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Genetic differentiation between natural populations of *Drosophila subobscura* in the Western Mediterranean Area with respect to chromosomal variation

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Summary

The chromosomal arrangement frequencies of 27 populations of *Drosophila subobscura* from the western Mediterranean region have been compared. To evaluate the relationships between these populations, factorial analysis of correspondences (BENZECRI, 1973) and a distance proposed by PREVOSTI (1974 a) have been used. The general clines present throughout the distribution of the species were also detected in the western Mediterranean area. Distinct chromosomal polymorphism was found in three areas : Tunisia, continental Europe and the whole of Sicily and Sardinia. Smaller islands were subject to stronger foreign influences. Iviza, Ponza and Ventotene showed small differences with the nearest continental populations. Ustica was rather similar to Sicily, its nearest major area ; however, Lipari, in spite of its vicinity to Sicily, showed greater similarity to the more distant continental Italian populations. The Corsican population seemed to be influenced by all its surrounding populations. The observed differences appear to be correctly interpreted as the consequence of adaptive selection (expressed in latitudinal clines) interacting with historical factors related to physiographical conditions which determine the degree of isolation between populations. Also, the size of the concerned regions seemed to be important : two of the three well differentiated areas were continental and the third included the two larger islands, Sicily and Sardinia. Corsica, next in size, showed a high frequency of a generally rare arrangement, O_{3+4+17} ; if genetic drift were a main factor in the differentiation of these populations, the reverse situation would be true.

Key words : Chromosomal polymorphism, Drosophila subobscura, *geographical variation, isolation, migration.*

Résumé

Variabilité génétique des populations naturelles de Drosophila subobscura
du bassin méditerranéen occidental : étude des remaniements chromosomiques

Cet article porte sur une comparaison des fréquences des remaniements chromosomiques présents dans 27 populations de *Drosophila subobscura* du pourtour méditerranéen occidental. Les relations entre ces populations sont étudiées grâce à l'analyse factorielle des correspondances (BENZECRI, 1973) et à une mesure de distance proposée par PREVOSTI (1974 a). Les clines généraux observés au niveau de la distribution globale de l'espèce se retrouvent dans cette aire méditerranéenne. Trois zones se distinguent vis-à-vis de ce polymorphisme chromosomique : la Tunisie, l'Europe continentale et l'ensemble « Sicile-Sardaigne ». Les îles plus petites sont soumises à des influences externes plus marquées. Ibiza, Ponza et Ventotene ne diffèrent que peu des régions continentales adjacentes. Ustica ressemble plutôt à la Sicile, sa proche voisine alors que Lipari qui est également située à proximité, se rapproche davantage des populations de l'Italie continentale. Quant à la Corse, elle est influencée, semble-t-il, par toutes les populations voisines. Les différences observées peuvent s'interpréter comme la conséquence d'une sélection adaptative (exprimée dans les clines latitudinaux) interagissant avec des facteurs historiques liés aux conditions physiographiques qui déterminent le degré d'isolement entre populations. De plus, la taille des régions concernées paraît importante à considérer : deux des trois zones bien différenciées sont continentales alors que la troisième regroupe les deux plus grandes îles, la Sicile et la Sardaigne. La Corse qui vient à la suite par sa dimension présente à une fréquence élevée un remaniement généralement rare ; le contraire eut été observé si la dérive avait été la principale cause de différenciation de ces populations.

Mots clés : Polymorphisme chromosomique, Drosophila subobscura, *variation géographique, isolement, migration.*

I. Introduction

Drosophila subobscura, a common species in a broad area of the Paleoarctic region, is found throughout Europe (with the exception of northern Scandinavia), North Africa and the Near East. The karyotype of the species has 6 pairs of chromosomes : five rods, all showing inversion polymorphism, and one dot.

Several authors have extensively studied inversion chromosomal polymorphism in the species in different areas of its distribution. A synthesis of the results obtained has been reported by KRIMBAS & LOUKAS (1980). The importance of historical factors in the geographical distribution of this polymorphism has been discussed by PREVOSTI *et al.* (1975) and PREVOSTI (1979) who stated the problem of the influence of adaptation versus that of historical factors on the characteristics of this polymorphism.

The physiography of the western Mediterranean region studied in this paper is especially suited to a deeper investigation of this problem. Two continental areas, North Africa and southern Europe, are separated by the sea. There are two mountain barriers in the western Mediterranean region of southern Europe : the Pyrenees between the Iberian Peninsula and southern France, and the Alps between southern France and Italy. There are also numerous islands differing in size and at varying distances from the mainland.

II. Material and methods

A total of 27 populations from the western Mediterranean region has been analysed (fig. 1). Data on 13 of these populations have already been published by several

