

Chromosomal polymorphism in *Drosophila subobscura* populations from Barcelona (Spain)

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1. INTRODUCTION

Drosophila subobscura, the commonest and most widespread of the indigenous European species of *Drosophila*, has six pairs of chromosomes, all of which, except the small 'dot' chromosome, show structural polymorphism. In this respect *D. subobscura* differs from the American species of the same group, *D. pseudoobscura*, in which the structural polymorphism is practically limited to one chromosome, the third, but *subobscura* resembles the neotropical *D. willistoni* in which 42 inversions have been described. However, there is an important difference since in *willistoni* there are a number of small inversions which frequently recombine to give rise to a large number of different structural types (da Cunha, 1955), whereas in *subobscura* the independent inversions of the chromosome form complexes which are rarely destroyed by recombination, i.e. they are alomeric complexes (Levitan, 1958). Possibly the polymorphism of *D. subobscura* is more akin to that of the North American *D. robusta* (Carson, 1958a) but in the latter species the number of different inversions is much lower.

Clearly the peculiarities of *D. subobscura* merit further study especially as data relating to frequency and distribution of the inversion types is still fragmentary. After a few early papers, e.g. Philips *et al.* (1944), recording the occurrence of polymorphism, the first report of quantitative data was that of Stumm-Zollinger (1953), which dealt with populations from Switzerland, France and Portugal, but this account recorded only heterozygote combinations in the populations. In another paper Richter & Hündler (1955) reported qualitative variation in the occurrence of inversions in a wide area which included Austria, Holland, Italy, Great Britain, Palestine and Syria. In more recent work quantitative data were included, as in the papers by Kunze-Muhl *et al.* (1958), dealing with two populations from Vienna; by Goldschmidt (1958) with one from Oranim in Israel; by Knight (1961) with two populations from Scotland; by Sperlich (1961) with a population from the Lipari Islands, Italy; and, finally, by Kunze-Mühl & Sperlich (1962) with a population from Formia in central Italy, and also one from each of the islands of Ponza and Ventonene. The present paper deals with quantitative estimates of inversion frequency in two populations from the district of Barcelona, Spain.

2. MATERIAL AND METHODS

One population, referred to hereafter as B, was derived from wild flies frequenting a garden in the urban area of Barcelona at a height of approximately 100 m. above sea level. The other population called R came from the Rabassada, an area of *Quercus ilex* and *Pinus halepensis* woodland, situated about 10 km. from Barcelona, at a height of approximately 400 m. above sea level. There are microclimatic differences between the two sites. First, there is the 300 m. difference in elevation. Secondly, they differ in orientation to the range of hills of Tibidabo which bound Barcelona on the inland side by being either SE. or NW. of the range. Such differences in orientation, coupled with differences in altitude, are responsible for a mean difference of temperature of 3–4° C.

The B population was sampled in May 1961. Chromosome structure was determined on 66 males (132 autosomal sets and 66 X chromosomes) by crossing the trapped males to virgin females of the Küssnacht strain, which is homozygous for the standard order in all chromosomes. From the progeny of these crosses 7 larvae were analysed to ensure a high probability (0.985) of observing both members of each pair of homologous chromosomes from the isolated males. Two samples were analysed in the case of the R population. In one, flies were trapped in May and, in the other, flies were caught in November. 70 males from the first and 50 from the second trapping were crossed to the Küssnacht females but only one larva from each set of progeny was analysed. The chromosomes were stained with acetic orcein (60%) and lactic acid (40%). The symbolism used here for the chromosomal orders follows the procedure of Mainx.

