SEVERAL COLOR "MUTATIONS" IN MICE OF THE GENUS PEROMYSCUS

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In the course of breeding experiments conducted by the author for more than two years past, certain rather striking "sports" have appeared, which seem to behave as discontinuous hereditary variations. Although sufficient time has not elapsed since their appearance to reveal the exact mode of transmission of these aberrant characters, a brief account of them seems justifiable at present.

PARTIAL ALBINISM

About December 29, 1915, a litter of five young were born, whose parents were brother and sister, both being F₁ hybrids between the subspecies *P. maniculatus sonoriensis* and *P. m. rubidus*. These two subspecies differ conspicuously in color as well as in some other characters, the former race being of a much lighter shade than the latter. Hybrids of the F₁ generation are on the whole intermediate in this respect. Of the five young F₂ mice above referred to, three developed a normal amount of pigment in the skin and eyes, while the other two remained extremely pale. At first glance, this might have been interpreted as a case of simple Mendelian splitting, resulting in the appearance of the grandparental color types. But a close inspection of the pale individuals, as late as the eighth or ninth day after birth, showed that they were nearly or quite pigmentless. Moreover, further breeding of hybrids between these two races has proved that no such simple segregation phenomena occur in the F₂ generation.

Unfortunately, all of the foregoing brood died in very early life, none reaching the age of two weeks. On January 8, 1916, a sister of the above-mentioned mother gave birth to a brood of two, the father being the same as in the preceding case. Both of these F₂ offspring, which are still living, are normally pigmented. But on October 5, 1916, a second litter was born of these same parents. This litter, when first examined, comprised two pale individuals, one of each sex. The skins
of these young mice failed to darken, as happens in normal animals, preceding the outgrowth of the hair, and the pigment of the eyes, which is usually conspicuous at this age, was not in evidence. The hair, at the time of its emergence, appeared nearly white.

Six weeks after birth, these mice, which were still in juvenal pelage, were covered, on the dorsal and lateral surfaces, with hair of a very pale gray shade, very near the “drab gray” of RIdgway’s “Color Standards,” though perhaps a trifle paler. (Two normal F₂ hybrids of the same age varied in shade between RIdgway’s “neutral gray” and “dark neutral gray,” perhaps averaging the “deep neutral gray”.) Viewed from a distance, in the subdued light of the murarium, the “albinos” did not differ widely in appearance from ordinary white mice, but the deeper shade was evident when one contrasted the faintly pigmented lateral region of the body with the truly white hair characteristic of the ventral surface of this species. Other peculiarities of these partial albinos are the complete absence of the black dorsal tail-stripe, the nearly white condition of the ears and the reddish color of the eyes. The latter are far from being of the pink hue found in domesticated white mice and rats, but they nevertheless contrast clearly with the jet black eyes of normal Peromyscus. Moreover, they differ notably in size, being smaller, or at least failing to protrude from the head as in the normal animals. Thus the mutation here considered involves several distinct characters, which may, of course, be physiologically related.

At the age of six weeks, a change of pelage was found to be in progress in both of these young mice, though the new hair had not appeared at the surface except in the male. In the latter, the customary replacement of gray by colored hair was evident on the antero-lateral surfaces of the body, but the color in this case was an extremely pale yellow.

Upon the completion of the post-juvenal pelage, some ten weeks after birth, these mice were of a very pale gray shade, suffused with a yellow, which is probably not far from RIdgway’s “ochraceous buff” or “cinnamon buff.” It would be impossible, however, to express their appearance in terms of any homogeneous shade or tint, covering a continuous plane surface. This second pelage is somewhat darker than the first one, as well as of a different color. In these aberrant mice, as in normal ones, the proximal zone of the hair differs in color from the distal, being of a somewhat “sooty” or “slaty” hue, contrasting with the colored tips. This underlying dusky zone is very much paler, however, in these “mutants” than in the more deeply pigmented animals.

