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CHROMOSOMAL POLYMORPHISM IN NATURAL POPULATIONS OF THE
DESERT ADAPTED SPECIES, DROSOPHILA MOJAVENSIS

The University of Arizona

PH.D.

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CHROMOSOMAL POLYMORPHISM IN NATURAL POPULATIONS
OF THE DESERT ADAPTED SPECIES, DROSOPHILA MOJAVENSIS

by

William Robert Johnson, Jr.

A Dissertation Submitted to the Faculty of the
DEPARTMENT OF ECOLOGY AND EVOLUTIONARY BIOLOGY

In Partial Fulfillment of the Requirements
For the Degree of

DOCTOR OF PHILOSOPHY

In the Graduate College

THE UNIVERSITY OF ARIZONA

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THE UNIVERSITY OF ARIZONA
GRADUATE COLLEGE

I hereby recommend that this dissertation prepared under my direction
by William Robert Johnson, Jr.

entitled Chromosomal Polymorphism in Natural Populations of
the Desert Adapted Species, *Drosophila mojavensis*
be accepted as fulfilling the dissertation requirement for the Degree
of Doctor of Philosophy.

William B. Heed
Dissertation Director

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Date

As members of the Final Examination Committee, we certify that we have
read this dissertation and agree that it may be presented for final
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William Johnson Jr.

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ABSTRACT

The karyotype variability of Drosophila mojavensis was examined from thirty-nine natural populations in southern Arizona and California, USA, and Sonora, Sinaloa, and Baja California, Mexico. The distribution and degree of heterozygosity of the four gene arrangements on the second chromosome and the two gene arrangements of the third in conjunction with observations of the species' genetics and ecology has led to a hypothesis of population structure and inversion heterokaryotypy. The baja race, found on the peninsula of Baja California is sub-divided into a mosaic of three marginal populations in three distinct phytogeographic regions. The description of these populations as being marginal or central is based on hypothesized trophic resource production in the host cactus, Machaerocereus, and population survival through time. The central populations have continuity in time in the same geographic area, while marginal populations, due to the ephemeral nature of the resource in those areas undergo frequent local extinctions and must be re-established by inter-deme migration. This latter description is also applicable to the host plants and populations of the mojavensis race (Ferocactus) in southern California and the sonorensis race (Lemaireocereus) in Sonora and Sinaloa, Mexico. In regions of sustained resource production, populations of D. mojavensis are able to increase fitness by utilizing heterokaryotypy. In marginal populations, directional karyotype selection maintains regionally (phytogeographic) specific inversions in a relatively homozygous state.

INTRODUCTION

Inversion polymorphisms of Drosophila have been for more than three decades one of the most widely studied genetic phenomena in the laboratory and in nature (Dobzhansky, 1970; White, 1973; Parsons and McKensie, 1972).

Before the advent of electrophoretic studies, inversion polymorphism was the most easily observable system that could be measured in natural populations and pioneered in the analyses of the genetic structure of populations both within and between species. The major effect of a heterozygous inversion in a population is to restrict gene recombination within the limits of the inversion in Drosophila. This is due to the exclusion of crossover products into the polar bodies during meiosis of the female heterokaryotypes and the lack of crossing-over altogether in the males. Lack of negative meiotic consequences (reduction in fertility) allows natural selection to increase linkage between the genes and their modifiers within the inversions to form co-adapted gene complexes, which together may behave in a heterotic manner (heterokaryosis).

Wasserman (1972) distinguishes three different levels of organization within inversions at which selection may be operating to produce heterokaryosis: the genic level, the karyotypic level, and the supergene level. Wasserman has stated, "With genic selection, the heterokaryotypes are heterotic because they have captured heterotic

loci which help to buffer them against the environment; the homokaryotypes are less fit because they are homozygous for deleterious recessive alleles and are less buffered against environmental variation. With karyotype selection each chromosome (inversion) is adapted to one or several aspects of the environment. The fitnesses of the karyotypes can be defined under given environmental conditions and would change if and when these environmental conditions are altered" (Wasserman, 1972). With supergene selection, the cooperation and organization of genes along the chromosome is considered and recombination between homologues of the same family of supergenes (same gene sequences) may break down this adaptive combination and produce frequency dependent selection against the homokaryotypes. In other words, offspring of heterokaryotypes inherit undisturbed blocks of previously selected supergenes, and individuals with better blocks of genes will be more likely to survive and reproduce. And if recombination between two well balanced supergenes destroys the integration of the genotypes, then the offspring of homokaryotypes will be less fit than those of the heterokaryotype.

Attempts to identify the specific environmental elements controlling inversion frequencies in natural populations have met with some degree of success in D. pseudoobscura, a North American temperate forest species (Dobzhansky, 1948; 1970; Strickberger and Wills, 1966); D. flavopilosa (Brncic, 1972), a forest species of South America; and in D. pachea, a desert adapted species (Ward et al., 1975), to name a few. Variation in temperature and precipitation, these related to latitude and elevation, were shown to be correlated with changes in

the chromosomal constitution of the species. Although the environmental-karyotype correlations give supportive evidence that natural selection is operating, how those variables influence the fitness of the karyotype is not precisely understood.

In addition, an extensive study of the tropical species D. willistoni indicated no particular environmental variable was correlated with inversion heterozygosity (Da Cunha and Dobzhansky, 1954; Da Cunha et al., 1959). A positive correlation was shown to exist between the inversion heterozygosity of this species and environmental diversity, evaluated by a quantitative rating based on climate, competitors, and other biotic conditions. This led Da Cunha and Dobzhansky to conclude that, in this species, inversion heterozygosity is related to more efficient utilization of the complex, multi-faceted environment: the number of inversions in a population is determined by the number of different ways the species can interact with the local environment.

Viewing the problem from a different perspective, Carson (1955), working with D. robusta, suggested that the amount of chromatin available for recombination is regulated by inversion heterozygosity and this in turn is regulated by the quality of the environment. He proposed that an ecologically unfavorable environment would select for a more open recombinant karyotype in order to produce novel genotype every generation whereas in ecologically optimal habitat, there would be a selection for a karyotype with little recombination. In laboratory experiments, Carson (1958) found that homokaryotypic flies responded more rapidly to selection than did those heterozygous for gene arrangements. However,

Carson (1959) later clarified the point that homokaryotypy in marginal populations was probably the result of directional selection for specific adaptive properties associated with the inversions, and that the free recombination represented by homokaryotypy is a by-product of this selection. Once homokaryotypy is achieved, the more open genetic system allows selection to be more effective for adjusting to novel environmental conditions. He argued further that in central, ecologically optimal parts of the species' range, where the population is generally very large and outcrossed and where random drift rarely operates, a premium is placed on heterotic buffering and developmental homeostasis, which is maximized by genic and inversion heterozygosity. In contrast, ecologically marginal parts of the geographic range, populations are small and subject to drift and inbreeding, and there is directional selection for specific gene arrangements attuned to local ecological conditions.

One feature of Carson's "heteroselection--homoselection" model is a hypothesized reduction of allelic heterozygosity in marginal populations. Subsequently, this hypothesized decrease has been shown not to be the case in Drosophila (Ayala et al., 1974). However, Soulé (1973) proposed a theory involving models of gene regulation and epistasis which would uncouple structural and allelic heterozygosity. He further proposed that these epistatic gene combinations (good candidates to be included within inversions) would be continuously incorporated into the gene pool as the population becomes more finely tuned to its environment. Therefore, the amount of heterozygosity

would depend heavily upon time, as measured by the duration of occupation of a particular geographical area. At the same time he rejects any effect of environmental complexity or heterosis upon chromosomal polymorphisms.

The authors of the studies of D. pseudoobscura (Dobzhansky, 1970), D. willistoni (Da Cunha et al., 1959), D. flavopilosa (Brncic, 1972) and D. pachea (Ward et al., 1975) appear to be supporting the idea of karyotype selection influencing and adjusting inversion polymorphisms of those species, while Carson (1955, 1959) appears to support an interplay of genic selection in central populations and karyotype selection in marginal populations to account for the ecogeographic variability of inversion frequencies.

Lewontin (1957, 1974), on the other hand, emphasizes temporal instability in marginal populations while accepting elements of both hypotheses of Dobzhansky and Carson. Lewontin believes that the unstable and unpredictable environment, which characterizes ecologically marginal populations, is selecting different genotypes at different times, necessitating a karyotype more open to recombination in order to produce new combinations of genes. In central populations with predictable, spatially diverse environments, highly buffered and canalized phenotypes, characterized by generalized physiological and anatomical adaptations would be favored.

The common theme throughout all the models on the ecogeographical distribution of inversion polymorphisms concerns the central-marginal population structure of a species. This view of population

structure has been discussed at length by many authors, especially with regards to speciation (Mayr, 1954, 1963; Wallace, 1959; Grant, 1977; Carson, 1955; 1959, 1973, 1975). The main points may be summarized as follows: since a species faces a wide range of environmental conditions, the adaptive norm of the species, as determined by its prior evolutionary history, establishes not only a geographic and ecological boundary but also manifests itself in the geographic variation of important parameters of population structure and dynamics, such as population density, temporal density fluctuations, interdeme interactions, and density dependent and density independent mortality. Central populations are characterized by optimal environmental conditions (diverse ecological amplitude), spatio-temporally stable population density, predominance of density dependent selection, and significant interdeme interaction (migration and outcrossing). This would be reflected in the genetic structure of the population by heterkaryotypy, restricted gene recombination, and highly buffered and generalized physiological and anatomical adaptations. Marginal populations, on the other hand, are characterized by depauperate ecological conditions, predominance of density independent selection, and relatively great fluctuations in population size leading to periodic deme isolation, inbreeding, and extinction. The genetic structure of these populations would exhibit homokaryotypy, open gene recombination, and relatively specialized and novel physiological and anatomical adaptations.

In contrast to the utilization of inversion polymorphisms as a form of population adaptation, Wasserman (1960) proposed that

differentiation of the chromosomal constitution of neighboring, but semi-isolated, populations could also be important for local adaptation and promoting further geographic differentiation by prevention of breakdown of locally adapted gene complexes. The existence of this kind of population differentiation and decrease in population fitness due to gene flow has been verified by experimental hybridization of different geographic populations of Drosophila (Wallace, 1968). Other studies indicate inferiority of F₂ offspring of crosses in such measurements as DDT resistance (King, 1955), fecundity (Vetukhiv, 1956), viability (Vetukhiv, 1953), longevity (Vetukhiv, 1957), and developmental rates (Wallace, 1955). The proposal made by Wasserman (1960) was prompted by his analysis of the chromosome phylogeny of the mulleri complex of the repleta species group of Drosophila. In this case, one or more of six fixed inversions are distributed in twelve extant species in such a manner that each species must have descended from a single ancestral species made up of several semi-isolated populations.

Inversion Studies in the Sonoran Desert

One of the major criticisms in studies of the ecogeographic variation of inversion polymorphisms in Drosophila is that too little is known about the ecology and population dynamics of the species studied. However, Fellows and Heed (1972), Spieth and Heed (1972), and Ward et al. (1975) have pointed out the relative simplistic nature of the ecology of the common desert adapted Drosophila. In these species, numerous feeding and breeding sites can be located in the field and observations can be made of their entire life cycle, including

mating behavior and dispersal (Johnston and Heed, 1976), larval niche ecology (Mangan, 1978), as well as sampling the micro-organisms in the substrate, the larvae, and in the adult flies (Starmer et al., 1976; Heed et al., 1976).

After Ward et al. (1975) analyzed the cline of a single inversion system in D. pachea, a characteristic species of the Sonoran Desert, and reported the climatic and host plant factors correlated with it, a geographic survey of the cytology of a second cactiphilic species, Drosophila mojavensis Patterson and Crow was initiated. Mettler (1963) reported this species to be polymorphic for five inversions in two of its six chromosomes. This degree of inversion polymorphism places D. mojavensis among those species of the Repleta group with the highest frequency of heterozygosity (Heed, 1979, pers. comm; Wasserman, 1976, pers. comm.). This was thought to be significant because inversion polymorphisms are known to be less frequent in arid-adapted species of Drosophila (Wasserman, 1960; Stone, Guest and Wilson, 1960). The reason for this scarcity is thought to be related to the ephemeral nature of the available feeding and breeding sites (Heed and Russell, 1971; Spieth and Heed, 1972), leading to periodic extinction or bottlenecks of local populations with interdeme replacement. In the hot, arid environment of the Sonoran Desert, populations of Drosophila are allowed to persist only due to the production by microbial agents of moisture and nutrient rich necrotic tissue in many of the native cacti (Fellows and Heed, 1972).

The geographic range of Drosophila mojavensis is coincident with the combined distribution of its two primary host cacti,

Stenocereus (Machaerocereus) gummosus (Engelm.) Gibson and Horak on the peninsula of Baja California and Stenocereus (Lemaireocereus) thurberi (Engelm.) F. Buxbaum on mainland Mexico and southern Arizona (Figure 1). The species is reported to utilize Ferocactus acanthodes (Lemaire) Britton and Rose in southern California (Patterson, 1943). This distribution occupies a wide range of climatic and vegetational regimes (Figure 1), including the coastal chaparral which is in the San Pedro Martir province (Shreve, 1936; Hastings and Turner, 1965); seven desert sub-divisions as defined by Shreve and Wiggins (1964); the subtropical thorn scrub in southern Sonora, and Sinaloa; and the Cape region of Baja California (Shreve, 1937). The Cape region is considered (or lumped with) in the Giganta-Laguna Province of Hastings and Turner (1965).

D. mojavenis was divided into two races by Mettler (1963), the baja race located in Sonora, Sinaloa, and Baja California, and the mojavenis race, an isolated population in southern California. Subsequently, Zouros (1973), using electrophoretic data, and Zouros and d'Entremont (1974), using behavioral data, proposed separation of the peninsular and mainland populations into distinct subraces as well.

