave the following numbers in 13 tests:

Dark-eyed: Pink-eyed...2: 6 4:2 5:4 1:5 3:3 5:3 4:6 1:5 5:5 3:4 3:2 1:5 6:3

Pink-eyed animals were classified as of formula RRpp on the basis of the following tests, which yielded only dark-eyed young:

No. of young.... 4 6 7 8 9 10 11 12 13 14 15 16 18
Cases........... 2 1 3 2 2 2 1 6 1 3 1 1 2=27

Pink-eyed animals were shown to be of formula Rrpp by the following tests:

Dark-eyed: Red-eyed...10: 7 8:4 1:4 7:8 6:7 5:6 3:1 4:6 4:2 8:2

Both red-eyed and pink-eyed yellow rats, when crossed with albinos, produce an F_1 generation consisting exclusively of black-eyed (black or gray) young. F_2 from the red-eyed cross consisted of black-eyed, red-eyed, and albino young, and F_2 from the pink-eyed cross consisted of black-eyed, pink-eyed, and albino young. If no linkage occurs the expectation in each case is 9 : 3 : 4, and we at first supposed that this was the ratio approximated. But a summary of all litters thus far obtained indicates a probable linkage between albinism and the two yellow variations.

Thus, red-eyed non-agouti yellows mated with albinos from our plus-selected hooded race produced 17 black F_1 young. These have given us 58 F_2 young, of which 30 are black-eyed, 18 red-eyed, and 10 albinos. A 9 : 3 : 4 ratio would call for 32.5 : 11 : 14.5. It is evident, therefore, that we have too many red-eyed young and too few black-eyed and albinos. Linkage (in this case, repulsion) between red-eye and albinism would tend to increase the number of red-eyed and to decrease the number of black-eyed without changing materially the expectation for albinos; hence, linkage seems probable. Linkage involving 1 cross-over to 3 non-cross-over gametes, or 25 per cent cross-over

gametes, would give an expectation of 29.9 black-eyed : 13.6 red-eyed : 14.5 albinos, which agrees much better with the observed numbers (30 : 18 : 10) than does the 9 : 3 : 4 distribution. But if red-eye is linked with albinism as well as with pink-eye, then albinism and pink-eye should be linked with each other. Apparently such is the case, for three F_2 litters from the cross pink-eye $\times$ albino include 12 black, 12 pink-eyed, and 3 albino young. A 9 : 3 : 4 ratio (expected if *no* linkage occurs) would call for 15 black, 5 pink-eyed, and 7 albinos. Linkage of 5 : 1 would call for 14 : 6 : 7, and perfect linkage would call for 14 : 7 : 7. It is evident that the observed numbers of blacks and albinos are too small on any of these hypotheses, but the existence of linkage would tend to *diminish* the number of blacks and albinos in proportion to the number of pink-eyed, which is the nature of the deviation observed. To determine definitely whether linkage really occurs between the yellow variations and albinism, and if so, what is its strength, further experiments are needed, which are now in progress. It will also be desirable to determine whether the linkage strength is the same in both sexes.

SUMMARY.

Two yellow variations in rats which have recently arisen as mutations show mutual repulsion in heredity. When crossed with each other they produce an F_1 generation composed exclusively of reversionary dark-eyed individuals. The F_2 young are of three apparent classes, dark-eyed, red-eyed, and pink-eyed. Their numerical proportions deviate somewhat from the typical 9 : 3 : 4 ratio. Further, the proportions of the several expected classes of red-eyed and pink-eyed young do not agree with those usually observed in an F_2 Mendelian population. But in both cases the deviations are largely accounted for by the supposition that the genes of the respective yellow variations are "linked" (in this case showing repulsion) and that the proportion of "cross-over" gametes is about 17 per cent, or in other words, that non-cross-over gametes are about 4.8 times as numerous as cross-over gametes.

NOTE.—In the foregoing discussion it has been assumed that the ratio of cross-over to non-cross-over gametes is the same among gametes which take part in producing yellows as among those which take part in producing black-eyed individuals. Theoretically it should be slightly different, as the following table will show:

Ratio cross-over to non-cross-over gametes.	Per cent cross-over gametes.	Per cent among gametes producing yellows.	Per cent among gametes producing black-eyed.
1 : 1	50	42.9	55.6
1 : 2	33.3	29.4	36.8
1 : 3	25	22.6	27.3
1 : 4	20	18.4	21.6
1 : 4.4	*18.5*	*17.1*	*19.8*
1 : 5	16.7	15.5	17.8
1 : 6	14.3	13.4	15.2

TABLES.

Table 141 shows the classification of extracted hooded *first* F₂ young obtained from crossing hooded rats of the plus-selected series with wild rats.

TABLE 141.

Hooded grandparents.	Grade of hooded grandchildren.											Total hooded.	Total non-hooded.	Means of hooded.
	1½	1¾	2	2¼	2½	2¾	3	3¼	3½	3¾	4			
♀ 5513, +4¼, gen. 10	1	..	3	2	1	7	8	6	5	7	1	41	107	3.05
♂ 6348, +4, gen. 10	..	..	1	..	1	2	4	3	4	6	1	22	68	3.28
♀ 6955, +4, gen. 12	..	..	..	..	..	..	1	1	3	..		5	27	3.51
♀ 5513, +4¼, and ♀ 6600, +4¼, gen. 12	..	..	..	..	..	..	..	2	..	1	..	3	12	3.17
♀ 5513, +4¼, and ♀ 6955, +4, gen. 12	..	..	..	..	..	..	..	1	1	..	..	2	5	3.37
Totals	1	..	4	2	2	9	14	11	12	16	2	73	219	3.17

Table 142 shows the classification of extracted hooded *second* F₂ young obtained from crossing first F₂ hooded rats (table 141) with wild rats. The hooded grandparents were themselves grandchildren of ♀ 5513, +4¼, generation 10, on the side of both parents.

