GENETICS OF NATURAL POPULATIONS. XXVI. CHROMOSOMAL VARIABILITY IN ISLAND AND CONTINENTAL POPULATIONS OF *DROSOPHILA WILLISTONI* FROM CENTRAL AMERICA AND THE WEST INDIES[1]

THEODOSIUS DOBZHANSKY

Department of Zoology, Columbia University

Received January 11, 1957

INTRODUCTION

Drosophila willistoni is one of the commonest, and often the commonest, species of its genus in a territory extending from the West Indies to La Plata, and from the Atlantic to the Pacific or to the eastern slope of the Andes. In this enormous distribution region, many populations carry great stores of polymorphs, the most obvious of which are the variant gene arrangements in every one of the three chromosome pairs which the species has. In fact, *D. willistoni* has the greatest number of chromosomal inversions found within populations of any species so far investigated—47 kinds of inversions, up to 9.4 heterozygous inversions per individual in a breeding population, and up to 16 heterozygous inversions in a single individual (Dobzhansky, Burla, and da Cunha, 1950; da Cunha and Dobzhansky, 1954, and unpublished data). The populations of different geographic regions show however some diversity, both with respect to the quality and especially with respect to the quantity of the polymorphs present. Thus, on the continent of South America, the number of heterozygous inversions per female fly varies from about 1 to more than 9 in different regions.

Owing to the generosity of Drs. H. L. Carson, W. B. Heed, W. S. Stone, and M. R. Wheeler, the writer has been privileged to examine population samples of *D. willistoni* collected by these colleagues on several islands of the Greater and the Lesser Antilles, as well as on the neighboring mainlands of Central and South America. The study of chromosomal variability in this material proved quite rewarding since it throws light on the mechanisms of racial differentiation, especially of the geographically marginal populations of the species. The results of this study are reported in the following pages.

MATERIAL

Tables 1–3 show the composition of the population samples from groups of localities indicated on the map in figure 1 and numbered from 1 through 15. The following list of the localities and collecting dates has been kindly supplied by Drs. M. R. Wheeler, and W. B. Heed. 1, Bucaramanga, Colombia, September 14, 1956. 2, Sierra Nevada de Santa Marta, Colombia, September 1956. 3A, Barro Colorado Island, Panama, November 1955. 3B, same, August 1956. 4A, Turrialba, Costa Rica, August, 1956. 4B, La Lola, Costa Rica, August 1956. 4C, San Jose, Costa Rica, August 1956. 4D, San Isidro de General, Costa Rica, August 1956. 5, Lancetilla, Honduras, April 1954 (see Dobzhansky and Pavlovsky, 1955). 6A, El Salvador, May and August 1954 (see Dobzhansky and Pavlovsky, 1955). 6B, San Salvador, September 1955. 7, Lake Placid, Florida (see Townsend, 1952). 8, Hot Mineral Spring, Bath, Jamaica, February 1956. 9A, Santiago de Cuba, February 1956.

[1] The work reported here has been carried out under Contract No. AT-(30-1)-1151, U. S. Atomic Energy Commission.

9B, Contramestre, Cuba, February 1956. 9C, 18 Km from Trinidad, Cuba, February 1956. 10, Petionville, Haiti, February 1956. 11A, El Yunque Resort, Puerto Rico, January 1956. 11B, Rio Piedras Agricultural Experiment Station, February 1956. 12, Monkey Hill, St. Kitts, January 1956. 13, St. Lucia, January 1956. 14A, Turner Hall Woods, Barbados, January 1956. 14B, Claybury, Barbados, January 1956. 15A, Sangre Grande, Trinidad, December 1955. 15B, Arima Valley, Trinidad, December 1955.

The specimens of the *willistoni* group of five sibling species collected in the above localities were shipped by air to the laboratory at the Columbia University. Single female cultures were next established from these wild flies, and the species were classified by Mr. B. Spassky by inspection of the genitalia in living F_1 males under a high magnification of a binocular dissecting microscope. The subsequent cytological examination of the chromosomes in the larval salivary glands disclosed no misdeterminations of the species. The cytological examination was carried out in September–October of 1956 by the writer, using the slides prepared by Mrs. O. Pavlovsky and Mrs. N. Spassky. Since, for some of the samples, several months elapsed between the capture of the flies and the cytological examination of their progeny, a slight amount of inbreeding might have taken place in the cultures. Although, after the first generation raised in the laboratory, the cultures were maintained by transferring at least two dozen adult flies, it was decided to examine the chromosomes in larvae coming from intercrosses of pairs of strains from the same locality. The numbers of such intercrosses were, of course, equal to the numbers of the strains from the respective localities, each strain being used in two intercrosses ($A \times B$, $B \times C$, $C \times D$, $D \times E$, etc.). The chromosomes of a single larva from each strain or each intercross were examined for heterozygous inversions. The inversion homozygotes are mostly not distinguishable with sufficient accuracy, at least without a prohibitive amount of work, in *D. willistoni*. Since no heterozygous inversions can be seen in the X-chromosomes of male larvae, females were chosen whenever convenient.

Distribution of Inversions Considered Separately

A summary of the data on the composition of the samples examined is given in table 1, by chromosome limb and by locality. A total of 36 different inversions are recorded. A majority of these, 33, were detected previously in Brazilian populations of *D. willistoni;* they are described, and some of them figured, by da Cunha, Burla, and Dobzhansky (1950). One inversion, A-1 in the third chromosome, was found by Townsend (1952) in two chromosomes from Florida. A new inversion was found in a single XR chromosome from Jamaica, and another new one in a single third chromosome from Santa Marta, Colombia. The former involves an inversion of the block of genes comprising the section 11 and the adjacent part of section 10 of the standard map (Dobzhansky, 1950). The latter inverts a part of the section 94 of the standard map. These inversions are marked in table 1 by asterisks.

