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Inversion polymorphism of *Drosophila pseudoobscura* (Drosophilidae) from the Baja California peninsula.

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For more than half a century, Dobzhansky and his associates (Dobzhansky and Epling, 1944; Olvera *et al.*, 1979; Anderson, *et al.*, 1991) studied the third chromosome inversions in populations of *Drosophila pseudoobscura*. The species has its main distribution in the United States and Mexico. In both countries most of the populations exhibit chromosomal polymorphism of their third chromosome gene arrangements. Over the years, it has been of special interest to study the chromosomal polymorphism of populations variously distanced from one another. This has been done in some cases, along east-west and north-south collecting transects. With regard to the United States and Mexico, the southward extension of the North American land mass has resulted in two parallel areas which are separated by the Sea of Cortes. They are the Peninsula of Baja California and mainland Mexico. Both areas contain populations of *D. pseudoobscura*.

In his pioneering 1944 paper, Dobzhansky reported, among other things, on the results of a north-south collecting transect along the Pacific coast of Washington, Oregon, California and three locations in Baja California. These three locations are Santo Tomas and Guadalupe, San Antonio Mesa and Cedros Island. The present investigation is an extension of the earlier studies of the chromosomal polymorphism of *D. pseudoobscura* populations along the Pacific coast.

Materials and Methods

The *D. pseudoobscura* populations studied herein were collected in the following localities: Las Animas, El Tigre, Mike Ranch, and Rancho Garrett, all of them in the State of Baja California, plus the locality Oasis San Ignacio in the State of Baja California Sur. Table 1 gives the relevant information on these places, as well as on the collections themselves.

The first four places are located in the northern third of the Baja California state, in the broadest part of the peninsula. Oasis San Ignacio is located in the middle of the peninsula, 250 km south of Cedros Island. The four northern locations in the state of Baja California share a very similar environment which is described by Delgadillo (1992). In contrast, the Oasis of San Ignacio has only palms as well as some introduced sugar cane and some grasses.

The prevailing temperature at the time the collections were done was 12° to 21°C. The collections were done from 5:30 to 10 AM. and from 5 to 8 PM. Flies were attracted to bait buckets containing fermenting bananas and collected by sweeping the buckets at regular intervals, 10 to 20 minutes, with a net. The trapped flies were put into a flask containing instant medium (Carolina Biological Supply Co., U.S.) and kept there until arrival at the laboratory. Once there, they were anesthetized and identified. Those belonging to the *obscura* group were separated from the others which were put in alcohol for future analysis.

Females belonging to the *obscura* group were put individually into separate 1/2 pint bottles with instant medium enriched with a heavy solution of live yeast and allowed to lay eggs. The female flies were incubated at 25°C for five days. After that they were placed at a lower temperature 15 - 17°C, and drops of live yeast solution were added for additional nourishment.

When mature third instar larvae crawled out of the food, a single larva from each culture was dissected, its salivary glands were extracted, and a smear was prepared using the regular lacto - aceto - orcein staining technique. Each slide was examined through the light microscope to determine the fly's gene arrangements, and the data obtained were used to get the respective inversion frequencies. In order to make comparisons, a statistical analysis was performed using the test developed by Steel and Torrie (cited by Everitt, 1992).

Results

Table 1 lists the data corresponding to the 7 collections (sites Las Animas and Rancho Garrett were sampled twice), with an overall analysis of 798 third chromosomes. Data from Dobzhansky (1944) is included. Unfortunately, the paper does not contain certain types of information recorded during our collections.

Table 1. Relevant information of the sampled localities.

Locality	Date of collection	km from Tijuana	Temperature °C	Females collected	Males collected
S.A.M.	Dobzhansky, 1944	50			
S.T.&G.	Dobzhansky, 1944	50			
E.T.	October 11, 1993	75	15- 23	10	6
L.A.I	May 14, 1993	135	15- 20	130	193
L.A.II	September 23, 1993	135	16- 21	7	6
M.R.	April 14 - 25, 1993	258	10- 22	420	522
R.G.I	July 28 - 30, 1993	268	12- 25	28	3
R.G.II	January 18 - 20, 1994	268	0- 19	10	14
C.I.	Dobzhansky, 1944	511			
S.I.	May 21 - 23, 1993	717	15-28	283	194

M.R.= Mike Ranch; L.A.I = Las Animas I; S.I. = San Ignacio; R.G.I = Rancho Garrett I; L.A.II = Las Animas II; E.T.= El Tigre; R.G.II = Rancho Garrett II; S.T.&G. = Santo Tomas and Guadalupe; S.A.M. = San Antonio Mesa; C.I. = Cedros Island

Temperature in degrees C

Of the 40 reported different gene arrangements known to occur in the third chromosome of *D. pseudoobscura*, we were able to detect six. Their frequencies in each collection are shown in Table 2. Depending on the locality, the different gene arrangements varied greatly in frequency: ST varied from 45.00% in El Tigre to 91.66% in Las Animas II; AR from 5.00% at El Tigre to 16.66% in Mike Ranch and 20.00% in Rancho Garrett II; SC from 4.12% in Las Animas I to 30.08% in Oasis San Ignacio; CH from 2.57% in Las Animas I to 50.0% in El Tigre; the remaining two gene arrangements, OL and CU, are quite rare. OL was found twice, one in the collection Las Animas I and the other in San Ignacio, CU only once at Mike Ranch. As has been found in other studies, the populations at the sites investigated here show a predominance of two or three gene sequences representing about 85 to 95% of the total sample with the remaining 5 to 15% being contributed in different frequencies by the other inversions. There is even the presence of one or two rare inversions, in our case OL and CU. Beside the analysis of the third chromosome, we were able to detect in the Mike Ranch locality the presence of the

Table 2. Frequencies of different gene arrangements.

