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Distances between Populations of *Drosophila subobscura*, Based on Chromosome Arrangement Frequencies

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Summary. Distances between populations of *Drosophila subobscura*, based on differences in the frequencies of chromosomal arrangements have been estimated using data from about 65 populations. The distances have been calculated using the formula:

$$D = \frac{1}{2r} \sum_{j=1}^{r} \sum_{k=1}^{s_j} |p_{1jk} - p_{2jk}| ,$$

where r is the number of loci or chromosomes (in the case of chromosomal polymorphism) considered, p_{1jk} the frequency of the allele or chromosomal arrangement k in the locus or chromosome j in the first population, and p_{2jk} the corrsponding value in the second population.

The main conclusion drawn from this analysis is that historical as well as adaptive factors are important in explaining the geographical distribution of chromosomal arrangements in *D. subobscura*.

In general, isolated populations maintain primitive features in their chromosomal polymorphism. This is reflected in a tendency to similarity between these populations. Also, a very sharp effect of geographical barriers is detected in the distribution of the chromosomal arrangements.

Two main factors are considered responsible for the strong effect that isolation has on geographical distribution of chromosome arrangements. These factors are the non-recurrence of rearrangements and the difficulty of establishing in one population the supergenes originated in another area, because of lack of coadaptation with the gene pool of the recipient population.

Introduction

The differentiation of populations through chromosomal inversion polymorphism can be expected to have peculiar features when compared with other genetic polymorphisms. Two main factors account for this. 1. Inversions are non-recurrent changes. 2. Inversions originate supergenes which can tie together more or less coadapted genes, having special possibilities to develop heterozygous superiority based on compound dominance and to be subjected to high selection coefficients.

In the polymorphisms arising from recurrent mutation the same alleles are expected to appear in different populations. On the other hand, because of the non-recurrence of inversions, when the same chromosomal arrangement is found in distant populations this is usually an indication of migration or gene flow between these populations. Therefore the geographical distribution of inversion polymorphism can be expected to be more strongly influenced by geographical barriers and by historical factors than single locus polymorphisms. Moreover, as it is likely that supergenes are subjected to high selection coefficients, its distribution would probably be specially affected by local adaptive selection.

The present data on the variability in natural populations are in agreement with these expectations. Single locus polymorphisms, as detected by differences in the electrophoretic mobilities of proteins, show more uniform geographical distribution than chromosomal polymorphisms. The data of Ayala *et al.* (1971), comparing the polymorphism in allozymes and chromosomal arrangements in island and continental populations of *Drosophila willistoni*, are an example of this. Also, in more general terms, Powell (1973) arrives at the same conclusion. However, these data can be accepted only with some caution. Within electrophoretic variants different allelic molecules can be included. In this case, the picture of the geographic distribution of these polymorphisms could change. A first hint about this possibility are the results of Bernstein *et al.* (1973) on the genetic variants in the xanthine dehydrogenases of the *virilis* group of *Drosophila*, with different sensitivities to heat denaturation.

In the present paper the characteristics of the geographical distribution of chromosomal polymorphism will be analysed in one species well suited for this purpose, *Drosophila subobscura* Coll. It is the commonest indigenous species of Drosophila in Europe and has a wide geographical distribution, corresponding to an area with complicated physiogeography and considerable diversity of ecological and climatic conditions. It is found throughout Europe, except above latitude 61° North, and also in North West Africa as far as the boundaries of the Sahara desert, in the Canary, Madeira and Azores islands and in Western Asia.

The karyotype of *D. subobscura* has 6 pairs of chromosomes, 5 pairs of achrocentrics and one pair of dots. One peculiarity of this species is its high degree of inversion polymorphism in the 5 pairs of achrocentrics. In the A chromosome (the X chromosome) 10 different arrangements have been described, 3 in the J, 11 in the U, 7 in the E and 23 in the O. At present, we have data (obtained by different authors, see Material and Methods) from 65 populations, distributed throughout most of the species distribution area. The main gap in these data corresponds to eastern Europe.

The analysis of the chromosomal polymorphism is approached quantitatively in the present paper. A general distance among the populations, based on differences between frequencies of the arrangements, is calculated. Powell *et al.* (1972) applied a similar method to the analysis of polymorphism of the third chromosome of *Drosophila pseudoobscura*. *Drosophila subobscura* offers the possibility of calculating general distances taking into account the polymorphism in all five chromosomes.