Drosophila mojavenis has also been reared from the columnar cacti, Carnegiea gigantea, Stenocereus (Rathbunia) alamoensis, Myrtillocactus cochal, and Pachycereus pringlei, as well as from its major host cacti. Considering the divergent biochemical constitution of those cacti (H. Kircher, 1978, pers. comm.), as well as the ability to maintain cultures for many years on standard laboratory medium, D. mojavenis proves itself to be widely tolerant of feeding and breeding

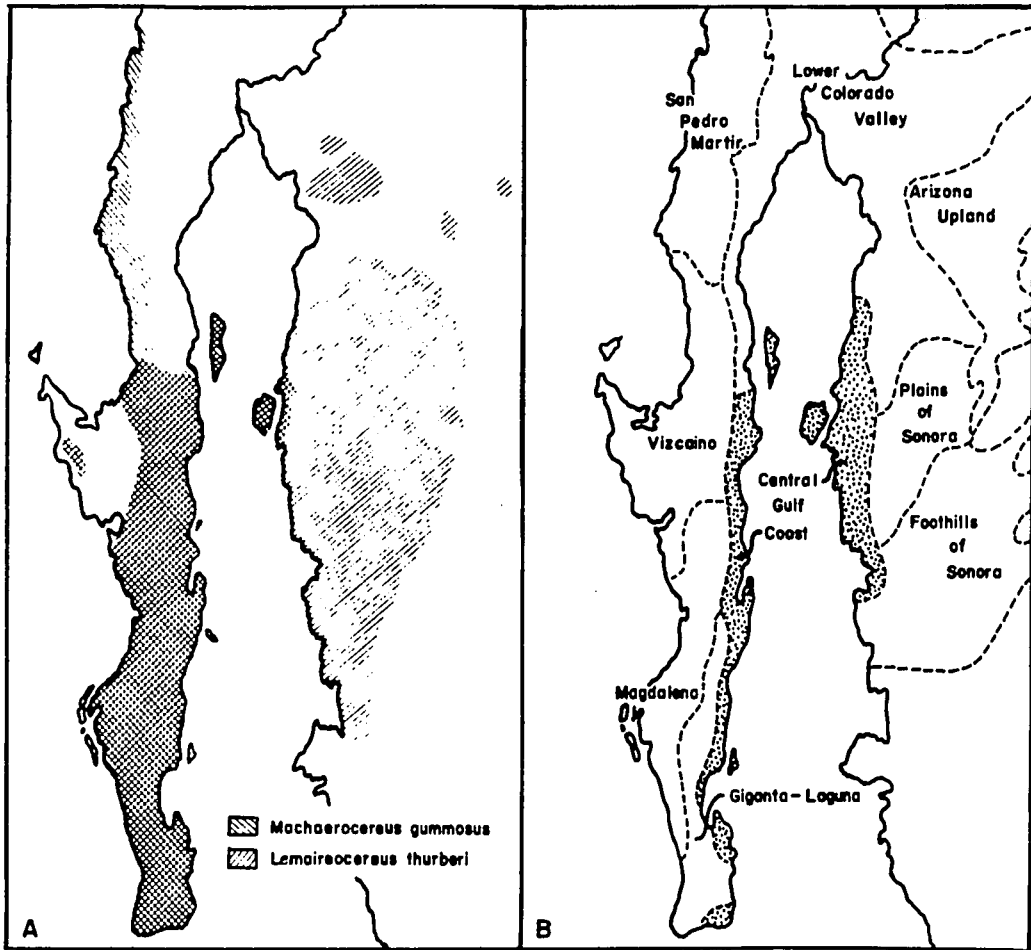


Figure 1. A. Geographic distribution of the primary host cacti, *Machaerocereus gummosus* and *Lemaireocereus thurberi*.
 B. The phytogeographic provinces of the Sonoran Desert.

substrates. In nature, however, this species restricts itself to its primary host cacti due to its poor competitive ability against other cactiphilic Drosophila on their respective host plants (Fellows and Heed, 1972; Mangan, 1978). At the same time, D. mojavenis shares its hosts, Machaerocereus and Lemaireocereus, with no other native cactiphilic Drosophila, most likely due to toxicity of certain biochemical compounds in the cacti (Mangan, 1978, pers. comm.).

When Mettler (1963) reported the inversion polymorphism of D. mojavenis from collections from Baja California and Sonora, Mexico, he designated the gene arrangements on the second chromosome as ST (Standard), LP (La Paz), and BA (Baja) and on the third chromosome, ST (Standard) and MU (Mulege) (Figure 2, p.15). Since then two more gene arrangements, SL (San Lucas) and SI (San Ignacio) have been discovered on the second chromosome and the present report documents the frequencies of all the inversions thus far discovered over the major geographic distribution of the species.

The conclusions reached following the preliminary geographic survey of the cytology of D. mojavenis (Johnson, 1973) were that the five known inversions were widespread over the species' range, but seemed to be fixed in various combinations in isolated demes distributed through the Sonoran Desert. Restriction of migration and inbreeding were considered to be the factors most important in developing this pattern. This agreed well with the hypothesis of Heed and Russell (1971) and Spieth and Heed (1972). However, continued field work and karyotype analysis of new populations indicated that these conclusions

were premature. Instead, there appeared geographic clines and geographic centers of inversion combinations which corresponded to observable ecological variables. The purpose of the present study is to define these relationships more clearly and to attempt to understand the ecogeography of the inversion polymorphism of D. mojavensis in the light of its well known ecology. This is important not only to visualize why D. mojavensis is more highly polymorphic than other repletas, but also to understand the working relationship between its basic reproductive and feeding ecology and its population dynamics and cytogenetics, which may shed more light on the understanding of inversions polymorphisms in general. There is no other species of Drosophila reported which allows such detailed study of all these aspects of its population biology.

MATERIALS AND METHODS

Adult flies from natural populations of Drosophila mojavensis were obtained from 39 localities in southern Arizona and Sonora, Sinaloa, and Baja California, Mexico. The collections were made from Spring, 1971, to Spring of 1976. Most of the population samples were collected by locating rotting arms of the host cacti, either Machaerocereus or Lemaireocereus, and aspirating the adult flies from the rots in the early morning and late evening. If adults were not available, rotting arms of the cactus were removed and wrapped in newspaper and returned to the laboratory, where adults could be reared from larvae within the rots.

Adult females collected in the field were isolated into separate vials in the laboratory at room temperature containing 15-20 ml of laboratory medium consisting of banana, agar, and yeast, supplemented with cactus powder derived from dried Machaerocereus. Adults reared from cactus rots were randomly pair-mated, one male, one female, and the progeny reared under the same conditions. One third instar larva was chosen at random from each vial and salivary glands were dissected out, fixed, and stained in 1% natural orcein in lactoacetic acid solution 1:1 5-10 minutes and squashed directly on a slide. The polytene chromosomes were then viewed with a standard light microscope with oil immersion.

The inversion designations used by Mettler (1963) and in the present report, 2-ST, 2-LP, 3-ST, and 3-MU, correspond to 2s, 2q⁵, 3d, and 3y respectively in Wasserman's classification (1960, 1962, and pers. comm. 1976). Wasserman has not given 2-BA or 2-SL a designation. ST is a single inversion removed from the hypothetical 2abcfghqr. LP is derived from and overlaps ST and the shorter inversions, BA and SL, are derived from and included within LP (Figure 2). However, BA and SL have not been recorded to be on the same homologue; therefore the four inversions may be treated statistically as though they were alleles at a single locus. On the third chromosome, ST (3d) is the ancestral arrangement and MU (3y) is a centrally located medium length inversion derived from ST (Figure 2).

The frequency of each gene arrangement was calculated from the observed karyotype frequencies. From the calculated inversion frequencies, an estimate of heterozygosity was determined for both the second and third chromosomes by the formula $h = 1 - X_i^2$, where X_i is the frequency of the i^{th} gene arrangement. The overall chromosome heterozygosity (H) for each collection is the arithmetic mean of the two chromosome estimates.

In all tables and figures N refers to the number of chromosomes identified per sample. This is usually twice the number of larvae examined. To estimate the annual temperature range (TMR) at each of the collection localities, the lowest monthly mean temperature and the highest monthly mean temperature were obtained from Hastings and Humphrey (1969) and the difference was calculated.

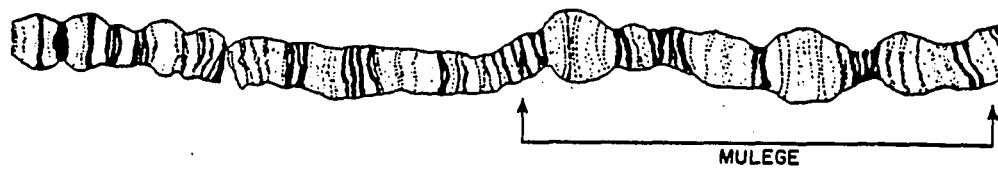
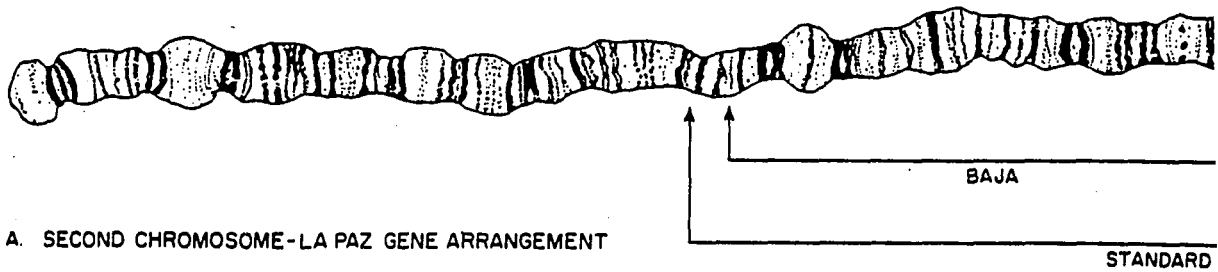
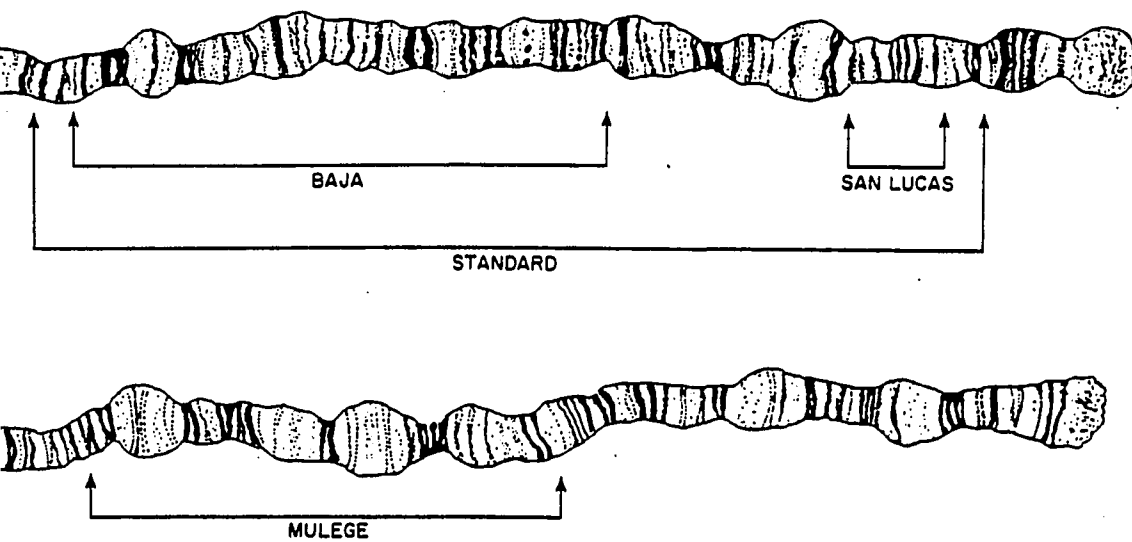


Figure 2. A cytological map showing the banding sequence and break-points of the common paracentric inversions, the second and third chromosomes of D. mojavenis.



ending sequence and break-
inversions, the second
vensis.

To prepare the inversion frequency isocline maps (Figures 6, 7, and 9, pages 28, 29, and 34, respectively) lines were drawn connecting those geographic areas whose populations have similar inversion frequencies (10% range). In regions where frequencies changed rapidly with few data points across the cline, lines were arbitrarily drawn to give a smooth transition.

RESULTS

The results of the salivary gland chromosome analysis are presented in Table 1. From the number of each karyotype observed, the relative frequency of each chromosome was calculated and is presented in Table 2. The inversion frequencies are graphically depicted in Figures 3, 4, and 5 for the second chromosome and Figures 6 and 7 for the third chromosome. Using the inversion frequencies estimates of heterozygosity were calculated for each chromosome and are presented in Table 3. Of the ten possible karyotypes expected from the four arrangements of the second chromosome (ST, LP, BA, SL) and the three possible from the third chromosome, all were identified in samples from natural populations except SL/SL. This previously undescribed short, basal inversion has been found in eight localities in Baja California and on Tiburon Island and appears to be restricted to the Gulf Coast region. The other new chromosome, San Ignacio (SI), is compound and was discovered by Wasserman (pers. comm, 1976) in a laboratory culture (A367) derived from a collection made in March, 1972, near San Ignacio, Baja California. When this culture was initially analyzed for inversion frequencies, the chromosome was not observed, and when other cultures from early collections were re-analyzed, the chromosome was found in one from San Lucas, Baja California (A422). Recent collections (A566) from the same region also indicated the presence of the chromosome in very low frequencies

Table 1. Number of each karyotype observed in a collection.--N is the total number of chromosomes observed.

1. El Socorro (A519) N = 132	ST/ST MU/MU 27
LP/LP ST/ST 44	ST/ST ST/MU 6
LP/LP ST/MU 13	BA/BA ST/MU 1
LP/BA ST/ST 7	LP/BA ST/MU 1
LP/BA ST/MU 2	LP/ST MU/MU 5
	ST/BA MU/MU 16
2. San Borja (A350) N = 54	ST/BA ST/MU 1
LP/LP ST/ST 1	ST/SL MU/MU 2
LP/LP MU/MU 4	
LP/LP ST/MU 1	5. San Ignacio (A566) N = 84
ST/ST ST/ST 1	LP/LP ST/MU 1
ST/ST MU/MU 2	ST/ST MU/MU 24
ST/ST ST/MU 1	LP/BA MU/MU 2
LP/ST ST/ST 4	LP/BA ST/MU 1
LP/ST MU/MU 10	LP/ST ST/MU 1
LP/ST ST/MU 3	LP/ST MU/MU 3
ST/BA MU/MU 1	ST/BA MU/MU 9
	LP/SL MU/MU 1
3. Punta Preita (A420) N = 106	
LP/LP MU/MU 11	6. Tres Virgenes (A567) N = 100
ST/ST MU/MU 3	LP/LP ST/ST 7
BA/BA MU/MU 4	LP/LP MU/MU 4
LP/ST MU/MU 3	LP/LP ST/MU 7
LP/BA MU/MU 20	ST/ST ST/ST 1
LP/BA ST/MU 2	ST/ST MU/MU 2
ST/BA MU/MU 3	ST/ST ST/MU 3
ST/BA ST/MU 2	ST/LP ST/MU 8
	ST/LP MU/MU 8
4. El Barril (A570) N = 54	LP/BA MU/MU 2
LP/LP MU/MU 8	LP/BA ST/ST 1
LP/LP ST/MU 1	LP/BA ST/MU 4
ST/ST MU/MU 8	ST/BA ST/MU 1
LP/ST MU/MU 8	LP/SL ST/MU 1
LP/ST ST/MU 1	LP/SL MU/MU 1
LP/SL MU/MU 1	
	7. San Lucas (A422) N = 132
5a. San Ignacio (A367) N = 54	LP/LP MU/MU 3
LP/LP MU/MU 2	LP/LP ST/MU 4
ST/ST MU/MU 16	ST/ST ST/MU 1
LP/ST MU/MU 4	ST/ST ST/ST 3
LP/BA MU/MU 4	ST/ST MU/MU 10
LP/BA ST/MU 1	LP/ST MU/MU 18
	LP/ST ST/MU 7
5b. San Ignacio (A421) N = 126	LP/BA ST/MU 1
LP/LP MU/MU 2	LP/BA MU/MU 1
ST/ST ST/ST 2	LP/SL MU/MU 1

Table 1, Continued. Number of each karyotype observed in a collection.