3. RESULTS

(i) *General*

There is well-marked homogeneity in the frequency of the inversion types in the Barcelona populations. This is true of the comparisons between the two sites for flies collected in spring and also for the two samples collected at the R site in spring

Table 1. *Test of homogeneity of samples from the Barcelona populations*

B and R sites sampled in spring		
Chromosomal elements	Degrees of freedom	χ^2
A	2	2.25
J	1	0.04
U	5	3.34
E	5	0.91
O	8	5.35
R site sampled in spring and autumn		
A	2	2.05
J	1	0.68
U	2	3.81
E	4	1.83
O	4	6.05

In no case is the probability less than 0.1.

and autumn. Table 1 shows the distribution of χ^2 according to structural type. If we calculate for the O chromosome, a χ^2 for O_{st} against all the other inverted orders, we get a χ^2 of 6.05 for one degree of freedom ($P < 0.05 > 0.02$), a statistically significant difference, but, since we are comparing one type against 18 alternatives, little confidence can be placed on the reality of this apparent difference.

From these data we might infer that the microenvironmental differences between the two sites B and R do not significantly influence the chromosomal proportions in the two populations which occupy these two habitats, nor is there any evidence of seasonal variation. This agrees with the evidence of Kunze-Mühl *et al.* (1948) who also failed to detect seasonal differences in Vienna, with the exception of the frequency of E_8 against a series of other types as in the O_{st} *versus* the rest, and these authors also attributed this difference to chance.

(ii) *Comparisons between the Barcelona and other populations*

Table 2 shows the array of 27 different chromosome types in the populations according to the authors noted above. Figure 1 shows the frequency in order from left to right of the chromosomal types in the populations of Edinburgh (Knight, 1961), Vienna (Kunze-Mühl *et al.*, 1958), Barcelona, Ponza, Formia and Ventonene (Kunze-Mühl & Sperlich, 1962), Lipari (Sperlich, 1961) and Oranim (Israel) (Goldschmidt, 1959). The order of these populations corresponds to decreasing latitude. The data from Formia, Ponza, and Ventonene have not been pooled, in spite of the small distance separating these populations, since there was heterogeneity in some of the chromosomal orders.

A general feature of the distribution of chromosomal types is the high frequency of the standard order in the more northern populations. In the other chromosome orders only U_{1+2} shows a similar trend with an apparent exception in the case of the population from Vienna. In A_2 , E_{1+2+9} , $E_{1+2+9+12}$ and O_{3+4+2} there is evidence of an inverse relationship since these types are more frequent in southern populations. J_1 shows a similar pattern, except for the Israel population, where J_1 is as infrequent as J_{st} , while J_{3+4} is the most frequent type. In most of these cases where there is a north-south gradient, the Barcelona array is intermediate between the arrays in Vienna and the Italian populations near Naples, in spite of the small differences in latitude between the Spanish and Italian localities. Only in the Iberian populations does O_{3+4+7} appear to play a significant role in the polymorphism of the O chromosome. According to Stumm-Zollinger's data this type is also frequent in Lisbon. In all other populations, even those from southern France, north of the Pyrenees, its frequency is very low.

O_{3+4} is rather frequent in Barcelona but its distribution seems to be rather irregular, and this is also true of E_8 which is rarer in Barcelona. U_{1+2+8} and E_{1+2} have high frequencies in Barcelona and the Italian populations but are rare or missing in Vienna, Edinburgh and Israel (Oranim). The same trend is evident in O_{3+4+8} but with lower frequency in the populations of both Mediterranean peninsulas.