Material and Methods

Data about the following 65 populations were used:

Dröbak, Norway (Sperlich, 1964)
Heriot and Dalkeith, Scotland (Knight, 1961)
Gröningen, Holland (Krimbas, 1964)
Fontainebleau and Montpellier, France (Prevosti, unpublished)
Lagrasse, France (Prevosti, 1964a)
Zürich, Switzerland (Burla and Götz, 1965)
Vienna, Austria (Kunze-Mühl et al., 1958)
La Coruña, Bilbao, Toro, Huelva and Ibiza, Spain (de Frutos, 1972)
Málaga and Valencia, Spain (Prevosti, 1966)
Barcelona, Spain (Prevosti, 1964b)
Caralps, Spain (Prevosti, 1968)
Guia, Las Mercedes, Esperanza, Las Cañadas, Vilaflor, Los Tilos, El Cedro and El Pinar, Canary Islands (Prevosti, 1971)
Terreiro da Lutta and Curral des Freiras, Madeira Island (Prevosti, 1972)
Corte, Corsica (Prevosti, unpublished)
Carasco and Alfano, Italy (Prevosti, unpublished)
Formia, Ponza Island and Ventotene Island, Italy (Kunze-Mühl and Sperlich, 1962)
Alghero, Foresta di Burgos and Sette Fratelli, Sardinia (Prevosti, unpublished)
Etna, Sicily (Prevosti, unpublished)
Lipari Islands, Italy (Sperlich and Kunze-Mühl, 1963)
Ustica Island, Italy (Sperlich and Kunze-Mühl, 1963)
Fruska, Gora, Yugoslavia (Andjelkovic and Sperlich, 1973)
Thessaloniki, Greece (Pentos-Daponte, 1964)
Pindos and Parnes, Greece (Krimbas and Alevizos, 1973)
Antalya, Silifke, Tarsus, Bursa, Zonguldak, Samsun and Trabzon, Turkey (Götz, 1967)
Rasht, Chalus and Shahi, Iran (Götz, 1967)
Oranim, Israel (Goldschmidt, 1956)
Gabes, Tunis (Orangerie and Belvedere), Tabarka and Ain Draham, Tunisia (Jungen, 1968)
Tangier, Marocco (Götz, 1965)
Asni, Essaouira and Agadir, Morocco (Prevosti, in press).

Among all these populations a simple distance was calculated, based on the differences between the frequencies of chromosome arrangements, as follows:

$$D = \frac{1}{2r} \sum_{j=1}^{r} \sum_{k=1}^{s_j} |p_{1ik} - p_{2jk}| . \qquad (1)$$

Here r is the number of different chromosomes (5 in the case of *D. subobscura*); s_j is the number of different arrangements in the chromosome j; p_{1jk} and p_{2jk} are the frequencies of the arrangement k of the chromosome j in the populations 1 and 2, respectively.

The logic of this distance corresponds to the following model. For each population and chromosome we have a set S of arrangements, which has s classes (s is the number of arrangements in the corresponding chromosome) with f_j equal elements ($j = 1, 2, 3, \ldots s$) in the s_j class. If we reduce proportionally f_j to f'_j to make $\sum_{j=1}^{s} f'_j = 1$, f'_j will correspond to the frequency of the arrangement j, and the set S will be reduced to S'. Then, the distance between S'_1 and S'_2, corresponding to the arrangement frequencies of the same chromosome in two populations, will be the symmetric difference between these sets: $D_{1,2} = (S'_1 - S'_2) \cup (S'_2 - S'_1)$. This value will

Table 1. *Arrangement distances*

	Dröbak	Dalkeith	Gröningen	Fontainebleau	Vienna	Zürich	Huelva	Barcelona
Dalkeith	0,307							
Gröningen	0,152	0,276						
Fontainebleau	0,271	0,225	0,150					
Vienna	0,260	0,370	0,187	0,195				
Zürich	0,235	0,300	0,112	0,120	0,128			
Huelva	0,782	0,657	0,695	0,580	0,640	0,623		
Barcelona	0,615	0,465	0,529	0,412	0,469	0,445	0,259	
Formia	0,780	0,657	0,693	0,607	0,606	0,609	0,373	0,309
Foresta di Burgos	0,879	0,790	0,801	0,764	0,760	0,761	0,396	0,490
Etna	0,941	0,846	0,873	0,813	0,818	0,817	0,414	0,524
Fruska Gora	0,560	0,505	0,470	0,442	0,342	0,391	0,577	0,460
Thessaloniki	0,668	0,545	0,592	0,514	0,434	0,500	0,502	0,392
Silifke	0,763	0,643	0,680	0,584	0,581	0,610	0,414	0,357
Trabzon	0,751	0,619	0,675	0,582	0,519	0,587	0,418	0,342
Chalus	0,709	0,489	0,636	0,548	0,531	0,549	0,595	0,489
Oranim	0,938	0,924	0,906	0,899	0,849	0,883	0,670	0,757
Orangerie	0,947	0,867	0,864	0,782	0,837	0,795	0,573	0,574
Agadir	0,927	0,834	0,844	0,803	0,789	0,792	0,428	0,498
Las Mercedes	0,931	0,699	0,846	0,749	0,802	0,792	0,404	0,485

oscillate between *0* and *2*; but if we want to have values between *0* and *1* we can divide by *2*, as is done in (*1*). If in order to obtain a general distance we are interested in considering all the chromosomes together, the single distances for each chromosome can be added and, dividing the sum by the number of chromosomes, we will have values between *0* and *1*. This method has the same basis as the one used by Powell et al. (1972) but it seems to reflect more clearly and directly the idea of distance.

