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FOUR DECADES OF INVERSION POLYMORPHISM IN *Drosophila pseudoobscura* FROM MEXICO

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Chromosomal inversion polymorphism has been study in different natural and experimental populations of *Drosophila* species. *D pseudoobscura* first studies in Mexico started during the late 30´s of last century, here are shown the relative frequencies of 48 populations in a period of 40 years with a grand total of 7266 third chromosomes analyzed. Globally in those populations a total of 26 inversions are present, in most cases their genetic structure is built by five main gene arrangements and three to six in minor frequencies not reaching a particular one more than six percent. This study includes the description of 15 new inversions reported else were. The most frequent gene arrangements found were TL, CU, SC, EP and OA that globally represent about the 90**%** of the whole sample. Remaining 21 inversions were found with individual frequencies varying from one to six per cent reaching in general the remaining 10%. In some areas the dominant inversions are CH. AR. ST and PP. in some areas. Important goals of this study are the discovery and description of 15 new gene arrangements as well new species description, *D. cuauhtemoci***.** All of them reported else were.

Key words: Drosophila pseudoobscura, natural populations, inversion polymorphism

INTRODUCTION

In the middle of the 30´ of last century DOBZHANSKY (1939) visited Mexico, and because he was much interested in make studies of inversion polymorphism in natural populations of *Drosophila pseudoobscura,* this was not possible until 1974. At that time and under his guidance and leadership a binational team of eight participants and with financial support of USNSF and CONACyT a project was started. At first initial objetives were: 1) to understand genetic variation

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and ecological basis of *D. pseudoobscura* natural populations*; 2)* to determine relationships between the amount of variation present in the populations and 3) to study patterns for chromosomal polymorphism of genetic distribution.

Paracentric inversions is the tool to measure genetic polymorphism in natural populations. They are present and very common in several *Drosophila* species, one of such cases is *D. pseudoobscura* first described by DOBZHANSKY and STURTEVANT (1938) since then many authors have been interested in this kind of studies focusing also in different *Drosophila* species.

Drosophila pseudoobscura was first monitored by DOBZHANSKY and STURTEVANT (1938) and later by his associates, and now for several researches looking for the third chromosome inversion frequency in natural populations. Here are a summary of those observations done in Mexico during a four decades interval.

DOBZHANSKY (1939) and DOBZHANSKY and EPPLING (1944) original studies *o*n nine Mexican populations of *D. pseudoobscura* where they found nine inversions as well on a first report as a team (DOBZHANSKY *et al.*, 1975). Concerning only three populations, eleven inversions including two new ones were found. After that, 48 natural populations, four of them sampled several times, were sampled covering most of the Mexican territory. Different aspects were studied, such are: seasonal variation; short and long-time variation in relative frequencies; clines presence; most frequent arrangements and geographic distribution; endemic gene arrangements and genealogical tree before and after this study. At present, a summary is the goal, in a similar way as DOBZHANSKY *et al.* (1964), ANDERSON *et al.* (1975) and ANDERSON *et at.* (1991).

MATERIALS AND METHODS

For each location, flies were attracted to plastic buckets containing fermenting bananas and collected by swinging an entomological net, this was done at regular intervals of 10-15 from sunrise to 9.00 h in the mornings and from 17.00 h until dark in the evenings during five days of each collecting trip. Trapped flies were sorted, and those belonging to *obscura* group were placed in vials with fresh food in groups of 20-30 individuals, males separated from females, to prevent double insemination, and ready to carrier them to Mexico City laboratory, once a collecting trip was done. At arrival to the laboratory each female was placed into separate one-half-pint bottle with fresh food and enriched with a heavy solution of live yeast and allowed to lay eggs for a week; when the amount of females was small we also used males, in such cases males were crossed individually with 2-3 females of a known karyotype strain in this case either Estes Park (EP/EP) or Tree Line (TL/TL) in order to increase the sample size. A week later, flies were transferred to a new bottle with fresh food to serve as a reserve, and some drops of live yeast heavy solution, were added to original cultures to allow developing larvae better nourishment, this way large salivary glands are assure and as a consequence large polytene chromosomes.

