COLD SPRING HARBOR SYMPOSIA ON QUANTITATIVE BIOLOGY

VOLUME XV

COLD SPRING HARBOR SYMPOSIA
ON QUANTITATIVE BIOLOGY

Founded in 1933

by

REGINALD G. HARRIS
Director of the Biological Laboratory
1924 to 1936

The Symposia were organized and managed by Dr. Harris until his death. Their continued usefulness is a tribute to the soundness of his vision.

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COLD SPRING HARBOR SYMPOSIA ON QUANTITATIVE BIOLOGY

VOLUME XV

ORIGIN AND EVOLUTION OF MAN

THE BIOLOGICAL LABORATORY
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FOREWORD

The two main groups brought together by this year's program were geneticists and anthropologists, both of which study the evolution of man. The ultimate purpose of science, perhaps, is to assist man in understanding himself and his place in the universe. All branches of science, even those studying celestial bodies or the structure of the atom, eventually contribute to this purpose. But the sciences most immediately concerned with man are anthropology and biology, which study him as a living organism and a social being. For nearly two centuries anthropology and biology have developed almost independently, although both have been profoundly influenced by such fundamental discoveries as Darwin's theory of evolution and his finding that man is a part of nature. In our century, the development of genetics, which studies the phenomena of heredity and variation, has caused a gradual drawing together of biological and anthropological research.

Man, like any other living organism, is a product of his heredity and his environment. Neither can be ignored, if we wish to reach a coherent understanding either of an individual human being or of a group of human beings such as a population or race. Nevertheless, until recently there has been relatively little contact and collaboration between anthropologists and geneticists or other biologists. The chief aim of the fifteenth Symposium on Quantitative Biology was to help establish such collaboration.

The group assembled at the Biological Laboratory started its nine-day session by considering the nature of the units of study with which anthropologists and biologists are concerned. The primary units that we observe are, of course, living individuals. These individuals, however, form natural units of higher orders—populations or groups, united by common descent, within which, rather than between which, marriages take place. Populations are of different orders. One of the largest of these is the human species, or mankind. Mankind is divided into races, subraces, and social, economic, linguistic, and other more or less clearly defined groups, each possessing its own heredity, or "gene pool." The human species has descended from prehuman ancestors, which in some respects resembled living apes and monkeys. Much progress has been made in recent years in studying these prehuman and early human forms, owing to the discovery of a large number of extremely interesting fossil remains in several countries, particularly South Africa. This evolutionary development of man was discussed in two daily sessions of the symposium.

A topic that interests both anthropologists and biologists equally is the genetic nature of traits that distinguish individual humans, or human populations such as races. Three sessions of the symposium were devoted to analysis of human traits. Both "normal" traits, such as blood groups and teeth, hair, and skin characteristics, and pathological traits, such as various hereditary diseases, were considered. This was followed by a discussion of the concept of race. Many misconceptions exist in the popular mind about the nature and significance of racial variations in the human species. Considered scientifically, the problem is simple

enough. Different human populations differ in the frequency of certain genes in their hereditary constitutions. The same genes that distinguish human races may also distinguish individuals within a race. Race differences are not absolute but relative. The symposium concluded with a discussion of the more general and philosophical implications of the modern Science of Man, and of the unsettled problems awaiting further study, in which anthropologists and geneticists will cooperate.

The program for this symposium was worked out in cooperation with Professors Th. Dobzhansky, of Columbia University, and S. L. Washburn, of the University of Chicago. One innovation was introduced in the proceedings: the chairman of each day's session not only presided at the meeting but also presented at its conclusion a discussion and synthetic summary of the topics dealt with. These summary presentations are published here. The editor of the volume was Dr. Katherine Brehme Warren.

The meetings were held from June 9 to June 17, 1950. The registered attendance was 129. The expenses of the symposium, particularly those connected with foreign guests, were covered by grants from the Carnegie Corporation of New York and The Viking Fund.

M. DEMEREC

SOME SYMPOSIUM PARTICIPANTS

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Second row: H. Strandskov, B. L. Hanna; J. V. Neel, J. B. Birdsell, L. D. Sanghvi, M. F. A. Montagu, Mrs. Montagu; Th. Dobzhansky, L. C. Dunn, W. H. Sheldon

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(Pictures were taken by M. Demerec, A. E. Mourant, K. B. Warren.)

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Top row: E. A. Hooton, J. B. Birdsell; S. L. Washburn, C. Kluckhohn, A. L. Kroeber; C. Stern, S. L. Washburn
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LIST OF THOSE ATTENDING OR PARTICIPATING IN THE SYMPOSIUM

Adams, Mark, New York University College of Medicine, New York
Allen, Gordon, The Research Laboratory, U. S. Public Health Service, New York
Angel, J. Lawrence, Jefferson Medical College, Philadelphia, Pennsylvania
Aronowitz, Olga, New York Zoological Society, American Museum of Natural History, New York
Barish, Natalie, Washington, D. C.
Bates, Marston, Rockefeller Foundation, New York
Belser, Nao, Carnegie Institution of Washington, Cold Spring Harbor, New York
Belser, William L., Carnegie Institution of Washington, Cold Spring Harbor, New York
Birdsell, Joseph B., University of California, Los Angeles, California
Bloom, David, New York City
Böök, Jan A., Institute of Genetics, University of Lund, Sweden
Böök, Mrs. Jan A., Institute of Genetics, University of Lund, Sweden
Boyd, Lyle G., Boston University, Boston, Massachusetts
Boyd, William C., Boston University School of Medicine, Boston, Massachusetts
Boyer, Donald, Princeton, New Jersey
Britton, S. W., University of Virginia, University, Virginia
Britton, Mrs. S. W., University of Virginia, University, Virginia
Broadfoot, Jean, Carnegie Institution of Washington, Cold Spring Harbor, New York
Brown, M. Jay, Columbia University, New York
Bryson, Vernon, Biological Laboratory, Cold Spring Harbor, New York
Buzzati-Traverso, Adriano, Istituto di Genetica, Universita, Pavia, Italy
Cain, Arthur J., Oxford University, England
Caspari, E., Wesleyan University, Middletown, Connecticut
Catlin, B. W., Carnegie Institution of Washington, Cold Spring Harbor, New York
Chance, H. L., University of Oklahoma, Norman, Oklahoma
Coon, Carleton Stevens, University Museum, Philadelphia, Pennsylvania
Count, Earl W., Hamilton College, Clinton, New York
da Cunha, A. Brito, Columbia University, New York
da Cunha, Mrs. A. Brito, Columbia University, New York
Dalton, H. Clark, Carnegie Institution of Washington, Cold Spring Harbor, New York
Dayton, Zlata Demerec, Cornell University, Ithaca, New York
Demerec, M., Carnegie Institution of Washington, and Biological Laboratory, Cold Spring Harbor, New York
Demerec, R., Swarthmore College, Swarthmore, Pennsylvania
Diaz Collazo, Ana M., University of Puerto Rico, Puerto Rico
Dissosway, Carolyn, Carnegie Institution of Washington, Cold Spring Harbor, New York
Dobzhansky, Th., Columbia University, New York
Dunn, L. C., Columbia University, New York
Ehrich, Robert W., Brooklyn College, Brooklyn, New York
Ewing, J. Franklin, Fordham University, New York
Freedman, Grenevere M., Jamaica, New York
Garn, Stanley M., Harvard University, Cambridge, Massachusetts
Glass, H. Bentley, The Johns Hopkins University, Baltimore, Maryland
Goodman, Reba, New York City

Grace, E. J., Grace Clinic, Brooklyn, New York
Hanna, B. L., University of Chicago, Chicago, Illinois
Haskins, Caryl P., Haskins Laboratories, New York
Hooton, E. A., Harvard University, Cambridge, Massachusetts
Howell, F. C., University of Chicago, Chicago, Illinois
Howells, W. W., University of Wisconsin, Madison, Wisconsin
Hsie, Jen-yah, Biological Laboratory, Cold Spring Harbor, New York
Hunt, Edward E., Jr., Harvard University, Cambridge, Massachusetts
Kallmann, Franz, Columbia University, New York
Kallmann, Mrs. Franz, Columbia University, New York
Kaplan, Bernice, Wayne University, Detroit, Michigan
Kaufmann, B. P., Carnegie Institution of Washington, Cold Spring Harbor, New York
Kemp, Tage, The University Institute of Human Genetics, Copenhagen, Denmark
Keur, Dorothy, Hunter College, New York
King, James C., Biological Laboratory, Cold Spring Harbor, New York
Kluckhohn, Clyde, Harvard University, Cambridge, Massachusetts
Koester, Mary L., Brookhaven National Laboratory, Upton, New York
Koopman, Karl F., Columbia University, New York City
Kostellow, Adele, Columbia University, New York
Kroeber, A. L., Columbia University, New York
Krogman, W. M., University of Pennsylvania, Philadelphia, Pennsylvania
Lasker, Gabriel, Wayne University, Detroit, Michigan
Laughlin, W. S., University of Oregon, Eugene, Oregon
Levene, Howard, Columbia University, New York
Levine, Louis, Columbia University, New York
MacDowell, E. C., Carnegie Institution of Washington, Cold Spring Harbor, New York
Mayr, E., American Museum of Natural History, New York
McCown, Theodore D., University of California, Berkeley, California
McCulloch, N. B., North Carolina State Agricultural College, Raleigh, North Carolina
Meyer, Natalie B., Carnegie Institution of Washington, Cold Spring Harbor, New York
Montagu, M. F. Ashley, Rutgers University, New Brunswick, New Jersey
Moody, Edward F., Jr., John Wiley & Sons, New York
Morison, Robert S., Rockefeller Foundation, New York
Moriwaki, Daigoro, Tokyo Metropolitan University, Tokyo, Japan
Mourant, A. E., Ministry of Health Blood Group Reference Laboratory, Lister Institute, London, England
Murphy, Douglas P., University of Pennsylvania Hospital, Philadelphia, Pennsylvania
Nappi, Raffaele, University of Naples, Italy
Neel, James V., Heredity Clinic, University of Michigan, Ann Arbor, Michigan
Nelson, Shirley, Jersey City, New Jersey
Oliver, Clarence P., University of Texas, Austin, Texas
Pittendrigh, C. M., Princeton, New Jersey
Plunkett, Geoffrey E., Biological Laboratory, Cold Spring Harbor, New York
Pollitzer, William S., Columbia University, New York
Prout, Timothy, Biological Laboratory, Cold Spring Harbor, New York
Prout, Mrs. Timothy, Biological Laboratory, Cold Spring Harbor, New York
Race, R. R., Medical Research Council Blood Group Research Unit, Lister Institute, London, England
Reed, Sheldon C., Dight Institute for Human Genetics, University of Minnesota, Minneapolis, Minnesota
Rickenberg, Howard V., Cornell University, Ithaca, New York

Rosen, D. E., New York Zoological Society, American Museum of Natural History, New York
Rosenbaum, Joan, Columbia University, New York
Royce, Joseph R., Drake University, Des Moines, Iowa
Sander, Gerhard, University of Wisconsin, Madison, Wisconsin
Sanghvi, L. D., Tata Memorial Hospital, Bombay, India
Scheinfeld, Amram, New York City
Schultz, Adolph H., The Johns Hopkins University, Baltimore, Maryland
Schwartz, A. D., Carnegie Institution of Washington, Cold Spring Harbor, New York
Seltzer, Carl C., Harvard University, Cambridge, Massachusetts
Shapiro, Harriett, Heredity Clinic, University of Michigan, Ann Arbor, Michigan
Sheldon, William H., Columbia University, New York
Simpson, George Gaylord, American Museum of Natural History, New York
Singleton, W. R., Brookhaven National Laboratory, Upton, New York
Snyder, Laurence H., University of Oklahoma, Norman, Oklahoma
Spuhler, Helen, Ohio State University, Columbus, Ohio
Spuhler, J. N., Ohio State University, Columbus, Ohio
Srb, Adrian M., Cornell University, Ithaca, New York
Steedman, Elsie, Hunter College, New York
Steinberg, Arthur, Mayo Clinic, Rochester, Minnesota
Stern, Curt, University of California, Berkeley, California
Stewart, T. D., Smithsonian Institution, Washington, D. C.
Strandskov, Herluf H., University of Chicago, Chicago, Illinois
Streisinger, George, Biological Laboratory, Cold Spring Harbor, New York
Tappen, Neil, University of Chicago, Chicago, Illinois
Taylor, Martha J., Carnegie Institution of Washington, Cold Spring Harbor, New York
Thieme, Frederick P., University of Michigan, Ann Arbor, Michigan
Tortora, Mario, University of Naples, Italy
Unger, Lester J., New York University Medical Center, New York
Visconti, Niccolo, Carnegie Institution of Washington, Cold Spring Harbor, New York
(Politecnico di Milano, Istituto di Chimica Generale e Analitica, Milano, Italy)
Vogt, Marguerite, Institute for Brain Research, Neustadt, Black Forest, Germany
Wallace, Bruce, Biological Laboratory, Cold Spring Harbor, New York
Warren, Charles O., Commonwealth Fund, New York
Warren, Katherine Brehme, Hofstra College, Hempstead, New York
Washburn, S. L., University of Chicago, Chicago, Illinois
Wenk, Eugene, Jackson Heights, New York
Wiener, Alexander S., Office of Chief Medical Examiner, New York, and Wiener Laboratories, Brooklyn, New York
Witkin, Evelyn M., Carnegie Institution of Washington, Cold Spring Harbor, New York
Wolff, Barbara, Swarthmore College, Swarthmore, Pennsylvania
Zelle, Max, Atomic Energy Commission, Washington, D. C.

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POPULATION AS A UNIT OF STUDY

GENETICS AND THE ORIGIN AND EVOLUTION OF MAN

HERLUF H. STRANDSKOV

The University of Chicago, Chicago, Illinois

Fundamental to an understanding of the origin and evolution of man are the concepts and principles of genetics. The most basic of genetic principles may be expressed most succinctly by the statement that organic inheritance is particulate. More explicitly this means that the biologic material contributed by a parent to an offspring consists, at least to a large extent, of discrete and specific units which through physiological processes direct the development of an individual. These units of heredity typically carried upon darkly-staining bodies or chromosomes within the nuclei of cells are commonly called genes, a name given to them by the Danish biologist, W. Johannsen.

Among sexually reproducing species each parent contributes what is called a complete or monoploid set of chromosomes and genes. Hence the fertilized egg or zygote possesses two homologous sets, also called a double or diploid set. In the division of the zygote or of any other body cell the entire diploid set is duplicated in an autocatalytic process and a diploid set identical to that of the mother cell is distributed to each daughter cell. Accordingly every body cell of an individual possesses a chromosome and gene contribution identical to that of the zygote from which he or she developed. Differences between tissues within an individual are a function of differences in the immediate and past environments of the cells which gave rise to or constitute those tissues.

In cell divisions leading to the formation of gametes by the sexually mature individual, the two existing monoploid sets of chromosomes and their contained genes are not duplicated as they are in ordinary cell divisions but are paired and separated in such a fashion that only a single or monoploid set is distributed to each daughter cell. Accordingly a gamete possesses only a single or reduced set.

Most of the principles of genetics mentioned above were discovered, at least formulated clearly for the first time, in 1865 by the Austrian scientist, Gregor Johann Mendel. Unfortunately the conclusions of Mendel remained unknown or unappreciated by the scientific world until 1900 when they were rediscovered independently by several investigators. Immediately upon rediscovery they became accepted and supported by investigators everywhere and have remained acceptable to all biologists to this very day. It is true that in recent years a few individuals have attempted to ridicule and belittle these principles, but the attacks which apparently were levelled for political rather than for scientific reasons have had little or no effect on the solid foundation on which Mendelian genetics is built.

Following the rediscovery of Mendel's laws in 1900 the science of genetics grew by leaps and bounds. As seems natural it was the genetics of the individual or of the mating unit which was studied first. Soon, however, attention was focused on the genetics of the smaller biologic unit, the cell. Marvelous correlations were discovered between the genetics of the cell and the genetics of the individual as well as that of the mating unit. Later, attention was turned to the genetics of the larger biologic unit, the intrabreeding population. It is specifically this topic, as it relates to the evolution of man, which I propose to outline.

May I, at the outset, emphasize that the genetics of man has been found to be identical in its basic principles to that of every other sexually reproducing species. Hence we may strengthen conclusions regarding man's evolutionary processes by conclusions based on a study of other forms. However, I recognize that we should, in so far as possible, look for and utilize only direct evidence. In other words, I subscribe to the statement that the best material for a study of man is man.

The genetics of a human intrabreeding population involves many interrelated processes occurring simultaneously in space and time. It is impractical to treat all of these concurrently. A more satisfactory procedure is to deal initially

with each one more or less separately, and as a final step attempt a consideration of the subject as a whole. I shall adhere rather closely to the following outline of topics:

I. Definition of the terms: (A) intrabreeding population and (B) populational genetic composition.
II. The mating systems of an intrabreeding population.
III. The ascertainment of the genetic composition of an intrabreeding population.
IV. Factors which may affect the genetic composition of an intrabreeding population.
V. Isolation.
VI. The interactions of the various interdependent evolutionary processes.

It must be obvious that the above topics can not be treated exhaustively within the confines of these few pages. All that I may hope to do is to introduce each one.

I. Definition of the Terms: (A) Intrabreeding Population, and (B) Populational Genetic Composition

A. Intrabreeding population

The evolution of a sexually reproducing species occurs in terms of intrabreeding populations. By an intrabreeding population is meant a group of individuals between whom mating takes place. Reference may be had to a species as a whole, but it may also be to a more limited group within which an individual has a greater chance of mating with another member of the same group than with a member of any other similar intrabreeding group. In other words an intrabreeding population, although recognized and considered as a unit, may be partially open. The primary isolating or limiting factor separating two or more nearly but incompletely closed intrabreeding populations may be only distance. However, in some instances it may be a nonbiological barrier such as a mountain range or a body of water or it may be some biological barrier, such as a predator. Relative to the human species it may be a psychological, social or cultural factor. In the latter event two or more incompletely closed intrabreeding populations may occupy the same spatial range without interbreeding to any appreciable extent.

B. *The genetic composition of an intrabreeding population*

The genetic composition of an intrabreeding population requires for its definition a brief review of a few concepts not hitherto introduced in the present discussion. Let us recall that variations in a given sexually reproducing species may be due to the effects of variations in genes at a single chromosome locus. (Genes which produce different effects in the same environment but which occupy the same locus on homologous chromosomes are called alleles.) Furthermore, let us understand that variations in a characteristic may be due to the interactions of the effects of genes at two or more different loci. It should also be appreciated that the development of every character of an individual is dependent, in a sense, upon the effects of the genes at all the different chromosome loci. No character or part of an individual develops completely independent of any other part, at least not completely independent of the rest of the individual considered as a unit.

The reference above to chromosome loci raises the question of the total number of loci on a monoploid set of human chromosomes. (The number is the same for all human individuals.) The exact number is not known, but estimates range from 5000 up to 120,000 (Spuhler, 1948, and Stern, 1949). A fairly conservative and often adopted estimate is 10,000. If this number should prove to be approximately correct and two alleles should be found to exist at each locus the possible number of genotypes for the human population would be approximately $3^{10,000}$ This is a large number. In fact it is more than large enough to include all the inherited variations ever observed among human beings. Of course, some loci may be represented only by one gene, but a fair number is very likely represented by three or more. Consequently it is probable that the possible number of human genotypes is as great as, or even greater than $3^{10,000}$. We emphasize this tremendous capacity for genetic variation which exists for the human and other sexually reproducing species, because some people ridicule modern evolutionary theory on the ground that the amount required by it is unattainable. Evidence indicates that the amount demanded is not only a possible one but also one that is readily and continuously realized.

As has been stated earlier a given individual normally possesses only two homologous sets of chromosomes. Therefore each of his loci may be represented normally by no more than two alleles and many will be represented only by one. In other words an individual may be homozygous or heterozygous relative to a given locus. His genetic composition or genotype may accordingly be represented as follows: *Aa BB cc Dd* etc. for

each of the 10,000 or more remaining loci. An intrabreeding population on the other hand consists of individuals all of whom may be genetically different. Therefore the genetic composition of a population cannot be expressed in the exact same way as that of an individual, but may be indicated by the percentage frequencies within the population of the alleles which exist relative to each locus. The following may serve as an example:

70% *A*: 30% *a*; 19% *B*: 81% *b*; 42% *C*: 11% C^1: 47% *c*; 100% *D*; etc.

It would be desirable to have a short term for the genetic composition of a population comparable to genotype for the individual. I have introduced on a previous occasion the term allelotype and have found it a convenient and a serviceable one. The allelotype is the genetic composition of an intrabreeding population expressed in terms of allelic percentage frequencies.

II. The Mating Systems of an Intrabreeding Population

Matings within an intrabreeding population may occur: (A) at random, or (B) in one or more non-random ways. Each differs somewhat in its effect relative to evolution.

A. Random mating

By random mating, as applied to a population consisting of males and females, is meant a system in which each individual has an equal chance of mating with any individual of the opposite sex within the population. Among species in which self-fertilization (autogamy) is possible every individual has an equal chance of being the mating partner of every other individual.

What we wish to consider briefly in the present section is the effect of a system of random mating on the genotypic and phenotypic proportions within a population. We may simplify the problem, at least initially, by examining the effect relative to a single pair of autosomal alleles. If we assume the existence of two alleles *A* and *a* in a population, the possible genotypes are *AA*, *Aa* and *aa*. If we let p equal the proportion of the gene *A* and q the proportion of its allele *a*, then under a system of random mating the proportions of the different genotypes in the population are given by the square of $pA + qa$.

$$(pA + qa)^2 = p^2AA + 2pqAa + q^2aa.$$

As the statement implies this result is an equilibrium of genotypic frequencies. In other words it is one which theoretically is not changed once it is reached. That it is an equilibrium may easily be proved by calculating the results expected if mating in this population should occur at random. This would be done by squaring $p^2AA + 2pqAa + q^2aa$, i.e., by obtaining the proportions of the genotypes expected among offspring from each possible type of mating. Table 1 shows the calculations.

TABLE 1. RANDOM MATING AND EQUILIBRIUM

The results of random mating in a population in which p equals the probability of an autosomal gene *A*, and q equals the probability of its allele *a*. Genotypic ratio: $p^2AA + 2pqAa + q^2aa$. (Reciprocal matings are combined.)

Matings	Proportion of all possible matings	Proportion of Genotypes expected among offspring		
		AA	*Aa*	*aa*
$p^2AA \times p^2AA$	p^4	p^4	...	...
$2(p^2AA \times 2pqAa)$	$4\ p^3q$	$2\ p^3q$	$2\ p^3q$	...
$2(p^2AA \times q^2aa)$	$2\ p^2q^2$	...	$2\ p^2q^2$	...
$2\ pqAa \times 2pqAa$	$4\ p^2q^2$	p^2q^2	$2\ p^2q^2$	p^2q^2
$2(2pqAa \times q^2aa)$	$4\ pq^3$	...	$2\ pq^3$	$2\ pq^3$
$q^2aa \times q^2aa$	q^4	...	...	q^4
Total	1.00	p^2	2 pq	q^2

It may be seen from an inspection of Table 1 that the proportion of each genotype expected among the offspring is the same as that of the parental generation. Hence we have demonstrated that the population is in a state of equilibrium relative to genotypic proportions. That equilibrium genotypic proportions under a system of random mating are reached and are given by the square of the initial allelic proportions was first pointed out in 1904 by the British biometrician, Karl Pearson, relative to a pair of autosomal alleles of equal frequency

in the population. Later the rule was shown by Hardy (1908) and by Weinberg (1908) to apply equally well to a pair of autosomal alleles of unequal frequency. Hence the general principle is usually referred to as the Hardy-Weinberg law.

The rate at which genotypic equilibrium is reached, relative to a pair of autosomal alleles, is surprisingly fast. Theoretically it is attained in at least two generations irrespective of size and genotypic proportions of the initial population. This was recognized as being true by Wentworth and Remick (1916).

If an autosomal locus is represented in a randomly mating population by three or more alleles the above rules also hold. In other words, if we let p + q + r, respectively, represent the proportions of the autosomal alleles A, A^1 and a, the equilibrium genotypic proportions expected in the population are given by the square of $pA + qA^1 + ra$.

$$(pA + qA^1 + ra)^2 = p^2AA + q^2A^1A^1 + r^2aa + 2pqAA^1 + 2prAa + 2qrA^1a.$$

As in the case of two alleles equilibrium genotypic proportions are reached in at least two generations.

If the locus involved is sex-linked the equilibrium genotypic proportions differ for males and females. If we let p equal the proportion in the population of the gene A, and q equal the proportion of its allele a, the equilibrium genotypic proportions among the males considered alone are $pA(y) + qa(y)$; whereas among females considered alone they are given by the square of $pA + qa$ or $p^2AA + 2pqAa + q^2aa$. This relationship obtains for species such as that of man in which the male is the digametic sex. (The letter y shown as part of the male genotype refers to the Y-chromosome which carries no sex-linked genes.)

From the above discussion it will be apparent that in a human population mating at random and at equilibrium fewer females than males are expected to show a recessive sex-linked character. The proportion expected among females is the square of the proportion expected among males. The ratio is as q is to 1. It follows, of course, that more females than males are expected to show a dominant sex-linked character. The ratio is as 1+q is to 1.

Equilibrium genotypic proportions relative to a pair of sex-linked alleles are not reached so rapidly as are those pertaining to a pair of autosomal genes, but they are attained for all practical purposes in a dozen or so generations. It is of interest to point out that they are not reached in a direct manner but in a zigzag course. By this is meant that in one generation the genotypic proportions of males or females are greater than those at equilibrium and in the next they are smaller. The shifts gradually become smaller and smaller until an equilibrium is realized. A comparable illustration would be an old-fashioned rocking chair started rocking and allowed to come to rest.

We have considered so far only alleles at a single locus. If two or more independent sets of autosomal alleles are considered jointly, the equilibrium genotypic proportions are given by the product of the squares of the separate sets of alleles:

$$\left[pA + qa\right]^2 \cdot \left[pB + qb\right]^2 \cdot \text{etc.}$$

This result was pointed out by Jennings (1917).

The rate at which genotypic equilibrium is reached, when two or more independent sets of autosomal alleles are involved, varies with the initial relations of the frequencies of the alleles, but in any event it is fairly rapid. Each set of alleles will reach equilibrium genotypic proportions in at least two generations as indicated earlier.

Even if the two or more loci involved are on the same chromosome, or as we say linked, the possible combinations of all separately inherited characters will soon appear at random, i.e., in accordance with the laws of chance. This will happen because of the phenomenon of crossing over. Of course, the closer two loci are linked the longer it will take for their alleles or characters to become randomly combined. An appreciation of the above fact is of importance in a consideration of the distribution of characters in a population which has been mating at random, or nearly at random, over a fairly long period of time. In such a population the repeated or consistent appearance together of two or more inherited characters is usually not evidence of linkage of responsible genes but rather of multiple effects due to a single gene or of multiple effects due to a certain combination of genes brought together by chance in the randomly mating population.

B. Non-random mating

Four major systems of non-random mating are possible. These are, (1) endogamy, (2) exogamy, (3) isophenogamy and (4) heterophenogamy.

1. Endogamy (inbreeding)

The two terms endogamy and exogamy were introduced by Mc Lennan in 1865. Endogamy or inbreeding may be defined as any system in which the mating partners are more consistently, i.e., more often closely related than would be true in a system of random mating. The closest form is self-fertilization. Others less close are parent-offspring, brother-sister and cousin matings.

a. Self-fertilization (autogamy)

Although self-fertilization does not occur within the human species we wish to consider briefly its consequences, because it is the closest possible kind of inbreeding and therefore shows most strikingly the effects of this type of mating system. Let us assume an initial population with genotypic frequencies of $p^2AA + 2pqAa + q^2aa$, and assume further that self-fertilization starts to operate within this population. If this happens the genotypic frequencies in the next generation will result as shown in the schematic representation of Table 2.

TABLE 2. SELF-FERTILIZATION (AUTOGAMY)

Initial population—	p^2AA	+	$2\ pqAa$	+	q^2aa
	↓				↓
	p^2AA				q^2aa
	$\frac{1}{2}\ pqAA$	+	$pqAa$	+	$\frac{1}{2}\ pqaa$
Next generation—	$(p^2 + \frac{1}{2}\ pq)AA$	+	$pqAa$	+	$(q^2 + \frac{1}{2}\ pq)aa$
	↓				↓
Equilibrium	$(p^2 + pq)AA$		+		$(q^2 + pq)aa$

It will be apparent from an inspection of Table 2 that under self-fertilization the proportion of the heterozygote is halved in each successive generation and the proportion of each homozygote is increased by ¼ the proportion of the heterozygote of the existing generation. Eventually heterozygosis disappears and homozygosis is established. The limiting or equilibrium genotypic proportions are $(p^2 + pq)AA$ and $(q^2 + pq)aa$, which incidentally are the initial A and a allelic proportions. Jennings (1912) was the first to point out the theoretical consequences of a system of self-fertilization.

b. Other endogamous systems

Among the closest forms of inbreeding which may obtain within a sexually reproducing species in which the sexes are separate, are parent-offspring, brother-sister and cousin matings. Each of these, if followed, consistently, will result in complete homozygosis within these lines, as is true for self-fertilization. The first two are rare events in most present-day human populations, but may have been more common during the early history of man. Cousin marriage is the closest form sanctioned by most present-day societal or governmental units. Even it is prohibited in some.

Less close systems of inbreeding may obtain. We have in mind uncle-aunt, uncle-niece and other somewhat more distant relative matings. If followed consistently each of these decreases heterozygosis to some extent but reaches an equilibrium short of complete homozygosis.

We have seen that any system of inbreeding affects genotypic proportions by increasing homozygosis and decreasing heterozygosis. What is the effect relative to phenotypic proportions? If a single pair of alleles with no dominance is involved the two homozygous phenotypes correspond, of course, to the two homozygous genotypes and, therefore, increase as they do until an equilibrium is reached. On the other hand, if dominance is involved only the homozygous recessive phenotype increases. (The alternative dominant phenotype must, of course, decrease to a corresponding degree.) This increase in the probability of a recessive phenotype correlated with the fact that many undesirable traits are inherited as recessive, is undoubtedly among the reasons why close endogamous marriages have been or are discouraged in many societal or governmental units. Other factors such as proximity tend to encourage them.

2. Exogamy (outbreeding)

Exogamy or outbreeding may be defined as any system in which mating between unrelated or

distantly related individuals occurs to a greater degree, i.e., more often than expected under a system of random mating. The genetic consequences of a system of outbreeding is an increase in heterozygosis. If dominance is involved outbreeding will result in an increase in the proportion of the dominant phenotype and a corresponding decrease in the recessive. Some of the reasons for the encouragement of outbreeding which is evident in many human societies are undoubtedly related to the fact that many favorable variations are inherited as dominants whose phenotypic proportions increase as a consequence of outbreeding.

3. Isophenogamy (mating based on somatic resemblance)

By isophenogamy is meant matings between individuals of identical or similar phenotype to a degree greater than that expected under a system of random mating. Illustrations are marriages between deaf-mutes or between individuals of similar musical accomplishments. If the phenotype in question has some genetic basis the consequence within a population is a higher proportion of homozygotes relative to the alleles in question than would be expected under a system of random mating. In other words the effect of isophenogamy is somewhat similar to that of a system of inbreeding which is based on relationship.

4. Heterophenogamy (mating based on somatic difference)

Heterophenogamy refers to matings between non-similar appearing individuals to a degree greater than that which would be true under a system of random mating. If the phenotypes in question have a genetic basis and are opposites the effect is an increase in heterozygosis and accordingly a decrease in homozygosis. In other words, the effect is somewhat similar to that of outbreeding.

With the consequences of systems of random and non-random mating outlined we may inquire into the extent to which each one occurred or occurs within human intrabreeding populations. Unfortunately very few empirical data are available pertaining to this question but such as do exist suggest that random mating is the one system most closely followed in most human populations relative to most sets of alleles. At least it seems clear that the consequences of random mating were or are closely realized relative to most sets of alleles for most partially isolated intrabreeding human populations. This seems true partly because, as we have stated above, random mating is the one system most closely followed, and partly because the effects of non-random mating systems, in so far as they do occur, tend to cancel one another. At least the effects of exogamy tend to cancel those of endogamy.

Among the major contributors to an understanding of the broad and general aspects of systems of mating, in so far as they pertain to evolution, are: Wright (1921, 1922, 1932, 1933, 1935, 1938, 1940, 1942, 1945, 1948 and 1949), Fisher (1930, 1935, 1940, 1949), Haldane (1932, 1937) and Dahlberg (1929, 1948). Many other investigators have contributed to certain special aspects of the problem. Among these are: Hogben (1946), Mather (1947), and Geiringer (1948). Not even all the contributions of the above mentioned investigators have been listed. We have selected those which are most general and give additional references.

III. The Ascertainment of the Genetic Composition or Allelotype of an Intrabreeding Population

In a previous section we outlined what is meant by the genetic composition or allelotype of a population. What we propose to present here are a few facts relative to the manner in which and the degree to which the allelotypes of populations may be or have been ascertained.

It is of importance to appreciate that the allelotype of a population may be determined only with respect to those sets of variations whose modes of inheritance are known. At the present time this means that they may be determined for only a few hundred sets, or for about that many chromosome loci. Hence we are far from being able to ascertain the complete allelotype of a single population, but we may determine the allelotypes of many populations relative to a few sets of variations whose modes of inheritance are known and whose allelic frequencies appear to be interesting from a comparative point of view. In fact, this is what has been or is being done.

The ease and reliability with which the allelotype of a given population may be determined, relative to a particular set of variations, varies with the complexity and the definiteness of the mode of inheritance of the characteristic in question. If the mode is of the simplest type the frequency of each allele in the population may be counted without a single one being missed. On the other hand, if the mode is complex or indefinite only an estimate may be obtained.

Among the human variations which are inherited in a relatively simple and definite fashion, and which have been investigated extensively from a populational point of view, are the three M-N blood types. These blood types were discovered in 1928 by Landsteiner and Levine and were shown by them to have a hereditary basis. The mode of inheritance was found to be one involving a pair of autosomal alleles neither member of which is dominant to the other.

If we adopt the symbols Ag^M and Ag^N for the two autosomal alleles involved, the genotypes of the three M-N phenotypes are as follows:

Phenotype	Genotype
M	$Ag^M\ Ag^M$
MN	$Ag^M\ Ag^N$
N	$Ag^N\ Ag^N$

In order to ascertain the allelotype of a population relative to a set of variations it is necessary to know, not only the mode of inheritance of the set, but also the phenotypic frequencies within the population. The latter necessitates an examination of each member of the population or at least each member of an adequate sample. Relative to the M-N blood types this would mean the testing of the blood of each member with M-N anti-sera.

When the phenotypic frequencies of a population have been ascertained the allelic frequencies, at least in so far as they pertain to the M-N blood types, may easily be derived. For illustrative purposes let us assume that the M-N phenotypic frequencies for a given intrabreeding population were found to be: 36% M : 48% MN : 16% N. In this event the frequencies of the Ag^M and Ag^N alleles in the population would be:

$$Ag^M = \%\,M + \frac{\%\,MN}{2} = 36\% + 24\% = 60\%$$

$$Ag^N = \%\,N + \frac{\%\,MN}{2} = 16\% + 24\% = 40\%$$

Note especially that every representative of each allele is counted. This is possible when dominance is lacking. Table 3 presents the M-N allelic frequencies of a number of populations throughout the world.

If the mode of inheritance of a set of variations is more complex or less definite than that of the illustration presented above an accurate or reliable determination is more difficult, but usually an acceptable estimate may be obtained. Wiener (1943), Fisher (1935) and Cotterman (1947) discuss estimation methods.

With the genetic compositions or allelotypes of many populations ascertained or being ascertained it seems appropriate to question the value or usefulness of such data. What purpose may they serve? A final answer may not be possible at the present time but it seems likely that as more and more allelotypes are ascertained they will contribute immeasurably to an understanding of the interrelationships of existing intrabreeding human populations. Furthermore it seems probable that they may add to an understanding of man's relationship to other primate species, especially as allelotypes of the latter are more extensively investigated. Allelotypes determined at different periods in the history of particular human populations should also contribute appreciably to an understanding of the manner in which the various factors of organic evolution bring about changes in allelic frequencies. And last but not least allelotypes should provide invaluable information relative to the biologic strength or health of a particular intrabreeding population, of a nation or of the human species as a whole.

IV. Factors Which Change the Genetic Composition or Allelotype of an Intrabreeding Population

Thus far we have considered only systems of mating among the factors which play a role in organic evolution. These, it may be recalled, may alter genotypic and phenotypic proportions within a population but, in and of themselves, do not change allelic frequencies. Hence, by themselves they cannot be responsible for evolution to any appreciable extent. In fact evolution is most properly considered in terms of changes in allelic frequencies. From this point of view the most elementary or basic evolutionary step is a change in an allelic frequency.

Four sets of factors are responsible for changes in the genetic composition or allelotype of an intrabreeding population. These are: A. mutation, B. selection, C. errors of sampling, and D. migration.

A. Mutation

Mutations are of two major types: (1) genic and (2) chromosomic. A genic mutation is a chemical change in a gene. A chromosomic mutation, on the other hand, involves only a mechanical change in the structure of a chromosome or a change in chromosome number. Chromosomic mutations have played an important role in the evolution of plants and of some animal species but probably have

TABLE 3. TABLE SHOWING THE FREQUENCY OF THE BLOOD TYPES M, MN AND N AND OF THE ALLELES Ag^M AND Ag^N IN VARIOUS POPULATIONS THROUGHOUT THE WORLD

Population	Investigator	Number investigated	Blood type frequency			Allelic frequency	
			M	MN	N	Ag^M	Ag^N
Caucasoids, (U.S.)	Landsteiner and Levine	532	26.1	53.6	20.3	52.9	47.1
English	Taylor and Prior	422	28.7	47.4	23.9	52.4	47.6
Germans	Blaurock	2,000	29.4	49.1	21.5	53.9	46.1
Russians (Leningrad)	Blinov	763	32.3	46.5	21.2	55.5	44.5
Hindus	Combined results	300	42.7	46.7	10.6	66.0	34.0
Negroes (U.S.)	Landsteiner and Levine	181	27.6	47.5	24.9	51.4	48.6
Chinese	Ride	1,029	33.2	48.6	18.2	57.5	42.5
Japanese	Haschimoto	1,000	29.5	50.9	19.6	55.0	45.0
Ainu	Kubo	504	17.9	50.2	31.9	43.0	57.0
Eskimos (East Greenland)	Fabricius-Hanson	569	83.5	15.6	0.9	91.3	8.7
Indians, U.S.	Landsteiner and Levine	205	60.0	35.1	4.9	77.6	22.4
Indians F.B. (Pueblo)	Allen-Larson	140	59.3	32.9	7.8	75.8	24.2
Indians F.B. (Blackfeet)	Matson, Levine and Schrader	95	54.7	40.0	5.3	74.7	25.3
Indians M.B. (Blackfeet)	Matson, Levine and Schrader	272	18.4	55.5	26.1	46.2	53.8

been relatively unimportant in the immediate evolutionary history of man. Hence we shall omit a consideration of them in the present discussion.

In terms of function a genic mutation implies the formation of a new gene which physiologically expresses itself in a different manner or to a different degree from that which was true of its parental gene. The new gene must, however, retain one characteristic of its parental gene, namely, the capacity for self-duplication. Furthermore, it is assumed that it retains the position or locus on the chromosome which was occupied by its parental gene. Therefore, it exists in the population as an allele of other genes of the parental type.

Of considerable interest and importance from an evolutionary point of view is the direction of the physiological effect produced by the mutant gene. There exists a widespread belief that the requirements or needs of a population direct its mutations toward a better fitness on the part of its members to their environment. Although this belief is widespread and apparently attractive to wishful thinkers the available evidence is entirely to the contrary. The facts are that the variations produced by mutations bear no direct relation to the requirements of the organism. Most of the effects produced by mutations are of a negative survival value, some are indifferent and only a very few are favorable. The distribution of the effects is that which one would expect if the mutations occurred fortuitously.

The rate at which mutations occur has been studied intensively and extensively among plants and animals other than man. The rate has been found to differ for different species, for different loci within a species and for the same locus under different environmental conditions. A rate of about 1 in 100,000 is often accepted as an overall average. A few attempts have been made to determine the rate at which various human genes mutate. Haldane (1935) estimated that the sex-linked recessive gene for hemophilia mutates from the normal gene at the rate of about 1 in 50,000 gametes per generation. Gunther and Penrose (1935) and Andreassen (1943) arrived at about the same figure for genes at other loci. A few estimates have indicated an even higher rate. For example, Mörch (1941) estimated that the gene responsible for chondrodystrophic dwarfs appears in Denmark at the rate of about 1 in 20,000 gametes.

Although these studies pertaining to mutations in man may not present completely reliable rates they do give unmistakable proof of the occurrence of genic mutations in man. Furthermore, they support the opinion based on other studies, namely, that human mutations, like those of other organisms, occur fortuitously.

Numerous studies have shown that special agents such as X-rays, ultra-violet light and certain chemicals will increase the mutation rate among organisms other than man. Since man is exposed to these agents on occasion the question has been raised as to whether or not these agents might not be inducing mutations in man at an appreciable rate. Muller (1949) is inclined to think that they may be. He at least thinks that the possibility exists and that every precaution should be taken to guard against such possibilities. No one could possibly object to such advice. Every precaution should be taken.

B. Selection

If mutant genes provide the raw materials of evolution and if they occur fortuitously, what factor or agent gives direction to the process of

evolution? This question was answered satisfactorily by Charles Darwin in 1859 when he suggested natural selection. It is true that the modern point of view relative to selection differs somewhat from that of Darwin, but his basic idea remains acceptable.

Natural selection is often thought of in terms of the elimination of the unfit and the survival of the fittest. In a sense this point of view is justifiable, but it is more proper to consider natural selection in terms of a differential contribution of alleles by one generation to the succeeding one. If a relatively higher proportion of one or more members of a set of alleles is contributed to succeeding generations evolution will proceed in the direction of the effect produced by those alleles.

Since it is the better adapted phenotypes which are most apt to contribute a relatively higher proportion of alleles to the next generation the evolution of an intrabreeding population is guided toward adaptedness. It should be remembered, however, that adaptedness or fitness for one environment does not necessarily mean adaptedness or fitness for another environment. Two entirely different organisms may be equally adapted but one to one environment and the other to another.

Many people are inclined to think of selection as being an all or none process and to involve fierce struggles between members of the same species or between members of different species. Although such struggles occasionally occur natural selection usually operates in a much milder and much less drastic manner. Usually the effect is a very slight change in allelic frequencies from one generation to the next but if continued in one direction through countless generations the change will of course become a major one.

C. Errors of sampling

In a population which is not indefinitely large allelic frequencies may be expected to change or drift from generation to generation merely as a consequence of errors or accidents of sampling. In fact, as a result of such drifts an allele may become completely established or completely lost. Professor Sewall Wright was the first to appreciate and emphasize the role of this factor in evolution. As implied above, it plays its most important role in small populations.

D. Migration

If an intrabreeding population is incompletely isolated its allelic frequencies may be altered by migrants. Immigrants may increase the frequency of some alleles or add new ones and emigrants may reduce or eliminate some.

V. Isolation

By isolation is meant the process whereby a single intrabreeding population is divided into two or more separately intrabreeding populations. The responsible factor may presumably be genetic from the start but unquestionably it is much more often non-genetic initially. It is clear, however, that if two intrabreeding populations are formed from a single one as a result of non-genetic factors and are kept completely or nearly completely isolated they will sooner or later become genetically isolated, i.e., incapable of interbreeding. When this happens one or possibly two new species will have been formed.

VI. The Interaction of the Various Interdependent Evolutionary Factors

It would be of interest to discuss in detail the interactions of the various factors which play a role in evolution but space does not permit this. We do wish, however, to emphasize that the facts known about: (1) the operations of the machinery of Mendelian inheritance, (2) the occurrence of numerous, small, fortuitous mutations, (3) the actions of natural selection and errors of sampling and (4) the semi-isolation and the complete isolation of populations, make it clear that all of these factors operating collectively can account without difficulty for the appearance of plants and animals as they are known to have existed in the past or to exist at the present time. Furthermore, it is clear, as has been emphasized, especially by Sewall Wright, that the conditions most favorable for evolutionary advance are those under which are found numerous small populations which are partially isolated. Indications are that man has presented these favorable conditions to a high degree throughout a major portion of his evolutionary history.

VII. A Few Concluding Statements

A summary of the contents of this paper may not seem necessary but for purposes of emphasis, I should like to present the following concluding statements:

1. The machinery of heredity of man is similar to that of other sexually reproducing species of plant and animal.

2. Man has evolved from some other species of primate.

3. The raw materials of human evolution have been and are primarily small genic mutations.

4. Pre-human and human genic mutations were and are fortuitous and not guided in

their direction by any mystical or supernatural force.

5. Natural selection has been and is the primary guiding factor of human evolution.

6. Man has evolved unique human characteristics not possessed by any other species of animal, but these have appeared as a consequence of the same natural evolutionary processes as have given rise to unique characteristics among other forms of life.

7. Some of man's unique characteristics are affecting the usual operation of natural selection in so far as it pertains to human evolution, and are giving a direction to human evolution which is not the most favorable from a survival point of view.

8. Man must accept his origin from some other species of primate and also his present biologic status but he need not accept completely his present evolutionary trend. It is within his power to redirect to some extent the present and future course of his own biologic evolution.

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DISCUSSION

STERN: To drop the adjectives "natural" and "artificial" when referring to selection in man would obscure the existence of some essential differences. Perhaps three terms like "natural" (biologically conditioned) vs. "sociological" (unconscious) vs. "eugenic" (deliberate) selection might approach reality.

STRANDSKOV: I did not mean to imply that adjectives descriptive of different types or forms of natural selection should not be used. What I object to is the placing of the term artificial in opposition to natural selection. In my opinion what has been called artificial selection is a form of natural selection. The whole subject of natural selection, in so far as it applies to man, should be thoroughly reconsidered. Several more or less distinct forms of natural selection apply to man. Stern has pointed up three major types. However, I am not sure that he has been fortunate enough to find the most descriptive adjectives for the three.

GENETIC STRUCTURE OF NATURAL POPULATIONS AND INTERBREEDING UNITS IN THE HUMAN SPECIES

ADRIANO BUZZATI-TRAVERSO

Istituto di Genetica, Università, Pavia, Italy

The main conceptual novelty brought about by genetic studies developed during the last two decades on taxonomic, biogeographic and evolutionary problems may be stated in these terms: the direct object of such studies is no more the species, nor other systematic categories, nor even single individuals, but populations. Of course these words do not have any meaning unless we try to specify what we mean by population; this is the task I have before me and I shall try to illustrate what population means to the present-day geneticist, both laboratory and field worker; and I shall endeavor to point out, too, those aspects of our studies which are likely to be of interest for the anthropologist in the widest sense, to the student of man as a sexually reproducing organism in the process of adaptation to its environment.

If we take a dictionary definition we find, for instance in Webster, that population is "all the people of inhabitants in a country or section"; it means, therefore, in this sense, the sum of the individuals present at a certain moment over a more or less arbitrarily limited area. If we take, on the other hand, the demographers' definition of population, we find a somewhat more extended concept; these students of human populations say that a population should not be considered only as a mere sum of individuals but as a living aggregate of human beings reciprocally related; it is sometimes stated that an analogy can be made between a population with its members and an organism with its cells. Even if we are prepared to accept such analogy we must point out, however, that it is too optimistic in the sense that while the spatial limits of an organism are, as a rule, clear cut and therefore the study of anatomical and physiological relations between its constituent cells is bound to no uncertainty as to the importance of the individual cells or group of cells to the whole organism, the limits of the populations in the studies of demographers generally correspond to some geographical, political, economic or administrative boundary; these are certainly not highly correlated with biological "boundaries." For our present purpose, however, let us not at once discard this analogy, for it may be useful as a focus for the differences between the various meanings of the word population. Granted this comparison between an organism and a population, we may say that the demographers' stage of analysis corresponds to the time when the biologist was mainly concerned with the anatomic, physiologic and, at most, ecologic description of the various living creatures dwelling on the earth surface, while the present status of the attack upon population studies from a genetic standpoint corresponds to the time when the biologist has given up the study of preserved specimens and histological microtome slides to devote himself to the analysis of how variability originates and can be transmitted from one generation to the next, by observing living beings continuously in time. While the previous concept of population was a static one, the present is dynamic. The task of studying populations from such a dynamic viewpoint becomes therefore more complex and difficult than it used to be under the static one.

On this view, then, a population is an array of interbreeding individuals, continuous along the time coordinate. In order to study a population directly we are compelled to draw a section across the time coordinate; in this way we are trying to seize a stage of the genetic relationships between previous and subsequent generations among interbreeding organisms. When we study the genetic make-up of a population, we analyze the genetic constitution of a sample of individuals existing at a definite time. Such analysis is being repeated at various intervals, and we may get in this way a picture of the shifts in gene frequencies brought about by evolutionary factors. It follows that the particular sum of organisms at a definite time, which we usually call a population, is of interest to the population geneticist only in so far as it is a representative of a certain evolutionary stage, not as an aggregate of single units of observation, not as a whole considered as the result of the interplaying units.

It therefore seems convenient at this point to distinguish the different sorts of populations which are being studied, in order to avoid confusion in terminology. Within the realm of biological objects we may state that a 'population' *tout court* is any aggregate of individuals, whatever the relations among them may be. A 'specific population' can be considered as the total sum of individuals belonging to a species living at a definite time within its distribution area; and for the purpose, we may accept Ernst Mayr's definition of the species (1942): "species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups." The next distinction concerns "natural populations," that is, that array of actually interbreeding individuals and of those thereby produced about which I said a few words before; these are natural units in the sense that there are actual breeding relationships between its members, which relationships can be referred to a number of factors which we shall examine later. These are the units of study of the population geneticist. As a further step in this distinction we may recall Sewall Wright's 'effective breeding population,' which is made up of only those individuals which actually breed and therefore contribute to the next generation, and which does not take into account the total number of individuals of all ages. This is a theoretical concept which may obtain quantitative consistency by means of observations on natural populations. And finally, for the sake of completeness, we may define as 'artificial populations' those arrays of actually interbreeding individuals and of their progeny that are kept under laboratory conditions for experimental purposes.

From the above definitions it necessarily follows that the most important aspect of natural populations lies in the actual breeding relationships among its members, and that this element permits a distinction between different natural populations belonging to the same taxonomic species. An ideal natural population is the one where its members have potentially equal chances to mate with any other member of the opposite sex, irrespective of whether there are factors which in practice act as a limit of true random assortment of the existing genetic constitutions. The classical definition of a random mating population states that mating is at random (1) when there is no tendency for gametes to unite with gametes carrying like genes and to avoid uniting with gametes carrying unlike genes and *vice versa*, (2) when there is no special tendency for like to mate with like, or with unlike, (3) when the probability of any particular sperm uniting with each kind of ovum is in proportion to the number of sperms and ova of their kind present. In such a case one could observe true random mating and the ratio of gametes would be exactly equal to the ratio of the parental generation. The true population, however, with which we are dealing in nature is made out of individuals, not of genes, and therefore I think that the definition I have previously proposed better meets the requirements of the experimental or field geneticist. The comparison between the ideal random mating population for any particular gene constitution and the results obtained by studying free living populations gives us a clue to the genetic and evolutionary mechanisms which are controlling the gene flow within the aggregate of individuals.

In most cases it is rather difficult to determine the boundaries of a natural population and, therefore, the number of its members. There are, however, practically no uncertainties about this point when the considered species is represented by only one small population living within a restricted area, or when there is a number of discrete and small natural populations isolated by geographical or ecological barriers. This is the case frequently found with large mammals living in civilized countries. The wild goat of the Alps (*Capra ibex*), which was abundant in the Alps up to the sixteenth century, was represented at the middle of the nineteenth century by less than 60 specimens living within a few square miles around the Gran Paradiso massif: in the year 1856 this region was declared hunting ground of the King of Italy and in 1921 it became a National Park; by 1935-38 the specific population amounted to some 3000 to 4000 individuals. During the second World War many of these were shot and by 1947 some 420 animals existed. In such a case we can assume that the specific population consisted of only one natural population. It must be added, however, that during this century several pairs of wild goats have been introduced from the Gran Paradiso to Switzerland and Austria. At present six populations of some 1,200 animals altogether are living in Switzerland (Baumann, 1949). It appears that at least 100 to 200 individuals are necessary to insure the survival of a population. The wild brown bear (*Ursus arctos*) is now represented on the Alps and the Appenines by only two or three

natural populations of just a few pairs each. The same scattered distribution of somewhat larger natural populations holds true for the European deer (*Cervus elaphus*) throughout Europe.

