

THE MORPHOLOGY OF HUMAN POPULATIONS

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Abstract

The breeding structure of the human population can be conceived as a pictorial model in which people are shown by dots at their place of residence. A series of superimposed maps show successive generations. Descent lines between successive maps show intergenerational migration. Loops indicate inbreeding. Largely vertical clusters of lines must soon form dense clusters of loops and these largely vertical fascicles of lines and loops bear some relationship to the isolates, breeding populations and races of classical anthropology. However, the universality of at least occasional strands between fascicles demonstrates the limitation of the classical concepts in that members of every isolate or race carry some origins from non-members and share descent from common ancestors in unequal proportions.

Anatomy is often thought of as a static subject whose chief facts were ascertained long ago. These facts are thought of as immutable —as true of the young as of the old— and indeed remaining after death to be seen by the student in the dissected cadaver. As a teacher of anatomy I have had to try to combat this static view. When I speak of morphology I do not imply anything embalmed and fixed. The morphological structure of populations, with which we shall now deal, is formed by movements and is subject to change. The structural elements are elastic and the purpose of the scientific study of

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the structure is to try to define the causes and the consequences of the changes.

What is human population structure? The earth is a globe and the human population occurs in a monolayer on its edgeless 2-dimensional surface. But the people do not fill the whole surface yet, despite the population explosion. The prediction made in the 1920's by the sociologist, E.A. Ross, of "Standing Room Only", is still unfulfilled. There are spaces between the people —big ones on seas, lakes, deserts and mountain tops and smaller ones in lush ecological settings with productive economies. In the irregular scattering of people we have a static two-dimensional image of the population structure with identifiable general features: absence of habitation on water but, usually, dense concentrations at its margins on the shores of rivers, lakes and ocean harbors.

Just as, in anatomy, an old-fashioned concern with static structure gave way to an emphasis on functional relationships, so also in the study of population structure, interest has turned to a concern with changes over time. In fact, the description of the simple distribution of people has been left to tradition-bound geographers. Those geneticists and demographers who are concerned with population structure deal with the dynamics. Changes with time give population distributions their third dimension.

Intergeneration migration

Of course, all population movements have sociological significance. Migrations for temporary labor or to retirement villages affect social life. From the point of view of human genetics, however, only permanent changes of residence from generation to generation are important. In the long-run perspective, the spacial units that give population structure its dynamic aspect are the movements from place of residence of parent to place of residence of offspring. The great wealth of evidence in such documents as birth certificates and baptismal records permit the collection of data on this useful measure of intergenerational movement: the geographic distance from place of birth of each parent to place of birth of each of their offspring. At present, when so many births occur in hospitals, the appropriate locus in each case is the place of residence of the parents at the time of birth of the offspring. In either case,

the unit is distance of movement per generation. As anthropologist you will see that this takes account to the factor of geography in choice of mates but ignores the factor of social distance. Some studies, such as those of Coleman (1979) show great social mobility so that, after a few generations, little trace remains of ancestral social class. Geographic migration is less marked, however, because mating requires meeting and meeting requires propinquity. Geographic distance is thus more important, at least in some cases, than social distance.

Marriage records can also be used for a measure of migration: the distances between the birthplaces of spouses. In fact, records which list residences at any stage of life are useful. However, the quality of data are important and it is not always easy to associate data concerning offspring with that concerning their parents.

Migration distances tend to be distributed in what is described as a gamma distribution —the greater the distances traveled, the rarer their occurrence. Because human beings use many modes of transport, most intergenerational migrations is by walking a short distance, but there is virtually always also some long distance migration by vehicle. The migration data permit an estimate of the degree of inbreeding from insolation by distance (Malecot, 1948, and extensions of his ideas by others including Morton *et al.*, 1968).

In our studies in northern Peru we found such a pattern of migration. Our censuses yielded in-migration rates of about 13-16% per generation in the town of Monsefú and 25-26% in the fishing village of San José; birth and death and studies in other towns and villages yielded more variable and generally higher migration rates but the same tendency to relatively frequent migration from places within about 30 kilometers, moderate amounts from surrounding regions, and occasional migration even from distant places including foreign countries and other continents (Lasker and Kaplan, 1964).