When mature third instar larvae crawled out of food, a single larva from each culture was dissected, its salivary glands extracted, and a smear prepared using the regular 5 % aceto orceine staining technique. Each slide was examined through a compound microscope to determine their corresponding karyotype, this was done, when necessary, with the help of a photographic atlas and figures reported by DOBZHANSKY and EPLING, (1944), KASTRITSIS and CRUMPACKER, (1966 and 1967) and OLVERA *et al.*, (1979). Data obtained such way were used to calculate inversions frequencies and Table elaboration.

Regular corn meal-agar-sugar-yeast food normally used in our laboratory was employed to rear flies and larvae. All cultures were incubated at 25 + 1º C and 65 percent of relative humidity.

Along these 40 years some localities were visited several times. Original three ones during first three year every three months and later for 3-5 years periods, the rest were visited at yearly intervals, and the remaining only once. Site names and their abbreviations are: Torreon, Coah. (TO), Los Lirios, Coah. (LL). Diego de Alcala, Dgo. (DA), Presa, Dgo. (PR), Presidio, Dgo. (PRE), Matehuala, S.L.P. (MA), Valparaiso, Zac. (VA), La Congoja, Ags. (LC), Rio Verde, S.L.P. (RV), Los Reyes, Gto. (LR), Tierra Nueva, Gto. (TN), Lobo, S.L.P.(L), Pinal de Amoles, Qro. (PA), Victoria, Gto. (VI), Huimilpan, Qro. (HU), Tulancingo, Hgo. (TU), Ciudad Guzman, Jal. (CG), Zirahuen, Mich. (ZI), Centro Nuclear, Mex. (CN), Amecameca, Mex. (AM), La Malinche, Tlax. (LM), El Seco, Pue. (ES), La Perla, Ver. (LP), Filo de Caballo, Gro. (FC), Oaxaca, Oax. (OA), Ocosingo, Chis. (OC), San Cristobal las Casas, Chis. (SCC), Cola de Caballo, N.L. (CC), Jerez, Zac. (JE), Mazamitla, Jal. (MAZ), Ixtlan, Oax, (IX), Tlaxcala, Tlax., (TLA), Sinaloa, Sin, (SIN), Juriquilla, Qro. (JU), Cuautemoc, Coah. (C UA), Catana, Coah. (CA), Chiflon, Coah. (CHI), Pachuca, Hgo. (PA), El Chico, Hgo. (ECH), Tequesquinahuac, Mex. (TE), Tres Marias, Mor. (TM), Xochimilco, D.F. (XO), Las Animas, BC; (LA), El Tigre, B.C. (ET), Mike Ranch, B.C. (MR), Rancho Garett, B.C.(RG), San Ignacio, B.C.S (SIG), Tehuacan, Pue. (TEH) .and Nevado de Colima, Col. (NC) (Table 1)

Results for population name and abbreviation for each inversion, sample size and main chromosome inversions present per population, their frequencies in percent and year of collection (Table 1).

A total of 53 populations as pointed out early sample and a grand total of 7266 analyzed chromosomes (Table 1), altogether 26 different inversions out of the 40 or so described gene sequences were found, they represent more than 60 per cent species variability for this trait, such inversion names and symbols alphabetically are: **Amecameca (AM)**, Arrow Head (AR), Chiricahua (CH), Cuernavaca (CU), Estes Park (EP), Hidalgo (HI), **Iztacihuatl (IZ), Los Lirios (LL), Michoacan (MI), Miraflores (MF),** Oaxaca (OA), Olympic (OL), **Ozumba (OZ), Patzcuaro (PA), Paxtepec (PA),** Pikes Peak (PP), **Popocatepetl (PO), San Antonio (SA),** Santa Cruz (SC), Standard (ST), **Tarasco (TA),** Tree Line (TL), **Tulancingo (TU), Tzinzunzan (TZ), Uruapan (UP),** and **Zirahuen (ZI).** Bold letters indicate new arrangements found during this study. Not all inversions are present on each locality neither they were found in every collection but they contribute to the particular genetic structure of each population, and also they are a reflection of high variability for this trait in Mexican populations of this species. As for their abundance, inversions could be catalogued as very common with more than 30 per cent of relative frequency, moderately common between 5-15 per cent and rare less than 5 per cent of relative frequency.