Table 2. *Frequency of the chromosomal types*

	Oranin (Israel) <i>n</i> = 115	Lipari <i>n</i> = 74	Formia <i>n</i> = 64	Ponza <i>n</i> = 134	Ventonene <i>n</i> = 84	Barcelona B <i>n</i> = 132	Barcelona R	
							Spring <i>n</i> = 70	Fall <i>n</i> = 50
A _{st}	6.9	35.1	35.5	35.8	33.3	51.5	64.1	75.9
A ₁	1.7	5.4	12.5	13.4	23.8	6.0	7.6	10.3
A ₂	91.4	59.5	50.0	50.8	42.9	42.4	28.2	13.8
J _{st}	7.0	6.8	17.2	11.9	11.9	29.3	28.5	22.0
J ₁	3.5	93.2	82.8	88.1	88.1	70.7	71.4	78.0
J ₃₊₄	85.2	—	—	—	—	—	—	—
U _{st}	—	2.7	1.6	3.7	—	4.5	4.2	6.0
U ₁₊₂	2.6	27.0	32.8	38.1	32.1	48.4	51.4	64.0
U ₁₊₂₊₈	—	51.4	20.3	29.1	32.1	45.4	42.8	26.0
U ₁₊₂₊₃	27.0	8.1	28.1	13.4	13.4	0.7	—	—
U ₁₊₂₊₆	—	5.4	4.7	11.2	10.7	0.7	—	4.0
U ₁	—	—	—	—	1.2	—	1.4	—
U ₁₊₂₊₇	68.7	—	1.6	0.8	—	—	—	—
U ₁₊₂₊₄	1.7	5.4	10.9	3.7	10.7	—	—	—
E _{st}	1.7	1.4	10.9	5.2	8.3	35.5	40.0	38.0
E ₁₊₂	—	29.7	39.1	41.0	22.6	24.4	24.8	30.0
E ₁₊₂₊₉	27.0	14.9	17.2	15.7	22.6	13.3	10.0	14.0
E ₁₊₂₊₉₊₁₂	55.7	39.1	17.2	15.7	16.7	19.2	20.0	12.0
E ₁₊₂₊₉₊₃	—	10.8	3.1	9.7	13.1	1.4	1.4	2.0
E ₈	15.7	4.1	12.5	12.7	16.7	5.9	4.3	4.0
O _{st}	—	1.4	10.9	5.2	7.1	38.3	37.1	20.0
O ₃₊₄	7.0	64.8	50.0	49.2	46.4	20.3	24.3	34.0
O ₃₊₄₊₇	3.5	1.4	—	—	—	22.5	20.0	20.0
O ₃₊₄₊₈	—	14.8	9.4	16.4	11.9	10.5	7.1	16.0
O ₃₊₄₊₂	85.2	9.4	4.7	10.4	9.5	3.0	2.8	2.0
O ₃₊₄₊₁	1.7	2.7	9.3	6.7	3.6	2.2	2.8	4.0
O ₃₊₄₊₂₂	—	—	—	3.0	1.2	1.5	4.3	—
O ₃₊₄₊₁₇	1.7	1.4	—	0.8	—	—	1.4	—
O ₃₊₄₊₂₊₇	0.9	—	—	—	—	—	—	—
O ₃₊₄₊₂₊₁₆	—	2.7	14.1	4.5	16.7	0.7	—	—
O ₆	—	—	—	—	1.2	—	—	—
O ₅	—	—	—	—	—	—	—	—
O ₇	1.7	—	—	—	—	0.7	—	4.0
O ₃₊₄₊₆	—	1.4	—	0.8	—	—	—	—

A₁ and especially U₁₊₂₊₆ are not rare in Vienna and the Italian populations but their frequency is lower in Barcelona. Type U₁₊₂₊₃, very rare in Barcelona, has rather high frequency in the other Mediterranean populations but has not been reported from Edinburgh or Vienna. O₃₊₄₊₁₆, which is rare in Barcelona, is rather frequent in some Italian populations. O chromosome types, rare in Barcelona, namely O₃₊₄₊₁ and O₃₊₄₊₂₂, are unimportant in any of the populations so far studied.

(iii) *The relative frequency of genotypes*

Table 3 shows the frequency of the four pairs of large autosomes found in the 66 males from the B site compared with the frequencies expected from the Hardy-Weinberg law. In the χ^2 test, chromosomal types of low frequency have been pooled.