In Mexico the same general pattern is apparent in the work of investigators of the Tajín Totonac, in Quiroga, in Tzintzuntzan, and in our studies in Mitla, Oaxaca, and Paracho, Michoacán (Lasker, 1954). About 35% of the individuals questioned in Paracho were born elsewhere. In a census of Paracho conducted in 1952 we asked: "What are the most distant places you have been?" Figure I shows the frequency of various answers. Foreign countries have been omitted. The

answers only concern the most distant places visited. Other places visited would form a thick mass of dots, the nearer Paracho the more densely massed.

The map can be compared with one of birthplaces of persons resident in Paracho (Figure 2). The distribution appears to be of the same general form observed elsewhere —*e.g.*, by Küchemann *et al.* (1967), in an English village. The shorter the distance the greater (by far) the frequency of migration. In Paracho many residents were born in the neighboring pueblos of Aranza, Ahuiran and Pomaquaron and from nearby ranchos and pueblitos. Some migrants had come from Zacán because of the eruption of the Paricutín volcano and a number had come because of troubles or financial necessity from such places as La Cañada and elsewhere in western Michoacán. Migrants from further away were fewer in number, but virtually all parts of Mexico—at least central Mexico—were represented.

Now imagine how the third dimension of population structure, movement through time, builds up generation after generation on a surface that is unevenly peppered with residences of individuals. Picture each preceding generation on a higher plane and each individual below connected by two lines to the map showing the parental generation's residences above. From the point of view of the individual at the bottom, the lines above form a tree branching into two each generation as they rise. The lateral extent of the branches equals the extent of intergenerational migration. From the point of view of the ancestors above, there is also branching along the lines of descent, but the number of branches is indefinite and limited only by the fertility of the subjects. Furthermore, lines of descent may reach deadends: the descending lines end wherever there is a childless individual. But the lines of ascent go on indefinitely doubling each generation as long as bisexual reproduction has existed and, assuming that all life evolved from simple self-replicating one-celled organism, single lines for asexual reproduction before that.

Inbreeding

The population has not decreased in half each generation, however. On the contrary, there has been a general increase in human numbers, at least in historic times, except for a brief