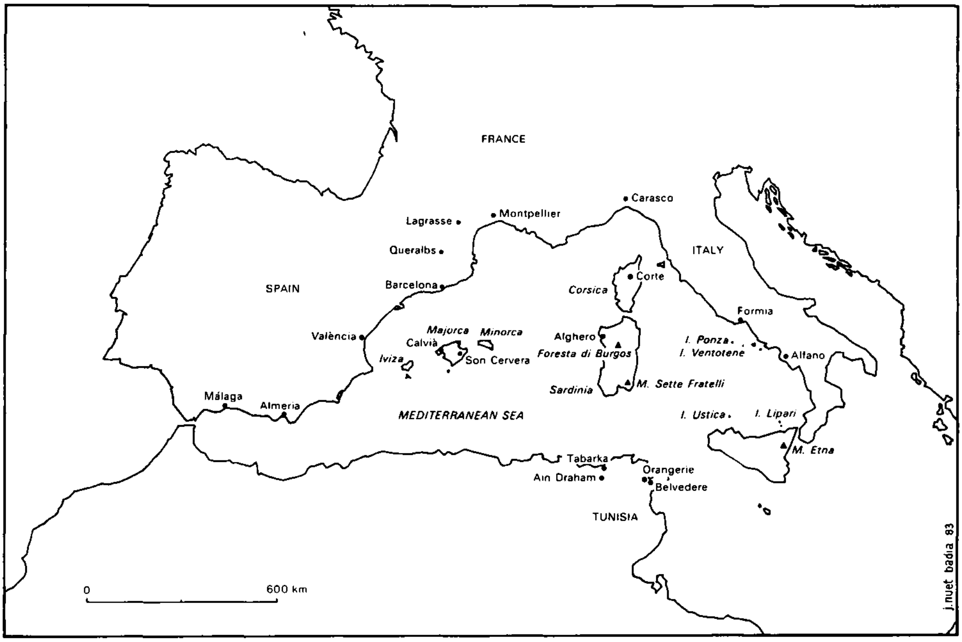

FIG. 1

Populations analysed.
Populations analysées.

authors : Spain (PREVOSTI, 1964 a, 1966, 1968 ; FRUTOS, 1972), France (PREVOSTI, 1964 b), Italy (SPERLICH, 1961 ; KUNZE-MUHL & SPERLICH, 1962 ; SPERLICH & KUNZE-MUHL, 1963) and Tunisia (JUNGEN, 1968). A newly collected sample of two other already published populations (Iviza in the Balearic Islands and Valencia in Spain) has been pooled with the old data since there were no statistically significant differences between the two samples. We also included unpublished data on 12 populations comprising continental Spain (Almería), continental France (Montpellier), Corsica (Corte), continental Italy (Carasco and Alfano), Sardinia (Alghero, Foresta di Burgos and Sette Fratelli), Sicily (Etna) and the Balearic Islands (one population from Minorca ; Calvià and Son Cervera from Majorca).

Factorial analysis of correspondences (FAC) (BENZECRI, 1973) was used to evaluate the general relationships between the studied populations. The formula proposed by PREVOSTI (1974 a) was employed to measure the overall differences between pairs of populations :

$$D = \frac{1}{2r} \sum_{j=1}^{r} \sum_{k=1}^{S_j} \left| p_{1jk} - p_{2jk} \right|$$

where r is the number of polymorphic chromosomes (5 in *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 populations 1 and 2, respectively.

The degree of polymorphism was expressed by mean heterozygosity and Carson's index of free recombination (CARSON, 1955). Besides considering heterozygote frequency, Carson's index takes into account the length of chromosomal fragments present in heterozygosity.

III. Results

A. *Latitudinal clines*

The frequencies of the arrangements in all the analysed populations are shown in table 1.

The latitudinal clines generally present throughout the distribution of the species were also detected in the western Mediterranean area. The arrangements A_{st}, J_{st}, U_{st} and E_{st} showed a decreasing frequency southwards as in other areas. The highest frequencies were observed in the French populations and in Carasco (northern Italy). On the Mediterranean shore of the Iberian Peninsula, their frequency decreased southwards, and in Italy the same trend was found, but it was less evident. Tunisian populations showed very low frequencies of these arrangements. U_{st} had much lower frequencies than the other standard arrangements in all the western Mediterranean populations and was not detected in the Tunisian populations or in Alfano (southern Italy). The distribution of O_{st} was a bit different. Its frequency was high in France and in the Spanish populations near the Pyrenees (Queralbs and Barcelona), but was low in northern Italy (Carasco) ; it decreased southwards much more in Italy than in Spain.

Complementary to the southward decrease of J_{st} was the increase of J_1 in the same direction. The variation of A_2 was similar to that of J_1, with the exception of the Tunisian populations where the high frequency of the endemic arrangements A_{2+6} and $A_{2+3+5+7}$ introduced a differential element. Populations from Italy and Spain differed in chromosomes U, E and O. Whereas U_{1+2+8} showed a gradual and sharp increase southwards in Spain, in Italy this increase was slighter and less regular due to the presence of high frequencies of U_{1+2+3}, U_{1+2+4} and U_{1+2+6}. The very high frequencies of U_{1+2+8} in Sicily and Sardinia must be considered not only in relation to the southern position of these islands but also to their isolation.

Some of the differences between Spanish and Italian populations in the western Mediterranean areas reveal that W-E clines are present in the whole Mediterranean region. This is the case of the increasing eastward frequency of A_1, U_{1+2+6}, E_{1+2+9}, E_8 and perhaps of O_{3+4+2}.

B. *Regional differentiation*

Figure 2 shows factorial analysis of correspondences for each chromosome and for all the chromosomes taken together. The diagrams of figure 2 represent only the

TABLE 1

Arrangement frequencies, mean heterozygosity (M.H.) and index of free recombination (I.F.R.).

Fréquences des arrangements, hétérozygotie moyenne (M.H.) et indice de recombination libre (I.F.R.).