of D. subobscura in several populations

Barcelona R + B n = 252	Kahlenberg (Vienna) n = 18	Schafberg (Vienna) n = 360	Vienna K + S n = 378	Dalkeith (Escocia) n = 60	Heriot (Escocia) n = 60	Edinburgh D + H n = 120
60.4	50.0	57.2	56.9	100	100	100
7.4	38.9	35.6	35.8	—	—	—
32.1	11.1	7.2	7.4	—	—	—
27.6	55.5	56.7	56.6	81.7	88.3	85
72.3	44.5	43.3	43.4	18.3	11.7	15
—	—	—	—	—	—	—
4.7	55.5	69.7	69.0	15.0	—	7.5
52.3	25.0	11.8	12.4	85.0	81.7	83.3
40.8	2.8	1.1	1.2	—	—	—
0.4	—	—	—	—	—	—
1.2	13.9	14.4	14.4	—	—	—
0.4	2.8	2.2	2.2	—	18.3	9.1
—	—	0.8	0.8	—	—	—
—	—	—	—	—	—	—
37.2	75.0	76.9	76.8	91.7	100	95.8
25.6	5.6	3.1	3.2	8.3	—	4.1
12.5	8.3	6.4	6.5	—	—	—
17.9	—	—	—	—	—	—
1.5	—	—	—	—	—	—
5.1	11.1	13.6	13.5	—	—	—
34.3	72.2	74.4	74.3	65.0	73.3	69.1
24.1	8.3	10.6	10.5	35.0	26.7	30.8
21.3	—	0.3	0.3	—	—	—
10.6	—	1.4	1.3	—	—	—
2.7	—	1.4	1.3	—	—	—
2.7	2.1	2.2	2.2	—	—	—
2.0	2.8	0.5	0.6	—	—	—
0.4	—	—	—	—	—	—
—	—	—	—	—	—	—
0.4	—	—	—	—	—	—
—	11.1	8.1	8.2	—	—	—
—	2.8	1.1	1.2	—	—	—
1.2	—	—	—	—	—	—
—	—	—	—	—	—	—

The test shows no significant discrepancy between the observed and expected frequencies. It does not necessarily follow, however, that the populations are in equilibrium, since we have no information about frequencies at different stages of the life-cycle or in successive generations (see Wallace, 1958; and Novitski & Dempster, 1958).

(iv) *The level of heterozygosity*

From the array of genotypes in population B we can calculate the average number of heterozygous inversions per individual. This is shown in Table 4 along with other comparable data. Since the latter refer only to males they only provide averages for autosomal inversions. The crude average is shown on the left of the table while a

Table 3. *Genotypes in the B population from Barcelona*

Genotypes	Observed frequency	Expected frequency	Genotypes	Observed frequency	Expected frequency
J _{st} /J _{st}	7	5.37	U _{st} /U _{st}	0	0.11
J _{st} /J ₁	24	27.27	U _{st} /U ₁₊₂	3	2.98
J ₁ /J ₁	35	33.37	U _{st} /U ₁₊₂₊₈	3	2.70
			U _{st} /U _x	0	0.10
E _{st} /E _{st}	8	8.25	U ₁₊₂ /U ₁₊₂	16	15.88
E _{st} /E ₁₊₂	12	11.12	U ₁₊₂ /U ₁₊₂₊₈	28	29.27
E _{st} /E ₁₊₂₊₉	5	6.46	U ₁₊₂ /U _x	2	1.00
E _{st} /E ₁₊₂₊₉₊₁₂	11	9.33	U ₁₊₂₊₈ /U ₁₊₂₊₈	14	13.06
E _{st} /E ₁₊₂₊₉₊₃	1	0.72	U ₁₊₂₊₈ /U _x	0	0.90
E _{st} /E ₈	2	2.87	U _x /U _x	0	0.01
E ₁₊₂ /E ₁₊₂	4	3.55			
E ₁₊₂ /E ₁₊₂₊₉	4	4.26	O _{st} /O _{st}	12	8.97
E ₁₊₂ /E ₁₊₂₊₉₊₁₂	6	6.15	O _{st} /O ₃₊₄	8	9.72
E ₁₊₂ /E ₁₊₂₊₉₊₃	0	0.47	O _{st} /O ₃₊₄₊₇	12	11.22
E ₁₊₂ /E ₈	1	1.89	O _{st} /O ₃₊₄₊₈	4	5.61
E ₁₊₂₊₉ /E ₁₊₂₊₉	2	1.17	O _{st} /O _x	2	4.11
E ₁₊₂₊₉ /E ₁₊₂₊₉₊₁₂	3	3.57	O ₃₊₄ /O ₃₊₄	4	2.48
E ₁₊₂₊₉ /E ₁₊₂₊₉₊₃	1	0.27	O ₃₊₄ /O ₃₊₄₊₇	4	5.95
E ₁₊₂₊₉ /E ₈	1	1.10	O ₃₊₄ /O ₃₊₄₊₈	2	2.97
E ₁₊₂₊₉₊₁₂ /E ₁₊₂₊₉₊₁₂	1	2.48	O ₃₊₄ /O _x	4	2.18
E ₁₊₂₊₉₊₁₂ /E ₁₊₂₊₉₊₃	0	0.40	O ₃₊₄₊₇ /O ₃₊₄₊₇	5	3.32
E ₁₊₂₊₉₊₁₂ /E ₈	4	1.59	O ₃₊₄₊₇ /O ₃₊₄₊₈	1	3.43
E ₁₊₂₊₉₊₃ /E ₁₊₂₊₉₊₃	0	0.01	O ₃₊₄₊₇ /O _x	3	2.52
E ₁₊₂₊₉₊₃ /E ₈	0	0.12	O ₃₊₄₊₈ /O ₃₊₄₊₈	3	0.80
E ₈ /E ₈	0	0.21	O ₃₊₄₊₈ /O _x	2	1.34
			O _x /O _x	0	0.42