It is possible to guess with good approximation the size of natural populations in animals which live in swarms, such as some fishes, birds or plankton animals, and in this case it is likely that each swarm can be considered as a well-defined natural population with definite boundaries. Of course the same holds true for organisms limited to restricted areas because of special ecological requirements as it often happens with plants, insects and parasites. When we come to consider organisms which are continuously distributed over vast territories, the difficulty of making good estimates of the size of natural populations becomes very great. Here, even though there are no geographical or ecological barriers, distance may act as an isolating factor, as Sewall Wright (1946) has pointed out. Here the range of activity, as Timoféeff-Ressovsky has called it (1940), which is connected with the active and passive possibilities of movement of the organism within its life cycle, plays a great role. The few data so far collected on the subject, as the very interesting ones for mammals and birds studied by S. A. Severtzov (1947), seem to indicate that the distribution is not even over the whole inhabited area, but that the population density is highly variable, so that what at first appears as a continuous distribution is in fact a discontinuous one or almost discontinuous. Migration of individuals from one natural population to the neighboring ones plays an important role and renders the study of such cases especially complex. Much remains to be learned on this difficult subject which may give unexpected results. The size of the natural population can be of great importance for its genetic make-up, since small numbers of interbreeding individuals bring about rates of inbreeding within the population, the rate of inbreeding being higher the smaller the number of individuals.

Theoretical considerations, developed mainly by Sewall Wright, on the size of natural populations have stressed the importance of this feature for their genetic structure, but the answer to the question of how organisms breed can be of greater importance than the answer to that of how numerous are the interbreeding individuals. When we are studying the problem of the genetic variability and of the evolutionary potentialities of natural populations over a number of generations, particularly if referred to an absolute time scale, several important factors must be taken into consideration.

Mathematical theories of evolution consider variations in gene frequencies as determined by selection, mutation, migration and population size. But a thorough study of the genetics of natural populations must take into account a number of biological factors which, too, are of paramount importance for the genetic structure of the species and populations. I wish it were possible to refer here to such factors in greater detail than the time limit allows, but I hope that it will nevertheless be clear how such factors may influence our conclusions about evolutionary trends in different plants, animals and man. As a matter of fact, if we are to examine the method of evolution in man as compared to other organisms we must try and get a clear picture not only of Mendelian factors but of how these may work under natural conditions, as well.

Any organism is characterized by its genetic structure, which determines its general physiology and behavior. In order to find out how selection, mutation and other evolutionary factors may affect the transformation of the organism in time, we must try to abstract its potential possibilities and see how these are being limited or enhanced by environmental conditions. We may therefore consider separately the following factors.

1. Number of generations per time unit, or length of generations. Of course, there are differences between the length of generation in experimental optimal conditions and the true length of generations in natural populations; the former data may, however, give useful information on the latter. Furthermore, if we know that an organism gives, say, one generation every ten days as in Drosophila, we are not justified in reckoning the number of generations of a population by dividing the considered time by ten days, for at the same time there are present in the population individuals born at different times which may breed. This is a difficulty not so far overcome in reckoning, for instance, the selection pressure in an artificial population where we have observed a change in gene frequencies. Haldane, however, has given a method for the estimation of generation time. As partial extremes we may remember some bacteria with 20 minutes for a generation, or even viruses which multiply by more than a hundred in the same time, and man with 25 years.

2. Number of gametes per individual, or fecundity. This is a factor of greatest importance for determining selection rates; recent experiments of mine have shown that this is the main factor

being improved by natural selection in artificial populations of *Drosophila melanogaster*. Here we may refer as extreme examples to the carp which lays 80,000 eggs at a time and mammals which give but few ovulations during the life cycle.

3. Number of offspring of a mating pair, or fertility. For a population this is even of greater importance than the preceding factor, from which it partially depends. If we consider the fertility of a single individual in the sense of Hadorn (1943) we must point out that it depends on the composition of the population, being the average of the fertility of this individual when mated to each of the various genotypes present in the population. When we say that a gene has a positive selective value as compared with its allele, it is likely that we are just stating that the individual showing the effect of that gene has a higher fecundity and fertility than the individual which does not show it.

4. Mortality rates at different stages of development. This is related to fertility in the above sense, and it and fecundity make up prolificity, or the main factor through which natural selection operates within a specific or natural population. Observations on living populations of mammals and of birds by Severtzov (1947) show that this factor is very constant for each particular species or population. Mortality rates are the lowest in man, amounting to one in ten, considering abortion and infant mortality rates during the first year of life; it is about 90% in most favorable cases in wild animals; it goes up to 99% in most terrestrial species (insects, arachnids, myriapodes, pulmonates), to 999 per thousand in terrestrial species with special life cycles (blister Coleoptera) and in many marine forms, where it may reach in many cases 999,999 per million.

5. Life cycle. There is no need to spend many words to show that the life cycle of an organism conditions its evolutionary trend. Holometabolous as compared to hemimetabolous development in insects, or ovoparity as compared to viviparity gives to the corresponding organisms completely different evolutionary possibilities.

6. Length of life cycle, or duration of development. On one side it may appear that the quickest the rate of development the greatest the evolutionary speed. But, on the other hand, we see that too fast a rate of development might not allow the organism to reach some stage of growth which would give him a chance to inhabit a new ecological niche. This fact is probably connected with the so-called high and low rate evolutionary lines. Duration of development, as well as length of generation, is inversely correlated with size.

7. Time of sexual maturity. This factor is connected with the preceding one, since for the breeding population only sexual maturity is the determining level of development.

8. Duration of sexual activity. This factor plays a role in determining the length of generations as reckoned in a natural population and may be of importance for selective forces acting differentially at different ages. Even within one class there might be great differences: Lepidoptera such as the silk worm die at once after egg deposition; Diptera such as Drosophila can reproduce throughout the whole adult life. The age of sexual maturity of females and the length of the period between successive births are coefficients which determine the numerical increase of the reproductive portion of the population.

9. Duration of life or longevity. This might be of importance if positively correlated with the length of sexual activity. Recent experiments of mine on artificial populations of Drosophila show that this factor is being selected for, even though selection does not directly favor this character under the particular experimental conditions. But it is likely that it can be considered as a correlated response to the positive selection for other characters. This, on the absolute time scale, seems to be positively correlated with size.

10. Mating systems. A number of more or less complicated devices have been developed, especially in the plant kingdom, to insure the prevalence of inbreeding or outbreeding, as the case might be. Homothally and heterothally among Fungi, monoecy, dioecy, incompatibility mechanisms, heterostyly among flowering plants, all these are examples of special mechanisms which determine the mating system of a species or of a natural population. Among animals, most of which are able to move, sexual reproduction insures a sufficient amount of crossing, but even here habits have been developed which hinder extreme inbreeding and extreme outbreeding; courtship behavior, sexual selection, dominance relationships within animal aggregates and protandry mechanisms in hermaphrodites are examples of such devices.

11. Sex-ratio, or the ratio between males and females. Sexual reproduction, which favors the greatest variety of genetic combinations, works at its best when the two sexes are represented by equal numbers, at least in the case of gene frequencies of intermediate values. It has been shown, however, that there might be great deviations with respect to the 1 : 1 ratio and that these may be different at different age levels. This raises a number of interesting cytological

and selective problems, which influence the genetic structure of natural populations.

12. Recombination index. As Darlington (1939) pointed out, for any particular inter-mating group there must at any particular time be an optimum amount of recombination and therefore an optimum number of chromosomes and an optimum amount of crossing-over between them. Taking the sum of the haploid number of chromosomes and of the average chiasma frequency of all the chromosomes per nucleus in a meiotic cycle we obtain the recombination index. As the optimum in the recombination index will depend on the number and concentration of gene variations to be recombined within the interbreeding group, the size of the group and its freedom of mating, this factor becomes of great importance for the genetic structure of natural populations.

13. Mutability or the capacity to mutate. We know that mutability is different at different loci, that it may be different in different populations (Berg, 1942), and even for the same locus in alleles of different origin as Timoféeff-Ressovsky showed in Drosophila (1932), that the general mutability can be different in stocks of various geographic origin as shown by Demerec (1937), that there are particular genes controlling mutability, that especially high mutability observed in wild populations can be maintained in laboratory stocks derived from them as I observed a few years ago (Buzzati-Traverso, 1942), and that, according to Mampell's data (1945) it can be produced by cytoplasmic factors. It surely is under the control of natural selection, since the amount of available variability is related to the genetic system and is kept at such an equilibrium as to insure the species or the population against extreme variation or stability with respect to the environmental conditions.

The interplay of the above factors and others of lesser importance, which would be too long to consider now, conditions the great variety of methods of reproduction or breeding habits of species and populations which we find in nature. Evolution depends on the action of natural selection on genetic variation, and we see that each animal or plant group aims at an optimum of hybridity in respect to the conditions in which the group lives. These breeding systems brought about by natural selection offer the best possibilities for the further work of selective mechanisms on Mendelian heredity, and the species or the natural population continuously changes its genetic makeup in order to reach a better adaptation. It follows therefore that adjustments of any property of the breeding system are under the control of natural selection even though they do not benefit single individuals. In the study of evolutionary problems we must then consider not only selection operating at the level of individuals but also selection acting on groups of individuals. Below visible variations, systems of genes and chromosomes are at work, which contain the variability and reveal it according to the principles of Mendelian heredity. This is why we are justified to consider the natural population as a unit, since individual variations must be referred to the genetic balance of the whole aggregate of individuals. The genetic structure of natural populations can not be solved only in terms of the individual variations which can be observed in the group, but must be integrated into a unitary research on changes in gene frequencies as related to the underlying breeding system.

This being the case, the problem facing the population geneticist can be stated in terms of: how do environmental and genetic factors, how does natural selection, how do evolutionary mechanisms act upon and transform such units?

In the endeavor to give an answer to this question in different types of organisms, during recent years the genetics of natural populations has been developed, and has brought us a number of very interesting data for a more thorough understanding of the mechanism of evolution. It has given sufficient data in several cases to explain observed changes at the subspecific and at the specific levels, it has made it possible to follow clear-cut evolutionary transformations taking place within a small number of generations both in natural and artificial populations, it has opened the way to a satisfactory interpretation in terms of known genetic mechanisms to some previously unexplained trends manifest in historical evolution. By these means systematics, biogeography, comparative cytology, paleontology and evolutionary studies have acquired a new significance because they have been put on a common basis, because an important step has been made towards the unification of several biological disciplines. We shall now see how this may help in a better understanding of the biology of the human species.

Surely there is no organism whose variability in physical and psychological traits and in behavior has been more thoroughly described than man. As is well known, there is an enormous mass of information accumulated by physical and cultural anthropologists, by physicians, by psychologists, by ethnologists, by social scientists, by glossologists and by historians. This evidence

has been of paramount importance for the description of the most obvious and even of some detailed subdivisions of mankind, but it is of limited value for the understanding of the genetic structure of human populations, because the observed characters have been considered only in their phenotypical aspect, to put it in genetic terminology. With few exceptions in recent years, which show the importance of the genetic attack upon the problem, human variability has been taken at its face value, and not as a symptom of the underlying genetic variability expressed in terms of gene differences and of the effects of genetic systems. On the other hand, it is interesting to remember the historical accident that the study of populations has been developed in man long before than in any other animal because of its social and political implications. Nevertheless, as I mentioned at the beginning, the results obtained by the school of demography on the statics and the dynamics of populations is of limited value for an understanding of the evolutionary mechanisms in man, because such populations were more or less arbitrary units, lacking in biological significance. The impact of genetics on biological sciences is transforming the outlook in this field, too, since new efforts are being made to relate variability, as determined by genetic factors, to the dynamics of populations, considered as natural interbreeding units.

In some respects the study of such natural interbreeding units is easier and more liable to give important results in the human species than in any other organism. Moral values which attribute importance to individuals determine this state of affairs. As a matter of fact, if, say, we are studying the variations of gene frequencies in the course of a few generations within a natural population of fruit flles, we may obtain a series of numerical data which may show the positive selective value of certain gene differences or gene combinations. But if we are willing to push our analysis one step or more further and we want to find out whether this selective value depends on differential fecundity, or fertility, or longevity, or selective mating, we are at a loss. We may, with great effort, try to reproduce in the laboratory the natural conditions and study these aspects of the problem, but we are liable to reach inconclusive results because we have only indirect evidence of the natural phenomenon. In man, on the other hand, data of this type are either already available or easy to collect, and therefore we have better chances to reach a clear insight on such problems as causes of death, fecundity and fertility rates, migration rates and mating discrimination, which are very important indeed as factors determining the genetic structure of natural populations.

In some other respects, man is a rather difficult organism for such research, in particular because the same moral values do not allow us to experiment on him, except perhaps in some very limited way. In animals and plants we can study the natural population from without, while in man we can study it only from within; therefore human beings may be better suited for some population problems while other organisms can offer better opportunities for certain other questions. In this way evidence coming from different sides can be integrated into one general body of knowledge on the mechanism of evolution.

If we come now to consider the nature of the thirteen factors affecting the genetic structure which we have taken into consideration previously in connection with animal and plant populations, it will appear at once the special position of man as compared to other types of organisms which are being studied from the population genetic standpoint. There is no need to enter into a detailed description of how these factors are manifest in man, because this is known by everybody, but I think it worthwhile to stress a few points.

A slow breeding species with long generations, with a small number of offspring, with a long period of sexual activity and with a conspicuous difference in the length of this period between males and females, man, at least in modern times, is characterized by a very low mortality rate. Since fertility can be voluntarily controlled by man and because of this low mortality as compared with other animals, from the viewpoint of natural selection differential fecundity and fertility must play a prevalent role in the trend of human evolution. At present we know something about the inheritance of longevity, but unfortunately almost nothing about the inheritance of fecundity. Furthermore, while we know why mortality rates are different in different populations, we are vague about the causes of differential fertility in human societies. We have several data about factors affecting mating discrimination in different populations, but we need a much more profound knowledge about the role played by this factor in determining the size of the interbreeding unit especially in white man. We know a great deal about sex-ratio at different age levels in western societies and we can rely upon the very ingenious interpretation of R. A. Fisher (1930)

about the importance of natural selection as the cause of its distribution from birth to sexual maturity; but we have no idea about the causes determining the prevalence of males at conception and why sex-ratio is different in different populations. Furthermore, even though man with few exceptions is a monogamous animal, the diminishing number of males after sexual maturity should be examined in relation to the longer period of sexual activity in males as compared to females. Professor Crew's review (1937) on the subject has raised a number of questions, most of which still wait for an answer. Finally we know that man has 48 chromosomes in diploid cells with a very interesting condition in the sex chromosomes, but we have no data on chiasma frequency, and therefore we can not study the relations between its recombination index and the prevailing mating systems in different populations.

The problem of the mating system in man leads us to examine the very important question of the size of the interbreeding unit. Here, if we could collect data throughout mankind we surely would have the best opportunities to analyze the effect of population size on its genetic structure and to get precious information about genetic variability with different amounts of inbreeding and outbreeding. On one hand we have the caste system in India which breaks up the Hindu community into some 2,300 mating groups, varying in size from a few hundreds to a few hundred thousands, and of ages varying from one to 50 generations (Darlington and Mather, 1949). On the other side, we have western white communities, particularly those of the New World, where no mating discrimination of long enough standing is likely to have affected the breeding system. Even if we limit our interest to white man, there still are very small communities with a high degree of inbreeding, where only a few family names are represented, as happens in valleys of the Alps and of the Pyrenees; and on the other hand, there are the populations of modern towns where a thorough mixture is taking place among genotypes which surely for centuries had no chance to come together. In this respect the recent Italian experience is worthy of study, in which the higher fertility of people inhabiting southern regions is changing at great speed the composition of the whole Italian population. Perhaps the cline of Rh-negative genotypes increasing as we proceed from south towards north in Italy, as shown by unpublished results kindly provided by Dr. Ç. Morganti, of Milan, may be a consequence of such differential fertility rates. Between the extremes of the small communities isolated by geographic barriers and by lack of means of transportation and that of great migrations from one continent to another, the size determination of interbreeding units or isolates, as determined by social and cultural factors in modern societies, raises special problems. Here the fundamental studies of Professor Dahlberg have opened an entirely new field of research; as this problem is very actively studied in this country I do not need to enter into it. I may only add that the recently discovered means of distinguishing between homozygotes and heterozygotes for the gene pairs determining M N blood groups and for genes *C c* and *E e* of the Rh-system may be a new approach to the determination of the size of the isolate.

As in many other sexually reproducing animals, natural populations in man are of such size and mating structure as to discourage both extreme inbreeding and extreme outbreeding; on one hand, social and religious taboos hinder incestuous matings, on the other hand, economic and cultural barriers do not allow a thorough panmixia but condition the establishment of a number of interbreeding units with few interchanges among them, at least for some generations. These interbreeding units integrate into larger aggregates, such as the demographers' populations, limited by, for example, national boundaries. Gene flow is more likely to take place within than without these aggregates because of the lack of strong geographic, psychological and linguistic barriers. We then find a third level where phenotypical classifications have been easier when we come to consider the great distinctions of races in mankind. Here geographical and psychological barriers have hindered gene flow for longer times, and therefore morphological differentiations are more clear-cut. But even here we find good evidence that a part of the underlying genetic make-up is the same, as the distribution of A B O blood groups frequencies clearly shows. The pattern of genetic polymorphism of the human species as revealed by the blood groups clines can be a sign of historical migrations or of the effects of selective forces over long periods of time, or of both such agencies. If it were already possible to draw a map of the frequencies of many genes in man over the earth's surface we would surely see some great pattern without relation to the great subdivisions of mankind, like the one of the A B O system, related to the remote ancestry of the human stock. Then we would see over this another pattern showing gene frequency densities corresponding more or less to the great races of

man, this being a sign of a differentiation of long standing; and finally we would observe a very minute variegation superimposed upon the two great patterns, due to the genetic variability among interbreeding units. While the two great patterns have been determined by unknown events of the past, the variegation is due to evolutionary factors at work now; on this we must concentrate our efforts if we want to reach a better understanding of what is happening now and of what has happened in the past.

There are good reasons to believe that the same evolutionary factors which are at work on animal and plant populations are determining the course of transformations in human beings. We have seen that size and structure of populations in man are no exception to the general rule of a great aggregate splintered into a large number of interbreeding units; if this is the case, we can reckon on the sort of effect which is being produced by genetic drift and has been thoroughly analyzed in the important contributions of Sewall Wright. Mutation is at work, as the recent works of Haldane (1948) and others have shown. The mutation rates per generation or per nuclear divisions are about ten times as high as those observed in fruit flies and in some flowering plants. We can therefore reasonably admit that they provide a sufficient amount of new genetic variability on which the human species can rely for any transformation that the environment may require.

Natural selection is the most important factor in the evolution of man, as it is for other organisms, and its study deserves much greater attention than it has had so far. We may state briefly that there are already many data showing that natural selection is changing the genetic structure of natural populations. Charles Darwin stressed the importance of differential mortality as a factor of selection, but we know that in man, as well as in many other species, differential prolificity may produce greater effects. The classical higher susceptibility to infectious diseases of some populations, such as the susceptibility to tuberculosis of African people or to influenza of the inhabitants of Spitzbergen Islands, are good examples of natural selection working at the differential mortality level. At the level of differential fertility we know that natural selection is active in the case of hereditary malformations and diseases, such as chondrodystrophy or haemophilia. The conflict between selection and mutation pressure determines in such cases the genetic polymorphism of human populations. But a more important cause of polymorphism can be ascribed to differential fertility of the heterozygotes as compared to both homozygotes. When fertility is lower in the heterozygote, as it happens for the *D d* gene of the Rh-system, the effect will be the production of polytypy or the formation of distinct races. When fertility is higher in the heterozygote a sort of heterosis is produced and a permanent polymorphism will occur; the high concentration of thalassemia minor observed in the Ferrara population in Italy has been explained recently on the basis of a heterosis mechanism producing higher fertility in marriages between heterozygotes, by Silvestroni and others (1950). As Haldane has pointed out recently (1949a), it is likely that the character of fertility itself, and of intelligence as well, are being selected for with a heterosis mechanism. The fact that these two factors are negatively correlated in modern populations has given rise to a vast number of studies and speculations, but we need a more profound knowledge of its hereditary mechanism before we can reach reliable conclusions.

According to several authorities natural selection is not a very effective factor in the evolution of man now, because man controls its environment and therefore diminishes the risks of being eliminated. I think that this viewpoint gives too much importance to some aspects of modern conditions in western societies; until food resources are even more abundant than they are now in this country for every man in the world, and as long as there are bacterial and other diseases, selection will be operating on human populations. But even then there will be genetic causes determining differential fertility, and the effects of natural selection will not be wiped out. In the study of interbreeding units in the human species we must consider furthermore natural selection operating not on the individual but on the interbreeding unit itself. Characters which are useful to the group as a whole can be selected for only by means of an inter-group biological competition. An hypothetic example is furnished by Haldane (1949b) for an organism such as man with a limited reproductive period. A small human community where every woman died of cancer at 55 would be more prosperous and fertile than one where this did not occur. With the impact of industrial civilization inter-group selection has diminished in intensity as Charles Darwin realized, or we may say has changed its direction. This interplay of inter-group and intra-group selection active in human societies shows us once more the importance of considering natural populations as units of study and makes us

realize the extraordinary complexity of the biological facts we are facing.

I am sure that in the course of this symposium we shall hear a great number of important facts illustrating the points I have touched upon as well as other aspects of the problem I have missed. Before closing I would like to add a few suggestions. From the standpoint of the population-geneticist, present-day human populations show two very interesting characteristics.

In the first place we are living at a time when the whole human population is increasing at a terrific speed. We do not know whether this phenomenon can be interpreted as just a part of the logistic curve typical for animal populations, that is, if the world population after having reached a peak will remain asymptotically around this value, or whether this increase will be followed by a not less dramatic decrease. This would mean that the present trend shall be considered by future biologists as a part of a population-wave, the importance of which for evolutionary mechanisms has been stressed by Timoféeff-Ressovsky (1939). At any rate, whatever future developments may be, this increase in number emphasizes some phases of the evolutionary process. A release of selection pressure takes place, new territories become intensely inhabited, therefore environmental variability increases and the new gene combinations being formed may become 'evolutionary candidates' for the permanent occupation of new ecological niches. If this is the case, why not undertake a comparative analysis of populations showing different rates of increase and sizes instead of concentrating on our western populations which are more or less at the same stage?

In the second place, the extraordinary development of medical sciences renders man the most interesting organism for the study of disease as an evolutionary factor. As Haldane pointed out (1949a) the struggle against disease, and particularly infectious disease, gives results rather unlike those of the struggle against natural forces, hunger and predators, or with members of the same species. We have already a good deal of data on the geography of disease, and for some of the most important endemic and epidemic diseases we know that they have been producing their effects for hundreds if not thousands of years. We know that every species of mammals and birds so far investigated show an extraordinary variety of biochemical constitutions revealed by serological tests. We know, furthermore, that in man and other warm-blooded organisms such biochemical properties are being inherited according to simple Mendelian rules, and there are a few data which show that a different capacity to produce antibodies is controlled by heredity, too. If we take now into consideration non-infectious disease, we have a number of data on the inheritance of some syndromes, and there are the old and devaluated conclusions of the constitutionalists; but we may have now a new line of attack on the problem, we may try to resuscitate and make efficient the study of constitution by using new biometrical techniques, particularly those of polygenic inheritance and multivariate analysis. On this ground, and considering, too, the practical importance of such investigation, I wonder if this line of work, the role of disease in evolution, may not become one of the most active research fields in the study of man.

In this communication I have merely attempted to suggest that man offers unusual possibilities for the study of some evolutionary problems and that the methods of the genetics of animal and plant populations can be applied with success on the human species. One clear lesson has been learned through the development of evolutionary studies based on genetical principles: that we must look after small and simple evolutionary events which are capable of being analyzed with present-day techniques, and that the results obtained by such means may give us, quite unexpectedly, the key for the solution of the great riddles of historic evolution.

I am sure that this splendid opportunity which is being offered to us, to build up a spiritually interbreeding population, if only for nine days, shall produce an hybridity optimum between our specialized disciplines which shall accelerate the rate of growth of the modern study of man.

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DISCUSSION

GLASS: I wish to comment on three points in Dr. Buzzati-Traverso's paper and illustrate them. (1) First, regarding the sex ratio at conception in the human species, I would like to call attention to the recent study by Dr. Christopher Tietze of the extensive collection of embryos at the Carnegie Institution of Washington's Department of Embryology. His studies show that, contrary to the long-held view, the sex ratio in these embryos of all ages is not significantly different from the sex ratio at birth. Point (2), regarding size of the mating group and its relation to the frequency of consanguineous mating. Several years ago I began searching for published figures on the frequency of cousin marriages in the United States and was unable to find any. I believe Dr. Arthur Steinberg can testify to a similar experience. Consequently we initiated a check on the frequency of consanguineous marriages at the Baltimore Rh Laboratory, through personal questioning of every patient visiting the clinic. The frequency of first cousin marriage found in over 8,000 white private patients of doctors in the city of Baltimore is .0005. This remarkably low figure is only one-tenth of the figure given for the city of London, and one-hundredth of the frequency recently reported by Neel from Japan. The theoretical size of the isolate, calculated from Dahlberg's formula, is 25,000. The frequency certainly indicates a far greater degree of exogamy than has previously been recorded for any human population. Point (3) relates to the higher fertility of a group against which selection is acting, as in the reported larger number of children in matings of heterozygotes for thalassemia in Ferrara. Dr. Race some years ago reported an increased fertility of a group of patients with dominant acholuric jaundice, and I have recently completed a study of fertility in Rh-positive and negative negro and white women in Baltimore. The Rh-positive negro women have more living children than the Rh-negative negro women, as would be expected from the action of selection against the Rh rh heterozygote. But among the white women, who have on the average much smaller families than the negro women, the Rh-negative women produce significantly more children than the Rh-positive women. This is no doubt a situation of relatively recent origin, and probably has little significance in explaining how the present Rh frequencies arose; but it clearly shows the importance of taking differential fertility into account in studies of changing gene frequencies. If the present situation persists in the white population studied, the frequency of *rh* will increase, and not decrease, in the future, and erythroblastosis will consequently become more common.

BUZZATI-TRAVERSO: Concerning the problem of sex-ratio in man, I would like to call attention to the differences in this characteristic shown by different human populations at birth. According to the Statistical Yearbook of the League of Nations (1944) there are populations in islands of the Pacific Ocean where the number of females is higher than that of males at birth. I think it worthwhile to analyze such data comparatively in order to establish the factors which may bring about such a difference in comparison with most human populations. Concerning the ascertainment of the rate of cousin marriages, I would like to call the attention of people interested in such studies to the fact that the Statistical Yearbook of the Italian Government publishes regularly such figures for various regions of Italy.

STERN: 1. Are Tietze's data on the sex-ratio of prenatal stages based on unselected material or does the Carnegie collection represent material selected in some fashion?

2. In regard to data on consanguinity in the United States, I might call attention to a paper by Aruer (1908) in the Columbia University Sociological Studies who on the basis of higher than random frequencies of marriages involving like surnames estimated the frequencies of cousin marriages as being several percent in certain groups living in the late 18th and late 19th centuries. Perhaps an important source for data on American consanguinity rates could be tapped with the help of Catholic authorities. The Catholic Church permits cousin marriages only by special dispense. The records of such dispenses might be made available as they were made available in Austria and Switzerland.

GLASS: In answer to Dr. Stern's first question, I think the Carnegie Institution's collection of embryos is a sample, essentially random, of embryos made available through spontaneous or therapeutic abortion and donated by a considerable number of obstetricians in different places. It does not represent all ages equally, but it includes a rather adequate number in each general age group. Tietze of course calculated the sex ratio separately for each of the age groups, but found no significant differences between them.

STEINBERG: Dr. Glass was right when he said that I experienced difficulties similar to his when I attempted to find figures giving the rate of cousin marriages in the United States. Like him I initiated studies to determine the rate in Rochester, Minnesota. The data are being gathered by interviewing women during the lying-in period. No instances of first cousin marriages have been found among the 1,000 patients interviewed to date. These data tend to confirm Dr. Glass's figures. The low figure obtained by him is especially interesting in light of the fact that Maryland does not prohibit first cousin marriages.

KEMP: Apparently the frequency of intermarriage varies very much in the different countries and is surprisingly low in the United States. When examining this problem one has to be very careful about the way the patients are questioned, because they do not always tell about consanguinity without being questioned thoroughly. In Denmark the frequency of cousin marriages in the total population was found to be about 1% and of marriages of other closely related persons (as far as cousins of 3rd degree) also about 1%.

NEEL: It is perhaps worth pointing out that there are certain assumptions inherent in the formula evolved by Dr. Dahlberg for calculating isolate size which are not met in all populations. The formula assumes that first-cousin marriage is contracted at random among the population. In our experience in Japan, to which Dr. Glass has referred, we felt that certain social factors favored first-cousin marriage. On the other hand, in this country there are widespread legal barriers against first-cousin marriage. In most countries, then, the population could be divided into two groups, namely, a group of related persons within which the relative chance of marriage might be high or low, depending on the country, and the remaining, unrelated persons. Presumably this fact could be taken into account by the appropriate correction factor, but the derivation of that factor would be rather difficult.

SANGHVI: A direct approach to an estimate of the average size of an "isolate" might be possible in some of the endogamous groups in India. In such groups marriages are largely arranged by the parents. An "offer" for marriage is sent by the parents of the girl to the parents of the boy. Such an "offer" is conveyed directly or through some person known to the two parties. Under ordinary circumstances no marriage can take place without such an "offer." The total number of such offers may indicate the number of potential mates for every individual, when he or she is passing through the marriageable age. This age may be roughly from 18 to 30 years in the case of the boy and 14 to 22 years in the case of the girl.

HUNT: I think that although the delimitation of human breeding aggregates in many places is difficult, some parts of the world offer considerable advantages for the study of human population genetics. Among these areas are the islands of Micronesia. I feel that the delimitation of such breeding populations would often be easy, especially wherever the inhabitants of a single island are a locally inbreeding group. To a large extent, the islanders of Yap whom I have measured are such a group.

The nature of their mating system in Yap, however, is complicated by social stratification, somewhat as it is in this country. As a result, physical differences among the social classes may be compared from a constitutional and genetic viewpoint.

In summation, Micronesia is an ideal laboratory for human biology. Its breeding populations have a cultural homogeneity and accessibility which lend themselves to the evolutionary approach. Small island populations have been invaluable since the time of Darwin in elucidating the evolution of lower forms. They can be equally valuable in the consideration of evolutionary and constitutional research on living human populations. I hope that some members of this symposium will be lucky enough to study the Micronesians.

PROBLEMS AND METHODS OF POPULATION SURVEYS

FREDERICK P. THIEME

Department of Anthropology, University of Michigan

Without pretending to discuss problems or methods of population surveys completely or in an historical manner, I propose to limit my attention to methods of study which might increase our understanding of human evolution. Within this narrower context, the methods proposed are the outcome of a recent investigation using, in general, such an approach.[1] Although the data of our research are not completely analyzed, the findings so far give considerable hope that this sort of study will be fruitful in helping to understand some of the processes of human variation and evolution. Some results of this particular survey are reported here.

As a general statement, it is probably safe to say that investigations of human populations make their greatest contribution to the interpretation of the general problems of evolution of man by virtue of the information they give about the results of innumerable small interacting evolutionary processes. Such studies allow us to examine the final summation or result, by individuals and characters, of many detailed effects which have gone to make up evolution. Such small effects are the result of the interaction of genetic factors, environmental forces, and selecting and isolating elements, all working through time. Or from another standpoint, such population studies allow us to reconstruct the process of interaction between these factors when exact evolutionary history is unknown. By examining the resulting individuals and characteristics of a population, we evaluate and reconstruct the past.

The problem for these studies is, in the last analysis, to examine and obtain knowledge about the inter-relationship between genetic and environmental factors in shaping the phenotype. The phenotype is largely our unit of study. This is the individual. He is studied in relation to his genetic and environmental background. For a given population, definable in terms of propinquity, isolation and history, we must know the description of all the individuals which comprise it. We accomplish this, in a measure, by examining the physical characteristics, both genotypic and phenotypic, of a defined sample of that population.

In addition to the physical characteristics of the sample population, the environment must be evaluated. The influence of environmental factors in shaping the characteristics of the human organism has always been given an important theoretical position, and proponents to defend this importance have never been lacking, particularly since the studies of Boas (1912) and Shapiro (1939) demonstrating changes of body measures attributable to environmental change. However, few investigations have been made of the influence of the environment, and most investigators merely give lip service to its importance. All racial studies can fairly be criticized for this. In addition, little work has been done to investigate the particular factors in the environment which elicit and are effective in causing physical response in the human organism. The degree of change possible and the limitations imposed by the genetic inheritance of the individual in resisting or modifying the environmental influences is quite unknown. In addition, the differential effects or potency of either genetic or environmental forces in changing different characters have never been examined for the individuals of a population. It is clear, however, that environmental factors may have a more marked effect on some phenotypical characteristics than upon

[1] A survey of the physical characteristics of the Puerto Rican population was carried out in 1948-49. This research was sponsored by the Social Science Research Center of the University of Puerto Rico and was under the supervision of H. L. Shapiro of the American Museum of Natural History and Columbia University. A field team composed of Miss Joan Finkle, R. I. Murrill and the author obtained data on a demographically representative sample made up of 3562 adult males and females. Anthropometric, dental and certain physiological data were obtained from each individual, and considerable other data on the nutritional status, physical and social environment, and general characteristics of the island were secured. The generous help of many persons and public agencies in Puerto Rico made this possible. This survey was carried out in conjunction with a research project in cultural anthropology which was under the same sponsorship and was supervised by J. H. Steward of Columbia University. No reports of either research project have yet been published.

others. For example, nutritional factors affect weight or soft parts more markedly than they do bone. The evaluation of these differential responses is important for study.

This importance has been recently affirmed by Muller (1949). He says, in speaking of prospects and problems of research in human genetics, "Yet in given situations, when dealing with particular characteristics, the actually existing differences in environment may be more or may be less effective than those of heredity in altering the observed outcome. There is no general solution, for the specific results will vary enormously according to the nature of the characters, the nature and range of the environmental conditions, and of the genotypes in question. Yet those specific findings are often highly important. They can be attained not by a-priori-based arguments, but only through observations and measurements made under suitably controlled conditions."

At the present time it is possible to study and control an analysis of the factors Muller mentions and thus contribute to an understanding of the nature of the elements which combine and interact to form some human characteristics.

Our theoretical objective is to describe the environment and the genotype so completely that we can understand the nature of and predict the outcome of individual development. However, with the genotype of any individual largely unknown, particularly as it is discernible for the important functional characteristics of man, it is necessary to frame these investigations in a particular fashion. We must use phenotype instead of genotype for the great majority of characters. Consequently, interpretation is more difficult but need not invalidate the results. This is so because individuals of a homogeneous environmental background, alike in phenotype, can be assumed to be alike in genotype. Actually, if we described the phenotype and environment in sufficient detail, we could, in effect, sort individuals into groups whose genetic difference would be little greater than between monozygotic twins. Although this is the objective, in large population surveys such detailed description, if it be possible, is impractical, and would result in sample groupings of too few individuals. Yet we can approach this goal. In the last analysis, our success in population studies is a function of the reality and significance of the sortings of phenotypical and environmental groups used. In these terms, our studies may have evolutionary meaning.

This approach has particular value for our purposes if certain methodology is used. It is necessary that the phenotype be described in terms of both adaptive and, so called, non-adaptive traits. The characteristics of each individual which are most responsive to environmental factors, as well as the quite resistant ones, need attention. Racial characteristics, as well as known genetic markers, give us information for sorting the sample into relatively homogeneous genetic groups. But in order to find out how these groups differ in their response to varying environmental background, functional or adaptive traits must be considered. Without these, the important evolutionary factors are likely to be missed. Because of this it is obvious that a description of a functional phenotype as well as the 'non-adaptive' phenotype must be done.

In the past, the failure of most anthropological population studies to add materially to the understanding of human evolution has been largely due to two things. First, they failed to examine environmental factors, and secondly, they did not use functionally important characters but rather sought and measured only so called 'non-adaptive' traits. If phenotype is to have meaning in terms of evolution, the characters studied must represent all degrees of adaptive value. Differences in biological fitness between groups, in terms of reproduction and survival, determine which group will dominate the population's future genetic structure.

In addition to the expected fruitfulness of a functional orientation, at the present time some other conditions enhance the likelihood of success for population studies. In the first place, some areas of the world have been studied quite completely. We have some excellent data on demography and physical environment available for use in our problem context. In the second place, the present availability of automatic electronic or electrical machines for data analysis make elaborate studies possible. If we realize that probably a minimum of one hundred detailed entries for each individual are necessary and that a sample of several thousand individuals is required, data analysis in itself may be a major problem. With present machines, not only may correlations which seem fruitful be investigated, but practically all possible combinations may be tested with only a small outlay of time. What previously would have been the work of weeks can be done today in minutes. This is an important change. Now we can do broad and voluminous surveys with field teams, using an interdisciplinary approach, with the knowledge that great amounts of laboratory, metrical and observational data may be readily analyzed in even less time than was previously

needed for very limited studies. Our type of study demands this breadth of approach.

Although we have a favorable climate of knowledge and techniques to support our studies, to achieve findings useful in understanding evolution requires an exacting methodology. Because evolution is a process working through time, change in populations must be measured. Consequently, studies must be planned in sequence. 'Bench marks' for a given time must be made, and later studies of the same group used for measuring change. In addition, the phenotype of the individual is not stable. We must know something of age and growth changes so that any particular phenotype will be described in this reference. Also, the environment may change and the influence of the environment, even though it remain unchanged, may have different effects through different genotypes. Although it would seem that the difficulties suggested here make effective study next to impossible, it is certain that gross effects can be described and the relative importance of environment and genes in terms of specific characteristics be revealed. In any event, we cannot predict their final value as long as we have not thoroughly examined the possibilities of these studies. The first will merely be pilot efforts which may direct us into more minute problems and map out effective methodology. They seem justified if only this is accomplished.

As previously stated, the problems of methodology are largely concerned with describing the phenotype and environment in sufficient detail. Of course, the observable genetic traits must be studied as well. Other papers in this symposium will deal with the methodology and importance of genetic surveys. Without a genetic description, as complete as possible, population studies of the sort proposed here would be very defective. In fact, I suppose the only justification for a population research which uses only phenotype instead of both genotype and phenotype is present ignorance of the genetics of functional and adaptive human characters. However, genetic surveys alone are not sufficient, for we must remember that the functional phenotypic organism reacting with the environment determines which genetic material will survive.

But whether our studies deal with genotype or phenotype or both, there is one important methodological consideration essential to all population studies which should be mentioned here. This is sampling technique. In order to obtain a valid estimation of human variation, genetic, phenotypic or environmental, the sample must be valid. In order to make statements about proportions or frequencies of genes or characteristics in a population, the population must have been sampled accurately. Unfortunately, this has not always been done in the past. The blood group gene frequencies which make up the known data have been gathered without sufficient regard for the importance of sampling. They often represent frequencies for special and mostly undefined sample groups and may not speak for real populations or races.

Populations must be sampled in terms of demographic information and each group must be present in the sample in the proportion that it is present in the parent population. This means that a representative sample and not a so-called stratified sample must be obtained. It is probably basic that the sample be valid for age groupings, sex, geographical region, race and socio-economic background. This socio-economic background, although it implies a great deal, is used mainly to give some sampling of economic status and place and type of residence, such as urban or rural. Of course, this basic list of sample control factors means that the sample structure is nevertheless complicated, and ideally it would be even more complicated for many additional isolating and selective factors are present in active populations which should be properly sampled. However, demographic data seldom give sufficient bases for further refinements. One objective of the type of survey proposed here is to define the additional environmental factors which have the most marked effect on physical characters. It is important to remember that these factors include socio-economic or cultural elements as well as those of the physical environment.

A large amount of background information is necessary before a basic sample structure can be designed. This requires that a sample of several thousand be planned if each grouping is to be represented by statistically significant numbers. In large populations a goal of one per cent of the parent population should probably be a minimum number, but the final test of sample size should be the expected numbers to be obtained for the smaller categories. This has the obvious disadvantage of making some groups very large, but if our objective is to know proportions of characteristics, genetic, or phenotypic or environmental, the difficulty is inherent in the method. Besides giving a basis for sample structure, the depth of knowledge about the studied population will affect the final interpretation of data. The knowledge of factors which establish the ecology, culture, history and environment of the population are of

particular value both for design of samples and interpretation of data. On this knowledge depends the validity and accuracy of results. The setting up of real ecologically homogeneous regions, reliable samples and the establishment of the true historical and social settings hinge upon this.

The value of the description of the phenotype depends upon the accuracy and choice of measurements taken. In addition, the reason for taking the measure must be known. It is not enough that the character be obvious, easy to measure or traditionally measured, but rather it must have physiological or anatomical reality in terms of function and problem. Although photographic records and detailed measurements and observations can be made ad infinitum, it must be remembered that the description of the individual is a tool and not itself the goal. In a study to describe the nature and extent of human variation in an evolutionary problem context, the characters chosen for measure should have a known or suspected value as isolating factors, selective factors, measures of vigor or biological success, indicators of developmental background, or marks of genetic ancestry. Obviously, much of the purpose of the type study proposed here involves finding just these things. However, if known information from various fields about human characters is applied to this particular problem orientation, we will find that our main problem is to integrate all this, in terms of the entire individual, and pick only the most important characters in terms of their known environmental or genetic functional background. The problem at present is to determine which of many known characteristics should be excluded. The achievement of results is largely a function of our choice of characters to be observed, plus our control of conditions.

In addition to judicious choice of characters, the phenotype description demands accuracy of observation. Some of the traditional methods of physical anthropology are not accurate enough. This is particularly so for attribute or observed characters. Tools designed for one man investigations in primitive scenes need no longer be used, nor are they justified when working in cosmopolitan settings. A variety of techniques and tools developed in other fields can be adapted to measure human characteristics.

The phenotype is the total of the anatomical, morphological and physiological characteristics of the individual. Consequently, physiological levels, biochemical values, past and present pathological involvements, as well as anthropometry and external observations must be determined. Techniques utilized in clinical practice, which are based upon clinical signs as well as findings resulting from analysis of fecal, urine and blood samples, should be included. These reveal much of the functional health of the individual and are sharply acted upon by environmental factors. Also, they reveal some of the internal environment of the individual, as well as a portion of his phenotype. From an examination of the blood system alone we can get information about pressure, hemoglobin values, cell counts, blood chemistry and nutrition, some parasitic infestations, cell characteristics such as the sickling trait, genetic blood type, and some hints about the general health of the individual. Other physiological systems of the body may be equally revealing. The present great wealth of medical information should not be neglected in our selection of characters to describe the functional phenotype.

While an adequate description of the phenotype is difficult, environmental factors are probably more difficult to evaluate and as hard to describe. This is so particularly as the environment has worked through time to produce the individual phenotype which we may observe. In practice, persons who have lived in one region all their lives are grouped together when testing for effects of the physical environment. The differences between regions are measured arbitrarily in terms of many things and the possible physical differences are then evaluated in terms of the environmental differences.

Environmental differences may be roughly handled by setting up ecological regions which take into consideration geography, climate, seasonal variability and social factors. This is, in part, the basis used for setting up the common United States census regions. These groupings are finally used to test whether the differences between regions have any discernible organic effect. If, in addition, the regions have historical and social reality, the amounts of heterogeneity within a population can be discerned. From these differences we may get ideas of the processes resulting in or causing regional isolation.

In our recent population study[1] we found that, in general, the effects of regional differences in the external environment in Puerto Rico had no discernible effect on the phenotype. In a group which was similar in racial phenotype and nutritional background, no important effects assignable to regional differences were observed. This was so in spite of the fact that Puerto Rico has varying ecological regions. This negative result may

be an artifact of our control accuracy and methods, however, and may not rule out the presence of small regional difference effects. In a broad evolutionary sense, marked environmental differences between populations or races probably have had an important evolutionary effect. However, within one population area the differences would be very slight, and, if they were to be measured, a very exact methodology designed to test just this would have to be used.

In Puerto Rico we can say that, although we found significant regional heterogeneity in phenotype and blood group proportions, the cause of these proportion differences cannot be assigned to regional differences. In only one thing, the relation of form to function, were certain body proportions altered by mode of life assignable to regional terrain. For instance, calf size is larger in mountainous regions. Some body proportions are also related to occupation not necessarily regional in character. Sedentary occupations affect particular anatomical areas.

The differences in Puerto Rico between regional frequencies of blood group genes is of interest and has important theoretical bearing upon genetic surveys of any sort. We find by Chi Square tests for homogeneity that significant proportion differences occur between regions for groups of homogeneous phenotype. This heterogeneity is in Rh blood type proportions. Phenotype in this test was based on skin color, hair form, nose shape and lip form which are the most racially variable and diagnostic characteristics in this particular negro-white mixed population. For the total population, without regard to phenotypic or racial similarity, the regional heterogeneity is very significant for all the blood type proportions tested. In this population, as might be expected when dealing with a negro-white mixture, the Rh factor proportions were of greater difference between the racial groups than the ABO. Also, of the four racial characteristics used, skin color gave the most revealing sorting in terms of expected proportions (lowest Chi Square values) than did any of the other three (hair form, nose shape and lip form). I believe these results clearly demonstrate that blood type studies of people estimated to be of the same race or population do not of necessity give a reliable estimate of gene proportions for that race or population unless a regionally representative sample is gotten. It is not enough to examine a sufficient number of one race in one location and then expect to get an accurate estimation of proportions for that entire race or population. Very often blood type surveys are insufficient in sample size though larger numbers are available, and I know of none that is demographically representative by geographic regions. While small samples affect the degree of accuracy of the proportion estimations, there is very limited value in unrepresentative samples and no way to estimate their accuracy.

In addition to the environmental factors already mentioned, there are two other portions of the human environment which are of considerable importance, particularly in terms of our problem of understanding human variability and evolution. The first of these is the cultural environment. The second is the nutritional environment.

The cultural environment of the individual not only adds to the complexity of the environmental factors involved, as such, but may account for much of human biological variability. Although each cultural form must provide for certain basic biological needs, such as reproduction, nutrition, care of the young, control of the body environment and other things, the varieties of cultural forms may not be understood only in terms of biological factors. Cultural form is the product of culture and not of biology, except in a very limited way.

Cultural practices, values and history may be very important in determining marriage selection, migrations, both internal and external in relation to a population unit, relative rates of inbreeding or outbreeding, phenotypic preferences, food taboos and patterns, differential fertility rates, disease immunities, fertility rates, differential mortality rates and isolating factors. These have obvious biological and evolutionary importance. Two individuals may live in the same geographical location and yet be isolated. This isolation is cultural and not due to biological reasons, yet has biological effects. These isolating processes may well give the result of small inbreeding population genetic effects even though in all demographic appearances the inbreeding group is a part of a larger population.

Elements of propinquity, class, wealth, politics, religion, language, occupation, social status, racial characteristics and endogamy or exogamy may act on the individual and affect his biological performance. In addition, the national cultural climate may affect all of these. War, industrialization, rates of culture change and degrees of cultural variability or rigidity may be important. It is certain that the validity of interpretations of human biological findings without consideration of cultural factors can be affected by this omission. Man is a cultural animal and his biology cannot be validly considered out of this cultural context. A

biologist may be properly considered a human biologist only by virtue of his cultural as well as biological knowledge. The student of human evolution should give more than lip service to cultural facts.

Nutrition, as previously mentioned, is another important part of the human environment. Differences in nutrition have dramatic effect in shaping the human phenotype. Some body characteristics are more responsive or resistant to these differences than others. In any event, if phenotype is used as a unit of study, the nutritional background which helped shape this phenotype must be known. The relationship of each unit character studied to nutritional differences and elements should actually be known.

Nutritional information about populations is very difficult to obtain. The voluminous discussion of this problem in the literature of nutrition is a tribute to this fact. However, reliable survey methods are known and must have been applied, or must be applied, in a population study of the type under discussion here. It is not difficult to get reliable nutritional groupings if this is done. Although these groupings may not achieve the accuracy which the nutritionalists strive for, they are adequate to point out the importance of nutrition in causing phenotypic variations of characters and the degree of this effect.

In Puerto Rico we were fortunate in having reliable nutritional information based on Roberts' (1949) research and other data. Some of the results of our study are given here to show the dramatic nature of nutritional effects on the human body. As our survey data are still being analyzed, the nature of nutritional variation on dental and certain physiological characteristics are not included. Although the data presented here are accurate, subsequent regroupings of our sample may vary slightly the estimation of the degree of nutritional effect.

The nutritional groupings presented in Table 1 and Figure 1 represent the following. Group 1 is the best in nutritional adequacy and is good by all present standards. Group 4 is made up of those persons who have very low caloric intakes and may be considered to verge on a starvation state at many times in their lives. Groups 2 and 3 are intermediate in that order between Groups 1 and 4.

The difference between the nutritional groups is not equal, and Group 1 is much superior to all others and the differences between Groups 2, 3 and 4 are not of the same order. The degree of homogeneity within each group also may not be equal and may have affected the size of group differences. In addition, the ability of individuals to adapt to a long history of nutritional inadequacy is not known or measured here. This may be an important factor and the ability of individuals to vary in internal efficiency may give different responses to similar nutritional histories, or vice versa. Whether the effect of variability in efficiency operates more or less in terms of levels of nutritional adequacy is not known but could have given us the lesser difference in Group 4 than their relative nutritional status indicated.

Table 1 gives a tabulation of the mean measurements with their standard errors for a selected number of body measures on Puerto Rican adult males and females. The measurements have been selected in terms of representing body areas and not in terms of magnitude of nutritional effect. These measures are given for the total population without regard to racial or regional background (the entire nutritional Group 2 has been reduced to a random sub-sample of 400 for ease of calculation). However, in view of the fact that each racial group is not represented in each nutritional group in the same proportion, the differences are not entirely due to nutrition. Therefore, a group of male individuals who were of the same racial phenotype group was selected from the total sample. Figure 1 gives the variations in stature for the nutritional groups in this racial type (Racial Group 3). Figure 1 also gives the stature of males in nutritional Group 2 who have then been sorted into eight racial groups. Racial Group 1 represents the Caucasian or white end of the scale and Group 8 the negro extreme. The intermediate groups are distributed equally on the scale of mixture between the extremes. Here we see that there is a tendency for the negro to be taller than his white counterpart in the same nutritional group. This makes the findings of nutritional differences for certain measurements more dramatic than indicated in Table 1 in view of the fact that the negroes are not as well represented in nutritional Group 1 as they are in the other groups. From what is given here it is apparent that marked and significant differences in body measurements may be caused by nutritional differences in one population or in one racial group. We also see that significant differences in stature (Figure 1) may be from genetic differences as well. For the persons in one nutritional group, in Puerto Rico, the negro is significantly taller than the white.