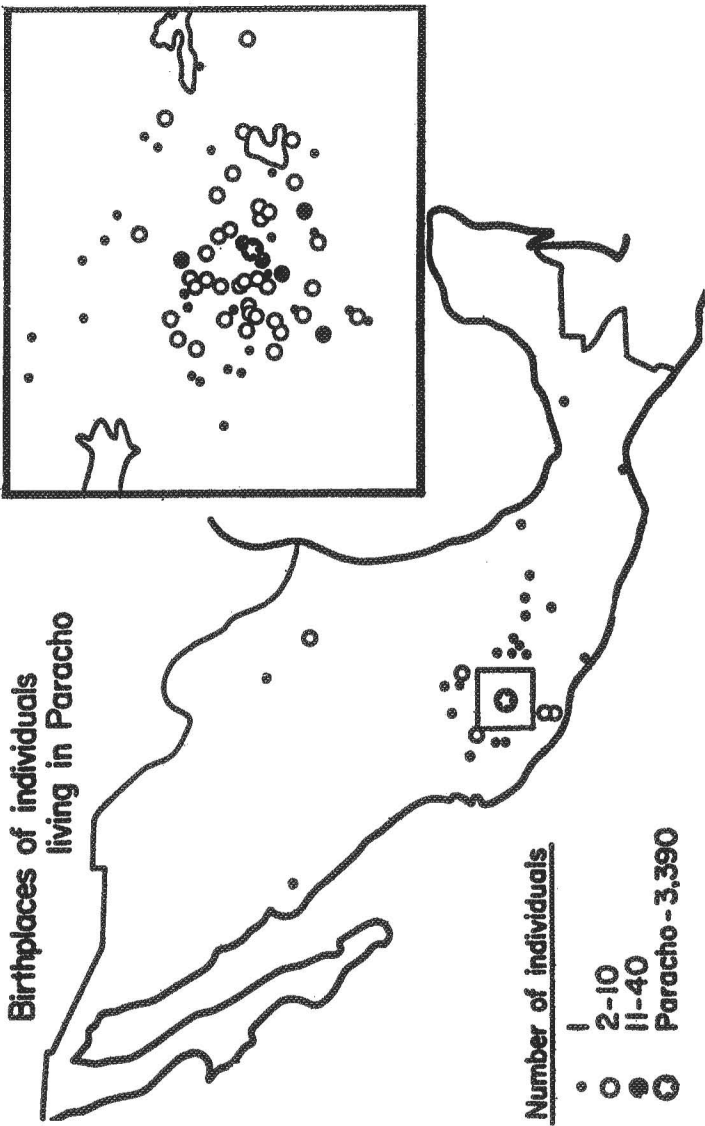


Fig. 1: Answers to the question asked in Paracho in 1952: "What are the farthest places you have ever visited?" foreign countries are omitted. (Courtesy of Bernice Kaplan).

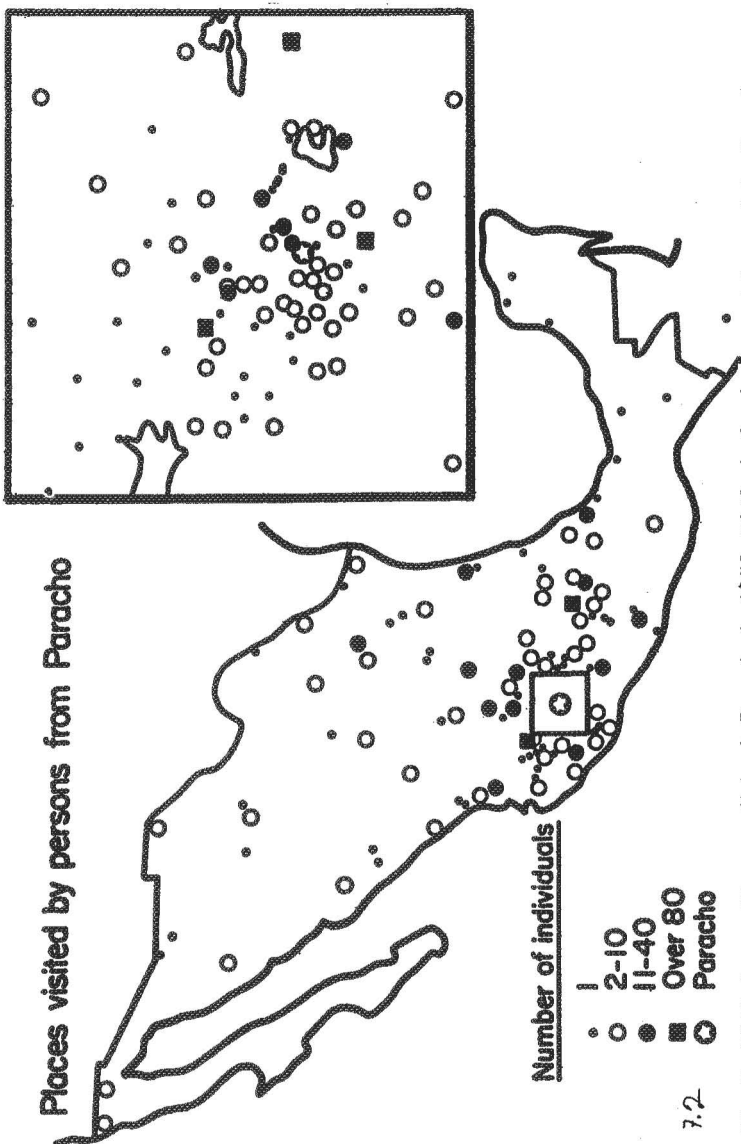


Fig. 2: Birthplaces of persons living in Paracho in 1952. Births in foreign countries and in Paracho are omitted (Courtesy of Bernice Kaplan).

