Modern European Cranial Variables and Blood Polymorphisms Show Comparable Spatial Patterns

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Abstract Spatial patterns in cranial traits for modern European populations are compared with patterns described by Sokal et al. (1989) for blood polymorphisms. Spatial patterns in these variables are described from both one-dimensional and directional autocorrelation correlograms. Manhattan distances computed among one-dimensional correlograms are used (1) to cluster variables with similar patterns and (2) to test the hypothesis that these clusters are to some extent accounted for by the type of variable. The one-dimensional correlograms for cranial traits do not show a significant contrast with either red cell antigens or the set of blood polymorphisms that excludes HLA. The only contrast that accounts for any of the cluster structure among one-dimensional correlograms is that between HLA and non-HLA variables. A cluster analysis of the directional correlograms demonstrates that cranial traits reflect patterns comparable to those for blood polymorphisms. This finding implies that patterns in cranial variables can be accounted for by the same, or similar, population processes as those inferred from patterns in blood polymorphisms. The implications of this finding for the likely origin of the northwest-southeast cline seen in some modern blood polymorphisms and modern cranial variables, but not in Neolithic cranial variables, are discussed.

Genetic pattern in modern European human populations has been described by Sokal et al. (1989) in their spatial analysis of blood polymorphisms. They showed that variation among the surfaces of these genetic markers could be summarized by a few major patterns. From these patterns the following population models were inferred: isolation by distance, ethnic settlement, Neolithic transition by demic expansion, and latitudinal selection. An earlier study by Sokal and Uytterschaut (1987) examined spatial variation of cranial traits in Europe. The present anal-

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Human Biology, December 1990, Vol. 62, No. 6, pp. 733–745.

KEY WORDS: CRANIAL VARIATION, BLOOD POLYMORPHISMS, SPATIAL PATTERNS, EUROPE

ysis addresses the question, Do cranial variables show the same range of patterns as the blood polymorphisms, implying the same underlying population processes?

Quantitative traits measured in preserved crania can be used to describe ancient or historical genetic variation in a population analysis, but compared with studies of modern blood polymorphisms, there arise additional reservations concerning the interpretation of such data. For instance, although each site in a spatial study is assumed to be represented by a homogeneous sample of the population cranial variation, sample sizes in the cranial data set are smaller and are more likely to be subject to problems of dating and of mixing age classes, sexes, and ethnic groups than are samples in studies of blood polymorphisms. It must also be assumed that genetic variability is not being confounded with environmental plasticity. Furthermore, because cranial traits are not functionally independent, as are most blood polymorphisms, they represent fewer separate components of variation than the actual number of traits measured.

Sokal and Uytterschaut (1987) analyzed spatial variation in cranial traits for three time periods: Early Medieval, Late Medieval, and Recent. When these cranial patterns were examined for similarities with the patterns in European blood polymorphisms, it became evident that the inclusion of some Asian and North African localities made comparison inappropriate. The data for the Recent period are reanalyzed here using a subset of the localities within the same boundaries for Europe defined by Sokal et al. (1989) for the study of blood polymorphisms. As in these two earlier studies, multivariable methods of spatial analysis (Sokal and Wartenberg 1981) are applied to summarize the total set of cranial variation surfaces by their major patterns.

The alternative outcomes—disagreement or concordance—between multivariable analyses of patterns in blood polymorphisms and cranial traits have the following implications. Finding different sets of patterns between modern blood polymorphisms and cranial traits would suggest that these variables reflect different population processes. In particular, this would be strong evidence for the impact of environmental factors in shaping spatial patterns of cranial variation [see Chakraborty (1990), Relethford and Lees (1982), and Rogers and Harpending (1983)]. Finding concordant patterns supports the working assumption that a genetic process is reflected without distortion in patterns of quantitative variables [e.g., Relethford and Blangero (1990) and Williams-Blangero and Blangero (1989)].

