# FURTHER DATA ON THE VARIATION OF THE Y CHROMO-SOME IN DROSOPHILA PSEUDOOBSCURA

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#### INTRODUCTION

S IX types of Y chromosome have been recorded in *Drosophila pseudoob*scura, three of them in race A and three others in race B. The six types differ from each other in size and in shape; the characteristics of the Y chromosome present in a given strain are constant. Each type is encountered in populations inhabiting a definite part of the species area.

Since the time of publication of the above observations (DOBZHANSKY 1935) the amount of available data has considerably increased due to accession of material from the hitherto unexplored parts of the area where the species is known to occur. One more (the seventh) type of Y chromosome has been detected, and the geographical distribution of the six previously known ones made clear.

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# OBSERVATIONS

The technique of collecting wild strains of *D. pseudoobscura* and of studying their chromosomes has been described (DOBZHANSKY 1935). The present series of observations differs from the older one only in that the cytological analysis has been performed in many cases on the first generation of flies hatching in the laboratory from parents collected in nature. This difference may account for several instances of two types of Y chromosome being found in the same strain.

The cytological characteristics of the seven types of Y chromosome are represented semi-diagrammatically in figure 1. The chromosome of type I is the largest in size, and all others may be derived from it by losses of sections. Whether or not they have been actually so derived in the history of the species is a different question. Type VII, which is here first described, resembles type II rather closely. The type VII is however smaller than type II, equal armed, and is known to occur in race A only, while type II has been recorded exclusively in race B. Type VII differs from type VI only in size, but the difference is large enough to make the classification reliable.

A list of strains of *D. pseudoobscura* which are known to carry the Y chromosome of a given type is presented below. This list is to be taken as GENETICS 22: 340 May 1937

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an addition to the records published previously (DOBZHANSKY 1935). Each strain in the list is designated by the name of the locality in which its wild ancestor has been captured, and by a serial number. Thus, Charleston-4 refers to the strain No. 4 from Charleston Peak, Nevada. The num-

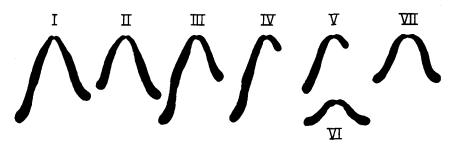


FIGURE 1. The seven types of Y chromosome encountered in Drosophila pseudoobscura (semi-diagrammatic).

ber of the spermatogonial metaphase plates examined in a given strain is indicated in parentheses.

Type I (Race A)

Arizona: Santa Rita-2 (7), Santa Rita-3 (10), Santa Rita-4 (9), Santa Rita-5 (10), Santa Rita-6 (5).

Mexico: Durango: Otinapa-7 (8); Morelos: Cuernavaca-5 (7); Oaxaca: Cerro San Jose-4 (12), Cerro San Jose-5 (15).

Type I (Race B)

California: Sequoia Park-8 (8), Lake Tahoe-1 (12), Tahoe-5 (15).

Type II (Race B)

Washington: Lake Quinault-13 (6).

Type IV (Race A)

Wyoming: Big Horn-5 (8), Big Horn-6 (8).

California: Tahoe-2 (7), Santa Cruz Island-1 (7), Santa Cruz-2 (7). Nevada: Charleston-4 (7).

Arizona: Santa Catalina-1 (4), Santa Catalina-2 (7), Santa Catalina-3 (7), Santa Catalina-4 (9), Santa Rita-1 (14), Santa Rita-4 (3), Santa Rita-7 (12), Chiricahua-3 (7), Chiricahua-5 (7).

New Mexico: Pinos Altos-1 (8), Pinos Altos-2 (6), Pinos Altos-3 (8), Pinos Altos-4 (6), Mountains near Carizozo-5 (7), Magdalena-4 (7), Zuni-6 (5), Taos-1 (8).

Colorado: Mesa Verde-1 (5), Mesa Verde-4 (8), San Juan-1 (7).

Mexico, Durango: Otinapa-3 (10); Morelos: Cuernavaca-2 (12), Cuernavaca-5 (13), Cuernavaca-6 (14), Cuernavaca-8 (7); Baja California: Guadalupe (8), Santo Tomas (6).

## Type V (Race A)

Idaho: Boise-1 (13), Boise-2 (9).

South Dakota: Black Hills-3 (10), Black Hills-5 (9).

Nebraska: Scottsbluff-3 (6), Scottsbluff-5 (5).

California: Providence Mts.-1 (8).

Nevada: Charleston-1 (6), Las Vegas-1 (3), Las Vegas-2 (5).

Utah: Cedar City-6 (5), Cedar City-9 (8), Cedar City-10 (6), Cedar City-11 (6).