LP/SL ST/MU	3		
ST/BA ST/ST	1		
ST/BA MU/MU	4		
ST/SL MU/MU	5		
ST/SL ST/MU	1		
BA/SL MU/MU	2		
8. Punta Concepcion (A352) N = 94			
LP/LP ST/ST	3		
LP/LP MU/MU	3		
LP/LP ST/MU	6		
ST/ST ST/ST	5		
ST/ST MU/MU	11		
ST/ST ST/MU	5		
ST/LP ST/MU	3		
ST/LP MU/MU	7		
ST/LP ST/ST	3		
ST/BA MU/MU	1		
9. Bahia Coyote (A427) N = 64			
LP/LP ST/ST	2		
LP/LP MU/MU	4		
LP/LP ST/MU	2		
ST/ST MU/MU	1		
ST/ST ST/MU	1		
LP/ST ST/ST	4		
LP/ST MU/MU	6		
LP/ST ST/MU	9		
LP/SL MU/MU	2		
ST/SL MU/MU	1		
10. Puerto Escondido (A428) N = 68			
LP/LP ST/ST	3		
LP/LP ST/MU	3		
ST/ST ST/ST	7		
ST/ST ST/MU	4		
LP/ST ST/ST	8		
LP/ST MU/MU	1		
LP/ST ST/MU	6		
ST/SL ST/ST	2		
11. Loreto (A385) N = 106			
LP/LP ST/ST	5		
ST/ST ST/ST	29		
ST/ST ST/MU	4		
LP/ST ST/ST	14		
LP/ST ST/MU	1		
12. Isla San Jose (A593) N = 54			
ST/ST ST/ST	16		
ST/ST ST/MU	2		
LP/ST ST/ST	5		
ST/BA ST/ST	4		
13. Sierra Giganta (A429) N = 70			
ST/ST ST/ST	25		
ST/ST ST/MU	1		
LP/ST ST/ST	6		
LP/ST ST/MU	2		
ST/SL ST/ST	1		
14. La Presa (A376) N = 102			
ST/ST ST/ST	50		
ST/ST ST/MU	2		
15. Villa Insurgentes (A430) N = 60			
ST/ST ST/ST	15		
ST/ST MU/MU	3		
ST/ST ST/MU	12		
16. Santa Rita (A564) N = 64			
LP/LP ST/ST	1		
ST/ST ST/ST	26		
ST/ST ST/MU	3		
ST/BA ST/ST	2		
17. S. Santa Rita (A431) N = 80			
ST/ST ST/ST	29		
ST/LP ST/ST	4		
ST/LP ST/MU	7		
18. San Augustin (A563) N = 82			
LP/LP ST/ST	9		
LP/LP ST/MU	5		
ST/ST ST/ST	3		
ST/ST ST/MU	2		
LP/ST ST/ST	14		
LP/ST ST/MU	3		
LP/BA ST/ST	5		
19. S. San Augustin (A587) N = 70			
LP/LP ST/ST	15		
LP/LP MU/MU	4		
LP/LP ST/MU	8		
LP/ST ST/ST	7		

Table 1, Continued. Number of each karyotype observed in a collection.

LP/ST ST/MU	1		
20. W. La Paz (A560) N = 86			
LP/LP ST/ST	5		
LP/LP MU/MU	11		
LP/LP ST/MU	19		
LP/ST ST/ST	1		
LP/ST MU/MU	1		
LP/ST ST/MU	1		
LP/BA ST/ST	1		
LP/BA MU/MU	2		
LP/SL MU/MU	2		
21. San Bartolo (A561) N = 56			
LP/LP MU/MU	19		
LP/LP ST/MU	8		
LP/ST ST/MU	1		
22. S. San Bartolo (A433) N = 80			
LP/LP MU/MU	36		
LP/ST MU/MU	4		
23. Punta Pescadero (A374) N = 78			
LP/LP MU/MU	30		
LP/LP ST/MU	9		
24. Santiago (A597) N = 82			
LP/LP MU/MU	35		
LP/LP ST/MU	4		
LP/SL MU/MU	1		
LP/SL ST/MU	1		
25. Santa Rosa Mtns (A572) N = 72			
LP/LP ST/ST	36		
26. O.P. Nat'l Mon. (A345) N = 30			
LP/LP ST/ST	15		
27. Altar Valley (A319) N = 58			
LP/LP ST/ST	29		
28. Caborca (A316) N = 44			
LP/LP ST/ST	22		
29. Punta Libertad (A514) N = 56			
LP/LP ST/ST	28		
30. Desemboque (A361) N = 56			
LP/LP ST/ST	19		
LP/LP ST/MU	7		
LP/ST ST/ST	2		
Desemboque (A366) N = 102			
LP/LP ST/ST	46		
LP/LP ST/MU	4		
LP/ST ST/MU	1		
Desemboque (A388) N = 100			
LP/LP ST/ST	46		
LP/LP ST/MU	2		
LP/ST ST/ST	2		
Desemboque (A509) N = 100			
LP/LP ST/ST	29		
LP/LP ST/MU	2		
ST/ST ST/ST	1		
LP/ST ST/ST	11		
LP/ST ST/MU	3		
LP/BA ST/ST	3		
LP/BA ST/MU	1		
31. Campo Vibora (A510) N = 100			
LP/LP ST/ST	41		
LP/LP ST/MU	9		
32. Rancho del Puerto (A580) N = 84			
LP/LP ST/ST	39		
LP/LP ST/MU	3		
33. Punta Chuecha (A581) N = 42			
LP/LP ST/ST	18		
LP/ST ST/ST	2		
LP/ST ST/MU	1		
34. Bahia Kino (A511) N = 46			
LP/LP ST/ST	17		
LP/LP ST/MU	6		
35. San Carlos (A512) N = 100			
LP/LP ST/ST	32		
LP/LP ST/MU	18		

Table 1, Continued. Number of each karyotype observed in a collection.

36.	Isla San Pedro (A513)	N = 100
	LP/LP ST/ST	50
37.	Isla Tiburon (A506)	N = 80
	LP/LP ST/ST	27
	LP/LP ST/MU	3
	LP/ST ST/ST	7
	LP/ST ST/MU	2
	ST/SL ST/MU	1
38.	Los Mochis (A337)	N = 110
	LP/LP ST/ST	50
	LP/LP ST/MU	5
39.	Topolobampo (A559)	N = 4
	LP/LP ST/ST	2

Table 2. Collection data and chromosomal inversion frequencies of D. mojavensis.

Name	Locality Region ¹	Collection		N ³	Second Chromosome				Third Chromosome		
		Number ²	Date		LP	ST	BA	SL	ST	MU	
Baja California Norte											
1	El Socorro	(SPM)	A519	7-74	132	0.93	0.00	0.07	0.00	0.89	0.11
2	San Borja	(Viz)	A350*	11-71	64	0.52	0.46	0.02	0.00	0.30	0.70
3	Punta Prieta	(Viz)	A420	2-74	106	0.44	0.18	0.38	0.00	0.04	0.96
4	El Barril	(CGC)	A570	3-75	54	0.52	0.46	0.00	0.02	0.02	0.98
Baja California Sur											
5	San Ignacio a	(Trans)	A367*	4-72	54	0.24	0.67	0.09	0.00	0.02	0.98
	San Ignacio b	(Trans)	A421	2-74	126	0.08	0.74	0.16	0.02	0.10	0.90
	San Ignacio c	(Trans)	A566+	11-74	84	0.11	0.74	0.15	0.00	0.03	0.97
6	Tres Virgenes	(CGC)	A567+	11-74	100	0.61	0.29	0.08	0.02	0.42	0.58
7	San Lucas	(CGC)	A422+	2-74	132	0.35	0.49	0.07	0.09	0.20	0.80
8	Punta Concepcion	(CGC)	A352*	11-71	94	0.39	0.60	0.01	0.00	0.38	0.62
9	Bahia Coyote	(CGC)	A427	4-74	64	0.58	0.38	0.00	0.04	0.37	0.63
10	Puerto Escondido	(CGC)	A428	4-74	68	0.40	0.57	0.00	0.03	0.78	0.22
11	Loreto	(CGC)	A385*	3-72	106	0.24	0.76	0.00	0.00	0.95	0.05
12	Isla San Jose	(CGC)	A593*	3-76	60	0.09	0.83	0.07	0.00	0.96	0.04
13	Sierra Giganta	(Gig)	A429*	4-74	70	0.11	0.88	0.00	0.01	0.96	0.04
14	La Presa	(Gig)	A376*	3-72	102	0.00	1.00	0.00	0.00	0.98	0.02
15	Villa Insurgentes	(Mag)	A430	4-74	60	0.00	1.00	0.00	0.00	0.70	0.30
16	Santa Rita	(Mag)	A564	11-74	64	0.03	0.94	0.03	0.00	0.96	0.04
17	50 km S. Santa Rita	(Mag)	A431	4-74	80	0.05	0.95	0.00	0.00	0.91	0.09
18	San Augustin	(Trans)	A563	11-74	82	0.61	0.33	0.06	0.00	0.88	0.12
19	10 km S. San Augustin	(Trans)	A587	3-76	70	0.89	0.11	0.00	0.00	0.76	0.24
20	22 km W. La Paz	(Trans)	A560	11-74	86	0.92	0.03	0.03	0.02	0.40	0.60
21	San Bartolo	(Cape)	A561	11-74	56	0.96	0.04	0.00	0.00	0.16	0.84
22	10 km S. San Bartolo	(Cape)	A433	4-74	80	0.95	0.05	0.00	0.00	0.00	1.00
23	Punta Pescadero	(Cape)	A374*	3-72	78	1.00	0.00	0.00	0.00	0.11	0.89
24	Santiago	(Cape)	A597	3-76	82	0.98	0.00	0.00	0.02	0.06	0.94

Table 2, Continued.

Name	Locality		Collection		N ³	Second Chromosome				Third Chromosome	
	Region ¹		Number ²	Date		LP	ST	BA	SL	ST	MU
Arizona											
25	Santa Rosa Mtns.	(Ariz)	A572	2-75	72	1.00					1.00
26	Organ Pipe Nat'l Mon.	(Ariz)	A345*	9-71	30	1.00					1.00
Sonora											
27	Altar Valley	(LC)	A319	4-71	58	1.00					1.00
28	Caborca	(LC)	A316	4-71	44	1.00					1.00
29	Punta Libertad	(CGC)	A514*	4-74	56	1.00					1.00
30	Desemboque a	(CGC)	A361*	12-71	56	0.96	0.04	0.00	0.00	0.88	0.12
	Desemboque b	(CGC)	A366*	3-72	102	0.99	0.01	0.00	0.00	0.95	0.05
	Desemboque c	(CGC)	A388	3-72	100	0.98	0.02	0.00	0.00	0.98	0.02
	Desemboque d	(CGC)	A509	3-74	100	0.78	0.18	0.04	0.00	0.94	0.06
31	Campo Vibora	(CGC)	A510	3-74	100	1.00	0.00	0.00	0.00	0.91	0.09
32	Rancho del Puerto	(CGC)	A580	7-75	84	1.00	0.00	0.00	0.00	0.97	0.03
33	25 km N. Chuecha	(CGC)	A581	7-75	42	0.93	0.07	0.00	0.00	0.95	0.05
34	Bahia Kino	(CGC)	A511	3-74	46	1.00	0.00	0.00	0.00	0.87	0.13
35	San Carlos	(CGC)	A512	3-74	100	1.00	0.00	0.00	0.00	0.82	0.18
36	Isla San Pedro Nolasco	(CGC)	A513	3-74	100	1.00	0.00	0.00	0.00	1.00	0.00
37	Isla Tiburon	(CGC)	A506*	11-74	84	0.87	0.12	0.00	0.01	0.93	0.07
Sinaloa											
38	Los Mochis	(TF)	A337	11-71	110	1.00	0.00	0.00	0.00	0.96	0.04
39	Topolobampo	(TF)	A559	11-74	4	1.00	0.00	0.00	0.00	1.00	0.00

¹Phytogeographic provinces of Shreve and Wiggins (1964). SPM = San Pedro Martir; Viz = Vizcaino; CGC = Central Gulf Coast; Gig = Sierra Giganta; Mag = Magdalena; Trans = transition zone between Magdalena and Cape; Ariz = Arizona upland; LC = Lower Colorado Valley; TF = Thorn scrub forest.

Table 2, Continued.

²Cultures and chromosome analyses derived from field captured isofemales except where indicated by an (*), which were derived from flies reared from cactus rots. + = S1 arrangement also present.

³N = number of chromosomes observed per collection.

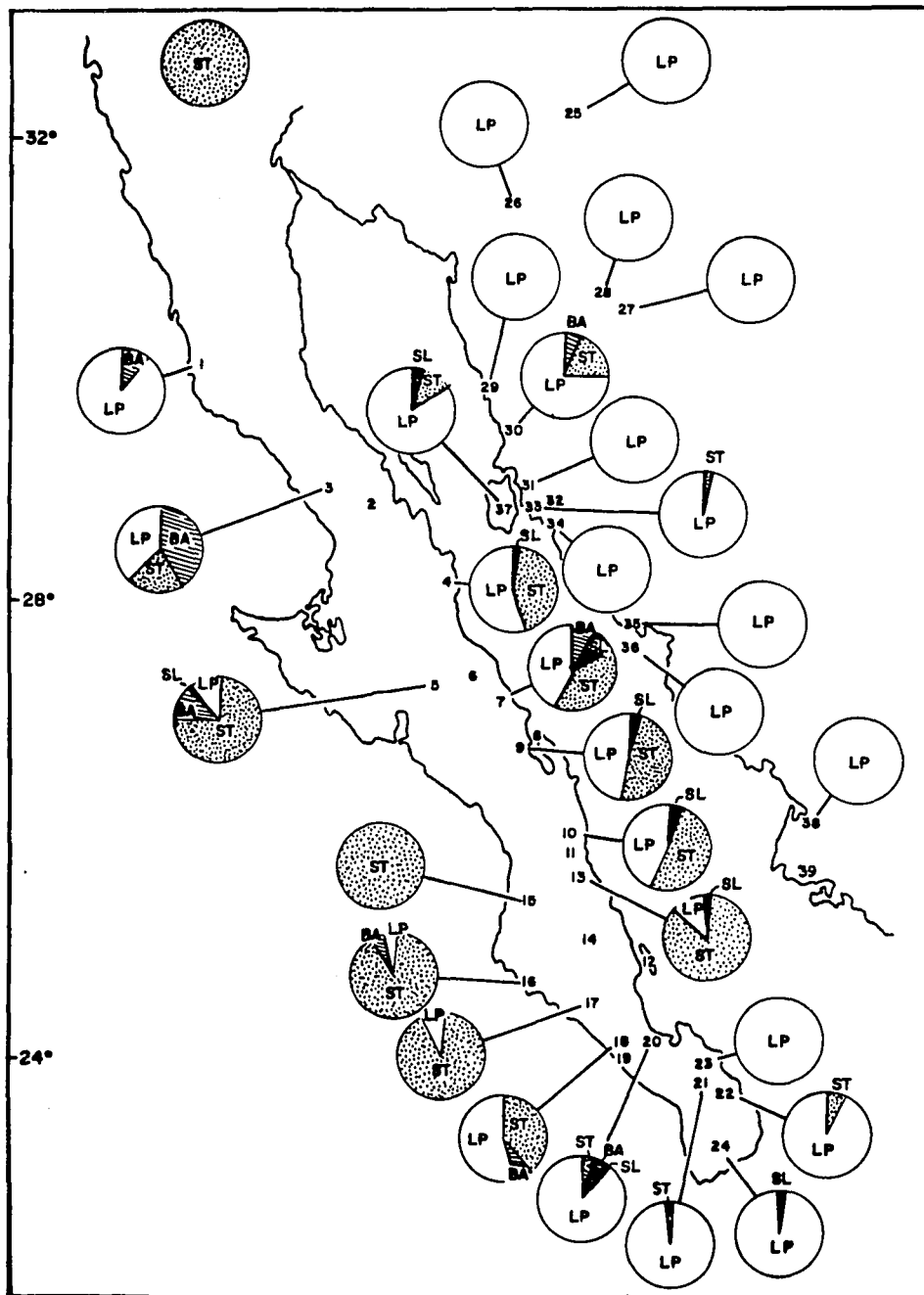


Figure 3. Graphic representation of the frequencies of the gene arrangements of the second chromosome of *D. mojavensis* from 28 localities in Baja California, Sonora, and Sinaloa, Mexico and from 3 localities in Arizona and California, USA.