Nutrition, in all probability, has the most marked effect of any environmental factor on body proportions and probably has some effect on all phenotypic characteristics. Certainly it is clear from

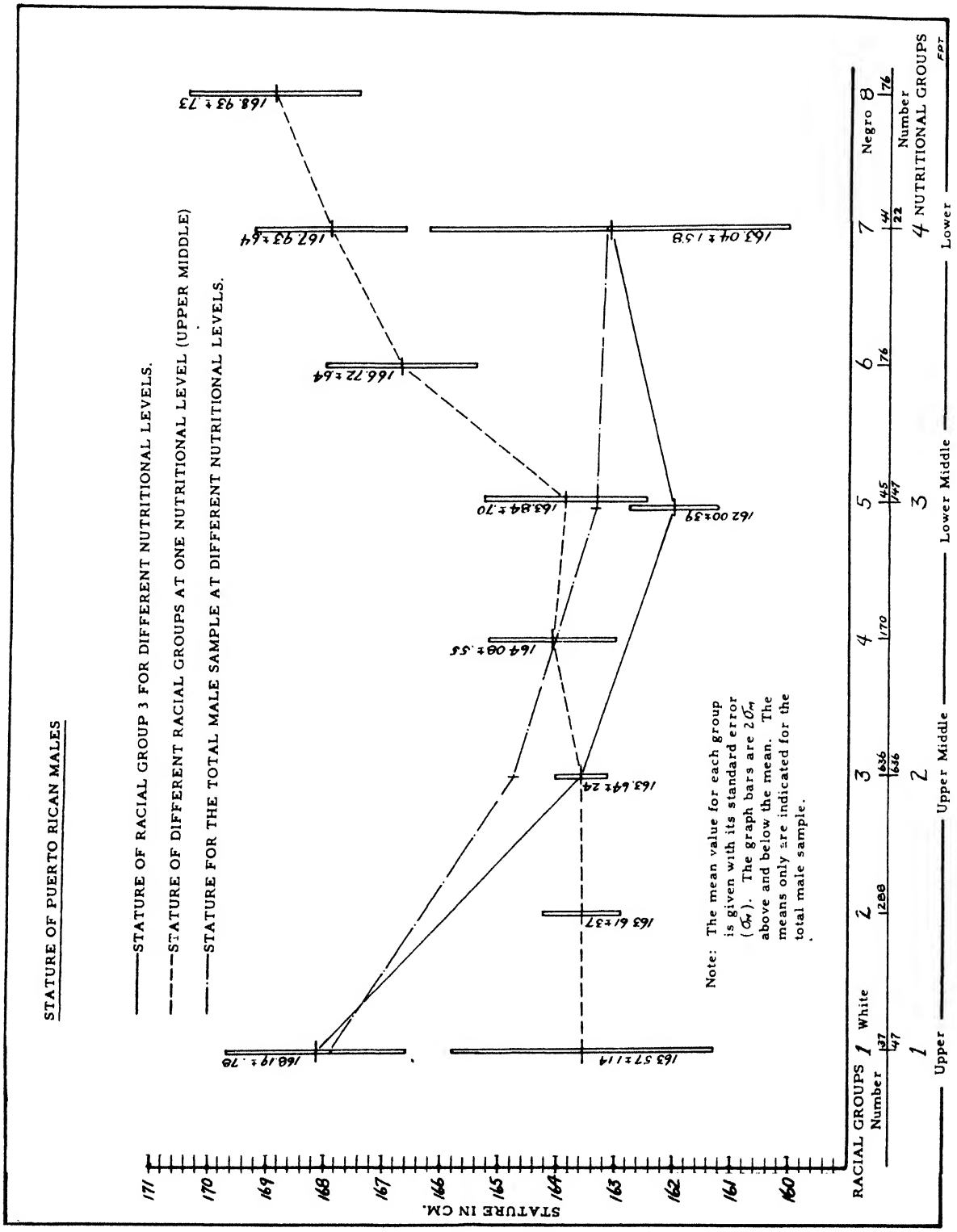
TABLE 1. MEASUREMENTS OF THE PUERTO RICAN POPULATION

Means with Their Standard Errors for Four Nutritional Groups

	Nutritional Group															
	Males								Females							
	1		2		3		4		1		2		3		4	
Number	100		400		274		35		103		400		302		42	
Measurement																
Weight (lbs)	145.26	2.18	127.10	.88	125.80	1.26	121.20	2.90	124.26	2.48	110.12	1.13	107.83	1.14	103.78	2.90
Stature	167.86	.57	164.77	.33	163.34	.38	163.11	1.01	155.05	.57	152.91	.30	151.96	.33	151.07	.81
Upper Arm	31.65	.18	31.27	.10	31.07	.12	31.07	.37	28.39	.19	28.39	.09	28.23	.11	28.44	.29
Lower Arm	22.92	.14	23.44	.10	23.05	.12	22.91	.33	20.74	.15	20.95	.08	20.73	.10	20.95	.24
Total Arm	73.43	.28	73.47	.21	72.71	.25	72.58	.63	66.24	.36	66.54	.18	66.07	.21	66.50	.61
Leg Length	80.56	.38	80.00	.26	79.00	.29	78.20	.74	73.95	.39	73.08	.21	72.66	.25	71.76	.59
Trunk Height	55.87	.25	53.57	.14	52.83	.18	53.39	.54	51.89	.29	50.37	.14	49.83	.14	49.69	.42
Bi-cristal	26.46	.24	25.59	.12	25.69	.14	24.38	.30	25.95	.26	24.85	.12	24.78	.13	24.12	.38
Bi-acromial	38.07	.18	37.52	.10	37.22	.14	36.58	.35	33.76	.20	33.36	.09	33.11	.10	32.53	.28
Abdominal Fold*	6.22	.50	4.33	.20	4.11	.19	3.64	.25	15.35	.89	9.25	.32	7.84	.33	6.38	.67
Knee Width*	94.15	.54	88.60	.20	89.00	.32	91.14	.95	83.31	.60	81.11	.25	80.53	.26	79.67	.68
Head Length*	189.67	.63	184.87	.38	184.55	.42	183.57	1.13	177.69	.74	175.79	.32	175.80	.40	174.57	1.03
Head Width*	153.07	.55	149.52	.30	149.61	.35	150.82	.94	144.65	.50	144.04	.26	143.80	.32	142.57	.75
Bi-zygomatic*	138.33	.49	135.59	.28	136.01	.32	135.80	.81	129.02	.52	128.35	.24	128.05	.29	126.64	.84
Bi-gonial*	100.46	.55	98.23	.35	98.71	.38	96.88	1.01	93.25	.55	91.63	.23	90.90	.29	91.93	.72
Total Face Ht*	123.33	.55	121.35	.31	120.58	.46	121.35	.93	113.51	.65	113.40	.31	113.19	.39	115.24	1.21
Upper Face Ht*	73.76	.42	71.33	.24	71.16	.36	71.60	.77	69.01	.48	68.22	.23	68.33	.32	68.66	.81
Nose Height*	56.68	.40	53.99	.21	53.87	.27	53.66	.55	53.30	.41	51.82	.19	51.47	.25	51.49	.68
Nose Width*	35.55	.28	36.28	.18	36.38	.22	34.97	.43	32.02	.29	32.43	.15	32.98	.20	33.16	.58
Leg Circum.	33.80	.24	32.11	.12	32.18	.16	31.34	.32	32.43	.32	30.98	.14	30.86	.16	30.04	.31
Waist Circum.	73.38	1.14	71.93	.42	70.56	.68	71.80	1.02	66.17	1.40	65.36	.40	60.78	1.03	58.05	3.67
Arm Circum.	25.90	.27	24.21	.11	24.08	.16	23.24	.37	23.91	.29	22.23	.13	22.09	.16	21.70	.35
Skin Color**	12.83	.25	16.83	.23	16.24	.26	15.14	.43								
Age (in years)	27.56	.60	28.80	.38	31.31	.59	34.42	1.56	28.60	.71	29.06	.37	30.05	.47	33.16	1.45

*Measures in millimeters, all others in centimeters except as noted.

**Von Luschan color scale. Highest numbers are the darker skin.


STATURE OF PUERTO RICAN MALES
STATURE OF RACIAL GROUP 3 FOR DIFFERENT NUTRITIONAL LEVELS.
STATURE OF DIFFERENT RACIAL GROUPS AT ONE NUTRITIONAL LEVEL (UPPER MIDDLE)
STATURE FOR THE TOTAL MALE SAMPLE AT DIFFERENT NUTRITIONAL LEVELS.
168.93 ± .73
167.93 ± .64
166.72 ± .64
163.84 ± .70
162.00 ± .39
164.08 ± .55
163.42 ± .24
163.61 ± .37
168.19 ± .78
163.57 ± 1.14
163.04 ± 1.38
STATURE IN CM.
171
170
169
168
167
166
165
164
163
162
161
160
Note: The mean value for each group is given with its standard error (σM). The graph bars are 2σM above and below the mean. The means only are indicated for the total male sample.
RACIAL GROUPS 1 White 2 3 4 5 6 7 Negro 8
Number 137 288 636 170 145 76 41 76
47 436 147 22
1 2 3 4 NUTRITIONAL GROUPS
Upper Upper Middle Lower Middle Lower
FPT

this that any description of the functional phenotype or an understanding of human variability without regard to nutritional environment is hardly possible. At least, until the order of the nutritional effect on each body character has been investigated, nutrition cannot be validly disregarded in population studies. The same is true for all other environmental factors.

In summary, the sort of population study discussed here is difficult to do but of promise in yielding fruitful results. By giving an understanding of the processes of change in present populations, these investigations can help us to discern the patterns of human evolution. They are complementary to other research bearing on the same problem and, although of specific value in themselves, have greater value in this cooperative context. In addition to the study of evolution, they have immediate and very great value as contributions to an understanding of the causes of human variations. Knowing what factors in the history and environment of the individual cause variations in functional performance will lead us to knowledge of how to improve populations. These studies, therefore, have practical value for medical, social and political purposes, as well as for the study of human evolution.

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DISCUSSION

GLASS: I want to emphasize further the importance and the difficulty of obtaining valid samples. To illustrate this, I might describe a personal experience. We found in the Baltimore Rh Laboratory in its first year of operation a frequency of the Rh-negative type of 15.6%, in approximately 5000 white persons typed. After three years and three months operation of the laboratory, the frequency of the Rh-negative type had risen to 17.7%, in approximately 28,000 white persons. The frequency has shown a steady rise in successive samples, and the differences are statistically highly significant. Since it is altogether unlikely that the Rh composition of the population of Baltimore has changed perceptibly in this brief time, it appears that the alteration of the Rh frequencies in the samples is due to a steadily increasing likelihood that Rh-negative women will come to the laboratory and conversely that Rh-positive women will not. This will almost surely happen anywhere as the population becomes typed and individuals learn to what type they belong, or as doctors learn to what types their patients belong. Consequently, in determining the frequencies of blood types in a population one cannot rely on visitors to a clinic after the first year or two during which the population has been typed for a given system of blood groups. The early random sampling of the population gradually gives place to definite biases, and new ways of obtaining a random sample must be sought. For these reasons, in the study of differential fertility in Rh-positive and -negative negro and white women I described in the discussion following Dr. Buzzati-Traverso's paper, the sample had to be limited to the women coming to the laboratory during the first two years of its operation, before any bias in the sample had been introduced.

SANGHVI: (Continuation of the discussion on heredity and environment in diseases.) An analysis of the first 10,000 cases registered at the Tata Memorial Hospital for the treatment of cancer in Bombay, for the period 1941-45, showed some interesting features regarding the effect of environment in the incidence of cancer at various sites in different groups. For instance, cancer of the cervix was 47.0% in Deccani Hindus, 30.8% in Indian Christians and 20.7% in Muslims of all types of cancer in women. Cancer of the base of the tongue in men was 58.9% in Gujarathi Hindus, 45.0% in Muslims and 27.0% in Indian Christians of the oral cancer. A large majority of the Muslims and Indian Christians are the converts from Hindus and the variations in the incidence suggest partly an effect of environment. (Cancer in India. Acta Unio Intu. Cancrum, 1949.)

STERN: While the at present overwhelming environmental source of racial difference in regard to tuberculosis morbidity and mortality has been rightly stressed it is also true that genetic differences exist between individuals within any racial group (*e.g.* studies on twins by Diehl and V. Veeschuer, and Kallmann). It is likely that genetic causes for susceptibility to infectious diseases have different allele frequencies in different human groups.

POPULATION AS A UNIT OF STUDY

CONCLUDING REMARKS OF THE CHAIRMAN

MARSTON BATES

Rockefeller Foundation, New York

Dr. Strandskov, in the first paper of this symposium, gave considerable space to the discussion of the genetic effects of different mating systems within populations. His classification of mating systems is germane not only to the primary objective of this symposium, the synthesis of material on the origin and evolution of man, but also to its secondary objective, the fostering of outbreeding, or exogamy, among the various tribal divisions of scientists. We have here tribal representatives from the geneticists, the anthropologists, the paleontologists, as well as a few strays from groups like ecologists and taxonomists, brought together in the hope that some sort of mental cross-fertilization will take place. These tribes tend to have endogamous reproductive systems, and consequently to follow divergent lines of development. This has gone far enough so that exogamous contacts may well produce ideas full of hybrid vigor—though we hope that the divergence has not gone so far that the filial ideas will be sterile.

The primary fertility barrier among the scientific tribes is specialized vocabulary, as Dr. Dobzhansky pointed out in his remarks on Dr. Strandskov's paper. It looks as though this would be no problem here, however, since the geneticists of the morning talks seemed perfectly at home with the anthropological vocabulary, as did the anthropologist of the afternoon with the genetic vocabulary. The first paper, in fact, though by a geneticist, presents us with two beautiful new anthropological words—isophenogamy and heterophenogamy. This terminology reminded me of my own field, ecology, which Karl Schmidt has defined as that science in which a spade is called a geotome. Perhaps population genetics will come presently to be known as that field of study in which caste is called obligate isophenogamy.

We are apt to consider man a very difficult subject for scientific investigation; but listening to the papers of today, and looking at the range of topics scheduled for the coming days, I have begun to wonder whether the opposite may not be true, whether man may not offer very special advantages for scientific study. The difficulties of course remain: in studying ourselves, we find particular difficulty in escaping the emotions and prejudices that impair 'objectivity'; the use of the experimental method is strictly limited by the value systems of our culture; the long generation span impedes the study of lineages and the accumulation of factual observation on inheritance.

But these difficulties may sometimes blind us to very real advantages. In the first place, man is the only animal for which we have reliable census data, with the exception of a few near-extinct animals like the Alpine goat and the European brown bear mentioned by Buzzati-Traverso. With these data, we can make precise descriptions of human population dynamics in a few areas over a limited time span. Buzzati-Traverso has pointed out the geographical and historical limitations of such demographic data for human political units; but within these limitations, they still provided an unequalled basis for quantitative studies.

In the second place, the needs of medicine and other technologies, and the curiosity of scholars of the humanities and social sciences, of history, anthropology, linguistics and the like, have provided us with an extraordinary accumulation of information about man and his environment. This is the sort of background information that makes possible studies like the one described by Dr. Thieme this afternoon.

In the third place, the 'subjectivity' of man studying man may be counterbalanced by the fact that the observer can put himself in the place of the observed. Watching a mosquito, or even a mouse, I have sometimes been overwhelmed by a feeling of the hopelessness of trying to understand the sense perceptions of the animal under observation, and the consequent difficulty of knowing how the environment impinges on the sensory apparatus of the organism to guide and control its behavior. I stand some chance of knowing what another man hears, sees, tastes, smells and feels; and I think this confers a real advantage.

This list is about long enough, but I might conclude with a fourth advantage—man's curi-

osity about himself, and his ever stronger realization that he must gain an understanding of his individual and aggregate behavior if he is to control the malignant aspects of his cultural equipment that have become so predominant with our recent progress in civilization. This curiosity and, even more, this urgent need, furnish a powerful drive. It is really academic to weigh the advantages and disadvantages of human study: we have got to the point where we must study man, whether he is an apt organism or not, if we are to gain the information that may enable us to attain our minimal biological objective of survival.

The general subject of this symposium, 'the origin and evolution of man,' may at first sight appear to have little relation to this pressing human need for treatment of the cultural malignancies of our civilization. It may seem quite irrelevant to discuss the morphology of Australopithecus, to speculate on the mating systems of Neanderthal man, to attempt the description of population allelotypes, to analyze the effect of nutrition on stature in Puerto Ricans, when man's problems so obviously revolve around the outlawing of warfare, the development of international understanding, and the adjustment of resources, population densities and economic systems.

Yet the relevance is, I think, rather direct. Treatment of our maladjustments, whether they be called cultural, social, economic, biological, or what, is going to depend on an understanding of the nature of man and of his social and environmental relationships. This understanding must be based solidly on studies of his present population structure, of the genetic and environmental forces that mould the human body and personality; and on studies of the historical processes that have governed his biological and cultural evolution.

The paleontologist and archeologist, studying fossil men and fossil cultures, must thus unite with the anthropologist and sociologist, studying contemporary men and contemporary cultures; and the work of these primarily descriptive sciences can be vitalized by the development of a closer symbiosis with an experimental science like genetics, which is primarily concerned with the general nature of the evolutionary process.

Hence this present symposium with its emphasis on the development of cross-relationships among the various human sciences. I only wish we had a larger representation of students of culture. The three speakers today, in dealing with the genetic and environmental aspects of human population dynamics, have all given considerable attention to cultural factors, and in closing this session, I should like again to emphasize this peculiar element in human study.

I have lately been attempting to review some of the literature on the factors governing birth rates and death rates in primitive cultures, and I have been greatly impressed by the influence of the cultural environment on these factors. Causes of death, for instance, in a food-gathering culture appear to be quite different from those in an agricultural or industrial culture. The epidemiology of disease in a food-gathering culture, where small bands wander over large territories with relatively infrequent intertribal contact, would be quite different from the epidemiological situation among a people settled in towns and villages. The common contagious diseases, like smallpox, measles, tuberculosis and so forth, seem largely to be phenomena of the civilized stage of culture, perhaps finding their origin along with agriculture in the early civilizations of Asia and the Mediterranean.

Since most of man's evolution surely occurred during the Pleistocene when he lived at a food-gathering level of culture, the understanding of population dynamics under such cultural conditions is surely basic to an understanding of this evolutionary process. It is disappointing, under these circumstances, to find how little we know, quantitatively, about population dynamics among contemporary primitive peoples. Such studies, surely, are difficult. As Kuczynski has said, "To appraise fertility, morbidity, mortality or migration is about as difficult in most African Dependencies as to appraise the frequency of adultery in England." But the fact that a study is difficult should be a challenge rather than a deterrent.

But I have talked long enough. As I remarked at the beginning, one objective of this symposium is to foster the exogamous meeting of minds among the tribal divisions of students of human evolution. Surely the beach is more appropriate for such purposes than the lecture room, so I suggest that we make such an environmental shift.

ORIGIN OF THE HUMAN STOCK

THE SPECIALIZATIONS OF MAN AND HIS PLACE AMONG THE CATARRHINE PRIMATES

ADOLPH H. SCHULTZ

Department of Anatomy, The Johns Hopkins University School of Medicine

INTRODUCTION

From all comparative-anatomical knowledge it has become abundantly proved that man belongs to the suborder of simian primates. This suborder is readily and naturally divided into two distinct, main groups, namely, one of the New World and one of the Old World. The animals of the first group possess without exception three premolar teeth on each side of both jaws, whereas those of the second group have only two of such teeth, and the former lack a bony auditory canal which develops in all the latter during postnatal life. On the basis of these and numerous other, constant anatomical differences between the American, or platyrrhine, and the Old World, or catarrhine, primates man must be assigned to the latter group. No fossil catarrhine has ever been discovered in the Western hemisphere, nor any fossil platyrrhine in the Eastern one, hence it must be assumed that the separation between these two series is an ancient and deeply rooted one and that man, as a typical catarrhine, must have had an Old World origin.

There exists a great deal of justification for dividing the catarrhines into lower and higher ones. The former all belong to the one family of Cercopithecidae which is composed of the great many species of Old World monkeys, characterized by the possession of ischial callosities and many other anatomical peculiarities. In the subfamily of Semnopithecinae (Langurs, Guerezas, etc.), which contains only highly arboreal monkeys with very long tails, the stomach has become sacculated, a specialization which has been avoided by all other catarrhines. The subfamily of Cercopithecinae (Macaques, Baboons, Guenons, etc.) includes the monkeys which are not nearly as exclusively plant-eaters, as all Semnopithecinae, and contains many forms with greatly reduced tails, especially among the more terrestrial species. In view of many basic, anatomical similarities it seems most reasonable to assume that the entire group of higher primates originated from some extinct primates, belonging to the subfamily Cercopithecinae, though this cannot as yet be proved palaeontologically.

The subfamily Hylobatinae (gibbons and siamangs) bridges to some extent the present gap between the lower and the highest catarrhines. In body size they are monkey-like and they still possess ischial callosities, though these develop not nearly as early in life as in monkeys. In general, however, the Hylobatinae share the main characters of the great apes and constitute with the latter the group of anthropoid, or man-like apes. This distinguished group is most justifiably assembled in the single family Pongidae which contains, besides the subfamily Hylobatinae, the second subfamily Ponginae. To the Ponginae belong the three recent types of great apes and a surprisingly large variety of fossil forms. Finally, the group of higher primates includes the family Hominidae, today represented only by the single genus *Homo*.

The two families, Pongidae and Hominidae, jointly referred to as the higher primates, have in common a great many important characters which have clearly become more highly developed than in the other, lower catarrhines. It is the exact place of man among the higher primates that is still in dispute and, particularly, its implications regarding human evolution. Even by disregarding the untenable claims of Jones (1948) for an extremely remote human origin, independent of any catarrhine source, we still find such widely different views as those of Straus (1949), who concludes that man's evolutionary course had begun before any typical anthropoids had appeared, or of Weinert (1932), who has convinced himself, but only few others, that man and chimpanzee became distinct only with the start of the Pleistocene period and long after all other apes had evolved. Palaeontologists have so far agreed no more than have comparative anatomists in regard to the exact place of branching of the Hominidae from the family tree of catarrhine primates. For in-

stance, Werth (1921–1928) derives man from the same ancestral stock that gave rise also to the gibbons, whereas Abel (1934) concludes also on palaeontological grounds that man and the African apes had sprouted from one family tree long after the branches for the Asiatic anthropoids had appeared.

Until recent years fossil finds have merely narrowed here and there the gaps between apes and men by producing a remarkable variety of extinct apes with some features less specialized than in the surviving anthropoids and by adding new forms to the Hominidae which, though more ape-like than modern man, are nevertheless already definitely human, justifying at most generic separation from recent man. It seems highly probable that the newly discovered group of Australopithecine primates, when more fully described and compared, will be outstandingly helpful in the determination of man's place among the higher primates and the understanding of the course of his evolution. From the latest reports it appears that in the Australopithecines have been found "anthropoids" which had walked erect, yet still had largely ape-like heads, thus closely resembling an expected, early stage in man's evolution.

For the great majority of the problems appertaining to man's phylogenetic specializations we will always have to rely upon thorough comparisons between recent primates, including all bodily parts and considering form and function. Only with such comparisons can we ever hope to detect which characters are really peculiar to man and to determine the degree and significance of such specializations. With the realization that all phylogenetic changes are primarily due to ontogenetic alterations, we have to discover when, where and, possibly, why human growth and development have become different from corresponding age changes in non-human primates and this, again, can be accomplished only by comparisons.

This paper deals with such comparisons between man and other catarrhines during and at the completion of their growth. The facts to be presented will here be given very briefly and mostly in the form of bare statements, or rough averages only, since nearly all these facts, their sources, the methods by which they have been obtained, the size of the series used, and the relevant literature have already been recorded and illustrated in other papers by the author, of which the more comprehensive ones are listed at the end.

Locomotion

Many of the Old World monkeys spend practically their entire lives in trees, whereas others are more at home on the ground. Most of them can and freely do *stand* for short times on their hind legs alone, but for locomotion they rely on all four limbs or, occasionally, swing by their arms alone. They can *walk*, or rather hop, on two legs no better than can a dog. All the man-like apes can readily stand on their feet alone and gibbons, siamangs and some chimpanzees and gorillas are well able not only to run, but even *walk* upright for short distances without support of their arms. Most of the time, however, gibbons, siamangs, orang-utans, and, to a lesser degree, chimpanzees move by means of brachiation and gorillas, specially when fully grown, in quadrupedal fashion. Permanent bipedal locomotion is a distinction of man—after infantile life. That evolutionary preparations for erect walk had their beginning in the ancestral stock of all higher primates is indicated not only by the limited ability for bipedal locomotion, found among recent apes, but also by certain anatomical requirements for the erect posture, unmistakably present in apes, but perfected only in man.

Life Periods

The acquisition of the erect posture was undoubtedly the first major step in man's evolution. As one of the recent steps must be regarded the great prolongation in the main periods of man's postnatal life. For instance, general growth is completed in about three years in prosimians, in seven years in catarrhine monkeys, in nine years in gibbons, and in eleven years in the great apes, but in man this period has increased to 20 years. Similarly, the normal life span has grown from at best 25 years in monkeys to about 35 years in apes and to over seven decades in modern man. The onset of female fertility falls in the sixth year in macaques, in the tenth year in chimpanzees and in the seventeenth year in civilized man. The general trend to lengthen these periods beyond their duration in lower primates has affected all the higher ones, but has reached its extreme in man, especially the more advanced races.

Among the many detailed growth processes the degrees of prolongation can differ widely and thus these processes can change their order in the ontogenetic time table of a given species. For instance, the eruption of the permanent dentition becomes completed at the very beginning of the period of epiphyseal union in the limb bones in all prosimians and monkeys. In the Asiatic anthropoids the last teeth appear somewhat later during the epiphyseal closure period and in the African apes later still. In some colored races of man there has occurred a further retardation in dental

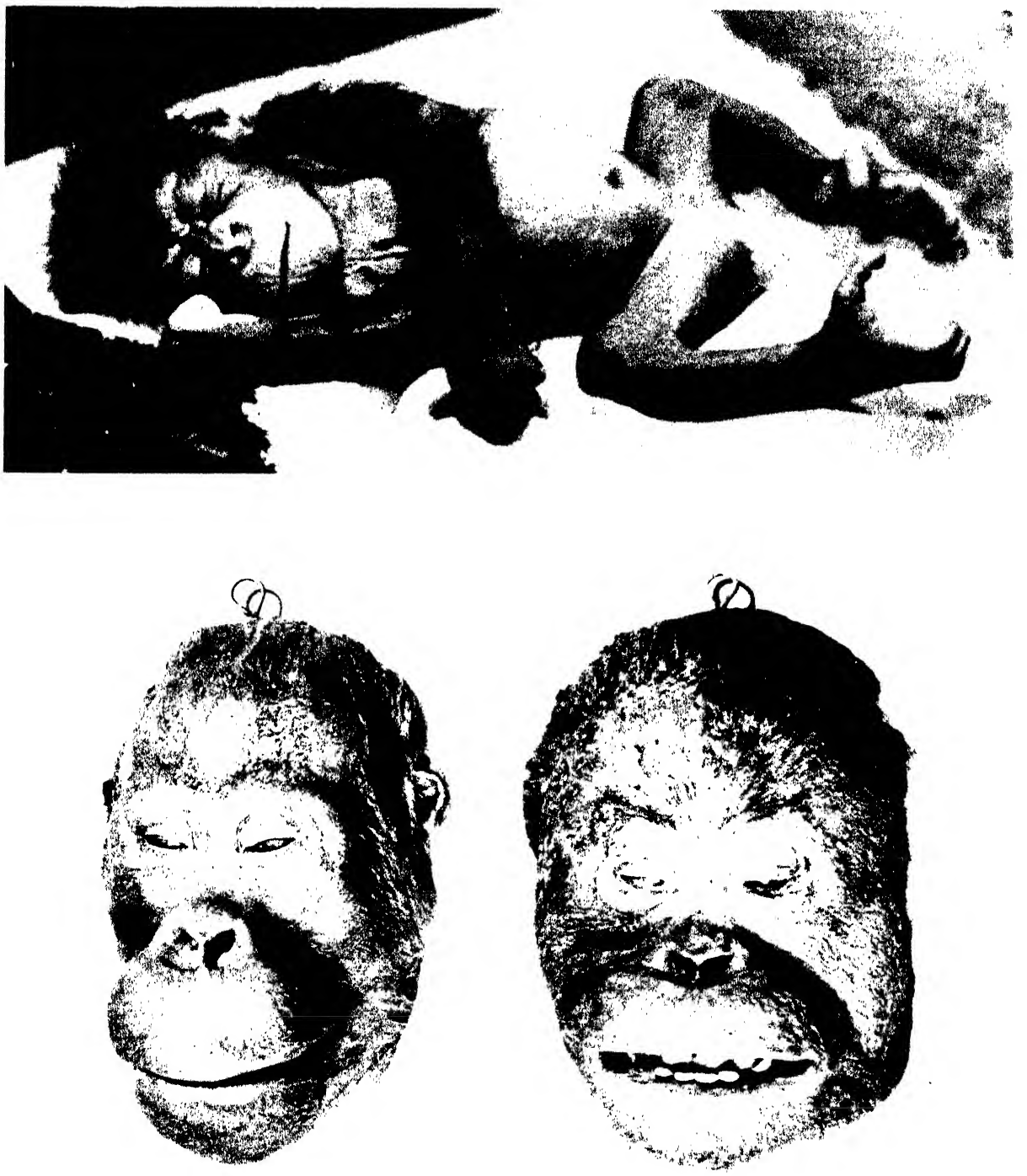

PLATE 1. Top = Sleeping chimpanzee baby "Panacea," 15 days old, showing long scalp hair, beginning long hair on arm and lack of long hair on remaining body surface. Bottom = Author's death masks of two female orang-utans with complete, but unworn dentition, showing striking differences in head formation.

eruption, relative to the period of epiphyseal union, and in whites this has reached its extreme, inasmuch as all epiphyses of the limbs are usually closed before the permanent dentition becomes complete.

Hair

One of man's most conspicuous specializations consists in his comparative hairlessness. In all catarrhine fetuses the first hair appears as eyelashes and eyebrows, to be followed rapidly by hair on the scalp and lips, while all other hair develops much more slowly. In newborns of, particularly, the African apes the hair on the scalp is strikingly long and strong in contrast to the fine, short hair on the rest of the body surface. This fetal prevalence of scalp hair, which exists in varying degrees in all catarrhines, disappears quickly in ape infants, but is retained and becomes even accentuated in man (see Plate I).

Per square centimeter of scalp, man and the great apes support practically equal average numbers of hairs (slightly over 300), whereas in the lower catarrhines the density of scalp hair is generally much higher (average over 900). On the back the density of hair is more than three times greater in monkeys than in the great apes and on the chest it averages about twice as much in the former than in the latter. In adult gorillas and some chimpanzees and orang-utans the chest can bear less hair than in some men. Hair density in general has become much reduced in all great apes in comparison with the lower catarrhines (which have a lesser hair density than prevails among platyrrhines) and this same evolutionary trend has reached its extreme in man. Just the opposite extreme has been acquired by gibbons which possess the greatest hair density of all catarrhines.

Trunk and Neck

Spinal Column:

The numbers of vertebrae in the different spinal regions have undergone some significant evolutionary changes in man and the man-like apes. This can here be shown merely by the following rough, general averages: The number of thoracic segments equals, as a rule, 12 in Old World monkeys as well as in orang-utan and man, but 13 in gibbons and the African apes. The number of lumbar segments, generally seven in lower catarrhines, has decreased to five in gibbon and man, to four in orang-utan, and to even less than four in chimpanzee and gorilla. The sacrum is usually composed of three vertebrae in monkeys, of four and more in gibbons, and of five and more in the great apes and man, the African apes having acquired the maximum average numbers. In the tail region the number of vertebrae has become less reduced in man (average = 4.2) than in any of the other higher primates among which the Asiatic anthropoids have reached the extreme reductions (averages = 2.4 to 2.7). The primitive numbers of lumbar, sacral and caudal vertebrae have become changed in all the higher primates in the same direction, but with differing intensity in the various forms. In general, man has remained more conservative in these conditions than the man-like apes.

The cervical portion of the spine, which is composed of seven segments in all primates with only rare, individual exceptions, has become proportionately much longer in apes and man than in the lower catarrhines. The lumbar region of the spine of higher primates has become reduced not only in the number of its segments, but also in its length, relative to the trunk height. Thus, it forms well over 40 per cent of the trunk height in Old World monkeys, about 37 per cent in man, 31 per cent in gibbons, and only 22 to 27 per cent in the great apes.

The formation of a promontory at the lumbosacral border through a deviation of the sacrum from the general direction of the presacral spine can become barely indicated late in growth in monkeys, develops earlier postnatally, and progresses farther, in all apes, especially the African ones, and appears already before birth and grows to an extreme in man.

In all catarrhine fetuses the spine projects very little into the chest cavity and this condition remains practically unchanged in monkeys. In apes, however, the spine migrates during growth toward the center of the thorax. The same ontogenetic shift takes place in man in whom the spine approaches even more closely to the center of gravity of the trunk with the completion of growth, as a mechanically advantageous adaptation to the erect posture.

Chest:

In comparison with Old World monkeys all higher primates have developed very stout trunks. The chest girth, the shoulder breadth and the hip breadth, in relation to the trunk height, all show much higher averages in apes and men than in monkeys. The higher primates as one group are furthermore sharply distinguished from the lower catarrhines by having acquired a more intense rate of growth in the transverse than in the sagittal diameter of the chest, so that in adults the

chest becomes much broader than it is deep. In monkeys these two chest diameters grow postnatally at equal rates and the chest index remains near 100. In the apes this index changes ontogenetically to far above 100 and reaches its extreme not in man, but in the gorilla.

The great widening of the entire trunk has affected also the sternum, which has become strikingly broader in apes and men than in any of the monkeys. In all catarrhine infants the sternum consists of separate bony sternebrae. Only rarely do a few of the lower sternebrae become united in old monkeys. In apes the separate bones of the corpus sterni tend to fuse at the caudal end when and after adulthood has been reached, but all parts become fused in only some of the oldest apes. In man this ontogenetic specialization has become accelerated and complete fusion between the segments of the corpus sterni occurs already during late juvenile life.

In Old World monkeys anywhere from seven to nine pair of ribs are directly attached to the sternum. Among apes and men this number of sternal ribs has decreased significantly, varying individually between only six and eight and averaging less in the great apes than in man.

Shoulder Girdle: (see Fig. 2.)

On the narrow chests of monkeys the shoulder blades lie lateral to the thorax, being held there by the proportionately short clavicles. In all apes and men the shoulder blades have moved far dorsally on the broad thorax and this as much in bipedal man as in the extreme brachiators. Thus the shoulder joints, which lie ventrally of the spinal column in all monkeys, have shifted dorsally into one plane with the spine in all apes and men.

In adults of the anthropoids the shoulders are situated high above the suprasternal notch, so that the clavicles point upward with their lateral ends and the neck appears to be short, lying between, rather than above, the shoulders. It is interesting to note that in early human fetuses the shoulders still lie far above the thorax and descend with growth less far in some races than, e.g., in whites in whom the clavicles at rest become usually horizontal, a position which is quite impossible for apes.

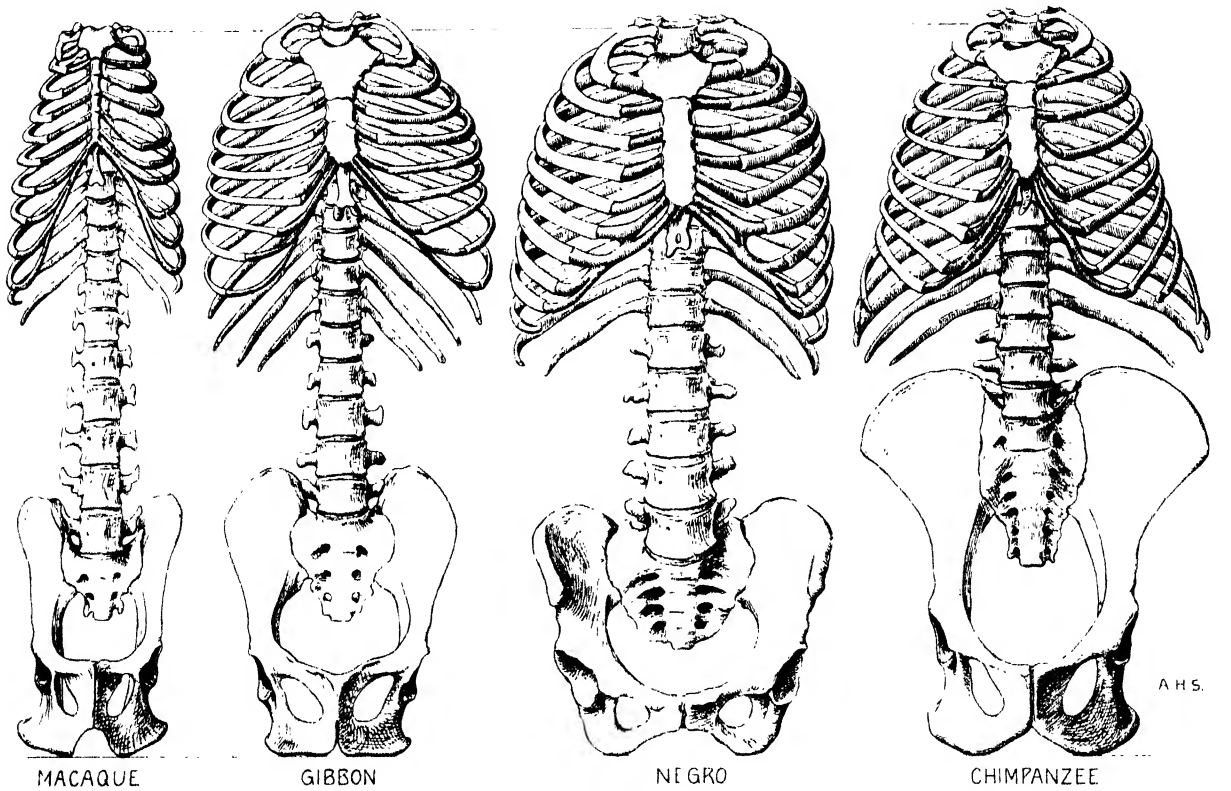

FIG. 1. Trunk skeletons of adult female macaque, gibbon, negro and chimpanzee, reduced to same total length, illustrating conditions discussed under "Spinal Column," "Chest" and "Pelvis."

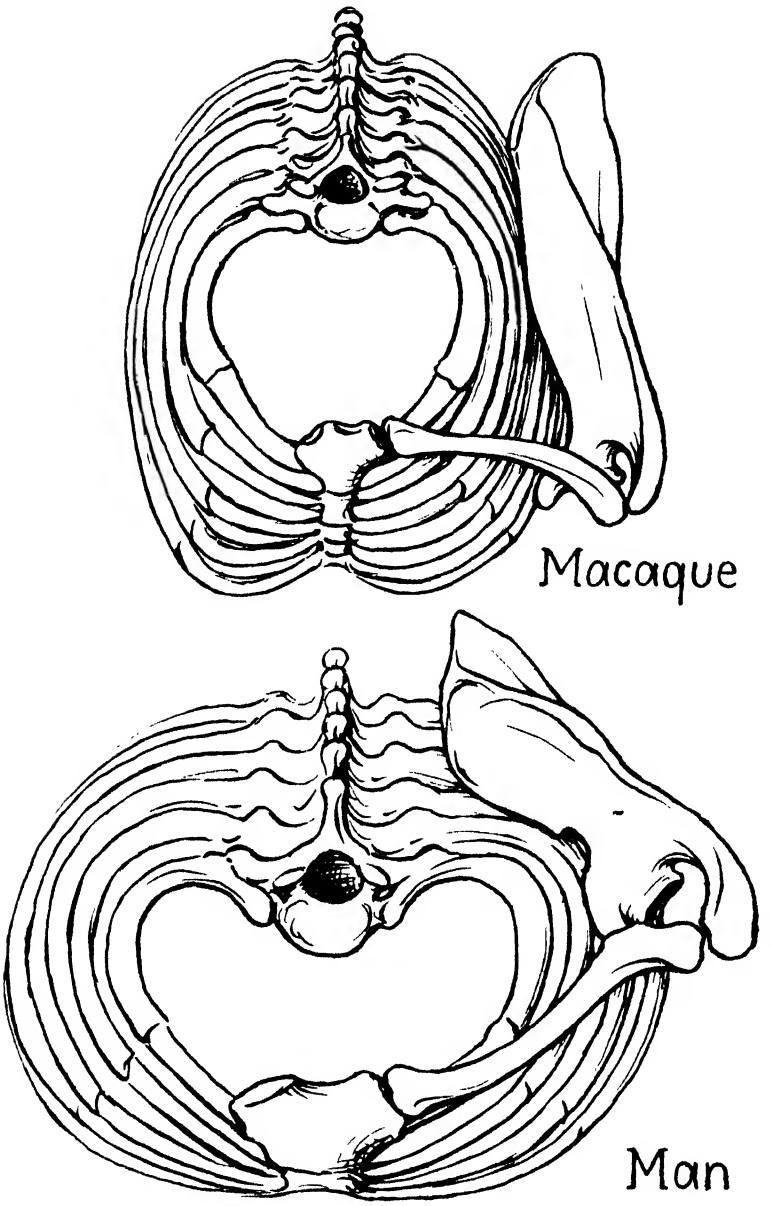

FIG. 2. Sketches of top views of thorax and left shoulder girdle in adult macaque and man, illustrating conditions discussed under "Shoulder Girdle."

Pelvis:

Just as the shoulder girdle, so has the hip girdle participated in the general great widening of the trunk, characteristic of all higher primates. Indeed, in the great apes the pelvic ring has become much larger than necessary for the passage of their comparatively small newborns. In these apes the exceptional size of the pelvis is determined largely by the requirements for muscle attachment and for leverage in muscular action. In the man-like apes the ilia have become relatively wider than in monkeys and, especially, very much longer, so that they extend on both sides of the spinal column to very near the last pair of ribs. The lowest lumbar vertebra often sits far down between the ilia, articulating with the latter, or has become sacralized in varying degrees of perfection. The pelvis of man has not shared these specializations in the anthropoid pelvis, but, instead, shows unique phylogenetic changes of its

own. The entire pelvis of man has become tilted and telescoped, so that the sacrum lies opposite, instead of far above, the pubic symphysis, the iliac fossae face medially, rather than ventrally, and the ilia have increased in width partly through the great enlargement of their sacral portions, but they have remained relatively as short as in monkeys.

LIMBS

Relative Length of Limbs:

Among all adult catarrhines man has acquired the greatest *average* length of the lower limbs, relative to the trunk height. This distinction develops only during postnatal growth and does not include all individual variations. In many adult gibbons and some chimpanzees the relative total lower limb length is as great as, or even greater than, in some human beings with completed growth.

The total upper limb length in relation to the trunk height has become greatly increased in adults of all higher primates, including man. This proportion averages roughly 120 in Old World monkeys, 150 in man, 154 in mountain gorilla, 175 in chimpanzee, 200 in orang-utan, and over 230 in gibbon and siamang. It is significant that man, though no brachiator, has clearly participated in the evolutionary trend of the apes to lengthen the upper extremities. Indeed, in many human beings the arms are longer, relative to the trunk, than in some gorillas and chimpanzees. As mentioned above, the latter are not nearly as specialized brachiators as the Asiatic apes. In the most accomplished brachiator, the gibbon, the relative upper limb length has become twice as great as in the average catarrhine monkey and thus has changed much more than has the relative lower limb length of man, which has reached only about one and a half times the size of that proportion in the average monkey.

In regard to the relation in length between the upper and lower extremities man does become distinct late in growth from all other catarrhines without any exception. This intermembral index (total upper limb length in per cent of total lower limb length) drops slowly in man from over 130 in early fetal life to 100 at birth and to well below 100 postnatally. In all non-human catarrhines this index remains above 100 throughout growth. It is only in a few platyrrhines and in a good many prosimians that one finds adults with intermembral indices equalling those of man by being below 100.

Hands:

The hand of man shows few and only minor distinctions and remains comparatively primitive at all stages of growth. The total length of the hand in relation to the trunk height is larger in man than in catarrhine monkeys, but much shorter than in the anthropoids, except the mountain gorilla. Man has a proportionately broader hand than any other Old World primate, with the exception of the gorilla, which develops the broadest of all hands at completion of growth. The human thumb is unusually long in relation to the greatest hand length, but it is not of exceptional length, if compared with arm length or trunk height. It is not the thumb which has become longer in man, as is commonly claimed, but the human fingers II to V which have failed to share the lengthening of these digits, typical of most apes. The rotation of the thumb, which develops only gradually in prenatal life of all catarrhines (and is practically lacking in platyrrhines), becomes more perfected in adults of the great apes than in the average adult man.

Feet: (see Fig. 3.)

The adult human foot differs strikingly from the feet of all adult non-human primates, yet it resembles unquestionably most closely the foot of gorilla. With the latter man shares especially the great increase in the relative size of the tarsus and the distal position of the base of the free portion of the first toe. The feet of the Asiatic anthropoids have become highly adapted to arboreal life by having the phalangeal portions of the second to fifth toes extremely lengthened and by having the first toe very extensively reduced in the case of the orang-utan, and greatly perfected for abduction and opposability in the case of the gibbon. The feet of the African apes have compromised in various respects between arboreal and terrestrial specializations, mountain gorillas favoring the latter most decidedly. In man the foot has lost its grasping ability much more completely than even in adult gorillas and has become highly adapted to its specialized functions for bipedal, terrestrial support and locomotion. These adaptations consist chiefly in the retention of the early fetal lack of rotation in the first digit, common to all simian fetuses, and in the far-reaching reduction of the phalangeal portions of the lateral toes. The latter increase in relative length during growth in monkeys and apes, whereas they decrease in man. This ontogenetic and phylogenetic degeneration in the human toes II to V has progressed so far that not infrequently some of the phalanges (the middle ones of the fifth and, more rarely, also the fourth toes) have become totally eliminated. It is exclusively this great shortening of the lateral toes which accounts for the fact that the human great toe appears to be so long. In rela-

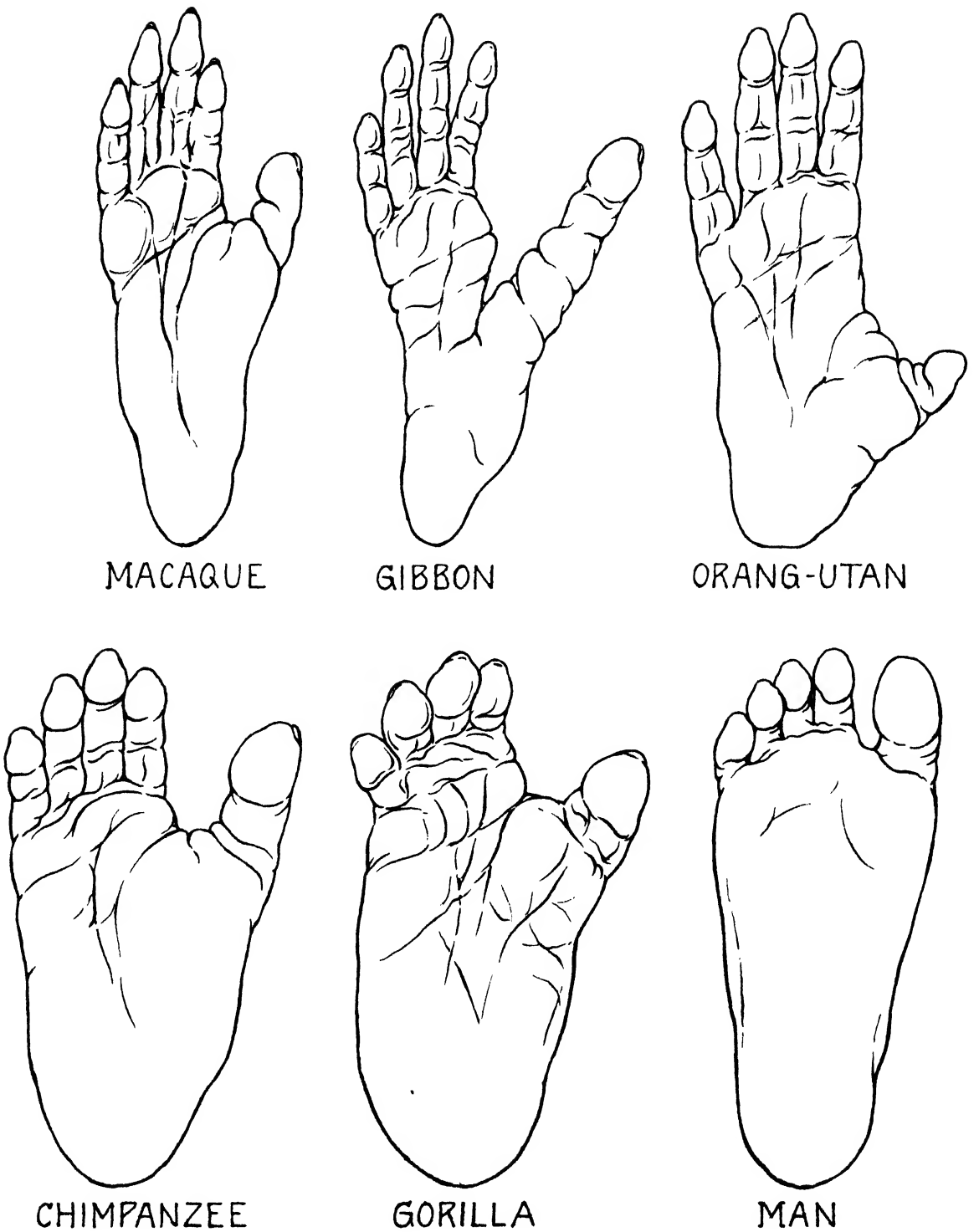

FIG. 3. Right feet of adult male catarrhine primates, reduced to same total foot length.

tion to tarsal length or to trunk height the great toe of man is actually no longer than in some apes. In all catarrhines the middle toe is the longest of all toes early in fetal life. This condition persists throughout growth in the monkeys and apes, but changes rapidly in man, in whom the second and often even the first toes become longer than the third.

HEAD

Brain Size: (see Fig. 4.)

