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Genetics and the Races of Man

by

WILLIAM C. BOYD



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Introduction

MAN is a curious animal, interested in many things. One of the things that interests him most is mankind itself, and he has devoted much thought, especially in the last few centuries, to the recording and interpretation of observations on the peculiarities of mankind. One of the features that impresses the common man and the scientist alike are the differences in customs, languages, skin color, and physique between human beings from different parts of the earth. It may be that we all have the makings of a taxonomist in us, for long ago people began, on the basis of such differences, to classify individuals from other nations and countries into races. The scientists who are most concerned with setting up such classifications are called anthropologists.

The first classifications were not very scientific. Originally people tended to confuse cultural traits, which are simply learned differences, with physical differences which are inherited and are not much influenced by environment. Thus the layman and early students of man attempted to classify mankind into races, for example, on the basis of language, and one heard of the Latin races, the Germanic races, the Slavic races, the Greek race, and even the Anglo-Saxon race. It is true that in some cases language is a guide to racial origins, as in the case of the French Canadians of Québec or the Pennsylvania "Dutch" of the United States, but languages can be, and are, forgotten by their original speakers and/or acquired by people of unrelated stocks, as the American melting pot shows us every day, so that the differences in the world's languages, fascinating and useful as they are to the linguist, are very shaky foundations for racial classification. Later skin color was utilized. One heard of a "white" race, a "yellow" race, a "red," "brown," and "black" race. The terms used are poor

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descriptions of actual human skin colors, but this method did have the advantage that color of the skin is only partly determined by the environment, being mostly an inherited characteristic. But it is too broad and vague a classification to be of much scientific value. Not all "black" races, for example, are closely related, as shown by the many differences between African Negroes, southern Indians of India, Australian aboriginals and Pacific Negritos. The color of the skin is evidently subject to fairly rapid change by natural selection, and the inhabitants of hot sunny regions all tend to develop high pigmentation because in this environment a dark skin is an advantage.

About a hundred years ago the Swedish anatomist, Anders Retzius, thought he had discovered a really scientific basis for racial classification, which was the shape of the head, in particular the ratio of the breadth of the head to its length. This is called the cephalic index, and has been much used by anthropologists. It has the agreeable feature that it can be applied to the skulls of ancient populations as well as to the heads of the living peoples of today.

It is true that the inhabitants of a given area tend to have similar cephalic indices, but it has not proved possible to erect a very satisfactory classification into races on the basis of this criterion alone, and we are now beginning to realize that no one criterion, even though based on an inherited character which is not influenced by the environment, can be enough for a good classification. The cephalic index, moreover, does not seem to be immune to changes which are presumably due to environmental influences and, although it is no doubt inherited, is determined by a genetic mechanism which we are as yet far from understanding. These and other considerations have led physical anthropologists in the last few decades to make more and more use, in racial classification, of characteristics inherited in a way which is completely understood. Instead of measurements of the proportions of the skull and other bones, we tend to make more use of the frequencies of certain genes in the population. For the present audience it is surely unnecessary to define a gene; let us say merely that the gene is the unit of heredity. The frequency of a gene can range from

1.00 (all members of the population have the gene) to zero (no member of the population has it). The use of gene frequencies has a number of advantages, of which I may mention three:

(1) The method of gene frequencies is completely objective. No element of subjective judgment enters into the determination of the frequency of a gene in a population, although the value of a frequency which divides two races is a man-made and arbitrary decision, as we shall see in a moment. (2) Tables of gene frequencies are more compact than tables of morphological and other features which may result from the action of the genes. In the Rh blood group system, for example, the frequencies of just 8 genes will summarize the variations in 27 possible blood types. (3) The gene method is quantitative rather than qualitative, so that the estimated gene frequencies give us an idea *how much* different races differ from each other, and enable us to predict the consequences of race mixture accurately.

This advantage in making quantitative comparisons is seen for example when we are dealing with a mixed race and wish to ascertain the proportions of the component races which went to make it up. Glass and Li were able to calculate from blood group data that North American Negroes have about 31 per cent white ancestry. From the rate at which race mixture has been progressing in this population Glass and Li were able to calculate that the American Negro will have become indistinguishable from the American white (in other words, be assimilated), *assuming mixture continues at the same rate as it has been going on in the past*, in some 1000 to 1100 years. In a later paper, Glass, using similar methods, was able to show that the common belief that North American Negroes have considerable amounts of American Indian ancestry is erroneous. Such results could not have been obtained by morphological and metrical methods, or by studies of skin color.