TABLE 142.

Hooded grandparents.	Grade of hooded grandchildren.									Total hooded.	Total non-hooded.	Means of hooded.
	2	2¼	2½	2¾	3	3¼	3½	3¾	4			
♀ 9619, +2	..	..	..	..	..	1	1	..	..	2	8	3.37
♂ 9686, +2¾	..	..	..	..	1	1	2	1	..	5	28	3.40
♀ 9620, +2¾	1	1	2	1	1	2	2	3	..	13	24	3.06
♀ 9729, +2¾	..	..	..	..	1	4	4	1	..	10	22	3.62
♂ 9727, +3	..	1	..	2	3	2	11	7	4	30	104	3.47
♀ 9728, +3	..	..	1	..	1	5	6	8	1	22	68	3.55
♀ 9621, +3¼	..	..	..	1	..	1	2	7	5	16	42	3.70
Totals	1	2	3	4	6	13	28	30	11	98	296	3.47

Table 143 shows the classification of extracted hooded *second* F₂ young obtained from crossing first F₂ hooded rats (table 141) with wild rats. The hooded grandparents were themselves grandchildren of ♂ 6348, +4, generation 10, on the side of both parents.

TABLE 143.

Hooded grandparents.	Grade of hooded grandchildren.										Total hooded.	Total non-hooded.	Means of hooded.
	1¾	2	2¼	2½	2¾	3	3¼	3½	3¾	4			
♂ 9639, +2	1	2	1	..	3	6	4	15	6	1	39	110	3.24
♀ 9704, +2¾	..	1	..	..	..	1	..	4	..	..	6	16	3.17
♀ 9765, +3	..	..	..	..	..	..	..	1	..	..	1	10	3.50
♀ 9747, +3¼	1	7	..	1	1	7	1	4	4	1	27	76	2.90
♀ 9703, +3½	..	..	1	1	2	2	1	5	2	2	16	47	3.28
♀ 9705, +3½	..	..	..	..	1	5	1	4	8	2	21	74	3.48
♀ 9748, +3½	..	..	..	..	1	2	1	2	3	..	9	40	3.36
♀ 9796, +4	..	..	..	..	..	..	..	..	1	1	2	3	3.87
Totals	2	10	2	2	8	23	8	35	24	7	121	376	3.22

Table 144 shows the classification of extracted hooded *second* F_2 young obtained from crossing first F_2 hooded rats with wild rats. The hooded grandparent, ♂9660, +3¾, was a grandson of ♀6955, +4, generation 12, on the side of both parents. The hooded grandparent, ♂9711, +3¼, was a grandson, on the side of one parent, of ♀5513, +4¼, generation 10, and on the side of the other parent, of ♀6955, +4, generation 12. (See table 141.)

TABLE 144.

Hooded grand-parents.	Grade of hooded grandchildren.									Total hooded.	Total non-hooded.	Means of hooded.
	2	2¼	2½	2¾	3	3¼	3½	3¾	4			
♂9660, +3¾...	1	..	..	1	1	2	5	9	2	21	44	3.50
♂9711, +3¼...	..	..	1	2	2	4	4	2	1	16	33	3.28
Totals....	1	..	1	3	3	6	9	11	3	37	77	3.40

Table 145 is a combination of tables 142 to 144, in which the second F_2 young are classified according to the grade of their first F_2 hooded grandparent.

TABLE 145.

Grade of hooded grand-parents.	Grade of hooded grand-children.										Total hooded.	Total non-hooded.	Means of hooded.
	1¾	2	2¼	2½	2¾	3	3¼	3½	3¾	4			
2	1	2	1	..	3	6	5	16	6	1	41	118	3.25
2¾	..	2	1	2	1	3	4	12	8	1	34	90	3.29
3	..	..	1	1	2	4	7	18	15	5	53	182	3.48
3¼	1	7	..	2	4	9	6	10	13	7	59	151	3.22
3½	..	..	1	1	4	9	3	11	13	4	46	161	3.39
3¾	..	1	..	..	1	1	2	5	9	2	21	44	3.50
4	..	..	..	..	..	..	..	..	1	1	2	3	3.87
3.02	2	12	4	6	15	32	27	72	65	21	256	749	3.34

Table 146 shows the classification of generation 12, plus-selection series. This is an enlargement of table 12 of Castle and Phillips.

TABLE 146.

Grade of parents.	Grade of offspring.													Totals.	Means.	Regression.
	2¼	2½	2¾	3	3¼	3½	3¾	4	4¼	4½	4¾	5	5¼			
3¾						4	20	7	4					35	3.83	−.08
3⅞						3	23	21	6	2	2			57	3.94	−.06
4				1	2	12	62	66	12	5	1	1	2	164	3.91	.09
4⅛	2			3	25	106	91	30	6	3	1			267	3.87	.25
4¼				1		11	25	35	16	5	2			95	3.95	.30
4⅜						3	6	14	10	7	3	1	1	45	4.17	.20
4½							1	4	1			1		7	4.14	.36
4⅝			1				3	4	3					11	3.91	.71
4¾																
4⅞																
5											1			1	4.75	.25
4.10	2			3	5	58	246	242	82	25	12	4	3	682	3.93	.17

Table 147 shows the classification of generation 13, plus-selection series.   This is an enlargement of table 13 of Castle and Phillips.