Dominant inversions for the main area distribution found are TL, CU, SC, EP and OA with relative high frequencies. In the peninsular region the dominant gene arrangements are CH, AR ST and PP who represent a different race more similar to those found in California. During the study 15 new inversions were discovery and described (OLVERA *et al.*, 1979), they names are printed in bold at early paragraphs, a new species of the group namely *D. cuauhtemoci* were found and described (FELIX *et al*., 1976).

Table 1. Location and inversion frequencies of 53 natural populations of Drosophila pseudoobscura from Mexico.

SITE	TL	CU	SC	EP	OL	OA	CH	PP	ST	AR	Other	n	Year col.
TO	36.6	11.6	16.1	9.8	16.1	---	---	7.1	---	---	2.7	113	2003
LL	42.1	---	---	1.7	13.1	1.7	---	38.1	---	---	2.3	176	1975
LL	35.7	23.1	10.5	5.6	21.8	1.4	---	---	---	---	---	143	2000
DA	6.5	---	52.1	6.5	2.2	---	21.2	2.2	---	2.2	6.5	46	2001
PR	6	4	56	---	---	---	18	6	4	6	2	54	2001
PRE	20.5	5.1	35.9	---	5.1	---	26.8	7.7	---	5.1	---	39	2001
MA	34.3	14.3	5.7	14.3	20	---	---	8.6	---	---	2.9	35	2002
VA	34.9	6.8	6.8	2.7	3.4	5.5	---	---	---	---	8.3	146	2001
LC	36.3	2.9	42.6	2.1	4.6	2.6	---	---	---	---	9.1	240	2001
RV	59.2	5.4	2.9	7.6	22.3	1	---	---	---	---	1.6	314	2000
LR	51.6	3.2	16.1	6.5	22.6	---	---	---	---	---	---	31	2001
TN	57.2	8.7	28.3	---	10.9	---	---	---	---	---	---	46	2001
L	54.6	14.6	9.1	1.8	12.7	1.8	---	---	---	---	5.4	55	2002
PA	56.9	6.3	4.9	---	25	---	---	---	---	---	7	144	2002
VI	28	17.1	28	1.4	3	8.1	---	---	---	---	10.8	74	2001
HU	45.2	26.2	4.8	4.8	14.3	2.4	---	---	---	---	2.4	43	2000
TU	50.8	38.5	6.2	2.3	---	0.8	---	---	---	---	1.5	130	1976
TU	67.6	22.9	---	6.3	2.5	0.4	---	---	---	---	0.4	240	2000
TU	29.8	31.6	8.8	5.3	17.5	7.0	---	---	---	---	---	57	2011
CG	21.4	8.6	8.6	5.7	1.4	2.9	---	---	---	---	1.4	70	2000
ZI	20.8	22.1	22.8	10	5.1	15.4	1.0	---	---	---	2.8	610	1974
ZI	30.5	25.7	20.9	10.5	2.9	9.5	---	---	---	---	---	105	2000
CN	66.2	21.1	---	12.7	---	---	---	---	---	---	---	71	2001
AM	37.9	55.5	0.8	3.8	1.0	0.3	---	---	---	---	0.4	1262	1975
AM	39	48	2.5	8	1	1.5	---	---	---	---	---	200	2000
LM	66.3	20.2	---	9	1.1	2.3	---	---	---	---	1.1	89	2002
ES	47.4	39.6	5.8	5.2	1.4	0.4	---	---	---	---	0.2	515	2001
LP	59.7	32.2	2.7	4.7	0.7	---	---	---	---	---	---	149	2002
FC	32.7	53.3	7.5	0.9	1.9	2.8	---	---	---	---	0.9	107	2000
OA	35.7	54.1	7.1	2	---	1	---	---	---	---	---	98	2000
OC	45.5	1.6	41.5	9.8	---	1.6	---	---	---	---	---	123	2000
SCC	33.3	1.3	61.5	3.9	---	---	---	---	---	---	---	78	2000
CC	9.7	6.4	32.3	22.6	---	9.7	---	---	---	---	---	31	2000
JE	30.9	7.1	33.3	11.9	2.4	4.8	---	---	---	---	9.6	42	2000
MAZ	25	25	25	---	25	---	---	---	---	---	---	4	2000
IX	---	33.3	66.7	---	---	---	---	---	---	---	---	6	2000
TLA	68.7	31.3	---	---	---	---	---	---	---	---	---	32	2002
SIN	25	50	---	25	---	---	---	---	---	---	---	4	2003
JU	78.8	---	---	15.4	1.9	---	---	---	---	---	3.8	52	2004
CUA	45.9	1.4	---	14.9	4.1	---	---	33.8	---	---	---	74	2004
CA	71.4	4.8	---	4.8	---	---	---	19	---	---	---	21	2004