As another example of point (2), we may mention the Australian aborigines and the Ainu. Both these peoples have been called by some authors "basic white." However, in the present state of our knowledge of the inheritance of skin color, we cannot state how much the very dark skin of the Australian marks him off from

the European. But a glance at his blood group frequencies tells us at once that he is pretty similar in regard to the original absence of B, but different in regard to M and Rh negative. We can probably account for the acquisition of the Rh negative gene by the Europeans on the hypothesis of mixture, and the peculiar M frequencies of the Australian by selection of random genetic drift, which I shall discuss later. Thus it is not impossible to imagine a common origin for these diverse peoples, although they have by this time differentiated into separate races.

It is only when characteristics are inherited in a completely understood manner that gene frequencies can be calculated. The best methods of estimating gene frequencies, a subject which has interested me, are too mathematical for presentation here, however. In man there seem to be two classes of characteristics whose mode of inheritance is understood: (1) Rare abnormalities such as Huntington's chorea, Marfan's syndrome, color blindness, and hemophilia, and (2) common normal characteristics, mainly blood groups.

Very rare characteristics are not satisfactory as a basis of comparison of different races and ethnic groups because the amount of data which would have to be collected is prohibitive. This rules out practically all the characteristics of type (1), and we are left with type (2).

It is presumably only an accident that the majority of characteristics of type (2) are blood groups, although there may be some feature of the blood groups which makes them peculiarly susceptible to genetic analysis. In any case, there is certainly no reason to suppose that other physical characteristics, if fully analyzed genetically, would be in any way inferior to blood groups as a basis for race classification, and I should not like my audience to think that my use of blood groups for this purpose is just a desire to use only the characters I have studied so long and understand relatively well, or in other words just an attempt to blow my own horn. When the genetic mechanisms of other physical characteristics such as head shape have been worked out, I propose to use them also.

It is surely unnecessary here to give much account of the human blood groups. They were discovered in 1900 by Karl Land-

steiner. You all know that for purposes of blood transfusion human beings may be classified into four groups depending on the kind of blood they possess, and that it is important that donor and recipient belong if possible to the same blood group. The details of the separation into four groups may be a little more hazy in your minds, but that is not important for our present purposes. What is more important is to know that these four blood groups can be considered as resulting from the action of three genes, which we designate as A, B, and O, each gene capable of occupying a particular point (locus) of the appropriate gene-carrying structure. Such structures are called chromosomes. Since we all have two chromosomes of any particular sort, one from our father and one from our mother, it follows that six combinations of these genes exist, namely OO, OA, AA, OB, BB, and AB. When the O gene is accompanied by A or B, it does not exert any perceptible action, and OA and OB are not distinguishable in the laboratory from AA and BB respectively, thus giving us the four basic kinds of blood.

Most of you probably know that this is a rather over-simplified version of the actual situation, and that more genes are actually involved. You doubtless also know that another blood group system, the Rh system, is important in some transfusions and sometimes responsible for a disease of infants known as erythroblastosis fetalis, and that there are other blood groups in addition to these. In fact there are nine well-studied blood group systems, all independent (probably) in their inheritance, and a number of systems more recently discovered which have not been so well studied. It is mainly on the basis of the data concerning the nine best-known systems that our racial classification must be erected.

Blood Group Systems

The ABO blood group system has been known the longest and is consequently the best studied. Thousands of populations have now been tested.

The ABO system is not the most useful, anthropologically, but the availability of much more extensive data than for any other

blood group system partially compensates for this, and even before such extensive information was available preliminary racial classifications based on the ABO system alone had been proposed.

The only populations having no A and no B are certain tribes of American Indians, although some American Indians possess moderate to large amounts of A. The Australian aborigines agree with the latter in possessing a high frequency of A. Nowhere besides North America is A so high, but on the other hand hardly anywhere else is it zero. The populations of the rest of the world differ mainly in the amount of B they possess; frequencies range from 0.04-0.05 in Western Europe and the Caucasus to nearly 0.30 in parts of Asia. The Basques, long thought to be an isolated remnant of a very early European people, have virtually no B.