	MALAGA	ALMERIA	VALENCIA	BARCELONA	QUERALBS	IVIZA	MINORCA	SON CERVERA	CALVIA	LAGRASSE	MONTPELLIER	CARASCO	CORTE	ALGHERO	FORESTA DI BURGOS	SETTE FRATELLI	FORMIA	PONZA	VENTOTENE	ALFANO	LIPARI	USTICA	ETNA	ORANGERIE	BELVEDERE	TABARKA	AIN DRAHAM
n	135	195	230	252	67	326	137	240	143	76	173	88	97	181	93	122	64	134	84	60	74	96	64	160	148	42	132
A_{st}	28.6	34.0	44.5	60.4	47.2	36.5	42.3	33.6	27.2	72.5	60.2	50.0	29.3	8.9	10.9	6.7	35.5	35.8	33.3	43.9	35.1	20.8			2.4	4.2	1.4
A_1	6.5		3.9	7.4	8.3	2.9	7.1	1.5	3.7	17.5	24.3	31.8	8.5	2.2	2.2		12.5	13.4	25.8	9.8	5.4	18.8					
A_2	64.9	66.0	51.6	32.1	44.4	60.6	50.7	65.0	69.1	10.0	15.5	18.2	61.7	88.9	87.0	93.3	50.0	50.8	42.9	46.3	59.5	60.4	100	17.6	21.4	29.2	20.6
A_{2+3}																									1.2		
A_{2+4}																								1.2	1.2	4.2	1.4
A_{2+6}																								57.6	60.7	41.7	57.5
$A_{2+3+5+7}$																								23.5	13.1	20.8	19.2
J_{st}	22.2	17.0	23.9	27.6	32.8	22.7	27.0	17.1	19.9	42.1	48.3	40.9	29.9	39.2	23.7	27.9	17.2	11.9	11.9	17.0	6.8	3.1	9.4	1.2	5.4	2.4	3.8
J_1	77.8	83.0	76.1	72.3	67.2	76.8	72.3	80.8	76.6	57.9	51.7	59.1	70.1	59.7	75.3	72.1	82.8	88.1	88.1	83.0	93.2	96.9	90.6	98.8	94.6	97.6	96.2
J_{3+4}						0.5	0.7	2.1	3.6					1.1	1.1												
U_{st}	0.7	2.1	3.6	4.7	6.0	1.6	11.0	0.9	0.7	15.8	26.6	12.5	1.0			1.6	1.6	3.7			2.7	1.1					
U_1	1.5	0.5		0.4						3.9	1.7	1.1				0.8			1.2								
U_{1+2}	47.4	47.2	48.2	52.3	59.7	47.7	51.1	44.2	36.4	57.9	53.8	45.5	48.5	11.6	11.8	17.2	32.8	38.1	32.1	46.7	27.0	12.5	6.2	30.0	21.0	19.0	28.0
U_{1+2+3}				0.4								15.9	4.1	0.6			28.1	13.4	13.4	18.3	8.1	6.2					
U_{1+2+4}										1.3			3.1	0.6	1.1	0.8	10.9	3.7	10.7	1.7	5.4						0.8
U_{1+2+6}		0.5	0.4	1.2			5.1	0.5		1.3	2.3	9.1	3.1	0.6			4.7	11.2	10.7	5.0	5.4	8.3	3.1	0.6			
U_{1+2+7}										1.3		2.3	3.1				1.6	0.8									
U_{1+2+8}	50.4	49.7	47.9	40.8	34.3	50.8	32.9	54.5	63.0	18.4	15.6	13.6	37.1	86.7	87.1	79.5	20.3	29.1	32.1	28.3	51.4	71.9	90.6	69.4	79.0	81.0	71.2
E_{st}	27.4	28.9	36.1	37.2	50.8	29.7	40.1	19.5	23.4	57.9	67.6	46.6	25.3	5.6	3.3	1.7	10.9	5.2	8.3	18.3	1.4			3.1	0.7		0.8
E_{1+2}	12.6	16.5	15.2	25.6	13.4	15.4	20.4	14.3	19.2	26.3	16.8	30.7	20.6	1.7	2.2	3.3	39.1	41.0	22.6	38.3	29.7	18.7	14.1	51.2	54.7	69.0	62.9
E_{1+2+9}	13.3	11.9	14.4	12.5	20.9	10.3	5.8	6.2	4.3	9.2	7.5	12.5	11.3	7.2	1.1	0.8	17.2	15.9	22.6	15.0	14.9	11.5	3.1	0.6	1.4		0.8
$E_{1+2+9+3}$	17.0	8.2	5.2	1.5		4.6			0.7		0.6		4.1	0.6		0.8	3.1	9.7	13.1	5.0	10.8	12.5	20.3				2.3
$E_{1+2+9+4}$						5.6	15.3	35.2	36.9				2.1	33.3	31.9	15.7				1.7			4.7	40.6	39.2	23.8	32.6
$E_{1+2+9+12}$	22.2	30.0	25.7	17.9	10.5	30.3	14.6	22.9	14.9	3.9	5.2	4.6	26.8	51.7	61.5	77.7	17.2	15.7	16.7	11.7	39.1	53.1	57.8	3.1	4.0	7.1	0.6
E_8	7.4	4.1	2.2	5.1	4.5	4.1	3.7	1.9	0.7	2.6	2.3	5.7	9.3				12.5	12.7	16.7	10.0	4,1	4.2		1.2			
C_{st}	6.7	14.9	17.4	34.3	40.3	14.8	16.1	19.9	19.8	40.8	61.1	23.9	9.2	2.8		2.5	10.9	5.2	7.1	5.0	1.4	1.1		1.9	2.0		
O_{3+4}	6.7	25.6	26.5	24.1	31.3	24.5	30.7	40.3	40.4	17.1	15.1	36.4	23.5	50.8	58.2	47.5	50.0	49.2	46.4	50.0	64.3	66.6	71.9	3.8	4.0		1.5
O_{3+4+1}		4.1	8.3	2.7	7.5	4.1	2.9	1.7	0.7	1.3		6.8	1.0	0.6			9.3	6.7	3.1	10.0	2.7	3.1					
$O_{3+4+1+8}$																	1.6	0.8									
O_{3+4+2}	1.5	3.1	3.9	2.7	1.5	2.6	7.3	11.3	7.4		2.3	9.1	5.1		1.1	1.7	4.7	10.4	9.5	12.7	9.4	6.2	4.7				
$O_{3+4+2+16}$				0.4								3.4					14.1	4.5	16.7	3.3	2.7	1.1					
O_{3+4+6}												1.1	15.3	18.2	18.7	27.0		0.8			1.4	1.1	1.6		0.7	4.8	
O_{3+4+7}	80.0	42.6	35.2	21.3	9.0	44.4	3.7	12.1	6.6	2.6				0.6							1.4						
O_{3+4+8}	3.0	4.6	3.9	10.6	7.5	5.6	34.3	13.0	22.8	36.2	20.9	14.8	14.3	24.3	19.8	18.8	9.4	16.4	11.9	8.3	14.8	16.6	20.3	78.3	70.3	40.5	77.3
O_{3+4+10}																		1.2	2.4			3.1					
O_{3+4+12}					1.5					1.3																	
O_{3+4+16}												2.3															
O_{3+4+17}		0.5		0.4									29.6		1.1			0.8			1.4						
O_{3+4+22}		3.1	2.2	2.0	1.5	2.0	4.4	1.7	2.2			1.1	2.0	2.2		0.8		3.0	1.2	11.7		1.1	1.6				
$O_{3+4+23+6}$															1.1									15.6	23.0	54.6	21.2
O_6											0.6	1.1		0.6					1.2								
O_7	2.2	1.5	3.0	1.2		2.0	0.7																				
M. H.	0.50	0.55	0.59	0.60	0.58	0.57	0.62	0.56	0.56	0.56	0.55	0.65	0.63	0.48	0.39	0.48	0.62	0.60	0.63	0.60	0.51	0.45	0.35	0.39	0.43	0.41	0.39
I.F.R.	83.80	80.24	79.17	79.80	83.82	79.68	78.98	81.08	81.40	81.30	88.78	78.46	87.47	85.34	86.95	86.39	78.20	82.50	82.10	81.25	83.80	83.70	90.27	86.80	85.76	85.66	86.52