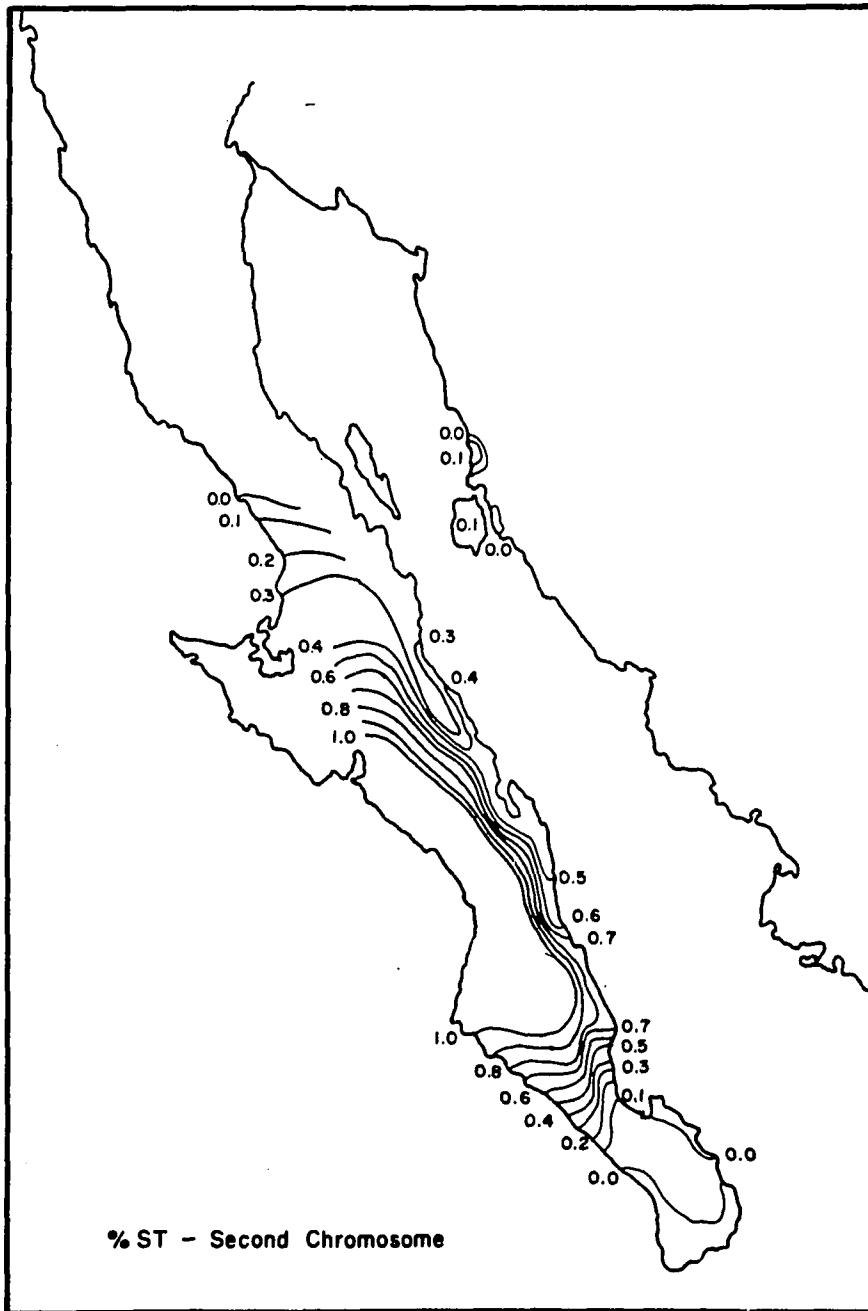


Figure 4. Isocline map of the frequency of the ST arrangement of the second chromosome.

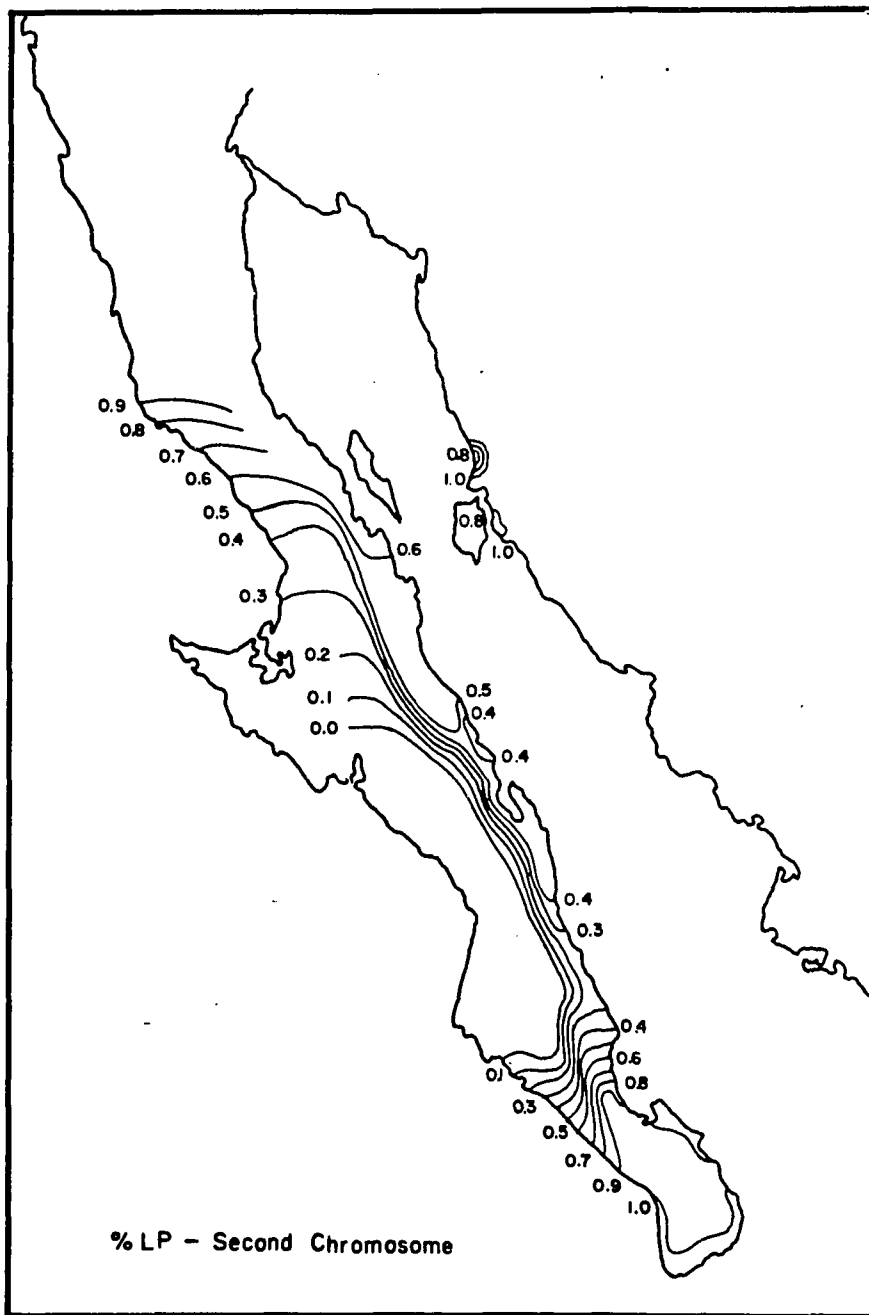


Figure 5. Isocline map of the frequency of the LP arrangement of the second chromosome.

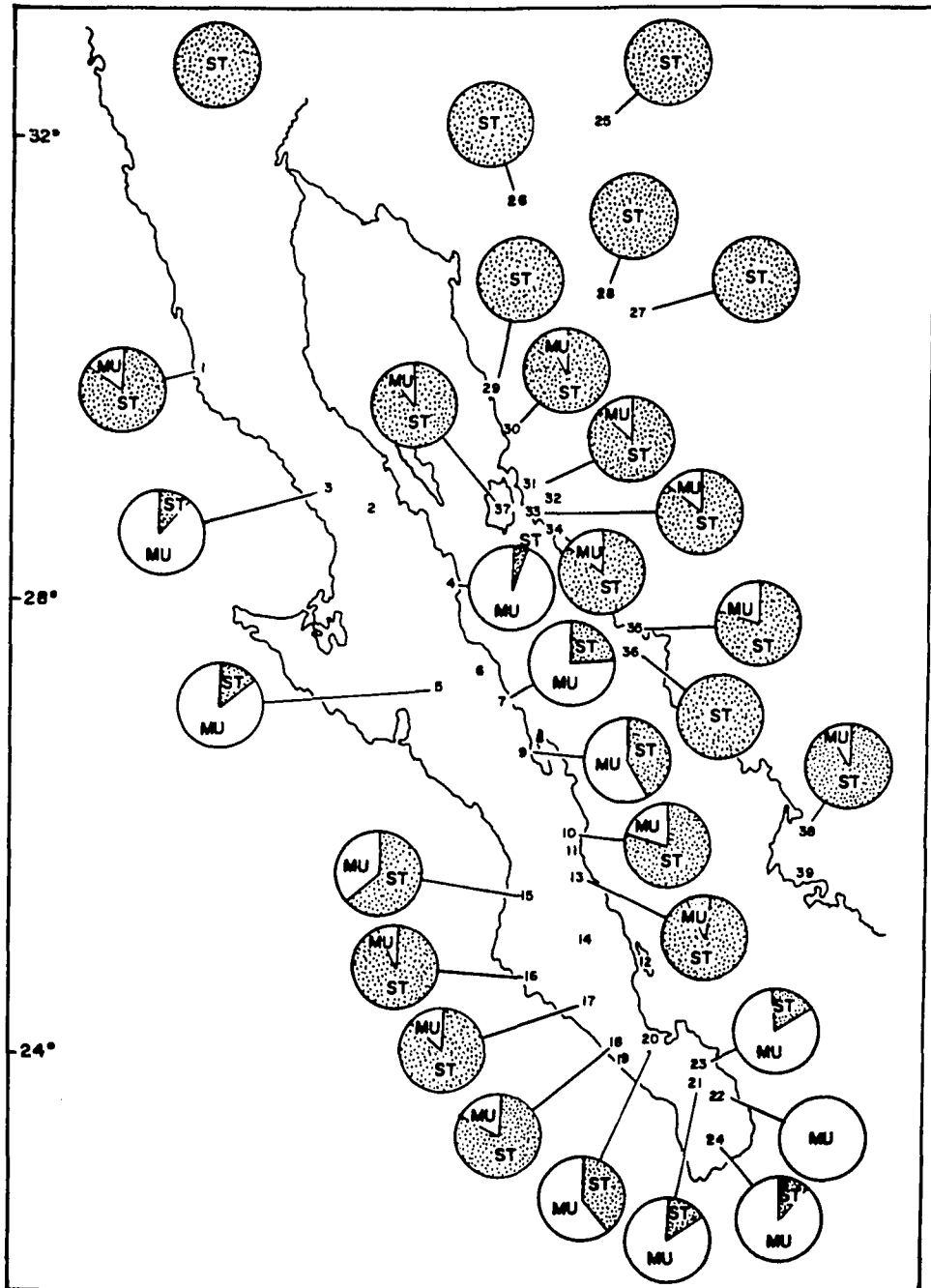


Figure 6. Graphic representation of the frequencies of the gene arrangements of the third chromosome of *D. mojavensis* from 28 localities in Baja California, Sonora and Sinaloa, Mexico and from 3 localities in Arizona and California, USA.

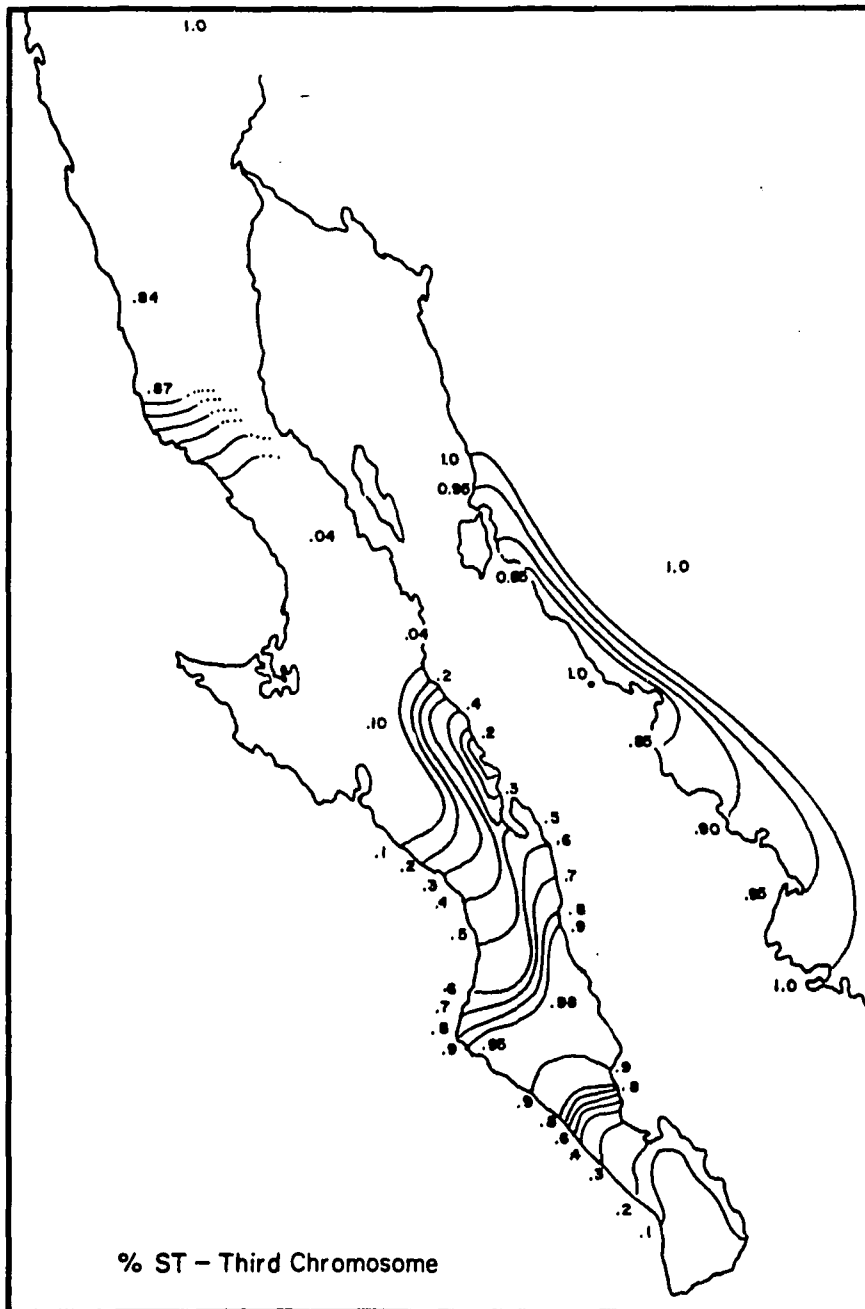


Figure 7. Isocline map of the frequency of the ST arrangement of the third chromosome.

Table 3. Inversion heterozygosity estimates of second (h_2) and third (h_3) chromosomes and their mean (H). ($h = 1 - \sum x_i^2$). TMR = (mean high temperature) - (mean low temperature). From Hastings and Humphrey (1969).