CasteL (1912) has discussed the finding of a “pure white albino” of
Peromyscus leucopus noveboracensis and the subsequent rearing of several specimens in the laboratory. Castle's mice evidently differed considerably from my own, which are far from being pure white. Morgan (1911, p. 106) describes some nearly white specimens of P. leucopus ammodytes, which appeared among his laboratory stock. These animals were apparently black-eyed, however, and retained part of their dark pelage. Morgan ascribes these changes to some unknown factor in their unnatural environment, acting during the lifetime of the individuals. Whether or not these "mutants" of mine be regarded as albinos or as "red-eyed yellows" is a matter of slight importance for present purposes. Their peculiarities of color obviously depend upon a loss of most of their normal pigment, and this loss affects all of the colored parts of the body. The condition is one which might reasonably be expected to be hereditary, since it has appeared in only two broods, derived from consanguineous matings, the father being the same in the two cases, and the mothers being full sisters. In ten F<sub>2</sub> broods of hybrids between these subspecies, but of other parentage,¹ as well as in three F<sub>2</sub> broods and a number of back-crosses with pure races, no single instance has been observed. The most plausible guess, at present, is that we have to do with a simple recessive character. Fortunately, the two "albinic" mice are of opposite sex, so it is not unlikely that a test of this point will be practicable.

Since the weaning of these two "albinic" young, their mother, mated to the same father, gave birth to two more offspring, both pigmented. Thus, of the six derivatives of this pair of animals, two were albinic, and four normal. Or, counting the brood of five, borne by the other sister, we have four albinos in a total of eleven young. This excess over the expected ratio for a recessive character has, of course, little significance where the numbers are so small.

I am aware of no case in which complete or partial albinism has appeared as a result of the crossing of two strains which were not known to carry this defect, and it is quite possible that in the present instance the association of this phenomenon with subspecific hybridization is purely accidental. On the other hand, hybridization may, as has been contended, tend to call forth germinal disturbances, independently of ordinary Mendelian segregation.

As stated above, no evidences of simple monohybrid segregation have

¹ That is, other parentage on both sides. The father was used with various females but no albinos appeared except among the offspring of the two mothers here considered.
A YELLOW RACE OF P. M. GAMBELI

In September, 1914, a young female of Peromyscus maniculatus gambeli was trapped by me on the grounds of the Scripps Institution, the appearance of which was so exceptional that the skin was saved. The pelage was still juvenal, but instead of having the usual dark gray tone, characteristic of this race in early life, it was relatively very pale. It is hardly possible that the strain described below is descended from the foregoing individual, though both may have had common ancestors within a very few generations.

In the spring of 1916, three peculiarly colored mice were found among the La Jolla gambeli stock of the second cage-born generation ("C₂," in my notation). They are of a peculiar yellow-brown hue, probably lying between the "cinnamon buff" and the "clay color" of Ridgway, and not unlike the most highly colored parts of the hair in P. m. sonoriensis. They differ from the latter race, however, in that this richer color covers the entire dorsal and lateral surfaces, instead of being confined to certain areas.² Proximally, the hairs are all of the normal slaty hue. Although no considerable attention was devoted to the first three of these "mutants" until the assumption of the colored pelage, it was noted in at least one case that the latter was preceded by an exceptionally pale juvenal coat.

These "yellow" gambeli contrast strongly with the brownish gray characteristic of the normal adults of this subspecies. Indeed, as already said, they diverge more widely from the typical condition of their own subspecies than do mice of a quite distinct subspecies. Thus far very few mice have been observed which show anything approaching an intermediate coat color. The existence of a few animals of somewhat intermediate appearance must be admitted, however, as well as the fact that the "yellows" themselves are far from being absolutely identical in color. The failure to report such departures from the "expected" condition of rigid distinctness is doubtless partly responsible for certain extravagances of neo-Mendelian speculation.

Upon looking over the pedigree of these first three "yellows," it was found that they were the offspring of three different mothers (C,♀6, C₁♀7 and C,♀77), and of two different fathers (C,♂7 and C₁♂49),

²The color is purest, it is true, on the head and lateral surfaces, the dorsal region being finely streaked with black.
none of which exhibited the peculiarity. It is noteworthy that these three females and two males were all the offspring of a single pair of grandparents (♀46 and ♂16). Besides these five, there were no other offspring of this pair (see figure 1).

Of the two grandparents, one was trapped in the immediate vicinity of the Scripps Institution, another at a point about a half mile distant. These mice were themselves killed for measurement before the peculiar condition of their descendants was realized. It may be safely assumed, however, that any such condition in the wild progenitors would have been noticed. All of the C₁ and C₂ representatives of this strain have been kept for further breeding purposes, and some other "yellows" have resulted.