reversal during the black plague and occasional local catastrophes caused by war and pestilence. The doubling of number of ancestors in each prior generation, but smaller total numbers of people in earlier times is possible because the same individual soon reappears as a progenitor in more than one ancestral line. Such lines thus form loops, a descendant being related to the same ancestor through both his or her mother and his or her father. The parents are related to each other and the individual is inbred. This is not the exception, it is true of everyone although in different degrees. The degree of inbreeding in any individual is exactly proportional to the number of links in the loops going back to the common ancestors. The inbreeding coefficient is $1/2$ raised to the power of one less than the number of lines (links) in the loop. If there is more than one common ancestor, the contribution to inbreeding calculated from each is summed over all of them to give the inbreeding coefficient of the individual (figure 3). The inbreeding coefficient of a population is the average inbreeding coefficient of its members.

Now where are we? The general structure of the human population can be expressed by migration rates or by inbreeding coefficients and can be represented by superimposed maps representing the distribution of population in successive generations (Figure 4). Through time in generations, the ascending branches and descending roots are all interconnected, but not at random. There is a general verticality of lines because of the prevalence of short intergenerational migration distances, especially in isolated subpopulations. Subpopulations of this kind are held together by denser networks of smaller inbreeding loops representing high coefficients of inbreeding. Even the most compact fascicles (bundles of lines held together by dense inbreeding loops) have some interconnections at least with nearby subpopulations, although in small groups these may be completely lacking for a few generations of purely endogamous unions.

The structure I have tried to picture poses some paradoxes. Although incest tabus and social patterns of mate selection restrict the numbers of tight inbreeding loops, the finite numbers plus bisexual reproduction demand masses of inbreeding loops to more distant relatives. One has two parents, four grandparents, eight great grandparents, over a thousand ancestors at ten generations, over a million at twenty generations,