It will be convenient to analyze the data by dividing the inversions observed into three groups: the universal, the widespread, and the endemic ones. Strictly speaking, the only inversion recorded universally in all populations of the species is III-J. It has been found from Argentina and Uruguay, throughout Brazil (da Cunha and Dobzhansky, 1954), throughout Central America and the West Indies (table 1 of the present work), and in Florida (Townsend, 1952). The inversions IIL-F and IIR-E may also be universal, although IIL-F has not been recorded in Florida and in Honduras, probably because the samples studied were too small. The inversion IIR-E has not appeared in a sample of 43 flies from La Plata, Argentina (da Cunha and Dobzhansky, 1954), and among 76 flies from

TABLE 1. *Frequencies (in per cent) of inversion heterozygotes in the populations studied* (Asterisks refer to single chromosomes with new gene arrangements mentioned in the text.)

Origin / Inversion	1. Bucaramanga	2. Santa Marta	3. Panama	4. Costa Rica	5. Honduras	6. Salvador	7. Florida	8. Jamaica	9. Santiago de Cuba	10. Haiti	11. Puerto Rico	12. St. Kitts	13. Santa Lucia	14. Barbados	15. Trinidad
XL Chromosome															
None	41.8	42.9	72.0	57.1	75.0	57.1	100.0	98.9	100.0	89.5	96.0	100.0	100.0	90.4	92.8
A	12.7	7.1	12.0	4.8	—	—	—	1.1	—	—	—	—	—	9.6	3.6
B	5.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—
C	5.5	14.3	—	23.8	—	10.7	—	—	—	10.5	—	—	—	—	—
D	1.8	14.3	4.0	—	16.6	—	—	—	—	—	—	—	—	—	—
C & D	34.5	7.1	12.0	9.5	8.5	32.1	—	—	—	—	—	—	—	—	—
D & F & G	9.1	42.9	12.0	—	—	—	—	—	—	—	—	—	—	—	—
D & H	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3.6
XR Chromosome															
None	36.4	71.4	12.0	57.1	58.3	85.7	98.6	96.7	100.0	100.0	92.0	100.0	90.6	66.3	57.1
A	18.2	21.4	32.0	9.5	—	—	1.4	—	—	—	—	—	—	13.3	17.9
B	5.5	—	—	—	—	—	—	1.1*	—	—	—	—	4.7	—	—
C	38.2	28.6	56.0	14.3	8.3	10.7	—	—	—	—	—	—	—	8.4	3.6
D	40.0	21.4	32.0	28.6	41.6	10.7	—	2.2	—	—	—	—	4.7	14.5	21.4
E	9.1	—	4.0	—	—	—	—	—	—	—	—	—	—	—	—
Females Studied	55	14	25	21	12	28	70	93	15	19	25	50	64	83	28
IIL Chromosome															
None	21.6	24.0	27.8	8.1	56.3	23.7	46.2	59.2	42.3	60.0	72.2	93.4	81.0	40.8	37.5
A or B	20.6	44.0	16.7	43.2	12.5	32.2	29.8	31.7	30.7	10.0	22.2	—	7.0	42.7	17.5
A & B	23.9	12.0	12.7	8.1	—	—	—	—	3.8	—	—	—	—	1.0	2.5
C	—	—	—	2.7	—	—	—	—	—	—	—	—	—	6.8	40.0
D or E	21.6	16.0	13.9	24.3	37.5	55.9	35.6	9.9	3.8	10.0	8.3	—	—	—	—
D & E	12.6	20.0	8.3	5.4	—	—	—	—	—	6.7	—	—	—	—	—
F	45.5	36.0	55.6	56.7	—	11.9	—	10.6	53.8	16.7	8.3	6.6	13.0	39.8	30.0
IIR Chromosome															
None	31.8	32.0	38.9	35.1	62.5	37.3	53.8	55.6	53.8	53.3	66.7	100.0	90.0	55.3	67.5
A	20.5	12.0	36.1	37.8	—	23.7	12.5	15.5	23.0	16.7	—	—	1.0	2.9	2.5
B	4.6	16.0	2.8	13.5	—	—	—	1.4	—	—	5.6	—	4.0	3.9	—
C	6.8	16.0	8.3	—	—	—	1.0	—	7.7	—	—	—	—	—	—
E	47.7	56.0	38.9	32.4	37.5	49.1	38.5	36.6	34.6	36.7	27.8	—	5.0	41.7	30.0
III Chromosome															
None	27.3	20.0	13.9	13.5	62.5	42.4	38.5	54.9	23.0	23.0	69.4	85.5	35.0	62.1	10.0
A-1	14.8	8.0	5.6	—	—	—	1.9	—	19.2	—	—	—	—	—	—
A or B	20.5	8.0	5.6	5.4	—	—	43.3	—	—	6.7	—	—	29.0	2.9	2.5
A & B	17.0	36.0	2.8	—	—	—	—	—	—	—	—	—	—	—	—
C	9.1	4.0	5.6	10.8	—	—	—	2.8	7.7	26.7	—	—	—	—	—
D	18.2	32.0	13.9	8.1	—	—	—	—	—	—	—	—	—	—	2.5
F	17.0	48.0	55.6	70.3	18.8	22.0	—	—	11.5	—	—	—	—	—	—
H	34.1	40.0	14.5	18.9	—	—	1.9	—	3.8	—	—	—	2.0	5.8	2.5
I	2.3	—	—	—	—	—	—	—	—	—	—	—	—	—	—
J	12.5	12.0	16.7	2.7	37.5	44.1	34.9	43.0	73.1	60.0	30.6	14.5	28.0	15.5	27.5
K	—	4.0†	—	2.7	—	—	—	—	—	—	—	—	—	—	—
L	35.2	32.0	21.8	43.2	—	6.8	—	—	—	—	—	—	28.0	11.7	40.0
L & M	4.6	14.0	16.7	27.0	—	—	—	—	—	—	—	—	—	2.9	22.5
Flies Studied	88	25	36	37	16	59	104	142	26	30	36	76	100	103	40

the island of St. Kitts. The latter absence may be real.