At the time of writing, the total number of broods born of the five C₁ mice listed above, is eight. The number of individuals surviving to an age at which the detection of this color peculiarity was possible was eighteen. Of these, twelve were of the normal color and six of the aberrant. Thus far, only four of the latter have matured sufficiently to show the definite yellow color of the adults, but this "mutation" appears to be nearly as recognizable in the juvenal as in the post-juvenal condition. In the former state the shade is much paler than the "deep neutral gray," which is characteristic of perhaps the majority of normal young gambeli, the difference between the two being most pronounced on the head. In these respects the young "yellows" reared in the laboratory agree closely with the young wild female mentioned at the opening of this section.

In contrast to the proportion of "yellows" appearing in this particular descent line, it must be mentioned that not a single other case has come to light among the four hundred or more cage-born gambeli which have been reared to maturity at La Jolla, since the commencement of the experiment. Moreover, with the single exception referred to at the beginning of this section, and a very few which are of somewhat intermediate appearance, no mouse resembling the yellow strain has been noted among the hundreds of these mice which have been trapped locally by my assistants and myself during the past two years.

Only two matings have been consummated in the case of the "yellows" themselves. The seven resulting offspring, while in the juvenal pelage, have agreed in being decidedly paler than the average young gambeli of this stage, the body shade being near the "light grayish olive" of

³ The birth of another brood (C, ♀6 × ♂49) on March 2, 1917, raises these figures to 14 normal and 7 yellow.
FIGURE 1.—Chart showing pedigree of the “yellow” race of *Peromyscus maniculatus gambelii* now being reared by the writer at the Scripps Institution. P denotes the original wild parents. C₁, C₂ and C₃ denote the first, second and third cage-born generations. Yellow individuals are designated by circles of solid black, normal ones by open circles. The small circles denote mice whose nature was not determinable, owing to early death.
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RIDGWAY, instead of the "deep neutral gray," and that of the head still lighter. On the other hand, they have certainly been darker than were some of the young "yellows" of the preceding generation, and have not been much paler than some exceptional individuals of the normal strain.

At the date of writing, the first-born of the two foregoing (C,) broods is about four months old, and the three young mice are in the completed post-juvenal pelage. In this second pelage, they are nearly or quite as pale as the yellows of the "C₂" generation, and differ rather widely from most gambeli of their age. On the other hand, they lack, to a large degree, the richer color of the parents, having, in comparison with the latter, a decidedly "washed out" appearance. The divergence from the normal condition is thus less marked in the younger generation than in the older, and this difference between the two is probably not a matter of age.⁴

If we may disregard these possibly significant differences between the C₃ young and their more brightly colored parents, the facts suggest that this aberrant color is a recessive character, dependent on a single factor (or lack of one). Unless I have been a witness to the origin of a bona fide mutation, rather than a simple case of gametic segregation, we must suppose that one or both of the grandparents were heterozygous for this character. The five C₃ individuals must all have chanced to be heterozygous, a coincidence, to be sure, for which the chances would have been only one in thirty-two. The ratio 12:6, in the C₃ generation, does not, of course, depart significantly from the "expected" 12:4. In view of the small numbers, the difference may well be accidental.

The question of a possible relation between this "mutation" and the one first discussed is a matter of some interest. To consider only the conditions of pelage color, it might be supposed that the difference was merely one of degree. In the mature state, the one stock is a dark yellow, the other a very pale yellow, in the early life, one is medium gray, the other very pale gray. Some might perhaps suspect that the difference could be accounted for in terms of "intensity factors" or the like. But there would still remain differences between the two strains which could hardly be thus explained, viz., the presence and the absence of the tail-stripe, and the difference in the color and size of the eyes, the latter being quite normal in the "yellows." Without further data, any attempt at a factorial interpretation would of course be premature.

The fact that one of the "mutants" was trapped in nature is of some

⁴ The second brood from the same parents approaches the yellow color more nearly. [Note added April 17, 1917.]
interest, since it shows that in this case at least, we are not dealing with a product of artificial conditions. Castle (1916, p. 124) states that “yellow sports” have been found among wild meadow-mice (Microtus) by Cole, Barrows, F. Smith and others. Apparently these have never been reared.