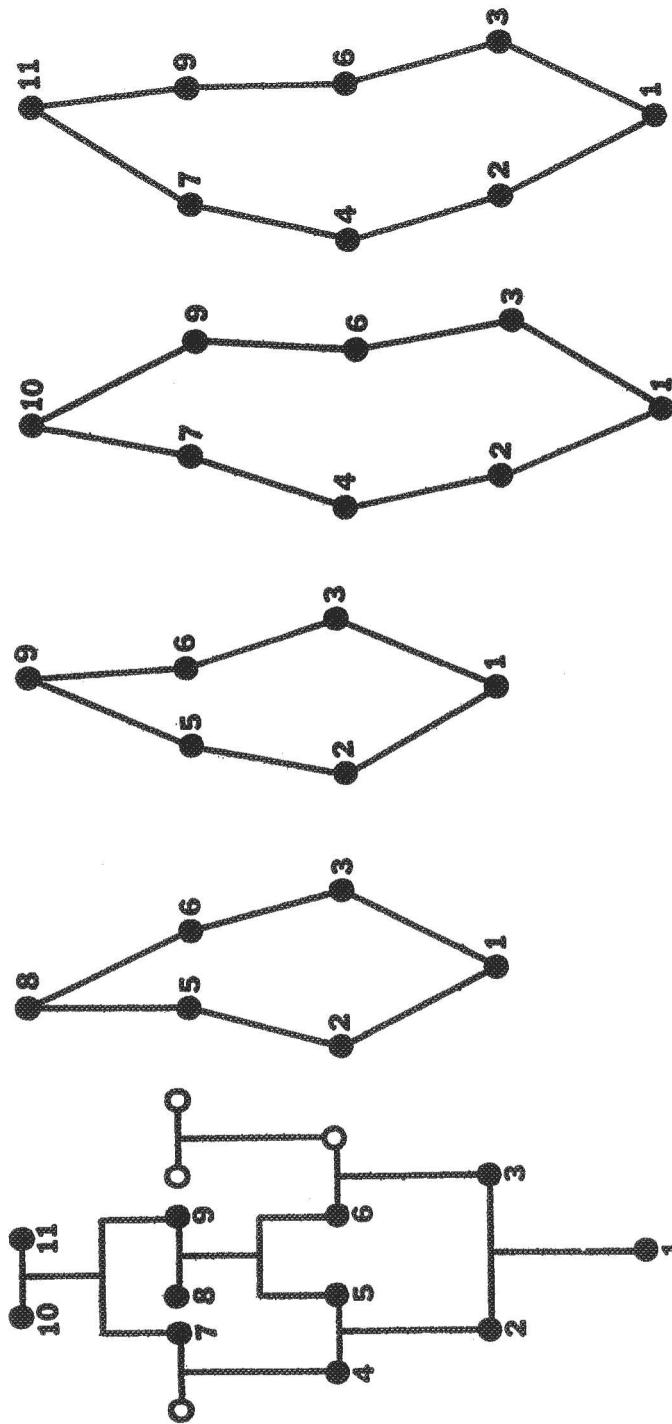


Fig. 3: Calculation of inbreeding from a Pedigree. An individual (1) is inbred to the extent that his mother and father (2 and 3) have ancestors in common (8, 9, 10 and 11). The degree of inbreeding is the sum of inbreeding in all the loops. The amount of inbreeding in each loop is one divided by 2 raised to the power of the number of descent lines in the loop less one. The four inbreeding loops at the right are abstracted from the pedigree at the left reading from left to right the inbreeding coefficient = $\frac{1}{25} + \frac{1}{27} + \frac{1}{32} + \frac{1}{128} = \frac{1}{10} + \frac{1}{128} = 0.078$

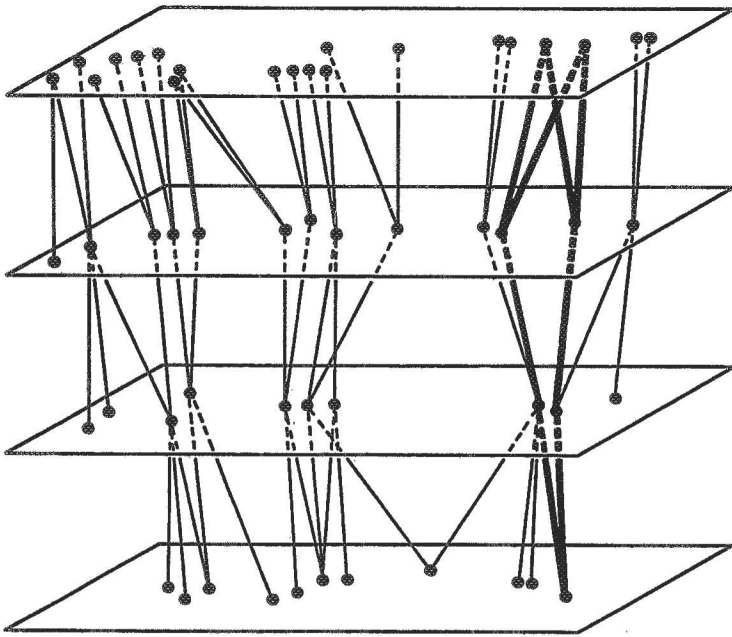


Fig. 4: *Superimposed maps representing the distribution of people in four successive generations connected by descent lines between generations. Laterality of the descent lines indicates migration. Most descent lines form generally vertical fascicles. These are held together by inbreeding loops (marked with thicker lines). Sooner or later all fascicles are connected either directly or indirectly.*

over a billion at thirty and a trillion at forty generations a mere ten centuries or so ago. But the population at that time was counted at millions in the whole world and all the rest of ancestry is represented by repeating the same ancestors and redoubling the inbreeding loops. Of course there are some gaps between the bundles of descent lines, gaps crossed by only a few migrations, but the numbers of lines are so enormous that any ancient interpopulation matings must now be represented in the ancestry of all of us. Since each inbreeding loop contributes a fraction to the inbreeding coefficient, we are by now all completely inbred. Because the cross connections are also additive, with enough time all human beings are as closely related to each other as brothers and sisters. With still more time, all members of the species become identical by origin.

