considerable) how difficult it is, otherwise, to avoid the occasions of personal disputes, or reflections; which, for my part, I heartily desire to shun" (Vol. V., p. 252b).

One can not but conclude, judging from the phraseology, that the passage in the *Phil. Trans.* cited by Dr. Bolton is from the same pen as Henry Oldenburg's prefatory note. Further evidence of the same authorship is found in the capitalization, following, as it does, the German method. Now Robert Boyle would not be likely to use this mode of writing, while Henry Oldenburg, being a native of Bremen in lower Saxony, might easily have lapsed into the style of his native tongue.

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SPECIAL ARTICLES.

COLOR INHERITANCE IN MICE.

Within the last few years great interest has been aroused by the rediscovery of Mendel's Law of Dichotomy in plant hybridization. This law has been confirmed for many species of plants, especially by De Vries (1902, pp. 146–151, etc.), Correns, Tschermak and others. The study of mice, rats and rabbits has yielded a partial confirmation of this law for animals. I wish here to contribute additional although too meager data drawn from my experiments of the past four years.

The two great laws enunciated by Mendel were these: Of the two antagonistic peculiarities possessed by two races that are crossed, the hybrid, or mongrel, exhibits only one; and it exhibits it completely, so that the mongrel is not distinguishable as regards this character from one of the parents. Intermediate conditions do not occur. That one of the two parental qualities that alone appears in the mongrels is called dominant; the other recessive. Second, in the formation of the pollen or egg-cell the two antagonistic peculiarities are segregated; so that each ripe germ cell carries either one or the other of these peculiarities, but not both. It is a result of the second law that in the second generation of mongrels each of the two qualities of their grandparents shall crop out on distinct individuals, and that the recessive quality shall appear in 25 per cent. of the individuals, the remaining 75 per cent. having the dominant quality. Such recessive individuals, crossed *inter se,* should never produce anything but recessive offspring.

Now experiments with animals have revealed the existence of recessive qualities—*e. g.,* in mice, when white and wild gray are crossed and the mongrel offspring are crossed *inter se,* the second mongrel generation will yield some white mice, and such white mice, bred *inter se,* will thenceforth produce only white mice. These results have been got by Crampe (1885), von Guaita (1898, 1900)—cf. Davenport (1900)—Cuénot (1902, 1903)—cf. Bateson (1902, p. 173)—Darbishire (1902, 1903), Castle (1903) and Bateson (1903). Is the percentage of the recessive individuals always 25? In such a second mongrel generation Cuénot (1902) found 162 gray and 57 albino individuals, or 74 per cent. to 26 per cent., and in von Guaita's breedings between walzing and albino mice the crossed gray hybrids gave 25 per cent. albinos; results that accord with theory. But instead of the 75 per cent. gray which Mendel's law calls for, von Guaita got 57 per cent. gray and 18 per cent. walzing mice of gray, gray-white, black, and black and white colors. Rabbits gave Woods (1903) only 21 per cent. instead of 25 per cent. of the recessive type in the second mongrel generation, and in crossing hybrids with albinos he got only 40 per cent. albinos instead of 50 per cent., as theory demands.

The discussion concerning the validity of Mendelism for mice has been based chiefly upon crosses between albinic mice on the one hand (Crampe, Cuénot, Castle and Allen) and gray or walzing mice on the other (Haacke, von Guaita, Darbishire). Bateson (1903) alone has recorded, without details, the results of crossing mice of varied colors. His data will be referred to in the following account of my experiments.

A. THE OFFSPRING OF MICE OF THE SAME COLOR.

I. *Albino* $\times$ *Albino.*—This cross appears to produce only albinos. Bateson (1903, p. 76) has examined the evidence and finds only one doubtful case where white mice produced colored offspring. In two crosses of white parents I got nine offspring; all were white.

II. *Yellow* $\times$ *Yellow*.—1. Yellow-red (8)* $\times$ yellow-red (7). The mother (8) was yellow-red with a patch of white below; the father was pure yellow-red. Of the offspring one was pure yellow-red like the father, two were brownish yellow above and much lighter below, one was brownish red with patches of white, and five were chocolate with yellow flanks and patches of white above and below. Thus, one bred true to the father but the remainder were much darker and had a mixture of colors.