Colorado: Estes Park-1 (10), Estes Park-3 (14), Estes Park-5 (20), University Camp-1 (6), University Camp-2 (8), University Camp-5 (11), Pikes Peak-2 (6), Tree Line on Pikes Peak-1 (10), Tree Line-2 (6), San Juan-4 (9), San Juan-5 (6), San Juan-6 (9), Mesa Verde-3 (6).

Arizona: Gila near Yuma-2 (11), Grand Canyon-1 (5), Grand Canyon-2 (7), Flagstaff-1 (4), Flagstaff-8 (7), Chiricahua-6 (7), Chiricahua-7 (10).

New Mexico: Zuni-2 (10), Zuni-5 (5), Taos-3 (5), Taos-4 (8), Magdalena-

1 (6), Magdalena-2 (8), Carizozo-2 (7), Carizozo-4 (7), Carlsbad-1 (7). Texas: Florence-2 (12).

Type VI (Race A)

Arizona: Chiricahua-2 (4).

New Mexico: Zuni-5 (11), Carizozo-4 (9).

Colorado: San Juan-2 (8), San Juan-3 (12).

Type VII (Race A)

Colorado: Estes Park-2 (16), University Camp-3 (11), University Camp-4 (8).

The available information on the geographical distribution of the seven types of Y chromosome is summarized in map form in figure 2 (for race A) and figure 3 (for race B). It is obvious from these maps that each type is encountered in populations inhabiting a definite area, outside of which it is met with seldom or not at all. In some localities the entire population seems to be homogeneous with respect to the type of Y chromosome, while in other localities mixed populations are found. For instance, in Chiricahua and Zuni mountains (Arizona and New Mexico respectively), and in San Juan mountains (Colorado) as many as three different Y chromosomes are represented.

Type I in race A is restricted to Mexico and to southern Arizona, where it exists side by side with type IV. In Oaxaca, Mexico, type I has been found without type IV, but since only two strains were examined from this region the absence of type IV is by no means certain. Type IV is very widely distributed; it is the only type of Y chromosome found in race A on the Pacific Coast from British Columbia to Baja California, and it occurs also in southern Arizona, New Mexico, southern part of Colorado, and in Mexico. East of the Sierra Nevada—Cascade mountains and north of Mexico type V is predominant, but two strains from Big Horn mountains,

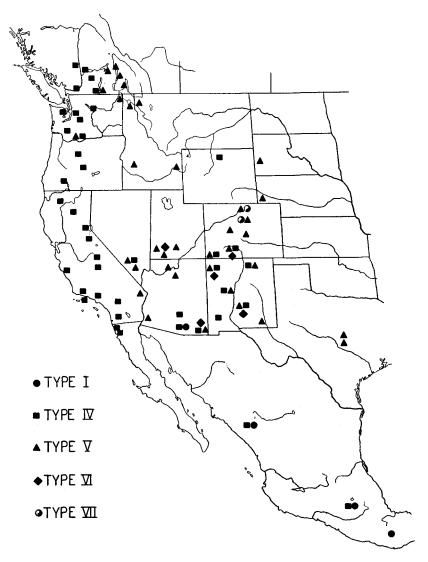


FIGURE 2. The geographical distribution of types of Y chromosome encountered in race A.

well within the territory occupied by type V, were found to possess type IV. Type VI is present as an admixture in the populations from some localities in the Southwest. Type VII is endemic to the highest part of Rocky Mountains, Colorado. In race B the situation is quite simple: type I is present almost throughout the range of the race, type II is restricted to the region around Puget Sound, and type III to southern Sierra Nevada and southern Coast Ranges.

Race A and race B of *D. pseudoobscura* appear indistinguishable morphologically. Apart from their physiology and their genetic behavior, the Y chromosome was supposed to represent the sole difference between the races. The older data showed (with one perhaps doubtful exception) that types I, II, and III are restricted to race B, and types IV, V, and VI to

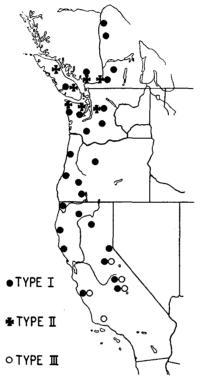


FIGURE 3. The geographical distribution of types of Y chromosome encountered in race B.

race A. At present the Y chromosome can no longer be regarded as a racial differential, since type I (or two types indistinguishable cytologically) occurs in both races. In this connection it is noteworthy that in the rather large area where both races are encountered (compare figures 2 and 3) type I is present in race B but never in race A. In Mexico, where race B does not live, race A may have the Y of type I. It follows that the occurrence of this chromosome in both races cannot be due to interracial hybridization going on in nature at the present time.