Widespread inversions are many. The following ones have been recorded in samples from Argentina to the West Indies and/or to Florida: XL-D (Argentina to Cuba), XR-A (southern Brazil to Florida), IIL-A and IIL-E (Argentina to Florida), III-B (Argentina to Florida, Townsend has recorded it as III-A), and III-F (Argentina to Cuba). However, XL-D and XR-A are rare or absent on the islands of the Antilles, except on Trinidad and Barbados. Similarly, IIL-A is absent on St. Kitts, and IIL-E on the Lesser Antilles. Inversion III-B, which is one of the commonest inversions in South America except in the Brazilian state of Bahia, is rare or absent in samples from Central America and the West Indies, but it was common in Townsend's sample from Florida. It can be confused with an adjacent inversion III-A, and for this reason is recorded usually as "A or B," except when both A and B are present. It can however be stated that

III-B is much more frequent in most populations than is III-A. Finally, III-F is rare or absent in northeastern Brazil and in the Antilles, except Cuba.

Inversion III-H is recorded from Argentina to Florida, but it reaches high frequencies chiefly in populations of equatorial Brazil, and, as seen from the data in table 1, in Colombia, Panama, and Costa Rica. Its not being recorded in some populations of southern Brazil may be due to the inadequacy of sampling, but the absence on some of the islands of the Antilles may be real. Inversions III-D, III-L, and the compound III-L&M behave very much like III-H. However, these inversions are rare or absent also in Argentina, in most of southern Brazil, and in Bahia. They occur on Trinidad and Barbados, and III-L reaches an unexpectedly high frequency on Santa Lucia, but they are absent on the other islands sampled in the Antillean chain. The compound of two overlapping inversions IIL-A&B is a further example of this distribution pattern; it is absent or rare in Argentina and southern Brazil, very common in equatorial Brazil, still fairly common in Colombia and Panama, and found only in scattered chromosomes in Trinidad, Barbados, and Cuba.

The geographically more restricted inversions are relatively few but perhaps most interesting. Inversion XL-C was originally found in a small sample from Costa Rica (8 females, da Cunha, Burla, and Dobzhansky, 1950) in conjunction with XL-D. It has never been found in the whole of Brazil, but it is common in the samples from Colombia and from Central America, again in the form of the compound C&D as well as by itself. It seems completely absent in the islands of the Antilles (table 1). Inversion III-A-1 was, as stated above, found by Townsend in Florida, but it reappeared as a moderately frequent chromosome in Colombia and in Cuba (table 1). It seems to be entirely absent elsewhere. The triple compound XL-D&F&G is common in the valley of the Amazon and in Colombia, but rare or absent elsewhere (table 2, page 124, in da Cunha and Dobzhansky, 1954, paper lists the frequencies of the inversions D, F, and G mostly separately rather than as a compound). Inversion XR-C, and the compound XR-C&D, behave like the XL-D&F&G compound, except that the former inversions occur also from Panama to Honduras and Salvador, and on Trinidad and Barbados.

Little can be said about the rare inversions, since their non-occurrence may mean only that the samples studied are small. However, their occurrence is significant. Inversion III-I was found originally in rare chromosomes from central Brazil, but it appeared also in Colombia. Inversion III-K was originally seen in two chromosomes from Goyaz, Brazil, but it was met with again in a single chromosome from Colombia. Finally, some conspicuous absences may be noted. Inversion XL-H is common in many parts of Brazil (fig. 2), but has appeared in only a single chromosome from Trinidad and in no other populations listed in table 1. The complete absence in Central America and the West Indies of the subterminal inversion IIL-H is noteworthy, since this inversion is rather widespread in most of Brazil and in Argentina, though not particularly common in any population studied.

Homozygous Inversions

As stated above, only heterozygous inversions have been recorded in the preparations examined. This technique permits the detection of the variations in the chromosome structure which occur within the populations of the localities sampled. It remains, however, to be discovered whether these populations differ from each other in the gene arrangements in their chromosomes. Suppose, for example, that the population of a certain locality is homozygous for some gene arrangement A_1 and that of another locality for an alternative gene arrangement A_2. Neither population will contain heterozygotes A_1/A_2, but such heterozygotes will

appear in the hybrids between the strains from the two localities. A series of crosses were, accordingly, arranged between flies from different localities in Central America and in the West Indies with flies from a strain from Marajo Island in Brazil. The Marajo strain has the standard gene arrangements in all chromosomes, as shown in the standard maps published by Dobzhansky (1950). The progeny of the crosses is expected to show in heterozygous condition all the inversions relative to the standard order which may have become established in homozygous condition in the strains from Central America and the West Indies.

Examination was made of hybrids between the Marajo strain and strains from the following regions: Colombia, Panama, Costa Rica, El Salvador, Jamaica, Cuba, Haiti, St. Kitts, Santa Lucia, Barbados, and Trinidad. With the exception indicated below, all the hybrids were heterozygous for the inversion compound XL-C&D, and for XR-C. This means that the populations in Central America and the West Indies differ from the standard strain by being homozygous for these inversions. The exceptions are the hybrids Santa Marta × Marajo, Costa Rica × Marajo, and Haiti × Marajo, some of which showed either the inversion XL-C or XL-D alone, or had a pairing configuration so complex that it was difficult to analyze. Reference to table 1 will show that in Colombia, Costa Rica, and Haiti the inversions XL-C and XL-D often occur alone or in combination within the populations, and in Colombia there occurs also the highly complex compound XL-D&F&G. The inversion XR-C was also absent in some of the hybrids Santa Marta × Marajo, Panama × Marajo, and Costa Rica × Marajo. Table 1 shows that this inversion occurs in some but not in all strains from Colombia, Panama and Costa Rica.