two main components of population differentiation. The percentages of variation corresponding to these components for axis 1 and axis 2, respectively, were : chromosome A, 76.24 and 17.31 ; chromosome J, 84.66 and 15.34 ; chromosome U, 57.44 and 22.66 ; chromosome E, 76.24 and 17.31 ; chromosome O, 31.53 and 21.48 ; all the chromosomes, 32.88 and 18.28. This could cause some distortion of the actual relative positions of the populations. To avoid this possibility, the distances between the populations given on table 2 were based on differences in the frequency of chromosomal arrangement and calculated with the formula proposed by PREVOSTI (1974 a).

TABLE 2

Distances between populations.
Distances entre populations.

DISTANCES ENTRE POPULATIONS

	ALMERIA	VALENCIA	BARCELONA	QUERALBS	IVIZA	MINORCA	SON CERVERA	CALVIA	LAGRASSE	MONTPELLIER	CARASCO	CORTE	ALGHERO	FORESTA DI BURGOS	SETTE FRATELLI	FORMIA	PONZA	VENTOTENE	ALFANO	LIPARI	USTICA	ETNA	ORANGERIE	BELVEDERE	TABARKA	AIN DRAHAM
MALAGA	131	137	262	307	130	305	248	278	467	477	447	246	459	446	447	362	349	355	326	328	382	450	587	588	589	593
ALMERIA		101	196	247	46	230	162	216	421	436	380	206	410	402	394	296	285	305	263	252	320	389	566	567	568	592
VALENCIA			161	177	82	205	188	230	377	392	330	214	397	401	384	302	308	331	277	282	360	441	597	597	598	602
BARCELONA				136	180	172	251	274	229	262	242	225	484	490	474	309	308	322	264	338	423	524	574	576	577	582
QUERALBS					400	171	269	290	223	251	232	254	474	497	482	313	317	325	257	374	446	539	630	631	632	640
IVIZA						201	164	206	400	415	367	191	382	383	382	307	308	328	273	271	338	410	566	567	568	572
MINORCA							205	191	261	306	249	205	402	413	402	286	261	297	230	315	385	462	522	524	525	533
SON CERVERA								77	435	447	370	237	300	291	325	285	272	289	256	245	310	356	475	477	501	492
CALVIA									422	440	378	246	270	264	300	307	293	314	290	280	308	342	439	439	466	455
LAGRASSE										130	205	376	574	633	621	435	440	462	404	509	573	676	610	619	642	625
MONTPELLIER											217	396	590	642	626	467	471	470	433	541	582	677	668	677	697	684
CARASCO												324	539	592	574	300	293	314	261	396	469	621	638	644	665	664
CORTE													370	381	368	274	261	285	247	273	334	433	585	586	578	590
ALGHERO														80	130	465	444	468	466	357	297	225	536	497	501	536
F. BURGOS															101	452	433	459	457	321	262	177	518	478	475	513
S. FRATELLI																456	436	458	463	343	291	203	547	505	491	541
FORMIA																	114	138	121	221	322	451	568	570	571	573
PONZA																		111	111	161	251	360	524	525	525	529
VENTOTENE																			178	201	261	414	564	566	567	569
ALFANO																				224	326	448	556	557	558	561
LIPARI																					131	259	506	497	495	502
USTICA																						183	513	495	479	509
ETNA																							535	496	486	526
ORANGERIE																								76	194	58
BELVEDERE																									157	66
TABARKA																										156