TABLE 147.

Grade of parents.	Grade of offspring.											Totals.	Means.	Regression.
	$2\frac{3}{4}$	3	$3\frac{1}{4}$	$3\frac{1}{2}$	$3\frac{3}{4}$	4	$4\frac{1}{4}$	$4\frac{1}{2}$	$4\frac{3}{4}$	5	$5\frac{1}{4}$			
$3\frac{1}{2}$	..	..	1	1	1	..	..	..	..	..	..	3	3.50	0
$3\frac{5}{8}$	..	..	..	..	..	..	..	..	..	..	..			
$3\frac{3}{4}$	..	..	..	1	3	11	3	1	1	1	..	21	4.08	−.33
$3\frac{7}{8}$	..	1	2	4	9	7	4	1	3	..	..	31	3.90	−.03
4	..	1	7	33	60	59	25	17	2	1	..	205	3.90	.10
$4\frac{1}{8}$	..	..	1	11	32	33	13	5	..	1	..	96	3.92	.20
$4\frac{1}{4}$	1	..	..	7	23	33	13	1	2	..	..	80	3.93	.32
$4\frac{3}{8}$	..	1	..	2	8	7	6	1	3	..	1	29	4.03	.34
$4\frac{1}{2}$	..	..	..	1	15	17	10	5	1	1	..	50	4.05	.45
$4\frac{5}{8}$	..	..	..	..	1	2	1	..	..	..	..	4	4.00	.62
$4\frac{3}{4}$	..	..	..	..	3	1	..	1	..	..	..	5	3.95	.80
$4\frac{7}{8}$	..	..	..	1	..	2	1	..	1	..	..	5	4.05	.82
4.13	1	3	11	61	155	172	76	32	13	4	1	529	3.94	.19

Table 148 shows the classification of generation 14, plus-selection series.

TABLE 148.

Grade of parents.	Grade of offspring.													Totals.	Means.	Regression.
	$2\frac{1}{2}$	$2\frac{3}{4}$	3	$3\frac{1}{4}$	$3\frac{1}{2}$	$3\frac{3}{4}$	4	$4\frac{1}{4}$	$4\frac{1}{2}$	$4\frac{3}{4}$	5	$5\frac{1}{4}$	$5\frac{1}{2}$			
$3\frac{1}{2}$	..	..	..	..	2	6	3	..	1	..	..	..	..	12	3.83	−.33
$3\frac{5}{8}$	..	..	..	..	2	9	4	7	1	..	1	..	..	24	4.02	−.39
$3\frac{3}{4}$	1	..	2	1	11	32	45	18	5	..	..	..	..	115	3.90	−.15
$3\frac{7}{8}$	..	..	1	.	28	52	63	28	8	3	1	..	..	184	3.97	−.10
4	..	..	..	2	40	84	122	50	6	2	..	..	..	306	3.92	.08
$4\frac{1}{8}$	..	..	..	..	19	74	72	56	15	3	1	1	..	241	3.99	.13
$4\frac{1}{4}$	..	..	..	..	6	25	48	42	8	1	..	..	..	130	4.04	.21
$4\frac{3}{8}$	..	..	..	1	2	24	36	29	6	2	..	..	..	100	4.04	.33
$4\frac{1}{2}$	..	..	..	..	3	12	31	37	12	3	2	1	..	101	4.16	.34
$4\frac{5}{8}$	..	..	..	..	..	11	13	15	11	5	2	1	..	58	4.23	.39
$4\frac{3}{4}$	..	..	..	..	..	5	16	14	8	2	..	..	..	45	4.17	.58
$4\frac{7}{8}$	..	..	..	..	..	1	7	14	6	3	1	..	1	33	4.33	.54
5	..	..	..	..	..	..	..	..	..	..	..	..	..			
$5\frac{1}{8}$	..	..	..	..	..	..	1	4	1	..	..	..	..	6	4.25	.87
$5\frac{1}{4}$	..	..	..	..	..	..	..	1	1	..	1	1	..	4	4.75	.50
4.14	1	..	3	4	113	335	461	315	89	24	9	4	1	1,359	4.01	.13

Table 149 shows the classification of generation 15, plus-selection series.

TABLE 149.

Grade of parents.	2½	2¾	3	3¼	3½	3¾	4	4¼	4½	4¾	5	5¼	5½	Totals.	Means.	Regression.
3¾	..	..	..	1	3	3	..	..	..	..	..	..	..	7	3.57	.18
3⅞	..	..	..	2	5	10	11	2	..	..	..	..	..	30	3.80	.07
4	..	..	..	1	16	58	46	28	7	..	..	..	..	156	3.91	.09
4⅛	..	..	1	2	29	184	255	165	29	3	1	1	..	670	4.00	.12
4¼	1	..	..	1	22	183	296	165	44	8	1	..	..	721	4.02	.23
4⅜	..	..	1	1	18	207	357	290	71	21	3	..	..	969	4.06	.31
4½	..	..	1	9	99	159	175	48	6	7	..	2	..	506	4.10	.40
4⅝	..	..	..	..	3	37	87	88	14	5	2	..	1	237	4.11	.51
4¾	..	..	..	..	3	25	38	58	24	5	9	6	..	168	4.22	.53
4⅞	..	..	..	..	..	13	25	42	34	15	12	4	1	146	4.37	.50
5	..	..	..	..	..	1	9	21	10	2	..	..	..	43	4.27	.73
5⅛	..	..	..	..	..	..	4	4	7	3	..	..	..	18	4.37	.75
5¼	..	..	..	..	..	..	2	10	5	1	1	..	..	19	4.36	.89
4.38	1	..	2	9	108	820	1,289	1,048	293	69	36	11	4	3,690	4.07	.31

Table 150 shows the classification of generation 16, plus-selection series.