Site	ST	AR	SC	CH	CU	OL	N
S.A.M.	58.33	23.61	-	18.06	-	-	72
S.T&G	59.37	28.13	9.38	3.13	-	-	32
L.A.I	82.47	10.30	4.12	2.57	-	0.51	194
L.A.II	91.66	-	-	8.33	-	-	12
E. T.	45.00	5.00	-	50.00	-	-	20
M.R.	72.22	16.66	7.63	3.12	0.34	-	288
R.G. I	84.21	7.89	7.89	-	-	-	38
R.G. II	75.00	20.00	5.00	-	-	-	20
C.I.	53.85	30.77	15.38	-	-	-	26
S.I.	56.19	7.96	30.08	4.86	-	0.88	226

M.R. = Mike Ranch; L.A.I = Las Animas I; S.I. = San Ignacio; R.G.I = Rancho Garrett I; L.A.II = Las Animas II; E.T.= El Tigre; R.G.II= Rancho Garrett II; S.T.&G. = Santo Tomas and Guadalupe; S.A.M. = San Antonio Mesa; C.I. = Cedros Island.

chromosome was found in each locality. In both case the gene arrangement was found in the ST/KL genotype. The importance of this finding is that the southern limit of this species has been thought to be in the San Jacinto mountain range in California.

Discussion

In making comparisons between the populations herein studied, one finds that all of them follow the same pattern of distribution, with two gene arrangements as main contributors of the gene pool: ST and AR in the Mike Ranch and Rancho Garrett populations. In the case of Las Animas I the pattern is the same, but Las Animas II looks less polymorphic with a total of only two inversions present, ST and CH. The small sample size of this population (12 chromosomes analyzed) could be responsible for that, as may also be the case in the El Tigre population. Two localities, Mike Ranch and Rancho Garrett, are quite similar in respect to the frequency of the SC inversion and close to the frequency of this arrangement in the Santo Tomas and Guadalupe population but differing in frequency of ST and AR. San Ignacio looks similar to Santo Tomas and Guadalupe, San Antonio Mesa and Cedros Island for ST, but differs considerably for AR and SC. In San Ignacio the prevailing gene arrangements are ST and SC, as is shown in Table 2. Correspondingly, Las Animas I and II and El Tigre are quite different from the others. The four northern populations are also different from our fifth locality of San Ignacio.

A statistical analysis of the present data was performed. To do it we chose the locations with the larger size of sampled chromosomes. They are: Mike Ranch, San Ignacio, and Las Animas, using as a baseline for comparison the population of San Antonio Mesa of Dobzhansky (1944). The respective sample sizes are: 288, 226, 194, and 72 chromosomes. Using these data we performed the statistical assay developed by Steel and Torrier in 1985 (see Everitt, 1992) to test for homogeneity of the samples. It was found that the localities in the Peninsula of Baja California are heterogeneous with respect to their chromosomal polymorphism.

Of interest for the present study is the presence in only one population, Mike Ranch, of the "sex ratio" inversion located in the X chromosome. It was found only in the progeny of five different females corresponding to 1.73% of the total sample of 144 females analyzed in that population. This finding is consistent with other studies that mention the broad distribution of this constitution in this and other species (Sturtevant and Dobzhansky, 1936). In the same publication, Sturtevant and Dobzhansky (1936) reported the frequency of "sex-ratio" in *D. pseudoobscura* from different localities varies from 0 to 40%

"sex ratio" inversion in the progenies of five females. This inversion, SR, is located in the X chromosome of *D. pseudoobscura*.

Of great interest is the presence in the collections from San Ignacio and Las Animas I of the Klamath (KL) gene arrangement, which is characteristic of the sibling species *D. persimilis*. Only one KL

of the X chromosomes studied. In Mexico only two locations, Durango and Oaxaca, have been investigated for this inversion, and it resulted as follows: in Durango one tested chromosome happened to be sex-ratio, and in Oaxaca two out of 10 chromosomes tested carried the condition (Sturtevant and Dobzhansky, 1936).

Of great interest was the appearance as far South as San Ignacio and Las Animas of the sibling species *D. persimilis* Klamath gene arrangement in the progeny of one female from each location which are 623 km apart. It was found in both cases in combination with the Standard gene arrangement. It is well known that the Klamath (KL) sequence is representative of the species *D. persimilis* and that both species share the ST sequence that links both species phylogenetically. The significance of this discovery must await further investigations. It is clear that more extensive studies should be carried out not only in the locations herein mentioned but in other representative areas of the Baja California Peninsula, in order to discover other possible patterns of distribution as well as of seasonality for the different gene arrangements.

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