The ABO data alone do not enable us to separate the peoples of the world into clear-cut races which make much sense geographically; they would for example force us to put some of the American Indians, the Australian aborigines, and the Baffin Land Eskimos into the same race, which hardly makes sense.

However, in view of the processes by which races are formed, we should not really expect to be able to make a satisfactory classification on the basis of any *one* series of genes. Also, the gradations (clines) between existing human populations are too gradual for sharp separation, and distant populations seem in some cases to have altered in the same direction.

The fact that blood antigen A can be divided into two main sorts of A, A_1 , and A_2 , probably determined by two corresponding genes, greatly increases the anthropological value of the ABO system. For it turns out that the A_2 gene is unknown in Eastern Asia, Australia, the Pacific and the American aborigines, being found only in the peoples of Europe, the Middle East, and Africa. The *proportion* of A_2 to A_1 is higher in Africa than in Europe, and the Middle East is in this respect as in others a transition area between Europe and Eastern Asia.

The second oldest blood group system, in order of discovery, is the MN system. The frequencies of M and N show less geographical variation than do the ABO frequencies, but two of the world's populations do differ sharply from the rest of the world

(and from each other). These are the American Indians on the one hand and the Australian aborigines and Melanesians on the other. High frequencies of N, and consequently low M, are found throughout the Pacific area, with the highest N in New Guinea. In American Indians N is very low.

The anthropological value of the MN system has been increased very much by the discovery of a pair of antigens, S and s, which are closely associated with it. As a result we now postulate that 4 genes (or chromosomes), Ms, MS, Ns, and NS are involved instead of merely 2. Use of anti-S enables us to distinguish sharply between the natives of New Guinea and the Australian aborigines, for antigen S is present in New Guinea and absent in Australia.

The *Rh system* is anthropologically the most useful blood group system, although fewer data are available than for ABO or MN. The 12 or more phenotypes distinguishable with the usual serums depend upon the action of more than 8 genes or chromosomes, and these genes, as I shall call them, vary significantly in frequency in different parts of the world.

May I note the high frequency of *r* (the Rh negative gene) in the Basques, the absence of this gene in Asians, American Indians, and Pacific populations, and the intermediate values of the black Africans? And finally the very high frequencies of R^o in black Africans, as opposed to its very low frequencies in the other populations (it seems to be actually absent in American Indians), make it practically an African gene.

More recently a new factor, *V*, has been found to belong to the Rh system. It is rare in whites but common in Negroes.

Time will not permit a discussion of the more recently discovered blood group systems, often identified by the name of the patient in whom they were first identified. I may mention one of them, however.

The *Duffy* blood groups promise to be among the most interesting of the new blood groups. In Europeans two genes, Fy^a and Fy^b are involved; in England the frequency of Fy^a is about 0.40. It is much higher than this in Lapland and Asia. In Africans there is another gene, which has been designated merely as *Fy*. This gene, unknown in Europeans save in rare individuals, is actually in

Negroes the most frequent at this locus, having a frequency of over 0.8. Fy therefore, constitutes another "African" gene.

Aside from R^o, Fy and V, blood group genes which are virtually restricted to one race are mostly conspicuous by their absence, as would be expected from the way in which races originate. That still others may exist, however, is suggested by the recent discovery that a blood antigen called *Diego* was not found at all in 200 white Americans, but individuals positive for Diego constitute over 30 per cent of certain American Indian tribes and all American Indians so far tested possess at least a moderate amount of this antigen. This may constitute the discovery of an "American Indian" or Asian gene.

The Races Defined by These Data

Definition of Race. Everybody knows what races are, he supposes, yet people constantly use the word in different senses. Even our later discussion of the mechanisms of race formation, although it should make the general meaning of the concept clear, does not provide us with a definition. The reason for this is partly that race is a more subjective unit than is species, and classifications into races depend to a large extent upon the purpose and even the whim of the classifier. Until the differentiation of different populations has reached the stage of making them different species, it is often almost a matter of taste whether we separate them into different races, or lump them together as members of the same race. In particular the amount of difference demanded by classifiers for a basis of classification of two populations as two different races will vary. Some will be satisfied merely with a difference in skin color, others will demand that the two populations differ in a number of ways. In a book published in 1950 I defined 6 races on the basis of blood group data. In the same year Coon, Garn, and Birdsell published a book on race formation in which, using mainly morphological data, they defined 30 (possibly equally valid) human races, no one of which was identical with any of mine. Our points of view were actually not so different. It simply suited the purpose of Coon, Garn, and Birdsell to divide mankind up

into 30 races, and it suited my purpose, at that time, to divide the human species into 6 races. Even if we had both been using only blood group data, there is the possibility that considerable differences in the number of races defined would still have been seen.