C. *Mainland populations*

Table 2 and figure 2 both show that the Tunisian populations were the most differentiated. The direction of greatest differentiation on figure 2 f is the vertical axis, and the North African populations diverge from all the other populations in relation to this axis. The A chromosome had the greatest influence on this general differen-

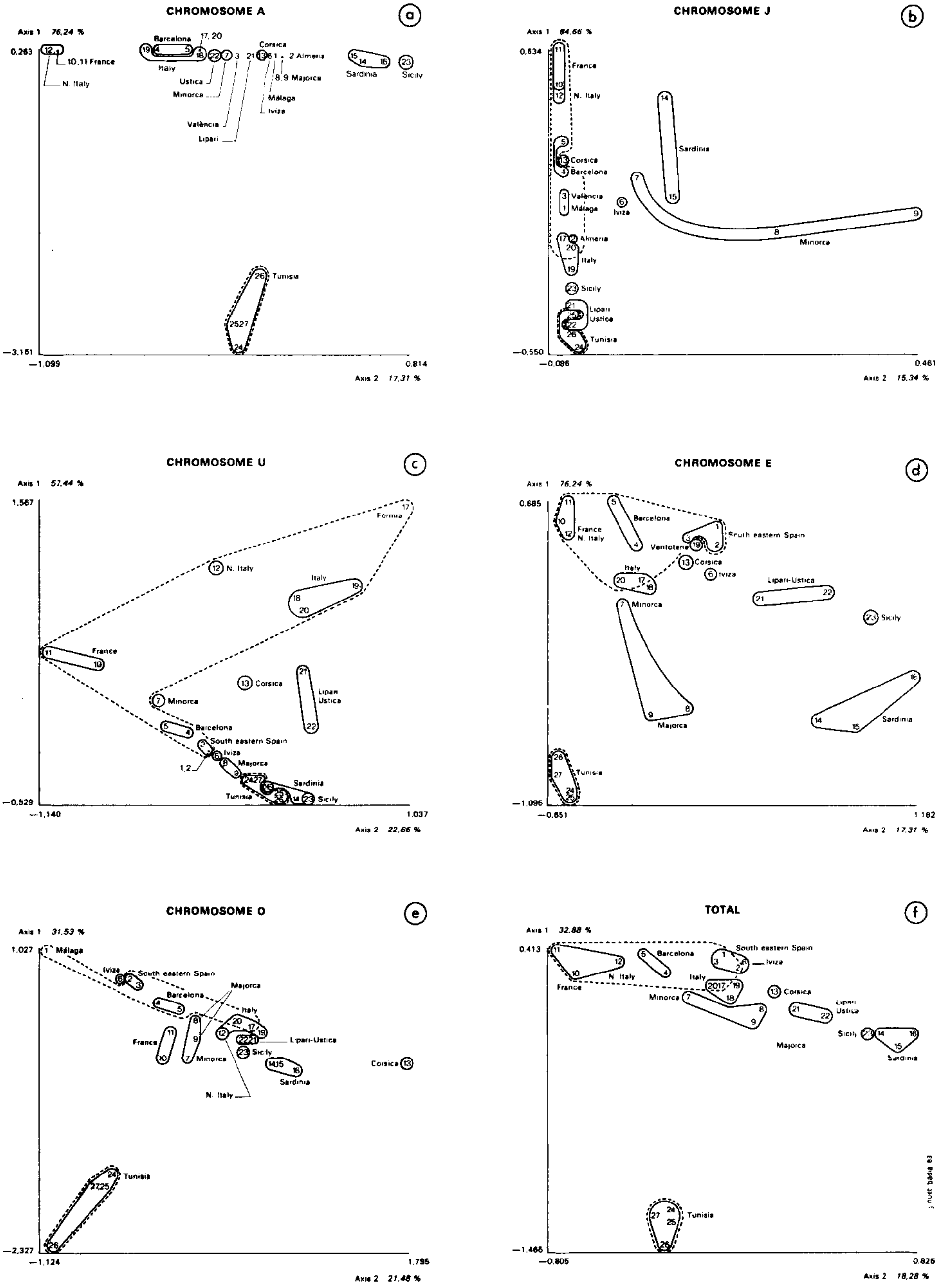

FIG. 2

Diagrams obtained with factorial analysis of correspondences. Axes 1 and 2 indicate the first two main components; the percentages of variability accounting for each of these components are indicated.

Diagrammes obtenus par l'analyse factorielle des correspondances. Les axes 1 et 2 figurent les deux premières composantes les plus importantes; le pourcentage de variabilité lié à chacune d'elles est indiqué.

