Microgeographic Variation in Drosophila pseudoobscura

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MICROGEOGRAPHIC VARIATION IN DROSOPHILA PSEUDOÖBSCURA

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Studies of recent years have revealed a prodigious amount of variability in the gene arrangement in the chromosomes of several species of Drosophila. In natural populations of *D. pseudoöbscura* the third chromosome is more variable than the rest; eighteen structural types, related to each other mostly as overlapping inversions, have been found in this chromosome alone.[1] Each type of the chromosome structure is restricted geographically to a part of the distribution area of the species, although in most localities several types coexist in the same population. Differences between populations are either quantitative, i.e., involving only the relative frequencies of the different types, or qualitative, when certain types occur in some localities but not in others. If population samples from a chain of localities sufficiently remote from each other are studied, the frequencies of the gene arrangements are commonly found to increase, or to decrease more or less regularly in a given geographical direction. Thus, the "Santa Cruz" arrangement is unknown in Washington and Oregon, is rare in the San Francisco Bay region, more common in southern California, especially on the islands off the coast, and very common in Mexico and in Guatemala.[1, 2] Such geographical gradients are familiar to students of geographical variation both in animals and in plants.

Differences between populations inhabiting neighboring localities seem to be of a somewhat different kind. Population samples were taken on eleven mountain ranges in the Death Valley region of California and Nevada. Only three ranges yielded samples the differences between which were not significant statistically; the others were all different. No geographical regularity is, however, observed in this variation, since adjacent ranges are no more likely to be similar than the remote ones, and vice versa. The elementary breeding unit in *D. pseudoöbscura* is therefore not a population inhabiting a large territory; it is no greater than the population of a single mountain range.[3] Next, population samples were taken in six canyons of one of the mountain ranges in the same region; these samples proved to be about as different from each other as those from separate mountain ranges. The breeding unit is, consequently, no greater than the population of a single canyon,[4] and it may be much smaller than that. Comparison of populations coming from localities even more closely adjacent than the above ones is clearly in order.

A small, but very carefully labelled, collection of strains of *D. pseudo-*

obscura from Texas has been received from Professor J. T. Patterson, whose generosity the writer takes pleasure to acknowledge. Each strain represented the offspring of a single fertilized female caught outdoors; with the exception of several cultures in which the wild progenitor has remained alive, all the rest contained the first generation offspring of the original flies. Two or three females and males were taken from every culture and inbred; the chromosomes were examined in the salivary glands of from ten to twelve larvae per culture. Since a fly has two chromosomes of each kind (except, of course, the X and Y-chromosomes), the offspring of a pair of wild flies carries combinations of the four chromosomes present in the parents. In wild flies these chromosomes may be either alike or different in the gene arrangement. Examination of a sufficient number of F_1 larvae permits, therefore, to determine the gene arrangement in four wild chromosomes. The same result may be accomplished also by examining F_2 larvae, although in some instances one, or even two, of the four chromosomes may be already missing. Since our F_2 cultures have descended from at least four F_1 flies, such instances must be very rare, however. Nevertheless, the difficulty just stated does introduce some uncertainty in the data.

The gene arrangement in the second, fourth and in the left limb of the X-chromosome was found to be constant in all strains. In the right limb of the X, the triple inversion characteristic of the "sex-ratio" condition was present in some cultures.[5] Six different gene arrangements were found in the third chromosome, namely, Pike's Peak, Arrowhead, Tree Line, Olympic, Standard and Estes Park; their descriptions have been published by Dobzhansky and Sturtevant,[1] and need not be repeated here. The number of the wild third chromosomes having each of the above gene arrangements found in the different samples is as follows:

	PIKE'S PEAK	ARROW-HEAD	TREE LINE	OLYMPIC	STANDARD	ESTES PARK	CHROMO-SOMES STUDIED
Aldrich Place, near Austin	33	1	..	..	..	2	36
Carrizo Springs	6	4	1	4	..	1	16
Catarina	19	1	5	3	..	..	28
Herrington Orchard, near Dilley	37	12	14	..	1	..	64
Redus Orchard, near Dilley	15	2	5	2	..	..	24
Forrest Orchard, near Dilley	19	2	..	3	..	..	24
Three Rivers	19	1	5	3	..	..	28

The figures suggest that at least some of the samples compared are unlike in genetic composition. The question is now whether the observed dissimilarities are real, or are due to sampling errors. The validity of the suspected heterogeneity of the samples may be tested by calculating the χ^2 values for the common gene arrangements (Pike's Peak, Arrowhead, Tree Line and Olympic), using the Brandt and Snedecor method.[6] The χ^2 values are found to lie between 13.6525 (for Arrowhead) and 20.5730 (for

Pike's Peak); for six degrees of freedom, the probability of such or greater heterogeneity being due to sampling is less than 5% (for Arrowhead).