$$U_x = U_{1+2+3} + U_{1+2+6}; \quad O_x = O_7 + O_{3+4+1} + O_{3+4+2} + O_{3+4+17} + O_{3+4+22}$$

corrected average is given on the right-hand side to enable us to compare data with the evidence from populations from Switzerland, France, Portugal and Israel (Stumm-Zollinger, 1953; Stumm-Zollinger & Goldschmidt, 1959). The correction involves adding the frequency of heterozygotes, expected in the X chromosome of females, according to the binomial distribution.

Table 5 shows the index of free recombination (IFR) (Carson, 1955) which refers to the length of chromosome free of inversions. Using the estimated heterozygote frequency in females and the observed frequency in males we can make a valid estimate of IFR which, of course, applies only to females since recombination does not occur in males. For this comparison the relative lengths of the chromosome used by Stumm-Zollinger & Goldschmidt (1959) have been used. Also, to allow comparison with the data of Sperlich (1961) and Kunze-Mühl & Sperlich (1962), the IFR has also been calculated for autosomes using the relative lengths of the inversions quoted by these authors.

The average number of inversions in Barcelona is the highest so far recorded for populations of *D. subobscura*, and as expected, the IFR has one of the lowest values.

Table 4. Average number of inversions in heterozygous condition, per individual

Locality	Total average	Average in the autosomes
Barcelona (Spain)	5.1*	4.5
Biaz (France)	4.8	
Formia (Italy)	4.7*	4.4
Tellay (France)	4.6	
Garonne (France)	4.4	
Lisbon (Portugal)	4.2	
Ventonene (Italy)	4.2*	3.9
Eilon (Israel)	3.9	
Ponza (Italy)	3.8*	3.5
Thun (Switzerland)	3.8	
Vitznau (Switzerland)	3.7	
Qirat'Anavim (Israel)	3.5	
Lipari (Italy)	3.5*	3.3
Chateauneuf (France)	3.4	
Vienna (Austria)	3.4*	3.1
Bex (Switzerland)	3.3	
Fetan (Switzerland)	3.3	
Küssnach (Switzerland)	3.3	
Oramin (Israel)	3.3	
Eglisau (Switzerland)	3.2	
Oberdorf (Switzerland)	3.2	
Braunwald (Switzerland)	2.4	

* This figure has been obtained adding to the observed frequency of heterozygosis in the autosomes, the expected frequency of heterozygosis in the X chromosomes of the females, based on the frequencies of the chromosomal orders of the X chromosome.