Locality	h_2	h_3	H	TMR	Locality	h_2	h_3	H	TMR
<u>San Pedro Martir</u>					<u>Cape</u>				
1 El Socorro	0.13	0.20	0.16	5.9	21 San Bartolo	0.08	0.27	0.18	10.7
<u>Vizcaino</u>					22 10 km S. San Bartolo	0.09	0.00	0.05	10.7
2 San Borja	0.52	0.42	0.47	11.1	23 Punta Pescadero	0.00	0.20	0.10	10.7
3 Punta Prieta	0.63	0.08	0.36	11.4	24 Santiago	0.04	0.11	0.08	13.5
<u>Transition zone</u>					<u>Arizona Upland</u>				
5 San Ignacio a	0.49	0.04	0.27	12.4	25 Santa Rosa Mtns	0.00	0.00	0.00	20.8
San Ignacio b	0.42	0.18	0.30	12.4	26 Organ Pipe Nat'l Mon.	0.00	0.00	0.00	20.8
San Ignacio c	0.42	0.06	0.24	12.4	<u>Lower Colorado Valley</u>				
<u>Central Gulf Coast</u>					27 Altar Valley	0.00	0.00	0.00	20.0
4 El Barril	0.52	0.04	0.28	15.3	28 Caborca	0.00	0.00	0.00	20.0
6 Tres Virgenes	0.54	0.49	0.51	15.3	<u>Sonoran Central Gulf Coast</u>				
7 San Lucas	0.62	0.32	0.47	16.3	29 Punta Libertad	0.00	0.00	0.00	17.3
8 Punta Concepcion	0.49	0.47	0.48	-	30 Desemboque a	0.08	0.21	0.15	18.0
9 Bahia Coyote	0.52	0.47	0.50	16.2	Desemboque b	0.02	0.10	0.06	18.0
10 Puerto Escondido	0.51	0.34	0.42	15.0	Desemboque c	0.04	0.04	0.04	18.0
11 Loreto	0.36	0.09	0.22	14.1	Desemboque d	0.36	0.11	0.24	18.0
12 Isla San Jose	0.30	0.08	0.19	12.1	31 Campo Vibora	0.00	0.16	0.08	-
<u>Sierra Giganta</u>					32 Rancho del Puerto	0.00	0.06	0.03	-
13 Sierra Giganta	0.21	0.08	0.14	14.9	33 25 km N. Chuecha	0.13	0.10	0.12	-
14 La Presa	0.00	0.04	0.02	14.9	34 Bahia Kino	0.00	0.23	0.12	-
<u>Magdalena</u>					35 San Carlos	0.00	0.30	0.15	13.1
15 Villa Insurgentes	0.00	0.42	0.21	12.4	36 Isla San Pedro Nolasco	0.00	0.00	0.00	-
16 Santa Rita	0.11	0.08	0.10	11.6	37 Isla Tiburon	0.23	0.13	0.18	-
17 50 km S. Santa Rita	0.09	0.16	0.13	12.0	<u>Sinoloan thorn scrub forest</u>				
<u>Transition zone</u>					38 Los Mochis	0.00	0.08	0.04	13.8
18 San Augustin	0.52	0.21	0.37	7.8	39 Topolobampo	0.00	0.00	0.00	13.8
19 10 km S. San Augustin	0.20	0.36	0.28	7.8	<u>Lower Colorado Valley</u>				
20 22 km W. La Paz	0.15	0.48	0.32	11.8	*Southern California	0.00	0.00	0.00	-

*(Wasserman, personal communication)

(1%). This chromosome is interesting in that it is derived via three paracentric inversions from the ancestral, hypothetical chromosome (2abcfghqr), which also gave rise to the Standard (ST) arrangement (Wasserman, 1977, pers. comm.) via one paracentric inversion. The proposed phylogeny for the arrangements of the second chromosome is presented in Figure 8. Hereafter, the SI chromosome is not included in the analysis which follows.

Temporal Variation

At localities where collections were made more than once, such as at San Ignacio, Baja California, and Desemboque, Sonora, some temporal change in inversion frequencies can be noted. The amount of change is small, and the number of successive samples is small, therefore, any conclusions are tentative.

At San Ignacio from spring, to fall (A421, A566) inversion frequencies in the second chromosome were identical, but in the third chromosome, the MU arrangement increased by 7%. At Desemboque (A361, A366, A388) the same variation in direction and magnitude may be noted (Table 2).

Over the five year study, long term changes in inversion constitution involve the minor arrangements, BA and SL. At San Ignacio from spring, 1972 (A376) to spring, 1974 (A421), BA increased from 7% to 14% with a corresponding decrease of ST. BA also became part of the Desemboque polymorphism from Winter, 1971, (A361, A366) to spring, 1974 (A509) at a frequency of 4%.

The other long term change in inversion frequencies was the appearance of the SL arrangement on the second chromosome. After its discovery in populations only on the Gulf Coast of the peninsula, (A421, A422, A427, A428) during the spring, 1974, it was later found in the Fall near La Paz (A560). Farther south, it had then not yet appeared (A561), but by spring, 1976, SL was found in the Cape region (A597).

Geographic Variation

Figures 3, 4, and 5 and Tables 2 and 3 illustrate that five categories of inversion polymorphism may be differentiated in the geographic distribution of the second chromosome. (1) Highly heterozygous populations occupy the Central Gulf Coast and portions of the Vizcaino region of Baja California. (2) Predominately homozygous LP populations occupy the Cape region south of La Paz. (3) There is a gradual exchange of predominately ST populations in the Magdalena plains of the peninsula through the heterozygous LP, ST, and BA populations in the Vizcaino region to predominately LP populations in the San Pedro Martir region. This situation is topographically separated from the previously described heterozygous populations by the Sierra de la Giganta. (4) Homozygous LP populations occupy southern Arizona, Sonora, and Sinaloa, with the exception of the limited populations in the Desemboque area west of the Sierra Seri in Sonora near Tiburon Island (Figure 9). (5) Homozygous ST populations are found in the Colorado Desert of southern California.

In contrast to the widespread distribution and high frequencies of LP and ST, the shorter and more derived arrangements on the second

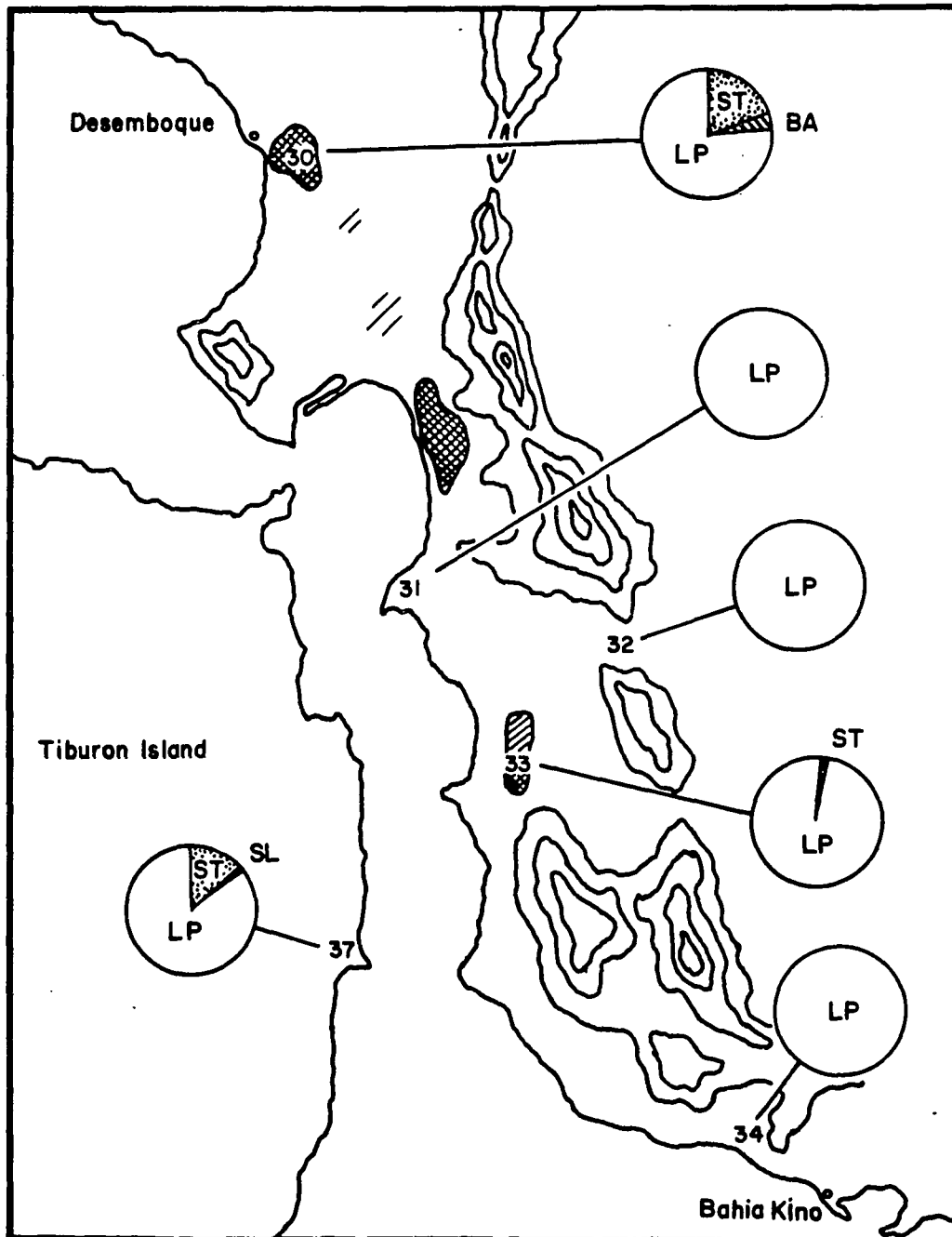


Figure 9. Graphic representation of the frequencies of gene arrangements of the second chromosome in populations west of the Sierra Seri and Isla Tiburon, Sonora, Mexico.

chromosome, BA and SL, have a more localized distribution and are relatively infrequent. BA is most abundant (6%-36%) in the Vizcaino region decreasing both northward and southward. It is present again in the narrow isthmus north of the Cape region and on Isla San Jose. From population samples, it appears that the distribution of BA is discontinuous east of the Sierra de la Giganta, but possibly it is continuous along the Pacific coast. BA is also present in some populations west of the Sierra Seri in Sonora.

SL has a distribution relatively confined to the Gulf Coast region of the peninsula from immediately north of La Paz (A560) to El Barril (A570), as well as on Tiburon Island. This short inversion was not discovered until the spring of 1974, even though four previous collections were made in this region (Johnson, 1973).

The geographic pattern exhibited by the frequencies of the arrangements of the third chromosome is similar to in some respects but distinct from in others the pattern of the arrangements of the second chromosome (Figures 7 and 8 and Tables 2 and 3). The important similarities are the complementary karyotypes between the Cape and the Magdalena regions, a north-south clinal exchange of the arrangements, and homozygosity in southern California, northern Baja California, and in Sonora and southern Arizona. The important distinctions are: (1) little east-west differentiation across the Sierra de la Gigante; (2) relative homozygosity in the Vizcaino region; (3) replacement of karyotypes between the Vizcaino and the San Pedro Martir regions, in contrast to the replacement occurring between the San Pedro Martir and southern California as observed in the second chromosome, and finally,

(4) the presence of heterokaryotypy in non-Machaerocereus populations along coastal Sonora (to be discussed later).

The similarities and distinctions between the second and third chromosomes can be best appreciated by comparing Figures 3 and 6 and Figures 4 and 5 with Figure 7.

Table 4 lists the average frequencies for each gene arrangement in populations of each phytogeographic province. The mean inversion heterozygosity is also presented for each region. However, the data from transition zones are excluded. These are localities 5, 18, 19, and 20 in Table 2. San Ignacio (5) is intermediate in geographic position as well as inversion frequencies to the Vizcaino, Magdalena and the Central Gulf regions. The latter three localities are intermediate to the Magdalena and the Cape regions. The data in Table 4 summarize the large differences that exist within relatively short distances within the Sonoran Desert and surrounding regions. In general, there is a close coincidence of inversion frequencies with the phytogeographic provinces.

An analysis of variance was made on the data from the 20 localities in Table 4 in Baja California grouped by province. The variables considered were individual chromosome frequencies (Table 2), the heterozygosity estimates of the second (h_2) and third (h_3) chromosomes, the mean of h_2 and h_3 (H) (Table 3), and temperature range (TMR) (Table 3) of the collection locality. They indicate that variability between groups is highly significant with respect to 2-LP ($\alpha < .001$), 2-ST ($\alpha < .001$), h_2 ($\alpha = .003$), 3-MU ($\alpha = .003$), and H ($\alpha = .002$); and nonsignificant ($\alpha > .05$) for 2-BA, 2-SL, and h_3 .

Table 4. The mean inversion frequency and heterozygosity (H) (with 0.95 confidence limits) of populations of *D. mojavensis* in each phytogeographic province.--Samples from ecogeographic transition zones excluded. N = the number of collection samples per province.

Province	N	2-LP	2-ST	2-BA	2-SL	3-ST	3-MU	H
San Pedro Mártir	1	0.93	0.0	0.07	0.00	0.89	0.11	0.16
Vizcaíno	2	0.48±0.08	0.32±0.27	0.20±0.35	0.0	0.17±0.25	0.83±0.25	0.42±0.10
Central Gulf Coast (Baja)	8	0.40±0.15	0.55±0.16	0.03±0.03	0.03±0.26	0.51±0.28	0.49±0.28	0.38±0.10
Magdalena and Sierra Giganta	5	0.04±0.06	0.95±0.07	0.01±0.02	0.002±0.005	0.90±0.16	0.10±0.16	0.12±0.06
Cape	4	0.97±0.03	0.02±0.03	0.0	0.005±0.013	0.08±0.09	0.91±0.09	0.10±0.06
Central Coast (Sonora)	12	0.96±0.04	0.03±0.04	0.003±0.006	0.001±0.002	0.93±0.04	0.07±0.04	0.10±0.04
Lower Colo. Valley and Arizona Upland	4	1.0	0.0	0.0	0.0	1.00	0.0	0.0

Even though the analysis of variance confirms the observation that there is a close coincidence of inversion frequencies with the phytogeographic provinces in Baja California, this variability is not seen in populations of Sonora. Populations of D. mojavensis occupy at least five distinct phytogeographic provinces on the mainland but are uniformly monomorphic, except for the special case along the coast between Desemboque and Los Mochis.

The phytogeographic provinces, each characterized by a distinct composition of perennial vegetation, have been climatically described by Hastings and Turner (1965). They showed how the complex nature of geography and climate in this region produces distinct precipitation patterns, and consider these patterns to be primarily responsible for the differentiation of the flora of the peninsula. Not only is each province characterized by a distinct mean annual amount of precipitation (map), but also the percentage of the average which occurs at each season differs (Table 5). More important to the flora and fauna of the peninsula is the reliability of the precipitation from year to year. This was estimated by Hastings and Turner (1965) using a coefficient of variation (CV). If $CV = 0.5$, the probability of getting the seasonal rainfall equal to or less than the seasonal mean is 0.5, and the probability is slight that a region will receive no precipitation if the CV is less than 1. However, as CV becomes greater than 1, the probability of no precipitation during a season increases rapidly, so if $CV = 1.5$, the probability of a completely dry season is 0.5 (Hastings and Turner, 1965).

Table 5. Seasonal mean amount of precipitation (mm) and coefficient of variation (CV) for each phytogeographic province of Baja California.--See text for explanation.