The second posited outcome, which can be anticipated from the title of this article, suggests new questions about spatial patterns in

blood polymorphisms for earlier time periods. Despite new technology for extracting DNA from ancient bone (Hagelberg et al. 1989), it is unlikely that genetic polymorphisms will ever be mapped for earlier ages of Europe. Yet it seems reasonable to back-project from patterns in modern genetic polymorphisms by cross-referencing to older patterns of anthropometric traits derived from preserved material. This approach leads to new inferences on the origins of spatial genetic patterns in Europe. These inferences will be discussed with reference to a third study of spatial patterns in Europe, in which Harding et al. (1990) examined the same cranial traits for three Neolithic time periods.

Materials

The data analyzed here consist of 97 means and sample sizes for each of the following 10 cranial variables: maximum cranial length, maximum cranial breadth, minimum frontal breadth, basion-bregma height, bizygomatic breadth, facial height, orbital breadth, orbital height, nasal breadth, and nasal height. The data were originally assembled by Schwidetzky and Rösing (1984) and are a subset of the localities for the Recent period (period 9), dated from A.D. 1500 to the present. The new data were selected by excluding sites with sample sizes of less than 25 individuals and all those located in Egypt and the USSR east of the Urals. However, despite these efforts to make the spatial sampling comparable to that for the blood polymorphisms, the cranial traits are relatively better represented in central and eastern Europe and less so in Iberia and northwestern Europe than the genetic data.

For the comparison of spatial patterns between the cranial traits and the blood polymorphisms analyzed by Sokal et al. (1989), some information from the latter study bears repeating. They analyzed 59 variables belonging to 26 systems, each corresponding to a genetic locus, with some exceptions. The numerical codes 1 to 65 identify red cell antigens, plasma proteins, and enzymes, following the scheme used by Mourant et al. (1976). The histocompatibility loci are coded 100 for locus A and 101–102 for HLA-B, and the immunoglobulin loci are coded 200 for Gm and 201 for Km.

It is important to note for the subsequent analysis that a reduced data set, composed of blood polymorphisms that were sampled for at least 66 localities, was used in computing average directional correlograms. For this reason the set of directional correlograms for blood polymorphisms is smaller than the comparable set of one-dimensional correlograms. It is also pertinent to explain why there are nine one-dimensional

cranial correlograms but ten directional cranial correlograms: The different arrangement of distance classes in these two types of correlogram sometimes leads to different decisions about the significance of spatial structure. Only significantly nonrandom correlograms enter the clustering and hypothesis-testing analyses.

Multivariable Methods

Several techniques from spatial autocorrelation analysis and numerical taxonomy are used in this study as part of the multivariable approach to the inference of population processes from spatial patterns. Because all of them are described in some detail by Sokal et al. (1989) and because further comments on multivariable analysis are made by Harding (1989), a brief account will suffice here.

The first step in this analysis is to compare average one-dimensional correlograms generated separately for blood polymorphisms and cranial traits. Second, UPGMA (unweighted pair-group) clustering is applied to the matrix of Manhattan distances (Sneath and Sokal 1973) among significant one-dimensional correlograms for blood polymorphisms and cranial traits combined. This is done to investigate whether correlograms cluster by type of variable. Third, the directional correlograms of cranial variables are grouped by *k*-means clustering (Späth 1980), a nonhierarchic clustering algorithm. The resulting average directional correlograms are presented, and the diversity of directional trends occurring among cranial variables is compared diagrammatically with that for the blood polymorphisms analyzed by Sokal et al. (1989). Finally, the hypothesis that type of variable accounts for some of the differences found among correlograms is tested by using methods of quadratic assignment (Hubert 1987). Because a greater number of variables are represented by the set of one-dimensional correlograms than by the set of directional correlograms, the one-dimensional correlograms are used for hypothesis testing.