SPECIAL MARKINGS

Various peculiarities in the distribution of pigment in the skin or hair have been observed in individuals of all of my subspecies. Thus the white “star” on the top of the head has been noted in both gambeli and sonoriensis, some other tufts of white hair on the head of sonoriensis, a white terminal segment in the normally black caudal stripe of rubidus, as well as peculiarities in the skin pigmentation of the tail and snout of the last-named subspecies and of the feet in all three. Judging from what we know of various other animals, we might confidently predict that some or all of these aberrations would be “genetic.” Indeed, the mode of inheritance of these various peculiarities might prove as worthy of investigation as most of the other subject matter of recent Mendelian investigation.

Since the present studies are only incidentally concerned with the search for “mutations,” or an inquiry into their mode of transmission, I can say little as yet regarding the inheritance of these special color markings in Peromyscus. In at least two cases, however, there are good reasons for believing that the markings in question are hereditary.

Before discussing the first of these cases, it must be stated that all of the subspecies of Peromyscus maniculatus have what is called a “bicolored” tail, i.e., one in which the hairs of the dorsal surface are dark, while those of the ventral surface are white. Thus there is normally a sharply defined dorsal tail-stripe, varying in width according to the race and the individual.

Now a very few cases have been noted in P.m. rubidus in which this stripe terminated in advance of the distal end of the tail, i.e., the terminal portion was white dorsally as well as ventrally. One instance was that of a female of the wild stock trapped near Eureka, California, in which about 2 cm of the dark stripe was lacking. Of the five offspring of this mouse by a normal male, one (a male) showed this character quite clearly, the dorsal tail-stripe terminating about 5 mm in advance of the end (excluding the “pencil”).

\footnote{Castle (1916, p. 125) states that “the production of white-spotted races from small beginnings... has been accomplished in the laboratory by Castle and Phillips in the case of Peromyscus...”}
Besides this female, no other wild mouse showing this character has been found among about 250 *rubidus* which I have trapped. But among the first cage-born generation, three others appeared in addition to the male referred to in the preceding paragraph. These last, it is worth noting, were all offspring of a single pair (♀ 40 × ♂ 15). A fourth mouse of the same parentage was indeterminate in respect to this character, owing to the loss of the tip of the tail early in life. Neither of the parents was recorded as showing this peculiarity, and it is quite unlikely that it would have been overlooked, unless present to a very inconspicuous extent.

If this character is determined by a single "factor," the latter seemingly cannot be a dominant one. If recessive, we must suppose that the mate of the P₁ generation female first mentioned chanced to be heterozygous for this character; also that both parents of the second brood mentioned were heterozygous. In the latter case, the number of recessive offspring (½ and possibly ¼) is much greater than the expectation, though it is needless to say that such small numbers prove nothing whatever. Indeed, it would be premature to assume a conformity with Mendelian ratios of any sort.

In relation to this aberrant tail character, it is of interest to note that Lloyd (1912, especially pp. 47, 112-116) records the occurrence of a similar condition in the house rat in India, and that he gives evidence for the existence of much restricted local strains in which this character has arisen more than once through independent mutations.

One further peculiarity of an apparently hereditary nature was found in ten or twelve specimens of the first cage-born generation of the subspecies *rubidus*. This was a white tip at the end of the snout, due to the absence of skin pigment as well as to the presence of white hairs. This character, with two doubtful exceptions, was found only among the progeny of two females (P♀ 40 and 41), by a single male (P♂ 15). It is noteworthy that 40 and 15 were the parents of three of the mice with white-tipped tails, and that these three all displayed the snout peculiarity as well as that of the tail. On the other hand, the fourth C₁ mouse having a white-tipped tail had a normally pigmented snout, showing that the two pigment defects are not inseparable.

Unfortunately none of the four C₁ *rubidus* with white-tipped tails has left descendants, so that the further study of this peculiarity is, for the time being, prevented.

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6 Unless, indeed, we have to do with the *de novo* appearance of a real mutation.
7 Save one in which the tail condition is indeterminate.
About ten cases of white-tipped snouts have appeared in the C2 generation, and the relationships of these animals implies that this character depends primarily upon genetic conditions. But whether the character is dominant or recessive, or whether it depends upon one or more factors cannot be settled without giving more attention to the matter than at present seems warranted.

LITERATURE CITED

LLOYD, R. E., 1912 The growth of groups in the animal kingdom. pp. 185. London; Longmans, Green & Co.