Adult man possesses by far the largest brain among all adult primates, but, relative to the total size of the body, the brain of some small monkeys can equal or even surpass that of man. It is a general law of nature that large animals possess proportionately smaller brains than closely re-

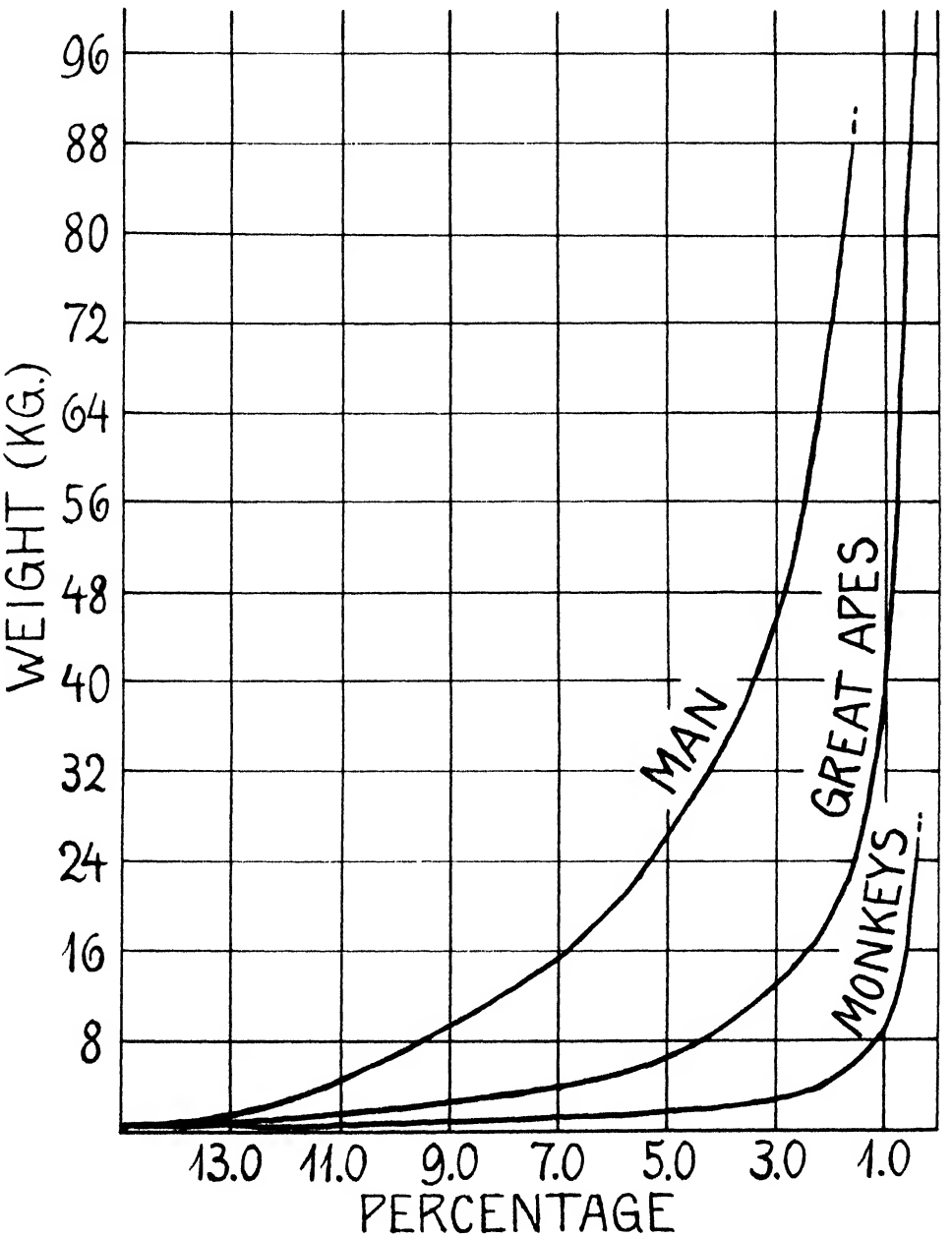

FIG. 4. Correlation curves between weight and relative brain size, represented by the cranial capacity (in cc.) and expressed in percentage of the body weight (in g.) in catarrhine primates of all ages.

lated, small animals and that during late prenatal and all postnatal growth the brain increases in size at a lesser rate than the whole body. In early human fetuses the relative brain size is as yet no greater than in equally large fetuses of many other primates. In man, however, the brain continues to grow for a longer period and at a more intense rate than in the apes, just as the brain size of apes has surpassed that of monkeys in consequence of their relative position with varying speed and intensity toward the back of the skull so that the head becomes hinged in front, rather than on top, of the spine in all Old World monkeys and apes. In man these fetal conditions remain practically unchanged throughout growth, so that the head of adult man is posed, relative to the spine, in a radically different manner than in adults of the non-human catarrhines. This ontogenetic special-

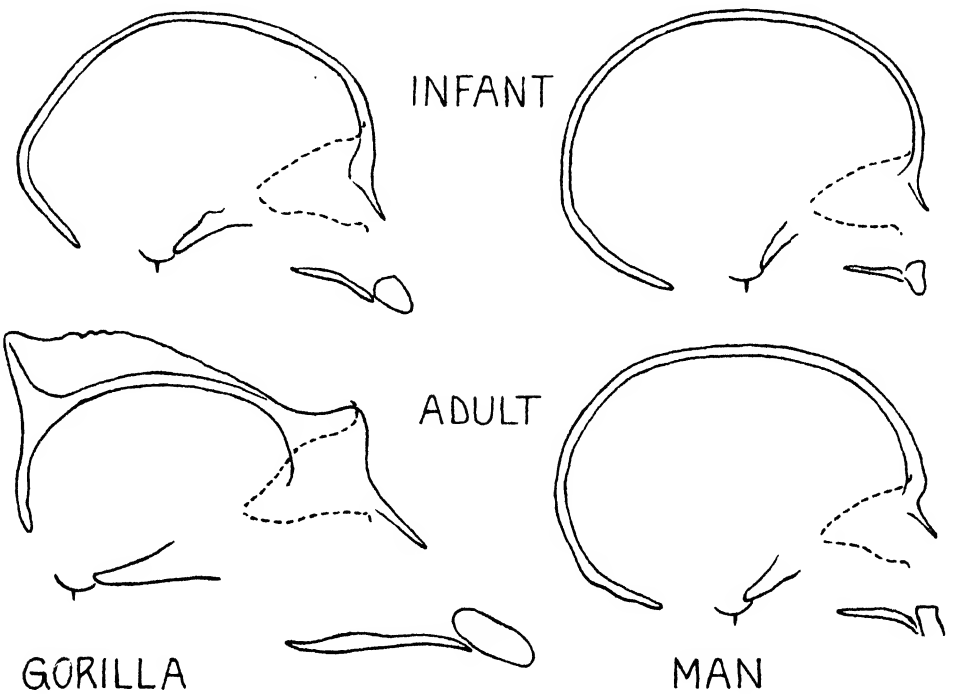

FIG. 5. Midsagittal sections of skulls of infantile and adult gorilla and man, reduced to same length of brain case, with projected sagittal section of one orbit and profile of one occipital condyle, illustrating "Head Balance" and relative position of orbit.

a specialized continuation and intensification of brain growth. If the growth curves for relative brain size are compared in the various major groups of catarrhines, it is found that the curve for the great apes has shifted away from the curve for catarrhine monkeys toward the curve for man.

These remarks suffice to show that the absolute size of the brain, or of the cranial capacity, in fossil primates remains meaningless until we have gained more adequately supported knowledge of the general body size and the age and growth rates in these extinct forms.

Head Balance: (see Fig. 5.)

During fetal life the head of all catarrhines is posed on top of the spinal column and the occipital condyles lie correspondingly far forward on the skull base. During growth these condyles shift

ization of man did not *have* to precede the great increase in brain weight, as is commonly assumed, since the weight of the whole head, relative to the entire body weight, is smaller in adult man than in many other adult primates which lack the near-equilibrium of the human head.

Outer Ears:

In their general configuration the outer ears of man resemble most closely those of gorilla. An ear lobule, free of cartilage, is not a human distinction, but exists in gorillas and chimpanzees, as well as in a variety of catarrhine monkeys, though it is lacking in the Asiatic anthropoids. The edge of the helix is most extensively folded over in most gibbons and all orang-utans and gorillas, somewhat less in the average man, and usually least among higher primates in chimpan-

zee. In nearly all monkeys of the Old World only the top of the helix is bent over, having posteriorly a more or less pointed end. The size of the outer ear, relative to the size of the entire head, has decreased extremely in some of the higher primates. This relative ear size can be represented by an index which averages in adults roughly 13 in Old World monkeys and in gibbons, 17 in chimpanzees, but only five in man, four in gorilla and three in orang-utan.

Face:

The face of even prognathous human beings does not protrude beyond the brain case nearly as far as in the apes and monkeys and thereby retains the common fetal condition much more closely than in other catarrhines. The human face remains to the completion of growth much lower than in the great apes, whether the total face height is expressed in relation to trunk height or to the size of the brain case. In gibbons, however, the face is proportionately no larger than in man and this in spite of the fact that the gibbon orbits are exceptionally large.

In all fetuses of monkeys, apes and man the orbits lie entirely underneath the brain case and there they are retained by man to adult life (see Fig. 5). In Old World monkeys and, particularly, in the great apes the orbits migrate after birth to a position largely in front of the brain cavity of the skull. It is mentioned here that this particular kind of 'fetalization' did not appear exclusively in man, but developed independently also in certain platyrrhines.

Dentition and Palate:

A great deal has been written regarding the dentition of recent and fossil catarrhines and in general this has produced only evidence for the close relationship between man and the anthropoids and, at the same time, for the remarkable variability and versatility which characterizes the higher primates. The latter is well exemplified by the fact that the canine teeth have acquired practically equal, enormous length in both sexes in gibbons, have become extremely thick and powerful in males of orang-utans and gorillas, show only moderate sexual differentiation in chimpanzees, and have been extensively reduced in size of, especially, the crowns in both sexes of man.

The diastemata, supposedly needed in connection with large canines, are not a constant feature of anthropoids, nor is their lack in man without exceptions, hence their taxonomic and phylogenetic significance is rather limited.

On the palates of all primates are found transverse ridges, or rugae, which are most strongly developed in prosimians. In all lower catarrhines the rugae are still comparatively large, regular and symmetrical, extending to at least the second molars. Among the Asiatic anthropoids they have changed to more irregular patterns and tend to become reduced in size and extent in occasional specimens. In the African apes the rugae usually reach to only the first molars and have become highly variable regarding number and pattern. In man these ridges are also very variable, have withdrawn most from the posterior part of the palate and have been reduced to the smallest average number. Individually, however, there can still be as many as eight ridges in man and as few as three in gorilla and not infrequently the last ridges still reach the first molars in man, as in the African apes.

Cranial Features: (see Figs. 6 and 7.)

A great many detailed cranial features have been claimed to be more or less specific for man and used in attempts to determine man's place among the primates. For instance, the conditions of the facial parts of the premaxillary bones have received a great deal of attention, since these particular parts become early hidden by the maxillary bones in man, but not in non-human primates. This localized human specialization does not appear to be as profound, as has been assumed, if it is taken into consideration that the premaxillary bones are extraordinarily variable in size among the great apes, can develop separate, lateral, alveolar parts in many gorillas, do surround the nasal aperture, meeting each other below the nasal bones, in snub-nosed langurs, and can reach all the way to the frontal bones in various monkeys without anyone ever having proposed radical taxonomic separations on account of these other, isolated, premaxillary specializations.

The relations between the bones in the temple, or pterion, region varies widely among catarrhines. In man the sphenoid usually meets the parietal, thus separating the frontal and temporal, but this condition, present in 98 per cent of whites, exists in much lower percentages of the cases in some of the colored races of man. In the non-human catarrhines the temporal meets the frontal as a general, but by no means universal, rule. Thus, in the Asiatic anthropoids the prevalent human condition is also found in a majority of specimens, whereas in the African anthropoids the temporal meets the frontal with very few exceptions, just as in most of the Old World monkeys. Among the latter, how-

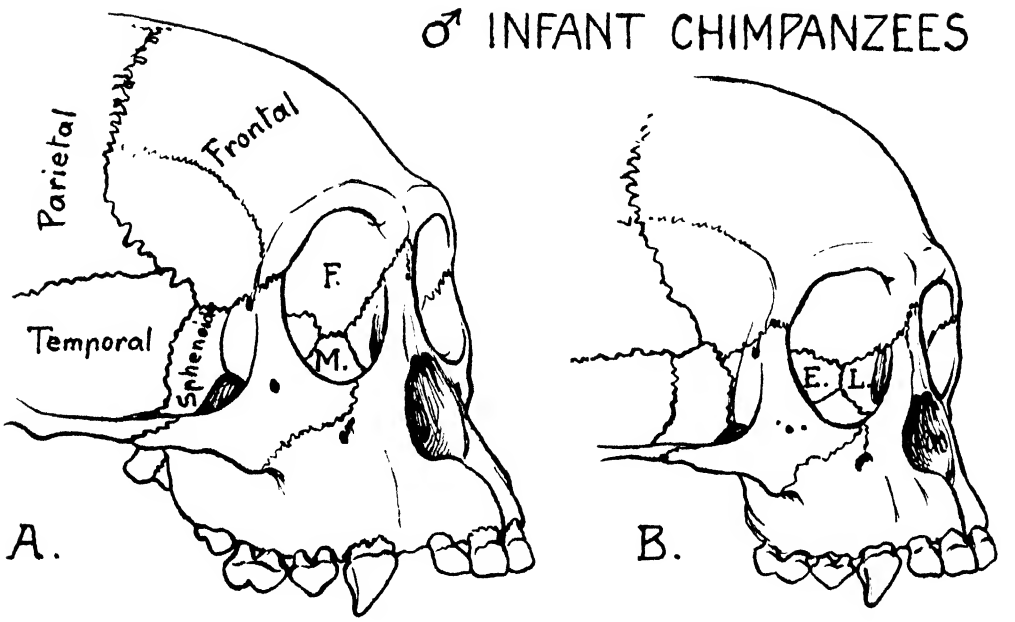

FIG. 6. Sketches of infantile chimpanzee skulls showing different relations between bones at temple and on medial wall of orbit. *A* from Cameroon, *B* from South of Congo river. *E* = ethmoid, *F* = frontal, *L* = lacrimal and *M* = maxillary bones.

ever, there are many species with highly variable pterions, and at least one in which the "human" condition seems to be more constant than in man. To be specific, in *Rhinopithecus roxellanae*, a langur-like monkey, the writer found a sphenoparietal suture, just as in most men, in every one of the 15 skulls examined.

The relation between the ethmoid and lacrimal bones is another of the cranial features which have been used for phylogenetic conclusions appertaining to man. In all monkeys, gibbons and orang-utans the ethmoid and lacrimal meet on a broad front, but this relation persists in only 50 per cent of chimpanzees, 43 per cent of gorillas and 93 per cent of men. In the remaining African apes and men the lacrimal and ethmoid have become separated by processes, extending from the frontal and maxillary bones, which meet in either a mere point, or else, more frequently, along a postlacrimal fronto-maxillary suture.

In all but one single specimen of the great many Old World monkeys examined so far, and in all Hylobatidae the frontal bones meet each other on the floor of the cranial cavity behind the

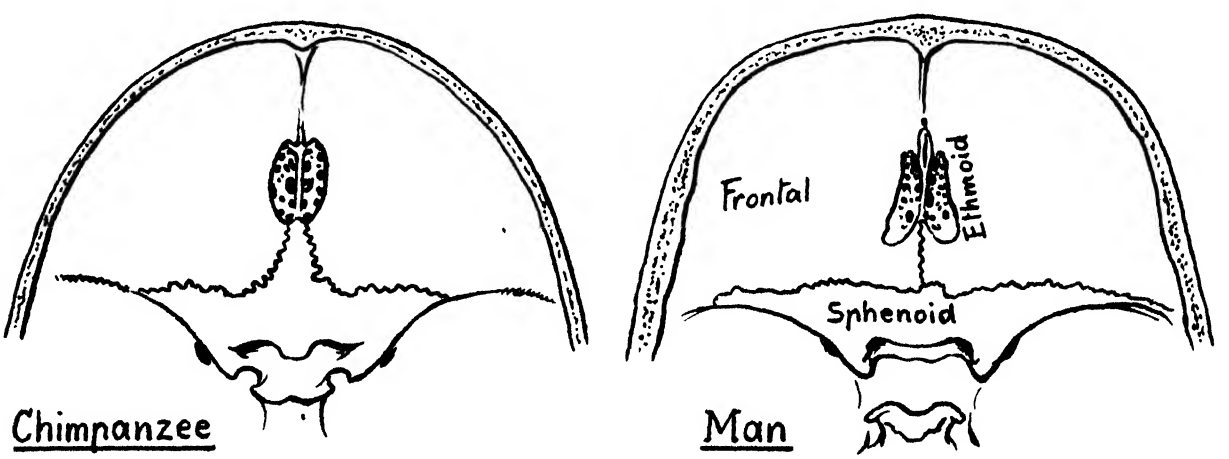

FIG. 7. Sketches of anterior floor of brain case showing different relations between sphenoid and ethmoid bones.

ethmoid, thus separating the latter from the sphenoid. This condition has persisted in only 52 per cent of gorillas, 23 per cent of chimpanzees, 3 per cent of men (in negroes alone in 9 per cent), and in even only 1 per cent of orang-utans. In the great majority of orang-utans, chimpanzees and men and in nearly half of all gorillas the sphenoid has pushed between the frontals to meet the ethmoid as a new, but still inconstant specialization.

The mastoid process, frequently claimed as a qualitative distinction of man and as supposedly acquired by him with the erect posture, is actually not limited to man, but found also among chimpanzees and gorillas. Indeed, in old gorillas this process can at times be fully as large as in any man. A mastoid process is at best rather poorly developed in orang-utans and totally lacking in all Hylobatidae and lower catarrhines. In man the mastoid processes appear comparatively early in postnatal life and grow to considerable size in all normal cases. In the African apes these structures have not been found before the late juvenile stage of growth and they do not reach their maximum size until advanced age and then only in some, but not all, cases.

Variability

An extremely high degree of variability has been claimed as a distinction of modern man, by some as an expected consequence of man's highly diversified environments, by others as the result of man's supposedly unique tendency for race formation and unlimited racial hybridization. Our present knowledge of the anthropoid apes is not in agreement with these preconceived conclusions of students, far more familiar with man than with the apes. Here it can merely be mentioned that in many respects, such as the numbers of vertebrae, the formation of the sternum and other skeletal characters, the anthropoids are vastly more variable intraspecifically than is man, including all of his races, and that such features, as body proportions or dermatoglyphics, are no less variable in apes than in man. The skin color of chimpanzees varies from black to white and this, in contrast to man, inclusive of palms and soles. Hair color in some gibbon species is amazingly variable, in others it is constant. The writer has the body of a young chimpanzee, born of black-haired parents, which had straw-colored hair at birth and later this color changed to a reddish tint. Many different races have been proposed for Bornean orang-utans on the basis of their widely differing skull shapes (see Plate I). Giants and pygmies have developed among chimpanzees and orang-utans and long-armed and short-armed varieties among gorillas. This is all the more remarkable, if it is considered that, of at least the great apes, each has a very limited distribution, in contrast to man, yet each has produced several species or subspecies which are morphologically, but not geographically, as different from each other as the main races of man. That all the distinct forms within an anthropoid genus *can* readily hybridize has been proved for gibbon, orang-utan and chimpanzee. Finally, it is mentioned here that modern man with his supposed "self-domestication" and restricted natural selection has not become unique in regard to the frequency of congenital malformations. Evidence of abnormal development can be at least as prevalent in wild ape populations as in civilized human groups.

Discussion

This condensed review of some of the similarities and dissimilarities between man and other catarrhines considers features of a more or less qualitative as well as those of a clearly quantitative nature. It has been maintained that qualitative specific characters support convincingly the assumption of a long independent evolution of the given species and that mere quantitative distinctions can be acquired so rapidly that they indicate a very recent phylogenetic separation of their owners. The writer questions the value of this generalization, having found that, at least in the case of man and the anthropoids, most of the characters, commonly regarded as "qualitative" ones, become quantitative ones, if fully analyzed. Many of the features, listed among the qualitative distinctions of man, actually are specific only in the frequency of their occurrence or in the degree of their specialization at a given stage of growth, including their relative size.

For instance, all catarrhines, except man, possess a penis bone and this fact, taken by itself, has been regarded as a highly significant, qualitative human distinction. To the writer this appears as a quantitative character in the light of comparative data of which only a few need here be mentioned: The length of the penis bone in adults measures in a primitive prosimian (*Nycticebus borneanus*) 16 mm., in a macaque 11 mm. and in a gorilla 12 mm., but the first weighs only 0.7 kg., the second 7.2 kg. and the third 142 kg. The total loss of the penis bone in man represents the extreme degree in the evolutionary reduction of this structure, which has clearly degenerated also in the gorilla in comparison with lower primates, if general body size is duly considered.

A free central wrist bone exists normally in adults of all catarrhines, except in the African apes and man. This, however, is not a radical, qualitative distinction of the latter, but merely a quantitative, ontogenetic difference. The os centrale of the wrist develops in man and the African apes, just as in all other catarrhines, early in embryonic life. In man it fuses with the navicular soon after its appearance and in the African apes not until near birth or even later. In the Asiatic apes an identical fusion takes place occasionally, but only among old animals, and such fusion has been observed even among a few old monkeys.

Man among all primates gives birth to the by far largest newborn, yet the human newborn attains the least degree of maturation. This purely quantitative, yet very important distinction may have appeared early in human evolution, or may represent a very recent innovation.

In attempting to determine man's place among the catarrhines on the basis of his specializations we should not only consider all of the latter, but try to evaluate them regarding their antiquity. The ease and speed with which the skeleton and dentition of man has changed will ultimately become determined by the fossil record. In the meantime and for problems impossible to solve palaeontologically, we can not infrequently gain an indication of the relative age of a phylogenetic innovation through the degree of variability in the changed structures. For instance, the number of segments in the caudal portion of the spine is extremely variable in higher primates, in which these parts have undergone comparatively recent and very profound changes. On the other hand, the number of cervical vertebrae, which has remained phylogenetically unchanged in all primates, varies only in extremely rare cases, even in the generally variable higher primates. Similarly, certain phalanges of the changing first toe of orang-utan and fifth toe of man are highly variable in contrast to the practical absence of noteworthy variations in the conservative digits of most other simian primates. Many additional examples could be quoted as illustrations of the general experience that the more recently a condition seems to have become changed the more unstable or variable it remains. It does not necessarily follow, however, that the less variable a peculiarity of a given primate species, the greater is its antiquity as an independently acquired and well established character. To this rule a good many exceptions have been found.

Conclusions

This paper has referred to only part of the numerous major and minor human specializations. The examples mentioned here suffice, however, to demonstrate that probably most of the distinctions of man represent no more than specific degrees of perfection along evolutionary trends which are common to all higher primates. A great many changes have progressed farther in man than in any of the anthropoids, but other characters have clearly remained more conservative in man than in the apes. In comparatively few respects can it be said confidently that man has diverged from all other catarrhines along really new evolutionary paths of his own, at least without leaving such specializations in a variable and unsettled state, so that man's range of individual variations has not yet become entirely separate from corresponding ranges in other primates.

In regard to the prolongation of the main periods of life, the enlargement of the brain, the erect position of the trunk with its correlated, manifold, structural adaptations, the reduction in hair density, etc. man has reached much greater extremes than have the apes, but the latter have undoubtedly shared the trends toward the same kinds of specializations. In respect to the reduction in the number of spinal segments, the widening of the chest, the lengthening of the upper limbs, certain detailed cranial features, etc. man and the apes show identical evolutionary tendencies, but in these specializations man has progressed less far than some, or even all, of the anthropoids. It is against experience and reason to assume that all these many and highly significant, common trends had evolved independently in man and the anthropoids.

Some of adult man's peculiarities can be understood as results of ontogenetic retardations, or "fetalizations," the most noteworthy examples being the unique relations between head and spine, the position of face and orbit relative to the brain case, the lack of rotation in the great toe, certain characters of hair distribution, and the late appearance of skin color. Other human distinctions, however, are due to ontogenetic accelerations or intensifications, such as the very early disappearance of a free os centrale, the comparatively early fusion of sternebrae, the great length of the lower limbs, the long continued growth of the brain, and the relatively early replacement of the first by the second dentition.

Considering all these diverse conditions, together with the mass of fundamental similarities in the higher primates, only one conclusion seems to be admissible today regarding man's place among the catarrhines. Taxonomically speaking, the place of modern man lies still alongside of the recent anthropoid apes. Phylogenetically speaking, all forms of man, past and present, and the entire profusion of fossil and surviving anthropoids must have had one common origin, most likely somewhere among early Cercopithecinae. This single ancestral stock started all higher primates with the same general endowment, unburdened by any one-sided specializations, and leaving them free to follow diverging evolutionary roads. The progenitors of gibbons and orang-utans, formerly ranging over a wider territory than today, took to the trees and perfected brachiation. Man, somehow, must have become "grounded" and bipedal nearly, or fully, as early and as rapidly as his Asiatic cousins had taken their fatal step. The African apes remained in some respects comparatively conservative by hesitating and compromising between arboreal and terrestrial adaptations, substituting strength, speed or bulk for the acrobatic perfections in the small and quick gibbons and the large and slow orang-utans, and by preferring their accustomed forest life and food to the adventurous environmental and dietary changes of their prehuman relations. In other words, on the catarrhine family tree man branched off in one direction somewhere very near where the Hylobatidae branched off in an opposite direction and this before the orang-utans had become committed to their specialized course and, certainly, long before the recent African apes had emerged as distinct forms. From this towering, fruitful stem of the primate family tree there must have sprouted continuously many more twigs, now dead, of which some may well have grown parallel to, or even from the branch for man. Such a former twig, quite likely, had produced the extinct Australopithecines.

The first and decisive specialization of man—erect, bipedal locomotion—would never have been possible, had it not been prepared for by his remote progenitor, who had endowed the apes as well with at least the potentiality of the erect position. This preparedness appears in all higher primates during growth and in varying degrees in form of the forward shift of the spine toward the center of the chest, the backward shift of the shoulders, the bending of the spine at its juncture with the hip bones, and other initial, anatomical and mechanical requirements for holding the trunk erect. It seems not at all unlikely that some of these preparations for the upright posture had become more pronounced in a few fossil anthropoids than in any of the surviving forms of apes.

After having discussed especially the first major human specialization, one should mention what must be recognized as the most recent and, perhaps, most fateful step in the evolution of mankind, namely our unique population growth. The shortest possible interval between successive generations, determined by the gestation period and the age of beginning female fertility, has increased with advance in primate evolution to an outstanding extreme in man. In spite of this, however, man has managed to multiply with unexpected rapidity and to spread over the entire globe. The total population of our species probably exceeds today the sum of the populations of the several hundred recent species of non-human primates. This represents an evolutionary specialization so recent that it has not yet become fully appreciated in regard to its far-reaching consequences and the inevitable risks inherent in all profound and precipitate phylogenetic changes.

Population growth in monkeys and apes has been held in check not so much by large predators and famine, as by disease. Especially parasitic diseases are shockingly prevalent among wild primates and, undoubtedly, had been also in prehistoric man. It is particularly with advance in medical knowledge and the consequent reduction in infant mortality that civilized man began to multiply at a previously unheard of rate and with results to which our typically simian bellicosity, possessiveness and other behavioristic qualities have not yet become phylogenetically adjusted.

Having discussed man's past evolution, with its many great bodily changes, these closing notes refer to man's present and future evolution, which will be less dependent on physical than on psychic perfections. The investigation of the past of mankind is largely the domain of the physical anthropologist; our future evolution represents chiefly a problem for the social anthropologist.

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DISCUSSION

DOBZHANSKY: The finding by Professor Schultz of a great variability in some species of anthropoids is very important. It shows how little basis there is for the often repeated statements that the genetic variability found in man is something abnormal, due to alleged absence of natural selection under civilized conditions, or to some rather mystical influence of so-called "domestication." In view of the importance of the phenomenon, one would like Professor Schultz to give a more detailed statement, especially whether the variability which he finds is intra-populational (polymorphism) as well as inter-populational (racial)? It is realized that some traits are more and others less variable in different species and populations. What we are interested in is Professor Schultz's judgment about the general, or average, variability of anthropoid species compared to man.

SCHULTZ: Professor Dobzhansky's questions I can answer best by means of some facts relating to chimpanzees, for which I have been collecting new data in the last few years. Chimpanzees have a practically continuous distribution from Sierra Leone along the West coast of Africa down to the Congo river and far East through the Equatorial forest, including an area South of the Congo. At least four subspecies inhabit different parts of this area. They can be distinguished more or less clearly and regularly on the basis of skin color, hair distribution, some skeletal details, etc. The great majority of the bodily characters of chimpanzees show nearly identical ranges of variations in all parts inhabited by these apes and regional differences have been found at best in regard to the relative frequency of certain variations. For instance, among the so-called pygmy chimpanzees from the left bank of the Congo there are many unusually small apes, but I have the body of one adult chimpanzee from Liberia which is as small as any of the "pygmies" I have been able to examine. Body weight can vary to a surprising degree among chimpanzees from most regions. In 25 adult females for which I have accurate records the minimum body weight is 21 kg. and the maximum 55 kg. That chimpanzees can vary more than human beings in regard to numerous features may be shown here by the following examples, taken at random from my records: The interorbital breadth, expressed in percentage of the breadth of the brain case, varies among 75 adult chimpanzees between 10.1 and 29.7, but in 75 adult human skulls in my laboratory (including Whites, Negroes, Indians, Eskimos, Chinese, and Australians) the same proportion varies only between 15.8 and 23.9. In 150 chimpanzee skeletons I found four lumbar vertebrae in 53 per cent of the cases and deviations from that modal number in the remaining 43 per cent. Human skeletons, on the other hand, contain five lumbar vertebrae in at least 90 per cent of the cases and at most only 10 per cent vary in this respect.

The variability of the other anthropoids is at least as pronounced as that of chimpanzees and is certainly no less marked than in man. For instance, the means of the variation coefficients for the most significant measurements and proportions of the limb bones of adults average 4.11 ± 0.28 in a total of 336 great apes and 3.96 ± 0.22 in a total of 744 human beings (Whites, Negroes,

Indians, Eskimos and Chinese), all of which I had measured with precisely the same methods (Schultz, 1937, Human Biol. 9: 281–328). In gibbons there exists a considerable number of different species and local races and the three genera of great apes contain from two to four subspecies each. All anthropoids, therefore, do show a considerable inter-populational variability. It is the intra-populational variability of the anthropoids, however, which appears so impressively great to all students with access to large series of these primates.

HUNT: I feel that the high variability in certain anatomical structures in both the giant anthropoids and man has great theoretical importance.

In the past, physical anthropologists have often studied modern anthropometric series through arbitrary morphological typing, assuming that each type is a survival of an ancestral type in a living mixed population. If such a type ever existed in an ancestral population, we must assume that ancestral human groups were less variable than living groups. I am not convinced that this conclusion is valid.

The evidence presented by Professor Schultz indicates that a breeding population of living higher primates is inconstant in many features. The same conclusion might be reached from fossil groups such as Sinanthropus and Mount Carmel. I feel that human evolution can better be regarded as genetic gains and losses than as an emergence of heterogeneous groups through the hybridization of homogeneous groups. A reassessment of the literature on present-day race mixture in these terms might reveal that most "hominoid" groups are and have long been heterozygous in many genes controlling physical proportions and size, and that even drastic mixtures of the living human races may not affect this condition in the resultant hybrid populations.

MONTAGU: It should, perhaps, be pointed out that most students who have referred to the great variability of man as compared with other animals have had external characters in mind, rather than such characters as the skeletal system, to which Dr. Schultz has referred. In this connection I should like to ask Dr. Schultz whether there is any other non-human primate species in which the variability is as great as it is in man in such characters, for example, as hair form, hair color, stature, eye color and the like? (Editor: See answer to question of Dobzhansky and Amer. J. Phys. Anthropol., N. S., 5: 1–14.)

STERN: In discussing various degrees of variability it is important to be aware of perhaps equal, perhaps different potential variability (types of genetic changes) and actual established variability. Mouse geneticists possess in their strains widest variability, but in nature mice do not realize most of this genetic potentiality. Is there a relaxation of natural selection in variable species?

SCHULTZ: I feel that this question could be answered only by a geneticist, together with, perhaps, some pathologist, since disease is the most potent selective factor in anthropoids.

SOME PRINCIPLES OF HISTORICAL BIOLOGY BEARING ON HUMAN ORIGINS

GEORGE GAYLORD SIMPSON

The American Museum of Natural History and Columbia University, New York

INTRODUCTION

The study of human origins is an attempt to determine a historical sequence of events from inadequate data. It is evident to all that the data are inadequate at present. It is highly probable that they will always be inadequate, because they must remain ambiguous in the sense that they will be consistent with more than one possible interpretation.

There are two sets of data: one derived from existing men and other animals and one derived from paleontological and archeological remains. Knowledge of what now exists is already extensive and may presumably be made essentially complete, but it will remain ambiguous for this particular problem. The problem is historical, and these data are not directly historical. They give only the results of historical processes at one particular time, and I see no way of determining from these results that they can have arisen, in all details, in one and only one possible way.

The paleontological and archeological data are directly historical and they supply the absolutely essential time element for these studies. If these data were essentially complete, they would provide unambiguous, unique solutions for some of the problems involved, such as the prime question of the phylogenetic lineations of men and other primates. The data are highly incomplete at present, but we are not willing to wait: we want provisional or alternative answers, at least, right now. Probably the data can never be complete because most of them are already irrevocably destroyed. It is most unlikely that samples of all the extinct races of man and other primates now exist as undiscovered fossils. Even complete data of this sort would not yield unambiguous answers to all questions, because such remains reveal little or nothing regarding some physiological, psychological and social factors that are, nevertheless, crucial to a full understanding of human origins.

Our task, then, is to take inadequate data, to reject interpretations that definitely do not fit these data, and then to judge the probability of the usually still multiple possible interpretations that remain. The most important aid toward such judgment is whatever knowledge we can attain of historical biological processes in general. Little knowledge of this sort has been derived from the study of man. This subject is recalcitrant both to observation and to experiment, and in many ways we know ourselves less well than we know flies or mice. There is hope for a repayment on the debt, but at present anthropology is more a consumer than a producer of historical biological principles. There may at times even be a certain reluctance or ineptness in this consumption.

My role in the present symposium is not to propose or to discuss any particular ideas as to the origin of the human stock, but to summarize some principles, derived from quite different sources, which may aid in forming and judging ideas in this field. Attention is called to the fact that my colleague, E. H. Colbert (1949), has already skillfully played a similar role in a previous symposium. Obviously I must mention some topics that he has already well treated, but I shall try to reduce repetition to a minimum. Attention may also be called to a more extended work (Simpson, 1949) in which some principles pertinent here are also discussed.

TIME AND SEQUENCE

Perhaps the most truly basic of all historical principles is that no one can be ancestral to his grandfather. This is unique among biological rules in that it really is a law, admitting no exceptions whatever. In vernacular form, the principle seems downright simple-minded, but really firm belief in all its implications would have forestalled much discussion and some blunders, in anthropology as well as in other fields.

Applied to the interpretation of contemporaneous data, the law means flatly that these are not historical in nature. *Tarsius* may or may not be more or less closely related to man—the point does not concern me here—but in any case *Tarsius* is not ancestral to anything. Not one of its structures can be taken as historically antecedent to any structure of any animal. We may, it is true, use

Tarsius as indirect evidence of some condition in an ancestor, but that is a different matter. Everyone will readily admit that *Tarsius* is not an ancestor, but this and analogous cases in the literature show how often such forms are treated and discussed as if they were ancestral.

Studies of brain evolution, simply to take one example, show how prevalent is this confusion and how often the obvious principle is violated. "With very rare exceptions, there is in the neoneurological literature no allusion to the fact that the evolutionary stages from living shark to living man do not illustrate a historical process." The quotation is from the only study ever made up to now of directly historical evolution of a brain over any considerable period of time: Edinger (1948) on the horse brain. This study shows that concepts of brain evolution in horses, indeed in ungulates as a whole or mammals in general, have been radically wrong in some respects as based on the comparative anatomy of living forms.

The usefulness of the comparative anatomical method is not impugned, but it is stressed that this usefulness is decreased when the true, non-historical nature of the method is overlooked and when its limitations are insufficiently understood. Edinger concludes that "the major trends of progressive mammalian brain evolution have been correctly derived from comparisons of extant brains.... Our material shows, however, that in actual, phylogenetic brain evolution there were phases different from the stages of brain evolution existing in living mammals.... The nature of our material suggests that its differences from the evolutionary levels of extant brains are due to a factor not recognizable in the living world; brain evolution seems to have depended on time."

The fortunate fact that some structures of some organisms have changed less than homologous structures of other organisms does make possible a structural seriation of contemporaneous forms. This non-historical seriation may approximate, although it can never equal, a historical sequence. There are many cases in which living forms, no matter how primitive, have characters wholly lacking in early historical stages and many others in which early historical stages have characters absent in all living forms. Moreover, since the comparative anatomical seriation has no time element, the direction of a more or less equivalent sequence in time is sometimes mistaken.

The true time sequence may begin at either end of the non-temporal seriation, or may even begin in the middle of the latter and work both ways. In fishes, there is a recent seriation from forms with no bone to forms with extensive bone. Comparative anatomists formerly unanimously agreed that this corresponded with a historical sequence in the stated direction, but directly historical studies (e.g. Romer, 1942) now indicate that the real time sequence was in the other direction. In some recent mammalian upper molars, there is a seriation from forms with a single, internal main cusp (amphicone or parametacone) through forms with a single or double homologous median cusp to those with two external cusps. There was considerable argument as to which end of this non-temporal seriation is 'earlier.' It now appears (e.g. Simpson, 1936) that an *intermediate* member of this series is historically the oldest condition and that both ends of the series were developed later.

Merely in passing, mention may also be made of the tremendous literature of biogeography, a large part of which consists of attempted historical interpretations of essentially non-historical data, i.e. the distribution of plants and animals at a single instant in time. Much of this laborious effort seems to me valueless or nearly so, simply because some workers have not fully appreciated the fact that their information has no time dimension and that it cannot be interpreted historically in its own terms but only by additional data and principles that are really historical in nature.

Even when paleontological, which is to say directly and inherently historical, data are used, there are frequent failures to appreciate the fact that ancestor and descendant *must* occur historically in that sequence. The late Franz Weidenreich (e.g. 1946) spoke of the "morphological age" of fossil hominoid remains and considered this as crucial in their historical arrangement, rather than the chronological age, even when the "morphological age" conflicted with the chronological age. The mental confusion implicit in such a term as "morphological age" reflects the fact that this truly great anatomist was not a paleontologist, but there are some examples of the same fallacy in work by generally competent paleontologists.

It is, of course, entirely possible to make a comparative anatomical study of fossil remains without regard for their age and to derive useful information therefrom, but historical inference by this method runs all the dangers already stressed for attempted historical interpretation of non-historical data. The dangers are, indeed, greatly intensified in such a case, because a historical element is factually present in the data and yet is

ignored in their interpretation. Part of the intense current discussion of the relationships of the Australopithecinae seems to a paleontologist rather sterile because it lacks the most essential historical datum, the age of these forms relative to other known fossil hominoids. If, for instance, the known Australopithecinae prove to be mid-Pleistocene in age and if some true hominids are correctly dated as this old or older, then dispute as to whether these Australopithecines are ancestral to man will become nonsensical. If, on the other hand, the known Australopithecines prove to be older than any true hominids, this of course will not establish their ancestral relationship, but it will show that the relationship is possible and will be valid supporting evidence.

The Principle of Morphological Correlation

The principle of morphological correlation or association is one of the most useful to the paleontologist and at the same time a source of annoyance. As a working principle, it belongs at a basic level of research where its application is in dealing with imperfections of the materials, (a) in associating parts found separately and (b) in restoring missing parts. Its pertinence to anthropology is obvious in such cases as (a) association of skull and jaw of Piltdown man or of skulls and skeletal elements of the Australopithecinae, or (b) restorations of skulls, jaws or skeletons of fossil men and their relatives, virtually none of which are complete. In passing, I may say that a prudent paleontologist is sometimes appalled at the extent of restoration indulged in by the anthropologists, some of whom seem quite willing to reconstruct a face from a partial cranium, a whole skull from a piece of the lower jaw, and so on. Of course this temerity is induced by the great popular interest of the subject and the fact that fragments do not impress the public. Then, too, the worst examples are in popular publications and are not likely to mislead the professionals, but still . . . !

The basic principle here involved was first clearly stated by Cuvier; it is "Cuvier's Law," if you like. Here is his own statement of it: "Every organism forms a whole, a single and closed system, all the parts of which are in mutual correspondence and collaborated by reciprocal reaction in the same final action. None of these parts can change without the others changing also, and consequently each of them, taken separately, indicates and gives all the others." (Somewhat freely translated from the first edition of the first great work on vertebrate paleontology. "Recherches sur les Ossemens Fossiles de Quadrupèdes," 1812.)

The last clause is the operative statement, one of the most fundamental principles of paleontology and also a source of misunderstanding and trouble. What it meant basically to Cuvier and what it still means to us today is simply that you can *identify* whole animals from parts of them. Given a jaw fragment of an unknown animal you can, with care and good fortune, determine that it belongs, for example, to a new genus and place it in a previously defined family. Unfortunately Cuvier, as a pioneer, could not see all the limitations of the method. He thought that given an ungulate-like tooth he could infallibly predict that it would be associated with a particular sort of hoofed foot, even though the feet had not yet been found. From this arose the belief (I am not quite sure to what extent Cuvier, himself, shared it) that Cuvier could restore a whole animal from one fragment of bone. That belief has become folklore. This marvelous ability is still almost universally ascribed to paleontologists, to their high distress. Even those who do not know what the word "paleontology" means *know* that "science" can perform this wholly impossible trick.

There is a classic case that finally put an end to confidence in their ability to extrapolate from fragments, as far as the paleontologists themselves were concerned. The case should be drummed into every student who ever deals with fossils and it is worth summarizing here, even though it is one of the well known esoterica within the profession.

In a later edition (the third, 1825) of the same work quoted above, Cuvier described a large fossil claw and concluded that "according to all the laws of coexistence [or, correlation] it is impossible to doubt that the closest relationships of the animal that carried it were with this genus of quadrupeds," i.e. with the pangolin or scaly anteater, *Manis*. Lartet soon named this creature *Macrotherium*. During the next sixty years many more specimens were found and the skeleton became tolerably well known, except for the skull. Almost all the paleontological worthies of the time discussed it, and all agreed that it was a giant pangolin or, at least, an edentate of some sort.

In the meantime one of Cuvier's eminent contemporaries, J. J. Kaup, had (in 1833) given the name *Chalicotherium* to fossil teeth identified as belonging to a pachyderm, in the terminology of

that day, and allied to *Lophiodon* and the rhinoceroses, which would make it a perissodactyl in modern terms. Abundant remains of this animal were also found in the following years and its dentition, jaws and skull became rather well known. All students agreed with Kaup that it was an ungulate of some sort, probably near groups we now place in the Perissodactyla, although the exact affinities were subject to some dispute. Edentates and ungulates are so distinct that no relationship between *Macrotherium* and *Chalicotherium* was indicated.

Although one happened to be extraordinarily wrong and one approximately right, the identifications of *Macrotherium* as an edentate and of *Chalicotherium* as an ungulate were methodologically justified as *identifications*. The principle that kept the two genera apart (edentate-like claws *cannot* belong with ungulate-like teeth because that violates "Cuvier's Law") and the envisioning of *Macrotherium* in restoration as a giant anteater were ludicrously wrong.

It was not until 1887 that anyone really began to wonder. *Macrotherium*, common skeletal remains without a head. *Chalicotherium*, common jaw and cranial remains without a body. The two frequently mingled in the same deposits. Filhol had suspicions in 1887, found head and body associated in 1888, and in 1890 published the news to his colleagues, who have been properly chastened ever since and who ever since have known that they cannot safely restore a whole animal from one bone unless they already have a complete skeleton of the same animal.

The example demonstrates in a spectacular way that the different parts of a given animal do not necessarily evolve with the same correlation as in any other animals. The same parts may evolve in different directions in different related lines, and different parts may evolve at different rates within the same line. There is thus no reason in principle why the brain may not in some cases have reached a *Homo*-like status before the lower jaw or why some primates may not have retained an ape-like brain after *Homo*-like posture was attained. Nevertheless Cuvier's principle is certainly entirely correct to this extent: every individual organism must be an integrated unit and all its parts must be workably correlated. Failure in application of the principle arises from the fact that workable correlations may be highly diverse and that correlation in one group may be quite different from that in a related group used as a model.

Association must also be judged by criteria other than those of Cuvier, especially by distribution, temporal, geographical and ecological. Beyond this, the fundamental anatomical and taxonomic criteria might be restated as a working principle more or less as follows: association of parts and restoration of missing parts are likely to approach correctness in direct proportion to nearness of established relationship to a form used as a model in which all the parts in question are known, or are likely to be incorrect in proportion to distance of affinity from such a form. And look out for surprises if there is so much as specific difference from the model! The restated principle makes the paleontologists' and anthropologists' work more difficult than Cuvier expected, but much safer.

Species, Lineages and Parallelism

The whole pattern of evolution consists of a fine mesh of genetically definable populations and a broader series of lineages, or of phyla in the sense of such lineages. The physical representation of a lineage at any given time may consist of a single, essentially panmictic population, but more often it consists of a number of such populations, each local in distribution, between which there is marginal or occasional genetic interchange. In the latter, usual case, the fine structure of the lineage or phylum as it extends through the time dimension is like a bundle of imperfectly separated or anastomosing fibers. Two or more separate phyla appear when definitive separation of populations, of fibers in the bundle, occurs and marginal genetic connection or occasional anastomosis ceases.

The crucial nature of this process has always been recognized in evolutionary studies. Most modern students (e.g. Dobzhansky, 1941; Mayr, 1942) equate the bundle with a species in taxonomy. Its separation into two or more phyla is the process of speciation and these separated groups become each a distinct species in its own right. It is, to be sure, impossible to define the word "species" in any way both theoretically acceptable and practically applicable to all cases without ambiguity. There have been endless discussions of this, "the species problem," and yet there is quite general agreement as to the essential nature of the unit intended when the word "species" is used. Both the diversity of approach and practice and the unity of essential concepts were well illustrated, for instance, in a symposium by two taxonomically specialized zoological societies a few years ago (Bogert *et al.*, 1943).

It has not been so generally recognized that this basic concept of a species is ambiguous and unusable, even in theory, unless a time element is implicitly involved. The concept is applicable only *a posteriori* or else as a prediction. Absence of actual interbreeding between two populations is not, even in theory, a sufficient criterion that they are distinct species unless there is evidence that this does in fact make them separate phyla with different evolutionary destinies or potentialities. To grant them specific status we should know that they did evolve separately without further sharing of their evolutionary stock, or we should feel able to predict that they will do so in the future. It is for its predictive value that the criterion of intersterility has often and properly been stressed for recognition of species. All biologists know that species, distinct and valid by genetic as well as by all other usual modern definitions, may still be richly interfertile. Such species *can* merge and lose their identities, although their postulated validity shows that they have not done so and are unlikely to. But when species are intersterile, as most are, then they cannot merge. They are irrevocably different lineages and their separate specific status depends on a prediction which is completely reliable (barring only the extremely slight possibility of genetic reversal of sterility, which has never been demonstrated, to my knowledge).

In the study of the origin of man, the existing races of man, and similar problems, it is certainly of great significance where the various groups, racial, tribal, etc., are placed in this evolutionary schema. As far as the words "species," "subspecies," "race," etc., are used merely as labels, they may not particularly matter, but it does decidedly matter whether a given group is only one strand in a broader genetic complex or is a phylum evolving independently from all others. To virtually all modern biologists, the word "species" has the latter meaning and the student of human evolution will not be clearly understood by other evolutionists unless he uses the word in this sense.

I also particularly want to stress the fact that discussion of human population groups has emotional and social significance to humans and that in dealing with this topic the scientist is responsible for the affective as well as for the technical significance of his terminology.

Once two or more separate lineages have arisen, they may continue to evolve in approximately the same way or they may soon exhibit markedly different evolutionary trends. Obviously there is no definite dividing point between the former course, which is parallelism, and the latter, divergence. It seems to be very rare for two lineages really to follow the same evolutionary course, indeed this may never occur in all detail, and some degree of divergence accompanies the closest parallelism. On the other hand, total divergence is almost equally unlikely and two lineages, especially while near their common origin, usually exhibit considerable parallelism even if divergence is their most striking or most important tendency.

The fundamental objective definition of parallelism is a geometric analogy; evolving lineages are considered parallel in a figurative sense just as two lines may be parallel in a literal sense. Nevertheless, almost all the diverse usages of the word "parallelism," usages extensively reviewed by Haas and Simpson (1946), involve the idea that the parallel lineages are rather closely related. It is a contradiction in terms to maintain, as some students of human evolution have done, that two groups are parallel but without special relationship, or that related lineages separately parallel others without being severally related to the latter. Such relationship is biologically inherent in the geometric figure of speech. The basis of parallelism is initial similarity of structure and adaptive type, with subsequent recurrent homologous mutation, and similar direction of natural selection. The initial similarity and the homology of mutations imply phylogenetic relationship. In fact, the existence of parallelism is in itself valid although not conclusive evidence of relationship, and closeness of parallelism tends to be proportional to closeness of affinity.

In the usual and fairly clear-cut sense, parallelism occurs between lineages or distinct, genetically defined species or higher categories and not within lineages or species. It is also usual for the strands within lineages, or the subspecies of a species, to evolve rather closely in the same direction. The basis for this, however, includes not only the same factors that make for parallelism but also an actual interchange, whether continual or spasmodic, of genetic materials. The existence of this additional factor is crucial in any comprehension of the evolutionary process, and it is necessary to distinguish such cases strongly from cases of true parallelism in the accepted sense of the term.

It is also essential to distinguish parallelism, similar changes in over-all adaptive type among related lineages, from the development of similar single characters in diverse groups. The phe-

nomena may well intergrade but are typically different. For instance, both Foraminifera and Mammalia commonly exhibit a trend toward increase in size. This is an interesting and important evolutionary phenomenon, but to speak of this trend as parallelism seems to me a misuse of terminology, and as interpretation it is more likely to obscure than to elucidate the phenomenon. As another example, dogs and horses both develop certain similar types of spotting, a fact highly interesting both for genetics and for broader evolutionary studies, but the rise of this particular character in both does not make these two radically divergent lineages parallel in any useful or usual sense of the word.

The widespread occurrence of parallelism in evolution is well known and has been stressed by almost all students, especially paleontologists. Numerous examples have been given, for instance in the previously cited study by Colbert (1949). A single striking example will suffice here. The Triassic mammal-like reptiles were split into numerous different phyla, almost all of which had similar adaptive trends toward becoming more mammal-like in posture and limb structure, in palate and respiration, in tooth differentiation, in jaw and ear, and in numerous other respects. For purposes of structural definition, it is customary to draw a purely arbitrary line between "reptile" and "mammal" on the basis of jaw articulation and middle ear ossicles. Probably four different lineages and possibly one or two more crossed this arbitrary line and thus separately became "mammals" by this definition. All the characteristics of classical parallelism are present. The phenomenon relates to separate lineages and to over-all changes in adaptive type, not only to single and isolated characteristics. The affected lineages were rather closely allied and all had a common origin not long antecedent geologically. (See, e.g., Olson, 1944.)

By definition, parallelism does not considerably *increase* the resemblance between different lineages. It therefore is unlikely to lead to false conclusions as to the presence or absence of special relationship between two groups of animals. It may, however, be extremely misleading as to the degree of such relationship, or the relative time of origin of groups from a common ancestry. The actually observed difference between two groups may be the same if they departed from a common ancestor long ago and have since been dominantly parallel or if their separation was relatively recent and their subsequent evolution dominantly divergent.

Many of the disputed questions of phylogeny and classification hinge on this point. It was long assumed that New World and Old World porcupines represent relatively late divergence from a common ancestor, unifying a Suborder Hystricomorpha, but recent studies strongly suggest parallel development from remote ancestry in a different suborder (Wood, 1949). Earlier students (e.g. Sinclair, 1906) concluded that the predacious marsupials of Australia and South America diverged within a rather specialized family or subfamily, but later evidence (Simpson, 1948) supports parallel development from primitive and very ancient forms. The monotremes may represent divergence from marsupial ancestors (Gregory, 1947) or parallel evolution from therapsid reptiles (Simpson, 1929; Olson, 1944). Anthropologists do not need to be reminded of disputes as to the extent of parallelism between man and apes.

The misleading element in parallelism is that it produces resemblances that did not occur in the common ancestry, that are homoplastic rather than homologous. (This use of words is subject to hearty disagreement, but I propose to continue it and cannot discuss the matter here.) The corrective is determination of the origin of the characters in question. The only conclusive evidence is paleontological, although the comparative anatomy of contemporaneous forms may indicate a solution. For instance, in the case of the porcupines comparative anatomical evidence suggests that their common ancestor had no quills and had simple and low-crowned teeth, although it leaves open the question as to whether peculiarities of the jaw muscles are homologous or analogous.

There is evidently another geometric possibility as to the direction of evolution of different lineages: they may also become more similar. This phenomenon of convergence is also very widespread in evolution and can be richly illustrated in the paleontological record. Parallelism and convergence intergrade, so that in some cases the designation as one or the other is necessarily somewhat arbitrary, and also one can be mistaken for the other. Some students, including students of human origins, have failed to distinguish them or have considered them as virtually identical. (On the history and varying usages of the term "convergence," also, see Haas and Simpson, 1946.) They are, nevertheless, quite distinct phenomena when typically developed, and the distinction is essential for the correct interpretation of phylogeny. Parallelism is the similar evolutionary modification of similar lineages. Convergence is the similar modification of dissimilar lineages.

Convergence may take place between closely as well as between distantly related lineages. The extent of the convergence, as such, is inverse to the relationship involved. Profound convergence implies profound initial dissimilarity, therefore distant affinities. The resulting degree of similarity, however, still reflects degree of relationship. If closely related and therefore only slightly dissimilar lineages converge, the slight accretion of convergent resemblance plus the initial similarity involves closer total resemblance than commonly results from longer convergence of initially more dissimilar groups. In all cases, convergence involves preceding divergence. The initial dissimilarity had necessarily arisen by divergence.

Parallelism is commonly adaptive in nature, although it does not seem always to be so, especially in lineages of particularly close relationship or with particularly small early divergence. It is probable that convergence is always adaptive. It is caused by adaptation of different groups to the same or similar ecological niches.

Convergence is more misleading than parallelism because it increases resemblance between lineages and may therefore suggest relationships where none exist. The old native faunas of South America include a host of striking convergences toward North American and Old World groups and almost all these were mistaken by the leading early student Ameghino for phylogenetic relationships (discussion and references in Simpson, 1948).

Fortunately convergence is generally easier to recognize than parallelism. Its process is fully adaptive and the resemblances developed by it are all functional. It involves strictly homologous mutation to less degree than does parallelism. It therefore does not wholly obliterate earlier differences between the groups involved, and even its functional resemblances may be achieved in structurally different ways. Some South American ungulates (notohippids) convergently developed grazing teeth functionally almost identical with those of grazing horses. The exact pattern of enamel folding has, however, little or no functional significance so long as an optimum length of enamel cresting is present, and this pattern is so different in notohippids and horses that the two groups can be distinguished at a glance. Knowledge of their quite different ancestry is hardly necessary to warn the modern student that this is convergence, not parallelism or phylogenetic continuity, although of course some confusion was inevitable before the principle of convergence was well understood.