TABLE 150.

Grade of parents.	3¼	3½	3¾	4	4¼	4½	4¾	5	5¼	5½	5¾	5⅞	Totals.	Means.	Regression.
4⅛	..	4	26	64	37	8	..	..	..	..	..	..	139	4.04	.08
4¼	..	4	34	64	40	5	1	..	1	..	..	..	149	4.02	.23
4⅜	1	9	149	316	271	58	9	1	2	..	..	..	816	4.08	.29
4½	..	7	25	82	69	18	5	..	..	..	..	..	206	4.10	.40
4⅝	..	..	12	50	61	26	11	4	1	1	..	..	166	4.24	.38
4¾	..	..	..	12	16	19	10	6	1	2	..	..	66	4.47	.38
4⅞	..	1	5	23	26	8	3	2	1	..	..	..	69	4.21	.66
5	..	..	..	8	25	15	7	2	2	1	..	1	61	4.44	.56
5⅛	..	..	1	1	8	6	..	1	1	..	..	..	18	4.39	.73
4.45	1	25	252	620	553	163	46	16	9	4	..	1	1,690	4.13	.32

Table 151 shows the classification of generation 13, minus-selection series.   This is an enlargement of table 28 of Castle and Phillips.

TABLE 151.

Grade of parents.	1¾	2	2¼	2½	2¾	3	3¼	3½	Totals.	Means.	Regression.
−2¼	7	43	25	28	12	1	..	..	116	2.25	0
−2⅜	8	74	80	87	56	19	5	..	329	2.39	0
−2½	8	65	65	92	46	11	2	1	290	2.38	.12
−2⅝	3	23	33	58	44	4	4	1	170	2.50	.12
−2¾	1	5	4	16	12	7	1	..	46	2.56	.19
−2⅞	..	7	8	10	7	2	..	..	34	2.42	.45
−3	..	4	1	6	5	3	2	..	21	2.59	.41
−2.49	27	221	216	297	182	47	14	2	1,006	2.40	.09

Table 152 shows the classification of generation 14, minus-selection series.

TABLE 152.

Grade of parents.	Grade of offspring (minus).											Totals.	Means.	Regression.
	1	1¼	1½	1¾	2	2¼	2½	2¾	3	3¼	3½			
−2¼	..	..	..	..	2	2	14	8	..	..	..	26	2.54	−.29
−2⅜	..	..	..	2	8	20	22	11	2	..	..	65	2.40	−.03
−2½	1	..	..	3	40	50	73	29	2	1	..	199	2.36	.14
−2⅝	..	..	..	2	23	32	59	44	10	1	1	172	2.44	.18
−2¾	..	..	..	..	7	20	42	43	11	4	..	127	2.60	.15
−2⅞	..	..	..	..	5	10	25	14	2	2	..	58	2.52	.35
−3	..	..	..	..	1	1	15	8	3	5	..	33	2.69	.31
−3⅛	..	..	..	..	..	6	3	7	4	..	..	20	2.56	.56
−3¼	..	..	..	..	..	..	..	4	3	..	..	7	2.85	.40
−3⅜	..	..	..	..	..	..	3	4	3	..	..	10	2.75	.62
−2.64	1	..	..	7	86	141	256	172	40	13	1	717	2.48	.16

Table 153 shows the classification of generation 15, minus-selection series.

TABLE 153.

Grade of parents.	Grade of offspring (minus).								Totals.	Means.	Regression.
	1¾	2	2¼	2½	2¾	3	3¼	3½			
−2⅛	..	1	4	4	4	..	..	..	13	2.46	−.33
−2¼	..	11	23	15	13	2	..	..	64	2.39	−.14
−2⅜	1	15	24	47	29	3	..	..	119	2.45	−.07
−2½	2	39	65	102	68	14	..	..	290	2.49	.01
−2⅝	1	41	97	137	99	24	6	2	407	2.50	.12
−2¾	..	7	37	91	70	31	3	1	240	2.60	.15
−2⅞	..	4	18	62	70	22	7	..	183	2.64	.23
−3	..	..	1	17	16	13	4	..	51	2.76	.24
−3⅛	..	..	4	11	17	7	1	2	42	2.73	.34
−3¼	..	..	..	5	12	8	3	1	29	2.85	.60
−2.65	4	118	273	491	398	124	24	6	1,438	2.54	.11

Table 154 shows the classification of generation 16, minus-selection series.

TABLE 154.

Grade of parents.	Grade of offspring (minus).													Totals.	Means.	Regression.
	1	1¼	1½	1¾	2	2¼	2½	2¾	3	3¼	3½	3¾	4			
−2¼	..	..	..	..	3	5	1	..	..	..	..	..	..	9	2.19	.06
−2⅜	1	..	..	..	5	4	3	1	..	..	..	..	..	14	2.16	.21
−2½	..	..	..	..	4	27	61	56	3	1	..	..	..	152	2.55	−.05
−2⅝	..	..	..	1	16	56	188	148	36	5	..	..	..	450	2.58	.04
−2¾	..	..	..	1	10	36	130	151	28	5	1	..	..	362	2.62	.13
−2⅞	..	..	..	1	11	45	187	230	71	16	1	..	1	563	2.66	.21
−3	..	..	..	..	2	12	95	128	65	12	1	1	..	316	2.73	.27
−3⅛	..	..	..	..	..	6	30	36	15	10	1	..	..	98	2.74	.38
−3¼	..	..	..	..	..	..	..	12	3	1	..	..	..	16	2.83	.42
−2.79	1	..	..	3	51	191	695	762	221	50	4	1	1	1,980	2.63	.16

Table 155 shows the classification of generation 17, minus-selection series.