Province	Winter		Spring		Summer		Fall		Annual
	map	CV	map	CV	map	CV	map	CV	
San Pedro Martir	92	0.54	41	0.96	18	1.81	27	1.09	178
Vizcaino	56	0.62	10	1.61	11	1.53	28	1.08	105
Central Gulf Coast	33	1.09	5	2.22	47	0.90	83	1.20	168
Magdalena	43	1.22	5	2.25	31	1.14	46	0.95	125
Giganta-Laguna	41	1.33	5	2.68	96	0.80	154	0.92	296
Lower Colorado V.	19	1.09	8	1.83	14	1.57	20	1.57	61

To summarize the climatic characteristics of the two non-desert regions; the San Pedro Martir province has a comparatively large mean annual precipitation (m.a.p.)--178 mm, which is reliable in winter (CV = 0.54) and spring (CV = 0.96), and the flora--California coastal chaparral--is attuned to this. The Giganta-Laguna (Cape) province also receives a large m.a.p. (296 mm), but is reliable during the summer (0.80) and fall (0.92). The flora here is predominately subtropical thorn scrub and short tree forest.

Of the four desert provinces, the Central Gulf Coast has the greatest m.a.p.--168 mm, reliable only in the summer (0.90). The flora in this region has affinities to the south and across the gulf in Sonora, which is also dominated by summer rain. The driest region is the Lower Colorado Valley, having no season of reliable precipitation, whereas the next driest region is along the southwest coast of the peninsula including the Magdalena plains and the Vizcaino desert. The Magdalena province receives reliable precipitation only during the fall (0.95), whereas further north in the Vizcaino province the reliable rainfall comes only in the winter (0.62).

The transition of desert flora to chaparral in the north and from desert to the thorn forest at the Cape has been described by Shreve (1936, 1937). It is across these environmental transitions that the most significant shifts of inversion frequency occur: Magdalena province (A564, LP-0.03, MU-0.04) to the Cape province (A561, LP = 0.96, MU = 0.84), with heterozygous populations situated within the transition zone. Across the chaparral-desert transition, populations heterozygous for LP, ST, and BA in the second chromosome,

and 4% ST in the third (A420), shift to 93% LP in the second and 89% ST in the third chromosomes (A519). Also, there is a reversal of gene arrangements LP to ST in the second chromosome between the chaparral populations of Baja California and the Colorado desert populations in southern California. This reversal can also be interpreted as between the Arizona-Sonora populations and those of southern California.

There are considerable differences in the mean annual temperature along the peninsula, but these are across the axis of the peninsula due to the cooling effects of the Pacific Ocean and the associated coastal fog (Hastings and Turner, 1965; Hastings and Humphrey, 1969; Felger, 1972). Not only is the Gulf Coast warmer in the summer, but it is colder in the winter, yielding a greater range of temperature of two to eight degree centigrade through the year than the Pacific Coast (Figure 10).

From Figures 3 and 6 and Table 3, it can be observed that the most polymorphic populations are those occupying the gulf coast of peninsula. A Pearson correlation analysis made with the data of all 24 localities in Baja California indicated a positive but relatively weak correlation between the temperature range (TMR) and h^2 ($r = 0.3364$, $\alpha = 0.05$) and between mean heterozygosity (H) and TMR ($r = 0.2829$, $\alpha = .09$). However, if four of the 24 localities (1, 2, 18, 19, in Table 23) are removed from the analysis due to explainable deviations (located in transition zones or suspected misidentification in early samples), the significance levels increase considerably, h^2 -TMR, ($r = 0.5622$, $\alpha = 0.005$) and H-TMR, ($r = 0.5764$, $\alpha = 0.005$). The

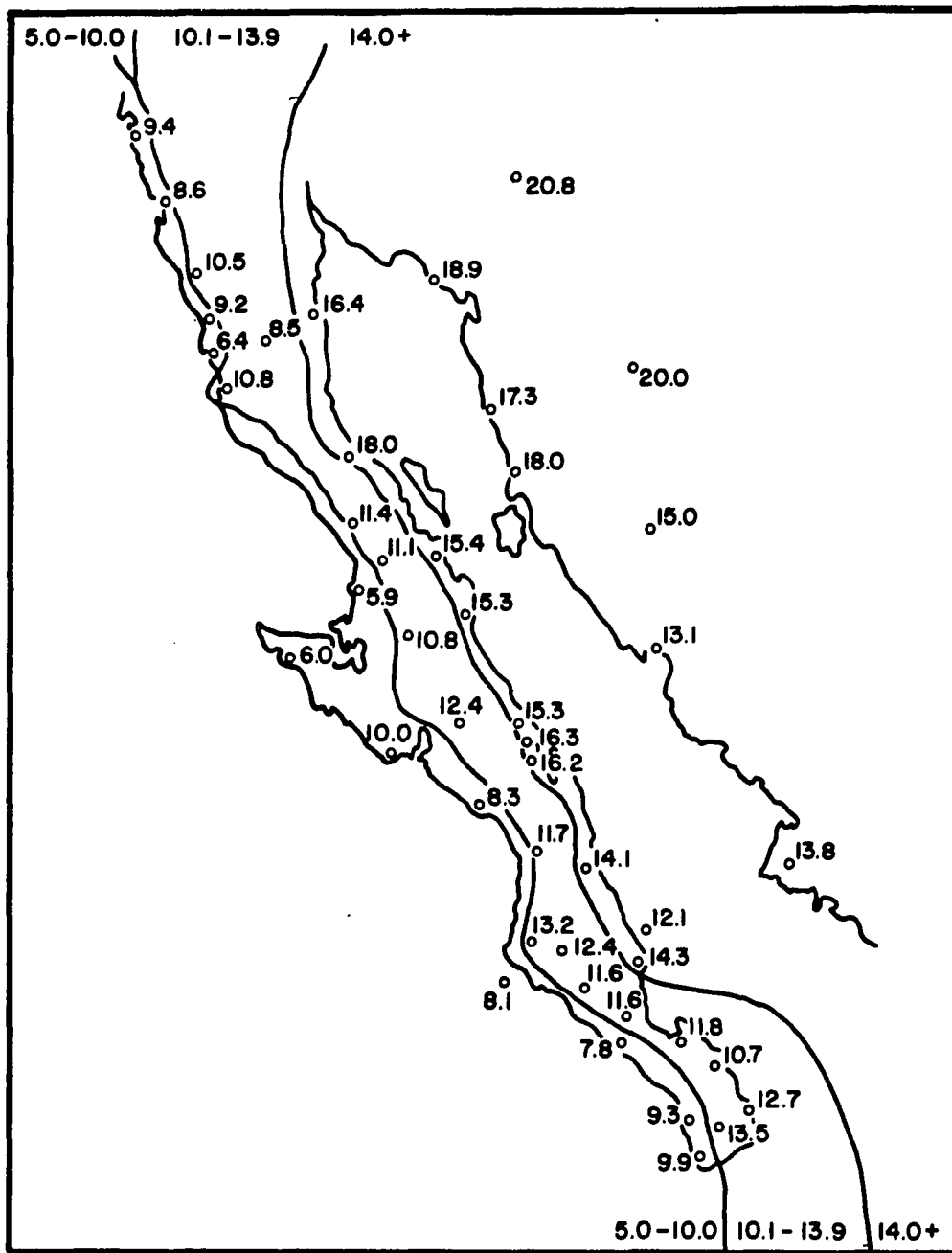


Figure 10. Map of Sonoran Desert region showing temperature range (TMR).

correlation coefficient for h_3 -TMR was conspicuously nonsignificant ($r = .33$, $\alpha = 0.097$, d.f. = 18).

Variation Correlated with Substrate

The major limiting factor of the geographic distribution of D. mojavensis is the presence or absence of the specific host cacti for feeding and breeding sites. The most important are Machaerocereus in Baja California, Lemaireocereus in Sonora and southern Arizona, and Ferocactus in southern California. Of all the various correlations of environmental variables with inversion heterozygosity, one of the most outstanding is with the distribution of Machaerocereus. This is especially true for the second chromosome, where all populations exhibiting heterozygosity were associated with Machaerocereus. This correlation is emphasized by two populations on coastal Sonora, one from Machaerocereus (A509) and one from Lemaireocereus (A510), separated by thirty miles of uninterrupted desert (Figure 9). The Machaerocereus population showed a significant heterozygosity, LP-0.78, ST-0.18, BA-0.04, while the Lemaireocereus population was homozygous LP. This substrate correlation does not hold completely true for heterozygosity in the third chromosome, the exception being the presence of MU in most of the populations along coastal Sonora where Machaerocereus is not present.

It should be pointed out that while heterozygosity in the second chromosome implies association with Machaerocereus, not all Machaerocereus populations of D. mojavensis are heterozygous. Therefore the spatial and temporal heterogeneity of useable necrotic tissue

may be very important variables in this respect. The density of Machaerocereus was estimated by Hastings (pers. comm., 1972) and by the author during field studies and no correlation could be drawn between absolute cactus densities and inversion heterozygosity. The cactus could usually be found in varying densities in most regions of the peninsula. The most abundant area is in the San Pedro Mártir region and east of the Sierra de la Giganta (C.G.C.). The region of lowest density is in the Magdalena plains, where the cactus is also quite stunted, as is all the vegetation in the region. However, the presence of rots in the cactus did vary geographically. Roughly, the areas of greatest difficulty in locating suitable rots were within the cool and humid regions near the Pacific Ocean, along the western side of the peninsula, and around the Cape region. The areas of greatest ease in locating rots were along the eastern side of the Sierra de la Giganta. Since these observations were recollected retrospectively, no conclusion can be made until they can be quantified by further field studies.

With the exception of a low degree of heterozygosity in the third chromosome along coastal Sonora, populations utilizing the other host cacti, Lemaireocereus and Ferocactus, are homozygous in their chromosome arrangements. While the rotting characteristics of Ferocactus is not known to this author, Lemaireocereus necrosis is considered to be a relatively rare event. These rots are usually very difficult to find in most localities except in regions exposed to frost or human disturbance. In my first four early expeditions to Baja California, only two Lemaireocereus rots were found that were considered useable by Drosophila, and in a recent expedition to the

southern peninsula, of the 107 rotting cacti found, only 8 were Lemaireocereus, while 73 were Machaerocereus. Only two of the 8 Lemaireocereus rots yielded flies when they were returned to the laboratory. Therefore, it is concluded that Machaerocereus is ecologically the preferred host in Baja California due to its production of abundant substrate, but that Lemaireocereus can be and is utilized sporadically. In addition, it has been noted in the field on mainland Sonora that a single Lemaireocereus necrosis can support enormously larger densities of D. mojavensis than Machaerocereus, presumably due to the greater size of Lemaireocereus. Due to this size differential, it can also be presumed that the duration of local deme can be supported by a single cactus necrosis is much longer with Lemaireocereus.

Deviations from Expected Patterns

However, there are a number of localities where the data collected appears at variance with the data of nearby localities. These are listed below, and possible explanations of the discordance are offered.

1. Collection #2 - San Borja (A350). The third chromosome has a frequency of MU at 71% in a region where all later samples (Collections #3, 4, and 5) indicate MU is around 96%. A350 was an early sample, analyzed when the author was inexperienced with polytene chromosome techniques. Table 1, #2 shows that there were 23 homokaryotypes observed but only 5 heterokaryotypes. A likely explanation is misidentification between the two homokaryotypes. These errors may also apply to collections 5 (A367) and 8 (A352). All these early collections

deviated significantly from Hardy-Weinberg expectations with excess homo-karyotypes.

2. Collection #6 - Tres Virgenes (A567). In this sample, 2-LP is 61% and 2-ST is 29% while further west at San Ignacio, 2-LP is 8-24% and 2-ST is 67-74%, and east and south at San Lucas, 2-LP is 35% and 2-ST is 49%. The same is true on the third chromosome; 3-ST is 42% at A567, further west it is 3-10% and eastward it is 20%. The data from this sample was derived from larvae reared from 2 Machaerocereus rots returned to the laboratory, and possibly may represent a biased oviposition sample.

A biased oviposition sample may also account for the absence of 2-BA on Tiburon Island, which was apparently present on the mainland Desemboque (A509).

DISCUSSION

Drosophila mojavensis provides classic examples of the response of inversion polymorphisms to varying stages of population isolation and differentiation, including heterokaryotypy in presumably large, contiguous, outbreeding populations; complementary karyotypes between semi-isolated, ecologically distinct populations; and homokaryotypy, not only as a response to increasing ecological marginality and small island founder effect, but also as a preliminary step towards speciation of geographically isolated, marginal populations (southern California) (Figure 11, p.58).

Tropic Resource Stability, Central Populations and Heterokaryotypy of D. mojavensis

One may ask why heterokaryotypy is tolerated and even actively exploited in D. mojavensis, while most arid-adapted species of Drosophila tend to be more monomorphic for chromosome arrangements? And secondly, why does this heterokaryotypy appear to be restricted to certain phytogeographic provinces? It has been discussed previously (Heed and Russell, 1971; Spieth and Heed, 1972), that the scarcity of inversion polymorphisms in arid-adapted species is probably related to the transitory nature of the breeding and feeding substrates in the desert, leading to a high frequency of periodic extinctions and inter-deme replacements. In other words, over the entire range of the species, all the populations are existing in conditions which would

be described as marginal in other species (Carson, 1955, 1959; Mayr, 1968; Soulé, 1973).

The major host cactus of D. mojavenis, Machaerocereus, differs from this rule in that in some geographic localities necrosis occurs at a relatively high frequency, such that these areas may be characterized by populations of relatively constant density and temporal stability. Furthermore, it is argued that D. mojavenis populations associated with Machaerocereus would have a high probability of remaining in the same area and would require a relatively limited dispersal rate due to the reliable production of new resources, while populations associated with Lemaireocereus would be highly clustered and transitory. In other words, eventhough the much greater size and rot longevity of Lemaireocereus would allow a local population to utilize a single necrosis longer, perhaps many generations, when the necrosis dried out, the population would be forced to disperse long distances in order to survive. This is in opposition to the condition in Machaerocereus, where rot size is smaller and duration would be relatively shorter. But the smaller resource units are more frequent and more evenly distributed, allowing the population to remain in the same geographic area for even longer periods of time.

The hypothesis considered here is analagous to and partially in accord with Valentine's thesis of grain strategy in regards to molecular heterogeneity of marine organisms as related to trophic resource stability (Valentine, 1976). Regions of poor resource stability are in the San Pedro Martir, Magdalena, and Cape regions where necrosis is

not encouraged in Machaerocereus and in southern California and Sonora-Arizona, where Lemaireocereus or Ferocactus are utilized. Here D. mojavenis adults must pursue a fine-grain spatial strategy, which, according to Valentine's model, requires "functional phenotypic flexibility". This kind of phenotypic flexibility would be best provided by a single karyotype adapted to the varying conditions of the local environment, and D. mojavenis would be expected to be homozygous for chromosomal arrangements, the characteristic condition of most arid-adapted Drosophila. This idea is very much like Carson's homo-selection (1959).

In regions of high resource stability (Central Gulf Coast, Vizcaino), D. mojavenis adults would pursue a coarse-grain spatial strategy. In this case, a highly buffered, strongly intra-specifically competitive phenotype as provided by heterokaryotypy would be favored (Carson's heteroselection). The key in each case is relative population persistence or lack of it as regulated by trophic resource reliability in an environmentally defined region.

Why necrosis in Machaerocereus might be frequent on the gulf coast and discouraged near the Pacific coast is not known, but observations made in the field while collecting adult flies and larvae in cactus rots indicate that this is probably true. It is possible that the additional physiological stresses induced by the greater annual temperature range prevailing on the gulf side of the peninsula would encourage necrosis, while conditions near the Pacific Ocean, and especially in the fog belt, with its cooling and moderating influences,

would inhibit the establishment of microorganisms which cause and maintain the necrosis. In addition the higher temperature and lower humidity on the gulf coast might induce organisms living in the region to attack the cactus for the available moisture.