Hypothesis Testing by Quadratic Assignment

If different variables reflect similar patterns, then their correlograms should show similar autocorrelation coefficients across all distance classes. Thus the Manhattan (city block) distances between similar correlograms will be small. Of course, this result is interesting only if the correlograms indicate significant structure. Pairs of variables showing different patterns will have larger Manhattan distances. Can Manhattan distance be predicted to some extent by whether the correlograms being

paired are for different *types* of variable? For instance, if cranial variables and blood polymorphisms show different patterns, then pairing such correlograms should produce larger Manhattan distances than, say, paired blood polymorphisms. In order to test this, I correlated the Manhattan distance matrices among significant correlograms with binary design matrices according to the method of Sokal and Wartenberg (1983). These Mantel correlations are tested for significance by Monte Carlo permutation methods (Smouse et al. 1986). The computations were carried out using the R package for multivariate data analysis (Legendre 1985).

The primary contrast tested is between the cranial variables and the blood polymorphisms, but various subsets of the blood polymorphisms are also contrasted with the cranial variables. The subsets are (1) non-red-cell antigens, including electrophoretic enzymes and HLA antigens, (2) HLA antigens only, (3) non-HLA variables, including red cell antigens, and (4) red cell antigens only. Five different binary design matrices are constructed using 0's for distances between variables within types and 1's for distances between types. The design matrices comprise the 9 (significant, one-dimensional) cranial correlograms against (1) 46 blood polymorphisms in a 55 × 55 matrix, (2) 26 non-red-cell antigens in a 35 × 35 matrix, (3) 15 HLA antigens in a 24 × 24 matrix, (4) 31 non-HLA antigens in a 40 × 40 matrix, and (5) 20 red cell antigens in a 29 × 29 matrix. Because I am examining five interdependent correlations, I have chosen a 1% permutation probability for rejection of a random association at a 5% experiment-wise error rate.

Results

Figures 1a and 1b show the average trend for significant one-dimensional *I*-correlograms by representing 46 blood polymorphisms and 9 cranial variables, respectively. Lines connect the mean autocorrelation coefficients in each distance class. For both sets of variables the mean autocorrelation coefficients decline from maximum positive values at interlocality distances of less than 300 km to low negative autocorrelations at intermediate and large distances. Monotonicity, consistent with the presence of a cline, is evident across most distance classes for blood polymorphisms (Figure 1a) but not for cranial variables (Figure 1b). In Figure 1b fluctuations in mean values between intermediate distance classes may be due to sampling error, because the set of nine cranial correlograms represents few independent dimensions. Negative autocorrelation appears to be stronger at intermediate distances than at far distances in the cranial correlograms but not in those for blood polymor-