TABLE 155.

Grade of parents.	Grade of offspring (minus).											Totals.	Means.	Regression.
	$1\frac{3}{4}$	2	$2\frac{1}{4}$	$2\frac{1}{2}$	$2\frac{3}{4}$	3	$3\frac{1}{4}$	$3\frac{1}{2}$	$3\frac{3}{4}$	4	$4\frac{1}{4}$			
$-2\frac{5}{8}$	..	2	10	40	49	11	1	..	..	..	..	113	-2.63	0
$-2\frac{3}{4}$	1	2	12	77	81	28	1	..	..	..	..	202	-2.65	.10
$-2\frac{7}{8}$	..	4	34	110	145	51	19	1	..	..	..	364	-2.71	.16
-3	..	..	3	28	42	18	7	..	..	..	..	98	-2.75	.25
$-3\frac{1}{8}$	..	..	..	5	18	17	6	1	..	..	1	48	-2.92	.20
$-3\frac{1}{4}$	..	..	..	3	16	15	6	1	..	..	..	41	-2.92	.33
$-3\frac{3}{8}$	..	..	..	..	..	1	..	1	..	..	..	2	-3.25	.12
-2.86	1	8	59	263	351	141	40	4	..	..	1	868	-2.70	.16

Table 156 summarizes the results of the plus-selection of hooded rats continued through sixteen successive generations.

TABLE 156.

Generation.	Mean grade of parents.	Mean grade of offspring.	Lowest grade of offspring.	Highest grade of offspring.	Standard deviation of offspring.	Correlation, parents-offspring.	Number of offspring.
1	2.51	2.05	$+1.00$	$+3.00$	.54	.29	150
2	2.52	1.92	-1.00	$+3.75$	.73	.31	471
3	2.73	2.51	$+ .75$	$+4.00$	.53	.33	341
4	3.09	2.73	$+ .75$	$+3.75$	.47	.06	444
5	3.33	2.90	$+ .75$	$+4.25$	.50	.16	610
6	3.52	3.11	$+1.50$	$+4.50$	.49	.18	861
7	3.56	3.20	$+1.50$	$+4.75$	.55	.21	1,077
8	3.75	3.48	$+1.75$	$+4.50$	.44	.09	1,408
9	3.78	3.54	$+1.75$	$+4.50$	.35	.21	1,322
10	3.88	3.73	$+2.25$	$+5.00$	.36	.11	776
11	3.98	3.78	$+2.75$	$+5.00$	.29	.23	697
12	4.10	3.92	$+2.25$	$+5.25$	.31	.16	682
13	4.13	3.94	$+2.75$	$+5.25$	.34	.13	529
14	4.14	4.01	$+2.75$	$+5.50$	.34	.31	1,359
15	4.38	4.07	$+2.50$	$+5.50$	.29	.30	3,690
16	4.45	4.13	$+3.25$	$+5.87$	.29	.31	1,690
Total ...	....	....	....	....	....	....	16,107

Table 157 summarizes the results of the minus-selection of hooded rats continued through seventeen successive generations.

TABLE 157.

Genera-tion.	Mean grade of parents.	Mean grade of offspring.	Lowest grade of offspring.	Highest grade of offspring.	Standard deviation of offspring.	Correla-tion, parents-offspring.	Number of offspring.
1	−1.46	−1.00	+ .25	−2.00	.51	...	55
2	−1.41	−1.07	+ .50	−2.00	.49	− .03	132
3	−1.56	−1.18	0	−2.00	.48	.20	195
4	−1.69	−1.28	+ .50	−2.25	.46	.02	329
5	−1.73	−1.41	0	−2.50	.50	.18	701
6	−1.86	−1.56	0	−2.50	.44	.16	1,252
7	−2.01	−1.73	0	−2.75	.35	.14	1,680
8	−2.05	−1.80	0	−2.75	.28	.09	1,726
9	−2.11	−1.92	− .50	−2.75	.28	.05	1,591
10	−2.18	−2.01	−1.00	−3.25	.24	.15	1,451
11	−2.30	−2.15	−1.00	−3.50	.35	.08	984
12	−2.44	−2.23	−1.00	−3.50	.37	.40	1,037
13	−2.48	−2.39	−1.75	−3.50	.34	.18	1,006
14	−2.64	−2.48	−1.00	−3.50	.30	.28	717
15	−2.65	−2.54	−1.75	−3.50	.29	.35	1,438
16	−2.79	−2.63	−1.00	−4.00	.27	.26	1,980
17	−2.86	−2.70	−1.75	−4.25	.28	.22	868
Total...	....	....	....	....	....	....	17,142

Table 158 shows the classification of the F_2 young obtained by crossing homozygous "mutant" with wild rats.

TABLE 158.

Mutant grandparents.	Grade of off-spring.						Totals.
	5	$5\frac{1}{4}$	$5\frac{1}{2}$	$5\frac{3}{4}$	$5\frac{7}{8}$	6	
♀ 0630, $+5\frac{1}{2}$..................	..	3	12	9	2	20	46
♀ 0698, $+5\frac{1}{2}$..................	1	2	22	29	1	59	114
♀ 0694, $+5\frac{1}{2}$..................	..	..	12	11	..	19	42
♀ 0630, $+5\frac{1}{2}$, or 0636, $+5\frac{1}{2}$.....	..	1	3	1	..	5	10
Total..................	1	6	49	50	3	103	212

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EXPLANATION OF PLATES.