2. Muddy yellow $\left(35\begin{cases}\text{white }(6)\\ \text{yellow }(7)\end{cases}\right)\times$ yellow (7). Of the four offspring one was a uniform light yellow (57); one was yellow above and white below and on the flanks (59); one was dirty yellow above, white below (58); and the last was wild-mouse gray (or agouti) above and white on belly and flanks. The result in both cases is seen to be very variable.

III. *Black* (*2*) *and Black* (*2*).—My blacks seemed delicate and relatively infertile, so that of two crosses only two individuals survived —both were black. Black behaves something like albinism. Is it not likewise recessive?

IV. *Chocolate* $\times$ *Chocolate*.—Chocolate is a broad class including various shades of color from a dark red-gray to a dark red-yellow. I raised four families as follows: 1 and 2. Chocolate (10) $\times$ Chocolate (1) with nine offspring, as follows: Uniform chocolate, nos. 22, 23, 26, 66 and 65. Chocolate above, more or less white below, nos. 67, 68. Chocolate with white spots, nos. 24, 25.

3. Chocolate $\left(66\begin{cases}10\\ 1\end{cases}\right)\times$ Chocolate $\left(25\begin{cases}10\\ 1\end{cases}\right)$.

These full siblings† of chocolate parents produced five offspring. All were of a uniform chocolate color.

4. Chocolate $\left(67\begin{cases}10\\ 1\end{cases}\right)\times$ Chocolate $\left(25\begin{cases}10\\ 1\end{cases}\right)$.

There was only one survivor of this pair; it was chocolate colored excepting for some white on the belly.

Thus the chocolate color shows itself rather stable, especially in the second pure bred generation.

B. THE OFFSPRING OF MICE OF DIFFERENT COLOR.

I. *Gray and White*.—This cross has been made by several investigators, as indicated above. The usual result is that the offspring in the first filial (mongrel) generation (F_1 in Bateson's nomenclature) are prevailingly gray like the wild house mouse. My own experience is partly confirmatory.

A wild house mouse (15) $\times$ albino (5) gave five offspring: nos. 47 to 51. Four of these resembled the wild mother in coat excepting that they were yellower on the back of the neck and of a cream color in the region between the fore legs and also between the hind legs. Also the coat had a richer, glossier look than the mother's. The other one of the offspring was generally agouti above and ashy below, but the hairs of the ventral part of the shoulder girdle were yellow tipped, there was a mid-ventral white patch and there were five distinct white patches on the dorsal side. These were unlike anything in the mother, and indicated particulate inheritance by the mongrel from both parents, but especially from the mother. My results agree with those of Crampe, who found that similarly bred rats give in F_1 either uniformly gray or gray and white. Darbishire (1903) crossing walzers and albinos finds that the mongrels have the less white the purer bred the albinos are, and von Guaita's pure-bred albinos gave all gray offspring when crossed with walzers. I know nothing of the ancestry of the albino (5); but it may be inferred that it was not pure bred. With an albino that had been bred pure for two generations I got the following result:

$$\text{Gray}\left(\mathbf{54}\begin{cases}21,\text{ chocolate }(10\times 1)\\ 29,\text{ house}\end{cases}\right)\times\text{white}\left(\mathbf{18}\begin{cases}4,\text{ white}\\ 5,\text{ white}\end{cases}\right).$$

Five offspring were obtained all gray like a

* The numbers in parentheses are those of the pedigree mice.

† Sibling (Pearson) is a term applicable either to brother or to sister.

house mouse, but of a lighter color. Probably the earlier crosses of Crampe (1877, p. 390, 391) with white and gray rats that led him to the conclusion that in inheritance the color of the species shuts out the color of the variety were made with pure bred rats. Cuénot crossing grays and albinos got gray mice without exception in the F_1 generation.

From the foregoing the conclusion may be drawn that the offspring of pure-bred gray mice crossed with albinos inherit chiefly from the wild form but that the color is slightly modified, particularly when the albinos are not pure bred, first by an increase in the yellow and, secondly, in some cases, by the presence of white. Gray is dominant over albinism but the soma derived from hybrid germ cells shows traces of the albinic blood. The dominance is incomplete. The dominance, so far as it goes, accords with De Vries's (1902, p. 145) generalization that the older type or the wild species is dominant over a more recent type or a cultivated variety.