CHI	28.6	---	---	14.3	---	---	---	57.1	---	---	---	7	2004
PA	53.9	39.5	---	2.6	1.3	---	---	---	---	---	2.6	26	1975
ECH	38	47.5	---	---	17.5	---	---	---	---	---	---	40	1975
TE	30.6	58.2	5.3	1.9	3.4	---	---	---	---	---	---	206	1974
TM	23.8	70.8	2.5	1.5	---	0.5	---	---	---	---	1	202	1976
XO	33.8	15.5	37.8	6.1	5.4	0.2	---	---	---	---	0.2	148	1979
LA	---	---	4.2	1.2	0.5	---	2.5	---	82.5	10.3	---	194	1993
ET	---	---	---	---	---	---	---	50	45	5	---	20	1993
MR	---	0.3	7.6	---	---	---	---	3.1	72.2	16.7	---	288	1993
RG	---	---	---	7.9	---	---	---	---	84.2	7.9	---	38	1993
SIG	---	---	30.1	---	---	---	---	4.9	56.2	8	---	26	1993
NC	20.3	5	65.3	---	6	1.5	---	---	.---	---	2	202	2000
Total	**39.9**	**22.7**	**21.2**	**7.2**	**8.4**	**3.4**	**13.9**	**19.7**	**57.4**	**7.7**	**3.5**	**7266**	**xxx**

DISCUSION

This report summarizes the analysis for relative frequencies of inversions in the third chromosome of *Drosophila pseudoobscura* in 48 localities along Mexico. Considering its extension and long time span study this number seems small, but developing the general project several tasks were achieved.

First, three populations were studied in central Mexico: Amecameca, Tulancingo and Zirahuen, they were sampled four times a year for three consecutive years and, later every 4-5 years in order to identify temporal changes and different patterns of chromosomal polymorphism among them. Last sample was taken in 2011 and the influence of temperature over changes in relative frequency of inversions were reported.

A second approach was to analyze several southern populations looking for a gradient starting from the central region such as: Tequesquinahuac, Xochimilco, Cuernavaca, Tehuacan, Oaxaca and San Cristobal las Casas, (OLVERA *et al*., 1982)

Another study was to determine yearly fluctuation for relative frequencies of inversions in two populations: namely Cuernavaca (GONZALEZ, 1976, personal communication) and a northeastern one in Saltillo, Coahuila, (ESPINOZA-VELAZQUEZ and SALCEDA, 1981)

At that moment, it is was possible to determine an east-west distribution of gene arrangements from Ciudad Guzman and Jalisco up to Orizaba in Veracruz covering five populations along the Volcanic axis, (Guzman et al 1993)

Later, attention was focus for populations from the Baja California Peninsula arrangements as CH, AR and ST, (SALCEDA, 2001) its behavior is very similar to Californian populations in USA broadly sampled by Dobzhansky and his associates.