### DISCUSSION

The geographical variation displayed by the Y chromosome of *Droso*phila pseudoobscura is interesting mainly because the character involved

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is in this case a chromosome, and intraspecific variations in the chromosome structure have been only very insufficiently studied from a geographical standpoint. It seems worth while to know that the situation which obtains here is not different from the ubiquitous picture encountered wherever one observes a geographical variation of a character modified by a single or a few genes producing clearly classifiable effects on the phenotype. Populations inhabiting different localities differ in the relative frequencies of the genotypes composing them, although populations in some areas may be homozygous for genes that are totally lacking in other areas. A population or a race can be described adequately only in terms of gene frequencies, not in terms of abstract "racial types."

The fact that Y chromosomes of type I occur in race B as well as in race A is very suggestive. As pointed out above, type I is the largest Y chromosome in the species, and all other types can be derived from it by losses of sections of one or of both limbs, and perhaps by shifts in the location of the spindle fiber attachment. The single close relative of D. pseudoobscura living on the American continent, namely D. miranda, also has a Y chromosome of type I. One may speculate that type I has been present in the common ancestor of both races of D. pseudoobscura and of D. miranda. This speculation receives no support if somewhat more distant relatives of our species are taken into account. The European species which FRO-LOWA and ASTAUROW (1929) take to be D. obscura Fall. seems to have a Y chromosome of type IV or V, and the same is true for species of the somewhat more distantly related affinis group in America (STURTEVANT and DOBZHANSKY 1936a). Unless the common ancestor of all these species was already variable with respect to Y chromosome, one is forced to assume that seemingly identical types of Y's have arisen independently in different phylogenetic lines. This is a situation which is familiar to many investigators who have attempted to trace phylogenies on the basis of comparative morphological and embryological data.

Comparative chromosome morphology is frequently supposed to furnish especially reliable information for the elucidation of phylogenetic bonds, a supposition founded on an implied but seldom stated assumption that the visible chromosome structure is a more conservative "character" than morphological structures at large. Proofs of the correctness of this assumption are lacking, and some facts argue rather against it. For example, the pair of species *D. melanogaster* and *D. simulans* have very similar gene arrangements in their chromosomes, while the pair *D. pseudoobscura* and *D. miranda* are very different in gene arrangement (Pätau 1935, KERKIS 1936, DOBZHANSKY and TAN 1936). And yet the external morphological and the genetic differences (as judged by their behavior in crosses) between the two species of a pair are of the same order of magnitude in

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the two cases. The genic differentiation and the differentiation of the chromosome structure do not necessarily go hand in hand. Only very special kinds of chromosome study, those on overlapping inversions (STURTEVANT and DOBZHANSKY 1936b) seem able to produce data of a more exact nature bearing on phylogenetic relationships.

### SUMMARY

1. The geographical distribution of the seven types of Y chromosome known in *Drosophila pseudoobscura* is shown in figures 2 and 3.

2. Type I of Y chromosome is encountered in both races of D. pseudoobscura as well as in D. miranda. The supposition that type I is the ancestral type of Y chromosome leads however to difficulties, since certain other species related to D. pseudoobscura have Y's which resemble the types IV and V of D. pseudoobscura.

#### LITERATURE CITED

DOBZHANSKY, TH., 1935 The Y chromosome of Drosophila pseudoobscura. Genetics 20: 366-376.

- DOBZHANSKY, TH., and TAN, C. C., 1936 Studies on hybrid sterility III. A comparison of the gene arrangement in two species, *Drosophila pseudoobscura* and *Drosophila miranda*. Z.i.A.V. **72**: 88-114.
- FROLOWA, S. L., and ASTAUROW, B. L., 1929 Die Chromosomengarnitur als systematisches Merkmal. Z. Zellf. mik. Anat. 10: 201-213.
- KERKIS, J., 1936 Chromosome conjugation in hybrids between Drosophila melanogaster and Drosophila simulans. Amer. Nat. 70: 81-86.
- PÄTAU, K., 1935 Chromosomenmorphologie bei *Drosophila melanogaster* und *Drosophila simulans* und ihre genetische Bedeutung. Naturwiss. 23: 537-543.
- STURTEVANT, A. H., and DOBZHANSKY, TH., 1936a Observations on the species related to Drosophila affinis, with descriptions of seven new forms. Amer. Nat. 70: 574-584.
- STURTEVANT, A. H., and DOBZHANSKY, TH., 1936b Inversions in the third chromosome of wild races of *Drosophila pseudoobscura*, and their use in the study of the history of the species. Proc. Nat. Acad. Sci. 22: 448-450.

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