In species in which the gene arrangement is as highly variable as it is in *D. willistoni*, the choice of the gene arrangement to be considered as the standard is an arbitrary matter. The gene arrangement in certain strains from Para and the Marajo Island was chosen (Dobzhansky, 1950). It happens that in some respects the populations of this area, the eastern part of equatorial Brazil are atypical if the species as a whole is considered. Indeed, heterozygous inversions XL-C and XR-C occur in hybrids not only between the Marajo strain and strains from Central America and the West Indies, but also between Marajo and strains from southern Brazil. In other words, the gene arrangements which have become established in a part of equatorial Brazil are relatively rare elsewhere in the species. To put it in another way, with respect to these particular gene arrangements the populations of the West Indies resemble those of southern Brazil more than either of them resembles the populations of a geographically intermediate region, which is equatorial Brazil.

Numbers of Inversions per Individual

Table 2 and figure 1 show the mean numbers of inversions found in heterozygous condition per individual in different regions. The data are given separately for females and for males; as expected, the means for the females are generally higher than those for the males, except on the

Table 2. *Mean numbers of heterozygous inversions per individual in the populations studied*

Population	Females	Males
1. Bucaramanga	6.80 ± 0.41	5.09 ± 0.35
2. Santa Marta	7.21 ± 0.65	5.45 ± 0.49
3. Panama	6.20 ± 0.44	4.73 ± 0.51
4. Costa Rica	5.81 ± 0.39	4.38 ± 0.44
5. Honduras	2.33 ± 0.45	1.50 ± 0.65
6. Salvador	3.14 ± 0.29	2.06 ± 0.26
7. Florida	2.06 ± 0.16	1.88 ± 0.19
8. Jamaica	1.58 ± 0.13	1.49 ± 0.16
9. Cuba	2.67 ± 0.30	2.91 ± 0.48
10. Haiti	1.84 ± 0.22	2.45 ± 0.39
11. Puerto Rico	1.28 ± 0.21	1.09 ± 0.29
12. St. Kitts	0.20 ± 0.05	0.23 ± 0.08
13. Santa Lucia	1.05 ± 0.12	1.17 ± 0.14
14. Barbados	2.45 ± 0.17	2.05 ± 0.29
15. Trinidad	3.18 ± 0.29	2.58 ± 0.29

FIG. 1. Mean numbers of heterozygous inversions per individual of *Drosophila willistoni* in different populations, symbolized by the diameters of the black circles. The numbers of the populations correspond to those in tables 1–3. The South American part of the distribution area of the species is not shown in this figure.

islands on which the X-chromosomes do not vary in the gene arrangement. It can be seen that the lowest mean number of heterozygous inversions is found on the Isle of St. Kitts. This is, in fact, the lowest concentration of inversions known in the species *D. willistoni* (cf. da Cunha and Dobzhansky, 1954). The highest means in table 3 are those for Bucaramanga and for Santa Marta, Colombia. They are higher than those found in the Amazon Valley in Brazil, and are exceeded only by those from some populations of central Brazil.

Figure 1 shows particularly clearly that the numbers of inversions are highest on the continent of South America, in Panama, and in Costa Rica. They become reduced in El Salvador and in Honduras, and even more so on the islands. The larger islands of the Greater Antilles have generally more heterozygous inversions than those of the Lesser Antilles, except that Trinidad, and possibly also Barbados, have again more inversions, presumably on account of their greater proximity to the continent of South America (see the Discussion). The geographically marginal but continental population of Florida about matches those of Cuba, Honduras, and Barbados.

The results are essentially the same if instead of the mean numbers of heterozygous inversions we consider the number of kinds of inversions recorded in a given locality. This information can be gleaned from table 1. The population of St. Kitts has a constant gene arrangement except for only 2 inversions, IIL-F and III-J. By contrast, Bucaramanga, Colombia, is the home of 32 different inversions, in a sample of about the same size as that studied from St. Kitts. The islands, have in general fewer inversions

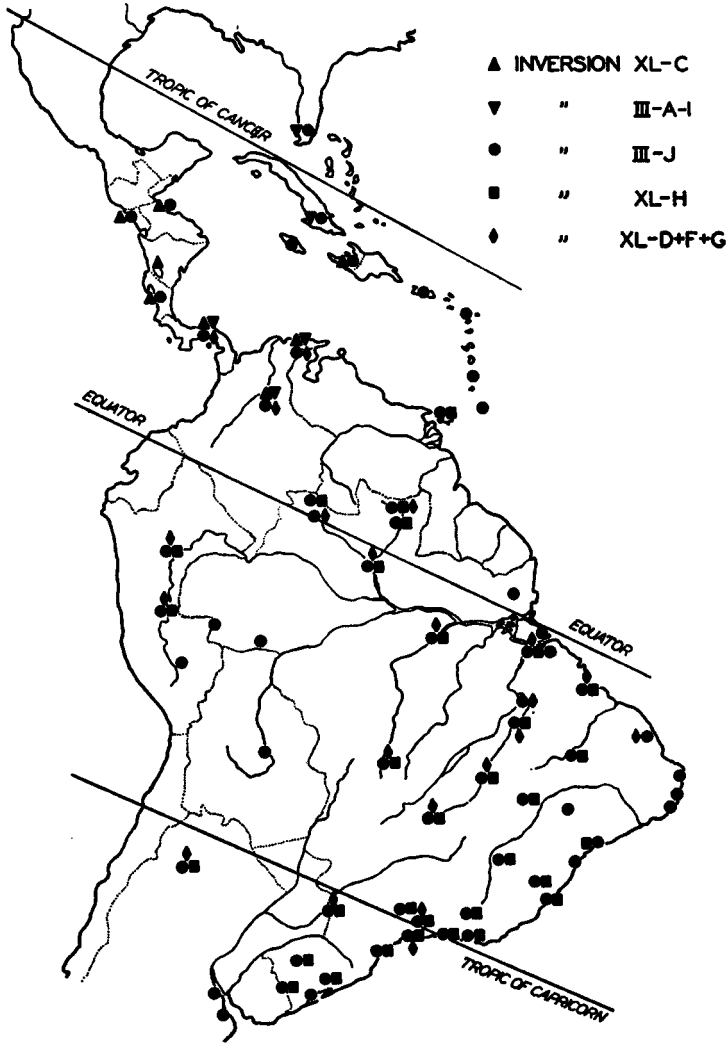

FIG. 2. Known distribution patterns of some inversions and inversion compounds in the chromosomes of *Drosophila willistoni*.

than does the mainland, except for Florida where the species is at its northern boundary. Among the islands, Trinidad and Barbados have more kinds of inversions than Santa Lucia, St. Kitts, and even Puerto Rico and Jamaica, which lie farther away from the continent of South America. Both the number of heterozygous inversions and the number of kinds of inversions show, therefore, descending gradients from the continent to the islands, especially to the small islands.