Finally, at the beginning of XXI century 32 populations were sampled scattered along Mexico, attempting to cover most of the territory trying to have a whole panorama for this trait in the country, (SALCEDA, GUZMAN and OLVERA, 2007a, SALCEDA *et al*., 2007b).

Several objectives were reached, first the great distribution of inversions as well elevated number of different gene arrangements that globally reach about 65% of the whole number of the already described. Also, presence of gradients were determined in four north to south transects. In two areas microclines were described (SALCEDA and ESPINOZA-VELAZQUEZ, 2006; SALCEDA and

GUZMAN, 2010) and for one population temperature as the main factor for relative frequencies of inversions modification (GRANADOS *et al.*, personal communication)

Other contributions are: discovery and description of a new species of the obscura group. Also, 15 new gene arrangements were discovered and described, that gives a new phylogenetic tree interpretation using relationships and origin of new inversion.

As for most abundant gene arrangements, as seen in Table 1, main area of distribution TL, CU and SC are predominant; in northeastern region predominates PP and TL an in Baja California ST and CH, Interpretation of this polymorphism is used to suggest the presence of several sub-races or subgroups in a similar way as DOBZHANSKY and EPLING did (1944), they are: Baja Californian represented mostly by inversions CH, AR and ST, this subcategory is quite similar to populations inhabiting California. Northeastern subgroup characterized by inversions PP, TL and OL as main components. Southern subgroups (TL and SC) where the predominant inversions. Central high plateau region coexist two close subgroups, predominant gene arrangements are TL and CU and the other represented by TL, CU and SC. In all cases, only more abundant inversions but in all populations 3-6 other gene arrangements are present with frequencies varying from 1-10 percent.

As shown in Table 1., Mexico represent an area of high genetic variability for this kind of polymorphism in the third chromosome of *D. pseudoobscura* that allowed to propose Mexico as the species birth place. This is supported not only by the elevated number of inversions but also to at least in two populations, the presence of up to 10 simultaneously different gene arrangements.

Finally, it is necessary to mention that there are at least four states, Chihuahua, Sonora, Sinaloa and Puebla remaining to be sampled, they are of great interest due to their extension and variety of ecological characteristics.

CONCLUSSION

Mexico represents a region of major variability for inversions in the whole distribution area of *Drosophila pseudoobscura* with about 65 percent of known inversions. Apparently, at least five subgroups are found, this is due to a great ecological diversity in the country. According to that great variability, this species probably was originated in central Mexico. Changes in temperature also determine changes in relative frequencies.

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ČETIRI DECENIJE INVERZIONOG POLIMORFIZMA *Drosophila pseudoobscura* U MEKSIKU

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Izvod

Vršeno je ispitivanje hromozomalnih inverzija kod prirodnih i eksperimentalnih populacija. Prva ispitivanja *D. pseudoobscura* u Meksiku su započeta u toku kasnih tridesetih godina prošlog stoleća i ovde su pokazala relativnu frekvenciju 48 populacija u period od 40 godina sa velikim brojem od 7266 analiza trećeg hromozoma. Globalno, u tim populacijama bilo je prisutno 26 inverzija, u većini slučajeva njihova genetička struktura se sastojala od aranžiranja pet glavnih gena, a tri do šest u minornim frekvencijama nisu dostizale više of 6 %. Studija uključuje opis i novih inverzija objavljenih ranije. Najveći deo nađenih čestih genskih aranžmana je TL, CU, SC, EP i OA što globalno pretstavlja 90 % ukupnog uzorka. Preostala 21 inverzija je utvrđena sa individualnom učestalošću koja varira od 1 do 6 % dostižući generalno preostalih 10 %. U nekim arealima dominantne inverzije su CH, AR, ST i PP. Značajan cilj ovih istraživanja je otkrivanje i opis 15 novih genskih aranžmana kao i opis novih vrsta , *D. cuauhtemoci***.**

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