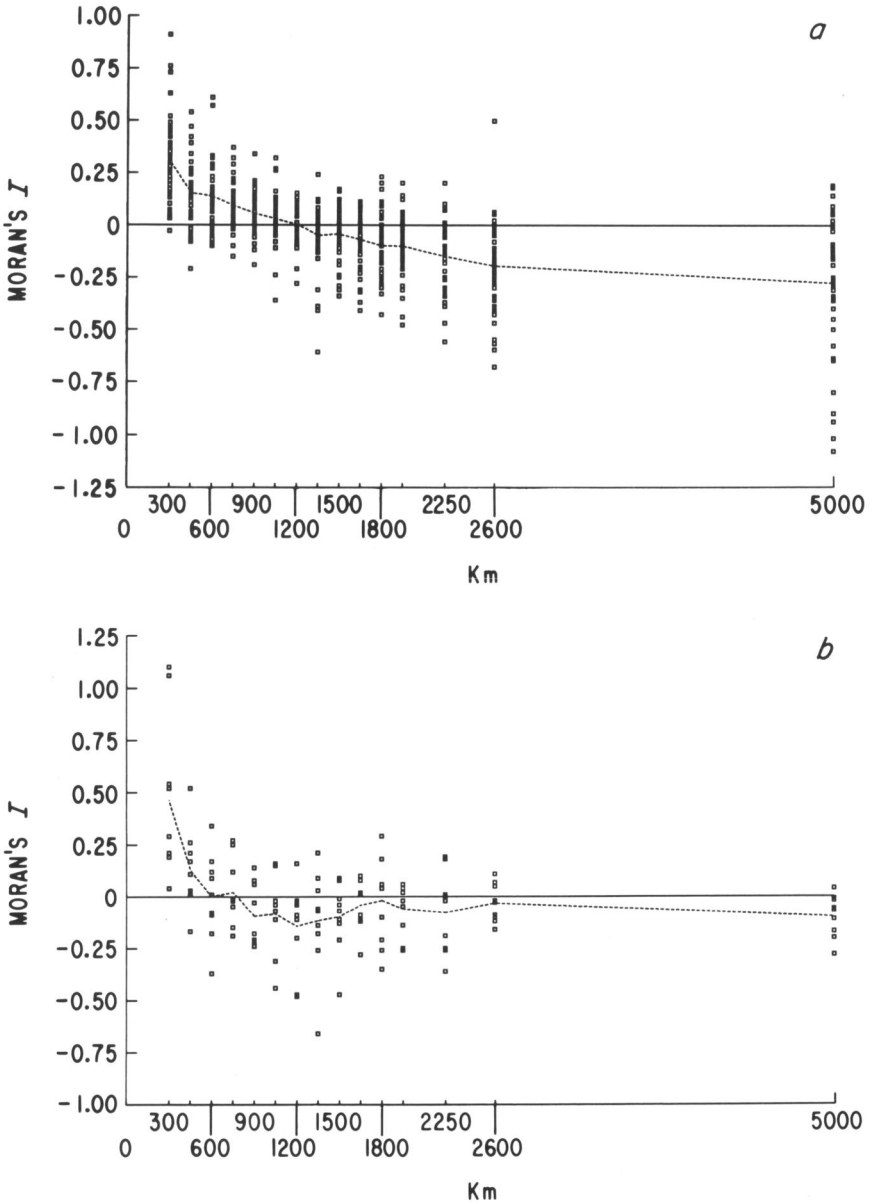

Figure 1. Combined one-dimensional correlograms. Ordinate, spatial autocorrelation coefficients (Moran's *I*). Abscissa, distance classes showing distance in kilometers. Distances indicated are upper limits of the distance classes. The average autocorrelations are connected by a dashed line. (a) Blood polymorphisms represented by 46 significant correlograms. (b) Cranial variables represented by nine significant correlograms.

phisms. Two cranial variables showing this trend are maximum cranial breadth and minimum frontal breadth. Inspection of their interpolated surfaces indicates considerable patchiness, with high values for sites in Switzerland, low values for Bulgaria, and intermediate values elsewhere.

Clustering the 55 significant one-dimensional correlograms for blood polymorphisms and cranial variables combined, by UPGMA, produces a phenogram of several branches with 14 mutually closest pairs. Two pairs are of cranial variables (basion-bregma height with orbital height; cranial breadth with minimum frontal breadth), and the others are all blood polymorphisms. The probability of this, or of a larger number of paired cranial correlograms, occurring by chance is less than 0.0004. Because cranial traits are interdependent variables, it is not surprising that some correlograms are similar. Yet these pairs and the other five cranial traits do not group together in a larger cluster but are intermixed with the blood polymorphisms. There is at least one cranial variable in four of the five major correlogram clusters. Cranial breadth and minimum frontal breadth, noted for their intermediate-distance negative autocorrelation, cluster with the Rhesus haplotype 4.19*cde*, indicating that this pattern is also represented by the blood polymorphisms.

Figure 2 shows the results of *k*-means clustering of the 34 significant directional correlograms for the blood polymorphisms. Each diagram is the average of the separate directional correlograms of the members of the cluster. These directional correlograms indicate a northwest-southeast gradient (Figure 2a), local patchiness (Figure 2b), a north-south gradient (Figure 2c), a north-northwest–south-southeast gradient (Figure 2d), and an east-west gradient (Figure 2e).