1. *Malaga;* 2. *Almeria;* 3. *Valencia;* 4. *Barcelona;* 5. *Queralbs;* 6. *Iviza;* 7. *Minorca;* 8. *Son Cervera;* 9. *Calvia;* 10. *Lagrasse;* 11. *Montpellier;* 12. *Carasco;* 13. *Corte;* 14. *Alghero;* 15. *Foresta di Burgos;* 16. *Sette Fratelli;* 17. *Formia;* 18. *Ponza;* 19. *Ventotene;* 20. *Alfano;* 21. *Lipari;* 22. *Ustica;* 23. *Etna;* 24. *Orangerie;* 25. *Belvedere;* 26. *Tabarka;* 27. *Ain Draham.*

tiation (fig. 2 a) due to the presence of endemic arrangements like A_{2+6} and $A_{2+3+5+7}$ with high frequencies in North Africa (table 1). Figure 2 e shows that chromosome O also contributed strongly to the separation of the Tunisian populations. This is explained by the presence of the endemic arrangement $O_{3+4+2+6}$ and the frequency of O_{3+4+8} which was much higher than in the other populations. In the diagrams of chromosomes J and U (fig. 2 b and c), the Tunisian populations are also situated at one end of axis 1, but there is no discontinuity between these populations. Actually, in these diagrams the populations are usually arranged along axis 1, according to the southward clines of increase of J_1 and U_{1+2+8} frequencies, respectively. On figure 2 d, the Tunisian populations are also at one end of axis 1, expressing their high frequency of E_{st}, E_8 and E_{1+2+9}. The main component of between-population differences in the E chromosome also included, to some degree, the effect of latitudinal clines since E_{st} affected this component.

The populations from continental Europe (fig. 2 f) are at the opposite end of axis 1 from the Tunisian ones. This means that maximal differentiation within the western Mediterranean populations occurred in these regions. On the other hand, differences within the continental European area are expressed by the direction of axis 2, and they are arranged along this axis according to latitude. At one end of the axis are the French populations and Carasco (northern Italy), followed by populations from the northern Mediterranean shore in Spain and lastly, a bit separated and towards axis 1, the populations from southern Spain and Italy.

Considering the chromosomes separately, the populations from continental Europe appear more scattered ; more similarity is found in the diagram of chromosome E. Also, population distribution along axis 2 is maintained ; more southern populations have higher values on this axis, although those from southern Italy are closer to populations from northern than from southern Spain. The populations from southern Italy and Spain are also slightly shifted in the direction of axis 1. The decrease of E_{st} southwards and the increase of $E_{1+2+9+12}$ and $E_{1+2+9+3}$ in the same direction account for the variation along axis 2. The higher frequencies of E_8 and E_{+1+2+9} in Italy account for the differences between the populations from southern Italy and southern Spain. The diagram of chromosome J also shows clustering of the populations from continental Europe. However, the populations in this diagram are arranged according to latitude along the axis of main differentiation (axis 1). The distributions of the other chromosomes show a greater complexity. Populations with chromosome A are also placed along axis 2 and, as with the E chromosome, increasing values along this axis tend to be arranged according to decreasing latitude. However, populations from southern Italy and southern Spain do not fit into this order due to the higher frequency of A_2 in Spain and of A_1 in Italy. Also, some populations from the islands are interspersed within the continental ones. Starting from the position of French populations at the lowest values of axis 1, the U chromosome values of the Italian and Iberian populations are situated on divergent lines. A decrease of U_{st} and U_{1+2} and an increase of U_{1+2+8} is found along the line corresponding to the Iberian populations. The divergent position of the Italian populations is mainly due to the presence of U_{1+2+3}, U_{1+2+4} and U_{1+2+7} arrangements and to the higher frequency of U_{1+2+6}. The greater complexity of polymorphism in this Italian chromosome explains the irregularities observed in the distribution of these populations in the diagram. Actually, this complexity is probably the main difference between the polymorphism of Italian and Iberian populations. In the diagram of the O chromosome, the French populations are closest to the Tunisian ones due to O_{3+4+8}. This arrangement is dominant in North Africa and also has a high frequency in France. The other populations from continental Europe are distributed along a straight line beginning with Malaga placed at minimal values of axis 2 and maximal values of axis 1. The Spanish populations are distributed on this line according to latitude, and the Italian ones are clustered at the other end of the line. The situation of the Spanish populations on this line depends on O_{st} frequencies, which are maximal in the north, and on the increase of O_{3+4+7} southwards. In Italy, O_{3+4+7} is almost lacking and O_{st} is replaced by O_{3+4} southwards and in the second term by O_{3+4+1}, O_{3+4+2} and O_{3+4+16}; the frequency of these arrangements explains the position of the Italian populations in this diagram.

D. *Island populations*

Perhaps the most interesting feature of this paper is the analysis of chromosomal polymorphism in the islands. The general FAC diagram shows that the island populations are more similar to those of continental Europe than to the Tunisian populations. A second observation is that the islands more differentiated from continental European populations, Sardinia and Sicily, are close together and shifted mainly in the direction of axis 2. On the other hand, the differences between European and North African populations are mainly expressed along axis 1. Thus the differentiation of these islands is not particularly influenced by their proximity to Tunisia. The high frequencies of A_2, U_{1+2+8} and $E_{1+2+9+12}$ explain the differentiation of these islands. The high frequency of $E_{1+2+9+4}$ in Sardinia and a rather high frequency of O_{3+4+8} in both islands are the only resemblances to the Tunisian populations.

Some islands situated near the mainland show very small differences with the nearest continental populations. This is the case of Ponza and Ventotene which are very similar to the mainland population of Formia. Also, Iviza, the smallest of the Balearic Islands and the nearest to the continent, shows very small differences with Valencia and Almeria. However, in terms of genetic distance (table 2), the population from Lipari island shows greater similarity to the more distant continental Italian populations than to Sicily. On the other hand, the genetic disance between Ustica and Sicily is much less than between Ustica and the continental populations.