When these gray mice are crossed *inter se* there result gray mice and white mice in the proportion of three to one (Cuénot; Castle and Allen, 1903), and the albinos show themselves purely recessive. That all recessive mice are, however, not alike, but differ according to their ancestry has been argued by Darbishire from the fact that pure bred albinos transmit less to F_1 than albinos do that are derived from a mixed ancestry.

II. *Wild Gray* (*45*) × *Black* (*9*).—Two offspring of this cross were essentially of the wild, maternal color.

$$\text{III. } \textit{Wild Gray (29♂)} \times \textit{Chocolate} \left(21 \begin{cases} \mathbf{10} \\ \mathbf{1} \end{cases}\right).$$

—Nos. 52 and 54 were marked like the wild gray but were darker. No. 53 had a dark back, a light yellow belly and white on the shoulders and in the middle of the right flank. No. 55 had a back like the house mouse, but its shoulders were white and its belly yellow and white. In these offspring there was an attempt at least at blending and there was a cropping out of an ancestral white, but on the whole the gray dominated.

IV. *Black* × *Albino*.—This cross was made twice.

$$\text{1. Black} \left(\mathbf{19} \begin{cases} \text{2, black} \\ \text{9, black} \end{cases}\right) \times \text{albino} \left(\mathbf{18} \begin{cases} \text{4, albino} \\ \text{5, albino} \end{cases}\right).$$

Five young were obtained, all reversions, being of typical wild mouse color except that two of them had white spots on the belly.

2. Black (126) × Albino

$$\left[\mathbf{102} \begin{cases} \text{57, reversion} \begin{cases} \text{35, yellow (6, albino} \times \text{7, yellow)} \\ \text{7, yellow} \end{cases} \\ \text{18, albino} \begin{cases} \text{4, albino.} \\ \text{5, albino} \end{cases} \end{cases}\right.$$

—The two offspring were reversions, but one had a white spot at the center of the belly. These two matings indicate that neither black nor white is dominant, but that the repressed ancestral gray character is, as it were, liberated.

V. *Black* (*137*) × *Yellow*

$$\left[\mathbf{136} \begin{cases} \text{102, albino} \\ \text{130, reversion} \begin{cases} \text{102, albino} \\ \text{126, black} \end{cases} \end{cases}\right].$$

—The single offspring was a typical reversion except that the front part of the belly and the flanks were white. Bateson (1903, p. 85) states that Miss Durham got sables and dingy fawns and even blacks from this cross. In any case there is no evident dominance.

The following cases are still more complex.

$$\text{VI. } \textit{Reversion} \left(32 \begin{cases} \text{6, white} \\ \text{7, yellow} \end{cases}\right) \times \textit{Gray} \left(47 \begin{cases} \text{15, wild} \\ \text{5, white} \end{cases}\right).$$

—There were two of the progeny of this pair that survived infancy—both were of the typical wild mouse color.

$$\text{VII. } \textit{Reversion} \left[109 \begin{cases} \text{57, gray} \begin{cases} \text{35, yellow} \\ \text{7, yellow} \end{cases} \\ \text{18, white} \begin{cases} \text{4, white} \\ \text{5, white} \end{cases} \end{cases}\right]$$

$$\times \textit{Reversion}\left[117\begin{cases}77,\ \text{yellow}\begin{cases}34,\ \text{yellow}\\42,\ \text{yellow}\end{cases}\\48,\ \text{gray}\begin{cases}15,\ \text{wild}\\5,\ \text{white}\end{cases}\end{cases}\right].$$

—There were three offspring; one was uniformly black (a color not found in the ancestry for at least three generations) and two were white. Black rats were got by Crampe (1877, p. 394) by crossing mongrels between wild and white-and-black rats; and black mice by von Guaita by crossing piebald dancing mice with albinos.

$$\text{VIII. } \textit{Piebald}\left(34\begin{cases}6,\ \text{white}\\7,\ \text{yellow}\end{cases}\right)$$

$$\times \textit{Gray-yellow}\left(42\begin{cases}8,\ \text{yellow}\\7,\ \text{yellow}\end{cases}\right).$$

—Of the six offspring four (nos. 77, 78, 79, 81) had the back colored yellow-red. In matching the color with the color wheel red, orange and yellow were found to constitute 60 per cent. to 70 per cent. of the color. In no. 82 the dorsal pelage was yellow-chocolate, with the color formula, N51, R28, Y12, W9;* and in no. 80 it was chocolate, with the color formula, N76, R13, Y4, W7. Four had some white on the belly or flanks. In this cross a new color—chocolate—arose, which I interpret to mean that some of the primitive gray was added to the yellow; that is, there was a partial reversion. Otherwise the yellow is dominant.