The proposal that greater resource stability afforded by Machaerocereus permits the utilization of heterokaryotypy as an adaptation only partially addresses this utilization in increasing the fitness of the population. Those same ecogeographic variables that probably determine resource production may also directly influence the relative fitnesses of the homokaryotypes and heterokaryotypes in both the larval and adults stages. Parsons and McKensie (1972) cite numerous examples of heterokaryotype advantage under stress conditions, specifically desiccation and high temperature. They pointed out that in adults, heterokaryotypes were much better fit to withstand periods of high temperature and/or low humidity. The geographic variability of both these environmental stresses in Baja California has already been pointed out with regards to resource production.

It is also possible that the relative longevity of a necrosis could play a role in selecting for heterokaryotypes at the larval stage of development. Machaerocereus rots in hotter and drier regions would be expected to be more short-lived as compared to necrosis in cooler and more humid regions or in the much larger cactus, Lemaireocereus. Examples of a more rapid developmental time of heterokaryotypes exist. For example, see Wallace (1955).

An additional stress which has already been documented to show heterokaryotypic advantage is population density. Dobzhansky (1947),

Dobzhansky and Pavlovsky (1961), and Beardmore, Dobzhansky and Pavlovsky (1960) have shown in population cage experiments that the heterokaryotypic advantage was only present under conditions of high density and overcrowding. These results in coordination with Wallace's (1975) concepts of density dependent and density independent selection (soft vs hard selection) provide the basis for the argument relating environmental stress, trophic resource stability, and population structure and selection for heterokaryotype.

It would follow that if the environmental variables influencing trophic resource production changed over the course of several years, which would involve many generations of Drosophila, one would expect this to be reflected in the amount of heterozygosity of inversions in the local populations. Such a change in heterozygosity has been observed in the results of a recent collection and karyotype analysis of populations near Desemboque and Kino, Sonora and the gulf islands, San Esteban and Tiburon. At Desemboque, between 1971 and 1974, heterozygosity increased from $h_2 = 0.08$, $h_3 = 0.21$, $H = 0.18$ to $h_2 = 0.36$, $h_3 = 0.11$, $H = 0.24$ (Table 3). However, the latest collection indicated that the second chromosome had become homozygous, while the third chromosome had remained relatively similar -- 3-ST = 0.95, 3-MU = 0.05; $h_2 = 0.0$, $h_3 = 0.08$, $H = 0.04$. Data from the two islands indicated the populations were homozygous for both chromosomes. Heterozygosity in the population on Isla Tiburon in 1974 was $h_2 = 0.23$, $h_3 = 0.13$, and $H = 0.18$. Apparently, in the last three years, conditions have changed such that the local Machaerocereus cannot provide the resource base for heterokaryotypic populations to be maintained.

The argument as presented so far has emphasized the following points; of paramount importance whether heterokaryotypy can or cannot be exploited as a population adaptation is a stable population structure determined by trophic resource stability. Once this criteria is met, heterokaryotypy increases the fitness of the population and heterozygosity of inversion should increase because (1) heterokaryotypes are better competitors; (2) they have less variance of anatomical structures; (3) they produce more biomass; (4) they are more fit to handle environmental stresses; and (5) they have a faster developmental time, which allows the larvae to pupate before the rot desiccates (Parsons and McKenzie, 1972).

Following the conclusion that environmental stress both directly and indirectly influences heterokaryotype in D. mojavensis, it would be helpful to evaluate the definition of "optimum environmental conditions" which presumably characterize heterokaryotypic central populations, at least with regard to desert species. This relationship between environmental severity and heterokaryotype departs from the traditional ideas of what is thought as being ecologically optimum. In the original studies (Carson, 1955; Da Cunha and Dobzhansky, 1954) and subsequent analysis of the phenomenon (Carson, 1959; Da Cunha et al., 1959; Mayr, 1963; Wallace, 1959) the precise nature of the variables which characterize "optimum conditions" of central populations are left undefined or defined only in a general manner (Soulé, 1973). However population size, its stability and its associated intra-specific competition is the one variable that all the main hypotheses considering the nature of the ecogeography of inversion polymorphism have in common.

In fact, from an anthropomorphic point of view, populations that are defined as optimum, might well be considered to be very "uncomfortable". In such populations, crowding would be high, competition in larval and adults substrates would be severe, and predation and parasitism high.

In regard to D. mojavnensis, the environmental stresses of temperature and humidity in combination with the utilization of Machaerocereus as host plant are considered to be the key factors influencing population structure and leading to increased inversion heterozygosity. The thesis presented in this report is in agreement with some aspects of the hypotheses of Carson (1959), Lewontin (1974), Wallace (1959), and Parsons and McKensie (1972) but in disagreement with several conclusions of Soulé (1973). Soulé believes heterosis is of little importance in maintenance of heterokaryotype, while the interpretations above assert that it has considerable importance. Also Soulé predicts an increase of inversions in marginal populations with age. This seems unlikely in light of the present interpretation of the population dynamics of most desert-dwelling Drosophila which have the cytological characteristic of marginal populations. Continuous local deme extinction and replacement does not lead to an age effect.

Lewontin's ideas are summed up best by his statement:

"Dobzhansky seems to me correct in his view that in central populations with predictable, spatially diverse environments a smaller number of distinct and diverse physiological and developmental modes will be selected. These modes are determined by coadapted genotypes tied up in inversions that prevent recombination. Carson seems to me right when he emphasizes the necessity of recombination in marginal populations in order to produce combinations of alleles that are not represented in the normal modes. But it is not some particular, specialized, homozygous genotype that is being selected in the marginal environment. In the highly

unstable and unpredictable environment of the margin, quite different genotypes are being selected at different times." (Lewontin, 1974, p. 151).

A subtle point of disagreement between Lewontin (1974) and Carson (1959) is the nature of the homokaryotype in marginal populations. As seen in Lewontin's statement earlier, he believes the homokaryotype is selected for the sake of increased recombination and theoretically any homozygous chromosome would do, while Carson believes that a particular specialized, homozygous gene arrangement is selected according to the local environment. In this regard, the data from D. mojavensis apparently supports the hypothesis of Carson. As will be seen in more detail in a later section of this paper, the marginal populations of D. mojavensis exhibit quite specific karyotypes corresponding to the mosaic of environmental regimes on the peninsula of Baja California.

Charlesworth (1976) applied theoretical models of genetic recombination and linkage disequilibrium to populations in a fluctuating environment and also concluded: (1) new inversions would be eliminated, (2) older, established polymorphism would breakdown, (3) inversion heterozygosity would be reduced by a shift from a constant to a fluctuating environment, and (4) the equilibrium level of a recombination system is influenced by both the amplitude of temporal variation and the periodicity of the cyclical environment. Maynard Smith also writes, "At equilibrium in a uniform environment, if there is any selection on recombination it will be for a reduction. It follows that, if there are situations in which selection favors higher recombination,

they will be ones in which the environment varies in space and in time or both." (Smith, 1978).

The ideas of Lewontin, Charlesworth and Smith considering an unpredictable and fluctuating environment provide a basis for the understanding of the paucity of inversions in ecologically marginal populations, but, being theoretical considerations, do not address precisely what in the environment is unpredictable and fluctuating. And I believe it is important to understand exactly what is of importance to the maintainance of genetic variation of a particular organism, as a lack of this understanding can lead to error. This point is illustrated in the case of D. mojavenis, where the geographic region with the highest inversion polymorphism is also the region with the greatest fluctuations of annual temperature and precipitation. However, if our thesis is correct, it is also the region of greatest stability of trophic resources and population size. Thus it is concluded that the predictability and fluctuations of trophic resources are of far more importance to the maintenance of heterokaryotypy than the more obvious variations of climate and vegetation.

Heterokaryotypy in Non-Machaerocereus Populations

The most serious objection arising from the data which disputes the heterokaryotypy-Machaerocereus-rot production model is the presence of ST/MU heterozygotes in Lemaireocereus populations from the Bahia Kino region south at least to Los Mochis, Sinaloa. There must be some heterokaryotypic advantage in this region independent of Machaerocereus,

and the population's temporal durability, and that homozygotes of MU/MU must be at a selective disadvantage (an MU/MU karyotype was not observed in any of the collection samples from Sonora). This issue was not pursued or tested to any great extent, but a few observations about the region are offered, in that they may have some bearing on the data.

(1) There is the presence of the cactus Stenocereus (Rathbunia) alamosensis, which is similar to Machaerocereus in many respects, and is utilizable by D. mojavensis. D. mojavensis usually does not use this host in nature due to competition from its sibling species, D. arizonensis (Fellows and Heed, 1972). (2) An enormous amount of agriculture has taken place in Sonora and parts of Baja California in the recent decade, and there has been considerable transportation of fruit and vegetables across the Gulf by ferries between Guaymas and Los Mochis and La Paz and Santa Rosalia.

High Heterozygosity and the Distribution of BA and SL

A subtle but interesting observation of the polymorphic populations is the distribution of BA and SL with regards to regions of high heterozygosity of LP and ST. While these less frequent gene arrangements are found primarily in the highly heterozygous central populations of D. mojavensis, they occur also in the region of high heterozygosity at the transition zone between the Cape and the rest of the peninsula. While the data at this stage is only tentative, it is possible that the two shorter inversions, both included within LP, could be serving to reduce the frequency of double crossovers between LP and ST where the latter two are in high frequency. This idea is

strengthened by the fact that the LP gene arrangement is a fairly long paracentric inversion--more than half the length of the entire second chromosome--and that BA and SL occupy about two-thirds of the length of LP (Figure 2).

The Distribution and Significance of the San Ignacio Chromosome

The San Ignacio chromosome (SI) apparently is a very rare relictual gene arrangement found only in the highly heterozygous central populations between San Ignacio and San Lucas, Baja California Sur. This chromosome represents a line of accumulated inversions independent from the modern widespread gene arrangements of D. mojavensis. The adaptive significance of this gene arrangement in natural populations is unknown, but it does appear to increase dramatically in laboratory stock populations (from less than 1% to over 30%). It was this increase that led to its discovery. Its presence is important in the present analysis in that it shows that these populations are relatively old and have maintained ancestral-descendent continuity over that long period of time in this area.

Ecogeographic Differentiation of Karyotype

The second most important cytological characteristic of D. mojavensis, aside from the decrease of inversion heterozygosity from central to marginal populations, is the major cytological difference exhibited between closely adjacent populations as the species emerges from the desert into different ecological regions (Figure 11). For instance, as the desert gives way to coastal chaparral in northern

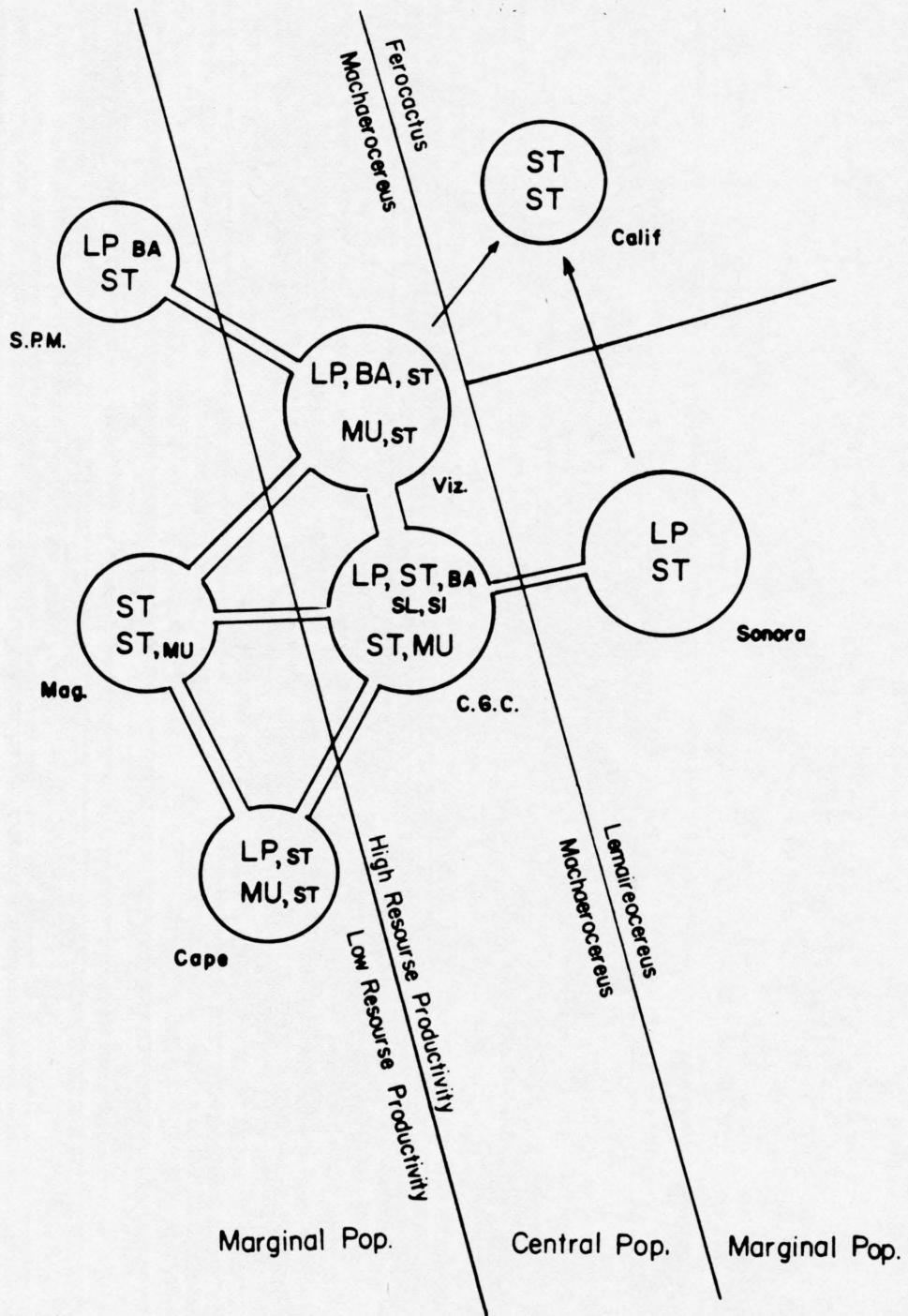


Figure 11. Diagrammatic representation of the geographic differentiation of *D. mojavensis* by karyotype.