In the high number of inversions the Barcelona populations resemble populations from southern France, Lisbon and Italy, especially Formia. Thus the high degree of structural heterozygosity appears to be a general feature of southern European populations while, in central Europe and especially in Scotland and Israel, the level of heterozygosity is lower.

In Table 6 we have calculated the contribution of the different chromosomes to the total level of heterozygosity of the population. There is good agreement between the data from Barcelona and Lisbon. Both Iberian populations, along with the one from Qirat'Anavim (Israel), show greater heterogeneity in the contribution of different chromosomes to the heterozygosity of the population. A further trait, common to the Iberian populations, is the relatively high contribution of chromosome E and the low contribution of chromosomes U, J and A.

4. DISCUSSION

In general, the chromosomal polymorphism in the populations of *D. subobscura* in Barcelona resembles that in populations occurring in similar environmental conditions, which seem to be more important than spatial separation. Thus, the

Table 5. *Index of free recombination*

Locality	IFR*	Locality	IFR†
Biaz (France)	79.4 ± 1.2	Formia (Italy)	78.2
Barcelona (Spain)	80.3‡	Barcelona (Spain)	79.8
Tellay (France)	82.1 ± 1.2	Ventonene (Italy)	82.1
Lisbon (Portugal)	82.5 ± 1.6	Ponza (Italy)	82.5
Garonne (France)	83.3 ± 1.0	Lipari (Italy)	83.8
Bex (Switzerland)	84.1 ± 1.2	Vienna (Austria)	84.8
Thun (Switzerland)	85.0 ± 1.1		
Chateauneuf (France)	85.0 ± 0.9		
Eglisau (Switzerland)	85.2 ± 0.7		
Fetan (Switzerland)	85.3 ± 1.1		
Vitznau (Switzerland)	86.0 ± 1.2		
Küssnach (Switzerland)	86.6 ± 1.6		
Oberdorf (Switzerland)	87.5 ± 0.8		
Braunwald (Switzerland)	87.8 ± 0.9		
Qirat'Anavim (Israel)	88.8 ± 0.6		
Eilon (Israel)	89.6 ± 0.8		
Oranim (Israel)	89.8 ± 1.3		
Dalkeith (Scotland)	92§		
Heriot (Scotland)	95§		

* IFR calculated with the relative length of the inversions according to Stumm-Zollinger & Goldschmidt (1959).

† IFR calculated with the relative length of the inversions according to Kunze-Muhl & Sperlich (1962).

‡ IFR calculated adding the estimated frequencies of heterozygous combinations of the inversions in the X chromosome to the data found for the autosomes in the males.

§ IFR estimated from the frequencies of the inversions.

data from Barcelona agree more closely with those from Lisbon (Stumm-Zollinger) than those from Garonne, a site situated some 30 km. south of Toulouse, France, which is a good deal nearer. However, there is greater environmental similarity between Barcelona and Lisbon than between either and Garonne, according to the bioclimatic map of the Mediterranean region (Gaussen *et al.*, 1962). A point of further interest is the occurrence at low frequency of O_{3+4+7} north of the Pyrenees although in the Iberian populations it is of major importance. Evidently this chromosomal order has circumvented the Pyrenean barrier but probably finds conditions on the northern side less favourable than the southern side of the mountain range.

Apart from the resemblance to the Lisbon populations, polymorphism in the Barcelona populations resembles that found in southern Italy, especially Formia; both the frequency of chromosomal types and also the level of heterozygosity are rather similar. Nevertheless in Barcelona there is some evidence of northern affinity. As shown in Fig. 1 Barcelona is intermediate between the Vienna and Formia populations. Stumm-Zollinger's data relating to Swiss populations indicate frequencies of chromosomal types not very different from those found in Vienna and therefore more similar to the Barcelona than to the Italian populations. Again, we

Table 6. Contribution of the different chromosomes to the heterozygosity of the population