I have previously suggested a definition of a human race which I propose to use here: "a population which differs significantly from other human populations in regard to the frequency of one or more of the genes it possesses."

There are clear-cut differences in blood group gene frequencies which distinguish a number of human populations one from the other, and we may accordingly call these populations races. Since these differences are generally merely quantitative, that is, one population has more of one gene and less of another, it is not easy to present such distinctions without recourse to tables which it would not be easy to show under the present circumstances. I shall try to show you the general procedure by presenting the basis for the distinction between *Northwest Europeans*, to which race many of the present audience will belong, at least by descent, and *Lapps*, a small but very distinctive European race in northern Scandinavia.

The Northwest Europeans have fairly high percentages of blood group gene A and relatively low B (gene frequency of B less than 0.1). The frequencies of M and N are "normal," meaning that M is roughly equal to N, but perhaps a little higher. The frequency of A₂ is higher than in Africa (A₂ is absent in most of the rest of the world). The Rh negative gene has the highest frequency in the world except for the values found in the Basques. Fy^a about 0.4.

The Lapps have the highest N frequencies in Europe, a high value of the Duffy gene Fy^a, a very low B frequency (B is present everywhere in Europe except possibly in the Basques), and the A₂ frequencies are 3 times those found anywhere else in the world. The Rh negative gene (r) is relatively infrequent, another of the Rh genes, R¹, is somewhat above the usual European values, and another, R², is high.

Thus we see that the Lapps, a small and at present minor European group, are sharply distinguished from the group we

think of as the principal European race. The distinction is so clear that the location of the Lapps is visible on a map of Europe on which virtually any of the blood group frequencies have been plotted. The distinctions between the other racial groups proposed below are mostly equally clear, and many subdivisions of these will undoubtedly become possible as more data accumulate.

At present I propose the following 13 races:

A. *European Group*

(1) Early Europeans, (2) Lapps, (3) Northwest Europeans, (4) Eastern and Central Europeans, (5) Mediterraneans.

B. *Africa*

I consider the Egyptians and North Africans to be predominantly European, and put only Africans south of the Sahara into (6) The African Race.

C. *In Asia* we have a very great diversity, but one can easily distinguish (7) the Asian Race, and (8) The Indo-Dravidian Race.

D. There are indications that the American Indians will prove to be separable into North American and South American types, at least, but at present I distinguish only (9) the American Indian Race. (I include the Eskimo in this race, although there are some differences.)

E. *Pacific Group*

The vast Pacific area still needs further investigation but the extensive studies of Simmons, Graydon, and associates have been largely summarized in papers dealing respectively with Micronesia, Indonesia, Melanesia with Australia, and Polynesia. Birdsell in the U. S. A., sometimes working in collaboration with the Australian investigators, has also done a great deal of fine work. Although it may be too soon to set up any definitive classification, it is tempting to classify the main Pacific populations (leaving Australia aside) into 3 races: (10) Indonesian Race, (11) Melanesian Race, (12) Polynesian Race.

F. *The Australian Aborigines* fall into the (13) Australian (aboriginal) Race.

It is now natural to ask ourselves how the differentiation of mankind into these various races came about.

Formation of Races

When populations are sufficiently isolated geographically from each other, or sometimes when other types of isolation exist, the formation of races and eventually species goes on by the process discovered by Darwin, namely the preservation and accumulation of small random variations which tend to make each race better adapted to its environment. Today we know something which Darwin did not, which is that these small heritable variations, which constitute the sole raw material of evolution, are genetic mutations. As most of you doubtless know, a mutation is a sudden change in a gene which causes it to have a different effect on the organism. This change is perpetuated; that is, the new gene reproduces itself, its *new* self, just as the old gene reproduced itself. As a consequence, it is possible to define evolution, as Dobzhansky has done, as "essentially nothing but a change in gene frequencies." Mutations provide the raw material, but natural selection provides the motive power, for it selects out, from the numerous mutations constantly being produced in each organism — nearly all of which are deleterious — those few which confer some advantage upon their possessors.