Figure 3, for the ten significant cranial variables, is the complement of Figure 2 and shows the averaged directional correlograms for three *k*-means clusters. They represent local patchiness (Figure 3a), a northwest-southeast gradient (Figure 3b), and complex patchiness (Figure 3c). These directional correlograms indicate that, despite the smaller number of variables represented by the intercorrelated cranial measurements, a diversity of patterns, including both patchiness and clines, is found for cranial traits, as it is for blood polymorphisms.

Testing the Manhattan distances between pairs of correlograms by Mantel matrix correlations with design matrices indicates that the difference between blood polymorphisms and cranial variables is not significant ($P = 0.028$, where 5% experiment-wise significance requires $P \leq 0.01$). The single significant contrast is between HLA and cranial correlograms ($P = 0.002$). This reflects the larger number of clinal patterns occurring for HLA variables than for any other type of variable, including cranial measurements. There is no doubt that cranial variables

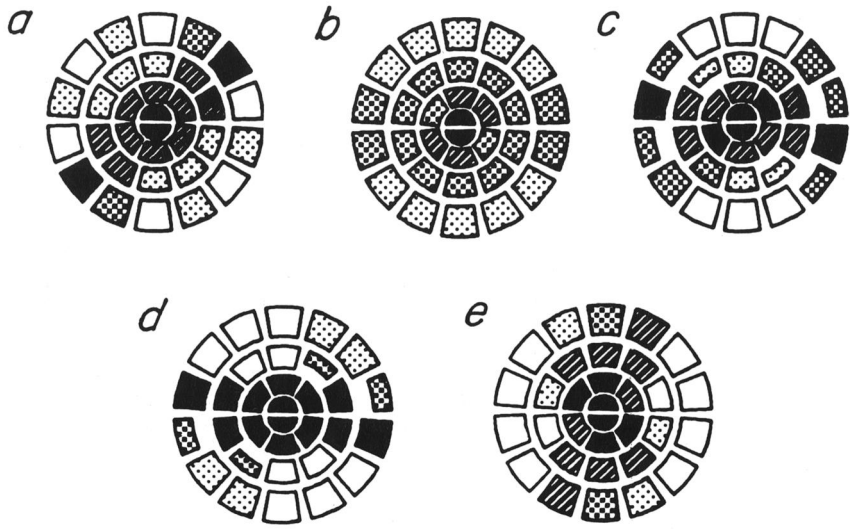

Figure 2. Average directional correlograms from clustering the 34 *I* correlograms for blood polymorphisms. Note the radial symmetry. The distance class limits from the center outward are 235, 840, 1815, and 3160 km. The different sectors represent average autocorrelation coefficients calculated for pairs of localities aligned with specified compass bearings. For all sectors shown, all constituent autocorrelation coefficients are based on 20 or more locality pairs. Sectors showing significant overall spatial structure are shown at full width of the annulus; those not significant are drawn at half-width. The shading represents approximate quintiles of the average autocorrelation coefficients from the 34 significant correlograms as follows: no shading, $-1.03 \leq I \leq -0.29$; small dots, $-0.26 \leq I \leq -0.05$; large dots, $-0.04 \leq I \leq 0.06$; stripes, $0.07 \leq I \leq 0.16$; solid, $0.18 \leq I \leq 0.56$. (a) First cluster: 53*PGM1–1*, 100*A10*, and 101*B13*, showing a tendency toward a northwest-southeast gradient. (b) Second cluster: 1.1I^{A}, 1.2I^{A1}, 1.2I^{A2}, 2.5*M*, 3.1*P*1, 4.1*D*, 4.13*Cde*, 4.13*cDe*, 4.13*cde*, 6.1*K*, 8.1*Fy–a*, 36.1*Hp–1*, 38.1*Gc–1*, 100*A1*, 100*A28*, 101*B14*, 102*BW17*, and 102*BW22*, showing little directional structure. (c) Third cluster: 4.13*cDE*, 50.1.1*P–a*, 100*A2*, 100*A3*, 101*B27*, and 102*BW15*, showing a north-south gradient over the 3160 km represented. (d) Fourth cluster: 100*A9*, 101*B5*, 101*B8*, and 102*BW35*, suggesting a north-northwest–south-southeast gradient, but this may be a more contorted surface than a simple cline. (e) Fifth cluster: 1.1I^{B}, 1.2I^{B}, and 101*B12* showing a diffuse east-west gradient. (From Sokal et al. 1989).