SIBLING SPECIES

Da Cunha, Burla, and Dobzhansky (1950) and da Cunha and Dobzhansky (1954) found that the amount of polymorphism observed in a population of a species is a function of the environment in which the population lives. One of the environmental variables to be considered in this connection is the presence or absence of closely related competing species. Other things being equal, the amount of

polymorphism is greater in the absence of such competitors than if they are present. Mr. B. Spassky has classified the sibling species of *willistoni* group by inspection of the genitalia of the males. Table 2 and figure 3 report the data on the occurrence of the four sibling species, *D. willistoni, D. equinoxialis, D. tropicalis,* and *D. paulistorum* in the samples from Central America and the West Indies. Relevant data for South American localities have been published in the articles of da Cunha, Burla, and Dobzhansky referred to above. The fifth sibling species, *D. insularis,* is described in the Appendix to the present article.

Only *D. willistoni* has been found in the samples from the islands of Santa Lucia and Barbados. On St. Kitts this species is joined by *D. insularis.* The sample from Trinidad is unfortunately small, but it contains *D. willistoni, D. paulistorum,* and *D. equinoxialis,* with proportions commonly met with in the Amazon Valley. The Greater Antilles are populated by *D. willistoni, D. equinoxialis,* and *D. tropicalis,* none of these species being dominant except locally. In Central

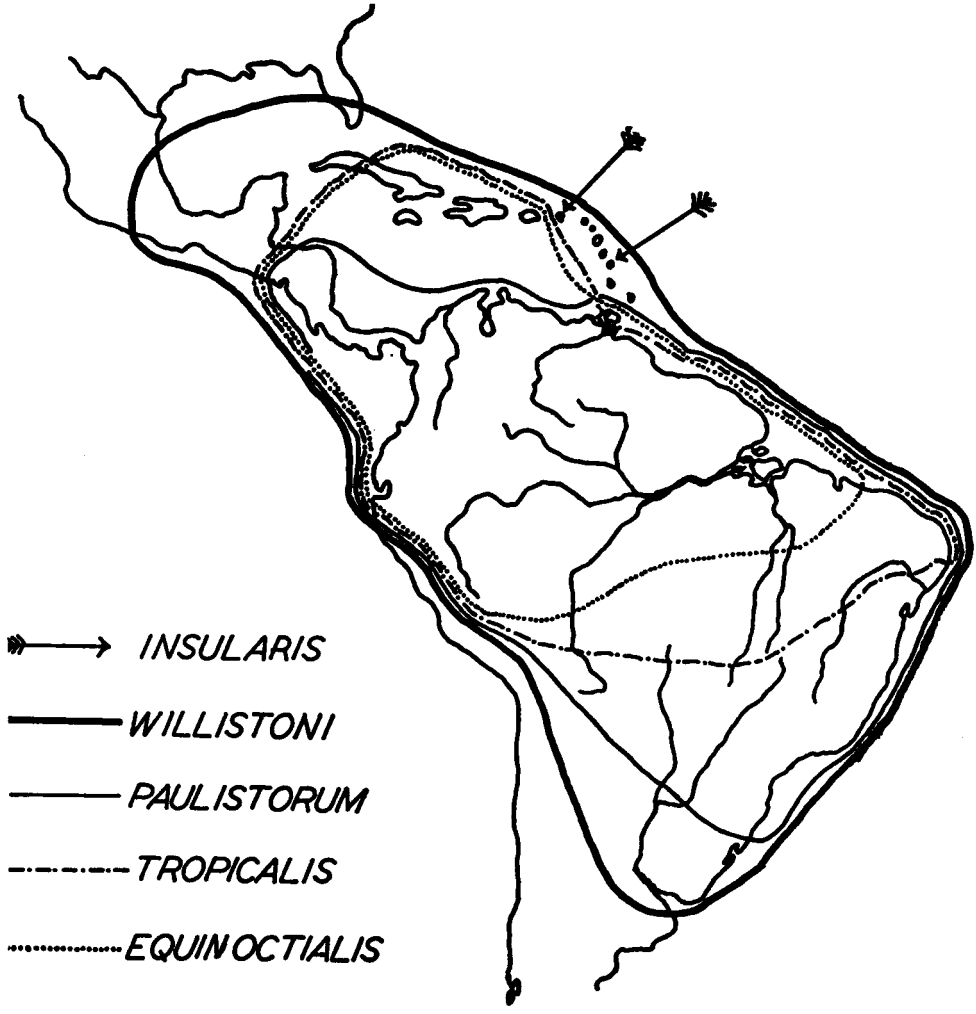

FIG. 3. Approximate distribution regions of the five sibling species related to *Drosophila willistoni.*

TABLE 3. *Observed proportions (in per cent) of the four sibling species in the samples examined*