Different geographical areas generally mean different environments; consequently a mutation which is advantageous in one environment may not be so in another. Also, since advantageous mutations are rare, it is a matter of chance whether in a given population a given advantageous mutation occurs or not. Both of these factors favor racial differentiation. On the other hand, the reverse of this process, called convergent evolution, which is the becoming more alike of two races placed in identical environments (if such exist) is not so certain to occur, for this process too is dependent partly upon the chance supply of the raw materials of change. Lacking the proper mutations, change in a given direction may not take place. It is possibly for this reason that the American Indians and Eskimos living in the cold extreme northern and southern portions of America have not developed blue eyes, blond hair, and light skins. Even if the same mutation does occur

in two different races living in the same environment, it may well be less favorable in one race than in the other, since it is projected in each case upon a different genetic background. We know that the final effect produced in an organism by a given gene depends not only upon the gene, but also upon the environment, and the environment includes the background of all the other genes the organism possesses.

The modern picture of race formation somewhat reverses the ideas of anthropologists of the last generation, such as Hooton, that the characters used for racial classification should be "non-adaptive" (Hooton later changed his mind). Racial characteristics have to be adaptive because they were created by a process which picks out adaptive characteristics. There is no other way in which racial characteristics can arise.

It was formerly believed that some human traits were much less subject to the action of natural selection than were others, and it was asserted that these characters were the most valuable for anthropology, since natural selection would change their frequencies in a population less rapidly than it would change the frequencies of the strongly adaptive traits. It was asserted by some (including me, I regret to say) that the blood groups belonged to the non-adaptive category. We now realize, however, that the blood groups are also subject to the action of natural selection, sometimes perhaps strongly, and modern anthropologists have come to realize that it is not easy, merely by inspection of a characteristic of an organism, to decide what its true selective value is. In fact it is now doubted if any truly neutral genes, in the evolutionary sense, exist.

In addition to the increase in the frequency of favorable genes by natural selection, other agencies may play a role in race formation. One of these, which has always been of importance in man, is mixture. When two or more different stocks occupy the same area, they may or may not fight, but they invariably interbreed. If this process is allowed to go on to its natural conclusion, a mixed race, different from either of the parent stocks, and more or less intermediate in appearance, results. Such a race may be now in the process of formation in Hawaii. At all times mixture has been

a force tending to counteract to some extent the natural tendency to racial differentiation.

The ever-present possibility of mixture between populations which are tending to diverge, but which are imperfectly isolated, and the fact that the environmental differences which lead to divergence are not sharply discontinuous, but often vary in a gradual manner from one locality to the next, cause the genetic differences between adjacent populations generally to be gradual instead of abrupt. Such gradual transitions in gene frequencies are called "clines."

Mixture may also result when one population migrates into an area occupied by another, with or without the use of force. Candela argued that the blood group B gene was introduced into Europe by the invading Mongoloid armies from the 5th to the 15th centuries.

Another process which may have operated, especially in early times when man must have been a rare animal in some areas, is genetic drift. By this we mean accidental random fluctuations in the frequency of a gene due to the fact that actual populations are finite in size. This is not difficult to illustrate. Suppose we have a population which has blood group B in about the amounts found in Europe, say 10 per cent. Let a boatload consisting of ten persons leave this population to settle in a new island or continent. It is clearly perfectly possible that merely by chance no person of blood group B (or AB) will be represented in our batch of emigrants; in fact the chances of this happening are about one in three. If this should happen, the population of the newly settled island or continent will never contain blood group B unless it arises later as a new mutation. And even if individuals possessing the gene B did reach the new world, it might happen that they would fail to leave descendants, or have only offspring who did not carry the B gene (as a general rule only about half of the descendants of a group B individual will carry the B gene). If this should happen, the B gene is completely and irreversibly lost, just as a consequence of random sampling of a small population. This process has been called by Professor Sewall Wright *genetic drift*. It should be noted that no restoring force acts to counteract random

fluctuations in gene frequencies and bring the frequencies back to their original values.

It is possible to lose by genetic drift even genes which have a positive selective value, if the population is small enough. It seems quite possible that this mechanism may explain the characteristic "patchy" distribution of some of the blood group genes in the American Indians and Australian aborigines, both of which at one time must have gone through the stage of being small populations.

