

termites by Holmgren; a similar account of the ants by Forel; descriptions of the termitophilous coleoptera by Wasmann; a description of a new cricket (*Myrmecophila escherichi*) which has become termitophilous, by Schimmer; termitophilous thysanura, myriopoda and coleopterous larvæ by Silvestri; a termitophilous earthworm (*Notoscolex termiticola*) by Michaelsen.

W. M. WHEELER

SCIENTIFIC JOURNALS AND ARTICLES

THE contents of *The American Journal of Science* for April are as follows:

"Ionization of Different Gases by the Alpha Particles from Polonium and the Relative Amounts of Energy Required to Produce an Ion," T. S. Taylor.

"Heat Generated by Radio-active Substances," W. Duane.

"Contributions to the Geology of New Hampshire. IV. Geology of Tripyramid Mountain," L. V. Pirsson and Wm. North Rice.

"Note on a Method in Teaching Optical Mineralogy," F. W. McNair.

"New Paleozoic Insects from the Vicinity of Mazon Creek, Illinois," A. Handlirsch.

"Results of a Preliminary Study of the so-called Kenai Flora of Alaska," A. Hollick.

SPECIAL ARTICLES

THE ORIGIN OF FIVE MUTATIONS IN EYE COLOR IN *DROSOPHILA* AND THEIR MODES OF INHERITANCE

The White Eye

In cultures of *Drosophila ampelophila*, that had been closely inbred for a year, a male fly, lacking the red pigment of the eye, appeared. The same stock has continued to produce these white-eyed mutants always of the male sex. A white-eyed father transmits the character to about one fourth of his grandsons, but to none of his granddaughters. In this sense the character is sex limited. The white eye can be transmitted, however, to the females, most readily by breeding any white-eyed male to red hybrids (F₁) out of white by red. White-eyed males and females give pure stock. When a white-eyed female is bred to

any wild male all of the female offspring have red eyes and all of the male offspring white eyes. The result shows that the male-bearing sperm of the wild flies lacks at least one of the factors essential for the production of red eyes. This statement does not mean that the male-determining sperm lacks all of the factors essential for producing red, but only that it lacks one of the factors necessary for the production of red. In fact, it is conceivable that all of the rest of the cell may be equally essential for the production of red, but in the absence of one condition (factor) the red fails to develop. It is in this sense that I understand the use of the word "factor" in inheritance; and in the same sense one might employ the word "unit character," although the latter word may seem to imply (from usage) that a particular character is represented entirely by some unit in the germ cells. We are not warranted, I believe, in extending to the results of Mendelian inheritance such an interpretation. Since I have discussed elsewhere the mode of transmission of the white eyes,¹ I shall omit further details here.

The Pink Eye

This eye color has appeared at least twice in cultures in no way closely related to the white-eyed stock. It is not due to a cross between red- and white-eyed flies. The color is much lighter and more translucent than red, and appears to contain more yellow. It is seen to best advantage soon after the flies have emerged. Later it becomes darker and casual observation might mistake it for red. As the flies get old the pink changes to a somewhat purplish color, and this change does not take place in the red eyes, so that with experience there is no difficulty in separating the two colors at all stages. No intermediate condition has been seen despite the fact that thousands of the pink-eyed flies have been examined.

Pink-eyed males bred to wild red-eyed females produce all reds in the first generation. These flies, inbred, have produced in the second filial generation 3,063 reds to 169

¹ SCIENCE, July 22, 1910.

pinks, males and females. The reciprocal cross, viz., pink-eyed females and red-eyed males, gives also in the first generation red-eyed individuals only. These inbred have produced 1,133 reds, males and females; and 237 pinks, males and females. The results show that pink is not sex limited. The simplest explanation of the difference between the modes of inheritance of pink and white eyes is found, I think, if we ascribe the factor involved in the formation of pink eyes to some other part of the mechanism than that involved in the formation of white eyes. If I am right in ascribing the sex-limited inheritance of white eyes to some change in one of the sex chromosomes, then the factor for pink eyes must be contained in some other part of the cell; possibly in some other chromosome. That this must be the correct interpretation is borne out by the results of the second cross just given, in which the male-producing sperm of the red-eyed male produces red-eyed males. Evidently this sperm adds the necessary factor to the pink-bearing egg to produce red eyes, which would not be the case if the factor in question was present in the sex chromosome which is assumed to be absent from this spermatozoon. The hypothesis also makes clear how important it may be to recognize that different parts of the cell may be involved in producing such a "unit character" as eye color.