Sample	*willistoni*	*equinoxialis*	*tropicalis*	*paulistorum*	Flies examined
1. Bucaramanga	78.2	17.7	1.6	2.4	124
2. Santa Marta	14.5	24.3	10.4	50.9	173
3A. Panama	5.3	82.1	3.3	9.2	509
3B. Panama	10.8	29.7	43.2	16.2	74
4A. Costa Rica	21.8	34.4	15.6	28.1	64
4B. Costa Rica	1.4	64.5	30.4	3.6	138
4C. Costa Rica	11.1	88.9	—	—	54
4D. Costa Rica	48.5	51.5	—	—	33
5. Honduras	11.1	34.1	54.8	—	135
6A. Salvador	35.4	44.7	17.9	2.0	246
6B. Salvador	8.8	80.9	10.3	—	68
8. Jamaica	53.9	31.1	15.0	—	254
9A. Cuba	55.3	19.1	25.5	—	47
9B. Cuba	—	75.0	25.0	—	4
9C. Cuba	41.7	—	58.3	—	12
10. Haiti	52.6	29.8	17.5	—	57
11A. Puerto Rico	58.1	2.3	39.5	—	43
11B. Puerto Rico	81.8	18.2	—	—	11
12. St. Kitts	100.0	—	—	—	77*
13. Santa Lucia	100.0	—	—	—	105**
14A. Barbados	100.0	—	—	—	97
14B. Barbados	100.0	—	—	—	18
15A. Trinidad	87.5	10.4	—	2.1	48
15B. Trinidad	12.5	—	—	87.5	8

* Also 4 strains of *Drosophila insularis*.
** Also one *Drosophila insularis*.

America the four sibling species (including *D. paulistorum*) occur together, as they do also in Colombia. *D. paulistorum* is common in Colombia and in Panama, and becomes rare northwards, being recorded in only a single sample from El Salvador.

It is interesting to compare these data with the situation in South America (da Cunha and Dobzhansky, 1954, and unpublished data). In South America *D. willistoni* and *D. paulistorum* vie with each other for dominance, the former being more successful generally in drier to humid and the latter in the superhumid tropical climates. *D. tropicalis* and *D. equinoxialis* are absent in southern Brazil (fig. 3). They appear in central Brazil and in the Amazon Valley, but are usually rare (except that *D. tropicalis* is common in the peculiar habitat of the Savanna on the Isle of Marajo). The four species occur also on the eastern slope of the Andes in Peru, *D. willistoni* and *D. paulistorum* being common and *D. tropicalis* and *D. equinoxialis* relatively rare. As shown in table 3, the situation is reversed in Central America, where *D. paulistorum* is rare (except in Panama and in one sample in Costa Rica), and *D. tropicalis* and *D. equinoxialis* are common.

A note should be taken of the fact that, judging by the structure of their chromosomes, *D. paulistorum* and *D. equinoxialis* are more closely related to each other than to the three remaining siblings. *D. paulistorum* is clearly most at home in South America, and *D. equinoxialis* in Central America and the Greater Antilles. It may be conjectured that these species evolved from allopatric subspecies, one of which occupied South America or a part of it and the other Central America. As reproductive isolating mechanisms developed between the nascent species, beginning with the zone of

contact, they penetrated each other's distribution regions and became largely sympatric, but *D. paulistorum* has not reached the Greater Antilles and *D. equinoxialis* failed to spread to southern and northeastern Brazil (fig. 3). The relationships between the members of the other pair, *D. willistoni* and *D. tropicalis*, are less clear. To judge from their chromosome structures, they are less closely related to each other than *D. paulistorum* is to *D. equinoxialis*. Nevertheless, there is in the data at least a suggestion that *D. tropicalis* is more at home in Central America and the Greater Antilles than it is in South America, while the opposite is true of *D. willistoni*. *D. tropicalis* and *D. willistoni* may have been in the past the northern and the southern subspecies respectively of a single species. However, since the reproductive isolation between all five sibling species is now secure, four of them have become sympatric in the equatorial zone of South America and in the southern part of Central America. *D. willistoni* proved ecologically most versatile; it has acquired the largest distribution area, including the areas of all other siblings and extending beyond them (fig. 3).

The position in the above scheme of historical relationships of the new sibling species, *D. insularis*, is rather baffling. It seems to be endemic on St. Kitts and Santa Lucia, although this may be due to inadequacy of sampling. According to Mr. B. Spassky, the genitalia of males of *D. insularis* resemble most nearly those of *D. willistoni*, but its chromosomes (in the salivary gland preparations) differ from those of *D. willistoni* at least as much as from those of other siblings. This may be a relict species formed on the Lesser Antilles from a source close to *D. willistoni*, and later depressed and restricted to some islands by a new invasion of *D. willistoni* from South America.

Discussion

D. willistoni is one of the rather few organisms for which some direct experimental evidence concerning its rates of dispersal is available (Burla *et al.*, 1950, and unpublished data). These rates, in uniformly favorable two-dimensional environments, happen to be rather low, lower than those in *D. pseudoobscura* and probably in many other species of Drosophila. A slowly moving species might be expected to have a narrow geographic distribution and a pronounced genetic differentiation of local populations. Exactly the opposite is true of *D. willistoni*. Its distribution extends from southern Florida to the Argentine pampa, and some of its chromosomal inversions have been recorded all over this vast area. In fact, *D. willistoni* is exceeded only by some species associated with and transported by man, such as *D. melanogaster* and *D. ananassae*, in having certain chromosomal variants recur throughout the species area. In *D. pseudoobscura*, as well as in the sibling species related to *D. willistoni*, namely in *D. paulistorum* and *D. tropicalis*, a much greater geographic differentiation of populations is observed.

The relative geographic homogeneity of the populations of *D. melanogaster* and *D. ananassae* is due to human intervention. Transport by man is, however, of little importance in *D. willistoni*, which is dominant in natural habitats and not particularly successful in man-modified ones.[2] As stated above, dispersal by active diffusion is far too slow to explain the wide distribution of the chromosomal variants. No matter where in the distribution region a chromosomal inversion may have arisen, it could hardly have reached Florida as

[2] Introduction by man cannot be dismissed as a possibly important agency in some geographically marginal populations, such as those in southern Florida and in the vicinity of Buenos Aires. Prof. Danko Brncic, of the University of Chile, kindly informs the present writer that he has collected *D. willistoni* in a cultivated oasis in coastal Peru. This may well be an introduction by man, since Prof. C. Pavan and the writer found thriving populations of *D. willistoni* and of its three siblings on the eastern (Amazonian) slope of the Peruvian Andes.

well as Argentina, Central America as well as northeastern Brazil, by this method alone. Dispersal by accidental transport, over much greater distances than normal dispersal can reach, has in all probability played an important role in the conquest of new and previously unoccupied territories by *D. willistoni,* and by the adaptively valuable components of the gene pool of this species. Under favorable conditions *D. willistoni* often builds enormous populations, and this should enhance the chances of some individuals of this species being transported passively by hurricanes and other means.