We chose this distance because it seemed to us the simplest one and to express better the actual differences between the populations, without any previous assumptions about the processes generating these differences. A general discussion, from a biological point of view, of the requirements to be fulfilled by a genetic distance is published elsewhere (Prevosti, 1974). Here we will only summarize the main conditions to be fulfilled by a distance, to be used according to our purpose.

1st. It should be independent of its generating processes or factors.

2nd. The distance between two populations should be independent of the other populations analysed.

3rd. A genetic distance should be independent of the number of alleles present in the loci considered and of the frequencies of these alleles.

4th. In general terms it is considered more convenient to calculate the genetic distance from gene frequencies than from genotypic frequencies.

5th. It would be very convenient to have a genetic distance of easy statistical handling. This is difficult, since the distributions of gene frequencies or their transformations rarely fit the usual statistical models.

Probably the main weakness of the distance used here is that it does not fulfil this last requirement. However, the numerous distances proposed in the literature usually do not fulfil others of the conditions mentioned above. This does not mean that at least some of these distances are not useful for specific purposes. After obtaining a simple and unbiased idea about the genetical differentiation of the populations, based on one method like that used here, it would probably be advantageous to use a more sophisticated distance to test specific hypotheses or to clarify some features of the differentiation.

Results

Table 1 presents the distances among 20 representative populations. The remaining populations have been omitted in order to make the publication of this table easier.

The Effect of long Distance

The main differentiation in chromosomal arrangements is found between populations from northern Europe and the Southern range of the distribution of the species. With the exception of Gabes-Oranim (see table 2), the populations having an arrangement distance of over 0,900 are always ones from the northern range of distribution of the species, while the others are from the South. This tendency to a strong North-South differentiation is also evident in the arrangement distances between Gröningen and the populations from Tunisia, South Morocco and the Canary and Madeira islands, as well as between the latter and Vienna or Zürich. In all these cases the distances are over 0,800 or around this value. Fontainebleau has an arrangement distance from the southern populations oscillating between 0,750 and 0,800.

Table 2. *Populations with genetic distances over 0,900*

	Arrangements distance	Geographical distance (in km.)
Dröbak — Etna	0,941	2.465
Dröbak — Oranim	0,938	3.479
Dröbak — Tunisia	0,942*	2.605*
Dröbak — Morocco	0,909*	3.355*
Dröbak — Canary Islands	0,928*	4.064*
Heriot Dalkeith } — Oranim	0,930*	3.878*
Heriot — Tunisia	0,907*	2.369*
Gröningen — Oranim	0,906	3.197
Gabes — Oranim	0,914	2.309

* Mean distance between the populations from the indicated areas.

among 20 representative populations

Formia	Foresta di Burgos	Etna	Fruska Gora	Thessaloniki	Silifke	Trabzon	Chalus	Oranim	Orangerie	Agadir
0,452										
0,451	0,177									
0,501	0,681	0,696								
0,363	0,590	0,630	0,315							
0,413	0,646	0,667	0,544	0,340						
0,399	0,587	0,648	0,439	0,269	0,286					
0,514	0,635	0,649	0,444	0,408	0,574	0,438				
0,642	0,618	0,623	0,795	0,740	0,698	0,712	0,805			
0,568	0,518	0,535	0,782	0,733	0,696	0,698	0,760	0,891		
0,485	0,329	0,302	0,666	0,661	0,642	0,631	0,710	0,730	0,321	
0,429	0,380	0,253	0,659	0,566	0,604	0,551	0,460	0,644	0,615	0,430

Although the area of distribution of the species is much wider in the West-East sense, the differences in the arrangements are much lower than in the North-South sense. The largest North-South distances hardly exceed 4.000 km., but the distance between the Canary Islands and North Iran exceeds 6.000 km.

Table 3. *Genetic distances between populations more than 4.000 Km. distant*

Dröbak — Canary Islands	930*
Heriot Dalkeith — North Iran	520*
Gröningen — Shahi (N. Iran)	673
Fontainebleau — Shahi Chalus (N. Iran)	561*
Lagrasse Chalus Montpellier Shahi (N. Iran)	465*
Spain — North Iran	600*
Huelva — Silifke Tarsus Samsum Trabzon (Anatolia)	435*
Huelva — Oranim	670
South Morocco — Anatolia	600*
South Morocco — North Iran	760*
South Morocco — Oranim	750*
Madeira — Anatolia	540*
Madeira — North Iran	450*
Madeira — Oranim	670*
Canary Islands — Anatolia	590*
Canary Islands — North Iran	490*
Canary Islands — Oranim	650*

* Mean distance between the populations from the indicated areas.

The populations over 4.000 km. apart, as well as their corresponding arrangement distances, are inserted in table 3. Only between Dröbak and the Canary Islands is North-South the main component of the distance, and only in this case does the arrangement distance exceed 0,900. In general, the arrangement distance oscillates between 0,500 and 0,700, but in two cases, South Morocco-Oranim and South Morocco-North Iran, the distance is over 0,700. On the other hand, the populations from Madeira and the Canary Islands have arrangement distances from North Iran of under 0,500. Huelva and Antalya also have an arrangement distance under 0,500; and the same is true of Lagrasse and Montpellier versus Chalus and Shahi in North Iran.