The relation of pink to white eyes is extremely interesting. When a pink-eyed female is bred to a white-eyed male all of the offspring have *red eyes*. These inbred produce red-, white- and pink-eyed offspring in the following proportions:

Red-eyed females	418
Red-eyed males	198
White-eyed males	222
Pink-eyed females	117
Pink-eyed males	35

White eyes appear again in this combination as sex limited. The pink eyes are relatively few in number, and the *females* are about three times as numerous as the males.

The reciprocal cross, viz., white-eyed females and pink-eyed males, gives in the first genera-

tion *red-eyed females and white-eyed males*. These inbred produce:

Red-eyed females	411
Red-eyed males	333
White-eyed females	377
White-eyed males	365
Pink-eyed females	76
Pink-eyed males	94

In this combination both males and females with white eyes appear in the second generation in about the same proportion as the red-eyed individuals. The pink eyes are again fewer than the other classes, but now the *females* are somewhat less numerous than the males. These peculiar results can, I believe, be accounted for theoretically, but the analysis is too elaborate to give here.

These results indicate that the white eye lacks one factor for red and pink eye, another factor for red. When combined all the elements for red are present. But the second generation shows that the reds formed in this way by recombination differ from the ordinary reds in that they produce reds, pinks and whites. The difference between these artificial reds and the normal reds consists in the presence of one dose of red in the artificial and two in the normal reds (at least in the female). The segregation is a consequence of this heterozygous condition. If this view is correct it should be possible to produce by the proper combinations some pinks and whites that when combined no longer produce reds, but only pinks and whites. I have made such races that have continued for several generations to produce pinks and whites only in very large numbers. In order to discover whether the induced change in this new race has taken place in the white or in the pink, the following experiment was carried out. One of the new pink females was crossed to a white male of the ordinary stock. This combination gave, it will be recalled, with ordinary pinks, red males and females, as stated above. The same thing occurred in the new experiment, showing that the pink had not been changed. On the other hand, when a white male of the new "pink-white" stock was crossed to an ordinary pink

female only pinks and whites were produced. Evidently the change has taken place in the white. If we express the ordinary red color as the outcome of two factors C and R then the *ordinary* whites will be OR while the *new* white will be represented by OO. The tests that I have made so far corroborate this view, giving the combinations expected from the formulæ. Theoretically the new white should behave towards the new pink as a sex-limited character in the same way in which the original white behaved towards the reds, and such, in fact, is the case. Moreover, it is clear why in the one case (white and pink) there should be sex-limited inheritance and in the other (red and pink) a different kind of inheritance, provided, as the facts strongly indicate, that the factor for pink is contained in another part of the hereditary mechanism than the factor for white. In other words, the factor for white (absence of red) is connected with the factor that determines sex, while that for pink is contained in a different part of the cell. It is this evidence that has seemed to me to show that the phenomenon of sex-limited inheritance is due to an intimate physical relation between the sex factors and the other factors in question; and the most obvious connection is that the relation is to be found in the chromosomes that carry both the sex factor and those factors that are sex limited.

The Bright Red Eye

This color arose in hybrids produced by breeding flies with miniature wings to wild stock. A small percentage of the male offspring had bright red eyes. This cross has been repeated a number of times and has always given some bright red-eyed flies. There can be little doubt that it is produced in some way by the cross. I found, it is true, one individual with bright red eyes in the wild stock from which the cross was made, but only once in many hundreds of flies examined, while the production of coral eyes is a constant feature of the hybrids.

The bright red eye is sex limited, as shown by the fact that in certain combinations it has appeared only in the males. When such males

were bred to their red-eyed sisters, bright red-eyed females as well as males were produced. When two bright red-eyed individuals are mated they produce only bright red-eyed offspring, and I have a large stock of these flies that originated in this way.

The bright red eye differs from the red eye in being *conspicuously* more brilliant in color. No intermediate condition has been found. The relation between this color and red and pink has not yet been fully worked out.