It must be noted, however, that the seven localities listed above fall into two geographical groups; Aldrich is at least 150 miles from the rest, while all others are relatively close. One may, then, disregard the Aldrich material, and test the heterogeneity in the remaining six samples. The χ^2 values turn out to vary from 7.7765 (for Tree Line) to 11.5080 (for Olympic), which, for five degrees of freedom, have a probability between 5 and 20% of occurring by chance. Finally, the three localities in the vicinity of the town of Dilley may be compared to each other. These three collecting grounds are indeed very close to each other: according to the information received from Professor J. T. Patterson, Herrington orchard lies $1^1/_2$ miles west of Redus orchard, while Forrest orchard is only $^1/_2$ of a mile north of Redus. Yet, no Olympic arrangement is detected among 64 wild third chromosomes studied from Herrington, and no Tree Line arrangement is found among 24 chromosomes from Forrest orchard. If the three localities are compared, the χ^2 values are 2.4313 for Arrowhead, 3.4403 for Pike's Peak, 5.1229 for Olympic and 6.2542 for Tree Line. For two degrees of freedom, an χ^2 value of about 5.1 has a chance of accidental occurrence between 5 and 10%, and a value 6.25 may occur due to sampling in from 2 to 5% of the trials.

Although the material at hand is clearly inadequate for an exact determination of the relative frequencies of the different gene arrangements in any one of the populations, and although the necessity of using F_2 instead of F_1 larvae introduces an additional uncertainty, still the data obtained strongly suggest a significant heterogeneity among the samples examined. The lack of similarity between the three samples from Dilley is, of course, most remarkable in view of the proximity of these collecting localities. The observations quoted above on the genetic differentiation of the local colonies of *D. pseudoöbscura* in the Death Valley region of California make the data reported in the present communication less surprising than they might have been otherwise. It may be pointed out, however, that the exceedingly rugged topography characteristic of the mountain ranges in Death Valley may offer a greater facility for the formation of isolated colonies of the fly than is likely to be the case on the relatively more uniform terrain of southern Texas. On the other hand, Professor J. T. Patterson informs me that *D. pseudoöbscura* is on the whole rare in Texas, the numbers of the trapped individuals of this species being much less than those of others; on the contrary, *D. pseudoöbscura* in California mountains is by far the commonest species. A lower population density per unit area may, under certain conditions, favor a genetic differentiation of local colonies.

Summary.—Data are presented that suggest the existence of genetic differences between colonies of *D. pseudoöbscura* inhabiting close localities.

[1] Dobzhansky, Th., and Sturtevant, A. H., "Inversions in the Chromosomes of *Drosophila pseudoöbscura*," *Genetics*, **23** (1938).

[2] Dobzhansky, Th., "Genetics of Natural Populations. IV," *Ibid.*, **24** (1939).

[3] Dobzhansky, Th., and Queal, M. L., "Genetics of Natural Populations. I," *Ibid.*, **23** (1938).

[4] Koller, P. C., "Genetics of Natural Populations. III," *Ibid.*, **24** (1939).

[5] Sturtevant, A. H., and Dobzhansky, Th., "Geographical Distribution and Cytology of 'Sex Ratio' in *Drosophila pseudoöbscura* and Related Species," *Ibid.*, **21** (1936).

[6] Mather, K., *The Measurement of Linkage*, Methuen, London (1938).

A REMARKABLE GROUP OF POSITION-EFFECTS

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The term position-effect is used here in the generally accepted sense though it would be advisable to replace it by a more neutral term, like "pattern-effect" which does not imply the explanation in terms of position of genes, an interpretation which does not work in the majority of cases. The effects to be described are nearly related to Dubinin's case of change of dominance of *cubitus interruptus* in the presence of a *IV-Y* translocation in *Drosophila melanogaster*.

A.—Years ago the senior author found in connection with very different work the following case: The dominant mutant Beaded (*Bd*) has been known, since Muller's well-known work, to be enhanced in its action by the presence of an enhancer somehow combined with an inversion in the homologous chromosome. When *Bd* was separated in our work from all the other chromosomes of the *Bd*-line by replacing these with marked chromosomes, the "dominant" effect of *Bd* consisted only in the production of a small per cent of flies with slightly nicked wings (actually a smaller effect than the one produced by some standard "recessive" loci like *px* or *bs*). The addition of the inversion (now called *In(3R)C*) again restored the high grade of specific scalloping called *Bd* and the percentage incidence up to 100%. It was then found that the action of this inversion could be replaced by some of the Payne-Inversions in the same chromosome, which were available at that time, thus showing that the presence of an inversion and not an enhancing gene was responsible for this effect. One of the junior authors (Gardner) has now reinvestigated this case. He finds that all inversions in the third chromosome which were tested, had the same enhancing effect, among them an inversion in the other end of the third