The Effect of Isolation

According to Prevosti (1974, in press) the chromosomal polymorphism of *D. subobscura* in the Canary and Madeira islands shows features of primitivism. The populations of these islands are considered old isolated populations, keeping the features of the period in which they became established or isolated. A comparison, by means of the arrangement distance, of the populations from these islands with other populations in which isolation may also have played a part is interesting from this point of view.

The distances between the population from Las Mercedes in the Canary Islands and all the other populations studied are given in the map of Fig. 1. We chose Las Mercedes, because the vegetation of this locality is the relic tertiary laurisilva. Whereas the arrangement distances between the populations from the Canary and Madeira islands are small, the values are clearly higher between the islands and South Morocco. This is a quantitative confirmation of the conclusion arrived at qualitatively in a previous paper (Prevosti, 1974 in press).

The differences between the islands and the mainland can not be explained by drift, because of the great similarity found among the islands. The populations from South Morocco show African characteristics, which are not found in the islands. This is supported by the arrangement distances between the populations from South Morocco and the population of Tangier, as well as between South Morocco and Tunisia. In spite of the greater geographical distances between these populations, the arrangement distances are all under 0,400, whereas those between South Morocco and the islands are over 0,400 (see table 4 and Fig. 1). The lack of African features in the populations from the islands can best be interpreted as an indication of early establishment, before the differentiation of the African features in the mainland.

The comparison of the populations from the Atlantic Islands with those from the European side of the Central and West Mediterranean area strengthens this interpretation (see fig. 1). The populations from Sicily and nearby islands (Lipari and Ustica) are the most closely related, according to the arrangement distance, to the populations from the Atlantic Islands. The populations from Sardinia follow this relationship; then come the populations from Tangier and southern Spain, some populations from southern continental Italy and the population from Corsica. The distances to the remaining west Mediterranean populations are similar or higher than to South Morocco. Therefore, the populations more similar to those from the Atlantic Islands are from another isolated area, the central Mediterranean islands, where influences from the European and African mainland arrive with difficulty.

In other areas in which isolation is to be expected, we also found a tendency to similarity to the populations from the Atlantic Islands. Such is the case for populations from North Iran which, according to Götz (1967), can be considered truly marginal and isolated, and show arrangement distances from the Atlantic Islands lower than others less separated in geographic distance, like those from Tunisia, Greece, Anatolia and Israel. Also the arrangement distances from the Atlantic Islands to the Scottish populations are lower than to North European and Central European populations in general, even including Fontainebleau in France.