The result of racial differentiation is generally a change in many gene frequencies. This of course cannot be observed directly since we cannot see the genes, but is reflected, in a human population, in two principal ways. The first of these involves changes in the appearance of the individuals who comprise the population, mainly as a result of modification of physique, hair form, and the color of the skin, eyes, and hair, etc. Since human genetics is unfortunately still in its infancy we cannot, in general, deduce from these visible changes which genes, or how many genes, have been affected, or to what extent their frequencies have changed. In racial classifications based upon inherited differences of this sort we deal entirely with *phenotypes*. (The phenotype of an individual is what can be found out about him by inspection or laboratory examination, the *genotype* is his genetic composition which in some cases can only be ascertained, if it can be ascertained, by examination of his parents or offspring or both.) When we consider blood group characteristics we are able to make use of genotypes, which results in our finding more distinguishable classes and greatly increases the usefulness of any given number of genes.

Stability of Races

If race mixture continues to increase, as a result of increased facilities for travel and of progressive decrease in race prejudice, some of the racial distinctions observable at present may disappear. We have mentioned Glass and Li's prediction of the eventual complete assimilation of the American Negro. It is therefore possible that the forces opposing racial differentiation may in the future be stronger than those promoting it. This will depend upon the course of future events.

There is another possible cause of racial instability which demands a brief discussion. On the basis of what I have said before, one might suppose that racial differentiation in isolated groups would go on to produce highly differentiated races or even species. Now some populations (e.g. the Australian aborigines and American Indians) were almost completely cut off from contact with other peoples, and consequent race mixture, for long periods of time. If race formation is the result of the selection of genes conferring an advantage in a particular environment, with consequent elimination of disadvantageous genes, and no genotype is selectively neutral, how does it happen that these isolated populations when they were discovered, differed from other races mainly in possessing different *frequencies* of certain genes, and not rather in having completely lost a number of genes, or in having acquired high frequencies of new characteristic genes, or even having become distinct species?

There are two possible answers to this question. In the first place, the rate of decrease or increase in the frequency of a gene depends of course upon the amount of selective disadvantage or advantage that it confers upon its possessors. Haldane showed that if we represent the ratio of the frequencies of the two alleles, A and a , at a given locus by v , and assume that in each generation only $1-k$ of the recessive genotype survive to breed, then if selection were slow (k small) the change in v with the number of elapsed generations n is given approximately by

$$kn = v_n - v_0 + \ln (v_n / v_0)$$

where v_0 is the ratio A/a initially and v_n at the end of the n th generation, and \ln means logarithm to the base e .

If we assume that the selective disadvantage of a gene is very small (k about 0.001), as it was natural to do in 1924, it could be calculated from this equation that to increase the frequency of an advantageous dominant gene from 0.05 to 0.50 would require about 3,000 generations, or about 60,000 to 70,000 years. The American Indians, for example, have probably not been in America as long as this.

More recent work, however, has forced us to consider the possibility of considerably higher rates of selection. The well-known effect of Rh incompatibility between mother and fetus is seen, in European populations, about once in 400 births. Since each abortion or erythroblastotic death due to this mechanism eliminates one Rh positive and one Rh negative gene, the result in most populations is to decrease the relative frequency of the Rh negative at an appreciable rate. Aird *et al.* have recently reported evidence for selection acting on the ABO blood groups. According to them, a person of blood group O has, at least in some populations, about a 35 per cent better chance of developing peptic ulcer than does a person of any other blood group. They also report that persons belonging to blood group A have a considerably better chance of getting cancer of the stomach than do persons of other blood groups. Other correlations of disease and blood groups have been reported, for example, by Pike and Dickins. It might of course turn out that these are due to the presence in the population of racial strata having a higher susceptibility to a specific disease, and a higher incidence of some particular blood group, but the situation nevertheless shows that it is not impossible that there exist selective coefficients, affecting the once supposedly "non-adaptive" blood groups, of many times the magnitude we formerly considered probable. Haldane's mathematical treatment would not strictly apply to such cases, but it is clear that these forces ought to change gene frequencies rapidly. This would make it a mystery why any amount of gene O remains in any human population exposed to the risk of peptic ulcer.