show a different set of patterns compared with HLA frequencies, but there is no accounting for the Manhattan distances by contrasting cranial traits with red cell antigens ($P = 0.054$), non-red-cell antigens ($P = 0.012$), or blood polymorphisms excluding HLA ($P = 0.064$).

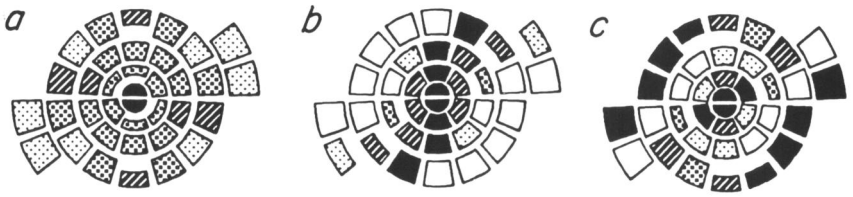

Figure 3. Average directional correlograms from clustering the ten significant correlograms for cranial variables. Explanation of the structure and shading is given in Figure 2, except that an extra distance class (4875 km) is also partially represented. (a) First cluster: cranial length, bizygomatic breadth, facial height, orbital breadth, nasal breadth, and nasal height, showing little directional structure. (b) Second cluster: basion-bregma height and orbital height, suggesting a northwest-southeast cline. (c) Third cluster: maximum cranial breadth and minimum frontal breadth, indicating a complex patchiness.

Discussion

Regardless of whetner blood polymorphisms or cranial traits are used as markers of population variability, the general findings reported by Sokal et al. (1989) and Sokal and Uytterschaut (1987) are the same, and this concordance is supported by the new computations. Spatial patchiness is found to be more common than clinal or random variation. The arrangements of these patches do not correlate strongly for functionally independent variables, but there is structure in the correlogram distance matrix, as revealed by clustering. These findings suggest that many different variables show similar spatial structure. This is consistent with the inference of one or two types of gene flow processes being the main causes of continental spatial patterning in Europe. Isolation by distance and ethnic resettlement are the processes that have been inferred (Sokal et al. 1989).

The spatial patterns found for cranial traits are largely indistinguishable from the patterns found for blood polymorphisms. This implies that the diverse evolutionary processes accounting for spatial variation among blood polymorphisms are sufficient to account for patterns in the ten cranial variables studied here. There is no evidence to gainsay the assumption that these quantitative variables respond to evolutionary processes in the same way as blood polymorphisms do. There is some evidence to suggest that HLA variables respond differently not only from cranial traits but also from other blood polymorphisms [see also Sokal et al. (1989)].

One interesting spatial pattern found in blood polymorphisms and in these modern cranial traits is the northwest-southeast cline. This

pattern has been interpreted as being consistent with evidence for a demic expansion into Europe during the Neolithic transition (Sokal et al. 1989; Sokal and Menozzi 1982). A northwest-southeast cline was first observed in a synthetic variable from a multivariate analysis of European blood polymorphisms (Menozzi et al. 1978). Application of both Fisher's (1937) wave-of-advance model by Ammerman and Cavalli-Sforza (1984) and a simulation model by Rendine et al. (1986) have been used to predict gene frequency gradients in the direction of the demic expansion. In these models demic expansion occurs because the spread of farming increases local population densities, causing settlement expansion into new territory and diffusive gene flow between the Neolithic farmers and the Mesolithic hunter-gatherers. Consequently, gene pools near the origin of the demic expansion in the Near East are swamped by the Neolithic farmers. Recruitment of the substrate Mesolithic population at increasing distances from the origin proportionally decreases the contribution of "marker" Neolithic genes, generating clines between the origin and the periphery of the expansion. This model fits well with archeological data (Ammerman and Cavalli-Sforza 1984) and accords with some current views on the origin of the Indo-European-speaking peoples (Renfrew 1987).

