

INVERSIONS IN THE THIRD CHROMOSOME OF WILD RACES OF DROSOPHILA PSEUDOÖBSCURA, AND THEIR USE IN THE STUDY OF THE HISTORY OF THE SPECIES

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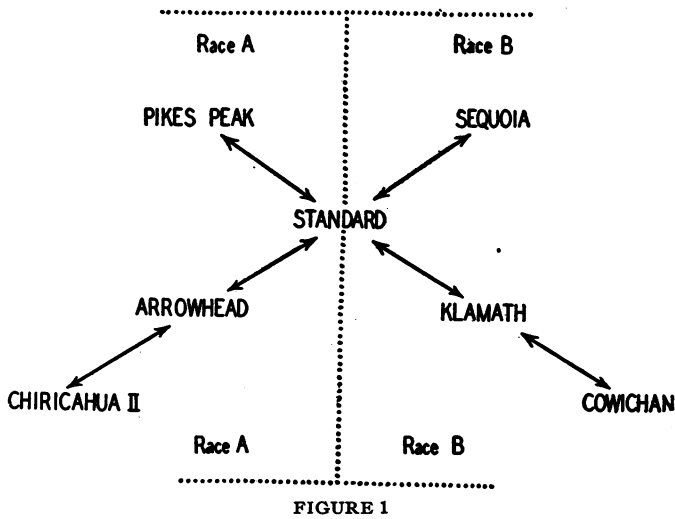
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Genetic studies showed several years ago that the third chromosomes of wild strains of *Drosophila pseudoöbscura* often carry suppressors of crossing-over. The salivary gland chromosome technique has made it possible to demonstrate not only that these are inverted sections, but also that there are many different inversions present in wild populations inhabiting different geographical regions. So far we have found at least fourteen different gene-sequences in wild stocks, and have found that in most geographical regions several sequences are present, though no single sequence appears to occur throughout the range of the species. There are a number of problems raised by these facts, most of which need further study; the present account is to be regarded only as a preliminary note.

One sequence has been arbitrarily designated as "standard," since it is the one in which most mutant genes are known and is also the only sequence that has been found in both of the cross-sterile races, *A* and *B*. This sequence is commonest in race *A* on the Pacific coast, from British Columbia to Lower California, but is found sporadically also in western Montana, western Nebraska, central Texas, central New Mexico (Carizozo) and southern Arizona (Santa Rita Mts.). In race *B* the standard sequence is predominant in the Sierra Nevada and the Coast Range south of the San Francisco Bay, California, but it has been found also in a single strain from the Olympic peninsula, Washington. Several other sequences represent single inversions with respect to the standard one; the "Arrowhead" sequence, found throughout the range of race *A* in British Columbia and the United States; the "Pikes Peak" sequence, found in race *A* from western Nebraska south to central Texas and southeastern Arizona; the "Klamath" sequence, found in race *B* from British Columbia south to Mono county, California; and the "Sequoia" sequence, known only in race *B* from Sequoia National Forest in California.

All the other known sequences differ from the standard by more than a single inversion; one of them, "Cowichan" in race *B* from Vancouver Island, differs from Klamath by a single inversion; "Chiricahua II," in race *A* from southeastern Arizona, differs from Arrowhead by a single inversion. All the others differ from all those so far named by more than a single inversion.

These facts give some information as to the historical relationships of the sequences concerned. If the sequence of the loci in the standard be arbitrarily designated *ABCDEFGH*, we may represent Klamath as *ADCB-EFGH*, Arrowhead as *ABEDCFGH*, and Pikes Peak as *ABCGFEDH*. It is clear that the standard sequence could give rise to any of the three others by a single inversion, or that any of the three could give rise to standard by a single inversion. But it is equally clear that Arrowhead cannot have given rise directly (i.e., by a single inversion) either to Pikes Peak or to Klamath. If Arrowhead was the original, ancestral sequence then Pikes Peak and Klamath are related to it (and to each other) only through the standard, unless one assumes the occurrence of a complex



series of coincidences (repeated breakages of the chromosome in exactly the same places). This method enables us to construct a phylogeny of the types concerned, though it does not give us a method of determining the direction in which that phylogeny should be read. For the types named the relations are shown in figure 1.

There is no direct method of determining which is the original sequence here; but if any one be selected, then the whole course of the evolution is thereby fixed. However, it seems likely that the standard sequence is, in fact, the ancestral one, for the following reasons among others: (1) it is centrally located in the diagram, being the only type to which several others are directly related; (2) it is the only sequence found in both races (*A* and *B*); (3) it has a wide geographical range, being equalled in this respect only by the Arrowhead sequence.

None of the other chromosomes of *Drosophila pseudoöbscura* shows a

diversity of sequence at all comparable to that of the third chromosome. Tan¹ has shown that races *A* and *B* differ by having three inversions with respect to each other—one in each arm of the *X*-chromosome, and one in the second chromosome. We have shown² that the right limb of the *X* often has an inversion associated with the "sex-ratio" gene, but the total number of sequences known for this limb is three. In the course of the present study three additional inversions have been found in wild strains: one in the second chromosome of a few strains from western New Mexico, one in the second chromosome of an *A* strain from Monterey county, California, and one in a fourth chromosome from the Mexican plateau. There are thus known from wild strains the following numbers of sequences: the left limb of *X*, two; the right limb of *X*, three; the second chromosome, four; the third, fourteen; the fourth, two. The reason for these relations remains unknown; it should, however, be pointed out that the third chromosome which shows maximum variation within the species *pseudoöbscura* is also the chromosome which shows maximum differences from the closely related species, *Drosophila miranda*.³

As stated, many localities yield several third chromosome sequences from a single collection. This is perhaps related to the fact that from 15 to 20 per cent of the third chromosomes tested from wild stocks have been found to carry lethal genes. This raises the question as to whether such stocks are in a condition approaching that of balanced lethals. The problem is now being studied; but two facts make us hesitate to conclude that diversity of sequence and frequency of lethals are causally related. (1) In northern and western New Mexico and in the parts of Colorado, Utah and Arizona near the point where these four states come together, extensive tests have failed to show any sequence other than Arrowhead; yet lethals were recovered here in a proportion not noticeably less than that found elsewhere. The number of tests for lethals was, however, small. (2) Preliminary tests indicate that the frequency of lethals is about the same in the second chromosome as in the third, despite the much greater uniformity in sequence in the former (complete uniformity in race *A* stocks from the regions studied).

¹ Tan, C. C., "Salivary Gland Chromosomes in the Two Races of *Drosophila pseudoöbscura*," *Genetics*, **20** (1935).

² Sturtevant, A. H., and Dobzhansky, Th., "Geographical Distribution and Cytology of 'Sex-Ratio' in *Drosophila pseudoöbscura* and Related Species," *Genetics*, **21** (1936).

³ Dobzhansky, Th., and Tan, C. C., "Studies on Hybrid Sterility. III. A Comparison of the Gene Arrangement in Two Species, *Drosophila pseudoöbscura* and *Drosophila miranda*." In press.