becoming manifest when conditions favoring transpiration are marked." The disease is therefore not due to the presence of parasitic organisms, but is what has been rather loosely called a physiological disorder.

IN a short paper in the *Annales du Jardin Botanique de Buitenzorg* (2d Ser., Supp. III.) Professor Ramaley enumerates and discusses the European plants growing without cultivation in Colorado. In addition to an annotated list of species the author discusses the region included, and the mode of introduction and occurrence of the species. Botanists who have not given attention to these immigrants will be much surprised at the extent of the list.

PROFESSOR SARGENT continues his studies of the species of hawthorns in Pennsylvania in a paper entitled "Crataegus in Pennsylvania, II.," published in the *Proceedings of the Academy of Natural Sciences of Philadelphia* (March, 1910). His first paper on the Pennsylvania hawthorns appeared about five years ago, since when much additional material has become available for study, resulting in a thick pamphlet of about one hundred pages. In this space the author enumerates and describes 110 species, of which 80 are described as new! Think of what the new editions of the botanical manuals will have to contain when these new species are added! We may have to grant the necessity of distinguishing these forms from one another in descriptive botany, but what an amount of work will have to be done by the taxonomists of the future in reducing these multitudinous forms to such categories as will be distinguishable by botanists, other than specialists in the hawthorns!

CHARLES E. BESSEY
THE UNIVERSITY OF NEBRASKA

## *SPECIAL ARTICLES*

### SEX LIMITED INHERITANCE IN DROSOPHILA

IN a pedigree culture of *Drosophila* which had been running for nearly a year through a considerable number of generations, a male appeared with white eyes. The normal flies have brilliant red eyes.

The white-eyed male, bred to his red-eyed sisters, produced 1,237 red-eyed offspring, ($F_1$), and 3 white-eyed males. The occurrence of these three white-eyed males ($F_1$) (due evidently to further sporting) will, in the present communication, be ignored.

The $F_1$ hybrids, inbred, produced:

2,459 red-eyed females,
1,011 red-eyed males,
782 white-eyed males.

*No white-eyed females appeared.* The new character showed itself therefore to be sex limited in the sense that it was transmitted only to the grandsons. But that the character is not incompatible with femaleness is shown by the following experiment.

The white-eyed male (mutant) was later crossed with some of his daughters ($F_1$), and produced:

129 red-eyed females,
132 red-eyed males,
88 white-eyed females,
86 white-eyed males.

The results show that the new character, white eyes, can be carried over to the females by a suitable cross, and is in consequence in this sense not limited to one sex. It will be noted that the four classes of individuals occur in approximately equal numbers (25 per cent.).

*An Hypothesis to Account for the Results.*—The results just described can be accounted for by the following hypothesis. Assume that all of the spermatozoa of the white-eyed male carry the "factor" for white eyes "W"; that half of the spermatozoa carry a sex factor "X" the other half lack it, *i. e.*, the male is heterozygous for sex. Thus the symbol for the male is "WWX," and for his two kinds of spermatozoa WX—W.

Assume that all of the eggs of the red-eyed female carry the red-eyed "factor" R; and that all of the eggs (after reduction) carry one X, each, the symbol for the red-eyed female will be therefore RRXX and that for her eggs will be RX—RX.

When the white-eyed male (sport) is crossed with his red-eyed sisters, the following combinations result:

WX — W (male)
RX — RX (female)

RWXX (50 %) — RWX (50 %)
Red female Red male

When these $F_1$ individuals are mated, the following table shows the expected combinations that result:

RX — WX ($F_1$ female)
RX — W ($F_1$ male)

| RRXX— | RWXX — | RWX— | WWX |
|---|---|---|---|
| (25 %) | (25 %) | (25 %) | (25 %) |
| Red female | Red female | Red male | White male |

It will be seen from the last formulæ that the outcome is Mendelian in the sense that there are three reds to one white. But it is also apparent that all of the whites are confined to the male sex.

It will also be noted that there are two classes of red females—one pure RRXX and one hybrid RWXX—but only one class of red males (RWX). This point will be taken up later. In order to obtain these results it is necessary to assume, as in the last scheme, that, when the two classes of the spermatozoa are formed in the $F_1$ red male (RWX), R and X go together—otherwise the results will not follow (with the symbolism here used). This all-important point can not be fully discussed in this communication.

The hypothesis just utilized to explain these results first obtained can be tested in several ways.

*Verification of Hypothesis*

*First Verification.*—If the symbol for the white male is WWX, and for the white female WWXX, the germ cells will be WX—W (male) and WX—WX (female), respectively. Mated, these individuals should give

WX — W (male)
WX — WX (female)

WWXX (50 %) — WWX (50 %)
White female White male

All of the offspring should be white, and male and female in equal numbers; this in fact is the case.