It is improbable that convergence ever produces literal identity in structure and certainly no such case has ever been demonstrated. It may nevertheless still cause errors in phylogenetic inferences, but in careful modern work these are most likely in marginal cases of convergence between groups that are, in fact, rather closely related although perhaps less so than we think. In such cases, too, convergence grades into parallelism.

In over-all comparisons of any two groups of organisms, it is extremely unlikely that they will be in all respects parallel, convergent, or divergent. Results of all three processes are almost sure to appear concomitantly in any particular case.

Gigantism and Reversibility

The suggestion by Weidenreich (1946) that the earliest humans were giants has evoked considerable interest in gigantism or more generally in size trends in evolution. Again, it is not my present function to judge the facts of this particular case or to criticize Weidenreich's interpretation of them, but to summarize knowledge of pertinent evolutionary principles.

That there is a frequent tendency for the size of individuals to increase in the course of the evolution of a group has long been one of the most widely recognized phylogenetic generalizations, from Cope (1885) to Newell (1949). This is "Cope's Law" of Rensch (1947), although it is not a law in any strict sense and although at least one other quite different principle (the survival of the unspecialized) has equally been honored with Cope's name, and the "law" of size increase has also been called "Depéret's Law." Practically every important group of animals provides some examples, from Foraminifera to Mammalia.

So striking and widespread is this tendency that it has been used as a rule in phylogenetic interpretation. Paleontologists have often assumed that if an older species is larger than a later one, *ipso facto* the relationship is not ancestral. Application of such a rule to Weidenreich's thesis would force immediate rejection of his human phylogeny. In the light of more advanced knowledge, however, such rejection is by no means forced on these grounds, although of course this does not necessarily mean that his views are correct, either.

Such rigid applications of "Cope's Law" involve thinking that it really is a law, mistaking what usually happens, or indeed merely what often happens, for what must happen. They imply belief in the complete and rigid irreversibility of evolution (which is "Dollo's Law" and will be mentioned again) or in over-all orthogenesis, necessitating the continuance of a trend toward larger size whenever this somehow gets started.

Yet there are numerous well-established examples of lineages that have become smaller, not larger. The pigmy mammoths of the Channel Islands (see Stock, 1935) are certainly much smaller than their immediate ancestors. In the evolution of the horse it is true that some lines at some times have become larger, corresponding with the over-popularized conception of this history, but it is also true that at least three horse lineages (in *Archaeohippus*, *Nannippus*, and *Calippus*) became smaller (see Stirton, 1940). Indeed there is increasing evidence that "Cope's Law" was repealed some tens of thousands of years ago and that present day mammals are usually somewhat smaller than their immediate forebears in the Pleistocene (Colbert, 1949; Hooijer, 1947; Schultz and Frankforter, 1946; etc).

These facts are inconsistent with some ideas of evolution, but they are strongly consistent with a generally adaptive control of size trends. "Selection for increasing size probably is the result of the statistical advantage that slightly superior bulk gives the individuals of some, but not all groups of animals, within a wide range of environmental conditions" (Newell, 1949). It would then appear that slightly smaller bulk might have the advantage for some groups under other conditions, and that the opposite trend, toward smaller size, would then occur as it factually has in numerous cases.

Sometimes the environmental conditions favoring smaller size can be specified. Pigmy mammoths are insular and it is well established that insularity often makes size decrease adaptive. Size decrease since the Pleistocene is probably a chronological example of Bergmann's rule that related warm-blooded forms tend to be smaller in warmer and larger in colder climates, an adaptive consequence of the ratio of bulk to surface. In other cases, such as the pigmy horses, the adaptive significance is unknown as yet and may be more subtle, although there is no reason to doubt that the smaller size was adaptive.

It remains true that increase of size is more common in evolution than decrease and that decrease seems to occur only under special and rather unusual ecological circumstances.

Clearly the principle of the irreversibility of evolution is not universally applicable to such cases as size increase or decrease. The principle has often been evoked in studies of human origins and others under the impression that it excludes any reversal of trend or any reduction in specialization. Such application is certainly wrong. "Dollo's Law" (which was known before Dollo stated it and which resembles the other "laws" of evolution in not really being a law) was much too rigidly stated by Dollo and by others in his generation. Subsequent friendly criticism (e.g. Gregory, 1936) has often involved the hopeful suggestion that Dollo did not really mean what he flatly said. A truly great man, Dollo needs no apologies, but neither do we need to hold fast to his mistakes. No one in his day could quite realize the extent and nature of the many exceptions to his "law," which nevertheless has a broad and important general validity.

True genetic reversal in evolution is theoretically possible in at least two ways, by straight back-mutation or by relaxation of some modifier which has changed the phenotypic effects of an otherwise unchanged ancestral developmental mechanism (see Wright, 1934). Neither process is likely to have really profound effects or to cause complete reversion to anything but a closely similar immediate ancestral stage, because only in such conditions are the genomes so closely similar that a single or simple change could make their effects essentially the same. I am aware of no particular examples or of any evidence that such a reversal has indeed occurred. As a rule, the genetic make-ups of distinctly different ancestor and descendant must differ in so many factors that true genetic reversal is statistically improbable to the point of practical impossibility (see Muller, 1939). This is the genetical basis for the essential truth of the principle of irreversibility.

We have, nevertheless, already seen that reversal in trend or in general development of particular characters can very well occur. Enlightenment as to the limits of reversal and criteria for interpretation can be had by considering reversal in evolution as convergence. It is convergence toward an ancestor. Convergence cannot produce identity; neither can reversal, and for much the same reasons. Convergence is identifiable because it is entirely adaptive in nature, extends only to functional characters involved in the com-

munity of adaptive type, and does not wipe out morphological dissimilarities acquired through earlier differences in adaptive and genetic history; the same, *mutatis mutandis*, is true of reversal to an ancestral condition.

There is also a broader significance in irreversibility and one that gives it some restrictions additional to those involved in convergence. It is a *historical* principle. Evolution is irreversible because history is irreversible. In spite of what they say, history does not and cannot repeat itself. Its causes can never be twice the same because its causes are cumulative in time. Groups simultaneously convergent might conceivably be adapting to identical conditions, but a group reversing or converging toward a more or less remote ancestor cannot be adapting to the ancestral conditions because these are in the past and cannot exactly recur.

Orthogenesis, Trends and Transformation

Among the many conflicting definitions of orthogenesis, the most usual is that it designates a tendency for evolution to continue steadily in the same direction over indefinitely prolonged periods of time regardless of influences directly involved in the interaction of organism and environment. No explanation for orthogenesis in this sense has ever been suggested. It is not explanatory merely to name a supposed cause (*"élan vital,"* "aristogenesis," "entelechy," etc.) and it is still less explanatory to speak of an inherent tendency, a perfecting principle, a divine purpose, or the like.

Orthogenesis is so firmly established as a paleontological principle among non-paleontologists that a paleontologist called on to discuss the theories of his profession generally feels that he cannot leave this subject out. Hence its inclusion here, and hence a rather large and peculiar recent literature. The peculiarity is that the extensive discussion seems to be about the non-existent. Practically every recent special study of the subject concludes that there is no such thing as orthogenesis.

Because there has been so much recent discussion and because it is also my opinion that orthogenesis, as defined above, is not real, the present purpose is sufficiently served by this statement and by reference to Simpson, 1944 and 1949; Colbert, 1949; and Jepsen, 1949. The last paper, especially, includes numerous references to earlier work on orthogenesis.

Although orthogenesis is rejected, there certainly are well-defined trends in evolution, a fact emphasized by the four studies cited above and by most others on this general subject. A trend may be somewhat loosely defined as directional, non-random change continuing progressively over appreciable lengths of time. As an objective phenomenon, this sounds about the same as orthogenesis, and it is trends that have given rise to belief in orthogenesis, but there are important differences. Orthogenesis in the usual definition implies constant and non-deviating progression; trends demonstrably vary in rate and in direction, even to the point of cessation or direct reversal. The cause of orthogenesis is unknown and undefined except for the usual negative assumption that the cause is not immediate and continuous adaptation; almost all authorities agree that trends are adaptive and are guided by natural selection.

There are some authorities who maintain that at least the more important changes in adaptive type are saltatory and instantaneous (Goldschmidt, 1940; Schindewolf, 1936), but to most of its students the fossil record seems conclusively opposed to this view. Changes in adaptive type usually, if not always, require an appreciable length of geologic time and therefore usually occur as trends in the record, shorter or longer according to whether the changes are smaller or greater and take place at faster or slower rates.

Among the basic adaptive processes involved in trends are the following:

1. Progressive improvement in efficiency or perfection of existing adaptive type.
2. Narrowing or specialization of adaptive type from more general to more specific, or ecologically from a wide to a narrow niche.
3. Converse broadening of adaptive type.
4. Change from one adaptive type to another.

There are also some sorts of adaptive trends that may be considered as special cases of the above or as dependent on them. Among these are:

A. Self-braking trends in a continuously adapted group in which there is, nevertheless, constant selective pressure for slow change.
B. Trends not representing direct environmental adaptation, but involving correlative adaptation to changes that are directly adaptive.

(As regards particular functions and associated structures, Sewertzoff, 1931, has given a more detailed classification and discussion of the sorts of changes, his "types" or "principles," involved in adaptive trends.)

With the probable exception of *2*, trends of all these sorts seem to have been involved in the evolution of man. It may therefore be useful to exemplify and discuss each briefly. Examples will be drawn from the well-documented evolution of the horse family, which contrary to frequent statement does not show any single and constant trend and therefore is not orthogenetic even in a descriptive sense, but which does have numerous different trends at different times and in different branches. (See Simpson, 1944; Romer, 1949.)

1, 2. Throughout the Eocene, about a quarter of the whole history of the family, changes in size and in skeletal characters of the horses (successive genera *Hyracotherium, Orohippus, Epihippus*) were slight or nil, hence without noteworthy trends. There was, however, a well-marked and essentially constant trend in the dentition. This involved mainly two functionally related sorts of modifications: the premolars became more molariform, giving the cheek tooth battery a larger and more uniform working surface, and all the cheek teeth became more crested or lophiodont, being modified from a grasping and crushing apparatus in the direction of cutting and grinding. This involved progressive increase in efficiency within the established general adaptive type of these small herbivores (*1*, of our list). It also probably involved some narrowing of adaptive type (*2*), for the teeth suggest that *Hyracotherium* (eohippus) was omnivorous with perhaps some preference for browsing on vegetation and that *Epihippus* was definitely restricted to browsing. As far as the teeth are concerned, this trend reached approximately complete effectiveness in the later Oligocene horses.

3, 4. In certain of the Miocene horses and especially within the rather protean genus *Merychippus*, there was a pronounced, relatively rapid trend from low-crowned browsing teeth to high-crowned, cement-covered grazing teeth. This was a new evolutionary direction and a decided change in adaptive type (*4* of the list). This is also an example, although not the best one possible, of the fact that structural progression, characterized as specialization, may nevertheless broaden rather than narrow adaptive relationships (*3*). The new feature, for which the specialization was adaptive, was the ability to graze, to eat harshly abrasive food. Nevertheless the ability to eat less abrasive food, to browse, was not thereby lost. The development of upright posture in man and utilization of the hands for manipulation, only, and not locomotion perhaps provide a better example of specialization that broadened rather than restricted the general adaptive type.

A. Increase in size did not noticeably occur among Eocene horses and was not universal among later lines, but it was common among them, especially in the Oligocene and Miocene. It is probable that this trend, when it occurred in the horses and in the numerous other observed cases, was of the continuously adapted, self-braking sort. Although a given size range may be fully adaptive, natural selection under appropriate conditions continuously favors variants *slightly* above the mean but well within the population range, so that slow increase in mean size will occur. Variants farther above the mean, or mutants for gigantism, are nevertheless opposed by selection or negatively selected, so that rapid change is prevented—this is the self-braking effect.

B. In some lines of horse evolution during the Oligocene and Miocene there was a distinct trend for the ratio of radius to humerus length to increase, that is, for the distal forelimb segment to become longer relative to the proximal. This has generally been considered a trend for progressive increase in speed and hence essentially of our type 1. There is, however, better reason to believe that it is an adaptation correlational within the organism to the changes of a different adaptive trend. The lines affected were those that also and at this same time showed the most marked trend for size increase. There are also other features of limb proportions and structure that changed in fairly close correlation with size changes, including some reversal in lines that became smaller. It is, moreover, improbable that *Equus* is a considerably faster runner than was eohippus.[1] The conclusion is that the changes in limb proportions were adaptations to changes in size, that their effect was to maintain approximately the *same* speed with different body bulks.

One other point needs to be stressed: the widespread occurrence of *transformation* in evolution, marked by radical changes in direction of trends and especially by initiation of quite new trends. When a trend has been observed in a given sequence, it seems to be almost irresistible to extrapolate the trend, to assume that it also occurred with about the same direction and rate before the historical segment actually observed. It is by this subjective process that wholly ortho-

[1] This statement, which has startled some of my colleagues, will be sufficiently defended elsewhere. In the meantime, note that eohippus was built like a whippet and was probably at least as fast.

genetic, and wholly imaginary, pictures of phylogeny are built up. It is noticeable that such extrapolated trends almost never intersect any actually known and possibly ancestral group, or do so only at quite impossible times. Here are grounds for grave suspicion, and in many cases it is obvious enough that orthogenetic extrapolation cannot possibly be correct. For instance, extrapolation backward of evolutionary trends in the bat wing from Eocene to Recent would not intersect a normal quadruped type within the two billion years of earth history. Yet it is virtually certain that change occurred from a normal insectivore fore limb approximately 75 million years ago or less. This change was a transformation.

It seems safe to generalize that when a transformation has occurred, bringing about a distinct change in adaptive type, its rate and course can never be correctly inferred by simple extrapolation backward of any trend occurring after establishment of the new type. For an enlightening contrast between phylogeny by extrapolation and by recognition of transformation, compare Osborn, 1936, 1942, and Watson, 1946.

Extrapolation forward from an earlier trend is less often attempted; the student is usually seeking ancestors, not descendants. When it is attempted, forward extrapolation is even less reliable than backward, because in the latter case we have, at least, the results of transformation as factual evidence, whereas a subsequent change in trend or new trend is unpredictable from preceding events. The future evolution of man has frequently been predicted in the Sunday supplements by extrapolation from trends (real or fancied) involved in the origin of man. In more sober science, it must be admitted that prediction on this basis, at least, is completely impossible.

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THE ANALYSIS OF PRIMATE EVOLUTION WITH PARTICULAR REFERENCE TO THE ORIGIN OF MAN

S. L. WASHBURN[1]

Department of Anthropology, University of Chicago, Chicago, Illinois

There are three reasons why this is an appropriate time to discuss the origin of man. The first is the finding of abundant fossils of a new kind of missing link in South Africa. The man-like apes indicate an unanticipated stage in human evolution which radically alters all current theories of human origins. The second reason is that, through the work of numerous geneticists, zoologists, and paleontologists, a theoretical framework is now available which is far superior to any previous evolutionary theories. The third is the fact that evolutionary speculations can be experimentally checked to a far greater extent than has been realized in the past. It is the combination of new facts, new theories, and new hopes of proof which makes this an auspicious moment to reconsider the problems of human origins.

Why the matter needs reconsideration after all the mass of work done on it deserves a word of comment, which may be divided again under the headings of facts, theories, and proof. The facts bearing on human origins were largely collected in the nineteenth century, or according to principles developed at that time, and there has been no "New Comparative Anatomy" comparable to the "New Systematics" or any "Modern Synthesis" as in evolution. The result is that the vast quantity of materials of very unequal value (Zuckerman, 1933; Simpson, 1945) is difficult to use. Each author tends to use only a small part of the easily available information, and the basis for selection is by no means clear. If the papers by Schultz (1936) and Straus (1949) on human origins were examined, it would be hard to tell that the same animals were under discussion, for few facts are mentioned in both papers and their evaluation is totally different. The mere collection of more facts will not advance the understanding of human evolution. Before progress can be made, methods must be outlined for deciding which facts are important.

The evaluation of differences in fossil bones and living primates leads to the question of theory. Certainly the ideas of orthogenesis, irreversibility, and the supreme value of nonadaptive characters have thoroughly blocked the development of effective thinking about human evolution. They have been used to rule every known kind of primate out of the line of human evolution. Actually, scholars who specialized in human evolution (and it should be stressed that this includes many human anatomists and others besides physical anthropologists) are in an extremely poor position to develop evolutionary theory. Since they are interested in the origin and classification of a single group of animals, and in actual practice almost entirely with man, there are not enough examples to develop and prove theories. Those interested in human evolution must borrow their general theories and principles from others who have access to wider data and more manageable subjects. The task of the anthropologist is to fit knowledge of the primates into the framework of modern evolutionary theory, as described by numerous authors in "Genetics, Paleontology, and Evolution" (Jepsen, Simpson, Mayr, 1949) and as developed in "The Meaning of Evolution" (Simpson, 1949).

The importance of experiment arises from the nature of the anthropologist's task. If he would demonstrate that one theory is better than another, he must have a method beyond personal opinion of deciding which facts are important. Facts and good theories are important, but people feel strongly on the subject of their own origin and there will be wide disagreement until a modern, experimental comparative anatomy can take its place among the tools of the student of evolution. At the moment, whether man is regarded as derived from an ape in the late Pliocene (Weinert, 1932) or an unknown, unspecialized, tarsioid of Eocene age (Jones, 1948) depends on personal evaluation of the same basic facts.

The origin of man has been studied by so many people, so many different ideas have been expressed, and the nomenclature is in such a complete state of confusion that it will clarify matters if I briefly outline my ideas first, then defend them in some detail and consider a series of problems of general zoological interest.

[1]Associate Professor of Anthropology, University of Chicago; Research Associate, Viking Fund.

The earliest primates were distinguished from other primitive mammals by the use of the hands and feet for grasping. This is anatomically a complex adaptation, involving elongation of the digits, flattening of the terminal phalanges and thinning of the nails (Clark, 1936). This basic adaptation has been the foundation of the whole history of the primates, which has been in other ways remarkably diverse. There is no single trend with regard to way of locomotion (which included slow clingers and fast hoppers), or dentition (there are forms with huge incisors, aye aye; or none, Lepilemur; canines may be huge, mandrill; or small, many female Old World forms and hominids), or diet (many primates eat a mixed diet, but one group of lemurs, Indrisidae, and one group of monkeys, Colobidae, have specialized in leaf eating and have developed specialized viscera). It is this great diversity in secondary characters and ways of life which makes primate classification so difficult. Particularly in fossils the hands and feet are usually not preserved, and the main pattern is not reflected in the jaws and teeth. I believe that this accounts for the difficulty in placing many of the Eocene genera (Simpson, 1940).

The early primates took to the trees with the special senses of the primitive mammal. There were tactile hairs, movable ears, and a sense of smell which was predominant. The changes which produced the forms we call monkeys were either present in the advanced lemurs (or tarsiers, I doubt that this is a fundamental distinction) or developed by parallel evolution. For in both New and Old World monkeys active, arboreal forms developed, with reduced external ears and ear muscles, reduced sense of smell, and with stereoscopic, color vision. These arboreal quadrupeds replaced the lemurs, except where the latter remained protected (Madagascar) or by being strictly nocturnal (as the tarsiers, lorises and galagos). The brain greatly increased in size, and Elliot Smith (1924) was the first to appreciate the multitude of differences which came from converting a primitive smell-brain into a sight-brain. Changes at this stage are clearly reflected in the skull by the reduction in parts associated with the olfactory mechanism (reduction in the turbinal bones, interorbital region, and cribriform plate with correlated changes in the anterior fossa).

The origin of the primates was primarily a locomotor adaptation. The first radiation lasted approximately a third of the age of the mammals, perhaps twenty million years. The second was a reorganization of the special senses, making the monkeys successful in the Old World tropical forests by day. The third radiation of Old World primates depended again on a locomotor adaptation. In the apes, a series of modifications in the arms and trunk leads to locomotion of a sort not found in the quadrupedal monkeys. (Spider monkeys brachiate; this is another example of the extensive parallelism in the New and Old Worlds. But spider monkeys also move in typical quadrupedal fashion and have prehensile tails. The combination of brachiation and quadrupedal locomotion is not found in the Old World and shows how the ape type of locomotion may have arisen). Brachiation involves changes in the motion of the arms and the abandoning of the use of the back in the typical quadrupedal manner. The anatomical changes are in the wrist, elbow, shoulder, and thoracic region. None of these are duplicated in any of the monkeys, and brachiation is an elaborate behavioral and anatomical complex, every essential detail of which is shared by man and the living apes.

Some idea of the profound changes in anatomy which accompany brachiation, as practiced by the apes, is given by the changes in the muscles of the trunk and arm. The scalenes migrate upward; psoas major, rectus abdominis, and the origin of sacrospinalis migrate down; serratus anterior increases in size, as does the deltoid; pectoralis major migrates up, pectoralis minor changes its insertion to the coracoid process; origin and insertion of arm extensors are reduced and the flexors are increased. These are correlated with the changes in the joints previously mentioned. (Loth, 1931, is the best general source of information on the muscles of primates.)

The discovery of the pelves of the South African man-like apes, or small-brained men, has made it possible to outline the basic adaptation which is the foundation of the human radiation. These forms have brains which are in the range of the living apes, and their teeth show both human and ape characters, but the ilia are practically modern-human. Men were bipeds first, and later large-brained, small-faced bipeds. Just as the differences between monkey and ape are in the upper extremity and trunk, so those between ape and man are in the pelvis and foot. To mention but a few differences: in apes gluteus maximus is not maximus, gracilis is not gracile, biceps femoris has one head, and semitendinosus and membranosus are not as the names imply. The bone-muscle-functional complex of the leg distinguishes man from the apes as sharply as the comparable complex of the arms shows their

similarity and distinguishes both from the monkeys.

The above outline differs from prevailing theories in several ways. The gibbons are regarded as typical apes and placed in the same family with the living apes and with numerous extinct forms. The South African forms are regarded as in the same family as man, part of the same radiation. However, the arrangement is in the main similar to many others (Hooton, 1946; Simpson, 1949; Zuckerman, 1933). Lemurs, monkeys, apes and men represent a series of radiations. Each is later in time and each is less variable than the one which preceded it.

Among the lemurs there are radically different locomotor, dietary, and dental patterns. At the other extreme man is represented by a single form, being far less variable (even if all fossil forms and the South African man-apes are added) than lorises, galagos, or indris-like lemurs.

Finally, anatomically speaking, man is highly specialized. He represents an extreme and odd form in his way of locomotion. In no other animal can the anatomy of pelvis and foot be matched. His trunk and thorax are very peculiar, their structure being shared only with the great apes. Obviously the brain is a recent and extreme adaptation. This modern, ground-living ape would amount to little without tools. The fact that we number more than a few thousand, ecologically unimportant bipeds living in the Old World tropics is due to the development of tools. And it is important to remember that tools are surely older than Java man. The appearance of all modern forms of men is long after tool using. The origin of the human radiation may be treated just as that of any other mammalian group, but the use of tools brings in a set of factors which progressively modify the evolutionary picture. It is particularly the task of the anthropologist to assess the way the development of culture affected physical evolution.

In defining the major groups of primates the effort has been made to use the most important characters, that is, to use the ones which made the evolutionary radiations possible. In general, characters may be divided into three categories: (1) Primary characters which are responsible for the radiations; (2) secondary characters which are a necessary consequence of the new selection, based on the acquisition of the primary ones; and (3) incidental characters which happen to be selected along with the primary ones. For example, if the group of apes which gave origin to man had a particular type of dentition, this would automatically become part of the original heritage of the hominids. Other features might be due to genetic drift in small groups of early men.

If modern man be examined, he is found to be a mixture of basic primate features, the primary characters of the first or lemuroid radiation. (The hands show a remarkable amount of the primitive grasping adaptation with long digits, nails, etc. It should be remembered that the most perfectly opposable and relatively largest thumbs among all the primates are found in the lorises, and not in man, as often stated. Human feet are a recent modification of the same pattern, fundamentally differing only in a single ligament and the length of the toes.) The next complex is that of the head, brain and special senses which is achieved, except for changes in proportions, in the monkey radiation. Then the arms and trunk become essentially modern. Perhaps then, many millions of years later, the bipedal complex was developed. Finally, the secondary features of the human radiation became general, the small face and the large brain.

Evolution proceeded at different rates in various parts of the body. This is not to suggest that at any time the animals were not functioning wholes adapted to a way of life, but it does mean that there may be a considerable degree of independence of a given part. The eye of monkey, ape, and man are remarkably similar despite major changes in other parts of the body. In spite of a variety of ways of life the same sort of visual mechanism was advantageous and was maintained by selection.

There are three implications of this scheme of evolution for the study of human origins: *First,* different characters are of very unequal taxonomic value at various stages in human evolution. If similarity in trunk and arm show the community of man and ape and if the difference lies primarily in pelvis and legs, a long list of characters in which both features of arm and leg are included may be misleading. Especially is it misleading to say that of so many characters man shares this percent with one form and that percent with another. Similarities in arms, legs, and skull have different meanings. The *second* implication is that there are real changes between ancestors and their descendants. To say that all apes have longer arms or canine teeth than man (Jones, 1948; Weidenreich, 1946) in no way bars them from human ancestry. The ancestors were parts of different radiations and were specialized accordingly. The search for the unspecialized common ancestor becomes either a denial of evolution or a hunt for an

illusory, philosophical archetype. The *third* is that there will be many incidental differences at each level which are of no major importance. Even if every ape had one form of pterion and every human another, it would be of no importance. Actually the form varies in both groups and experimental alteration of suture patterns shows that this type of difference does not change the functional pattern of the cranial vault.

It is clear that adaptation to life on the ground is the basis of the human radiation. Many groups of Old World primates have come to the ground at different times and places, but no group of New World monkeys has taken up life on the ground. Two, perhaps three, different groups of baboons, patas monkeys, vervets and macaques have become ground-livers. On the other hand not a single group of the leaf-eating monkeys (Colobidae) have taken up life on the ground. The restriction here is clearly diet. The soft leaves and fruits of the tropical forests are not available in plains country, and monkeys adapted to this diet have not become ground-livers, although there seems no reason as far as the locomotor system is concerned why they could not. If the ground-living and tree-living Old World monkeys are contrasted, a series of differences appear which are of the greatest importance for the understanding of human evolution. The ground-living forms, which have far greater ranges and are divided into less distinct varieties than the tree-livers. For example, the vervets, which are only partially ground-livers, still are very similar from Uganda to the Cape. Whereas in the *nictitans* group of cercopiths there are several perfectly distinct varieties in Uganda alone. Or, to take an Asiatic example, macaques of the irus group (long-tail, long face, small size), are distributed throughout South East Asia, while the arboreal leaf-monkeys of the same area are divided into four major groups, three of which are subdivided into numerous species. As far as monkeys are concerned, the sort of difference which Dobzhansky (1950) has shown between the tropical and temperate forms exists in the tropics between the strictly arboreal forms and those well-adapted to the ground. The great number of forms are in the rain forests. The implication for classification is that the ones well-adapted to life on the ground will not divide up neatly into the sort of localized varieties which the tree-livers do. The attempt has been made repeatedly to divide the baboons into sharply defined groups. The chaos which has resulted is the result of expecting that plains forms, which have vast reaches of similar habitat open to them, will subdivide as the tree-restricted monkeys do.

The implication for human evolution is clear. Once man's ancestors were efficient plains-livers, they probably occupied large ranges with anatomical variation but without separation into distinct forms. In the case of early man-like forms, more difference should be demonstrated before taxonomic groups are set up than in the case of fossil anthropoids believed to have been tree-livers.

Turning from the general implications of efficient ground-living to the anatomy involved, I think that we have every reason to believe that this was fully achieved by the South African man-apes. The pelvis of these forms (known by three specimens, described by Broom, 1950a and b, and Dart, 1949b) is so human in form that some have argued that it must belong to an early hominid which became mixed in the man-ape deposits. Although the ilium is short and broad and of essentially human form (although differing in detail, especially in the shape of the iliac crest) the ischium is ape-like. The muscular attachment area of the ischium is separated from the glenoid cavity by a greater distance than is the case in modern man (Broom, 1950a). The differences are not great but are sufficient to preclude the possibility of the pelves belonging to other animals than the man-apes. The pelvis of a large baboon found in the same deposits is utterly unlike that of the man-apes, being typically baboon. According to all investigators (Broom, 1950a; Dart, 1949c; Camp, 1949; Barbour, 1949) there has been no great change in the climate of South Africa since these forms lived. They are associated with the bones of baboons and numerous antelope, the typical fauna of the African plains, and forest forms are lacking. The man-apes were bipedal, plains-living forms, derived from the forest-living apes. Morphologically they are ideal representatives of a stage in our evolution and chronologically they may be actual ancestors or the first cousins of the same (Clark, 1950). That is, these forms may be representative of populations which were directly ancestral to such humans as Java man.

The derivation of this type from an ape is best regarded as a case of rapid or quantum evolution (Simpson, 1944). It may soon turn out to be one of the best-documented cases. Since the South African materials are abundant and more are being found, and since there are an impressive number of well-preserved human fossils, the

main features of the transition should soon be fully known.

Since this is the beginning of the human type of locomotion, the principal problem is to understand the locomotor changes. If an ape stands erect, it can walk, and the gibbon can get along fairly rapidly, but it cannot complete powerful extension of the leg. It should be stressed that it is not the extent of the motion which is different but the ability to finish with a real drive. When walking on a flat surface, the ape goes with a bent-knee gait (Hooton, 1946). In modern man the muscle which finishes swinging back the thigh is gluteus maximus. This is an exceedingly massive and powerful muscle, arising from the posterior part of the ilium and the sacrum. In modern man, if gluteus maximus is paralyzed, the trunk is said to jack-knife. That is, the extreme extension of the thigh necessary for normal human walking is not possible, but a flexed gait, comparable to that of the apes, is perfectly easy. The paralysis of this single muscle makes the human type of very-extended bipedal locomotion impossible. It shows that the form and function of this particular muscle is critical in the evolution of man's posture and gait.

In the apes gluteus maximus is a small muscle. In monkeys it is about one-half the size of gluteus medius! Since the ilium of the living apes is long, gluteus maximus lies primarily lateral to the greater trochanter and is an abductor of the thigh. (The relation to the hip joint, and so its function, varies with the position of the leg. A study based on action current is needed to tell when the muscle is really in action.) The primary effect of bending back the ilium is to bring gluteus maximus behind the hip joint, thus making it an extensor. Gluteus medius now lies lateral to the joint and becomes an abductor, taking over the old function of the maximus. Since selection is for function, it is clear that bending the ilium will change the selection on the gluteal muscles. It is my belief that this single change is the thing which initiates human evolution.

Before continuing to an examination of the circumstances under which such a change might occur, it should be pointed out that the statements above are susceptible to experimental verification. The function of these muscles in man and ape can be checked. This should be done. Further, I believe that it is impossible to reconstruct a gluteus maximus on the pelvis of a man-ape which is anything but an extensor. The importance of gluteus maximus in human locomotion, the effect of bending the ilium on the function of gluteus maximus, and the position of gluteus maximus in the man-apes can all be determined independently by as many people as want to take the trouble. In this sense there can be an experimental and ultimately quantitative study of the critical events in human evolution.

The pelvis has several different functions. It serves to connect the hind limb and the trunk, gives origin to many muscles, and serves as a bony birth canal. If the ilium becomes shorter, it must have a greater angle with the ischium in order to keep the same diameter of the canal. This is illustrated in the accompanying figure (Fig. 1). The figures for apes are from Weidenreich (1913). Many monkeys would be much the same, but in the leaf-monkey (*Presbytis rubicunda*) with a very short ilium the angulation of the ilium, relative to the ischium, is greater. Man and the man-apes are characterized by exceedingly short ilia, far shorter than apes of equivalent size. Without fossils it is impossible to tell whether shortening or bending came first, but a considerable shortening of the ilium (of the sort actually seen in other primates) would of necessity result in bending it, which would give the necessary pre-condition to the change in function of gluteus maximus. It should be noted that the difference between the langur and the "hypothetical" form is no greater than that between the hypothetical and the known human extremes. In the Bush race the sciatic notch is extremely wide (Orford, 1934; Washburn, 1949). Comparing an extreme human type to an extreme monkey type gives a totally different idea of the gap than comparing male European to living ape. It should be noted that continued bending, although an advantage from the locomotor point of view, is disadvantageous in females because it narrows the outlet of the birth canal. This accounts for the fact that the bending has been carried further in human males than in females. There is a notable sex difference in the sciatic notch which is directly related to locomotor and postural differences between men and women.

The argument runs as follows: among apes who were living at the edge of the forests and coming to the ground, were some who had shorter ilia. These ilia had to be more bent back for obstetrical reasons and in some this carried gluteus maximus far enough so that it became effective in finishing extension. This started a new selection which favored bigger gluteus muscles and ilia still further bent. The beginning is, of course, supposition, but the functional results can be experimentally checked and the initial shortening

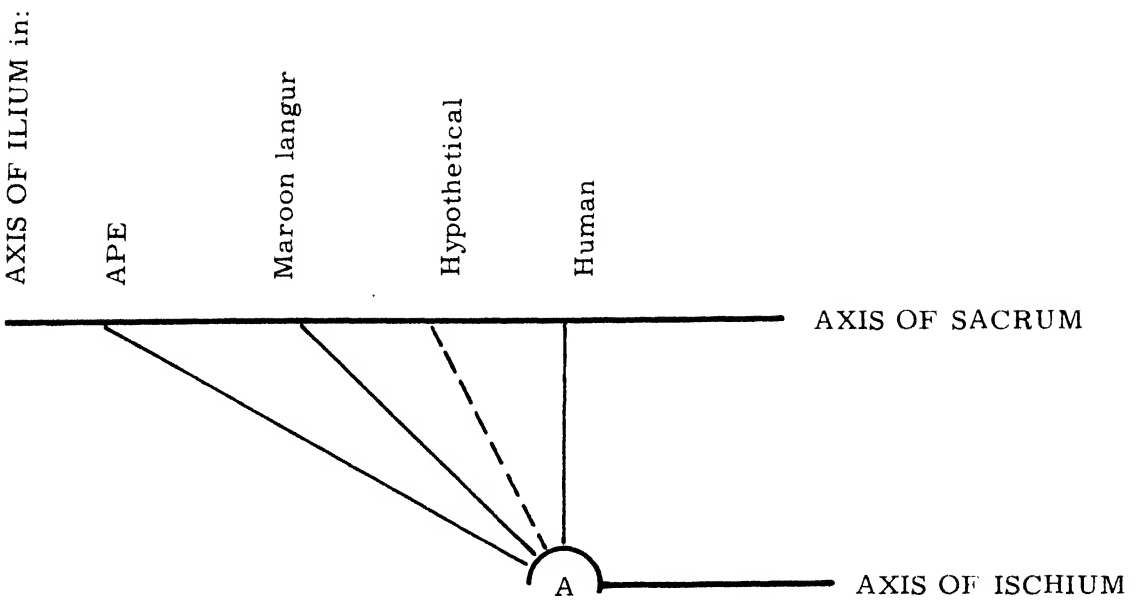

FIGURE 1.
The effect of shortening the ilium on the angle between the ischium and the ilium. A= the acetabulum.

and bending is not much beyond the range of known forms.

Characters closely associated with the primary changes in the pelvis are those in the feet and in the muscles of the legs. The feet of the mountain gorilla have approached the human condition in many ways (Schultz, 1934). Changes from a foot of such a sort to the human would not involve any major evolutionary changes. After all, the joining of the first metatarsal to the second by a ligament may well account for a great many of the features which differentiate the feet of apes and men.

Changes in the muscles are extensive but follow a pattern already seen in the monkeys. When a man walks, he straightens the leg primarily with the muscles on the front of the thigh (Q. ex. femoris). This is the same action which an ape or monkey uses in climbing. In running, the apes and monkeys use primarily the muscles in the back of the thigh. If the mass (weight) of the muscles on the front of the thigh is compared to that of those on the back, (quadriceps to the hamstrings), it is found that the relation is 2/1 in man, 1.2/1 in mangabeys, 1/1 in arboreal cercopiths (nictitans), and 1/1.2 in mixed ground-livers (vervets), and 1/2 in baboons. The first and last figures are from Haxton (1947), the others from monkeys obtained in Uganda. Even by such a crude method it is clear that the proportions of the major muscle masses closely follow the habit of the animal. Climbing is pre-adaptive for human walking. Quadrupedal running tends to build a different pattern of muscles. Aside from mass, there are a number of differences in the leg muscles of man and ape, which can best be described as the attenuation of the muscles other than quadriceps, and the migration of the insertions closer to the knee. These changes are of degree only, and the functions are the same. There is no radical alteration of form and function as in the case of gluteus maximus. Once the major change in the pelvis had taken place, these other changes may well have followed rapidly.

It is difficult to determine to what extent these changes had already taken place in the man-apes. There are only fragments of limb bones. However, the ape-like character of the ischium suggests that the hamstrings may not yet have achieved modern human form. The lack of an iliac tuberosity suggests some differences, but many changes in the leg muscles are little, if at all, reflected in the skeleton. The differences between mangabeys and baboons for example,

which are functionally important, make no discernible difference in the femur. However, in the man-ape, the distal end of the femur is very large. This is the critical point. If these forms were walking erect, the femur must have borne the weight and given origin and insertion to the enlarged muscles concerned with locomotion. I believe that the argument between Le Gros Clark (1947) and Kern and Straus (1949) over the details of morphology of the femur is irrelevant. Any different group of animals may have somewhat different features of a particular bone. There is no reason why the femora of the man-apes should be identical with man, ape, or monkey. The morphology is of a general primate type and the size is in accord with the idea that these forms were bipeds. Granted a reasonable conformity of shape, the important thing functionally is size.

Considering the arms of the man-apes, the distal end of the humerus has been discovered, and Clark (1947) has claimed that it is of the human type and Straus (1948) that it is catarrhine. However, according to the plan suggested here, one would not expect any fundamental difference in the end of the humerus. The basic ape features, still preserved entirely in modern man, are the great size of the trochlea and conforming width of the proximal ulna and the rounded capitellum. The meaning of these features is that the stability of the elbow joint is determined by the fit between the trochlea and ulna, the radius being freed from stability and support is better adapted for rotation. Naturally, the precise detail of this pattern varies from group to group. These little variations are not of evolutionary significance. The major features and their importance can be easily determined. Cut the annular ligament (which holds the head of the radius in place) in a monkey, and the elbow joint loses its stability. Do the same in man, chimpanzee, or gibbon, and the hinge part of the joint functions nearly normally. The distal fragment of the humerus of the man-apes shows that they were typical members of the ape-human stock. The proximal humerus, clavicle, and scapula tell the same story, although detailed study will surely reveal some minor differences from other known forms.

Several authorities have claimed that forms such as the great apes could not be ancestral to man. The reasons given are that the ape's arms are too long and thumbs too small (with the thumb muscles reduced) and that changes in these proportions would break the law of irreversibility of evolution. First, it should be stressed that no one thinks that man is descended from one of the living apes (see Simpson, 1949, for discussion on this point). The question is: could man be descended from a form which had relatively longer arms and smaller thumbs than modern men? Precise differences from living forms are not the issue, but the relations of two kinds of organization. First for the facts: Schultz (1936) has shown that man's arms are, in fact, very long by general primate standards. There is far less difference in length between man and gorilla than between gorilla and orang. The same is true relative to the proportions of the hand. With regard to the thumb muscles, the long flexor is present in all gibbons, over half of chimpanzees, and lesser percentages of gorillas and orangs (Straus, 1949). Once our ancestors had become bipeds, the selection on the arms, hands and associated muscles would have been different from that of tree-living apes. Selection must be quite different for the living gorilla and orang. The issue is, then, could a trend toward long arms and small thumbs in apes be reversed in their descendants when selection pressures were radically changed? That such reversals can and do take place has been recently emphasized by Colbert (1949), Gregory (1949), and Simpson (1949). The idea that such reversals cannot take place seems to be based on the idea that the trends are due to orthogenesis, rather than to continued selection of the same sort over a long period. The fact that orthogenesis is not necessary to explain the facts of evolution seems well established and was dealt with at length by several authors in the volume "Genetics, Paleontology, and Evolution," also by Simpson's "Tempo and Mode in Evolution," and more recently by Jepsen (1949). In spite of all this one reads in "Races" published in 1950 (Coon, Garn and Birdsell) that, "Evolution, we are told, is irreversible." Wright (1934) has shown that the missing digits of the foot of the guinea pig may be brought back by mutation. These digits are normally not there at all. It seems that this is precisely the sort of situation in which the cooperation of geneticists, paleontologists and anthropologists is needed. Great knowledge of the proportions and variations of the primate arm and hand is rendered useless by outmoded concepts and by the failure to realize that reversals, far greater than changing the hand of the living chimpanzee into a human-proportioned hand, have actually been produced in the laboratory.

Turning to the skull, the teeth have been most extensively studied and the evidence has been carefully reviewed by Clark (1950). There is

nothing in the dentition which would militate against the idea that these forms are direct ancestors of late Pliocene age. The molars of ape, man-ape, fossil man, and modern man form as nearly perfect a morphological record as one could hope to find (Gregory, 1949). There is no gap in the record at all, and, on the basis of molar teeth, one would have an exceedingly difficult time in deciding where apes left off and man began. This gradation is in marked contrast to the pelvis. It supports the idea that there was no sudden moment when selection on the dentition changed, rapidly producing a new type. These molar characters would then be regarded as incidental, useful in sorting, but not fundamental. It should be remembered that some arboreal monkeys have dentitions identical with plains-living ones. There seems to be no reason why the dentition should be different and, in fact, it is not.

The size of the molar teeth is of interest. As Broom (1946) has indicated, the best match for the teeth and jaws of the man-apes outside of Africa is the form named "*Meganthropus*" (Weidenreich, 1945). But the limb bones associated with the African forms are not large, the best match being with a small female Bushman, about the lower limit of size of living humans. This shows that large molars do not necessarily mean giant bodies. After all, a small monkey may have larger molars than a modern man. The correlation of body-size and tooth-size among primates is not high. Of course, if non-primates were considered too, the correlation would be far lower. Think if human standards were used to reconstruct body-size from a wart hog's molar! It is particularly dangerous to reconstruct body-size from the teeth of an unknown form.

The canine teeth offer points of interest. Von Koenigswald (1948) has shown that some at least are not as small as has been claimed. However, they are small compared to those of male apes. Of course, in female apes the canines may be exceedingly small, wearing like incisors and narrower than the first premolar (gorilla). In male monkeys the ground-living forms tend to have larger canines than the tree-livers. The extremes in canine size are all in male ground-livers (baboons, mandrills, some macaques) (Washburn and Howell, in preparation). The function of these teeth is in the organization and protection of the group. The males dominate in the social organization (Zuckerman, 1932), and no female has a chance in fighting against the great canine teeth of the males. The big males likewise act as sentries and guards. From the evidence of other primates one would expect a male plains-living ape to have at least as large canines as the forest-forms. The fact that they are much smaller in the man-ape suggests that the teeth were less important in protection and fighting than among the living apes. This supports Dart's (1949a) hypothesis that the man-apes were already using tools. However, this cannot be definitely proved at the present time. Differences in the size of the canine teeth should not be overemphasized because there is a complete series in size and form linking man and ape.

At least some of the problems of the dentition can be dealt with experimentally. It would be useful to know to what extent size and pattern of the teeth are independently inherited. The simpler pattern of the molars of some of the small modern domestic pigs suggests that reduction of cusps may be only one aspect of size reduction. Weidenreich (1941) indicated the same in small dogs. This could be checked experimentally. Also, it would be possible to prove the importance of the large canines in the social organization of the monkey. With groups such as those on an island off Puerto Rico, the social organization could be studied, the dominant male trapped and his canines removed. A quantitative, experimental approach is possible so that the significance of the changes shown in the evolutionary record could be documented by fact and raised beyond the level of individual opinion. Tree shrews would be ideal experimental animals for this type of problem. They are small, hardy, and can be raised in the laboratory. If anthropologists and geneticists plan to cooperate in the solution of problems of mutual interest, it will be necessary to develop some new laboratory animals, and tree shrews may well prove to be the most suitable. Some experimental analysis of cranial form has been attempted (Washburn, 1947).

The evolution of the brain has always been of particular interest in the primates. Since the brain of modern man is so big and since man likes to think of himself as a rational animal, there has been a tendency to define man in terms of brain size. (Keith, 1949, defined the border of man and apes as 750 cc.) The idea that mammals as a group have triumphed over the reptiles because of better brains received a set-back from the work of Edinger (1948). She showed that the brain tends to follow in evolution, that the earliest mammals did not have brains in advance of reptiles, and that at least several of the orders of mammals had established locomotor and dental

adaptations prior to having their characteristic brain form. The hominids follow Edinger's pattern perfectly. The range of variation in cranial capacity is:

chimpanzee and gorilla	325 - 650
man-apes	450 - 650
Java man	750 - 900
Pekin man	900 - 1,200
Neanderthal	1,100 - 1,550

The range for Java man is too small, because of the small number of specimens. The figure for the man-apes should perhaps be raised because of a later, partially-described find (Broom, 1949). So there is either a complete series or very close to one. There is no doubt that all human fossils described so far have human pelves and limb bones and the man-apes were remarkably human in these features. Therefore, it appears that the differences in the brain between apes and man, just as those in dentition, were attained after full human status had been achieved in the limbs and trunk (Clark, 1950).

If one considers the primates in general, the same pattern seems to hold. The lemurs have bigger brains than the tree shrews, the monkeys than the lemurs, the apes than the monkeys. With each major advance in primate evolution the brain doubled or even tripled its size. If the human brain is viewed from this point of view, the remarkable thing about man is that his ancestors went through three major different locomotor adaptations during the age of mammals and one major reorganization of the special senses. After each of these the brain at least doubled its size. Viewed in this way the remarkable size of the human brain is due to the number of times this organ had to adjust to new ways of life. This is added to the general tendency for mammalian brains to increase in size, and to the fact that at least the last doubling was after the use of tools, which may have greatly increased the selection for large brains.

The final adjustment in brain size seems to have been rapid. If capacities of 800-1000 were common in the early Pleistocene (and they may well have been less in the beginning), and 1200-1400 common in the third inter-glacial, the same rate of change would make the man-ape capacities expected in direct ancestors of the late Pliocene age. If the change in brain size follows the change in locomotion, it might be expected to continue rapidly until a new plateau is reached. If so, there is some justification in projecting the known rate back for at least a short period of time, and even a short prolongation of the known rate would reduce brain size to that of the apes and man-apes. Brains of this size may have been characteristic of apes for many millions of years. There is almost no direct evidence, but the skull found by Leakey (Clark, 1950) would be in accord with such an idea.

In summary, the critical primary adaptation initially responsible for the origin of man as a distinct group is in the pelvis. Efficient, bipedal locomotion of the human type involves primarily the pelvis and gluteus maximus, but a series of secondary changes in thigh, leg, and foot must have followed soon to complete the adaptive complex. This complex may have been further improved by continued selection, but, as far as can be determined from the skeleton, had reached modern form in the early Pleistocene. Changes in the teeth, brain size, and many other parts of the body took place at a much slower rate and continued on into late Pleistocene times. These changes are the result of the secondary selection patterns which followed after the establishment of the primary human pattern. Finally, there are many little differences between any two forms. These incidental features may be due to a variety of causes and should not be allowed to confuse the major patterns.

It is customary to present the results of phylogenetic speculations in the form of a classification. There has been so much overemphasis on classification and names, especially with regard to the primates, that common names have been used here as far as possible. At the moment they are better guides to the identity of living primates than the supposedly scientific ones. Without wishing to stress names or overemphasize their importance, the views expressed in this paper imply a reduction in the number of names of categories among the primates. If the term "family" is reserved for a group of animals representing a major adaptive radiation (such as the Indridae, Lorisidae, or Galagidae), then the gibbons belong in the same family as the great apes. Bipedal man might be put in a separate family. The reasons for granting bipedal man more taxonomic distinction from apes than the ground-living monkeys from the tree-living monkeys, is that there is a much greater series of anatomical changes in the case of man. Within the human family one genus, *Homo*, might easily include all the Pleistocene large-brained hominids (Java man, Pekin man, etc.). One other genus, *Australopithecus*, might contain the man-apes (*Australopithecus*, *Plesianthropus*, *Paranthropus*, and perhaps *Meganthropus* and even

Gigantopithecus). Obviously, since little is known of the time when these forms lived, the extent of their range and how many local forms there may have been, the significance of this category is uncertain. If such forms were widely spread over the Old World in late Pliocene and early Pleistocene times probably there were quite distinct local groups. It seems convenient to place these small-brained men in a single genus, at least until there is more evidence to the contrary. The number of names is a function of the kind of interest of the investigator (Broom, 1950). If one is primarily interested in classification, in type specimens and priority, then the less there is known about fossil primates the more names there will be. If one is interested in the mechanics of evolution, in the understanding of process, a cumbersome and constantly changing classification is a great liability and the tendency will be to lump, to leave fragmentary bits unnamed, and to create new groups only when absolutely necessary.

In conclusion, it might be repeated that this is an appropriate time to reconsider the problems of the origin of man; for the traditional phylogenies have been upset by the discovery of new fossils; the old theories of orthogenesis, irreversibility and the supremacy of non-adaptive characters have been proved false; and because experimental procedures offer methods of raising some conclusions beyond the level of individual opinion. Looking to the future, fossils are being found at a rate undreamed of in the past. The cooperation of geneticists and paleontologists has produced a rich evolutionary theory which places the fundamental contribution of Darwin in modern form. Facts are increasing and new theories are challenging, but methods must be developed for proving and checking the importance of particular facts and the fit of any given theory. Such testing requires a knowledge of fossils, of living forms and the application of experimental procedures. All three types of evidence are necessary and a science of human origins can be built only upon this triple foundation.

Without fossils, ancestors can be reconstructed only by what has been called "mental triangulation." With all the vast effort which went into the comparative anatomy of the primates, no one reconstructed an animal with a human ilium and an ape's head. There were attempts in this direction and Weidenreich (1947) recognized that the evolution of the locomotor system preceded that of the head, but before the discovery of the man-apes, and before Edinger's investigations, it remained equally logical to maintain that the brain was the primary and initial factor in human evolution. The actual course of evolution can be determined only from fossils.

But, fossils, at best, constitute a very limited source of information. Adaptations in the digestive, circulatory, reproductive systems, and special senses affect the skeleton little or not at all. The significance of many changes in the skeleton cannot be determined, unless living forms of comparable structure are available for study. Unfortunately, much of the fossil record of primates is limited to teeth and jaws, and the extent to which these parts can be misleading is well-shown by the living lemurs. The skulls of lorises and galagos show not only detailed similarity but comparable trends, yet the whole post-cranial skeleton is different and the animals represent opposite extremes in locomotor adaptations. From the point of view of the comparative anatomist the primates have definite advantages, for there are living representatives of all the major primate radiations, and numerous parallel series offer opportunities for the analysis of the causes of anatomical similarity. Of course, the living forms are not ancestors and will not reveal the detailed anatomy of extinct types, but a far fuller understanding of a lemur can be gained by studying fossils and living forms than by the study of either one alone. Obviously, the chimpanzee is not studied to prove that it is *the* human ancestor but to understand the kind of organization which may have been characteristic of the ancestral forms.

After the study of fossils and living animals, when theories take definite form, then experiments should be planned. Particularly the importance of adaptive complexes and the precise nature of adaptation can be advanced far beyond the level of individual opinion. The fact that gluteus maximus functions differently in man and ape is not a matter of opinion but can be precisely determined. Again, the importance of gluteus in walking can be quantitatively investigated and placed beyond the realm of debate. The study of human origins requires an appreciation of the nature of evolutionary change in animals, an understanding of the specific problems of the primates, and a detailed comprehension of form and function of man and ape. Solution of the problems will require the cooperation of many scientists, and it is hoped that this conference may be the beginning of much close cooperation between anthropologists and others interested in the origin and differentiation of the human stock.

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DISCUSSION

ANGEL: It seems clear that the bone mass genetically available to cover various sizes of brains must play a major part in both cranial index and details of cranial form. As in the examples you gave, a functional breakdown of head-form into antero-posterior and radial growth of the skull base and bone mass or brain size would, through the principle of relative growth, greatly reduce the number of genic factors apparently needed.