A propensity for passive long-distance transport may enable a land-dwelling species to reach and to secure a foothold in island habitats. This is the way the biota of oceanic islands are formed. Darlington (1938) and Simpson (1956) have argued that the land animals of the Greater Antilles have reached these islands across the sea, from the mainlands of South and Central America. The same applies to the Lesser Antilles, excepting Trinidad. The Lesser Antilles are mostly volcanic in origin; they were never connected with any continent and probably not with each other. Trinidad alone was until a geologically recent time a part of the continent of South America. The data reported in the present article fit neatly into the framework of the Darlington-Simpson views. This is the more remarkable since Simpson was at pains in his work to point out that his inferences apply to generic and higher groups, and not necessarily to species. Our data are concerned with intraspecific variants and with sibling species.

The small sample from Trinidad contained the same three sibling species, *D. willistoni, D. paulistorum,* and *D. equinoxialis,* which are common in equatorial South America. The variety of the inversions found in the Trinidad population of *D. willistoni,* as well as the numbers of heterozygous inversions per individual, are not far from what is known to exist in the Territory of Rio Branco in Brazil, directly to the south (da Cunha, Burla, and Dobzhansky, 1950). Only *D. willistoni* has been found in the samples from Barbados, while the only other islands in the chain of the Lesser Antilles studied, namely St. Kitts, and Santa Lucia, have *D. willistoni* and the endemic *D. insularis.* The genetic composition of the populations of *D. willistoni* becomes progressively depauperate, the order of impoverishment being Trinidad-Barbados-Santa Lucia-St. Kitts. A glance on the map will show that this coincides with the increasing distances between the respective islands and the continent of South America. Only two different inversions have been found in the St. Kitts population, and the average number of heterozygous inversions per individual is near 0.2 (see table 2), which is the lowest number ever found in any population of *D. willistoni* (see da Cunha and Dobzhansky, 1954, the lowest numbers previously recorded being in the state of Bahia, Brazil). This is exactly what one might expect if the island populations are derived from small numbers of migrants passively transported across water. Simpson (1956) has described this as linear dispersal.

The Greater Antilles (Cuba, Jamaica, Hispaniola, and Puerto Rico) are a different, but a parallel, story. Three sibling species occur on these islands, namely *D. willistoni, D. tropicalis,* and *D. equinoxialis.* The same three siblings are common in Central America, where the fourth sibling, *D. paulistorum,* also occurs, but is seemingly rare north of Costa Rica. The genetic composition of the populations of *D. willistoni* shows a progressive decrease in diversity from the continent to the islands. As a matter of fact, one can see a drop in diversity from the continent of South America (Colombia), through Panama, Costa Rica, Salvador and Honduras, Cuba, Jamaica and Haiti, and Puerto Rico (table 2 and fig. 2). This is consistent with the view that *D. willistoni* is native in South America, and that it has spread gradually to Central America, and thence to the

Greater Antilles. Examination of table 1 will show that the Greater Antilles have very few inversions in the X-chromosomes, which are common in Central and South America, and even on Trinidad and Barbados. There are also the striking absences of such chromosomal variants as the inversion compound A&B in the IIL chromosome (except in the small sample from Cuba) and the inversion F in the third chromosome (except again in Cuba). Both variants are common in Central America. The population of Florida behaves as though it were another island population, which is exactly what it is since the species does not live on the continent of North America.

Some interesting details must now be mentioned. The inversion A-1, discovered by Townsend (1952) in Florida, has now turned up in Cuba, in Colombia, and in Panama, but not elsewhere in Central America or on the other islands (table 1 and fig. 1). This is most consistent with Simpson's (1956) view that Cuba received immigrants directly from the continent of South America, and particularly from what is now Colombia. The Florida population might, on this basis, be regarded as derived from Cuba, but it shows a high frequency of the inversion B in the third chromosome which is rare in Cuba. This must be either a result of a later differentiation or of a later introduction. Jamaica does not stand out in our data as being particularly rich in genetic diversity, although Simpson regards it, like Cuba, to be the probable receptor of migrants from the continent and a source of migrants to Hispaniola and Puerto Rico.

Looked at from a different angle, the data show quite a striking correlation between the sizes of the islands and the amount of genetic diversity in their populations. Taking the data in table 2 at face value, the amount of diversity decreases in the sequence Cuba–Hispaniola–Jamaica–Puerto Rico in the Greater Antilles, and in the sequence Trinidad–Barbados–Santa Lucia–St. Kitts in the Lesser Antilles. This is the order of decreasing sizes of the islands, except that Barbados and Santa Lucia should be reversed. This relationship between size of the island and the diversity of the population has been found recently by Lowe (1955) for mammals and reptiles of three islands in the Gulf of California, and by Kramer and Mertens (1938) for lizards on islands near Istria in the Adriatic. Now, the authors just referred to studied typically continental islands lying fairly close to mainlands, while the Antilles are, as indicated above, oceanic islands, which were not parts of any continent recently enough to matter for our purpose.