PLATE 1.

Colored photographs of the fur of guinea-pigs, showing grades of dilution due to different combinations of the allelomorphs of albinism. The skin of each animal from which fur is shown was opened along the median ventral line and a complete section across the middle of the body is shown in skins 1, 6, 9, 10, and 11. But in the other skins 2, 3, 4, 5, 7, and 8, only a section extending from the mid-dorsal to the mid-ventral line is shown. Figures 1 to 4 show agouti fur (AAEE); 5 to 8, non-agouti fur (aaEE); and 9 to 11 show fur in which the extension factor is wanting (ee). The uppermost row of skins are intense pigmented, all others are dilute of intensities, diminishing toward the bottom of the plate. Factors A and E are written as homozygous, though this is not known in all cases.

Fig. 1. Black-red agouti................ C C AAEE
2. Dark sepia-yellow agouti......... C_d C_d AAEE
3. Dark sepia-cream agouti......... C_d C_r AAEE
4. Light sepia-cream agouti......... C_d C_a AAEE
5. Black........................ C C aaEE
6. Dark sepia$_1$................... C_d C_d aaEE
7. Dark sepia$_2$................... C_d C_r aaEE
8. Light sepia$_5$................... C_d C_a aaEE
9. Red.......................... C C aaee
10. Yellow$_4$...................... C_d C_d aaee
11. Cream$_6$...................... C_d C_a aaee (C_d C_r similar)

PLATE 2.

Photographs of guinea-pig skins, showing further grades of reduction in color due to albinism and its allelomorphs. Sections of skin extending entirely across the body are shown in all cases. The arrangement is similar to that of plate 1.

Fig. 12. Dark sepia-white agouti (red-eyed)...... C_r C_r AAEE
13. Light sepia-white agouti (red-eyed)..... C_r C_a AAEE
14. Albino (known to transmit agouti)...... C_a C_a AAEE
15. Dark sepia (red-eyed)................. C_r C_r aaEE
16. Light sepia (red-eyed)................. C_r C_a aaEE
17. Albino (transmits only non-agouti)...... C_a C_a aaEE
18. White (red-eyed)..................... C_r C_r aaee (C_r C_a similar)
19. Albino (from yellow stock)............. C_a C_a aaee

PLATE 3.

Colored photographs of the skins of guinea-pigs.

Fig. 20. A half-grown guinea-pig of race C; color, pale cream. The eyes were brown-pigmented.
21. An F_1 male hybrid whose mother was an albino of race B and whose father was a pure *cutleri*. Compare figures 23 and 34.
22. An F_1 male hybrid whose mother was a brown-eyed cream animal of race C and whose father was a pure *cutleri*. Compare figures 20 and 23.
23. A pure *cutleri* male.
24. A pure *cutleri* female.

PLATE 4.

Colored photographs of the skins of F_2 hybrids produced by crossing brown-eyed cream guinea-pigs with *Cavia cutleri*. Compare figures 20, 22, and 23.

Fig. 25. Golden agouti.
26. Pale black (sepia).
27. Brown or chocolate.
28. Cinnamon.
29. Yellow.
30. Albino.

PLATE 5.

Colored photographs of skins showing new color varieties of guinea-pigs.

Fig. 31. Silver cinnamon or red-eyed cinnamon.

32. Red-and-pink-eyed black spotted with white.

33. Pink-eyed golden agouti spotted with red and with white, hence a "tri-color."

34. Albino with sooty fur and black pigmented extremities, similar to race B.

PLATE 6.

Femurs of hybrid guinea-pigs and of their parent races, natural size, to show extent of variation. The longest and the shortest femur in each group of individuals is shown with 3 or 4 others of intermediate length placed between them. In the left half of the plate are shown the femurs of males, and in the right half the femurs of females. Top row, *Cavia cutleri*. Second row, race B guinea-pigs. Third row, F_1 hybrids produced by the cross of *C. cutleri* ♂ × race B ♀. Fourth row, F_2 hybrids from the same cross.

PLATE 7.

Fig. 35. A scale of grades used in describing the pattern of piebald rats. Rats like the pictures toward the left of the scale are known to fanciers as "hooded"; the grade at the extreme right would be called "Irish" by fanciers.

36. Skins of a pair of rats and of their 9 young. One parent was an "Irish" rat, the other "hooded." Four of the young are hooded, five are Irish. Hooded is recessive to Irish in crosses. The Irish parent in this case was a heterozygote. Note individual variation in each group of young.

37. A typical smooth-coated guinea-pig.

38. A rough-coated guinea-pig, well-rosetted, grade A.

39. A poorly-rosetted rough guinea-pig, grade C.

PLATE 1

Variations of intensity of coat pigments, due to albino allelomorphs, in agouti series (1—4), black series (5—8), and yellow series (9—11).