Baja California, MU is replaced by ST as the most frequent gene arrangement on chromosome 3. In southern Baja California as the desert changes into subtropical thorn scrub, a similar exchange occurs, only it is ST replaced by MU. On chromosome 2, ST is replaced by LP as the most frequent arrangement (Figure 12). Also the shift from 2-LP to 2-ST between the San Pedro Martir populations and the Mojave desert population in California represent a major replacement but in this case there is no evidence that the two populations are contiguous. The differentiation of the species by karyotype and its correlation with conspicuous environmental variables, perennial vegetation, precipitation, temperature range, suggests that these populations are being adapted to the local ecological conditions by way of selection for complementary karyotypes in the respective geographic centers. The superior fitness of the undisturbed co-adapted gene complexes adapted to the local conditions of the environment is the proposed mechanism for this selection (Wasserman's karyotype selection). The polymorphism in the transition zone is maintained because the populations occupy a heterogenous environment and there is frequency-dependent selection against the homo-karyotypes, or an additional possibility is the maintenance of the cline via migration pressure. However, if this were the case, then both second and third chromosomes should exchange gene arrangements in a coordinated manner. Figure 12 illustrates that the inversions on the second and third chromosomes are not being replaced in a similar manner across the transition zone. On the second chromosome, the greatest rate of exchange occurs west of and across the environmental

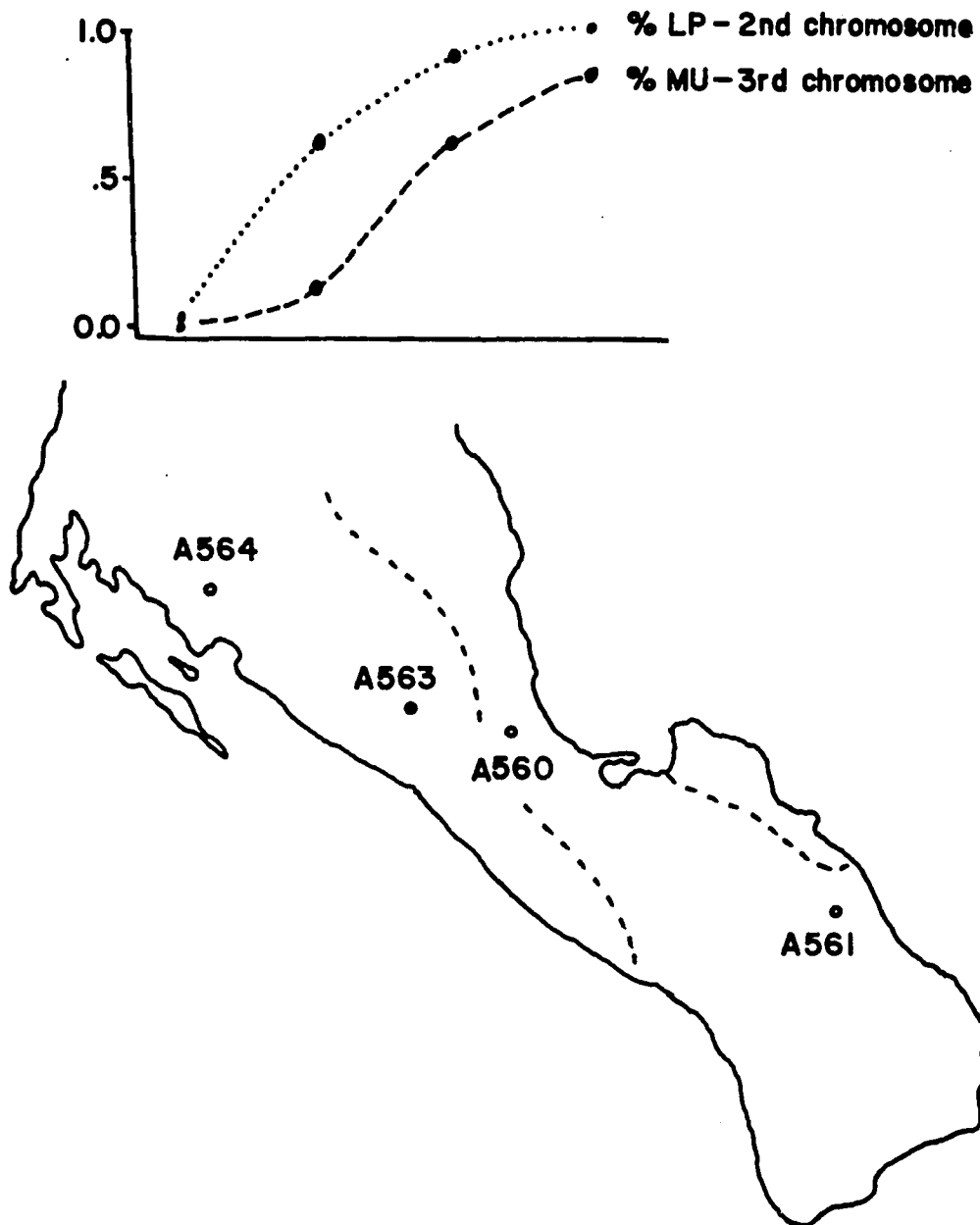


Figure 12. Transition zone between the Cape and Magdalena regions in southern Baja California showing the relative change of inversion frequencies on the second and third chromosome.

transition zone, while on the third chromosome, the greatest rate of inversion exchange is across and east of the transition zone.

These chromosome replacements mimic somewhat the hypothetical ancestral population structure postulated by Wasserman (1960, 1962) to account for the cytological evolution of the mulleri complex species group of which D. mojavensis is a member (Figures 11 and 13). Wasserman suggests that in these cases migration is sufficiently restricted between neighboring populations to permit gene complexes to adapt to differing local conditions. But these data indicate migration is sufficient to infiltrate adaptive rearrangements into neighboring populations if they are selectively advantageous there. The result is a series of populations with overlapping ranges of inversions, where each inversion occurs in a specific environmental regime.

Geographic Race Formation in D. mojavensis

Wasserman hypothesized that this geographic differentiation of karyotype in semi-isolated populations could lead to speciation events if different sexual behavior characteristics were linked to the inversions. Preliminary hybridization tests (unpublished data from W. B. Heed lab) of various geographic stocks from Baja California and Sonora indicated no obvious reproductive barriers in the F_1 and F_2 generations. However, a more sensitive test may reveal some differences.

There is evidence, however, for differentiation in D. mojavensis but it coincides with areas showing geographic isolation rather than areas of adjacent chromosomal replacement. First, individuals from Sonora and Arizona are noticeably larger and darker than those from

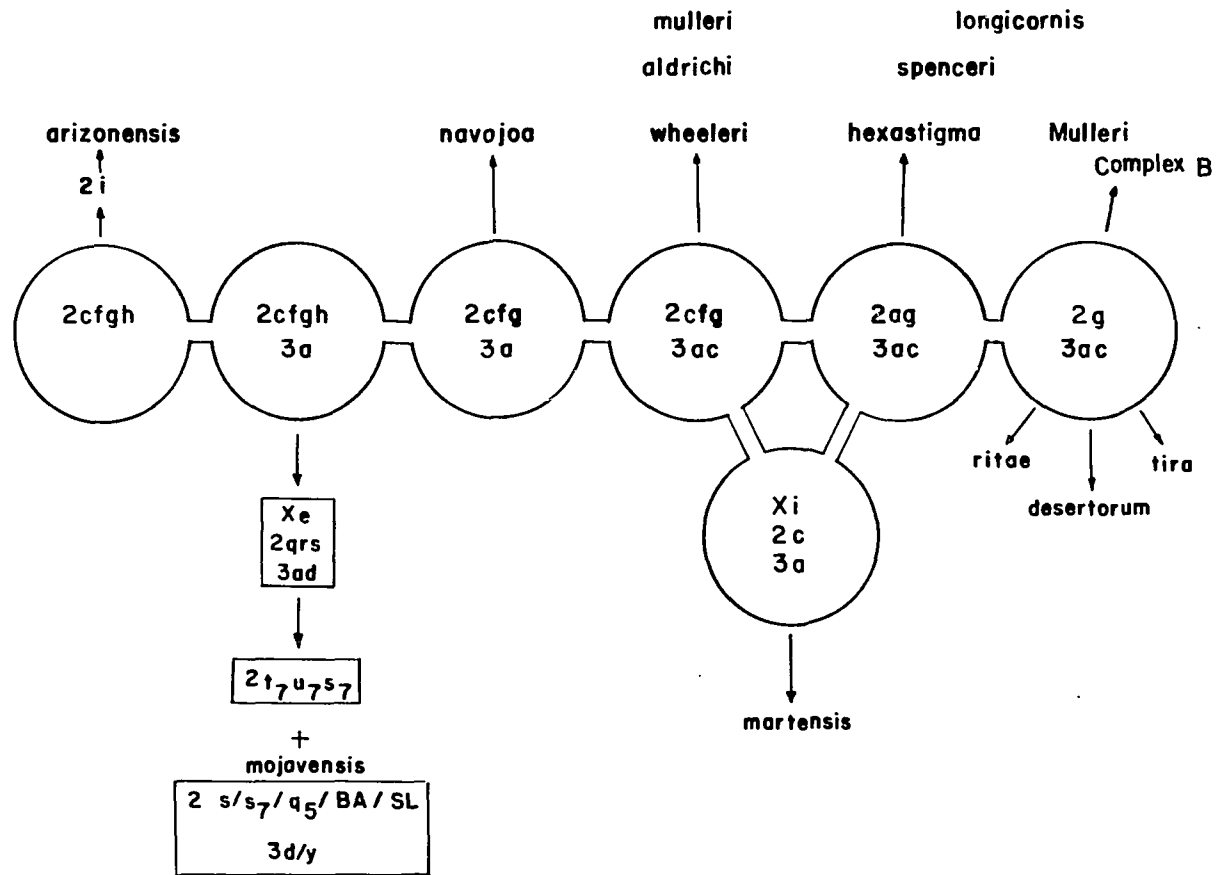


Figure 13. Chromosome inversion distribution in the hypothetical ancestral species of the mulleri subgroup.

Baja California. Second, Zouros (1973) demonstrated significant allelic frequency differences between the mainland and the peninsula, including many islands in the Gulf, for the Pt-8 protein and ADH enzymes. Third, Zouros and d'Entrement (1974) reported behavioral isolation between the mainland and peninsular strains of this species. And finally, Starmer et al. (1977) reported a significant difference between strains from the peninsula and those from Sonora with regard to longevity when exposed to atmospheric ethanol. All these differences between the Sonoran and peninsular populations also correspond very closely to host plant preference which could be a factor in addition to geographic isolation that is actively contributing to the differentiation.

The *mojavensis* race was not studied in the course of this investigation, but it is possibly an example of Carson's and Mayr's hypothesized marginal population becoming geographically isolated and taking up a new evolutionary path, in this case, switching to a novel host cactus, Ferocactus, developing distinct morphological characters, while becoming homozygous for the two polymorphic chromosomes. The *mojavensis* race is probably entirely isolated from the main body of the species due to the presence of unsuitable habitat (the high altitude temperate forest on the Sierra San Pedro Martir), and the lack of necessary host cacti in the Lower Colorado River valley at the head of the Gulf of California. D. mojavensis has not been collected anywhere between the Arizona-Sonora Lemaireocereus populations and those in the Colorado Desert of southern California.

The Sonoran race is evidently not as well isolated from the other populations in Baja California. Populations sampled on Isla

Tiburón and coastal Sonora have the same inversions as those in Baja California, including the more derived inversions, BA and SL, but at a much lower frequency. Because it is well known that inversions are monophyletic and can spread through the populations of a species only by migration, there must have been some trans-gulf migration, possibly via island hopping and sweepstakes dispersal. Further north and inland, where only Lemaireocereus is found, Sonora and Arizona populations of D. mojavensis are homokaryotypic. On the third chromosome, 3-MU shows a frequency of 3-18% along the coast from Isla Tiburón south, as discussed previously. The MU arrangement was not found on Isla San Pedro Nolasco, 16 km from the mainland, possibly a result of founder effect. The island is, however, only 3.5 square kilometers in area, and with limited resources, this population might be subject to many population size bottlenecks. Loss of inversions on the islands of the Gulf was noted earlier in recent collections from Isla San Esteban and Isla Tiburón. The latter is noteworthy since the Tiburón population was polymorphic in 1974. The only other island population sampled was Isla San José, and while the differences in inversion frequencies could be accounted for by sampling error (culture derived from a single rot pocket), an important feature is the presence of BA. BA is not found in the peninsular populations further north than Loreto (A385), but is found in the transition zone populations north of La Paz (A560, A563). More field research in this region will be necessary to clarify the biogeographic relationship of the Isla San José population.

The protein allele analysis by Zouros (1973) indicated that the Gulf island populations were almost identical to the populations on the

nearest main land mass, and that the differences (absence of rare alleles) could be accounted for by sample size error. One conclusion that could be drawn from the cytological and allelic data is that migration is sufficient between the peninsula and mainland and to the nearby islands to infuse all of the genic alleles and chromosomes into those populations, but that selection and population dynamics maintain the observed differentiation. If population size fluctuations, including local extinctions and biased founder replacement, are responsible for the attrition of inversions on the islands, it apparently does not affect the genic heterozygosity (Zouros, 1973).

CONCLUSIONS

From the data accumulated from all workers and present observations on the cytogenetics, genetics, and ecology of D. mojavensis, the following conclusions concerning its systematics and biogeography have been drawn:

- (1) D. mojavensis can be considered to be differentiated into three distinct geographical races (the mojavensis race, the baja race, and the sonorensis race).
- (2) The mojavensis race is probably entirely isolated from the other two and is the most differentiated morphologically and genetically.
- (3) The baja and sonorensis races undoubtedly exchange migrants across the gulf via the Midriff islands, and most of alleles and chromosomes can be infused between them and into neighboring island populations.
- (4) In spite of this contact zone, strong natural selection (and in some cases, coordinated with population fluctuations) maintain the observed allelic, cytogenetic and anatomical differences between the two races. Both races are probably evolving more or less independently of the other.
- (5) Historically, the mojavensis and sonorensis races are probably derived populations; and D. mojavensis probably underwent most of its evolution and reproductive isolation from other mulleri Drosophila on the peninsula in a similar manner as being observed between the baja and sonorensis races at the present. Supporting points for this

conclusion are the following, (a) Baja California is the region of highest genetic diversity, (b) the ecologically preferred host plant occurs there, (c) all of the secondary host cacti occur on the peninsula, (d) the relict chromosome SI occurs on the peninsula, (e) the more derived inversions, BA and SL, probably had their origin in Baja California, (f) there is the presence of the geographic and ecological complement of D. mojavenis on mainland Mexico, its sibling species, D. arizonensis.

(6) As an evolving unit, the baja race is subdivided into a mosaic of three marginal populations in three distinct phytogeographic regions around a central population occupying two phytogeographic regions. The description of these populations as being marginal or central is based on hypothesized trophic resource production in the host cactus, Machaerocereus and population survival through time. The central populations have continuity in time in the same geographic area, while marginal populations, due to the ephemeral nature of the resource in those areas undergo frequent local extinctions and must be re-established by inter-deme migration.

(7) This latter description is also applicable to the host plants and populations of the mojavenis race (Ferocactus) and the sonorensis race (Lemaireocereus).

(8) In regions of sustained resource production, populations of D. mojavenis are able to increase fitness by utilizing the cytological specialization of heterokaryotypy.

(9) In marginal populations, directional karyotype selection maintains regional (phytogeographic) specific inversions in a relatively homozygous state.

(10) In the transition zones between two distinct differentiated populations, a second type of inversion polymorphism is observed, which is qualitatively different from that seen in the central populations.

SUMMARY

Drosophila mojavensis appears to be utilizing two strategies of cytological adaptation in different geographic populations: (1) chromosomal polymorphism within certain populations and monomorphism within other usually peripheral populations; and (2) complementary chromosomal replacement between adjacent localities, which show fixed differences or have a low degree of polymorphism. There is a strong relationship between the geographic mosaic of karyotypes and prevailing environmental conditions, as reflected by perennial vegetation. No single climatic variable is suggested as being responsible for the occurrence but it is believed the overall differences of the environment in each region necessitate different adaptive responses. There is a positive relationship between inversion heterozygosity, especially in the second chromosome, with the regions of greatest variability in annual range of temperature in Baja California. It is proposed that this is mediated by increased necrosis by the major host cactus Machaerocereus, which affects population duration. In addition, inversion heterozygotes are probably more highly buffered in the region of presumably greater stress.

The replacement of one major chromosomal type by another occurs principally across the boundaries of the Sonoran Desert in Baja California where the identical host plant (Machaerocereus) enters the coastal chaparral in the north and the subtropical thorn scrub in the Cape region. This extreme local adaptation leads to a low degree of heterokaryotypy on either side of a narrow hybrid zone and mimics

somewhat the hypothetical ancestral conditions postulated for the mulleri complex of species by Wasserman. Retardation of gene flow within the limits of the inversions is inevitable under these conditions but whether speciation events also are initiated is not resolved.

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