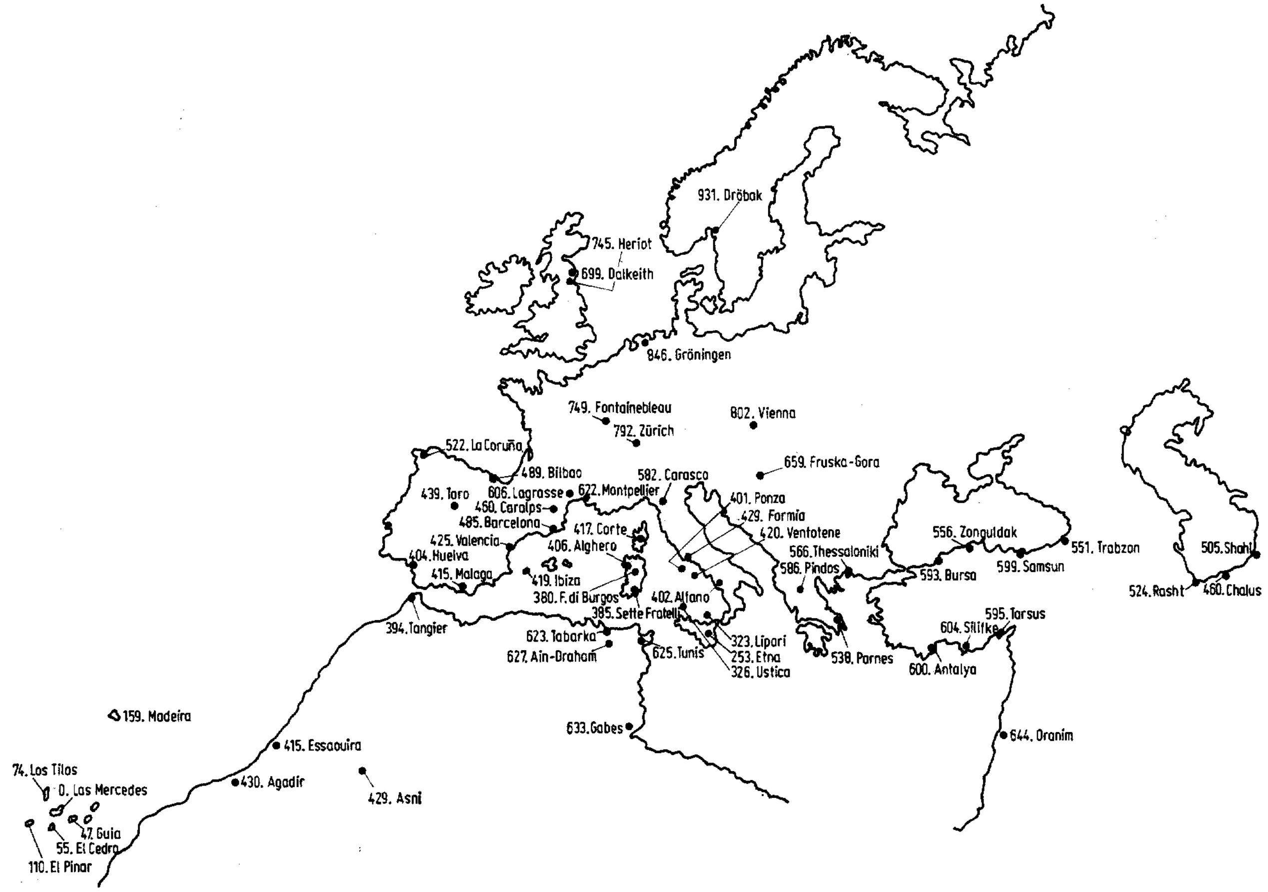

Fig. 1. Arrangement distances to Las Mercedes (Canary Islands) (in order to make the figures on the map shorter, the distances are multiplied by 1000)

Table 4. *Arrangement distances between populations from South Marocco and other African populations*

Tangier	Gabes	Orangerie	Belvedere	Tabarka	Ain Draham	
Asni	0,209	0,333	0,287	0,318	0,342	0,303
Essaouira	0,215	0,370	0,335	0,344	0,352	0,337
Agadir	0,228	0,323	0,321	0,292	0,319	0,316

The Effect of Barriers

Here we shall present some examples demonstrating that geographical barriers, either sea or a mountain range, have a sharp effect in increasing the arrangement distance.

The correlation between geographic distances and arrangement distances is not linear. The relationship between both distances $\left(\frac{\text{arrangement distance}}{\text{geographical distance}}\right)$ decreases considerably when the geographic distance increases. We are studying this relationship, but for the moment it seems convenient to analyze some cases in which the raw data demonstrate the barrier effect. For this purpose we will mainly compare arrangement distances between populations separated by similar geographical distances. To make the comparison easy, apart from the figures corresponding to the arrangement distances and the geographical distances in kilometers, in tables 5 to 9, the ratio $\frac{\text{A. d.}}{\text{G. d.}} \times 1000$ is also given. As the relationship between both distances is not linear, this ratio has little meaning for the comparison of populations separated by different geographical distances.

The data presented in table 5 illustrate the effect of the Gibraltar straits. Tangier and the nearby populations of Málaga and Huelva, on the other side of the straits, show arrangement distances between 2 and 3 times greater than do populations separated by similar geographical distances but which are both on the same side of the straits (see the distances Málaga-Huelva, or Asni-Essaouira, Asni-Agadir and Essaouira-Agadir). High figures for the ratio, arrange-

Table 5. *The effect of the Gibraltar Straits*

	Valencia	Málaga	Huelva	Tangier	Asni	Essaouira
Málaga	0,187 465 0,402					
Huelva	0,202 612 0,330	0,104 228 0,456				
Tangier	0,314 625 0,502	0,285 160 1,781	0,296 193 1,534			
Asni		0,425 720 0,590	0,415 680 0,610	0,209 550 0,380		
Essaouira		0,392 810 0,483	0,383 720 0,532	0,215 650 0,331	0,123 189 0,650	
Agadir		0,443 900 0,492	0,428 825 0,518	0,228 750 0,304	0,064 182 0,351	0,133 135 0,992

Comparison of Spanish with Moroccan populations:

━━━ Populations neighbourt to the straits
— — — Populations neighbour to the straits on one side, far from the strait on the other side.

Comparison between populations from the same continent:

——— Neighbour populations
— — — Not neighbour populations.

In tables 5, 6, 7, 8 and 9 for each comparison are given three figures: First figures = arrangements distance; second figures = geographical distances (in km.); third figures = $\frac{\text{arrangem entsdistance} \times 1000}{\text{geographical distance}}$

ment distance: geographical distance, are also an indication of discontinuity in the distribution of the chromosomal arrangements conditioned by the straits. When we compare more distant populations, the effect of the straits is partially masked. This is because it is pooled with the differences corresponding to the mainland space separating the populations. Nevertheless, compare the distances Tangier-Valencia, and Málaga or Huelva-Asni, Essaouira or Agadir on the one hand, with Málaga or Huelva-Valencia, and Tangier-Asni, Essaouira or Agadir on the other hand. The arrangement distances between the populations on different sides of the straits are almost double.