The differences between Corsica and Sardinia are considerable, in spite of the close vicinity of these islands. Populations from Sardinia show more southern features : the frequencies of the standard arrangements are lower, and those of typically southern arrangements like U_{1+2+8}, $E_{1+2+9+12}$ and O_{3+4} are much higher. Also, in Corsica O_{3+4+17} has a frequency of 29.6 p. 100 but in Sardinia it is only present in one population (Foresta di Burgos) with a frequency of 1.1 p. 100. However, there is a point of similarity between the two islands : in all the western Mediterranean area, the only populations having a high frequency of O_{3+4+6} are those from Sardinia and Corsica. In spite of its pecularities, the Corsican population is fairly similar to those from continental Italy and southern Spain.

The populations from the Balearic Islands are characterized by their dispersed position in the general FAC diagram ; only those from Majorca are closely located. The populations from each of these islands resemble different populations, producing a distortion of their position in the diagrams which does not fit completely with the genetic distances between them.

The distribution of the Balearic Islands in the diagram of the E chromosome fits the best with the general one. The vicinity of Majorcan populations to Tunisian ones is strongly influenced by the polymorphism of this chromosome, especially by the frequency of $E_{1+2+9+4}$. The frequency of $E_{1+2+9+4}$ in the Majorcan populations approximates that in the Sardinian populations. The frequencies of E_{st}, E_{1+2}, E_{1+2+9}, $E_{1+2+9+3}$ and $E_{1+2+9+12}$ in Iviza considerably resemble those of Almería and Valencia. The A chromosome of the Balearic Islands shows a scattered distribution. Majorca and Iviza are rather similar and situated in the vicinity of populations from southern Spain due to their frequencies of A_{st} and A_2 ; Minorca is more similar to populations from Catalonia and Valencia. In the J chromosome diagram, Sardinia and the Balearic Islands are outside the line expressing the latitudinal cline of J_{st} and J_1 arrangements. Axis 2 of this diagram corresponds to the variation of J_{3+4}, a rare arrangement in the western Mediterranean region and only found on these islands. Even considering that axis 2 is represented in this diagram in large scale, the effect of J_{3+4} seems to be exaggerated since the highest frequency of this arrangement is only 3.6 p. 100 in Calvià (Majorca). In the U chromosome diagram, the Balearic Islands, Sardinia and Sicily appear on one line of populations according to the cline of the arrangements U_{st}, U_{1+2} and U_{1+2+8} ; Sardinia and Sicily are at one end of this line due to their high frequency of U_{1+2+8}. The Balearic Islands are scattered as in the other diagrams : Iviza and Majorca resemble those of southern Spain and even Tunisia ; Minorca approximates French populations even more than those from northern Spain.

The characteristic scattering of the position of the Balearic Islands also appears in the diagram of the O chromosome. Iviza stays very near to the populations of southern Spain and far from those of Majorca and Minorca ; the reason for this is the frequency of O_{st} and O_{3+4} and the high frequency of O_{3+4+7} in Iviza. Besides having a higher frequency of O_{st} and O_{3+4}, Majorca and Minorca also have a high frequency of O_{3+4+8} ; this shifts the position of the populations of these islands near to those of France and Italy.

E. *Mean heterozygosity and index of free recombination* (table 1)

The greatest polymorphism is found in continental Italy, including the small islands of Ponza and Ventotene, and in the islands of Corsica and Minorca. These populations show the highest values of mean heterozygosity (over 0.600). Thus, free recombination reaches its lowest values in these areas, Ponza, Ventotene and Alfano in southern Italy excepted.

In contrast with the high polymorphism of populations from continental Italy and the island of Corsica, the lowest values are found in the nearby islands of Sardinia and Sicily. Polymorphism is also low in Tunisia. High I.F.R. values correspond to low values of mean heterozygosity in these populations. The highest value of this index is 90 in Sicily, where mean heterozygosity is minimal.

In the islands of Lipari and Ustica, the degree of polymorphism is intermediate between that of continental Italy and Sardinia and Sicily. This agrees with the situation of these islands in the FAC diagrams.

The greatest polymorphism in the Mediterranean area of the Iberian Peninsula is found in the north and decreases gradually southwards. There is also less polymorphism in the Mediterranean populations from France and the Balearic Islands, with the exception of Minorca.

IV. Discussion

Three main areas have been distinguished in the western Mediterranean area according to the characteristics of chromosomal polymorphism in *D. subobscura* populations. These areas are Tunisia (which seems to be representative of North Africa in general according to data on the non-Mediterranean populations of Morocco ; PREVOSTI, 1974 b), continental Europe, and the whole of Sicily and Sardinia. The population of the island of Corsica, although presenting some peculiarities like a high frequency of O_{3+4+17}, is generally at a small genetic distance from most of the other populations, Tunisia excepted. The population of this island seems to be more influenced by all its surrounding populations.

Two important factors may explain the differentiation of the three regions. First, they are isolated from each other. As pointed out by PREVOSTI *et al.* (1975), geographical barriers like sea arms or mountain ranges limit migration between populations and are important factors in the differentiation of chromosomal polymorphism in *D. subobscura* populations. Genetic distance, based on the frequency of chromosomal arrangements, is much greater between populations separated by a barrier than between populations of equal geographical distance but with no barrier between them. Second, differentiation of chromosomal polymorphism depends on the size of the regions concerned. The importance of this second factor has been discussed by PREVOSTI *et al.* (1975) but appears very clearly in the western Mediterranean data. Two of the three main areas of differentiation are continental and the third is formed by the two larger islands, Sicily and Sardinia. Corsica is next in size and is noteworthy due to its high frequency of O_{3+4+17}. If genetic drifts were a main factor in the differentiation of these populations, the situation would be exactly the reverse, and the populations from small islands like Lipari, Ustica and the Balearics would show more differentiation .