The Orange Eye

A cross between a white-eyed male and a red-eyed female (heterozygous for pink) produced flies with red, bright red, pink, white eyes, and a few flies with eyes having a faint orange tinge. The eyes are much lighter than pink eyes, and do not seem to intergrade with them. The appearance of the orange color in this and in other cultures followed the appearance in them of the bright red eye, and seems to be connected with the factor for bright red. As yet this relation has not been clearly worked out. Orange bred to orange has given in some cultures stock that has produced many hundred flies with orange eyes only. The orange eye has not been found to be sex limited in any of the many combinations that have so far been made. Thus while white and bright red eye colors are sex limited the other two colors, pink and orange, do not show this form of inheritance. Now that pure cultures of all the stocks have been obtained, their interrelations will be further studied.

The Spotted Eye

On two or three occasions flies appeared in which some of the ommatidia of the compound eye were red and the rest white. The last individual of this kind that appeared was obviously a white fly with about one fourth of the area of one eye red, the rest white. The other eye was entirely white. Unfortunately the fly died before she could be tested. The occurrence of this mutation is of interest in its bearing on the origin of the spotted condition in many of our domesticated animals.

These cases are comparable to heterozygous flies with one long wing and one short,

proportionate—one the dominant, the other the recessive type. Two such flies have been bred to the recessive form and have given long- or short-winged offspring—no fly with both types of wing. Inbreeding these longs to shorts again has not yet produced a single fly with both types of wings. Evidently the asymmetrical condition is due to a somatic change that takes place in the development of the individual; a change comparable to that that takes place in the germ cells of Mendelian hybrids. The same explanation applies to the case of the spotted eyes also. The spotted condition appears therefore to be an ontogenetic segregation.

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HEREDITY IN INSANITY

THE fact that nervous and mental diseases are often transmitted by heredity was known to Hippocrates and has since his time been amply illustrated by insane-hospital statistics, but the exact conditions under which such transmission occurs have never been fully understood. A recent study has, however, revealed some data which seem to indicate that certain forms of insanity are transmitted from

actual findings recorded in the study here referred to; these findings, it will be observed, are in fairly close correspondence with theoretical expectation, which is as follows:

1. Both parents being neuropathic, all children will be neuropathic.

2. One parent being normal, but with the neuropathic taint from one grandparent, and the other parent being neuropathic, half the children will be neuropathic and half will be normal but capable of transmitting the neuropathic make-up to their progeny.

3. One parent being normal and of pure normal ancestry and the other parent being neuropathic, all the children will be normal but capable of transmitting the neuropathic make-up to their progeny.

4. Both parents being normal but each with the neuropathic taint from one grandparent, one fourth of the children will be normal and not capable of transmitting the neuropathic make-up to their progeny, one half will be normal but capable of transmitting the neuropathic make-up, and the remaining one fourth will be neuropathic.

5. Both parents being normal, one of pure normal ancestry and the other with the neuro-

Types of Mating	Number of Matings	Total Offspring	Neuropathic Offspring	Normal Offspring			Died in Childhood	Data Uncertain
				Neuropathic Progeny	Without Progeny	Normal Progeny		
RR × RR ∞ RR	3	16	10	0	0	0	5	1
DR × RR ∞ DR + RR	19	129	45	14	20	27	20	3
DD × RR ∞ DR	5	18	0	8	2	7	1	0
DR × DR ∞ DD + 2DR + RR	7	54	12	6	18	10	8	0
DD × DR ∞ DD + DR	1	4	0	1	0	3	0	0
DD × DD ∞ DD	0	0	0	0	0	0	0	0

D = Dominant. R = Recessive.

RR = Neuropathic subject (nulliplex inheritance).

DD = Normal subject of pure normal ancestry (duplex inheritance).

DR = Normal subject with neuropathic taint from one parent (simplex inheritance).

parent to offspring in the manner of a trait which is, in the Mendelian sense, recessive to normal.¹ The accompanying table shows the

¹“Preliminary Report of a Study of Heredity in Insanity in the Light of the Mendelian Laws,” by G. L. Cannon and A. J. Rosanoff. Read before the New York Neurological Society, October 4, 1910.

pathic taint from one grandparent, all the children will be normal, half of them will be capable and half not capable of transmitting the neuropathic make-up to their progeny.

6. Both parents being normal and of pure normal ancestry, all the children will be normal and not capable of transmitting the neuropathic make-up to their progeny.