On the other hand, one inherits roughly half of ones DNA base sequences from each parent, a quarter from each grandparent, and so on, and the point is reached where one will have received no genetic information along most of the numerous branches of the ancestral tree. Small differences in the likelihood of survival or reproduction of individuals with particular genetic information—Darwinian fitness—differentiate, but only in part, populations that are identical by long-time descent but live in different habitats or by different cultures. Chance mutations and chance survival also play a part so we become identical by descent but still differ genetically.

Races

Where do races fit into this scheme? They can be seen as the largest bundles of fascicles, attached by numerous migration lines to other bundles, but with descent lines among themselves much denser still. And, at least historically, they tended to inhabit more or less contiguous lands and to respond to selection to a limited part of the range of human environments.

The concept of race is one of the most controversial in physical anthropology. The term race has been used in different ways by different writers. Many researchers think that the concept is of limited usefulness and some think that races do not exist at all. What relationship does the model drawn have to the concept of race? to make such a comparison one must limit the race concept to its biological sense: a race is a subpopulation of a biological species whose members share a common descent. Thus individuals belong to the same race by reason of shared ancestors and *not* because of any shared physical characteristics. Examination of the detailed structure of the model will show that, ordinarily, only siblings share all the same ancestors in exactly the same proportions. The filaments coming from without the fascicles connect to individuals within it in different proportions so that membership in the group by descent is a *relative* matter. The boundaries of groups must be vague and no matter how many groups are described, there will always be individual who could reasonably be classed in any of several groups or in none. In fact, there will be no sizeable number of individuals who can be

securely grouped together. Different classifiers, even when they try to follow the same rules of classification, will group individuals somewhat different. Even if objective criteria are followed, individuals do not fall into clear natural groups. Thus the categories of races are only roughly applicable to geographic groups or groups whose geographic origins are known or can be inferred. If that is all one wants to say by it, a racial term may serve, but its extension into a dynamic model of human population structure is only roughly approximate at best.

Thus far we have drawn a picture of the human population structure which consists of a series of parallel planes with lines between them. These lines form inbreeding loops and tend to cluster into perpendicular fascicles. The number of parallel planes traversed before dense clusters of loops must form is governed by the size of the breeding population, but inbreeding can be, and often is, more intensive because the fascicles consist of subfascicles and small inbreeding loops may occur even within the family. Various kinds and degrees of endogamy give the structure its fascicular appearance, marriages within clans, within tribes, within local groups and within nations. There always are some exogamous unions, even between tribes and nations, however, so the whole structure of the species is held together by more or less frequent interfascicular strands and isolated filaments.

What are the shortcomings of such a model? First of all, the generations do not show temporal planes. A hundred years may span three generations or six. The inbreeding loops therefore can be asymmetrical polygons. An animated moving picture of the population might show individuals symbolized by dots on a map. As the film rolls the dots migrate over the surface of the map. Occasionally a pink dot and a blue dot, representing individuals of opposite sex, come together. In some of these cases a new dot subsequently appears and is usually closely associated with the pink dot from which it emerged. Later the new dot may move farther and farther and may in turn become associated with another dot and give rise to still further dots. If we want to show inbreeding loops the dots will have to be drawn as leaving trails of their past movements and as we run the film forward two trails from the same ultimate source will sometimes again merge to form an inbreeding loop.

To approach the model with fields studies of real communities, it will be necessary to examine small segments of it separately. To see the whole thing at once one would need complete pedigrees of everyone and considerable time depth. Unfortunately that is not possible. After a few generations many of the lines are lost in uncertainty. Remember that in about ten centuries with four generations per century one would have to consider up to two trillion lines of descent for a single individual today. The best we can do is sample the patterns and I encourage anthropologists to do so.

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