Larger islands, whether continental or oceanic, will, by and large, have more diversified environments than will be found on smaller islands. A greater diversity of environments means, however, a wider variety of ecological niches available for occupation by the inhabitants. To be sure, the area of an island and the diversity of biotic environments which it offers will not always go hand in hand. A flat sandy bar will offer probably fewer ecological niches (except for sand-dwelling forms) than an island of equal area but having a mountain range, dry and humid valleys, forests as well as grassy fields, etc. Of course, this rule can be expected to hold only in a statistical sense. Proximity and remoteness from the mainland will be obvious disturbing agents. The fact that Trinidad has a genetically richer population of *D. willistoni* than do Santa Lucia and St. Kitts is due to its proximity to the continent of South America more than to its larger size. Nevertheless, the correlation between the areas of the islands and the genetic diversity of their inhabitants is probably genuine. It clearly reflects the operation of a more general rule, which holds in island as well as in continental populations. This rule, stated by da Cunha, Burla, and Dobzhansky (1950) and da Cunha and Dobzhansky (1954) is that the amount of adaptive polymorphism carried in a population is a function of the

diversity of environmental opportunities, of ecological niches, which the population exploits. This is, in turn, a deduction from a still more general proposition, that genetic diversification is a method which life uses to master environmental diversity with which it is confronted. In island populations the composition of the gene pool is governed primarily by historical factors, the chief of which is probably the origin of island biota through chance introduction of immigrants from other islands or continents. The finding that the relationship between the amount of polymorphism and the environmental opportunity is nevertheless discernible in island populations is certainly an additional testimony that this relationship is a real and valid one.

Summary

The genetic polymorphism, as manifested in heterozygosis for chromosomal inversions, has been studied in populations of *Drosophila willistoni* from the West Indies and Central America, and compared with the situation in South American populations. The genetic variability is depauperate in island and marginal populations compared to continental and central ones. The reduction of the genetic variability is especially pronounced on the Lesser Antilles, except for Trinidad which has a population not very different from some continental ones. The island of St. Kitts has the most nearly monomorphic population known in the species *D. willistoni*. The populations of the different islands differ from each other rather more strikingly than do continental populations living at comparable distances. Larger islands tend to have more polymorphism than smaller islands. This agrees with the more general rule, that the amount of adaptive polymorphism in a population tends to be proportional to the diversity of environmental opportunities which this population exploits.

Acknowledgments

As stated in the Introduction, the present investigation became possible only thanks to the sending by Drs. M. R. Wheeler, W. S. Stone, W. B. Heed, and H. L. Carson of samples of *willistoni*-like flies collected in Central America and the West Indies. To these colleagues the writer wishes to express his heartfelt appreciation. Mr. and Mrs. B. Spassky and Mrs. O. Pavlovsky have taken care of the maintenance of the stocks and the preparation of the slides for cytological examination. Drs. Daniel Marien and Karl Koopmann taught to the writer his first lessons in the zoogeography of the West Indies.

Appendix

Drosophila insularis, species nova

Male and female: Arista with 10–11 branches, both numbers being about equally frequent. Front dusky yellow. Anterior orbital shorter than the posterior, middle orbital one-third posterior. Two prominent orals. Face yellow. Carina short and broad, not sulcate. Cheeks yellow, their greatest width about one-tenth greatest diameter of eye. Eyes bright red with a short brownish pile.

Acrostichals in 6 to 8 rows, often quite irregular. Thorax dusky yellow, darker than in *Drosophila willistoni* Sturtevant, pleurae lighter. Anterior and middle sternopleurals at most half as long as the posterior and much thinner. Legs greyish yellow. Abdomen yellow with diffuse dark brown bands expanded in the middle and fading out laterally. Wings clear, proportions like in *Drosophila willistoni* but darker in color, especially in old individuals.

Length of body ♀ 2.9–3.2 (mean 3.03), ♂ 2.5–2.8 (mean 2.65) mm; wings ♀ 2.1–2.3 (mean 2.16), ♂ 2.0–2.1 (mean 2.04) mm.

Reproductive organs of the adults, eggs, larvae, and pupae like those in *Drosophila willistoni,* except for minute but constant differences in the external male genitalia which will be described in a separate publication by Mr. B. Spassky.

Remarks—Closely related to *Drosophila willistoni,* from which it differs by a slightly larger body size and a darker

pigmentation. These differences, though fairly clear in flies grown in similar environments, are not reliable for identification of single specimens grown in diverse environments. Reproductive isolation between *Drosophila insularis* and *Drosophila willistoni* is however complete, since cross-insemination occurs only with difficulty, and the few hybrids that are produced are wholly sterile.

Geographic Distribution—Four strains derived each from a single female collected on the island of St. Kitts in January 1956; one strain derived from a female collected on the island of Santa Lucia in January 1956.

Literature Cited

Burla, H., A. B. da Cunha, A. R. Cordeiro, Th. Dobzhansky, C. Malogolowkin, and C. Pavan. 1949. The *willistoni* group of sibling species of *Drosophila*. Evolution, **3**: 300–314.

da Cunha, A. B., H. Burla, and Th. Dobzhansky. 1950. Adaptive chromosomal polymorphism in *Drosophila willistoni*. Evolution, **4**: 212–235.

——, and Th. Dobzhansky. 1954. A further study of chromosomal polymorphism in *Drosophila willistoni* in its relation to the environment. Evolution, **8**: 119–134.

Darlington, P. J. 1938. The origin of the fauna of the Greater Antilles, with discussion of dispersal of animals over water and through the air. Quart. Rev. Biol., **13**: 274–300.

Dobzhansky, Th. 1950. The chromosomes of *Drosophila willistoni*. J. Heredity, **41**: 156–158.

——, H. Burla, and A. B. da Cunha. 1950. A comparative study of chromosomal polymorphism in sibling species of the *willistoni* group of *Drosophila*. Amer. Natur., **84**: 229–246.

Lowe, Ch. H. 1955. An evolutionary study of island faunas in the Gulf of California, Mexico, with a method for comparative analysis. Evolution, **9**: 339–344.

Kramer, G., and R. Mertens. 1938. Rassenbildung bei west-istrianischen Inseleidechsen in Abhängigkeit von Isolierungsalter und Arealgrösse. Arch. Naturgeschichte, **7**: 189–234.

Simpson, G. G. 1956. Zoogeography of West Indian land mammals. Amer. Mus. Novitates, **1759**: 1–28.

Townsend, J. I. 1952. Genetics of marginal populations of *Drosophila willistoni*. Evolution, **6**: 428–442.