The observed differences seem to be correctly interpreted as a consequence of adaptive selection (expressed in latitudinal clines) interacting with historical factors related to physiographical conditions which determine the degree of isolation of populations. The larger the separated areas, the greater would be the differentiation effect of barriers imposing an equal degree of isolation. The important parameter of differentiation is the coefficient of migration and the number of migrants passing a barrier being equal, this coefficient would be smaller the larger the areas receiving the migrants. Also, if the frequency of migrants is low, the new arrangements occurring in the populations might often be lost, etiher by chance or because they are carriers of gene complexes not coadapted with the gene pool of the receiving population. As a consequence of this lack of coadaptation, the progenies of crosses between migrant and autochthonous individuals would be less fit to survive, and the newly introduced arrangements would have low probability of being maintained in the population. This interpretation is supported by observations carried out in the Canary Islands (PRE-

VOSTI, unpublished data) where arrangements typical of continental Africa (like $A_{2+3+5+7}$ which never rise to substantial frequencies) are sporadically found.

If genetic drift were an important factor influencing the characteristics of chromosomal polymorphism in *D. subobscura,* we would also expect that variability in chromosomal arrangement would be low in small islands. This should be expressed by the values of mean heterozygosity, but these values are low only in the larger islands such as Sardinia and especially Sicily. The characteristics of chromosomal polymorphism in these islands have been discussed by PREVOSTI *et al.* (1975) on the basis of their genetic distance from other populations. It was found that the populations nearest to Sicily were those from the Canary Islands and, reciprocally, the populations closest to those of the Canary Islands, were those from Sicily followed by those from Sardinia. Chromosomal polymorphism in populations from the Canary Islands seems to be in a rather early stage of development. The similarity of Sicily and Sardinia indicates that in these islands some old features may also have been retained due to isolation.

The greater variability of the smaller islands is a consequence of the relatively greater frequency of migrants from other areas and of the more successful establishment of the arrangements brought by the migrants. A greater variety of influences was detected in Corsica, perhaps because of its position. Besides the general influence of continental European populations, a specific relationship with Italian populations is expressed by the presence of U_{1+2+3}, U_{1+2+4} and U_{1+2+7} and with Sardinia and Tunisia by the presence of O_{3+4+8} and $E_{1+2+9+4}$, respectively. A high frequency of O_{3+4+17} is only found in some Anatolian populations in the eastern Mediterranean area. These various influences explain the high degree of polymorphism in Corsica.

In the Balearic Islands, J_{3+4} (also observed only in Sardinia in the western Mediterranean area) was found. This arrangement, typical of eastern Mediterranean regions, reaches its highest value in Israel (GOLDSCHMIDT, 1956) and Crete (KRIMBAS & ALEZIVOS, 1973) and substantial frequencies in Greece and Anatolia. It is difficult to explain the presence of this arrangement in the Balearic Islands, unless carried there by man. Communication among the Balearics and Sardinia with the eastern Mediterranean region is old. In any case, the establishment of this arrangement in the islands, and not in continental European populations, is another fact pointing to the easier establishment of foreign arrangements in the islands. Communication with the eastern Mediterranean was also intensive in several continental areas such as the Iberian Peninsula, and J_{3+4} has not been found there. Another foreign influence in the Balearic Islands is the high frequency of $E_{1+2+9+4}$, especially in Majorca. It could have arrived from Sardinia or directly from North Africa. Transport is also a plausible explanation due to the distance from possible areas of origin. Rather important differences are also observed within the Balearic Islands. Iviza is very similar to continental Iberian populations, whereas the influence of Iberian populations seems to be much weaker in Majorca and Minorca. O_{3+4+7}, typical of the Iberian Peninsula, shows a high frequency in Iviza, but is low in the other islands. $E_{1+2+9+3}$, not rare on the Peninsula, shows an appreciable frequency in Iviza but has been found only once in the other islands. On the other hand, O_{3+4+2}, and especially O_{3+4+8}, have higher frequencies in Majorca and Minorca than on the Spanish mainland. The high frequencies of O_{3+4+2} and O_{3+4+8} in these islands are perhaps better interpreted as a consequence of isolation rather than of a foreign influence. The differences among the islands of the Archipelago could also be generally interpreted this way. These differences are greater than in the Canary Islands where the arrangement distances are usually less than 100, except for those of Hierro Island (the greatest distance between Vilaflor in Tenerife and Pinar in Hierro amounts to 116). However, the uniformity of the Canarian populations is mainly due to monomorphism in the A, J and O chromosomes. In fact, there are differences among the islands as to arrangements of the U and, especially the E chromosome which are polymorphic Thus, in both archipelagos polymorphism tends to differentiate in the different islands, probably due to isolation, although in the Canary Islands only polymorphic chromosomes can differentiate. This monomorphism of Canary Island populations, interpreted as a primitive feature (PREVOSTI, 1971), has not been observed at all in Balearic Island populations.

Continental European populations show greater frequencies of the standard arrangements northwards, fitting with the general latitudinal clines found in these arrangements. Accordingly, the characteristically southern arrangements show higher frequencies in the southern populations. On the other hand, French and Italian populations are distinguishable within these populations because of the high frequency of O_{3+4+8} in France (a general feature in other French populations) and the polymorphism of the U chromosome in Italy (a general characteristic of Italian populations).

The populations from Spain and Italy have the above-mentioned latitudinal clines in common with all of Europe in general. They are rather different in other aspects : the polymorphism of the O and U chromosomes is richer in Italy, and the high frequency in Spain of the O_{3+4+7} arrangement practically lacking in Italy.

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