

The Apportionment of Human Diversity

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INTRODUCTION

It has always been obvious that organisms vary, even to those pre-Darwinian idealists who saw most individual variation as distorted shadows of an ideal. It has been equally apparent, even to those post-Darwinians for whom variation between individuals is the central fact of evolutionary dynamics, that variation is nodal, that individuals fall in clusters in the space of phenotypic description, and that those clusters, which we call demes, or races, or species, are the outcome of an evolutionary process acting on the individual variation. What has changed during the evolution of scientific thought, and is still changing, is our perception of the relative importance and extent of intragroup as opposed to intergroup variation. These changes have been in part a reflection of the uncovering of new biological facts, but only in part. They have also reflected general sociopolitical biases derived from human social experience and carried over into "scientific" realms. I have discussed elsewhere (Lewontin, 1968) long-term trends in evolutionary doctrine as a reflection of long-term changes in socioeconomic relations, but even in the present era of Darwinism there is considerable diversity of opinion about the amount or importance of intragroup variation as opposed to the variation between races and species. Muller, for example (1950), maintained that for sexually reproducing species, man in particular, there was very little genetic variation within populations and that most men were homozygous for wild-type genes at virtually all their loci. On such a view, the obvious genetical differences in morphological and physiological characters between races are a major component of the total variation within the species.

Dobzhansky, on the other hand (1954) has held the opposite view, that heterozygosity is the rule in sexually reproducing species, and this view carries with it the concomitant that population and racial variations are likely to be less significant in the total species variation.

As long as no objective quantification of genetic variation could be given, the problem of the relative degree of variation within and between groups remained subjective and necessarily was biased in the direction of attaching a great significance to variations between groups. This bias necessarily flows from the process of classification itself, since it is an expression of the perception of group differences. The erection of racial classification in man based upon certain manifest morphological traits gives tremendous emphasis to those characters to which human perceptions are most finely tuned (nose, lip and eye shapes, skin color, hair form and quantity), precisely because they are the characters that men ordinarily use to distinguish individuals. Men will then be keenly aware of group differences in such characters and will place strong emphasis on their importance in classification. The problem is even more pronounced in the classification of other organisms. All wild mice look alike because we are deprived of our usual visual cues, so small intergroup differences in pelage color are seized upon for subspecific identification. Again this tends to emphasize between-group variation in contrast to individual variation.

In the last five years there has been a revolution in our assessment of inherited variation, as a result of the application of molecular biological techniques to population problems. Chiefly by use of protein electrophoresis, but also by immunological techniques, it has become possible to assess directly and objectively the genetic variation among individuals on a locus by locus basis. The techniques do not depend upon any *a priori* judgments about the significance of the variation, nor upon whether the variation is between individuals or between groups, nor do they depend upon how much or how little variation is actually present (Hubby and Lewontin, 1965). As a result, the original question of how much variation there is within populations has now been resolved. In a variety of species including *Drosophila*, mice, birds, plants, and man, it is the rule, rather than the exception, that there is genetic variation between individuals within populations. For example, Prakash et al. (1969) found 42% of a random sample of loci to be segregating in populations of *D. pseudoobscura*, producing an average heterozygosity per locus per individual of 12%. A study of a number of populations of *Mus musculus* by Selander and Yang (1969) gave almost identical results. Two analyses for man, one on enzymes by Harris (1970) and one on blood groups by Lewontin (1967), give respective estimates of 30% and 36% for polymorphic loci within populations, and 6% and 16% for heterozygosity per gene per individual.

The existence of these objective techniques for the assessment of genetic variation, and their widespread application in recent years to large numbers of populations, in conjunction with older information on the distribution of human