The Central Mediterranean is another interesting area, in which we can compare the populations from Tunisia in Africa with those from continental and insular Italy (see table 6). Here the sea barrier is considerably wider and so are the arrangement distances also. The situation is also complicated by the existence of islands, big ones like Sardinia and Sicily and small ones such as Ustica, Lipari, etc. Three clearly differentiated areas can be distinguished: continental Italy, the great islands of Sardinia and Sicily, and Tunisia. Within these areas the arrangement differentiation is small (see the boxes encircled by straight, thin line, in table 6); between these areas the differences are considerably greater. Between different islands, Sardinia-Sicily, Ustica-Sicily, and Ustica-Sardinia, the arrangement distances are a little greater than between populations from the same continental area, but the geographical distances are also greater between the islands. The similarity between the islands is remarkable. The same situation was found when the populations from the Atlantic islands were compared with one another or with the nearby African mainland. Since the populations from the Italian islands are most like those from the Atlantic islands, it appears logical to conclude that isolation has maintained primitive features in both areas. The arrangement distances between the islands and Tunisia are a little greater than between the islands and continental Italy.

Consideration of the European populations situated outside the Mediterranean area allows us to detect the effect of the straits of Dover. There is also in this case a clear effect of isolation and again its consequences seem to be the conservation of more primitive features in the insular populations. Among the seven populations compared in table 7, the most different are the British ones. The arrangement

Table 6. *Genetic and geographical distances in the Tyrrhenian Area*

	Formia	Alfano	Alghero	Foresta di Burgos	Sette Fratelli	Ustica	Etna	Tunis	Ain-Draham
Alfano	0,125 207 0,603								
Alghero	0,465 445 1,045	0,465 598 0,777							
Foresta di Burgos	0,452 392 1,153	0,457 555 0,825	0,080 63 1,269						
Sette Fratelli	0,456 413 1,106	0,463 508 0,911	0,129 168 0,767	0,099 126 0,785					
Ustica	0,322 285 1,129	0,327 245 1,334	0,297 458 0,648	0,262 400 0,655	0,291 325 0,895				
Etna	0,451 407 1,108	0,448 265 1,690	0,225 645 0,348	0,177 585 0,302	0,203 503 0,403	0,184 192 0,958			
Tunis	0,569 575 0,989	0,556 585 0,950	0,516 443 1,164	0,478 420 1,185	0,524 282 1,855	0,504 332 1,518	0,515 430 1,197		
Ain-Draham	0,573 653 0,877	0,560 693 0,837	0,536 418 1,281	0,513 400 1,282	0,539 282 1,911	0,509 443 1,143	0,527 560 0,941	0,063 130 0,484	
Gabes	0,634 879 0,721	0,619 846 0,731	0,544 762 0,713	0,527 678 0,777	0,557 563 0,989	0,533 588 0,906	0,550 601 0,910	0,152 340 0,447	0,161 345 0,466

━━━ Comparison of populations from the islands with closest populations from the African mainland

▬ ▬ ▬ Comparison of Sardinia with the African and European mainland.

═══ Comparison of Sicily and nearby islands with the African and European mainland.

⋯⋯ Comparison of the African mainland with Continental Europe.

— — — Comparisons between different islands.

——— Comparisons within the same continent or island.

distances between continental and British populations are greater than between continental populations, whatever the geographical distance. There is only one exception: Fontainebleau has a greater arrangement distance to Dröbak than to the British populations.

The arrangement distances between the Canary Islands and Scotland are lower than between the Canary Islands and the other populations from non-Mediterranean Europe. This supports the view that in the British populations, as in the Italian islands, there is preservation of primitive features.

Another case of interest is the comparison of Greek with Anatolian populations separated by the Dardanelles and the Bosphorus. The barrier here separates western from eastern populations, instead of northern from southern ones. Moreover, around the Black Sea there is a land connexion, non-existent in the situations analysed before. Owing to these factors the populations from both sides of these straits could be less differentiated than in other situations. However, these populations (see table 8) show greater arrangement distances than the populations situated on the same side of the straits, when the geographical distances are of similar magnitude. Compare the arrangement distances between Parnes or Thessaloniki and Antalia or Bursa, with those between Silifke-Bursa, Silifke-Zonguldak and Antalia-Zonguldak.

Finally we will analyze the effect of another kind of barrier, a mountain range. We have data on 4 populations situated on both sides of the Pyrenees. Two populations, Caralps in the south of the range and Lagrasse in the north, are almost 100 km. apart. We have two other populations, Barcelona, about 100 km. southwards of Caralps, and Montpellier, at approximately 100 km. North-East of Lagrasse (table 9). The arrangement distance is clearly greater