*Second Verification.*—As stated, there should be two classes of females in the $F_2$ generation, namely, RRXX and RWXX. This can be tested by pairing individual females with white males. In the one instance (RRXX) all the offspring should be red—

RX — RX (female)
WX — W (male)

RWXX — RWX

and in the other instance (RWXX) there should be four classes of individuals in equal numbers, thus:

RX — WX (female)
WX — W (male)

RWXX—WWXX — RWX—WWX

Tests of the $F_2$ red females show in fact that these two classes exist.

*Third Verification.*—The red $F_1$ females should all be RWXX, and should give with any white male the four combinations last described. Such in fact is found to be the case.

*Fourth Verification.*—The red $F_1$ males (RWX) should also be heterozygous. Crossed with white females (WWXX) all the female offspring should be red-eyed, and all the male offspring white-eyed, thus:

RX — W (red male)
WX — WX (white female)

RWXX — WWX

Here again the anticipation was verified, for all of the females were red-eyed and all of the males were white-eyed.

*Crossing the New Type with Wild Males and Females*

A most surprising fact appeared when a white-eyed female was paired to a wild, red-eyed male, *i. e.*, to an individual of an unrelated stock. The anticipation was that wild males and females alike carry the factor for red eyes, but the experiments showed that all wild males are heterozygous for red eyes, and that all the wild females are homozygous. Thus when the white-eyed female is crossed with a wild red-eyed male, all of the female offspring are red-eyed, and all of the male offspring white-eyed. The results can be accounted for on the assumption that the wild male is RWX. Thus:

RX — W (red male)
WX — WX (white female)

RWXX (50%) — WWX (50%)

The converse cross between a white-eyed male RWX and a wild, red-eyed female shows that the wild female is homozygous both for X and for red eyes. Thus:

WX — W (white male)
RX — RX (red female)

RWXX (50%) — RWX (50%)

The results give, in fact, only red males and females in equal numbers.

*General Conclusions*

The most important consideration from these results is that in every point they furnish the converse evidence from that given by Abraxas as worked out by Punnett and Raynor. The two cases supplement each other in every way, and it is significant to note in this connection that in nature only females of the sport *Abraxas lacticolor* occur, while in *Drosophila* I have obtained only the male sport. Significant, too, is the fact that analysis of the result shows that the wild female *Abraxas grossulariata* is heterozygous for color and sex, while in *Drosophila* it is the male that is heterozygous for these two characters.

Since the wild males (RWX) are heterozygous for red eyes, and the female (RXRX) homozygous, it seems probable that the sport arose from a change in a single egg of such a sort that instead of being RX (after reduction) the red factor dropped out, so that RX became WX or simply OX. If this view is correct it follows that the mutation took place in the egg of a female from which a male was produced by combination with the sperm carrying no X, no R (or W in our formulæ). In other words, if the formula for the eggs of the normal female is RX—RX, then the formula for the particular egg that sported will be WX; *i. e.*, one R dropped out of the egg leaving it WX (or no R and one X), which may be written OX. This egg we assume was fertilized by a male-producing sperm. The formula for the two classes of spermatozoa is RX—O. The latter, O, is the male-producing sperm, which combining with the egg OX (see above) gives OOX (or WWX), which is the formula for the white-eyed male mutant.

The transfer of the new character (white eyes) to the female (by crossing a white-eyed male, OOX to a heterozygous female ($F_1$)) can therefore be expressed as follows:

OX — O (white male)
RX — OX ($F_1$ female)

| RXOX— | RXO — | OOXX— | OOX |
|---|---|---|---|
| Red female | Red male | White female | White male |

It now becomes evident why we found it necessary to assume a coupling of R and X in one of the spermatozoa of the red-eyed $F_1$ hybrid (RXO). The fact is that this R and X are combined, and have never existed apart.

It has been assumed that the white-eyed mutant arose by a male-producing sperm (O) fertilizing an egg (OX) that had mutated. It may be asked what would have been the result if a female-producing sperm (RX) had fertilized this egg (OX)? Evidently a heterozygous female RXOX would arise, which, fertilized later by any normal male (RX—O) would produce in the next generation pure red females RRXX, red heterozygous females RXOX, red males RXO, and white males OOX (25 per cent.). As yet I have found no evidence that white-eyed sports occur in such numbers. Selective fertilization may be involved in the answer to this question.

T. H. MORGAN

WOODS HOLE, MASS.,
July 7, 1910

ELECTROLYTIC EXPERIMENTS SHOWING INCREASE IN PERMEABILITY OF THE EGG TO IONS AT THE BEGINNING OF DEVELOPMENT

It has been shown that at the beginning of development of the egg there is an increase in the absorption of oxygen (Warburg) and excretion of carbon dioxide (Lyon). This is evidently accompanied by increased oxidation within the egg, but varying views as to the cause of the increase have been advanced. The more rapid oxidation might be due to the