The solution to this mystery probably lies in a phenomenon which had already become familiar from studies on lower organisms, namely the phenomenon of balanced polymorphism. This phenomenon provides a mechanism which tends to counteract the selective force acting to eliminate some disadvantageous genes. This mechanism depends upon an advantage possessed by the heterozygote.* Fisher had shown in 1930 that if any three genotypes, FF , Ff , and ff , have selective advantages in the ratio $a:b:c$,

* The heterozygote has one dose of a gene; the homozygote has a double dose.

then the gene frequencies of F (p) and f (q) will have the equilibrium values such that

$$p/q = (b - c) / (b - a)$$

It is thus possible for selective forces to produce a situation in which two (or more) alleles are present in a population and the frequencies of these alleles do not change.

What the advantages of persons heterozygous for the blood group genes are, if such advantages indeed exist, we do not know, but what may be an example of the operation of this mechanism in man has been reported by Allison. There is a "sickle cell" gene in African populations which in heterozygous condition causes the erythrocytes of the individual, when they are deprived of oxygen, to shrink and assume strange shapes sometimes reminiscent of sickles. In homozygous condition this gene causes a profound anemia which probably leads to the early death of the affected individual. Allison calculated that the "fitness" of the homozygous recessive was not over 25 per cent of that of the heterozygote. There is thus a strong selective force acting to diminish the frequency of this gene. Noting that high frequencies of the sickle cell gene occurred in populations living in very malarious areas, Allison reasoned that compensating selective advantage possessed by the heterozygote might be greater resistance to infection with *falciparum* malaria, and, in an experiment with volunteer normal and "sickle cell" individuals, he apparently demonstrated this greater resistance. Allison calculated that the heterozygote in these regions possesses about a 26 per cent advantage over the normal homozygote.

If balanced polymorphism is in fact operative in connection with the human blood group systems, as now seems very probable, it is to be expected that blood group gene frequencies will tend to be stable, like other racial characteristics, so that in the absence of race mixture or changes in the environment, these frequencies will change but slowly, and then in such a way as generally to leave in each population appreciable frequencies of each of the various alleles.

This is now seems likely that the gene frequencies which characterize any particular race today are the result of the joint action of a number, perhaps all, of these evolutionary forces, and as a consequence of being the reflection of an equilibrium state may change relatively slowly with time. Thus race, though to some extent an arbitrary creation of the taxonomist, does have a certain degree of stability.

Summary

The advantages of blood grouping data for anthropological classification are described, and a summary of the principal blood group systems is given. A classification of the human species into 13 races based upon blood group data is given, and a description is given of the mechanism of balanced polymorphism, which possibly acts to stabilize the gene frequencies of human races.

A survey of the mechanisms of race formation is given. It is concluded that the main agency is the action of natural selection on spontaneous mutations, to preserve and accumulate genes advantageous in the particular physical and genetic environment in which an isolated population finds itself. Consequently one expects to see races differing with respect to the frequencies of a number of genes.

Note on the Author

WILLIAM CLOUSER BOYD

A graduate of Harvard College (A.B. 1925), Professor Boyd received his A.M. from Harvard University (1926) and his Ph.D. from Boston University (1930). During World War II he worked on problems of plasma fractionation in the Department of Physical Chemistry at the Harvard Medical School, and in 1949-1950 he was head of the Department of Biochemistry and Immunology at the United States Navy Medical Research Institute in Cairo, Egypt.

At Boston University Dr. Boyd served as instructor, 1926-1929, assistant professor, 1935-1938, associate professor, 1938-1948, and professor of Immunochemistry since 1948.

Professor Boyd was awarded Guggenheim fellowships, 1935-1936 and 1936-1937, and a Fulbright fellowship, 1952-1953. He is a member of several scientific societies, a member of the Council of the American Association of Immunologists and of the American Academy of Arts and Sciences, and President of the American Society for Human Genetics. He is also chairman of the subcommittee on the Sociological Impact of Space Flight of the American Rocket Society.

Dr. Boyd has contributed about two hundred scientific papers to some fifty-five professional journals, and is the author of the following books: *Blood Grouping Technic* (with Fritz Schiff) 1942, *Fundamentals of Immunology* (1943, 1947, 1956), *Biochemistry and Human Metabolism* (with B. S. Walker and I. Asimov) (1952, 1954, 1957), *Genetics and the Races of Man* (1950), *Races and People* (with I. Asimov) (1955). *Fundamentals of Immunology* has been translated into Russian and *Genetics and the Races of Man* into French.

Professor Boyd is an accomplished linguist, reading and speaking German, French, Spanish, Italian, Russian, and Arabic. In 1935 he gave lectures in Russian in the Soviet Union.