Table 7. *The effect of the straits of Dover*

	Dröbak	Heriot	Dalkeith	Gröningen	Fontainebleau	Vienna
Heriot	0,307 913 0,336					
Dalkeith	0,307 913 0,336	0,083 16 5,187				
Gröningen	0,152 760 0,200	0,290 677 0,428	0,276 689 0,400			
Fontainebleau	0,271 1,354 0,200	0,263 906 0,290	0,225 921 0,244	0,150 601 0,249		
Vienna	0,260 1,326 0,196	0,399 1.558 0,256	0,370 1.571 0,235	0,187 884 0,211	0,195 1.010 0,193	
Zürich	0,235 1.373 0,171	0,331 1.222 0,270	0,300 1.237 0,242	0,112 663 0,168	0,120 450 0,266	0,128 591 0,216

━━━ Comparison between British and Continental populations
——— Comparison between Continental populations
……… Comparison between British populations

Table 8. *The effect of the Dardanelles and Bosphorus*

	Pindos	Parnes	Thessaloniki	Antalya	Bursa	Silifke
Parnes	0,119 273 0,435					
Thessaloniki	0,162 162 1,000	0,200 272 0,735				
Antalya	0,322 865 0,372	0,265 632 0,419	0,366 789 0,463			
Bursa	0,248 647 0,383	0,232 510 0,454	0,288 519 0,554	0,110 395 0,278		
Silifke	0,305 1.061 0,287	0,231 893 0,258	0,340 1.066 0,318	0,120 296 0,405	0,138 603 0,222	
Zonguldak	0,306 924 0,331	0,268 878 0,305	0,312 745 0,418	0,136 514 0,264	0,098 267 0,367	0,154 594 0,259

Comparison of Greek with Anatolian populations:

━━━ Populations not far from the straits;
——— Populations more distant from the straits.
……… Comparison between populations from the same continent.

between the populations separated by the mountain range. On the southern side it is interesting to note that Valencia, 385 km. southwards of Caralps, shows an arrangement distance to this population of only 0,184. Also, the arrangement distance between Barcelona and Montpellier, separated by the Pyrenees,

Table 9. *Effect of the Pyrenean range*

	Montpellier	Lagrasse	Caralps
Lagrasse	0,130 117 1,111		
Caralps	0,251 197 1,274	0,223 89 2,505	
Barcelona	0,262 281 0,932	0,229 189 1,211	0,136 104 1,307

Comparison of populations situated at different side of the Pyrenees:

━━━ Population close to the Pyrenees;

——— At least one of the populations not close to the Pyrenees;

……… Comparison between populations situated at the same side of the Pyrenees.

is greater than between Barcelona and Valencia (306 km. apart) and Montpellier and Fontainebleau (541 km. apart), which are 0,123 and 0,211, respectively.

Discussion

It should be specially noted that the work of Dobzhansky and his school in several species of Drosophila, both in natural and experimental populations, has accumulated a great deal of evidence supporting the fact that chromosomal polymorphisms in Drosophila have an adaptive value.

The existence of North-South clines in several arrangements of *D. subobscura* (see Prevosti, 1964b; Krimbas, 1964) was an indication of their adaptive significance, also found in this species. The greater arrangement distances found between northern and southern populations than between eastern and western ones corroborates this conclusion. Thus, at this point the use of arrangement distances only gives new support to an already established conclusion.

A less documented fact derived from the present analysis is the importance of historical factors in the geographical distribution of chromosomal polymorphism.

As indicated in the introduction, simple consideration of the origin of the chromosomal arrangements induces us to believe that historical factors should be important. Inversions are practically non-recurrent changes that have happened in just one population. Their presence in other populations requires migration or gene flow. Radial distributions of chromosome arrangements, such as those found by Mainx *et al.* (1956) in *Liriomyza urophorina*, constitute evidence of this non-recurrent origin and distribution by gene flow. Of course, the situation of the original population, as well as the facilities for gene flow or migration to other populations can be greatly important for the future geographic distribution of a new arrangement.

Even the adaptive significance of an arrangement is conditioned by its site of origin. The supergene originated by an inversion ties together an aggregate of more or less coadapted genes operating well in the environment of the locality where it appeared. This original assemblage of genes can be expected also to influence the future fate and distribution of the inversion. Then, on theoretical considerations, the interaction between historical factors and the adaptive value of the arrangements seems to be the main cause of distribution of the gene arrangements of the chromosomes. The data of *Drosophila subobscura* analysed here are easily interpreted from this point of view.

For both the Atlantic and the Italian islands there is much more similarity among the islands than between the islands and the neighbouring mainland. In a previous paper (Prevosti, 1974 in press) the situation in the Atlantic islands was analysed; it was concluded that primitive features have been kept in their populations. The comparison carried out in the present paper allows us to give a more general significance to that conclusion, since we found a similar situation in central Mediterranean islands. The similarity between the populations from the islands of both areas is further evidence for the primitivism of their populations. In fact, in the central Mediterranean islands we found that the populations were more like those from the Atlantic islands. The lower arrangement distances between the Atlantic islands and Scotland than between the Atlantic islands and less distant populations from continental Europe are another indication of the same tendency. In this case the barrier of the straits of Dover would help to conserve some primitivism in British populations. Finally, yet another case supports the contention that isolation contributes to the maintenance of primitivism. This is the similarity between the populations from the Atlantic islands and those from North Iran, in the eastern range of the distribution of the species, which according to Götz (1967) are marginal and isolated.