Spatial patterns in morphology of crania dated to the Neolithic period do not, however, support a genetic model of Neolithic transition in Europe by demic expansion and variable admixture (Harding et al. 1989). Interestingly, Sokal and Uytterschaut (1987) show a directional correlogram that indicates a weak northwest-southeast gradient in European cranial variation of the Early Medieval Ages (A.D. 500–1000), but there is no comparable pattern in the Late Medieval Ages (A.D. 1000–1500). This evidence suggests that, at least for cranial variables, some microevolutionary process in the last 500 years has acted to produce or recreate the northwest-southeast gradients of variation found for modern times. From what is known of Europe's migration history during the last 500 years, however, no migration hypothesis in this direction seems plausible. One important migration event in Europe in the fourteenth and fifteenth centuries was the conquest and occupation of the Balkans by the Turks. But a limited portion of Europe was involved, and there was a relatively small proportion of Turkish settlers in these areas; thus it is unlikely that this migration generated a major northwest-southeast directional shift in spatial patterns of genetic markers.

If the northwest-southeast cline in modern cranial variables was brought about by a microevolutionary process effective during the last 500 years, then perhaps such a process could account for northwest-southeast clines in modern blood polymorphisms as well. Another line

of inference follows from the description of temporal variation in cranial patterns by Sokal and Uytterschaut (1987): Spatial patterns in blood polymorphisms have also varied over time, weakening the argument for the persistence of spatial genetic patterns since a one-time demographic event in the Neolithic period.

Despite the finding of this analysis that modern spatial patterns in cranial variables are similar to those for blood polymorphisms and the subsequent inference that additional processes are unnecessary to explain cranial patterns, it must be noted that cranial variables are widely recognized as sensitive to environmental change. Immediately preceding the 500-year period of this analysis, a still not well understood process of brachycephalization occurred in Europe; this process differentially modified eastern and western populations (Creel 1968, Fig. 12; Schwidetzky and Rösing 1984, Fig. 8; Sokal and Uytterschaut 1987, Fig. 5). The brachycephalization was probably ecophenotypic and would not have produced parallel changes in blood polymorphisms. Undoubtedly, there is still more to learn about the biological history of Europe.

Certainly little is known of the role of selection in shaping patterns of variation across Europe. It has been suggested that selection may account for some of the observed genetic pattern in Europe (Sokal et al. 1989). Possibly, clinal patterns produced by systematic selection have been disturbed in various time periods by historic migrations, reemerging more clearly at other times. The difficulty with evaluating the role of selection, as noted by Lynch (1989), is that there are too many possibilities. Using a phylogenetic analysis, Lynch (1989) concluded that a neutral mutation-drift hypothesis was sufficient to explain interracial differences in human cranial dimensions. Likewise, multivariable spatial analysis of European genetic variation suggests that a neutral model is sufficient to account for observed geographic patterns. However, a migration hypothesis must be proposed to explain the emergence of northwest-southeast clines in Europe in the last 500 years.

Acknowledgments I am grateful to Robert R. Sokal for his advice and statistical expertise, which I sought at several stages of the analysis. Comments on the manuscript by Robert R. Sokal and two anonymous reviewers were also much appreciated. Barbara Thomson and Donna DiGiovanni provided computing and technical assistance, and Joyce Schirmer helped with the figures. The work was supported by the National Institutes of Health, under grant GM 28262, awarded to Robert R. Sokal. This is Ecology and Evolution Contribution 760 from the State University of New York, Stony Brook.

Received 31 August 1989; revision received 27 April 1990.

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