Chromosomes	A (%)	J (%)	U (%)	E (%)	O (%)
Switzerland:					
Fetan	17.6	16.0	27.8	15.6	23.0
Braunwald	18.7	15.8	27.7	15.1	22.8
Thun	19.7	14.6	29.5	12.3	23.9
Vitznau	14.2	14.2	24.1	17.5	30.1
Küsnacht	17.4	15.9	30.0	16.4	20.4
Eglisau	16.9	16.9	31.7	12.8	21.6
Oberdorf	18.2	17.2	31.8	13.3	19.5
Bex	12.8	12.3	29.6	22.2	23.0
France:					
Chateaufneuf	13.3	12.7	26.0	22.5	25.4
Tellay	10.0	10.1	27.8	22.0	30.1
Biaz	17.0	12.5	25.4	23.8	21.4
Garonne	12.2	11.6	24.5	16.6	35.1
Portugal:					
Lisbon	17.4	9.6	11.4	38.2	23.4
Spain:					
Barcelona	12.1	7.1	13.3	40.1	27.4
Israel:					
Qiryat'Anavim	4.8	26.9	22.3	39.0	7.0

find that distance is not of paramount importance in the differentiation of the populations, but in this case climatic conditions seem unrelated to the observed differences. Climatic differences appear unimportant also with respect to the differences between Barcelona and Formia. Both places have a Mediterranean maritime climate with a July isotherm of 24°C. in Barcelona and 25°C. in Formia, with a higher rainfall in the latter. In the Italian population there is also some evidence of features characteristic of drier habitats. In Israel, according to Goldschmidt (1958), and also in the Italian populations, according to Kunze-Mühl & Sperlich (1962), *D. subobscura* is found in relatively high numbers only during a few weeks in the spring. The hot and dry summer leads to a drastic reduction of numbers and the autumn recovery is weak. In Barcelona there is also a peak in the annual occurrence in April and May but in November there is a second peak, not very different from that encountered in spring, and this suggests that conditions are generally more favourable for the development of this species in the Barcelona area.

Thus, as in other *Drosophila* species, chromosomal polymorphism seems to be relevant to ecological features, especially those associated with differences in latitude and the July isotherm. Prevosti (1954, 1955) found an association between the July isotherm and body-size in the species. Both types of variation could be inter-related but there is no confirmatory evidence on this point. There is also evidence of differentiation between populations according to distance, e.g. J_{3+4} and U_{1+2+7} in Israel and O_{3+4+7} in the Iberian peninsula.

Another feature of the Barcelona population is its high level of heterozygosity or low level of IFR which it shares with Lisbon, populations from the south of France and also the continental populations from Italy. According to the data reported by da Cunha & Dobzhansky (1954) for *D. willistoni* and by Carson (1955, 1958) for *D. robusta*, low IFR values are found in the central areas of the distribution of a species. This is not so evident in the case of *D. subobscura* on existing data. The central and west Mediterranean regions are not the central areas of its distribution but they may not be far from the most favourable areas for the development of the species. Hadorn *et al.* (1952), in a trapping expedition in S.W. Europe, collected the