The general picture given by the present analysis is the existence of two main areas of differentiation in the populations of *D. subobscura*, corresponding to the European and the African mainlands. More local differentiations are found in subareas separated by less powerful barriers, like the Iberian Peninsula or Israel. On the other hand, more isolated areas keep some degree of primitivism and show a tendency to have more similar chromosomal arrangements than other non-isolated but equally distant areas. These areas are the Atlantic islands, Scotland and North Iran on the periphery of the distribution of the species; and the Central Mediterranean islands not in this periphery.

The presence of an inversion in one geographical area depends on the probability of its appearing in situ, or of arriving there from other populations, but in both cases the inversion has to become established.

Because of the smaller area involved, it is less probable that a new arrangement will appear in the islands than in the mainland; also, the probability of arrangements arriving from other populations to the islands is lowered by isolation. Logically, both of these factors should contribute to the conservatism of island populations. However, consideration of the data on the Drosophilidae of the Hawaiian islands (Carson *et al.*, 1970) leads us to suspect that the difficulty of establishing new arrangements could also contribute significantly to the conservatism of the isolated populations of *D. subobscura*. In the Hawaiian Drosophilidae the establishment of inversions has been much more frequent than in the insular populations of *D. subobscura*. In Hawaii, the factors of isolation and small area are both present, and we have no reason to assume that the probability of new arrangements appearing is higher in the Hawaiian Drosophilids. Instead, the biology of the Hawaiian Drosophilids, especially the small number of individuals in the populations, as well as the different evolutionary phase of the species of these islands compared with *D. subobscura* (this is a much older species), could explain a higher probability of new rearrangements being established in Hawaii.

The probability of establishing a new inversion in a large and old population, with a genotypical structure already very advanced in the process of coadaptation, is possibly very low. This seems to be particularly the case when the new inversion arrives with migrants from other populations. In continental areas, the establishment of a new arrangement is statistically more probable, since its passage to neighbouring populations through genetic flow can be a steady and slow process allowing for gradual coadaptation. In isolated areas, because of the lack of this steady genetic flow, the integration of the genes or supergenes brought with the migrants becomes more difficult.

The fall in viability observed by Prevosti (1957) in the F_2 of crosses between stocks of different geographical origin is experimental support for diminished coadaptation between the gene pools of geographically separated populations. Similar data have been obtained for other species by other authors (see Vetukhiv, 1954; Brncic, 1954; Wallace, 1955). A logical consequence of this diminished coadaptation is that it is difficult for a supergene originating in one population to become established in another differentiated population when carried there by migrants. The difficulty of establishment could be more important than the restriction of migration in explaining the strong effect of apparently rather weak barriers, like the Gibraltar Straits or the Pyrenees. At least, the effect has to be explained by interaction of both factors. Sperlich and Feuerbach (1966) concluded that the chromosomal polymorphism of *D. subobscura* corresponds to the type of rigid polymorphism. This conclusion refers especially to buffering properties of the genotypical structure of the population, in reaction to variations in environmental factors. Perhaps, another expression of this rigidity could be the difficulty of integrating into the gene pool the supergenes arrived from different populations. In cases such as the Pyrenees or the Gibraltar Straits, in which the barrier separates two mainland areas, the sharpness in differences between the populations on both sides is probably due to an asymmetric rate of gene flow. In these populations the genetic flow from one side of the barrier is very limited, whereas it is open on the other side. This situation restricts the arrival of genetic variants from the other side of the barrier, but at the same time favours integration in the gene pool of the continental area where the population is situated.

Saura and Lakovaara (1973) studied allozyme polymorphism in 20 systems, and González-Duarte *et al.* (1973) studied two esterases and one alcohol dehydrogenase of *D. subobscura*. The differences between populations were much smaller than in chromosomal polymorphism. Powell (1973) calculated genetic distances among some of the populations studied by Saura *et al.* and confirmed quantitatively that the differences between populations are lower in the allozyme systems than in chromosomal polymorphism.

The supergenes probably integrate differences in several or many single locus alleles; hence, in general, it should be expected that selection coefficients acting on the supergenes are higher than the coefficients acting on the alleles of the allozyme systems. This, plus the non-recurrence of the chromosomal rearrangements is, probably, the basis of the higher differences found in chromosomal polymorphism.

However, in species like *D. subobscura*, with very developed inversion polymorphism in all chromosomes, we should expect important differences among populations at least for the loci contributing to the adaptive value of the arrangements. The data on association between loci and arrangements of the third chromosome of *D. pseudoobscura* (Prakash and Lewontin, 1968 and 1971), and between alleles of the est-5 and chromosomal arrangements of the O chromosome in *D. subobscura* (González-Duarte *et al.*, 1973), are in line with this expectation. This is an interesting point about which we are short of information. It would also be very illuminating to know, in each particular case, if the alleles detected by electrophoretic mobility are actually single alleles or groups of alleles.

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