MACDOWELL: Dr. Washburn suggests that genetics can step in after experimental studies, such as those he has just reported on the depend-

ence of certain bone configurations on muscles, have separated traits that are directly inherited from the secondary effects of such traits. It happens that genetics has already stepped in by contributing a mutation[1] among others that performs a similar experiment. In this case the configuration of a bone, the sternum, is found to be dependent upon the timing of growth of other bones, the ribs. This mutation occurred in a mouse, but it has led to an interpretation of the division of the sternum into segments, or sternebrae, applicable to all mammals including man and the apes. Dr. Schultz showed drawings of several primate sterna varying from broad to narrow, with sternebrae varying in number and degree of separation. It now appears highly probable that all these variations, and countless others, are expressions of differences in the ontogenetic timing of rib elongation, and that, in regard to the pattern of this bone, the tissues of the different sterna are intrinsically alike. The anlage of the sternum appears as a pair of diverging bands, which the elongating ribs meet and push together. Differentiation towards cartilage and bone proceeds uniformly in the sternum, except at the points of contact with ribs. At these points, and in a zone radiating from them, differentiation is inhibited. This is the essential point revealed by the mutation. With normal rib growth the inhibited zones for a pair of ribs overlaps, so that differentiation first proceeds only intercostally, and, in the mouse, four slender sternebrae, with epiphyses, as in long bones, are formed. The recessive, monogenic mutation, called *screw-tail* from one of its various effects, temporarily retards the elongation of ribs[2] at a time when they would normally be uniting the halves of the sternum. Nevertheless, the halves do unite by cell migration from the inner margins, at the sacrifice of length and thickness. Thus the paired zones of inhibited differentiation do not meet, and at birth, instead of a series of four intercostal bone centers, there is a single elongated bone center. Since the ends of the 6th and 7th ribs are attached side by side, a single zone of inhibition is formed but this is so large that it meets its opposite mate and so the xiphoid process starts with a separate bone center. Subsequently, instead of the inter-sternebral epiphyses lengthening the sternum, the zones of continued growth are lateral and a broad short, shield-shaped sternum is formed, with deep lateral indentations at the ends of the ribs resulting from the inhibition of differentiation. By the time rib-growth is resumed the new pattern of the sternum has been established. The adult ribs give no suggestion of abnormality or of their responsibility for the dramatic appearance of a sternum lacking sternebrae from the beginning.

In other mice, deviations in the position of attachment or growth of individual ribs or single pairs of ribs, which in some cases may fail to join the sternum, have given a wide range of sternal patterns, all in perfect accord with the interpretation that the rib-end induces an inhibition of differentiation of the sternum. The most bizarre of these patterns appeared in a strain in which rib growth was normal, but occasionally all the ribs on one side were attached slightly higher than those on the other, so that each rib-end was opposite an intercostal space, and the zones of inhibited differentiation were staggered and did not overlap. In these cases, at birth, the sternum had a single continuous bone-center, in the form of a wall of troy (meander pattern).

WASHBURN: I want to thank Dr. MacDowell for contributing this excellent example of the way genetics can aid our evolutionary thinking. If many apparently complex morphological changes can be the result of a single change in a process, in this case the slowing of growth of ribs, then it will be far easier to account for the sort of differences seen between various primates. As Dr. Angel points out, studies of relative growth will also help. At present there is a vast quantity of descriptive data, and what we need is more studies of the type recommended by Dr. Angel and so beautifully illustrated by Dr. MacDowell.

[1]MacDOWELL, E. C., J. S. POTTER, T. LAANES, and E. N. WARD, 1942, J. Hered. *33*: 439–449.

[2]BRYSON, V., 1945, Anat. Rec. *91*: 119–141.

ORIGIN OF THE HUMAN STOCK

CONCLUDING REMARKS OF THE CHAIRMAN

W. W. HOWELLS

University of Wisconsin, Madison, Wisconsin

PRESENT OUTLOOK ON HUMAN ORIGINS

The three preceding papers, though different in topic, agree strikingly in presenting a rejuvenated point of view on human-primate relationships. It has been in preparation for some years, with the finds of fossil material and the synthesis of genetic and paleontological thought, but in these three papers, written independently, it comes to a culmination. Simpson calls for a belated testing of our ideas by the principles of paleontology—not a Pharisaical praising of them when they happen to serve our hypotheses aptly, but a strict attention to their true significance and the limits they lay upon us. Washburn carries this theme out by showing how function is the key to the charting of human phylogeny, by discriminating between the anatomical features which are the basic adaptations and those which follow in train, and have their significance on quite a different scale. Schultz gives us an extremely judicious recapitulation of the comparative features of man and the apes, agreeing closely with Washburn as to which are the essential distinctions and which are the non-essential—e.g. articulations of the vault bones, and even the dentition—and furnishes the excellent summary statement that "in the great majority of the instances the distinctions of man represent no more than specific degrees of perfection along evolutionary trends which are common to all higher primates."

In addition, Le Gros Clark (1950) has published a recent paper on "New palaeontological evidence bearing on the evolution of the Hominoidea," which might also, in a perfect world, have been part of this symposium.

Given all of these papers, I can think of little that is fresh to add. What I shall try to do is show how, as it seems to me, these papers reflect very definitely a new plateau of appreciation of man's place among the primates. That is my principal point. A secondary point is the continuity of the problem of human origins with that of later human types, and the constant importance to all of this of what Dr. Simpson has said.

The first impression one gets from these papers is that thinking has been freed from the bonds of many minutiae formerly held to be too important, and a reaffirming in a more integrated way of man's general position with the apes. This is made not only on the basis of fuller information but also with a better sense of perspective than before; this in fact is the main apparent difference. It results in a much more positive rejection of special theories like Wood Jones' tarsian hypothesis, which embraced irreversibility so heartily, and told a rosary of special differences between man and the apes. It is a thorough vindication of Gregory, who himself has lately (1949) reviewed the history of these ideas. It seems to be general; we note Le Gros Clark using the word "hominoid," in Simpson's (1931) classificatory sense.

The most prevalent attitude of the past has not been that man was not allied to the apes, but rather that there were a lot of mysteries and special difficulties connected with the assumption that he was. The basic reason was the lack of fossil material, as Simpson says, forcing students to rely on comparative anatomy, which is actually not in its nature historical evidence. Le Gros Clark also says "The comparative anatomist who attempts to solve evolutionary problems solely by reference to the anatomy of living forms is severely handicapped by the limitations of this sort of evidence. For he is dealing with the terminal products of evolution, which can at the most provide evidence of a very indirect nature regarding their past evolutionary history. This has been particularly apparent in the field of study which deals with the inter-relationships of the primates, where the diversity of opinion expressed by anatomists only serves to emphasize the uncertainty of conclusions based on such evidence. Nor is it to be expected that attempts at a quantitative study of metrical characters in living forms will clarify the problem to any significant degree, for, while many similarities and differences can no doubt be expressed numerically, there is at present no means whereby the relative importance of *individual* characters in the appraisal of genetic relationships can be assessed quantitatively. Any degree of certainty on the evolutionary history of living forms, it will probably be agreed, can ultimately be attained only by a

study of their fossil record." Now Washburn has put his finger on one answer to the problem of the relative importance of characters, a point also made by Schaeffer (1950). Attention to the principles laid down by Simpson is another answer. But in the main situation described, too much reliance has been placed, as Washburn says, on personal opinion. The net effect of the paucity of fossils is to be seen in the history of theory on human evolution.

Darwin and Huxley proceeded of course from comparative anatomy; practically speaking, human or anthropoid fossils were unknown. Their allying of man and the apes was a great victory for the day. At the same time, however, men were men and apes were apes. The two could meet, all right, at a hypothetical crotch where their branches came together in the past. This is the diagram which has fascinated us, and plagued us, ever since. Added to this, the apes outnumbered us four to one which, with other facts, made us look like the aberrant animal, and the apes like the more natural, conservative primates. It is worth remarking that this particular prejudice is notably absent from the papers of this panel, and is specifically rejected by Schultz.

Probably the most devoted recent student of the general problem has been Gregory, who is a paleontologist as well, and has had the benefit of fossils. Here the dates of discovery become important: his syntheses followed the important finds of dryopithecine remains which, taken all together, tended evermore to make these ancestral anthropoids appear more directly parental to the living, arboreally-adapted great apes. Take the date of Gregory and Hellman's review of the evolution of human dentition in the Anthropological Papers of the American Museum—1926—and consider what had *not* been discovered by that time: *Proconsul*, *Ramapithecus*, the australopiths, *Meganthropus*, the bulk of the *Pithecanthropus* material including teeth, and *Sinanthropus*. Gregory has of course continuously adapted his own view to later finds, but the "Dryopithecus pattern" of the molars had a great influence on anthropological thinking. Furthermore, the jaws and teeth of this group in general were certainly suggestive of the living anthropoids, and the fossils themselves had come from so wide an area as to indicate, quite fairly, that the Miocene and Lower Pliocene anthropoids had been pretty well sampled.

At any rate, there was continued production of branching diagrams, largely expressing the same view of man as a highly special kind of ape, difficult to explain. The canine tooth was a particular stumbling block. The foot also gave trouble; however, Morton (1922–1924) and Straus (1926) took a more positive view of this, finding it understandable only as a derivative of an arboreally adapted foot, and Morton, after analyzing the foot mechanically and functionally, deprecated the complexity of the differences between apes and man, and proceeded to anticipate much of what has been discovered and concluded since then, as to a stage of small-brained, terrestrial man-apes in the human line.

From approximately 1925 to the present was another period, with discoveries of quite another order. The main story of this quarter century is of course that of the australopiths. Here was the first suggestion of something different, and it is a peculiar fact that as one discovery followed another in this group, each one tended to be more revealing than the last. The Taungs skull, of *Australopithecus*, which first came under discussion in 1925, was very provocative, with its general form, its brow, its relatively large brain and its small incisors. But it was after all the skull of a child, and only the first permanent molars were really allowed in evidence; and so strong was general opinion that *Australopithecus* was promptly set down by the majority of those who went on record as an anthropoid allied primarily with the gorilla and chimpanzee, albeit more "advanced." This following of a pattern is a sign of the times.

In 1936 and 1938, fragments of adults of the group were found at Sterkfontein and Kroomdraai which confirmed previous forward-looking estimates of the nature of the dentition, palate, details of skull form and probable head posture. The australopiths appeared to have "ape" skulls with strongly humanoid features, especially in the dentition. The term "man-apes" was introduced by Gregory. A few fragments of the limb bones were taken by some to indicate that they belonged to upright walkers, but others pooh-poohed the idea as premature. From this prepared ground, the discoveries of 1947 and 1948 carried things much further. Broom's excellent skull no. 5 from Sterkfontein was complete, rendering obsolete the discussion as to the correct restoration of the skull of *Plesianthropus*. Dart's occipital fragment from Makapan is striking in its contour and placement of the neck muscles, suggesting an even more human-looking skull and upright carriage. The two pelvic bones finally made it evident that the posture was truly bipedal and fundamentally of human type.

Also, collections from the new sites at Makapansgat and Swartkrans provided two new forms of the group, showing variation on the general pattern, especially in skull and brain size, indicating that the whole group was successful in the adaptive sense instead of being a local special curiosity, taxonomically isolated—that is to say, what earlier students seem to have implied by referring to *Australopithecus* as an extinct side-branch. All this South African material since 1925 has constituted a sort of creeping barrage, driving the anthropologists from the notion that the australopiths were just another kind of ape to the acceptance of the fundamentally important fact of their bipedal adaptation.

At the same time, other finds of consequence were coming to light. In 1933 Hopwood reported the first fragments of *Proconsul* and *Limnopithecus*, which were followed in 1947 and 1948 by much better material, including a skull of *Proconsul*; this last revealed surprising features of form both in the skull and the mandible, especially in the incisors and symphysis of the latter, which were rather unexpected, either in the light of the *Dryopithecus* material or in the light of the 1933 remains of *Proconsul*. From 1931 on, new anthropoid forms were found in the Siwalik Hills, with *Ramapithecus* being especially divergent toward man from the typical "anthropoid." In 1939 and 1941 von Koenigswald collected two more jaw fragments in Java of intermediate or "human" form, at least one of which could immediately be named *Meganthropus* and hailed as a true hominid. In general, all these finds of the last quarter century furnish us with forms which do not fit simply into a dryopithecine-pongine phylum of the strictest sort; i.e. a line of punt-jawed, apparently arboreal, apes, but show variety, and in the case of all but *Proconsul*, a much greater resemblance to man than previous fossils.

Where does this bring us? I said that the papers of this group mark the attainment of a new vantage point, and that this is due in part to the fossil finds I have described. It is also due to the stepped-up communication of evolutionary and genetic knowledge from one field to another, partly in symposia such as this one. How are our views affected by what has happened? First, let us consider the most general aspects of interpretation, and second, the specific matter of human phylogeny.

In interpreting our fossils it is more than ever obvious that we must remember the hazards of discovery, something well known to the paleontologists, but much too easily forgotten by the anthropologists. Let us remember that, as I have indicated, the earlier finds, being largely of dryopithecine types, made it easy to suppose that the main line of ape evolution led straight up to gorillas and chimpanzees, until the South African finds of the open-country australopiths made it obvious that this was a special view only. This is the view which left the interpretation of human origins very difficult. I am not aware that anyone explicitly ascribed anthropoid evolution to orthogenesis, but it gave an orthogenetic impression in the descriptive sense. Evolutionary principles, properly understood, would have warned us that something different was to be looked for, and various instructive examples of phyletic histories should tell us what to expect, regardless of fossils. Jepsen (1949) has recently cited an instance, in the apatemyids of the Paleocene and Oligocene, which not long since gave the appearance of an "orthogenetic" line but which, because of a few recent discoveries, now appear to have a family tree sprouting roots and branches in new directions—a perfectly good parallel and lesson for the situation among the higher primates.

Dr. Simpson can therefore hardly have emphasized the point too strongly. Let us remember that the fossil record is never complete, and that from present indications, the Pliocene still has the principal secrets of human ancestry. Let us look at the fossils first as indicators of the general process and scheme of development, until we have far more of them, instead of feeling obliged to put them into a given line at whatever effort, or use them as links in a chain already visualized. This was Dr. Weidenreich's impatient attitude: he constructed a chart, which always reminded me of Dalton's table of atomic weights, not only giving all the known human fossils precise places, but providing other precise places, like a stamp album, for those not yet discovered.

At the same time, I do not mean that practical reconstructions of human phylogeny, and consideration of its problems, need be stultified. I mean only that a less slavish attitude toward particular details of fossil material seems to be in order; not a disregard of detail but a subjecting of it to known general principles. That is certainly a note common to the three papers before us, as well as a ruling motive in organizing this whole gathering. As Simpson says, we are obliged to furnish hypotheses of human ancestry now, not when the record in some never-never time is complete (and it is our favorite pastime anyhow). He states it as well as possible: the job is to take the data, however inadequate, and to reject inter-

pretations that definitely do not fit them, and to use knowledge of general principles to judge among the possible hypotheses remaining.

For example, I agree heartily with Dr. Simpson when he says that the discussion as to whether the australopiths are directly ancestral to man is futile, because of the uncertainty of the time element. However, I do not think it is carrying water on both shoulders to say that they are nevertheless the key to our latest understanding of human phylogeny, and I mean by what they disprove rather than what they prove. They disprove the unity and simplicity of the "ape" family, and once more they indicate the importance of a general education in paleontological principles in human evolution. As Washburn says, after all the work on the comparative anatomy of the primates, no one thought to reconstruct a human ancestor possessing a human ilium and an ape's head. Yet, given present grasp of evolutionary theory in general, someone conceivably might have done this, before the finds of the australopiths showed such an actuality. Morton, it is true, concluded that the foot led the body, and the brain followed bipedism. Weidenreich also deduced that the growth of the brain was a consequence of the upright posture, and that what was primitive for the human stock was not necessarily ape-like—that is to say, convergent upon the anthropoids. (This was despite his apparent lack of enthusiasm for the australopiths.)

Turning from generalities to the actual matter of human origins, what appears to have emerged? There seems to be increasing agreement on a number of matters. What is old, so to speak, is the reaffirmation of man's affinity with the apes. He is that general kind of animal. In Washburn's terms, both are participators in the third radiation, that of the Old World primates, connected with adaptations to brachiation. This reaffirmation rests in turn on what is new. This is largely the realization that the apes of today are just as peculiar as man is; that it is not a case of some aberrant offshoot of the ape stem giving rise to man but more one, as Schultz says, of both branches developing different potentialities inherent in the basic form. In other words, the fossils have broadened our knowledge of the apes so that many disputes as to just where the human line should be joined to them, and similar issues, seem inconsequential, and various formerly differing views can be reconciled. *Proconsul* seems particularly important in this respect, giving us a Lower Miocene ape of generalized form, possibly cursorial, but in any case a new kind of ape which does not settle comfortably into the assumed lineage running from a chimpanzee right back to *Propliopithecus*.

It is true that bipedal walking was the more radical line of change. As Washburn says, this was undoubtedly a case of quantum evolution, a conceptual contribution of Simpson's (1944). The australopiths show it in what was probably a fulfilled, if not perfected, stage, and illustrate the meaning of it in creating a systematic division among the apes, giving rise to what may have been a major group, of which we happen to be the only survivors. At any rate, for human evolution there can no longer be any doubt that we know the fundamental point of change, and its general nature. There is no gainsaying Washburn's interpretation of the transformation in the ilium, and the adaptation for upright walking involved, as the basic character, with others, such as the dentition or the size of the brain, being secondary and postadaptational or fortuitous.

Acceptance of these things involves us in matters of terminology and classification, not because such formal considerations are essential to the above points, but because the terms we use are still the matrix of some fossilized conceptions. As to classification, the australopiths go with man. It does not matter whether they are actually ancestral; that question can well be left to the future. It does not matter whether Washburn's suggestion be followed, and we recognize two genera, *Australopithecus* and *Homo*, or whether we transfer the subfamily Australopithecinae to the Hominidae and recognize differences approximating those between the Dryopithecinae and Ponginae of Simpson by creating a subfamily for living man and the present human fossils down to *Pithecanthropus*. The main thing is a realistic relationship of all these animals on significant principles.

But classification is, practically speaking, less material than terminology, at the moment. There is a good deal of confusion now inherent in our ordinary terms. It is not a matter of splitting hairs; it is a real difficulty, and Le Gros Clark (1950) and Straus (1949) both recognize it specifically in recent papers, the latter adding that a lot of disagreement is semantic in origin, which is undoubtedly true. We have reached the point where some terms, especially "human," "ape," "anthropoid" and "man-ape" are actually embarrassing, except as applied to living forms, or in the case of the last, to the South African australopiths. When we talk about anthropoid and human history, the word "ape" keeps changing

its meaning. Le Gros Clark in his last paper deliberately meets the situation by adapting Simpson's superfamily name, and using "hominoid" for the whole anthropoid-human group back to its beginnings; this gives a term clear in its functional and historical meanings; he uses "hominid" for the human line since its divergence from the "anthropoid ape" sequence, which functionally, and clearly historically, must automatically apply to the Australopithecinae. Yet in the same paper Clark uses the usual terminology, e.g. the australopiths were "in some respects ... definitely ape-like creatures, with small brains and large jaws." We have to read into this that he means living apes. Schultz, in his paper, obviously finds the same difficulty: "in the Australopithecines we have found 'anthropoids' which had walked fully erect, yet still had very ape-like heads." I have been doing the same, of necessity, in this paper. "Man-apes" is particularly unsatisfactory now, which is why I have been barbarously referring to this group as "australopiths."

Although we cannot sweep them away by fiat, we should recognize that these terms, carried over from living animals, have their ambiguities. They do not represent well enough the actual quantities with which we are now dealing; these would be better represented by hominoid (for the whole group in all aspects), hominid (for the fruit of the bipedal adaptation), and pongid (for the arm-dependent apes, and their forerunners as well as we can distinguish them). From this year on, we ought to be able to make greater use of such terms and need hardly keep saying "man is a member of the anthropoid group," any more than we need to say "man is a primate" when we use this term in connection with him.

It is true that there is not universal consent to these conclusions. As for the tarsian hypothesis, I should say that it finds itself in World War II wearing World War I armor plate. It is Straus (1949) who remains the principal objector to grafting the human branch directly onto the apes, and above all to the idea of a brachiating apprenticeship, which Washburn considers a basic tack on the human course. On that point there is a flat disagreement. Yet otherwise I doubt that Straus differs from others as much as might appear. In the first place, he is writing very much from the point of view of comparative anatomy: "To me, an anthropoid ape, extinct or living, primitive or otherwise, would possess an ensemble of characters (of skull, dentition, trunk, and limbs, and of soft parts as well as hard ones), that would definitely allocate him to the group of living anthropoids .... The same criteria would apply in the definitions of monkey and hominid." Secondly, he lists a number of primitive or generalized—non-anthropoid—features of man distinguishing him from the apes (hand and limb proportions; lack of simian shelf, ischial callosities or sexual skin, etc.), but these contain an implied plea to irreversibility, and when it comes to applying them to the fossils I do not find them very serviceable, and cannot separate man from the australopiths or *Proconsul* by them, nor can I readily include either of these latter under his definition of an anthropoid ape. Therefore I think the issue is less sharp than it appears. Notice that Le Gros Clark includes all our forms under hominoid—i.e. non-cercopithecid—while leaving open the question of whether the hominids might have arisen from a brachiator or from a Proconsul-like creature not yet adapted to brachiation. Finally, to return to Straus, he explains the *special* resemblances between man and the apes as the result of parallelism. If I read Simpson and Colbert (1949) aright, they would not be parallelisms; they would either be a set of fortuitous homologies or an implausibly large number of convergences, working against diverging adaptive trends, rather than a proper parallelism, flowing out of parallel adaptive trends. Therefore it would appear that general evolutionary principles rule against interpreting these likenesses as parallelism and in favor of interpreting them as indicating genetic relationship.

The discussion of the origin of the human stock has been concerned with its appearance as a distinct hominoid line. Certain problems concerned with later developments are also important to this, however. One is the origin of what we have been wont to call men, or human beings. With the australopiths technically becoming men, any dividing line above them has now become difficult to find. As in the past, we can simply take *Pithecanthropus* as the most primitive specimen we know of. But definite criteria do not at the moment exist for setting him and the rest apart from the South African fossils. Certainly brain size will not serve: as Washburn points out, a continuous series exists now, especially with the latest Swartkrans finds; on the basis of a jaw, Broom (1950) estimates a skull, constructed along the lines of the other skulls of the group, which would have a capacity of 850 and possibly 950 cc. In the skull generally the features overlap, with the preponderance of them being specifically hominid and not pongid; it is the relative propor-

tions of the jaw and brain case which give the so-called "ape-like" character to the australopith skulls. The skeletons will probably provide the clearest distinction when they are sufficiently known. In the meantime the teeth will probably be most serviceable, although these also do not provide simple distinctions.

This is an area where we lack material. We have nothing positively preceding *Pithecanthropus*, and can only say, as Washburn does, that the australopiths represent the next step down by extrapolation. In actual phylogeny the time element, as Simpson says, becomes important; neither do we know any precise date for the South African finds, nor can we estimate rates of transformation such as would produce Lower Pleistocene human types from the australopiths, or derive these last in turn from their own ancestors.

Actually, of course, we have the general picture, and it would take a considerable amount of new material from new areas to satisfy our curiosity on this point. Heretofore we have been given to talking about "the appearance of man"—the tyranny of terminology—as if he had suddenly been promoted from colonel to brigadier general, and had a date of rank. It is now evident that the first hominids were small-brained, newly bipedal, proto-australopith hominoids, and that what we have always meant by "man" represents later forms of this group with secondary adaptations in the direction of large brains and modified skeletons of the same form.

In the past, this business of the arrival of man has tended to be couched in terms of special problems. One such was the question of an external cause: the disappearance of forests harboring arboreal apes, perhaps due even to the onset of the Ice Age. Beyond saying that such an event is hardly likely to have been connected with the Pleistocene, no fruitful comment can be made on it. Another problem is that of giantism (Weidenreich, 1946). There is no reason why there should not have been giants in the hominid line, but the same paleontological information which makes this likely also suggests there is no reason why such giants should have been the ancestors of later men generally (Hooijer, 1949). Weidenreich's evidence for his hypothesis was largely his own special phylogeny for the Javanese types. The principal fossil evidence was *Gigantopithecus*, and this is cancelled by the australopiths who, as Washburn says, show that large teeth do not mean large bodies.

A further question sometimes brought up is whether man evolved more than once; whether there was a multiple appearance of really human types, several phyla crossing that imaginary line which made them men. It depends in part, of course, on where that line is to be placed, but in another way it is a problem of how far various known human types trace back their ancestries separately. This turns up in various guises, most recently that given it by Gates (1948). Weidenreich had the same idea, though he expressed it less explicitly; he believed that man evolved continuously during the Pleistocene in separate phyla, in parallel in the strict geometric sense, and he carried these lines from present races back to his earliest human stage, the "archanthropine," without apparently drawing them closer together, and without amplifying his notion of giant ancestors in connection with this other than as a "stage." As I have said, however, this kind of discussion tends to be circular unless it can be made concrete in terms of actual phyletic lines, and for that sort of thing we lack any evidence.

It does, nevertheless, suggest another aspect of human origins which I think is generally overlooked. This is that in fact only a single problem is involved, from the derivation of the hominids all the way up to the races of modern man. I do not mean that we are not to distinguish between major adaptational shifts and minor local variations, but rather that the same body of principles—those covered by Dr. Simpson—must rule. Anthropologists and others with different backgrounds, interested in different phases of this sequence, can easily forget the fact. Here I return to Simpson's paper and consider it relative to other material. This of necessity anticipates the next part of the program, on fossil man.

Knowledge of the evolution of man, of archaeological history, and of genetics and race, advances only by actual research and finds. Understanding of the facts, however, can and does advance by appreciation of the general setting, provided by indirect sources of evidence and evolutionary knowledge generally. As Simpson implies, only in this way can we discipline our hypotheses and keep the weeds down, and at least teach our own students less in the way of year-to-year fads in interpretation, and more of the basis of evaluation of the material, present and future. Another virtue of formally considering principles, as we are doing in this symposium, is that it forces one to stand off and take a more general view, and to try to bring all parts of a problem into coherent relations. In the case of

man, as of course it does in others, this means that higher and lower taxonomic categories cannot be considered in isolation from one another. In fact the recent spectacular synthesis of genetics and paleontology came about after the two fields were able to drop their total preoccupation with the lower and higher categories respectively (Jepsen, Simpson, Mayr, 1949).

In anthropology such a synthesis has not taken place. Hypotheses as to race have not been made to jibe with hypotheses as to general human origins, or at least not successfully; what genetics may have to say about race has not been made to fit what paleontology has to say about the human line over a million years, nor have the principles discussed by Simpson and Colbert (1949) been used correctly as often as they have been misquoted; consequently the literature contains various illicit references to parallelism, orthogenesis, species and so on. I refer especially to Gates and Weidenreich, who have not, I think, seen what they are implying by some of their deductions. Weidenreich's chart of human lines developing during the Pleistocene calls for an unparalleled parallelism, in fact for an incredible convergence following an original radiation, so that what finally became the modern races were the descendants of more diverse forms, who had been staggered in their relative progress until the very end, when all arrived at the tape together, since modern man is skeletally strongly uniform.

Dr. Weidenreich felt that he had the essence of the picture of human types, and derided those who were doubtful that the ancestors of modern man were known. I do not agree that this was a safe conclusion. If Neanderthal Man in Europe, *Sinanthropus* in China, and *Pithecanthropus* in Java all give us representative populations with known cultures at specific, and even extended, periods in given areas of the world, then on the other hand, other finds, sometimes as tantalizing as the lost mutter of a dying man, only warn us to be careful: the Rhodesian and Piltdown skulls, both practically dateless and cultureless, found as single specimens under conditions of the sheerest luck, and lonely in their regions; and the first interglacial *Meganthropus* and Heidelberg jaws, splendid in their isolation.

I do not mean to digress too far into the Pleistocene fossils. I am simply saying that the material is actually uneven and fragmentary, and does not justify drawing up any complete set of relationships. Against the background of the well-known forms, like *Pithecanthropus* and *Sinanthropus*, such fossils as the Piltdown skull (which need not be early to be significant), the Heidelberg jaw, and the *Meganthropus* jaw indicate a marked diversity of early forms, but still we can hardly say that we have a structure which tells us something reliable as to the degree of division of the human stock existing in the Lower Pleistocene or just before, or otherwise inform us as to the morphological variety of this stock as it rose from its australopithecine ancestors. What I want to do through this last discussion is to bequeath what Dr. Simpson has said, especially with regard to species and lineages, to later parts of the symposium.

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CLASSIFICATION OF FOSSIL MEN

THE GENUS PALAEOANTHROPUS AND THE PROBLEM OF SUPERSPECIFIC DIFFERENTIATION AMONG THE HOMINIDAE

THEODORE D. McCOWN

Department of Anthropology, University of California, Berkeley, California

The intent of this paper is to consider the nature of the Old World population represented by the fossil remains of palaeoanthropic man, of *Homo neanderthalensis*. The propriety of the particular name used to define the systematic position of these human beings can be usefully considered at a later point in this paper. My reasons for dwelling primarily on the Neanderthal group is that it provides the largest sample of fossil man now extant, has a considerable time range and a wider geographic distribution than do the fossil men of Peking or of Java, and in all these respects is also somewhat superior to the fossil men of the terminal Pleistocene. Lastly, I know quite intimately a part of this fossil Neanderthal material.

A century ago problems with regard to Neanderthal Man were non-existent. The adult Gibraltar skull was reposing in the collections of a local scientific society at the military post of Gibraltar and the discovery of the holotype was not to take place for another six years. As a preliminary to some later considerations I want to review the nature of the evidence that has accumulated in the preceding hundred years and which is the source material for the facts, the inferences and the hypotheses that have been developed concerning Neanderthal Man,

The present use of the term Neanderthal is in a collective sense, without taxonomic implications, and the first question I propose to answer is what is the number of the specimens which can be used as a sample on which to generalize with regard to Neanderthal Man as a Pleistocene population. My count indicates that there are between 80 and 90 individuals which can be assigned to or have been attributed to Neanderthal Man. Such a count cannot be precise at the present time. For convenience the material can be grouped in several categories, the major one being the state of completeness of the material. There are 16 individuals in which skull, mandible and some skeletal parts are present. Thirteen of these are adults, the sex ratio being eight to five; there is one adolescent and two children. The second subgroup is composed of 10 individuals each represented by a reasonably intact cranium only one of which has an associated lower jaw. There are eight adults, equally divided as to sex, and two children.

A third group represents 11 individuals and here the representation is based exclusively on mandible or maxillary fragments, few of them complete. Most of these are of adults; sex attribution is unreliable. The total count thus far comes to 37.

The next grouping contains a great variety of material, all of it fragmentary. There is included among these 50 or more individuals the material from Krapina in which 14 separate mandible fragments give one a minimum number of individuals represented in that particular local population. There are however a variety of other remains and consequently the number undoubtedly should be increased to approximately a score although an exact count is clearly impossible. Similar to the Krapina material are the fragmentary individuals from the Skhūl and Tabūn caves of Mt. Carmel where I estimate that a dozen individuals are represented over and above the more complete specimens which have been included in the earlier mentioned categories. Another group of remains represents Henri Martin's finds of what he believes to be 18 individuals, additional to the two crania from La Quina. Then there are the four La Ferrassie children. There are others but I shall not enumerate them here.

The evidential value of this material in terms of morphology is highest for the first group. But even here one is faced with the problem that the exclusion of the three sub-adults and of two adult specimens, the La Ferrassie individuals, reduces the total number usable for study to 11. Seven of the 11 individuals come from Palestine. The situation can be improved somewhat if one restrict the principal morphological consider-

ations to the skull. The sample can then be increased by six more adult individuals. I am excluding in this enumeration the Galilee skull and the specimen from Monte Circeo since the first is incomplete and the latter is not yet fully described. Additional specimens from Palestine, recovered near Nazareth will increase this sample by certainly one and perhaps two or more individuals when Professor Vallois concludes his studies of them. The total is still less than 20.

The group of individuals represented by jaws contributes relatively little and the fragmentary material from Krapina, Mt. Carmel and so on is occasionally useful for particular points of morphological information but in general its evidential value is moderate. Uncertainties of age and sex restricts its value sharply in a study whose purpose is to provide a well rounded picture of the total morphology of Neanderthal Man.

I have made the assumption in the foregoing that the over-all goal is to get as full a picture of the cranial and skeletal morphology of Neanderthal Man as it is possible to obtain. To my knowledge no recent comprehensive and inclusive study of the dental morphology of Neanderthal Man has been attempted. There is no question that this subdivision of morphology would be rewarding from the standpoint of statistically adequate samples because the most numerous single items are teeth, which I estimate must run to between two and three hundred. The difficulty here however is that the comparative studies of Gregory and others leads me to the conclusion that the general outcome of such research would not be fundamentally different from that of the partial studies that have already been made.

Thus far I have been considering only the physical characteristics of the specimens as concerns their completeness, their age at death, and sex. There are additional important considerations which involve the time associations of the specimens. In nearly all the recent general expositions the specimens which I have mentioned above as part of the Neanderthal collective group are usually referred to as Mousterian Man. When we look into the details of the paleontological and archaeological associations of the material one again finds great disparity with respect to the value of that evidence. The specimens from Spy, Le Moustier, La Chapelle, La Ferrassie, from Mt. Carmel and from Teshik Tash all have archaeological associations that range from excellent to fair. Their known paleontological associations range from excellent to poor and it is ironic that the usually accepted holotype for the Neanderthal species lacks both archaeological and paleontological associations. In the second group of material, that composed of crania without postcranial remains, any kind of certain associations for the Gibraltar adult are lacking although it is customary to use the good associations of the Gibraltar child as the basis for inferring the probable associations of the older skull. The remaining material has archaeological associations as well as paleontological ones. Among the jaw fragments a specimen such as the large mandible from Tabūn has first rate associations and at the other end of the scale are specimens such as Šipka and La Naulette whose associations are extremely difficult to evaluate. One finds considerable variation with regard to the value of the evidence for the fragmentary remains. In general it is no worse than the associations of the previously mentioned material. The critical problems however are concerned with the over all interpretation of what the associational evidence means, of relating the specimens to particular parts of the Pleistocene. Most prehistorians when faced with this problem continue to react as if the classic sequence of Palaeolithic industries in Western Europe were still a complete and infallible guide to the time relations of the human specimens found with them. The problem was really posed as long ago as 1895 with the discovery of the material at Krapina. In my opinion it was not solved by calling the artifactual remains pre-Mousterian although this has been widely accepted as a solution to the problem. The same type of difficulty became evident again with the discovery of the Galilee skull and was quite fully exemplified with the Mt. Carmel discoveries where the industries have an important and predominant industrial tradition, the Levalloisian, which is not characteristic of the cultural associations of the European Neanderthal specimens.

In Europe it has been convenient to contrast the faunal associations occurring with Mousterian industries and Neanderthal man with the late Pleistocene I 'Age du Renne. It was of course fully recognized fifty years ago that some remains of Mousterian Man occurred with animals which were regarded as indices of a cold climate and other remains with a fauna which was generally accepted as living under temperate conditions. The general problem became more acute with the discovery of extra-European remains such as Galilee, Mt. Carmel and Kafzeh. To exemplify one aspect of this general problem I want to lay

before you certain facts which had to be faced in connection with the study of the material from Mt. Carmel.

Great care was used in accumulating in the field as much evidence as possible with regard to the faunal associations of the skeletal material in both the Tabūn and Skhūl caves. The result of this care in the field plus the extremely illuminating studies of the recovered paleontological materials by Miss Bate provided us with a considerable body of evidence as to the inter-cave associations of the human material. The long series of deposits in the Tabūn cave provided two major items of information. The first was that at a point in the sequence of strata subsequent to the deposition of layer C there was a very definite change in the composition of the fauna marked by the disappearance of certain species and some genera. The second item was of a somewhat different nature and had to do with the change in the relative number of fallow deer and gazelle. At the same point in the time sequence marking the change in composition of the fauna there was a related change in terms of the relative proportions of the two ungulates. Both of these have been interpreted as indicating a change from dry to wet conditions as far as moisture is concerned. Temperature associations are less certain but may well have undergone deterioration, that is, the change was from warmer to cooler. At Mt. Carmel these two changes are quite marked. Miss Bate is of the opinion that the probabilities favor an interpretation that the changes are equivalent in time to a similar situation noted for some European deposits. The generally accepted opinion is that the comparable European phenomena marked the onset of the Würmian glaciation and that the deposits and their contents laid down before this change was manifest fall into Third Interglacial times and that deposits laid down immediately subsequent to the change fall within the period of the Würmian glaciation.

The situation with regard to the faunal associations of the more numerous Skhūl burials is this. The over all picture one gets of the animals that were being eaten by these human beings is that it was drawn from a fauna that was closely similar to the fauna of level C and D in the Tabūn. Characteristic forms are present in levels B and C of Skhūl but since the site ceased to be occupied in a real sense of this term subsequent to B we can not duplicate the changing proportions of fallow deer and gazelle as represented by the B layer of Tabūn and the later Upper Palaeolithic layers of the Mugharet el Wad. What we can specify is that the skeletal bearing levels of the Skhūl were laid down some time prior to the faunistic changes that are manifest between levels B and C of the Tabūn. The Skhūl fauna contains a relatively higher proportion of specimens of wild cattle than do any of the layers of the Tabūn sequence. Unfortunately this information is not particularly useful in making a closer time approximation. It may represent an indication of a time difference but until we can rule out the possibility of cultural preference on the part of the human beings who were responsible for the animal material being present, one has to proceed with caution in evaluating this information.

The similarity between the artifacts made by the Skhūl people and the Tabūn people are very great. As far as I can see on the basis of a reanalysis there are no differences that cannot reasonably be attributed to sampling error.

The upshot of these considerations is that there is no clear cut evidence to establish a time difference between the two sets of human remains and some evidence in favor of their contemporaneity. I have a nagging suspicion that there is a time difference but no evidence to settle my doubts. The result was that Keith and I decided that the most economical hypothesis was to assume contemporaneity but we were never unaware of the fact that it was an assumption that additional evidence from sites elsewhere might prove invalid.

I have dealt at some length with this particular situation because it exemplifies certain general conditions that apply to the context of all of the remains of ancient man. Even where there is an awareness of the problem, where every effort is made to gather as full information as possible which will help in elucidating it, one still may be faced and usually is faced with an inability to come to a positive and precise conclusion which will define the time period of the human material with precision. The point here is that if we were dealing with a period of two and a half to five million years it would matter less than where we are dealing with a period which with great generosity may be estimated at not more than two hundred thousand years.

One of the problems which the palaeoanthropologist will have to undertake is that of persuading competent and interested paleontologists to re-assess, where it is possible to do so, the evidences of faunistic associations with the earlier found specimens of the Neanderthal

group. Many of the decisions which were reached in the past hundred years with regard to the time associations of fossil humans have used as primary evidence their cultural associations and as secondary evidence the value of particular species that were regarded as index fossils of the glacial and interglacial climates of the Upper Pleistocene. It may well be that a number of the older discoveries cannot be effectively better integrated into our knowledge than they are at present but I certainly would like to see an attempt in this direction.

The earlier attempts at a definition of the morphology of Neanderthal Man all had as a collateral purpose the demonstration that the specimen or specimens were ancient and different from the living races of mankind. The general question of the validity of the Darwinian evolutionary hypothesis was inseparably connected with any account of the remains of Upper Pleistocene human fossils. There is quite naturally a notable decrease in the emphasis and amount of space given to these considerations but it was an important theme of Marcelin Boule's comparative studies and his general recapitulation of the status of Neanderthal Man which he included in the long and detailed account of the specimen from La Chapelle-aux-Saints. Boule's opinions have become incorporated in the general body of scientific knowledge. He treated the remains known to him in 1908 as being essentially a unified group possessing a common culture, the Mousterian, and living at the same period of time. The group as he then knew it and treated it consisted essentially of the Neanderthal find, the specimens from Spy and the La Chapelle male. He paid a little attention to the Krapina material but hardly any to the Gibraltar skull.

When he wrote his popular book, Les Hommes Fossiles, he had the additional evidence of the two adult individuals from La Ferrassie and he used it to supplement and round out his conception of Neanderthal morphology. In all important respects however it is the morphology of the La Chapelle individual, and for a variety of reasons he delayed publishing a full descriptive account of the La Ferrassie individuals. They remain incompletely described to the present day.

These ideas provided a foundation on which a very large number of later writers built. Weidenreich's acute sense of problem made him aware of the fact that the Ehringsdorf skull differed both from the holotype and the La Chapelle paratype and it seems to me he deserves great credit for posing a series of questions regarding the essential variability of Neanderthal man which have been useful in later work. The same sorts of questions were raised in Keith's descriptions of the Galilee skull and it became possible to consider them more fully with the recovery of the human specimens from the Levalloisean strata of the Mt. Carmel caves.

These questions are all related to a fundamental one: Is there really unity of type among Neanderthal specimens or are the divergences great enough so that they overlap extensively with the characteristics of modern races on the one hand and with ancient races on the other?

The answer which Hrdlička gave to this question was that morphologically there was an overlap with modern man. His views gave rise to vigorous restatements of the accepted opinion that there was a real morphological hiatus. Not only was there the reiteration of the views of Boule, Keith and others, but using a somewhat different technique of investigation Morant came to the conclusion that while there was unquestioned variability in the European Neanderthal specimens nevertheless it was extremely difficult to find good and valid grounds for the demonstration of real overlapping of characteristics between this group and the means for a wide variety of living races. In retrospect it seems difficult to see that Hrdlička was able to establish a clear case and to conclude that the Neanderthal group was only a "phase" in the evolution of modern men.

The discoveries of Neanderthal and Neanderthal-like individuals since 1929 have provided new material which increases by about 50 per cent the number of good specimens to use as a sample in estimating the morphology of the Neanderthal group. The principal discoveries are those of Mt. Carmel, the material from near Nazareth in Palestine, the two crania from Saccopastore and the cranium from Monte Circeo. The discovery in Uzbekistan of an immature individual cannot yet be fully evaluated and, in any event, standard practice and common sense indicates that adult individuals are more useful in the first assessment of the morphology of a population than are immature ones.

In studying the very full reports which Sergi has published on the two Saccopastore specimens it is evident that on balance they are not sharply distinguishable from the crania of Gibraltar, La Chapelle, and Spy and while a similar comprehensive treatment of the Monte Circeo specimen is not yet available it is apparent that it too falls close to the modal tendencies of male west European Neanderthals.

This situation is not paralleled in the material which has been recovered from the several Palestinian sites. As is well known, there is great diversity of physical patterns among the individuals from the Skhūl and Tabūn caves. On the assumption which has been mentioned previously that we are dealing with a single population as far as time and culture are concerned there is more heterogeneity of pattern in the Mt. Carmel group than there is among the Belgian, French, Italian and Spanish finds. It cannot be demonstrated, however, that if specimens such as Steinheim, Ehringsdorf and Krapina are added to the previously mentioned group of Neanderthal specimens, the Mt. Carmel material is more variable. The difficulty here is that the European material which is most suggestive of marked variation is that from Krapina and as I have stated above evaluation of it on the basis of the published descriptions is by no means easy.

Adding the Palestinian material to the collective group of European Neanderthals does not, in my view, negate the morphological distinctiveness of the Neanderthal pattern on the one hand and a generalized *Homo sapiens* pattern on the other. The variability increases but the central tendencies remain much the same. These are statistical figures of speech, because the analysis of variance and of the means for the group can give a misleading effect of greater preciseness of information than is actually warranted. In using the phrase "generalized *Homo sapiens*" I have in mind that no one known group of living races or of their terminal Pleistocene forebears of themselves form a simple transition to the morphological pattern of the greater Neanderthal group. One has to use many different kinds of individual characteristics or special subpatterns among particular living groups of man as a basis for this transition. Keith and I emphasized the number of points in which the tall rugged Skhūl males approximate the tall rugged kind of human being which usually bears the name Cro Magnon. In particular points the Skhūl males are nearer to some living Australians and in other points the overlap is indifferently with Caucasoids, Negroids or American Indians. I do wish to emphasize that while the pattern for the group is distinctive, it seems to me impossible to hold any longer to the view of a morphological hiatus between modern man and the Neanderthal population.

In interpreting this Palestinian material several hypotheses were framed on the general basis of the physical variability of that population. One of these was that reproductive isolation between a Neanderthal group and some unspecified form of man, basically with a *Homo sapiens* pattern, had disappeared before the time of the Mt. Carmel population and that the morphology could be interpreted as the result of a long-time mixture of genetic factors from both groups. We were reluctant to accept this hypothesis for several reasons. One is that it is by no means easy to transfer the range of variation evident in bone morphology into genetic terms and it is particularly difficult to interpret the morphology of possible hybrids in terms of ancestral components when breeding experiments are impossible. The second main reason was that we felt that to make such an interpretation meaningful we ought to be able to specify what particular kind of pattern the supposed *Homo sapiens* ancestors exhibited and the evidence known to us then and the evidence available even now makes it extremely difficult to state with certainty what the nature of the morphology of Third and Second Interglacial *Homo sapiens* individuals may have been. I am aware that these reasons will be regarded as excessively cautious ones by some colleagues. In the long run caution will do less harm than to have pushed the evidence as hard as we might have.

The second hypothesis which we suggested can be paraphrased in genetic terms somewhat as follows. The whole Neanderthal collective group was reproductively and genetically isolated early in its history, certainly by the commencement of the Third Interglacial, but that even at this time it manifests evidences of an approach in some characters to morphological features that are widely found among *Homo sapiens*. This view essentially relies on the idea that mutations at particular loci were taking place frequently enough to produce individuals that in some but not all features mimicked the later and better known *Homo sapiens*. The Mt. Carmel population, living at the close of the Third Interglacial, would represent the accumulation of this type of tendency within the Neanderthal population.

Is such a process probable, granting a community of genetic origin earlier in the Pleistocene for both Neanderthal Man and *Homo sapiens*? What we know with regard to the living habits of Neanderthal Man and what we can guess with regard to the size of the group as a whole, and of the sub-groups which formed its component parts, would indicate that there is reasonable ground for believing in factors promoting local differentiation. Selection, mutation and genetic drift

would combine to produce the variable morphology possessed by the group.

This general hypothesis cannot clearly be ruled out as impossible but I am less certain now of its inherent probability. The reasons for my uncertainty are that within the known span of time for the Neanderthal group it would imply considerably higher mutation rates than are believed to exist in modern man and a considerably larger population than was the case, if we are to account for the wide geographic spread of the known variability.

A third hypothesis is that by Middle Pleistocene time geographical and cultural isolation might have been established between the Neanderthal group and groups that are genetically ancestral to modern man. There would, however, have been no reproductive incompatibility but the degree of isolation would have been sufficient to maintain considerable constancy of established patterns. Then, towards the close of the Pleistocene, some local groups of Neanderthals may have begun to draw on the *Homo sapiens* gene pool. This raises the problem as to whether the amount of gene flow between these two major populations was equal or whether the major current was more in one direction than the other.

The rarity of even individuals in populations of *Homo sapiens*, only a little later in time, that could be mistaken for a Skhūl V is evidence, I believe, for the major flow having been from the ill-definable *Homo sapiens* gene reservoirs to the Neanderthal one.

What is the systematic position of a human group which was largely but not completely isolated in space from a similar human group with which it was reproductively and genetically compatible? Among living groups of mankind the widely accepted answer is that the differences are those of races of a single species. Human history is full of examples in which groups never or rarely did interbreed, maintained constancy of pattern for varying lengths of time but could interbreed successfully. The morphology of Neanderthal man, as I assess it now, makes it difficult for me to believe that differentiation during the Pleistocene had resulted in genetic isolation of the two groups. The polymorphism of the Neanderthal group seems similar in kind to racial polymorphism among *Homo sapiens*. Such being the case I am inclined to the view at present that a subspecific name and a taxonomic position in the species *sapiens* better represents a genetic interpretation of the phenotypic characters of the Neanderthal group. I am convinced that this is one of several possible answers and that among the critical pieces of evidence we need is some real demonstration of the existence of a *Homo sapiens* population earlier than the Würmian, and its nature.

The structural differences between the majority of Neanderthal specimens and individuals or groups of *Homo sapiens* are real phenomena that indicate separateness of genetic history. Consequently I find it hard to believe that local populations of Neanderthals of Third Interglacial or later times were the groups which gave rise to *Homo sapiens*. If they did, this also implies a combination of mutation rates and the selection of these mutations in a span of time which seems somewhat short to have produced the existing polymorphism of the known Upper Palaeolithic peoples. As a structural stage the Neanderthal group still occupies a position intermediate for cranial, facial and dental characters between *Pithecanthropus* and *Homo sapiens*. Conversion of structural stages into systematic categories has led to varying results—species differences and genus differences. Keith and I, on the assumptions and the hypothesis we used, placed the emphasis on structural difference and suggested a difference of generic value to place Neanderthals in the family Hominidae. Knowing the imperfections of our material but using cautiously what we have, we still can suggest useful answers to the questions as we conceive them. Many of the genetically oriented questions we now ask cannot be answered from the material because of its imperfections but the questions are worth putting even though the answers are partial and should avoid a tone of finality.

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DISCUSSION

EWING: The following date, derived from a site near that of Mount Carmel, may possibly affect our thinking about the hypotheses discussed by Dr. McCown, even though the data are admittedly often vague and in this case founded on a reticulate of hypotheses concerning chronology.

At Ksâr 'Akil, near Beirût, the Boston College -Fordham University Expedition excavated a rock shelter, the layers of which represent cultural periods from the Upper Levalloiso-Mousterian to the dawn of the Mesolithic. This site is up the coast from Mount Carmel. One of the most striking of our finds was a set of layers, whose geology admits of only one interpretation, namely, that they were deposited during very moist times. Without going into details,[1] I may content myself

[1] This situation has been described semi-technically, but with full documentation, in *Thought* (Fordham University Quarterly), Vol. 24 (1949), pp. 255–288.

with saying that we have equated our three humid periods with the first, second and third maxima of the Last Glaciation in Europe. This hypothesis is supported by associated faunistic and cultural evidence, and itself corroborates the climatic conclusions drawn by Miss Bate from the fauna at Mount Carmel. According to our hypothesis, the Upper Levalloiso-Mousterian occurred at the end of the Third Interglacial and up to the peak of Phase 1 of the Last Glaciation; the "Lower Aurignacian"[2] immediately preceded Phase 2.

Now, the justly famous Mount Carmel skeletons were laid down in a cultural period immediately antecedent to our Upper Levalloiso-Mousterian. In our "Lower Aurignacian" we unearthed the skeleton of a completely *sapiens* youth. I should like to consider the chronological implications of this situation, in terms of genetical possibilities.

There are other factors, of course. We have found at Ksâr 'Akil the first detailed documentation of a transition in tool techniques between the flake Levalloiso-Mousterian and the blade Aurignacian. Other interpretations are possible, but at present I favor the view that Mount Carmel exhibits hybridization between *sapiens* and Neanderthal types; from this union, and in this area, eventually grew the blade cultures, the tools of which were employed by a completely *sapiens* type of Man. However that may be, I wonder whether the alleged shortness of time elapsing between the "classical" Neanderthals and the Cro-Magnons, has not influenced me in rejecting out of hand any evolution of one from the other; and influenced me falsely. It is solely this chronological aspect I wish to present.

Even allowing for our ignorance of absolute chronology, we may hazard a guess of the time intervening between the Mount Carmel skeletons and the Ksâr 'Akil youth. Ksâr 'Akil's earliest layers (later than those of the Mount Carmel skeletons) may be 125,000 years old; our youth may be as old as sixty or even seventy thousand years (although probably more recent than that). This gives us 65,000 years; at twenty-five years to a generation, we have 2,600 generations. Making a necessarily even wilder guess at the population of the Near Eastern littoral at that time, we could put it at something like 200 persons of one sex, at a given time. This would afford us over 500,000 persons of *one* sex, living successively in the area of the Palestinian and Lebanese coast.

I am sure that the geneticists would grant the possibility: that the rule-of-thumb one in 100,000 mutation rate plus the even quicker recombination rate could accomplish the necessary changes with such material during such a time.

Thus the time and population available would allow of either hypothesis: local evolution of the *sapiens* type from the Neanderthal type (a hypothesis which is, of course, seriously controverted by earlier *sapiens* specimens elsewhere), or the replacement of a hybrid population by a purely *sapiens* one.

HUNT: On cultural grounds, Professor Hallam Movius believes that the Mount Carmel Neanderthaloids are somewhat more recent than the Riss-Würm Interglacial. Instead, he considers them as living between the first and second advances of the Würm glaciation.