IX. *Gray and White*

$$\left(57\begin{cases}37,\ \text{yellow (6, white} \times \text{7, yellow)}\\7,\ \text{yellow}\end{cases}\right)$$

$$\times \textit{White}\left(18\begin{cases}4,\ \text{white}\\5,\ \text{white}\end{cases}\right).$$

—There were eight offspring, three albinos and five gray. Four of the latter had white patches on the sides, legs or middle of the belly. This is like the case described by Castle (1903, p. 542).

C. SUMMARY OF RESULTS.

When the parents are of the same color, especially if they are pure bred, there is a strong tendency for the offspring to be of the same color as the parents. In the case of albinos this tendency is so strong that the offspring are probably always albinic; if both parents are black the tendency to black offspring is likewise very strong; if chocolate, the result is more variable; if yellow, still more intermediate. The results indicate that there are different degrees in the strength of inheritance of different colors.

When the parents are of dissimilar color the offspring show different kinds of inheritance in the different cases. When gray and white are crossed the offspring are gray with a little white, and this white is the more reduced the purer bred the albinic parent; the gray is dominant. Likewise in the cross of gray and black, black is quite shut out, and the same is true of gray and piebald rats (Crampe, 1877, p. 394). The wild, gray color is strongly prepotent. Melanism and albinism act quite similarly in crossing. Both are in the nature of 'sports.' Perhaps 'purity of the germ cells' is the mechanism of isolation for which we have been so long looking, by which mutations are preserved from the 'swamping effects of intercrossing.'*

When gray and chocolate are crossed the gray is incompletely dominant. When black and white are crossed, typical reversions appear; neither color is dominant. When black is crossed with yellow the result is highly variable. If white and yellow be mixed in various proportions for several generations the progeny takes on various shades of yellow and may acquire the wholly new color of chocolate. Similarly, black may result from a mixed ancestry in which there is no black. The study of the cropping out of new colors certainly forms an enticing subject for further inquiry.

D. BEARING OF THE RESULTS ON MENDEL'S LAW.

The enthusiasm kindled by the discovery of a new law leads us to go to extremes, to as-

* N, nigrum, black; R, red; Y, yellow; W, white. The numbers are percentages.

* Since the above was written I have received Castle's paper in SCIENCE for December 11, 1903, in which he states that the long-haired character in the Angora guinea-pig is recessive. This character is probably a mutation, and as such behaves in accordance with the above hypothesis.

sume its universal validity, and to overlook apparent exceptions. Those who insist upon a critical examination of all evidence against as well as for the theory run the risk of being regarded as lukewarm and as clogs on the wheels of progress; but they should not be deterred on that account from a full examination of all the facts in the interest of truth.

Mendel's Law is an hypothesis of great value both because it fits so many cases of inheritance and because it is stimulating to experimental investigations which will determine the limits within which it is valid.

The first limitation of Mendel's Law is stated by De Vries (1902, p. 141), who certainly can not be accused of lukewarmness toward the theory, since he was its rediscoverer. He says in effect: Mendel's Law of dichotomy holds in general only for phylogenetically recent characters, the so-called racial characters; and for only a part of those—what part we do not know. Even Mendel recognized that his rule was not generally applicable.

The second limitation of Mendelism concerns his theory of dominance. Sometimes when dissimilar racial characters are crossed one of them is dominant, and sometimes not. For example, gray is (within limits) dominant over white or black in mice, but when black and white or black and yellow are crossed there is no dominance of one color over the other; both are recessive and a reversion to the primitive gray occurs. The whole hypothesis of the purity of the germ cells will bear careful scrutiny. The best example of a recessive character in animals is albinism, but even in this case, as Darbishire has pointed out, the recessives can not be perfectly pure and independent of ancestry, for the mongrel mice coming from a recessive crossed with a gray differ according to the ancestry of the recessive. The result of this study is, I think, to add evidence that Mendel did not discover all the important laws of inheritance, and that further investigation will unquestionably reveal other and still broader principles of heredity.

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December 13, 1903.

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