PLATE 2
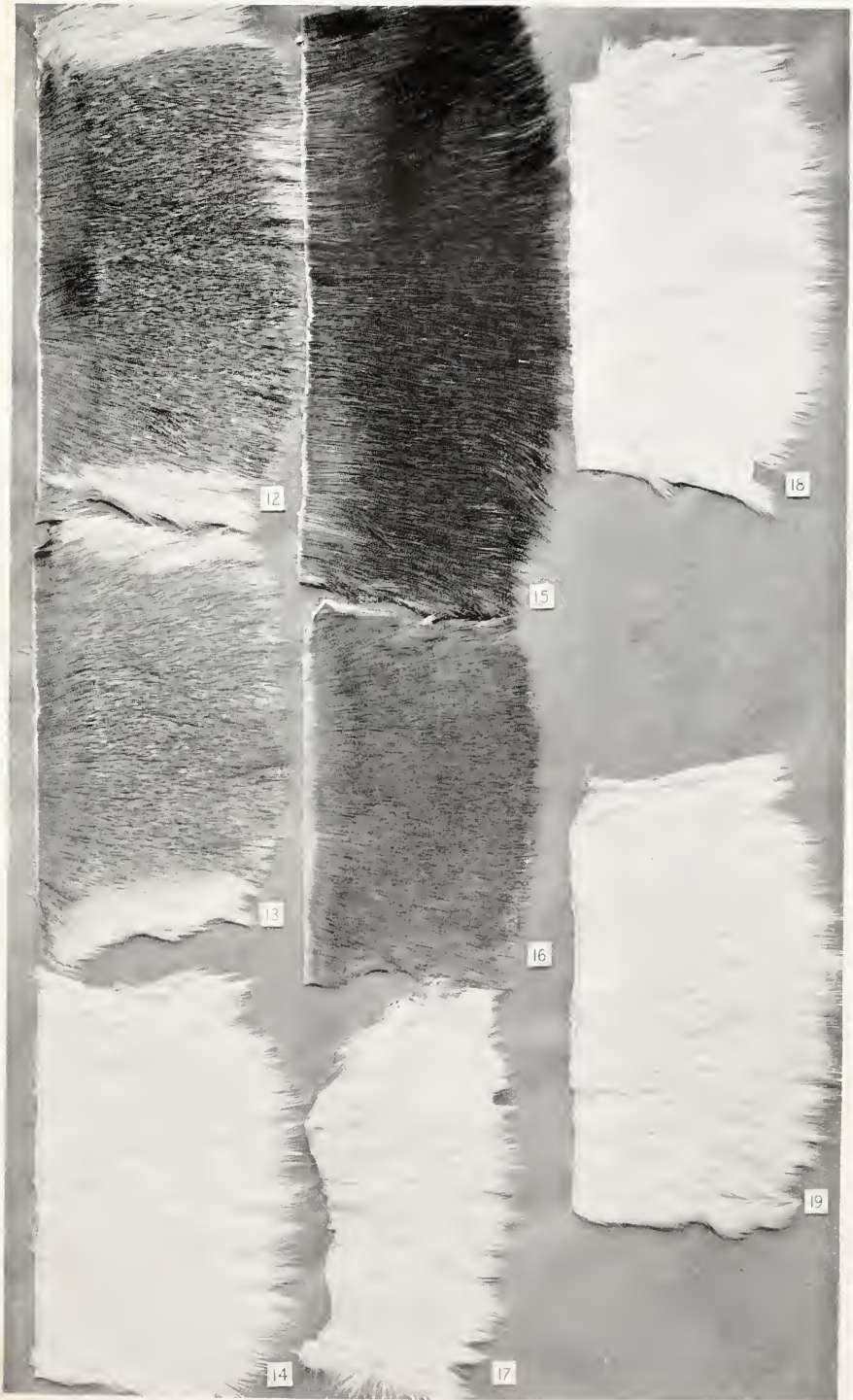
Albinism and its non-yellow allelomorphs in agouti series (12—14), black series (15—17), and yellow series (18, 19).

PLATE 3

Fig. 20, half-grown guinea-pig, race C.   Figs. 23, 24, male and female Cavia cutleri, adult.
Fig. 22, F₁ hybrid, race C x Cavia cutleri, adult.   Fig. 21, F₁ hybrid, race B (Plate 5,
Fig. 34) x Cavia cutleri, adult.

PLATE 4

F₂ hybrids, race C x Cavia cutleri.   Fig. 25, agouti; 26, black; 27, chocolate; 28, cinnamon; 29, yellow; 30, albino.