The later these people lived, in my opinion, the more likely it is that they were hybrids between fully Neanderthals and modern man.

Considering Neanderthal man in zoogeographic terms, I should like to suggest that the various faunal areas which Henry Fairfield Osborn postulated for Pleistocene land mammals in Europe may each have included some taxonomically distinguishable race of fossil man. In the third interglacial, for example, perhaps the coastal faunal assemblage in Europe included the Piltdown-Fontéchevade race. Further inland was a zone of intergradation represented by the "progressive" Neanderthals. Still further east may have lived the fully Neanderthal race, which from a zoogeographic viewpoint may be regarded as the human representative of the central European fauna. At any rate, the limits of past mammalian faunal assemblage during the Pleistocene may some day provide valuable clues as to the racial boundaries of early man, even though these boundaries are not yet clear now.

WASHBURN: In considering past classifications of fossil men, I think that it is well to keep in mind that until recently many thought that modern man (as represented by Galley Hill) had existed in Europe prior to and with Neanderthal forms. This made the forms seem different by the test of living in the same area and remaining distinct. The recent work of Oakley has shown that Galley Hill was actually later than Neanderthal. The

[2] This is the equivalent of Professor Garrod's "Chatelperronian," locally. Actually, it demands, and will receive after final study, a local name. It may be remarked, that even if our dating hypothesis must be eventually changed to make our three moist periods equivalate Phases 2, 3, and 4, the time element invoked in this argument would not be too seriously affected.

question now seems to be can men of modern type be found earlier than the Mount Carmel finds? If a modern-type ancestor cannot be found, these forms cannot have been hybrids. My own feeling is that the Mount Carmel finds are not more variable than apes from a single area and that they may actually be representative of the sort of population which gave rise to modern man.

THE PROBLEM OF THE EARLIEST CLAIMED REPRESENTATIVES OF HOMO SAPIENS

T. D. STEWART

Division of Physical Anthropology, U. S. National Museum, Washington, D. C.

In a recent publication (Stewart, 1949), I outlined the development of the concept of morphological dating in connection with early man in America. My purpose in writing this was twofold: First, to illustrate in this particular field, the extent to which judgment had become warped by personal bias; and second, to emphasize the absurdity of placing full reliance on morphology as a guide to human evolution. Although American man probably dates back no further than the late Pleistocene and little, if any, change in his physical type could have taken place since his arrival in the Western Hemisphere, the late Aleš Hrdlička insisted on judging the antiquity of all putatively early skeletal remains by morphology alone. In other words, because these specimens resembled the remains of recent Indians, he set aside the evidence of geology and denied their antiquity. As long as this fallacious concept prevailed (its demise pretty well coincides with the year 1937 and the International Symposium on Early Man in Philadelphia), few anthropologists were able to grasp the simple idea that the earliest remains of man found in America do not differ essentially from those of recent Indians.

In order to surmount the provincial setting of my subject and to give it universality, I mentioned also two examples from the Eastern Hemisphere having to do with the opinions of Sir Arthur Keith and the late Franz Weidenreich. The reference to Keith cited his long adherence to the principle of geological dating and his unfortunate recent wavering therefrom. The reference to Weidenreich raised doubts about his morphological ranking of fossil hominids. In the present paper, I am going to expand my previously brief reference to this broader phase of human evolution and classification.

In expanding from the New to the Old World, I am aware of my limitations. With one exception, I have not handled the actual ancient specimens to which I am making reference. My basis for judging their evolutionary status, therefore, is primarily a knowledge of modern man. Also, I am aware that an individual's experience in the field of biology provides his angle of perspective on human evolution. Weidenreich, to continue the same examples, viewed this subject, at least in his later years, from the standpoint of Asia, the prehominids or archanthropines, and the Early Pleistocene. Keith, on the other hand, has had a different outlook, at least geographically and morphologically. The British Isles have presented him with examples of man which are not very primitive looking, even though coming sometimes from Middle Pleistocene deposits. And even the Palestine caves furnished him with the most advanced looking Neanderthal remains yet recovered. Such diverse perspectives and the opinions based thereon, may profitably be reviewed, it seems to me, from the more objective position that I occupy, and in spite of its handicaps.

Everyone who scrutinizes the literature on fossil man becomes more or less aware of the psychological elements that shape the authors' conclusions. Hooton discussed this subject in his entertaining fashion at the International Symposium on Early Man in Philadelphia in 1937. Yet so subtly hidden are some of these elements that they are not easily recognized. Their exposure thus becomes an important step in reviews of this field. However, this does not mean that subjectivism is not a useful thing. As Kroeber has said so aptly in a related connection (1940):

> . . . All phenomena connected with man and his history seem to demand a greater or less degree of intuitional judgment if they are to be dealt with understandingly; and a good intuition, which proves to be supported by the majority of the facts without forcing, does definitely carry us forward. It certainly has until now been difficult in the field of physical anthropology to make much progress by pure empirical work with the element of subjective judgment entirely eliminated. The argument, in short, is not against subjectivism, but in favor of the perpetual recognition of how great a part is really played in larger interpretations by the subjective factor. This recognition is perhaps particularly important in physical anthropology because its anthropometric techniques are likely to give a spurious impression of a high degree of objectivity in all its procedures. (p. 462)

A little thought should make it clear that the subjective element has great opportunity for expression in connection with those fossil finds

which show the least morphological departure from the modern human type. Primitive forms like Pekin man or classic Neanderthal man scarcely need to have their antiquity demonstrated. Yet in the case of modern-looking forms investigators are likely either to doubt the claims of antiquity or to exaggerate the primitiveness of certain features so as to make them seem more convincingly old. If, on the other hand, there is undoubted geological evidence of antiquity, investigators may resort to the concept of morphological dating to minimize the geological findings. All of this is unscientific, of course, but in keeping with human nature.

These generalizations, already demonstrated for American man, require further documentation from the Old World. Since about 1911 Keith has assembled the records of human fossils that indicate or suggest a considerable antiquity for the "*sapiens*" type. Even at this early date he stated clearly his opinion of the significance of these finds:

> The deposits of the Thames, of the Somme, of the Seine, of the Arno, from one side of Europe to the other, have revealed the same story—the existence of a man, a mere variant of modern man, one with a thick skull, a big brain, and a long head. How are we to account for this unexpected revelation? There are two ways: we may hold with the majority of anatomists and geologists, and simply refuse to believe in the authenticity of these discoveries because they run so contrary to our preconception of how and when modern man was evolved. Or, with Sergi and with Rutot, we may put our preconceptions aside, and, as we are bound to do, accept the revelations of those discoveries as facts, and alter our conception of man's evolution to harmonize with our facts. We have, in the first place, to conclude that man of the modern type is much older than we supposed. We expected to find him in a process of evolution during the Pleistocene period, but we have traversed more than the half of that period and find our own species much as we find him at the present day. (Keith, 1915, p. 209)

If anything, Keith has been inclined to minimize the doubts regarding the circumstances surrounding the discoveries of the modern-looking human remains—and especially the doubts regarding their primary inclusion in the geologically old deposits in which they have been found. Indeed, he has even gone beyond the geologists in claiming an older age for at least one of them. Thus, in stating (1931) his position regarding the London skull, he says:

> A full consideration of the evidence has led me to transfer this skull to an older geological horizon than the discoverers have given to it, and to assign it, not as they have done, to an unknown type of modern humanity, but to a recognized type of ancient man, viz. man of the Piltdown type. (pp. 31–32)

Even though Keith now (1949, p. 265) has "had to abandon the claims of the 'modern type of man' to a high antiquity, the very thesis which [he] set out to prove so long ago," his defection has not stopped the trend of thought to which his efforts gave rise. It is legitimate therefore still to cite his earlier position for purposes of comparison.

In contrast, Weidenreich tended to ignore the finds of early "*sapiens*" types, or to emphasize their dubious qualities. For example, in his estimation the Piltdown skull—a find that Keith early championed—"should be erased from the list of human fossils. It is an artificial combination of fragments of a modern-human braincase with orang-utang-like mandible and teeth" (Weidenreich, 1943, p. 273). Elsewhere, he says (1947, p. 194) "...any claim to geological priority for recent human types must be based on incontestable geological facts and not on speculations and conjectures.... As long as uncertainties...last, the morphological analysis is the only reliable means of tracing the line of human evolution."

This disinclination on the part of Weidenreich to accept any fossil find lacking in primitive features, and in spite of geological documentation, may be further illustrated. The incomplete Swanscombe skull, another "*sapiens*"-like find from the Middle Pleistocene, is placed by Weidenreich (1947, p. 194) "on the list of the dubious cases so far as its classification is concerned." His argument is that "If it could be proved that the missing frontal bones had a frontal torus, the skull could be placed in the same group with the Steinheim Skull or the Skhūl population of Mount Carmel. As long as this proof is *not* brought forward, the nature of the skull remains doubtful." (1943, p. 273). This comes very close to morphological dating.

Other anthropologists who have written about fossil man may be ranged in, or somewhere between, these extreme positions of Keith and Weidenreich. Since Keith's retreat from what Hooton (1937, p. 97) has called "his palaeontological Verdun," the latter has announced his occupancy of this position. As a teacher and as the author of "Up from the Ape" (1946), Hooton has been largely responsible for the tolerant reception of Keith's idea in America. Thus Howells in his "Mankind so Far" (1944) devotes separate chapters to Piltdown man and to the "ancient moderns" of the Lower Paleolithic. Note, how-

ever, this bit of conservatism: The chapter on "Ancient Moderns: Lower Paleolithic" follows one on "The Upper Paleolithic: Enter *Homo sapiens.*"

For contrast again, Hrdlička's position may be cited. In his "Skeletal Remains of Early Man" (1930) Piltdown alone of the modern-looking skulls is described. From this specimen he drew the following conclusion:

> ...it must be plain that any far-fetched deductions from the Piltdown materials are not justified. This applies particularly to the superficially attractive conclusions that the Piltdown remains demonstrate the existence in the early Pleistocene, long before the Neanderthal and even the Heidelberg forms, of men with practically modern-sized and modern-formed skulls and brains and directly ancestral to *Homo sapiens* or recent man. This hypothesis is a proposition that would change the whole face and trend of human prehistory, and that against all other and better substantiated evidence in this line. Such a theory, all science will agree, could only be established as a fact by the most ample and satisfactory material demonstration, which is quite impossible in the present case. (pp. 89–90)

Like Hrdlička, Boule in his "Les Hommes Fossiles" (1923) ignored all of the "ancient moderns" except Piltdown. Even in the third edition (1946 edited by Vallois) there is but brief mention of other finds. However, Boule looked upon Piltdown man more charitably than did Hrdlička. As translated his opinion reads:

> The Piltdown relics are, unfortunately, incomplete. The interpretation of them, an extremely difficult task, is still doubtful regarding certain essential points. But in spite of all the uncertainties, they form a most important and one of the most instructive discoveries. Even although it be admitted that the skull and jaw are perfectly independent, it is at the same time none the less true that the fragments of the skull tell of the existence, at a period probably very early in the Quaternary era, of a man with an essentially human brain-box, and that this Man is more closely related to the ascending line of Modern Man than to that of Neanderthal Man. The beginning of our direct ancestry must thus date from a very remote past. Up to the present time, this hypothesis had been supported only by a certain number of discoveries which possessed no geological sanction, and, in consequence, were of no value as proofs. Now we have brought before us a new, carefully observed fact, of which the significance seems clear and definite, always allowing that the Piltdown skull is really as ancient as is supposed. (English ed., 1923, p. 172)

These examples will suffice to show the division of opinion, amounting to personal bias, that has existed through the better part of this half-century, regarding the validity of the earliest claimed representatives of *Homo sapiens.* They adequately demonstrate, too, that the controversy over early man in America is but a geographical distinction in a world-wide problem, which everywhere presents different time depths but the same personality factors.

Up to this point I have purposely ignored some recent developments in this field. These newest developments, being in part destructive of old evidence and in part constructive by way of new evidence, tend to cancel out and to yield a result that is little if any changed. It seems likely, indeed, that if the authorities I have quoted could be reached for further comment on this point, none would be inclined to alter his stated position.

We may note in passing that Keith's change of position, to which reference has been made, came about not so much because of the new evidence, but because of his general studies in human evolution. As his doubts began to appear in 1931, they take this form:

> The racial body is unstable; it must change with the passage of time. It is the application of this law which makes me more and more sceptical of the geological evidence which assigns a high antiquity to modern types such as are represented by Galley Hill man and the Olmo man. (p. 30).

Writing in 1949 Keith reviewed his position thus:

> My first book on fossil man... was written to vindicate the claims of modern man to a high antiquity—claims which were rejected out of hand by the leading authorities of that time. The test case was that of "Galley Hill Man"; his remains were found in 1888 at a depth of 8 ft. in the 100-ft. terrace of the Thames valley; the geological evidence gave him a high antiquity, but carrying all the modern marks...he was placed by the leaders of opinion on the list of rejects. The fossil remains of Piltdown man were found at a depth of only 3 ft., but were immediately accepted because they carried primitive marks and were devoid of the modern ones [sic]. This mode of discrimination seemed to me unscientific; I clung to the geological evidence at Galley Hill, but the tide of discovery went dead against me. Even in 1926, when I brought out a new edition...I was still a defender of the antiquity of Galley Hill man and of his many compeers, but a change had overtaken me by 1931.... By 1936 the evidence...convinced me that it was easier to believe that there was a flaw in the geological evidence of the antiquity of Galley Hill man than that a race or type of mankind could continue for 100,000 years without undergoing evolutionary change. And so I have had to abandon the claims of the "modern type of man" to a high antiquity, the very thesis which I set out to prove so long ago. (p. 265).

The newest evidence, that which is too recent to have influenced the opinions cited, will now be reviewed. This consists, as I have stated, of destructive and constructive elements. On the de-

structive side are the results of the fluorine test as applied by Oakley to some of the English specimens—Galley Hill, Swanscombe and Piltdown. On the constructive side is the finding of new "*sapiens*" skull fragments of undoubted geological age in the French Fontéchevade cave.

The fluorine test is based upon observations from the last century indicating that in general the fluorine content of bones increases with geological age. To achieve this result a constituent of the bone, hydroxyapatite, is said to trap fluorine ions from the ground water and to convert them by a process of ionic interchange into fluorapatite, a stable mineral resistant to weathering. However, since ground waters vary in fluorine content, depending upon available geological sources of the element, it is impossible to use the fluorine content of a bone as a direct indicator of geological age. Also, there is some danger in comparing bones from different sites. When such comparisons are made they carry the assumption that the fluorine environment of the different sites has been the same throughout the geological interval since the bones were deposited.

In the report on the Galley Hill-Swanscombe tests, comparisons have been made between five lots of bones from various loams and gravels in the *Swanscombe region.* Two of the sample lots, of which one represents the Swanscombe skull, came from the 100-ft. terrace and is of Middle Pleistocene age. The percentage of fluorine is the same in both lots of bones. Another sample lot came from the 50-ft. terrace and is of Upper Pleistocene age. The percentage of fluorine in this lot is slightly reduced as compared with those from the 100-ft. terrace. The remaining sample lots represent recent bones and the Galley Hill skeleton. The percentage of fluorine in both of these lots is about the same and much less than in the samples from the 50-ft. terrace. Montagu and Oakley, the authors of this report, draw the obvious conclusion: that Galley Hill is recent and Swanscombe is of Middle Pleistocene age.

In the report on the Piltdown tests, comparisons have been made between six lots of bones representing "every available bone and tooth from the Piltdown gravel and from neighbouring deposits." The two lots of Piltdown human remains (*Eoanthropus* I and II) are distinguished from other mammalian remains that have been grouped according to known or probable age as follows: 1) Lower Pleistocene, 2) Possibly Middle and Upper Pleistocene, 3) Holocene or Pleistocene and 4) Holocene (Recent). The percentage of fluorine fails to differentiate the skull bones and mandible of *Eoanthropus* I, or in general the remains of Piltdown Man from the Recent mammal remains. Here again the high fluorine content of the mammal bones attributed to the Lower Pleistocene is in distinct contrast to that of the more recent remains. Oakley and Hoskins, the authors of this second report, conclude that "1) all the remains of *Eoanthropus* . . . are contemporaneous; 2) *Eoanthropus* is, at the earliest, Middle Pleistocene." (1950, p. 381) That the authors do not follow the example of Galley Hill and call Piltdown recent is due probably to the ape-like lower jaw.

I am not in a position to debate these interpretations, but I am reminded of the errors that characterized the early efforts in dendrochronology and Carbon 14 dating. I am disturbed, for instance, by the failure to define exactly the "Swanscombe region," the source of several bone samples. Thus, are the fluorine histories of the samples from the 100-ft. and 50-ft. terraces strictly comparable? Also, how have the variant stratigraphic layers at the Barnfield (Swanscombe) and Galley Hill pits affected the flourine environment of the contained bones? Is it true, as the authors say (Montagu and Oakley, 1949, p. 366), that just because no fossil animal bones were found at Galley Hill this means that they were once present but have since been completely decalcified by percolating water owing to the absence of a capping layer of clay? Again, if it is true as the authors say (Oakley and Hoskins, 1950, p. 381) that iron sulphide can inhibit fluorine absorption, what about the possibility of errors due to unrecognized inhibitors? And is it true that "free fluorine ions have apparently been remarkably deficient in the ground-water" at the Piltdown site since the final rearrangement of the gravels?

Today most everyone accepts at once and without question the findings in an exact science like chemistry. Anthropologists are only human, therefore, when they extend this acceptance to chemical experiments set in the framework of the less exact biological and geological sciences. In short, my reservations stem not from the chemical side but from the biological and geological side; from those elements of the experiment that require personal evaluations. I am not defending the antiquity of the Galley Hill and Piltdown skeletons, but, just as in the case of morphological dating, I am sounding a warning about the subjective pit-falls that surround chemical dating.

From Galley Hill's "bones of contention"—the symbol of Keith's "paleontological Verdun"—let us pass to the Department of Charente in France where the newly discovered and thus far geologi-

cally undisputed Fontéchevade skulls were found. The cave deposit which included these specimens was separated into two parts by an uninterrupted stalagmitic layer representing a long and presumably wet period when the cave was unoccupied. Above this layer the strata contained Upper and Middle Paleolithic artifacts. The stratum below the stalagmitic layer, in which the human remains were found, contained "Tayacian" type artifacts of the Lower Paleolithic, together with the remains of a "warm temperate" fauna. According to Vallois (1949, p. 339) "Archeology and paleontology therefore agree in placing the date of the level with the human fossils in the last interglacial phase, the Riss-Würm. This is the first time that fossilized human bones of such an antiquity have been found in France."

Unfortunately, like all other claimed early representatives of *Homo sapiens*—now that Galley Hill is excluded—the Fontéchevade skulls are incomplete. Number 2, the more complete one, consists of the left parietal, the upper half of the right parietal and the upper part of the frontal. Number 1 consists simply of a piece of frontal 5.5 cm high and 4 cm wide, including, however, the glabella region and the left supraorbital ridge. A Neanderthalian type of frontal torus is lacking and the type of parietal is regarded as that of *Homo sapiens*. In Vallois' opinion

> The interest of the Fontéchevade discovery is that it clarifies the problem. In contrast to earlier finds of human remains we have here, in effect, a specimen which is well dated and found in a stratigraphic context which allows of no dispute: *this is the first time that man, certainly not Neanderthal although earlier than the Neanderthals, has been found in Europe under such conditions.* Now this type... taking all its characters together, aligns itself with the Piltdown-Swanscombe forms. This confirms in turn the correctness of associating these two fossils themselves. (1949, pp. 357–358).

It is still too early to tell whether Vallois' opinion of Fontéchevade, like Keith's of Galley Hill will be regarded in some quarters as a patriotic gesture. Certainly, the anatomical characters, and especially the interpretation of the missing parts, will be argued. Yet it is unlikely that the dating can be denied. To this extent, then, the problem is clarified: In and before the last interglacial period there existed in Europe, and probably elsewhere, men with less "primitive" cranial features than those of the succeeding more advanced cultural period—the Neanderthal men of the Mousterian age.

Thus far I have avoided coming to grips with the term "'*sapiens*' type" and the other synonymous terms I have been using, such as "ancient moderns." What right have we to identify the Fontéchevade skulls as authentic representatives of this type or group? There seems to be some confusion on this point. Vallois is careful to say that the cranial characters of Fontéchevade, particularly the lack of a frontal torus, do not oblige us to accept it as *Homo sapiens*. Then he retreats into vagueness by saying that the only stand he can take is to range Fontéchevade man "with the men of Piltdown and Swanscombe, and in their area of taxonomic significance." Yet in Movius' opinion "Certainty that [the pre-Neanderthal Europeans] were of fundamentally modern type with respect to the [brain case] can no longer be denied, even by the most profound skeptics." (Movius, 1948, p. 367). And Eiseley, writing it must be admitted for popular consumption, goes the limit:

> There is nothing Neanderthaloid about it. This woman could have sat across from you on the subway yesterday and you would not have screamed. You might even have smiled. (Eiseley, 1948, p. 19).

Much the same sort of confusion appears in the literature regarding the taxonomic position of the Swanscombe skull fragment. This specimen was observed *in situ* at a depth of 24 ft. in gravels that yielded also an Acheulean industry and faunal remains attributable to the Mindel-Riss Interglacial Period. After his definitive description of this specimen, Morant (1938, p. 96) cautiously concludes that

> Owing to the incompleteness of the single specimen, the failure to find distinction from *Homo sapiens* in the case of all characters examined, except possibly the thickness of the bones, cannot be considered a good reason for assigning [it to] this group...
>
> Hence it is necessary to admit that the missing parts of the Swanscombe skull *may* have been so formed as to provide clear evidence of differentiation from modern man.

The same caution is echoed by Howells when he says "...the Swanscombe find fails to be conclusive about *Homo sapiens*." (1944, p. 201). Yet Hooton says:

> ...case after case of finds of *Homo sapiens* in apparently mid-Pleistocene deposits has had to be relegated to the "not proven" category. Now at last, however, the persistent searches of archaeologists among the glacial gravels have been rewarded by one cast-iron irrefragable case that serves not only to establish the main point of contention, but also to validate or, at any rate, to strengthen numerous other claims previously dismissed. (1946, p. 359).
>
> ...there is no denying the conclusion that Swanscombe is either mid-Pleistocene *Homo sapiens* or something so close to it that the differences are zoologically inconsiderable. (1946, p. 363).

Coon says much the same thing in his "The Races of Europe" (1939) under the heading "*Sapiens* Men of the Middle Pleistocene" (p. 30). But on the other hand, Le Gros Clark in his "History of the Primates" (1949) carefully qualifies his opinion, saying that "*on the evidence of the two bones available*, the remains of the Swanscombe skull suggest that Acheulian Man in Europe was not markedly different in anatomical features from *Homo sapiens*" (p. 94).

This should be sufficient to demonstrate that in coming to grips with the term "'*sapiens*' type," or its equivalents as applied in the anthropological literature to a certain group of fossil men, we are up against a controversial issue abounding in subjectivity. Indeed, there seems to be a tendency, as the information about these fossils is conveyed from the primary to the secondary literary sources, to modernize the morphological characters. Undoubtedly, the generalization that the modern form of mankind is older than the Neanderthals, is attractive because it provides a simple solution for many difficulties, not the least being the organization of the fossil record for lectures and books.

At this point it is pertinent to note that certain other fossil finds besides those we have been considering, have been described as having modern characters. Some of these, usually the less complete ones, are regarded as well on the side of *Homo sapiens;* the others, in spite of possessing modern characters, for the most part are granted Neanderthal status. Mention has already been made of the Piltdown skull and its assignment by chemical dating to the Middle Pleistocene at the earliest. In their original description of this specimen, Dawson and Woodward (1913) were impressed not with the modern character of the cranial pieces, but with the primitive character of the assembled form. Indeed, Woodward's reconstruction is very much on the primitive side. It remained for Keith (1915, 1938-39) to correct this impression by showing that the pieces could be fitted better into the form of a modern skull. Only the associated ape-like jaw, the great thickness of the cranial bones, and the uncertainty about the character of the supraorbital region have given pause to those who have been tempted to rank the calvarium as *Homo sapiens.*

Coming up in time there is the relatively complete Steinheim skull from Germany, dating probably from the second or third interglacial periods (Weinert, 1936). Although this specimen is usually assigned to the Neanderthal group, largely because of the prominent brow ridges, much emphasis is placed upon the modern character of the back part of the skull.

Another German find, the Ehringsdorf skull, again relatively complete, dates from the second half of the last interglacial period (Weidenreich, 1928). Being associated with Mousterian implements and having prominent brow ridges, this fossil is ranked with the Neanderthalians. However, the otherwise close resemblance of the vault, especially in its height, to that of modern man is usually stressed.

In this respect Ehringsdorf is rather like the high vaulted Skhūl people of the Mount Carmel caves in Palestine (McCown and Keith, 1939). These finds date probably from the third interglacial period and the beginning of the last glaciation. Of this type I can speak with more personal assurance, because I have seen and handled the famous Skhūl V specimen at Peabody Museum, Harvard University. It is my impression that, except for the brow ridges, the form of this skull falls within the range of some modern populations. The brow ridges alone, I repeat, are quite outside the modern populations of my experience.

Going still farther afield, Africa offers other examples referred to the "*sapiens*" type. Among these are Leakey's Kanam and Kanjera specimens, attributed to the Lower and Middle Pleistocene, respectively (Leakey, 1935). Although the age of these specimens is debated (the fluorine test cannot be applied because the deposits are of volcanic origin), Leakey feels that the underlying reason against their acceptance "seems to lie in the fact that they represent true *Homo sapiens*" (1948, p. 167).

This review could be extended to include other cases that were at one time or another advanced as early "*sapiens*" types. According to Vallois' recent listing of European cases (1949, p. 356), these include: Denise, Castenoldolo, Moulin Quignon, Olmo, Clichy and Grenelle, Ipswich and London. He disposes of these summarily as follows:

> ...The nature of the deposit bearing the Denise specimens cannot be verified, but it was determined, a short while ago, that even the bones which were certainly indigenous to the deposit were not fossilized; the Castenoldolo men came from recent burials; the Moulin-Quignon jaw is modern and was fraudulently introduced; the skeletons of Clichy and Grenelle cannot be precisely dated but are very probably recent, since they likewise are not fossilized; the Ipswich and London skulls probably belong to the Upper Paleolithic, and this perhaps applies also to the Olmo

skull, which was found under conditions which lend themselves to discussion... (pp. 356–357).

Still another claimant is the Bury St. Edmunds cranial fragment. Montagu has reviewed its history (1949) and is now inclined to accept it as "an authentic representative of neanthropic man of the upper or middle Acheulean." (p. 33) The bare mention of these cases, regardless of the accuracy of their disposition, serves to indicate the extent and complexity of the problem.

Closer inspection of these cases reveals an historical factor in the descriptions. Until recent years—that is, before the finding of the so-called progressive Neanderthals (Steinheim, Ehringsdorf and Mount Carmel)—the skulls of Mousterian man available to Morant (3 male, 3 female) were, as he showed (1927), remarkably homogeneous as to type. Between this type and all modern racial types there was, as he pointed out also, a distinct hiatus. It was possible, therefore, during the earlier period, to make a clearcut morphological diagnosis of such new findings as were reasonably complete. If the new finds did not exhibit the main anatomical features of these classic Neanderthal skulls, they were regarded as *Homo sapiens*. The progressive Neanderthals, especially the Skhūl crania of Mount Carmel, have altered this situation. The Neanderthal type can be regarded no longer as having low variability. Hence it is not so simple any longer to decide the status of a new find, particularly when it is incomplete.

This situation is well illustrated by Weidenreich's pronouncement on the Swanscombe skull which I quoted earlier (p. 98): "If it could be proved that the missing frontal bones had a frontal torus, the skull could be placed in the same group with the Steinheim Skull or the Skhūl population of Mount Carmel." The converse of this statement, which Weidenreich could not face, seems equally true, namely: If it could be proved that the missing frontal bones *did not have* a frontal torus, the skull could be placed in the same group with modern man.

Incidentally, Montagu has recently (1950) demonstrated that the modern-looking Wallbrook frontal looks natural when joined with the equally thick Swanscombe parietal. Interesting as this is, it does not constitute proof and only the Swanscombe frontal can settle the morphological status of Swanscombe.

This emphasis on the frontal torus as the principal remaining morphological difference between the Neanderthal and modern types is significant. The frontal torus would seem to be a slender basis for distinguishing two contemporary hominid types or for giving them separate specific, much less generic, status (McCown and Keith assign the Neanderthals to the genus *Palaeoanthropus*). Moreover, it is beginning to appear that these types were not only contemporary but occupied overlapping territories. (The Fontéchevade cave is in the area of the classic Neanderthals.) From these emerging facts we may well begin to wonder about the spatial and chronologic separation that would be required to maintain the genetic distinction between these two types. Could it be that the older concept of the Neanderthals—especially of the homogeneity of this group—lacks reality in terms of population characteristics? From our knowledge of modern populations of *Homo sapiens* should we not allow for more variability in the Pleistocene human populations? These are questions that I feel merit consideration, although not being a population geneticist I am not able to argue them convincingly.

The fixation on the distinctiveness of the Neanderthal population has had its counterparts in other spheres of physical anthropology. Here in America, for example, the Basket-maker group for a long time was considered long-headed and otherwise different from the deformed but "evidently" round-headed Pueblos. Recently (1944) Seltzer showed that there were no grounds for this distinction; that not all of the Basket-makers are so long-headed and the undeformed Pueblos are not round-headed. As another example, an exaggerated sex distinction has been made from time to time in series of ancient skulls, because size was used as the primary criterion in sexing. Simmons (1942) has demonstrated with skulls of known sex that size is a false guide in such matters.

The tendency to exaggerate the distinctiveness of Pleistocene populations and to disregard their variational probabilities has received encouragement from current interpretations of the differences between the Mount Carmel Neanderthals. To be duly critical of these interpretations requires a review of the Mount Carmel finds, which can be considered the best sample of Neanderthals from one place thus far recovered. Although these skeletons come from two caves and from different parts of a stratum having a depth of six to eight feet, which must have taken a long time to accumulate, they are often referred to loosely as a "population." Moreover, the Tabūn woman, which may even be Upper Levalloiso-Mousterian,

according to Garrod (1937, p. 64), is compared morphologically with the Skhūl men of the Lower Levalloiso-Mousterian. This so-called population, therefore, consists of male and female individuals who were not necessarily contemporaneous and may have lived hundreds of years apart.

One of the stressed differences between the Mount Carmel types is the height of the vault. Actually, it is low in the Tabūn woman and considerably higher in only one of the Skhūl men. In terms of the mean height index (basion-bregma height × 100 / mean of length + breadth) this difference may be expressed as 71% for the woman and 77% for the Skhūl V man. This is a range of only 7 points. Greater ranges are not uncommon in some modern populations of the same sex. In individual cases the index of modern man is known to go below 71% (for example in the Aleut, Hrdlička, 1945, p. 520), although admittedly such modern low vaults are better filled out than are those of the low Neanderthals. Modern skulls usually have mean height indices higher than 77.

The chin is another variable feature in the Mount Carmel people. Although the Tabūn woman has a retreating chin, whereas most of the Skhūl men have projecting chins, the fact is often overlooked that the Tabūn II jaw, from a lower level than that of Tabūn I, is completely modern looking. Receding chins occur occasionally among native Australians today (Hrdlička, 1929, pl. 3).

Curiously, the low vault of the Tabūn woman is not accompanied by an equally low face and orbits. By comparison the high-vaulted Skhūl V skull has a low face and orbits. The upper facial indices are: 60.8 in the Tabūn woman; 50.3 in the Skhūl V man. Using maxillo-frontale as a landmark for measuring orbital breadth, the resulting orbital indices are 78.5 in the Tabūn woman; 65.2 in the Skhūl V man.

McCown and Keith have used individual modern skulls, among them an Australian, in their Mount Carmel comparison. I am unable to learn much about this Australian, but judging by the measurements in Hrdlička's Catalog of Crania (1928), there is a vast range to pick from. If McCown and Keith's Australian was selected to represent the average, then the result has been, as in the case of Morant's use of racial means, to emphasize morphological differences between Neanderthals and moderns.

It is another matter to show that the characters of fossil men are outside the modern range. Hrdlička often (for example, 1929, pl. 3) pictured a Piegan Indian skull that he regarded as Neanderthaloid. It was low vaulted, but otherwise entirely modern. My candidate at present for this position is an Australian skull brought back recently by the Arnhem Land Expedition (USNM no. 380,451). It is not particularly low headed (MHI 81.4), but has larger browridges, amounting almost to a torus, than any I have seen heretofore in modern man. This same skull has a lower facial height (upper) than the Skhūl V man (45.5 vs. 50.3) and almost equally low orbits (65.9 vs. 65.2).

In view of these considerations it seems more romantic than realistic to attribute the variability of the Mount Carmel people to structural instability and the throes of evolutionary change, as McCown and Keith (1939, pp. 13–14) have done, or to hybridization, as Montagu (1940) and Dobzhansky (1944) have done. Both of these explanations require the assumption of contemporaneity for the sample, as well as an emphasis on morphological differences. As I see the evidence of stratigraphic position at Mount Carmel, the primitive and advanced types could have been separated widely in time. Given the element of time, equally large morphological differences, resulting simply from population shifts, could accumulate in a habitation site as desirable as this one seems to have been.

As a modern counterpart, Hrdlička found in Aleutian middens—sometimes exceeding 20 ft. in depth—low heads superimposed on high heads. The accompanying culture had an Eskimoid character and could be divided into early and late periods (Quimby, 1945). It has never occurred to anyone to explain Hrdlička's discovery on the basis of evolutionary throes or hybridization. The populations of *Homo sapiens* are credited with a variability sufficient to encompass this range.

The great variability of modern man is the cause of a difference of opinion among biologists regarding his classification. Some regard the major subdivisions as different species. Gates (1948), for example, arguing that "the primary so-called races of living man have arisen independently from different ancestral species in different continents at different times" has named 5 species under the superspecies *Homo sapiens* (pp. 366–367). Gates' species are: *H. australicus*, *H. capensis*, *H. africanus*, *H. mongoloideus*, and *H. caucasicus*. On the other hand, probably the majority of modern systematists regard *Homo sapiens* as a polytypic species. According to this favored view the subspecies or races of modern man are largely the product of geographic isolation. Obviously, at the rate that group iso-

lation has been breaking down during the historic period, it will be more and more difficult to distinguish human races. I leave to the population geneticists all predictions as to what will happen in the future to human variability.

Our interest here is not alone in the "horizontal" species concept, but also in the "vertical." As we have seen, many anthropologists would carry the earliest representatives of *Homo sapiens* back into the Middle Pleistocene. At the same time, almost no one hesitates to so designate the men of the Late Pleistocene and Upper Paleolithic. Yet there is little reason to believe that what we are calling "*sapiens*" at these various levels is quite the same thing. Upper Paleolithic or Late Pleistocene man differs in general from modern man in being more massive. This is fairly well documented (Morant, 1930-31). In turn, the evidence shows that Middle Pleistocene man differs in various ways from Upper Pleistocene man. Certainly such a feature as the frontal torus, except possibly in the earliest claimed representatives of *Homo sapiens*, shows a progressive diminution from Pleistocene to Recent times. In other words, the revealed general human evolutionary trend cannot be denied. If this point of view has validity, then the forms which are being called "*sapiens*" in the vertical species concept must represent somewhat different and progressively more extreme parts of the horizontal ranges as we go back in time. Thus a so-called "*sapiens*" in the Middle Pleistocene could not have been typical of that time level. This general idea is implied in the term "progressive Neanderthals."

I have questioned already the wisdom of subdividing the human populations of earlier time levels into species or genera. The "*sapiens*"-like forms of the Middle and Upper Pleistocene are not widely different from the "progressive Neanderthals"; and the latter are but natural variants of the classic Neanderthal. The total variability represented by such forms—and they or their equals were probably contemporaneous through the latter half of the Pleistocene—does not appear to exceed that of present-day man, although naturally the range of variability of present-day man has shifted in the progressive direction. Considering that modern man as a whole is commonly regarded as a polytypic species, then these Pleistocene populations likewise qualify for such status. Like Dobzhansky (1944, p. 265), therefore, I can see no reason at present "to suppose that more than a single hominid species has existed on any time level in the Pleistocene." However, I arrive at this conclusion not as he does, from assumed evidence of hybridization, but from the available evidence of population variability.

If there is merit in this argument, then it becomes necessary to express its full implication in terms of systematics. This, it seems to me, is the primary problem presented by the growing need for acceptance of the earliest representatives of *Homo sapiens*. How, for example, does one distinguish taxonomically the somewhat different characteristics of human populations on different time levels? If no more than a single hominid species has existed on any time level in the Pleistocene, where does one species leave off and another begin? If the range of polytypic *Homo sapiens* includes Upper Paleolithic man, how much more can it include? The solution of such questions and of the problem in general I leave to others better acquainted with the aims and rules of taxonomy. All that I set out to do was to show how the problem appears to me in the framework of present knowledge.

In developing this framework I have made a special effort to expose the subjective elements. The glitter of subjectivism in this phase of anthropology, appearing in forms such as morphological and chemical dating, has blinded many to the emerging outlines of the picture. As stated in the beginning (p. 97), I go along with Kroeber in favoring "...the perpetual recognition of how great a part is really played in larger interpretations by the subjective factor."

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DISCUSSION

DOBZHANSKY: The great variability of the Neanderthaloids, so ably described by Drs. McCown and Stewart, bears upon one of the basic problems of human descent. It is now clear that the Neanderthaloids and the so-called *sapiens* type were at no time two reproductively isolated species, but rather component races of a single species. Some modern populations may carry genes that were present in the Neanderthaloids, and other moderns may not carry such genes. But this does not mean, of course, that mankind consists of races descended from Neanderthaloids and other races which came from the *sapiens* type contemporaneous with the Neanderthaloids. In general, the old anthropological alternative of monogenic versus polygenic descent of man ceased to exist when considered from the vantage point of the present evolution theory. Different populations (races) of a polytypic species may be descended largely from different races of the ancestral species and may differ in some genes in which these ancestral races differed. And yet, a polytypic species may still evolve as a single genetic system. Favorable mutants or gene combi-

nations arrived at in one part (race) of such a species may, under the influence of natural selection, eventually spread to all other parts and thus become a common property of the entire species. Thus, local autonomy of the gene pools of racial populations does not preclude retention of a basic unity of the species as a whole. I would like to point out that this view agrees quite well with the conclusions reached by the late Weidenreich on basis of purely morphological analysis of pre-human populations. This is worth while stressing because Dr. Weidenreich has sometimes used expressions which seemed to put him close to the old-fashioned polygenist camp, which he actually rejected absolutely.

BIRDSELL: Without speaking of any particular point on the two preceding papers, I should like to stress an aspect of the consequence of the fluorine redating of the Piltdown remains. In the flurry resulting from its change from first to third Interglacial dating, some seem to have considered that the problem of the interpretation of Piltdown has vanished. The contemporaneity of the mandible and skull have been affirmed by Oakley. This is no guaranty of their organic association, but it increases such a probability. Further, at the late date now given, it becomes increasingly awkward to attribute the mandible to some unknown form of non-human primate. Considerations of time, climate, and ecological competition all make it increasingly improbable that the mandible can be in this fashion disassociated from the vault. Piltdown as now dated, presents a more embarrassing problem than it did in its pre-fluorine chronology.

STEWART: I agree with Dr. Birdsell's new evaluation of the Piltdown problem. If this problem still is not simple, at least it is now shorn of some of the subjectivity formerly connected with the dating of this specimen. The removal of the subjective factor in relative datings of fossils seems to me to be the great contribution of the fluorine method.

TAXONOMIC CATEGORIES IN FOSSIL HOMINIDS

ERNST MAYR

The American Museum of Natural History, New York

It is one of the most fruitful procedures of modern science to bring specialists of various fields together to discuss the problems that concern the zone of overlap of their fields. Not possessing any first-hand knowledge of paleoanthropology, my own contribution to the question of the taxonomic categories of fossil man will be that of a systematist. Significant progress has been made within recent years among biologically thinking taxonomists in the understanding of the categories of subspecies, species, and genus, and it is my hope that this knowledge may help in a better understanding of fossil man.

The whole problem of the origin of man depends, to a considerable extent, on the proper definition and evaluation of taxonomic categories. But, there is less agreement on the meaning of the categories species and genus in regard to man and the primates than perhaps in any other group of animals. Some anthropologists, in fact, imply that they use specific and generic names merely as labels for specimens without giving them any biological meaning. The late Weidenreich, for example, stated that in anthropology "it always was and still is the custom to give generic and specific names to each new type without much concern for the kind of relationship to other types formerly known." Broom (1950) likewise states, "I think it will be much more convenient to split the different varieties [of South African fossil ape-man] into different genera and species than to lump them." The result of such standards is a simply bewildering diversity of names. In addition to various so-called species of *Homo*, the following names for various hominid remains have been found by me in the literature: *Australopithecus*, *Plesianthropus*, *Paranthropus*, *Eoanthropus*, *Giganthopithecus*, *Meganthropus*, *Pithecanthropus*, *Sinanthropus*, *Africanthropus*, *Javanthropus*, *Paleoanthropus*, *Europanthropus*, and several others. No two authors agree either in nomenclature or in interpretation. It seems to me that an effort should be made to give the categories species and genus a new meaning in the field of anthropology, namely, the same one which in recent years has become the standard in other branches of zoology.

A re-evaluation of the terminology of hominid taxonomy is facilitated by the fact that in recent years a magnificent body of new data has been accumulated by anthropologists, partly based on comparative anatomical studies and partly on significant new discoveries of fossil man in southeast Asia and in eastern and southern Africa.

The nomenclatorial difficulties of the anthropologists are chiefly due to two facts. The first one is a very intense occupation with only a very small fraction of the animal kingdom which has resulted in the development of standards that differ greatly from those applied in other fields of zoology, and secondly, the attempt to express every difference of morphology, even the slightest one, by a different name and to do this with the limited number of taxonomic categories that are available. This difference in standards becomes very apparent if we, for example, compare the classification of the hominids with that of the *Drosophila* flies. There are now about 600 species of *Drosophila* known, all included in a single genus. If individuals of these species were enlarged to the size of man or of a gorilla, it would be apparent even to a lay person that they are probably more different from each other than are the various primates and certainly more than the species of the suborder Anthropoidea. What in the case of *Drosophila* is a genus has almost the rank of an order or, at least, suborder in the primates. The discrepancy is equally great at lower categories, as we shall presently see. It is not mere formalism to try to harmonize the categories of anthropology with those of the rest of zoology. Rather, the evaluation of human evolution depends to a considerable extent on the proper determination of the categories of fossil man.

There are two recent developments in general systematics that will be particularly helpful in our efforts. The first one is that the biological meaning of the categories species and genus is now better understood than formerly, and second, that, in the attempt to close the gap between the complexity of nature and the simplicity of categories, the number of existing categories has been augmented by intermediate and group categories, such as "local population" or "local races" and

"subspecies groups." The adoption of these intermediate categories facilitates classification without encumbering nomenclature.

The Taxonomic Categories

The work in the new systematics has led to a far-reaching agreement among zoologists on the meaning of the categories subspecies, species, genus, and family. In the following an attempt shall be made to see how far the current usage of these categories can be extended to fossil hominids and what such a reclassification means in terms of human evolution.

The genus: The genus is a taxonomic category for a group of related species. It is usually based on a taxonomic group that can be objectively defined. However, the delimitation of these groups against each other, as well as their ranking, is frequently subjective and arbitrary. A conventional definition of the genus would read about as follows: "A genus consists of one species, or a group of species of common ancestry, which differ in a pronounced manner from other groups of species and are separated from them by a decided morphological gap."

Recent studies indicate that the genus is not merely a morphological concept but that it has a very distinct biological meaning. Species that are united in a given genus occupy an ecological situation which is different from that occupied by the species of another genus, or, to use the terminology of Sewall Wright, they occupy a different adaptive plateau. It is part of the task of the taxonomist to determine the adaptive zones occupied by the various genera. The adaptive plateau of the genus is based on a more fundamental difference in ecology than that between the ecological niches of species.

Unfortunately, there is no such thing as a recognized or absolute generic character. This was known already to the earlier taxonomists, in fact, Linnaeus stated, "It is the genus that gives the characters, and not the characters that make the genus." The genus is a group category and it defeats the object of binomial nomenclature to place each species into a separate genus, as has been the tendency among students of primates.

The acceptance of the new concept of biologically defined polytypic species (see below) necessitates the upward revision of all other categories (Mayr, 1942). Often what was formerly a group of allopatric species is now a single polytypic species with numerous subspecies. To leave each of these polytypic species in a separate genus deprives the genus of its significance as a truly collective category. I shall illustrate this need for the combining of genera by an example. Gorilla and chimpanzee are two excellent species which, as Professor Schultz has shown, differ from each other by a wealth of characters. At one time several species of gorillas and of chimpanzees were recognized, but the allopatric forms within the two species are now considered subspecies. Being left with one species of gorilla and one species of chimpanzees, we are confronted by the question whether or not they are sufficiently different to justify placing them in different genera. A specialist of anthropoids impressed by the many differences between these species may want to do so. Other zoologists will conclude that the differences between the two species are not indicative of a generic level of difference when measured in the standards customary in most branches of zoology. To place these two anthropoids into two separate genera defeats the function of generic nomenclature and conceals the close relationship of gorilla and chimpanzee as compared with the much more different orang and the gibbons. Recognizing a separate genus for the gorilla would necessitate raising the orang and the gibbon to subfamily or family rank as has indeed been done or suggested. This only worsens the inequality of the higher categories among the primates.

The same is true for the fossil hominids. After due consideration of the many differences between Modern man, Java man, and the South African apeman, I did not find any morphological characters that would necessitate separating them into several genera. Not even *Australopithecus* has unequivocal claims for separation. This form appears to possess what might be considered the principal generic character of *Homo,* namely, upright posture with its shift to a terrestrial mode of living and the freeing of the anterior extremity for new functions which, in turn, have stimulated brain evolution. Within this type there has been phyletic speciation resulting in *Homo sapiens.*

The claim that the many described genera of hominids and Australopithecines have no validity, if the same yardstick is applied that is customary in systematic zoology, is based on two major points. Both of these are admittedly somewhat vulnerable. One is the overall picture of morphological resemblance with a deliberate minimizing of the brain as a decisive taxonomic character. To this point we shall return presently. The other point is the assumption that all these forms, including *Australopithecus,* are essentially members of a single line of descent. Additional finds

might easily disprove this. However, taking all the available evidence together, it seems far more logical and consistent at the present time to unite the hominids into a single genus than to continue the current multiplicity of names.

This re-evaluation of the generic status of the fossil hominids forces us to consider also the categories above the genus. Does *Homo* belong to a separate family Hominidae? The morphological differences between *Pongo*, the genus to which the chimpanzee and gorilla belong, and *Homo* are so slight that there seems to be no jus tification for placing them in separate families. There is even less justification for placing South African man in a separate subfamily, the Australopithecinae. The most primitive known hominids, those of South Africa, combine certain typical hominid characters, such as upright posture, with others that are usually considered simian, such as small size of brain and protruding face. It is noteworthy, however, as pointed out by several investigators, that these hominids, even at this primitive stage, lack certain other simian features that were formerly considered as primitive: powerful canines, large incisors, a sectorial form of the first lower premolar, an exaggerated development of the supra-orbitals, a simian shelf, and powerful brachiating arms. It now appears probable that many of these characters are functional specializations which were acquired by the anthropoid apes after the hominid line had branched off.

The fact that the hominids lack these specializations has been used by some authors as evidence to postulate a very early human origin and a very isolated position of the hominid branch. This is by no means the only possible interpretation. Rather it seems to me that most of these typical characters of the living anthropoids may well be a single character complex evolved in response to a highly arboreal mode of living. It now appears probable that the African anthropoids, the orang, and the gibbons, may have acquired most of these characters independently and are therefore, in a sense, a polyphyletic group. The available evidence seems to indicate to me that man may be more closely related to the gorilla-chimpanzee group than this group is either to the orang or to the gibbons. The degree of similarity in certain morphological traits cannot necessarily be used to measure degree of phylogenetic relationship. The arboreal, brachiating large anthropoids are exposed to a similar type of selection and will therefore evolve in a parallel, if not convergent, manner. When the *Homo*-line acquired upright posture it entered a completely different adaptive zone and became exposed to a severely increased selection pressure. This must have resulted in a sharp acceleration of evolutionary change leading to the well-known differences between man and the living anthropoids. This factor must be taken into consideration when the phylogeny of man and the anthropoids is reconstructed. It would therefore appear to be misleading from the purely morphological-phylogenetic point of view to separate man from the anthropoid apes as a special family. It would be equally misleading to go to the other extreme and to use the evidence of the somewhat independent evolution of man and the various anthropoids as a means to deny their close relationship.

Denying the genus *Homo* family rank is based on purely morphological considerations. It does not take into account man's unique position in nature. Man has undoubtedly found an adaptive plateau that is strikingly different from that of any other animal. There are some who feel that there is only one way by which to emphasize this uniqueness of man, namely, by placing *Homo* into a separate family. The conventional standards of taxonomy are insufficient to decide what is correct in this case.

From the purely biological point of view man is certainly at least as different as a very good genus. We have thus the evolution of a new higher category in the geologically short period of one to two million years. This is another significant illustration for the rapidity by which one major taxonomic entity can be transformed into another one, without any jumps.

The subspecies: Before we can attempt to answer the question how many species of fossil man have existed, we must say a few words on infraspecific categories. The species of the modern systematist is polytypic and multidimensional. It has the geographical dimensions of longitude and latitude and also the time dimension. It is polytypic because it is composed of lower units, such as subspecies and local populations. Customarily in anthropology, distinct local populations have been referred to as races, and a similar custom exists in some branches of zoology as, for example, in ichthyology.

The amount of geographical variation and the degree of difference among the geographical subdivisions of a species are different from case to case. Some species appear quite uniform throughout their entire range; other species have a few or many more or less well defined subspecies. For instance, the two African forest anthropoids, chimpanzee and gorilla, show only a moderate

amount of geographical variation, although both have well-defined subspecies, and attempts have been made to split the chimpanzee into several species. Geographical variation is much more pronounced in the orang and even more so in some of the South American monkeys where geographical races are often different enough to be considered full species by conservative authors.

Modern man is comparatively homogeneous because there is much interbreeding between different tribes and races. Still, we find in close neighborhood to each other such strikingly different races as bushmen and Bantus in South Africa, or the Congo pygmies and Watusi in central Africa, or the Wedas and Singhalese in Ceylon. There is much indirect evidence that primitive man was much more broken up into small scattered tribes with little contact with each other, intensely subject to local selective factors.

In addition to this much greater geographical variation of primitive man, there is evidence also of greater individual variation (including sexual dimorphism). The variability of Mt. Carmel man has been commented upon in the literature. It seems possible, if not probable, that the various South African finds, *Australopithecus*, *Plesianthropus*, and *Paranthropus*, might well be age or sex stages of a few related tribes, notwithstanding Broom's (1950) assertions to the contrary.

Differences between young and adult and between male and female appear to be greater in the gorilla and orangutan than they are in modern man. Variability may increase or decrease in the course of evolution. Abundant proof for this statement can be found in the paleontological literature. I interpret the available literature to indicate that primitive man showed more geographical as well as individual variation than modern man.

Why primitive man should have been more variable than modern man is not entirely clear. A study of the family structure of anthropoids might shed some light on this problem. Perhaps there was a greater functional difference between male and female than in modern man. Perhaps the ancestral hominids had a system of polygamy that would favor the selection of secondary sex characters in the male. We don't know. Whatever the reasons, we should not use the variability within populations of modern man as a yardstick by which to judge the probable variability of extinct populations.

This point is important because it bears on the question whether or not more than one species of hominid has ever existed on the earth at any one time. Indeed, all the now available evidence can be interpreted as indicating that, in spite of much geographical variation, never more than one species of man existed on the earth at any one time. We shall come back to this point later.

The species: As described in several publications, the concept of the species has undergone a considerable change during recent years. The morphological and typological species of the early taxonomists has been replaced by a biological species. The species is now defined "as a group of actually or potentially interbreeding natural populations that is reproductively isolated from other such groups." When this concept is applied to man, it is at once obvious that all living populations of man are part of a single species. Not only are they connected everywhere by intermediate populations but even where strikingly distinct human populations have come in contact, such as Europeans and Hottentots, or as Europeans and Australian aborigines, there has been no sign of biological isolating mechanisms, only social ones.