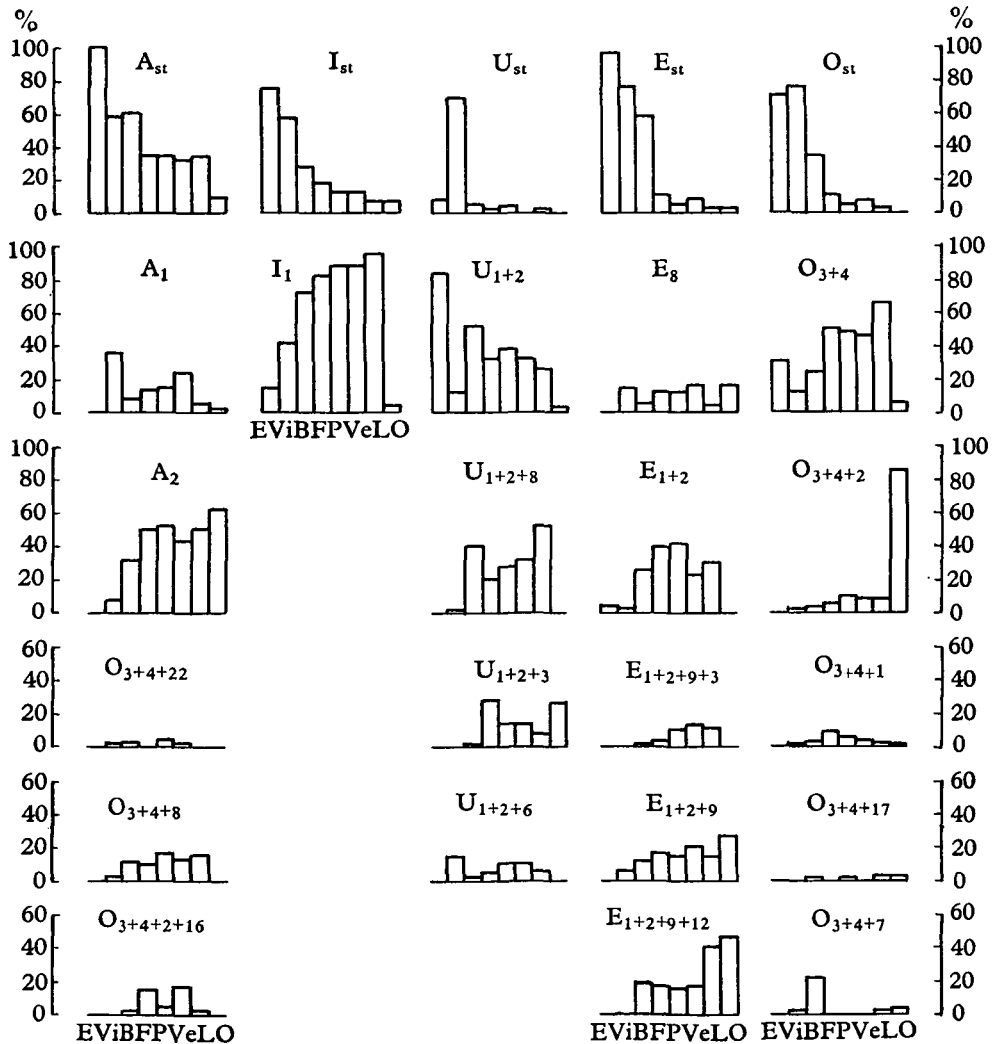


Fig. 1. Frequencies of the chromosomal orders of *Drosophila subobscura* in several localities. E = Edinburgh, Vi = Vienna, B = Barcelona, F = Formia, P = Ponza. Ve = Ventonene, L = Lipari, O = Oranim. The order of the localities corresponds to its decreasing latitude.

highest number of *subobscura* in populations from the south of France, just north of the Pyrenees, and the species is also abundant in Barcelona. However, the data from Formia do not suggest optimal conditions for this species at this site. In the island populations from Ventonene, Ponza and Lipari (not far from Formia), in spite of the insular condition, the IFR is lower than in mainland populations, e.g. Vienna. This suggests that lower values of this index are characteristic of Italian populations generally. There is some evidence which is consistent with the generalizations of American authors in the high values of IFR in Scottish and Israel populations (Knight, 1961; Goldschmidt, 1958), which may be regarded as marginal areas. Both Swiss and Viennese populations are intermediate between these and the southern European ones.

SUMMARY

1. Chromosomal polymorphism in two populations of *D. subobscura* from Barcelona has been analysed and compared with the polymorphism which has been reported from other populations.

2. In spite of microclimatic differences between the Barcelona sites, there is no evidence of differences in the frequency of inversion types nor of seasonal differences within one of these sites.

3. Regularities in the array of frequencies of chromosomal types in Barcelona and other populations suggest that the polymorphism is mainly adaptive although there is also evidence of differences due to distance which are not obviously associated with differences in habitat.

4. In general the index of free recombination gives higher values in the marginal populations of *D. subobscura*, but further data are needed to arrive at a definite conclusion on this point since the present evidence is rather ambiguous.

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