PLATE 5

Some new guinea-pig color varieties.   Fig. 31, red-eyed cinnamon; 32, red-and-pink-eyed black spotted with white; 33, pink-eyed golden agouti spotted with red and with white; 34, albino with sooty fur and black pigmented extremities, similar to race B.
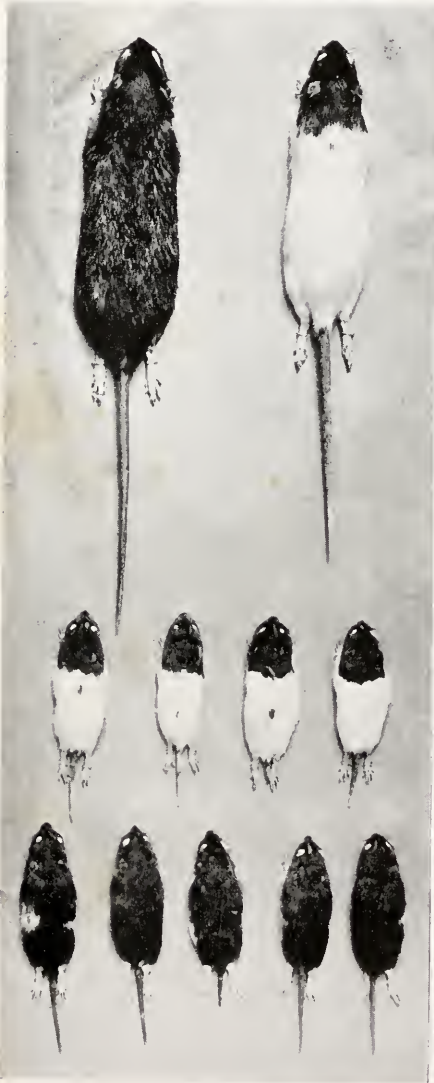
PLATE 6
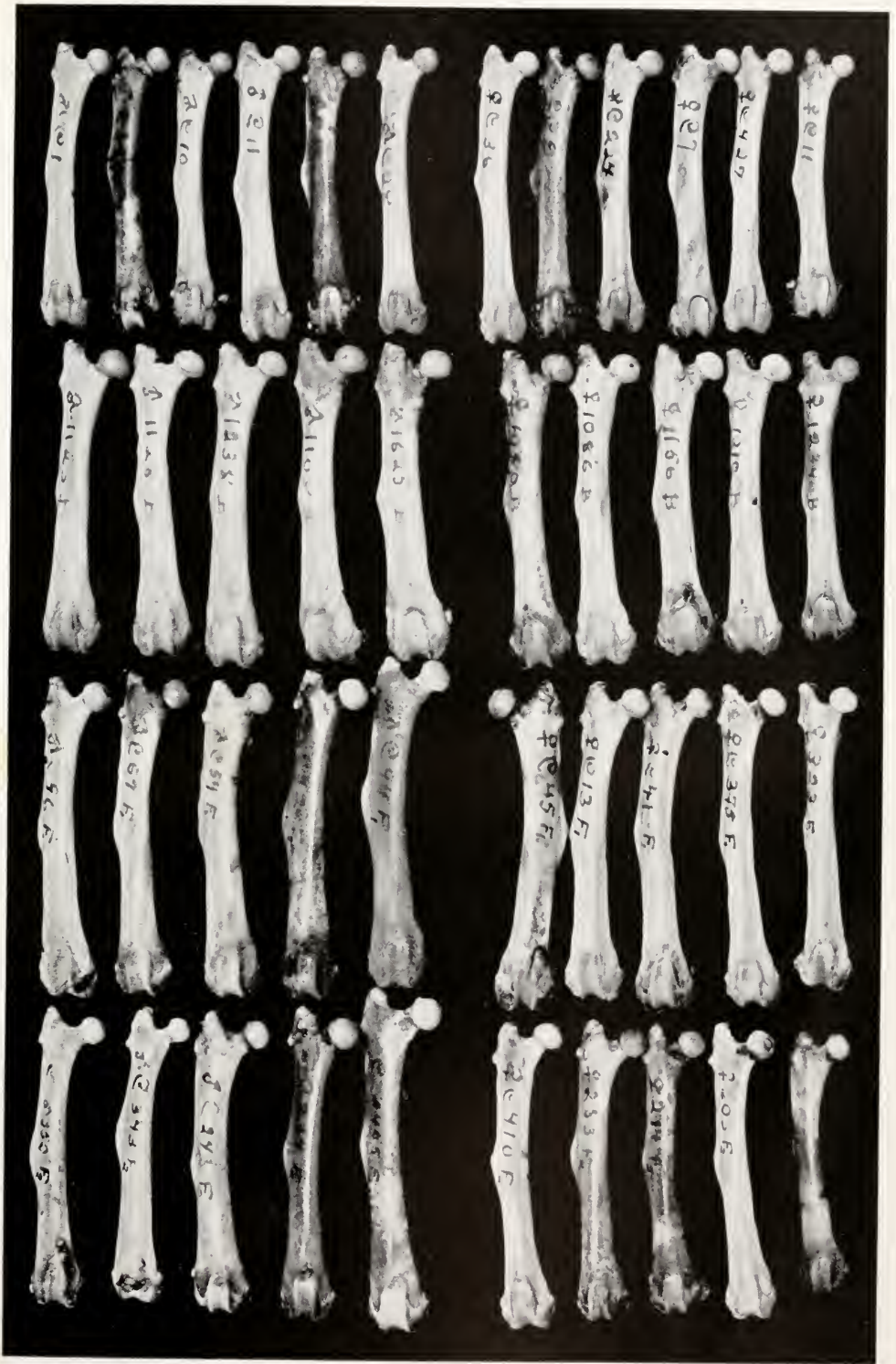
Femurs of Cavia cutleri (male and female), of race B, and of their F_1 and F_2 hybrids, showing complete range of variation in each. Natural size.

PLATE 7
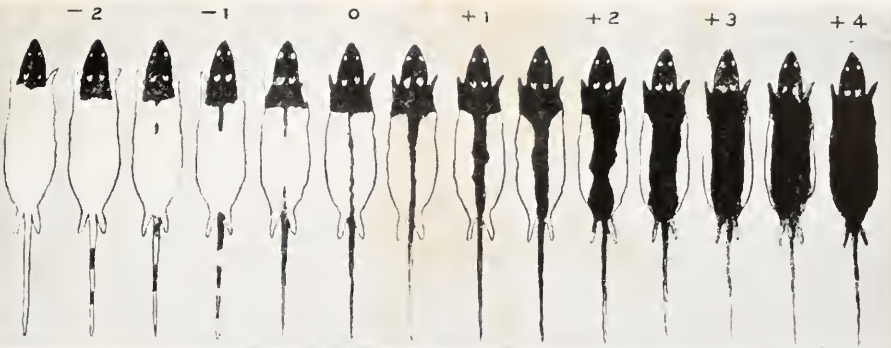
Fig. 35, a scale of grades for piebald rats.   Fig. 36, a pair of piebald rats and their nine young.   Fig. 37, a smooth guinea-pig.   Fig. 38, a well-rosetted rough guinea-pig, grade A.   Fig. 39, a poorly rosetted rough guinea-pig, grade C.

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