The problem of species delimitation is much more difficult with respect to fossil man. How shall we determine which populations are "actually or potentially interbreeding"? It is evident that we must use all sorts of indirect clues. The first concrete problem is what types of fossil man should be included in the species *Homo sapiens*. Cro-Magnon man is so nearly identical with *Homo sapiens* that its inclusion in that species is not doubted by any serious student.

The problem of Neanderthal man is much more difficult. Should he be included in the same species as modern man or not? When the first finds of Neanderthal man were made there seemed to be no problem. These fossils were characterized by distinct morphological features and were clearly replaced by modern man in Europe on a distinct chronological level. There is no morphological or cultural intermediacy. Additional finds, however, have caused various difficulties. In Palestine the Mt. Carmel finds belong to a population that combines some features of Neanderthal with some of modern man. It is immaterial whether we interpret this as a hybrid population, as an intermediate population, or as a population ancestral to both. The fact remains that Mt. Carmel man makes the delimitation of modern man from Neanderthal exceedingly difficult, if not impossible, as pointed out by Dobzhansky (1944). Weidenreich supported the theory that modern man was a direct descendant of Neanderthal man. Boule and others have raised serious objections to this theory. But how can we reconcile the

apparently incompatible views that modern man and Neanderthal are conspecific and that modern man is *not* a descendant of typical European Neanderthal? A possible clue is furnished by the hominids that were widespread in Europe in mid-Pleistocene. The skulls of Steinheim, Swanscombe, and of Fontéchevade combine features of modern man and of Neanderthal man, together with primitive and specialized features of their own. They lived apparently in inter-glacials and were more closely linked with a warm climate than Neanderthal man.

If I understood the evidence correctly, it is possible to interpret these early European fossils as remains of populations of *Homo* that were ancestral both to *sapiens* and to "classical" Neanderthal and from which these two forms evolved by geographical variation. Tentatively the working hypothesis can be made that Neanderthal in its classical form was a geographical race that occurred in central Europe and was represented in Africa by Rhodesian man and in Java by Njandong man, while a more *sapiens*-like population occurred at the same period as some of these Neanderthaloids either in north Africa or western Asia or in some other area that has not yet yielded remains of fossil man. When *sapiens* began to expand and spread, he eliminated the other contemporary races just as the white man drove out the Australian aborigines and the North American Indians. The process of elimination of the Neanderthal characters in mixed populations was presumably helped by selection preference in favor of the characters of modern man.

It is very probable that additional finds will make the delimitation of *sapiens* against Neanderthal even more difficult. It seems best to follow Dobzhansky's suggestion and to consider the two forms, as well as the ancestral group that seems to combine their characters, as a single species.

Homo erectus: Java and Peking man are sufficiently distinct from modern man so that they have to be considered a separate species, which must be called *Homo erectus*. This is true regardless of the fact that on Java, at least, Njandong and Wadjak man may have formed a practically unbroken chain of hominids leading from Java man to modern man. Peking man (*Homo erectus pekinensis*) is, on the whole, so similar to Java man that it should be considered merely subspecifically distinct, as I proposed previously (Mayr, 1944).

In spite of its obvious similarity to *Australopithecus* too little is known of the still earlier Java *Meganthropus* to assure a correct classification. This is even more true of *Giganthopithecus* whom some authors consider hominid and others anthropoid. One thing about *Giganthopithecus* is, however, very probable, namely, that it was not necessarily a giant in spite of its giant teeth. Jaws and teeth of early fossil man were relatively much larger than they are in modern man.

Homo transvaalensis: South African ape-man again is one level further back and is sufficiently far removed from Java man to be considered a full species. Actually, no less than three genera and five species of South African ape-man were described which, in Broom's terminology, have the following names: *Australopithecus africanus* 1925 (Taungs), *A. prometheus* 1947 (Makapan), *Plesianthropus transvaalensis* 1936 (Sterkfontain), *Paranthropus robustus* 1938 (Kromdraai), and *Paranthropus crassidens* 1949 (Swartkrans). Most of these names may not have any validity, according to the Rules of Zoological Nomenclature, Article 25A, as revised in 1930. According to these Rules a name has validity only if the description includes diagnostic characters. Since one of these names was based on a child, another on an adult female, a third on an adult male, an enumeration of diagnostic differences is virtually impossible. The extant skulls are somewhat altered in shape due to crushing, and the fact that the cephalic index in the Taungs child is 62.4 while it is 83.5 in the Sterkfontein male is therefore not as significant as Broom thinks. Nor is the fact that the finds are associated with different faunas. Contemporary modern man can be found associated with okapis or elephants or tigers or kangaroos, or South American edentates or with polar bears. The various finds of South African man are presumably not contemporary, but there is nothing in the evidence that has so far been presented (e.g. Broom, 1950) that would prove that more than one species is involved.

Until a real taxonomic distinction has been established, it will be safer and more scientific to refer to the different South African fossils by vernacular names. There is no danger of confusion if we speak of the Sterkfontain or Makapan finds, while it implies an obviously erroneous conclusion, namely that of generic distinctness, if we refer to them as *Plesianthropus* and *Australopithecus*. New discoveries are still being made in these cave deposits and many of those that have already been made have not yet been fully worked out. There is good reason to believe that it will be firmly established in the not-too-distant future how many different tribes, temporal subspecies,

or even species of South African ape-man once existed. To consider them all as one species is the simplest solution that is consistent with the available evidence.

A more important question is whether South African man is ancestral to modern man or merely a specialized or aberrant sideline. The exact dating of these fossils has not yet been achieved but they are believed to be very early Pleistocene or latest Pliocene, in fact, they presumably ranged over a considerable period of time. There is thus no definite chronological reason why the South African ape-man could not be considered a possible ancestor of modern man. The principal objection that has been raised is that South African man shows a combination of characters that "should not" occur in an early hominid. This argument is based on typological considerations. Adherents of this concept believe that missing links should be about half-way between the forms they connect and that they should be half-way in every respect. This undoubtedly is not the case with *Australopithecus*. It is apparently amazingly like modern man in its upright posture, structure of the pelvis, and other features, while it is very simian in its massive mandibles, large molars, prognathism, and small brain. *Australopithecus* lacks those specializations that stamp gorilla, orang, and gibbon as typical anthropoids.

The peculiar combination of characters that is found in *Australopithecus* is due to the fact that during evolution of man different characters evolved at different rates. If we would set the point where the human line branched off from the other anthropoids as zero and the *Homo sapiens* stage as 100, we might give arbitrarily the following points to the various organs of *Australopithecus*: pelvis, 90; premolars, 75; occipital condyles, 80; incisors, 55; the setting of the brain case, 70; shape of the tooth row, 70; the profile of the jaw, 30; the molar teeth, 40; the brain, 35; etc. It is obvious that one type does not change into another type evenly and harmoniously, but that some features run way ahead of the others.

The inability to understand this has been the reason for Weidenreich's insistence that *Eoanthropus* was an artifact. He maintained with respect to Piltdown man: "Form and individual features of the brain case are generally acknowledged as those of modern man; those of the lower jaw have anthropoid characteristics. Therefore, both skeletal elements cannot belong to the same skull." As a matter of fact, the skull cap is not strictly modern nor is the jaw strictly anthropoid and the recent fluorine content determination by Oakley (1950) indicates that, indeed, jaw and skull cap may be of the same geological age.

It may take a long time before the Piltdown puzzle is completely cleared up. As a working hypothesis it might be suggested that Piltdown man represents a geographical race of man that was restricted to northwestern Europe. Some of the characters, particularly in the jaw, appear to be specializations rather than indications of primitiveness, perhaps developed in connection with the large size of the individual. The phylogenetic and chronological relationship of Piltdown to the other hominid finds indicated by the the words Heidelberg, Steinheim, Swanscombe, and Fontéchevade still remains to be determined.

The simplified nomenclature of fossil man: Reducing the bewildering assortment of genera and species of hominids to one genus with three species results not only in simplicity but it also makes certain conclusions obvious that were previously not apparent. Before discussing these conclusions, however, I might point out some of the disadvantages of such a simplified classification.

There have been two trends in human evolution as, indeed, there are in the evolution of all organisms. First of all, there is a continuous evolutionary change in time, the so-called phyletic evolution, starting in the hominids with the most simian forms and ending with modern man. Simultaneously a centrifugal force has been operating, namely, geographical and other local variation, which tries to break up the uniform human species. This geographic variation leads to the formation of races and subspecies, and if this trend would go to completion, to the formation of new separate species. There are all sorts of intermediate stages in both these trends and it is obvious that all the many possible differences and gradations between the various kinds of hominids cannot be expressed completely in the simple nomenclature of species, genus, and subspecies.

For instance, man as he exists today, has pronounced racial groups, such as the Whites, Negroes, and Mongoloids, which might well deserve subspecific recognition. But there are minor racial differences within each of these subspecies. Furthermore, preceding modern man there have been types of *Homo sapiens* that are now extinct, like Cro-Magnon man and his contemporaries. This, no doubt, is a different level of subspecies from those of living man. Neanderthal man is a third level, and the pre-Neanderthal man, who combines certain features of *sapiens* and Nean-

derthal, is a fourth level. It is unsatisfactory for biological, as well as for practical reasons, to treat each of these levels as a separate species. On the other hand, combining them into a single species conceals the pronounced differences between these levels and reduces the taxonomic difference between Neanderthal and modern man to the level of difference between White Man and Negro. How can this be avoided?

First of all, we must realize that no system of classification and nomenclature can ever hope to express adequately the complicated relationships of natural populations. However, by giving species and genus the well-defined meanings that we have assigned to these categories, we make at least an attempt to standardize taxonomic categories and make them comparable. A possible solution of our particular difficulties may come from a refinement of the levels of infraspecific categories. In addition to the subspecies we may use such infrasubspecific categories as "race" and "local population," as well as the suprasubspecific category of the "subspecies group." Hence, we should be guided by the following practical rules:

1. Not to assign a formal name to any local population or race that does not deserve subspecific rank.

2. To give trinomials to all forms that do not deserve higher than subspecies rank.

3. To group together as subspecies groups all those subspecies within a species that form either geographical or chronological groups.

Such subspecies groups in *Homo sapiens*, for instance, might be:

(a) modern man
(b) Neanderthal group
(c) pre-Neanderthal group

4. Not to give formal generic and specific names to new fossil finds that are not sufficiently known. Vernaculars, such as "Steinheim man" or "Piltdown man," are just as useful and much less misleading. The formal application of generic and specific names simulates a precision that often does not exist. To give the impression of an unjustified precision is as much of a methodological error as to make calculations to the fifth decimal when the accuracy of the original data extends only to the first decimal.

Anthropologists should never lose sight of the fact that taxonomic categories are based on populations, not on individuals. Different names should never be given to individuals that are presumably members of a single variable population.

Conclusions

The arranging of all finds of fossil hominids into a single genus with three species helps to focus attention on the following conclusions.

The question of the "missing link." Ever since there has been an appreciation of man's anthropoid origin there has been a search for the "missing link." Some anthropologists may disclaim this and say that they realize the gradual evolution of mankind but the fact remains that accurate criteria of humanhood are elaborated even in the most recent literature, such as Sir Arthur Keith's criterion of the brain volume of 750 cc.

The analysis of this problem will be facilitated by the realization that it is an oversimplification to use in this case the uninomial alternative "ape" versus "man." Taxonomists know by experience the inadequacy of uninomialism. Classifying man binomially as *Homo sapiens*, it at once becomes apparent that we must look for two missing links, namely that which connects *sapiens* with his ancestor and that which connects *Homo* with his ancestor. Or, to express this differently, the two points of interest are the one on the phyletic line of man where he reached the *sapiens* level and second the place where the *Homo* line branched off from the other primates.

Let us look more closely at these two problems of the origin of man. The branching off of *Homo* from the other anthropoids was a case of orthodox speciation distinguished only by the fact that the new species simultaneously reached a new adaptive plateau. It is now evident, as has been stated by many authors, that a change in the mode of locomotion and a corresponding alteration of the entire organization of the body, in other words, the assuming of the upright posture, were the essential steps that led to the evolution of *Homo*. This evolutionary trend apparently affected first the pelvis and posterior extremities, followed closely by the anterior extremities. The corresponding re-organization of the skull lagged apparently behind. It is therefore singularly difficult to localize both in time and space this important evolutionary step of the attainment of the upright posture with the help of jaw and tooth fragments, such as constitute most of the primate and anthropoid remains in eastern Africa during Pliocene and Miocene.

To determine the exact point in the phyletic evolution of *Homo* where the *sapiens* level was reached, is quite impossible. It was a very gradual process leading from *erectus* to *sapiens*

and no particular form can be singled out as the missing link. However, there is a lower level in the phyletic evolution of *Homo* that is of special evolutionary interest, namely, the level at which the hominids first displayed those intellectual qualities that are considered distinctly human rather than simian.

Attempts have been made to measure the attainment of this *Homo* level in terms of brain size. This method is fraught with difficulty. First of all, brain size is to some extent correlated with body size. If, for instance, a large gorilla should have a brain of 650 cc. this is not at all necessarily equivalent to the brain of a fossil hominid of 650 cc., if that hominid were much smaller than a gorilla. If the brain of the gorilla averages one-fourth larger than that of the chimpanzee, it does not mean that he is on the average 25 per cent more intelligent. The correlation between brain size and intelligence is very loose. There is good evidence that the brain size of late Pleistocene man may have averaged larger than that of modern man. If true, this does not mean necessarily that there has been a deterioration of man's intelligence since the Pleistocene, for intelligence is determined not only by brain size. It is, of course, still unknown what neurological structures affect intelligence but the folding of the cortex and all sorts of specializations within the cortex appear to be as important as size. It is therefore dangerous, in fact, outright misleading, to use size as an absolute criterion and to say that the *Homo* stage was reached when brain size reached a level of 700 or 750 cc.

It has been suggested to measure the attainment of the human level by some cultural achievement, such as the use of fire, rather than by an anatomical standard like brain size. This is unquestionably a superior approach, but has the practical difficulty that the first moment of fire making was not fossilized and can never be dated accurately. However, the first making of fire may have occurred not much after the first use of tools by hominids and some lucky finds may shed light someday on the period when that occurred. South African man was presumably already a user of tools, and the first use of tools may be coincident with the evolution of South African man.

Speciation in man: In the strict sense of the word, speciation means the origin of discontinuities through the origin of reproductive isolating mechanisms. How often has man speciated? The answer is that he has speciated only once if our assumption is correct that never more than one species of man existed on the earth at any one time. This single event of speciation was the branching off of *Homo* from the anthropoid stock. That some fairly distinct hominid remains have been found in approximately contemporary deposits does not prove their specific distinctness. The sub-division of the human species into independent tribes favors diversification. If fossils of Congo pygmies and of Watusi were to be found in the same deposit by a paleontologist, a million years hence, he might well think that they belonged to two different species. As stated previously, the known diversity of fossil man can be interpreted as being the result of geographic variation within a single species of *Homo*. This led to the evolution of such aberrant types as Piltdown man of England, but apparently nowhere to the simultaneous occurrence of several species of *Homo*. What is the cause for this puzzling trait of the hominid stock to stop speciating in spite of its eminent evolutionary success? It seems to me that the reason is man's great ecological diversity. Man has, so to speak, specialized in despecialization. Man occupies more different ecological niches than any known animal. If the single species man occupies successfully all the niches that are open for a *Homo*-like creature, it is obvious that he cannot speciate. This conforms strictly to Gause's Rule. Also man is apparently slow in establishing isolating mechanisms. This is indicated by the numerous instances of incomplete speciation in the history of the hominids. In no case was this speciation completed because the segregating populations were either absorbed by intermarriage or exterminated. Man is apparently particularly intolerant of competitors. The wiping out or absorption of primitive populations by culturally more advanced or otherwise more aggressive invaders, which we have witnessed so many times during the eighteenth and nineteenth centuries in Australia, North America, and other places, has presumably happened many times before in the history of the earth. The elimination of Neanderthal man by the invading Cro-Magnon man is merely one example.

There is one striking difference between man and most of the animals. In animals whenever there is competition between two subspecies the one that is better adapted for a specific locality seems to win out. Man, who has reached such a high degree of independence from the environment, is less dependent on local adaptation, and a subspecies of man can quickly spread into many geographically distant areas if it acquires generalized adaptive improvements such as are described by the social anthropologist. Such improvements do not need to and probably often do not have genetic basis. The authors who have claimed that man is

unique in his evolutionary pattern are undoubtedly right. Even though the phyletic evolution of man will continue to go on, the structure of the human species at the present time is such that there appears to be very little chance for speciation, that is, for the division of the single human species into several separate species.

SUMMARY

1. There is no conclusive evidence that more than one species of hominids has ever existed at a given time.

2. It is proposed to classify fossil and recent hominids tentatively into a single genus (*Homo*) with three species (*transvaalensis*, *erectus*, *sapiens*).

3. The recognition of subspecies groups within the species facilitates classification.

4. The ecological versatility of man and his slowness in acquiring reproductive isolating mechanisms have prevented the breaking up of *Homo* into several species.

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DISCUSSION

LASKER: I wonder how Professor Mayr would justify considering men, gorilla and orang to belong to three different genera, but man, the australopithecines and Piltdown man to belong to one genus. Considered purely morphologically, an animal with "ape-like" jaw and "man-like" skull cap, such as Piltdown, if the parts really belong to one form, differs greatly from one with anthropoid brain case and more human jaw, such as *Australopithecus*.

Incidentally, I can think of no adequate anatomical reason for associating the Heidelberg jaw with "*Pithecanthropus*" rather than with the Neanderthaloids.

MAYR: Since there are no absolute generic characters (see above), it is impossible to define and delimit genera on a purely morphological basis.

MONTAGU: I think it should be noted that convenience can be pushed to such a point that it becomes a confounded nuisance. When, to paraphrase A. E. Housman, the ambiguity of language is brought in to add to the already existing confusion of thought, as has been done in the anthropological taxonomy of fossil man, confusion is rendered worse confounded, and "convenience" becomes an impediment to clear thinking and further progress. The terminology of palaeoanthropology provides an unfortunate example of the systematics of confusion. When types such as Java man and Pekin man can be referred to by generic names—*Pithecanthropus* and *Sinanthropus* —when, in fact, they represent no more than two subspecies or geographic races, it were high time that we did something to bring the taxonomic practice of palaeoanthropology more into line with its own theory and the practice of the newer systematists. I should therefore seriously suggest that a committee, consisting of such men as Drs. Mayr and Dobzhansky, and several palaeoanthropologists, be appointed to consider the matter of revising the nomenclature which is at present confusing the field of palaeoanthropology.

SCHULTZ: It has been long overdue and is most welcome that expert taxonomists come to the aid of anthropologists in modernizing the nomenclature of the Hominidae which has reached such absurdities as the *generic* separation of Java man and Peking man. Doctor Mayr's highly valued proposals for taxonomic reforms are rather startling to anthropologists who still hope that their Latin or Greek binominal terms can imply consistently degrees of distinction. To recognize only three species of *Homo*, of which one is assigned to the Australopithecines and another to everybody from Neanderthal man to ourselves, is a very sudden jump from one, old extreme to an opposite, new extreme, even though the latter is undoubtedly more consistent with general usage in modern systematics.

Doctor Mayr's interesting suggestion that gorilla and chimpanzee represent only different species of one genus, because the skulls of the latter are very similar to female skulls of the former, deserves comment as an excellent example to remind us, how unjustifiable it can be at times to assume close relationship between animals on the basis of close cranial resemblance alone (in one sex only). Even though the skulls of adult female gorillas differ from those of adult chimpanzees to only limited degrees, the skulls of adult male gorillas are vastly different, because sex differences in gorillas are extremely pronounced in

contrast to those of chimpanzees which are generally less marked than in man. In other bodily features the two African apes can differ enormously. For instance, the proportionate size of the testes is extremely small in gorillas, whereas extremely large in chimpanzees, the female sexual skin shows very different changes in the two types, chimpanzees have relatively huge outer ears, gorillas very small ones, the hand is long and slender in chimpanzees, but relatively broader in gorillas than in any other simian primates, etc. If these and many other constant distinctions are mere species differences, then the comparatively few known differences between Peking man and Rhodesian man, e.g., would deserve at most subspecific rank.

With these remarks I wanted to point out chiefly that it will require more such profitable meetings between anthropologists, primatologists and taxonomists before we can expect a generally acceptable, detailed, and much needed change in the systematics of past and present higher primates.

WASHBURN: I feel that it is useful to have separate names to specify each of the major adaptive groups of the primates. Traditionally, such groups as galagoes, lorises, or monkeys were given family status. If this continues to be done, then it is convenient to put apes and men in separate families, indicating the difference between arboreal brachiation and bipedal ground living. Within the human family two groups may be recognized, the small-brained man apes and large-brained, tool using man. It may be well to keep the generic names *Australopithecus* and *Homo* for these. I thoroughly agree with Dr. Mayr on the desirability of abolishing most of the genera he has mentioned. But too few names can be confusing, and I wonder if Dr. Mayr would feel this suggestion is counter to his idea.

MAYR: An unequivocal decision on the ranking of the groups that are included in the higher categories seems impossible. However, the morphological difference between galagoes, lorises, and monkeys seems much greater than that between anthropoids and man. Furthermore, within the single family Cercopithecidae (old world monkeys) there seems to be greater morphological variation (e.g., between macaques, baboons, langurs) than there is morphological difference between man and the anthropoids.

As far as brain size and use of tools is concerned, there has been apparently a continuous line of development from the primitive hominids to modern man. Java man (? or ape-man) is so completely intermediate between South African man and modern man, and the difference between these two terminal forms so much a matter of degree, that it seems questionable whether these evolutionary stages justify generic separation. The difference is certainly not equivalent to a generic difference in most groups of animals.

CLASSIFICATION OF FOSSIL MEN

CONCLUDING REMARKS OF THE CHAIRMAN

WILTON MARION KROGMAN

Graduate School of Medicine, University of Pennsylvania

It is the function of a Chairman to synthesize and to evaluate; synthesize, in the sense that he should try to draw together, to coordinate, the content of the several essays; evaluate, in the sense that he should point the common theme or concepts in the presentations.

There is one thing in common to all the essays: they are talking about us, however remote in time, however modified in form. Moreover, two are by physical anthropologists, so they have that in common; one is by a systematist—and there's nothing common about that! It is not strange, therefore, that all three essays stress the oft confusing role of the personal or subjective element in the vexing problem of human evolution. McCown points out the basic need of early students of human evolution to prove the "primitiveness" and "difference" of Neanderthal Man in order to uphold a time-established Darwinian hierarchy. In his opus major, Boule—using the La Chapelle male as the archetype—felt impelled to demonstrate a homogeneity of type, time, and culture for Neanderthal Man. Stewart strikes the note of the morphologist, who in a blind adherence to "pure morphology" as a criterion of evolutionary stage, was able to disregard ancillary geologic, paleontologic, and cultural evidence. But he also quotes Kroeber on the value of a "good intuition" (my intuition tells me that the intuition of the other chap is apt to be faulty).

Mayr strikes a much more serious note when he says that "the whole problem of the origin of man depends... on the proper definition and evaluation of taxonomic categories." Even after he has defined the genus he goes on to say that "there is no such thing as a recognized generic character." Here problems of human origin and classification meet on the same ground: the need to set up a mechanism whereby traits of taxonomic import may first be defined—in a functional, meaningful direction—and secondly, evaluated, in a morphogenetic sense. There is little value in a trait-list that is merely a roll-call of observed morphological difference; there is even less value in an assumption of traits presumed either to be genetically unique (independent) or in a complex (linked, in various categories). The glutaeus maximus may have played an important role in human evolution; that does not give it the right to be the literal basis of arm-chair speculation!

The problem of sampling has been stressed by all three essayists. McCown has in a very illuminating fashion demonstrated how the 80-90 Neanderthalers really breaks down to a mere handful of less than 20 skulls. Stewart has, by enumerating the finds, called our attention anew to the fact that the finds are chance, are scattered, are incomplete, and are often unique. Mayr has struck at the heart of this situation by pointing out that "taxonomic categories are not based on individuals, but on populations." In a strict sense, therefore, the genetic analysis of fossil man faces the almost insurmountable barrier of the inadequacy of the available material. It is well-nigh impossible to speak of fossil "populations," except as it is assumed that the finds—most of them unique—somehow represent either a typical representative of an assumed stable population, or that the small total samples that are available are truly random.

This brings us to the problem of variability, a problem which, in the present discussion, must be referred to evidence from organic evolution generally. It is, I think, an accepted concept that, within a given form, variability may increase or decrease during the course of evolution; presumably the stimulating or selective factors—whatever they may be—vary directly. Certain it is that we dare not use the relatively homogeneous modern *Homo* as a standard, i.e., we cannot predicate ancient variability (or non-variability) upon present variability. Mayr throws out the suggestion that early *Homo* may have been more heterogeneous, with greater individual variability. If this be so then the problem is compounded: to inadequate and dubious sample must be added doubt as to representativeness.

What, then, can be done about it? The answer is simple, but not clear: we have to do the best with what we have. This inevitably means analytic description, both morphologic and morphometric—we observe and categorize, we measure

and evaluate. All of the essayists have mentioned this, either directly or by implication. Stewart discusses the caution necessary in the morphologic approach, and in evaluating the Neanderthal -*sapiens* problem mentions specific morphologic traits. McCown follows the trait trail when he says that "structurally in skull, face and teeth Neanderthal is intermediate between *Pithecanthropus* and *Homo sapiens*." Mayr goes even further in a trait-for-trait evaluatory sense when he takes up the problem of "primitive" in establishing a Family category. He enumerates such traits as powerful canines, larger incisors, sectorial lower molars, etc. In this categorical sense he concludes them to be specializations. Again, he employs the trait-evaluation technic with a slightly different emphasis when he illustrates the unequal rate of evolution in the Australopithecines by giving a percentage equivalent (taking the Anthropoid-Homo split-off as zero) for each of 9 traits, listing pelvis, teeth and brain-case as win, place, and show, with brain an "also ran."

It does not appear as tho either the physical anthropologist or the taxonomist has gone very far in solving the very complex problem of "weighting" traits of potential use in classification. Here, once more, we join with those concerned with problems of ultimate Primate origins. With them, we agree that observation and experimentation must combine to isolate meaningful traits in terms of genetic independence, or in terms of functional adaptiveness. If, as it fully appears, different traits evolve at different rates, and one type does not blend into another evenly or harmoniously, then it is encumbent upon us, jointly, to try to find out why these observations are true (assuming that they are).

There is a further stricture that might be added here, viz., that the physical anthropologist has often listed every cranial and skeletal trait as if, by sheer weight of numbers, he could resolve the basic fallacy of trait-categorization, i.e., the assumption, tacit or stated, that all traits are of equal value. The fossil hand of tradition has extracted so-and-so many measurements, indices, observations; the time is ripe to concentrate upon the ascertained and evaluated few, reject the futile many.

The crux of classification of fossil men has sort of dwindled to an "is-you-is or is-you-ain't?" situation, at least as far as the Neanderthal-*sapiens* problem is concerned. In the first place, as Stewart points out, a definition of *sapiens* has been very carefully avoided. We are aware of *sapiens* man more because of his "non-Neanderthal" and "advanced" traits than by an exact definition. Stewart goes on to say that "in and before the last inter-glacial period there existed in Europe, and probably elsewhere, men with less 'primitive' cranial features than those of the succeeding more advanced cultural period—the Neanderthal men of the Mousterian age." On this point McCown observes that "while the pattern for the (Neanderthal) group is distinctive, it seems to me impossible to hold any longer to the viewpoint of a morphological hiatus between modern man and the Neanderthal population." Mayr, after defining the species, says that all living *Homo* is a single species, *sapiens*, but specific traits are not given. We are left with the feeling that the *sapiens* category is set up, but not precisely defined. Obviously, then, we must fall back upon such adjectival delimitations as "primitive" vs. "advanced," "gerontomorphic" vs. "pedomorphic," "Neanderthal" vs. "non-Neanderthal," and so on. As a result the Neanderthal type becomes the nucleus of the argument.

There is, among the essayists, a general agreement that the Neanderthal type is a recognizable morphologic entity. There is, however, a variable interpretation as to its relation to a *sapiens* form; the feeling seems to be that differences do exist, of a degree, however, rather than of a kind. Stewart observes that "the '*sapiens*'-like forms of the Middle and Upper Pleistocene are not widely different from the 'progressive Neanderthals'; and the latter are but natural variants of the classic Neanderthals." McCown feels that there is a greater distinction to be made; when the Palestinian and European Neanderthalers are pooled this still "does not negate the morphological distinctiveness of the Neanderthal pattern ... and a generalized *Homo sapiens* pattern." He further adds "that no one known group of living races or of their terminal Pleistocene forbears of themselves form a simple transition to the morphological pattern of the greater Neanderthal group." Mayr is quite clear on the point: he places Neanderthal and *Homo sapiens*, together with their ancestral forms, in a single species. The Neanderthal type is regarded by him as a geographical race, with possible representatives in Africa (Rhodesian) and Java (Ngandong).

The problem of the classification of fossil man has been illuminated by the three essayists, but not fully clarified, and certainly not settled. Several propositions emerge which seem basic to the general discussion.

1. Since the genus is a rather arbitrary construct, and since a dichotomy between ape and

man must be made at some point, we may tentatively accept the suggestion of the systematist that there is good reason to regard all fossil hominids, including the South African "man-apes," as belonging to a single genus, *Homo*.

2. With the recognition in principle—though not in precise morphological detail—that the Neanderthal-*sapiens* relation is a biological continuum, we may further postulate three species of Homo: *H. transvaalensis*, for the S. African forms (including therein Australopithecus, Paranthropus, and Plesianthropus); *H. erectus*, for Sinanthropus, Pithecanthropus, Soloensis, and (doubtfully) Heidelberg; *H. sapiens*, for Neanderthal and Cro-Magnon (as well as the numerous other early "*sapiens*"-like forms), and modern man.

3. It is not likely, on a time basis, that any two species of hominids were contemporary, i.e., the three species above named represent a phyletic and sequential series.

4. The taxonomic classification of the fossil hominids, as above suggested, greatly reduces the plethora of genera and species now a part of anthropological terminology. Terms such as Pithecanthropus, Sinanthropus, now become merely historically descriptive, losing all classificatory import. It is still correct—and might be less confusing—to refer to specific fossil finds by their place names, as "Java Man," "Taungs," "Kromdraii," and so on.

5. The co-operation between morphologist and taxonomist has been a stimulating and fruitful one. The re-evaluation of morphological traits from a classificatory viewpoint has served to broaden the perspective of the anthropologist. Further types of co-operative endeavor, as exemplified by the "fluorine test" will aid in elucidating problems arising from chronological uncertainties.

6. A final word of caution is necessary, viz., that any taxonomic system cannot hope to provide for all the variables in the classification of fossil men. There must inevitably be a certain amount of arbitrariness in any reconstructive taxonomic framework.

GENETIC ANALYSIS OF RACIAL TRAITS (I)

CLINICAL AND GENETICAL ENTITIES IN HUMAN POPULATIONS

WITH SOME REMARKS ON SCHIZOPHRENIA, MANIC-DEPRESSIVE PSYCHOSIS AND MENTAL DEFICIENCY IN A NORTH SWEDISH POPULATION

J. A. BÖÖK[1]

Dept. of Medical Genetics, Institute of Genetics, University of Lund, Lund, Sweden

I

All grades of genetic diseases or defects exist. One extreme is represented by those initiated by highly penetrant genes which cause a specific pathological condition such as Huntington's chorea. The other extreme is represented by conditions in which the genotype as a whole, in the existing environment, makes the individual especially susceptible to various noxious influences. Tuberculosis may serve as an example of the latter interrelationship.

The fact that a disease or defect has been proven to be the result of a specific gene does not mean that the etiology is entirely known. A study of gene action, presumably of a biochemical nature and interfering with normal metabolism and development, will furnish the only way to a better understanding of genetic pathology. It may even open possibilities for causal therapy. Surely the noxious gene cannot be removed from the individual but there is a chance that its effect can be counteracted.

The development of biochemical genetics by Beadle and his collaborators is one of the most important events in genetics since the discovery of the Mendelian Laws. Its bearing on clinical genetic research in the future can hardly be overemphasized. Here an attempt is made to diagnose also on the genotypical level. Consequently knowledge of primary gene actions is extremely important. With very few exceptions, among which oligophrenia phenylpyruvica should be mentioned (Følling, 1934), this field is still rather speculative.

II

The science of genetics was based, originally, on the analysis by means of mathematical and statistical methods of rather easily defined biological characters. In most cases highly penetrant genes have been studied in suitable organisms. Man, however, is a much more complicated organism, especially from the phenogenetic point of view. This is not always fully realized when different diseases and defects are studied. Penetrance of a gene, for instance, depends not only on various constellations of genetic modifiers and all kinds of extra-genic factors but is also a function of organic time. Genic indicates here the main genes responsible for specific diseases, whereas genotypical means the total of genes in an individual. The longer the embryonic development and the life cycle of an organism is, the more phenogenetic complications can be expected and the more difficult will be the diagnosis of the genic background. In this respect man and most experimental organisms used in genetic research are quantitatively different.

III

Two principal proceedings have been employed for the study of human genetics, the twin method and the pedigree method. When using these methods in clinical genetics it is important to make clear the possibilities of using clinical diagnostics as a means of interpreting the genic background. Known clinical entities cannot, without a critical trial, be interpreted each as being the expression of specific genotype. Actually, the situation is extremely complicated. Entities which from a clinical point of view are considered quite different may be caused by one and the same gene. This is, for instance, presumably the case in pernicious anemia and subacute combined sclerosis of the spinal cord. More often two or more different genes (allelic or at different loci) may cause similar or even identical clinical conditions. The different inherited types of retinitis pigmentosa may serve as an example. The more unstable the genes are, i.e., liable to be influenced by extra-genic factors, the more difficult it will be to connect the clinical symptoms with a definite genic background.

[1]Special Research Fellow of the U. S. Public Health Service during 1950-51. Fellowship taken at the Dight Institute for Human Genetics, University of Minnesota.

Considering this, which gives but a vague picture of some of the interwoven relationships between genotype and phenotype in genetic diseases, it is obvious that no general rule of thumb exists for clinical genetical research. The usual way of collecting a relatively large number of propositi, all having the same clinical diagnosis, and later looking for the same symptoms among the sibs, can often be subjected to criticism. Other symptoms or different kinds of subclinical manifestations, all due to the same genic background, may be overlooked. Furthermore, this procedure always implies the risk that the material is heterogeneous from the genic point of view. What we obtain in this way is in most cases actually more like empirical risk figures than genetic ratios.

One important task of medical genetics is to break up heterogeneous groups and better analyze clinical genetical entities. Before this is done, speculations about mode of inheritance and attempts to classify genetic diseases will in many cases be entirely fruitless. Large data or refined statistical methods will not help in this situation. The obvious discrepancy between clinical analysis and advanced statistics used in many investigations should be noted.

IV

Theoretically the genic factor starting a process that results in a pathological trait forms the basis of a clinical genetical entity. This concept therefore is dynamic. In cases with highly penetrant genes the relationship between the genic factor and the clinical picture is simple from a diagnostic point of view. In most cases the genic factor presumably starts or inhibits a biochemical process which leads to clinical disease but only if certain extra-genic influences also exist. Different extra-genic factors may, in different individuals, give rise to different symptoms although the genic action is basically the same in all. To diagnose the genic factor it is necessary to obtain all the different types of clinical or subclinical symptoms produced in different individuals and attempt to analyze the basic phenogenetic process. The whole picture then could be called a clinical genetical entity.

V

The analysis of clinical genetical entities has to start with the collection of data which can be assumed to be more homogeneous for the special genic factor under consideration than if ordinary clinical series are used. If a dominant or recessive sex-linked gene is suspected responsible for the disease the simplest way will be to study large pedigrees. Especially as concerns the thorough clinical analysis this line of research has been far from fully utilized.

Especially for recessive conditions complete investigations of isolates are important. The term isolate is used here according to the definition given by Dahlberg (1948 and in earlier papers). A number of genetic diseases and defects appear to occur with different frequencies in different populations. In certain isolates a specific disease may be rather common. As it is reasonable to assume that genetic diseases arise as mutations, such uneven distribution is apt to occur especially in populations with rather small geographical isolates. Convincing data for the mutational origin have already been obtained for a number of diseases such as chondrodystrophy (Mørch, 1941), hemophilia (Andreassen, 1943, Haldane, 1947), juvenile amaurotic idiocy (Sjögren, 1931) and fibrosis of the pancreas in children (Lowe, May and Reed, 1949).

Hanhart in Switzerland and Sjögren in Sweden were pioneers in applying this method and we owe a number of the best clinical genetical studies to these scientists. Only a few places give really good opportunities for such studies, i.e. those having old geographical isolates as well as reliable population statistics and registration. At the present time there is a strong tendency for these isolates to break down and disappear and it is to be hoped that the excellent possibilities which still exist in some countries can be utilized before it is too late.

VI

For a number of years the present writer has had the opportunity to study an isolated population of 9,000 in Northern Sweden, mainly from the point of view of genetic neuropsychiatric disorders. Some of the proceedings and results will be given here partly for the sake of their newness and partly to illustrate what has been said above. It should be understood that most of the figures which will be given are of a preliminary nature and may later be subjected to minor corrections.

The population is scattered over an area of 1,826 sq. miles (4,732 sq. km.) and is from an environmental point of view very homogeneous. No cities, railroads or industries exist. Most people make a living as lumbermen and have small additional household farms. The birth rate is high. In 1949 the figure was about 28 per thousand. In spite of the fact that more people move away from

this region than into it, the population is steadily increasing. Figures from the last 5 years show a net increase of about one per cent per year. An important feature of this population is furthermore that no less than 50 per cent are under the age of 20 years.

Mainly as a result of geographical isolation the incidence of consanguineous marriages is rather high in some parts of the district (Böök, 1948). The average figure of first cousin marriages for the total area is 2.21 ± 0.41 per cent. Actually, however, several smaller isolates exist. Thus the most isolated region (parish of Muonionalusta) had an incidence of first cousin marriages of 6.80 ± 1.82 per cent.

On the other hand the sums of these psychoses do not differ too much in the two samples. The figure for manic depressive psychosis (0.8 per thousand) furthermore does not give the correct picture of the situation as in some cases the diagnosis was very questionable and some had moved into the area recently from other parts of the country.

Table 2 gives a calculation of the morbidity risk for schizophrenia. The high figure of 2.85 ± 0.30 per cent is significantly different from the figure of 0.89 ± 0.13 from the West Swedish population. An explanation of these findings is still premature as the analysis of the pedigrees is under way. However, it seems reasonable to assume the differences are biological. In the first place one would think of true differences in gene frequencies between the two populations. On the other hand, extra-genic factors which would increase the manifestation of schizophrenia may have a similar effect.

TABLE 1. ROUGH FREQUENCY (I.E. IN RELATION TO THE TOTAL POPULATION LIVING) OF SOME NEURO-PSYCHIATRIC DISORDERS IN THE PRESENT POPULATION AS COMPARED WITH A WEST SWEDISH ISLAND POPULATION

(Sjögren, 1948). Incidence per one thousand individuals.

	Schizophrenia	Manic depressive psychosis	Idiocy and imbecility	Total population
Present data. Three North Swedish parishes	9.5	0.8	11.9	8651
Sjögren's data. West Swedish island population.	4.5	2.8	6.8	8736

To start with all cases of mental deficiency, psychoses and convulsive disorders were collected through official channels (parish registers, social relief organizations, archives of the district physicians, mental hospitals and institutions) for the period 1900 to 1946, and later followed up to September 1949 when the field work was finished. During the field work from 1946 to 1949 practically all cases alive, living in the area or institutionalized, have been examined by the writer together with their families. A number of new cases and secondary cases were found and added to the data. All possible means have been used to secure a complete registration of the whole population and it can now be claimed that only very few cases may have escaped.

VII

The rough frequency of the three most important neuro-psychiatric disorders is given in Table 1. A comparison of Sjögren's (1948) data from a West Swedish population of almost exactly the same size reveals several interesting facts. The incidence of schizophrenia in the present population is much higher whereas the incidence of manic depressive psychosis is exceedingly low.

VIII

According to the principles mentioned earlier in this paper it was possible to define one special group of mentally deficient as reasonably constituting a clinical genetical entity. About 10 per cent of the mentally deficient in this area belong to this group. Only idiots and imbeciles have been included in the data. The clinical characteristics of this group as they appear from complete examinations of 14 cases are as follows.

All are of low mentality (8 idiots and 6 low-grade imbeciles). They all show impairment of the pyramidal system with clinical signs of mainly spasticity of the lower extremities (spastic diplegia). Five cases were unable to walk, three could not walk without aid and six were able to walk with great difficulty. The patellar reflexes were highly hyperactive in all cases. Ankle clonus were present in seven cases. The toe signs

TABLE 2. MORBIDITY RISK FOR SCHIZOPHRENIA ACCORDING TO WEINBERG'S "ABGEKÜRZTES VERFAHREN"

(cf. Sjögren, 1948).

	Number of cases	Risk period	"Bezugsziffer"	Morbidity risk
Three North Swedish parishes, Böök.	83	20–45 years	2,911	2.85 ± 0.30%
West Swedish island population Sjögren, 1948.	40	20–45 years	4,500	0.89 ± 0.13%

were extensor in five cases, atypical in two and flexor in seven cases. Muscular atrophies of the legs were present in nine cases. Congenital deformities of the feet were found in 11 cases (5 equino-varus and 6 plano-valgus). Convulsive disorders were absent with the exception for one case who belonged to a family where other members had convulsive disorders without mental deficiency.

At the end of September 1949, thirteen cases with this specific condition were alive and resident in the area. This gives a frequency in relation to the total population of 1.5 per thousand. However, due to an excess mortality this figure should be corrected. For an estimate it is sufficient to take the frequency in relation to the population under the age of 45 years. This will give a figure of 1.8 per thousand.

For the genetical analysis so far six additional cases with enough information to allow a definite diagnosis are available. The total of 19 cases belong to 11 families. Seven cases are females and 12 males. In two families the parents are first cousins, in two, second cousins and in further two, third cousins. Furthermore it has so far been possible to show that six of the families belong to the same pedigree complex. In all families the parents are unaffected.

As all cases in the area have been registered as propositi, the Macklin test for simple recessivity can be used. The calculation is shown in Table 3 and supports the theory of simple recessive inheritance. This conclusion is furthermore supported by the high rate of consanguinity among the parents.

Clinically the above condition belongs to the group infantile spastic diplegia (also called Little's disease) which from an etiological point of view is very heterogeneous. The genetic etiology seems conclusive in the present cases. No histories of birth trauma, cerebral infections or other types of exogenous injuries have been obtained. The condition is strictly congenital and stationary. It seems justified to regard this *oligophrenia spastica* as a specific clinical genetical entity to be separated from other similar conditions. A similar or perhaps identical recessive type was described by Hanhart (1936) who found seven cases belonging to the same pedigree in a Swiss community. Both findings confirm the view that specific hereditary types exist within the group of congenital spastic diplegia and dem-

TABLE 3. OLIGOPHRENIA WITH SPASTIC DIPLEGIA

Simple recessive test according to Macklin's (1938) "percentage affected method."

Number of children per family	Total number of children	Affected		Not affected		$(o - c)^2/c$
		o	c	o	c	
4	4	2	1.46	2	2.54	0.30
5	5	1	1.64	4	3.36	0.36
6	0	0	0.00	0	0.00	0.00
7	7	1	2.02	6	4.98	0.71
8	40	7	11.08	33	28.92	2.07
9	9	4	2.43	5	6.57	1.38
10	10	2	2.65	8	7.35	0.20
11	11	2	2.87	9	8.13	0.35
Totals	86	19	24.15	67	61.85	5.37

$\chi^2 = 5.37$, DF = 7, $0.50 < P < 0.70$

onstrate how combined clinical and genetical research can contribute to nosological differentiation.

SUMMARY

In sections I—V of this paper the possibilities of the clinical genetical method as an aid in nosological differentiation is discussed briefly.

Sections VI—VIII give some preliminary data of a study of a North Swedish population (about 9,000 individuals) mainly from the point of view of neuro-psychiatric disorders. The incidence of schizophrenia in this population is unusually high (roughly 9.5 per thousand; morbidity risk 2.85 per cent). A special type of mental deficiency with spastic diplegia (oligophrenia spastica) from this area is concluded to constitute a clinical genetical entity.

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DISCUSSION

KEMP: May I ask if there was increased consanguinity among the parents of the patients suffering by schizophrenia, because two possibilities must be considered in explaining the high frequency of schizophrenia in the population mentioned, viz. 1) schizophrenia being recessive and thus frequent owing to the high intermarriage in the population, and 2) the population in this north-Swedish isolated population chiefly being of the leptosomic constitutional type. The last explanation seems to be the most probable.

It would be very interesting to get some new information concerning isolated groups of population in U. S. A.

BÖÖK: I cannot yet answer the question of increased consanguinity. About 100 schizophrenic index cases with extensive pedigrees are available but the analysis is still under way. However, Dr. Kallmann in his extensive twin study of schizophrenia found increased consanguinity among the parents, which seems to be further evidence that this disease depends upon recessive factors. On the other hand it is true that the leptosomic and athletic type is prevalent in this population. It seems probable that both these factors are at work. I intend to discuss this more thoroughly in a coming paper when exact data are available.

LASKER: Dr. Kemp has raised the question of isolates in America and Dr. Oliver mentions Mexican populations in some parts of the United States. Such communities are likely to manifest the introduction of new members from Mexico from time to time. However, in Mexico there still remain some more or less genetically isolated communities. In the town of Paracho, Michoacan, which has approximately 3,000 inhabitants, we interviewed approximately one-third of the adult population concerning their parents. Although we found few cases of intermarriage of recognized relatives, the great majority of individuals interviewed were related to each other through marriages if not directly. Consequently, if we could have pushed the analysis back one or two generations more (at which time the population of the town was smaller), most of the marriages would certainly prove to be consanguineous. The great majority of spouses of those interviewed were born in the same small town and in the few cases where this was not true the spouse was from within the immediate vicinity (the Sierra Tarascan region).

SANGHVI: In connection with Dr. Kemp's remarks about the availability of isolates, the people of India offer interesting human material for the study of the question of "isolates." At present, there are more than 5,000 endogamous groups varying in size from a group consisting of 87 individuals to a group of more than 4,000,000 individuals. Barriers of custom are and have been in the near past, sufficiently rigid to prevent intermarriages to any appreciable extent, between

different endogamous groups. Social customs regarding consanguineous marriages are of varied patterns. For instance, first cousin marriages are prohibited by social custom in some groups and supported by the same authority in some others. In the latter cases, first cousin marriages constitute a large proportion of all marriages. Similarly for the marriages between uncle niece and some other consanguineous relations. The history of the origin of a large number of these groups is buried in the past. Some groups are, however, known to have been endogamous for 100 generations or more.

THE FREQUENCY OF DISEASES AFFECTED BY HEREDITY IN DENMARK

TAGE KEMP

The University Institute of Human Genetics, Copenhagen, Denmark

The future development and genetic composition of a human population are dependent on a variety of factors, hereditary as well as environmental, endogenous as well as exogenous, eugenic as well as euthenic.

A very important group of these factors which determine the fate and survival of a race or a nation is composed of the hereditary anomalies, abnormalities, defects and diseases occurring in the population.

This is why the study of the hereditary lesions is of so great consequence for the population problems, human genetics, medical statistics, public health, clinical, preventive and social medicine, sociology and politics. In democratic countries during recent years, an increasing social consciousness has been manifesting itself, a growing feeling that society must make living conditions tolerable for everybody; this has necessitated the study of the hereditary diseases, and not least of their frequency in the population. It is of importance to the governmental powers and social authorities to know the number of people who, because of hereditary lesions, are socially incapacitated and have to be given social relief, to be treated, or to be placed in hospitals or institutions.

Furthermore, the study of the incidence of defective traits is an essential part of medical genetics. It is fundamental for investigations on the significance of mutation as a cause of disease and on the way the hereditary lesions arise through mutation; for investigations on their mutation rate and on the manifestation, penetrance and expressivity of the pathological genes; and for studies on the distribution of these genes through the generations in the various social strata and geographical localities. These processes are dependent on the effects of selective mating, centers of inbreeding, isolates, differential fertility, migrations and other similar factors.

The knowledge of the frequency of the conditions affected by heredity makes it possible to follow and control the development and the fluctuation of the hereditary diseases in the population, and to check up on the behavior of these diseases down through the ages.

Many attempts by various methods have been made to estimate the incidence of hereditary defects and diseases in various countries or groups within populations. Some information concerning the incidence of hereditary diseases was obtained centuries ago through vital and medical statistics, yet health services are still collecting material elucidating this question.

Direct investigations concerning the problem have been carried out for the most part during the last fifty years, originally on mental defects and diseases, but later within the whole field of medicine.

Several types of methods have been used to investigate the morbidity in the average population and to ascertain the amount of hereditary tainting, as, for instance, census investigations, sampling methods, and morbidity, mortality and hospitalization statistics. These methods may be used in various ways:

Sampling methods are often applied combined with proband materials or propositi investigations; and it must be considered whether the sample is representative of the average population and fulfils certain assumptions with regard to selection and composition.

Census investigations may include greater or smaller geographical units, states, counties, municipalities, communities, islands, valleys and so on, or population-groups delimited according to sex, profession, social class, race, nationality etc.

Various age groups may be examined, for instance, new-born, school-children, military conscripts or certain age classes; or mortality statistics may be used.

The point must be considered that a group of hereditary lesions cannot be diagnosed throughout the lifetime of the tainted individual, but only within a certain period, the period of manifestation or the period of risk, the age-class during which the disease may develop. In the case of these diseases it is often appropriate to settle, besides the frequency figures, the morbid risk or the "expectancy" for the disease in question; that is, the risk of a person becoming ill during his lifetime if he lives long enough to pass the

period of manifestation or risk, the time during which the disease may develop. It is possible to calculate the morbid risk from frequency figures with certain cautions, *inter alia*, taking the age of onset and the mortality of the disease in question into consideration.

During recent years two outstanding genetic-psychiatric studies have taken place in Denmark, namely: one based on census investigations by Strömgren (1938), and one using sampling methods by Fremming (1947).

Strömgren made a census among the ca. 40,000 inhabitants of the Danish island of Bornholm, situated in a rather isolated area in the Baltic Sea, relatively near Sweden. The population on the island is very homogeneous, and there is no intermarrying of any importance. Strömgren attempted to count and identify all psychotic, ex-psychotic or mentally defective persons living on the island at a certain date. Furthermore Strömgren made a more thorough census of a small district of Bornholm, inhabited by about 1,000 persons, where it was easy to get adequate information about every individual inhabitant.

Fremming carried out an investigation applying the sample-method originally indicated by Klemperer (1933). Fremming's basic material of probands consisted of the persons born at Bornholm in the five-year-period of 1883–1887, somewhat more than 5,500 persons. More than 92 per cent of the propositi, most of them more than 55 years of age, were traced and examined, and the incidences of psychoses, psychopathy, oligophrenia, epilepsy, criminality, tuberculosis and some other diseases were computed, and a thorough demographic analysis of the material was performed.

Some of the results of Strömgren's and Fremming's investigations are cited in Tables 1, 4 and 5.

During the last ten years new possibilities have been created for investigations on the frequency of hereditary lesions and for following, controlling and studying the whole body of hereditary lesions in the Danish population.

In the University Institute for Human Genetics in Copenhagen a Medico-Genetic Registry has been established. The registry includes a systematic registration, a card index, complete as far as possible, covering all the more serious hereditary conditions observed in Denmark during recent years.

At present more than 150,000 patients and their families are registered in the registry and every year several thousands are added. The registry forms the starting-point for more thorough studies into the inheritance of the various lesions and diseases. The procedure then is as follows: The physician, who is trained as a specialist in the field concerned, makes a thorough investigation of the individual patient having the disease or lesion in question, and for the more rare diseases it is attempted as far as possible to compute all cases of the disease in the country; for more common lesions it is generally not possible to accomplish a complete census and then a representative sample is collected.

In this way more or less thorough information concerning the frequency of several hereditary lesions in the Danish population is obtained, and some of the results will be mentioned in the following sections.

In 1945 the total population in Denmark was 4,045,000 inhabitants, about one million living in Copenhagen, one million in other cities and two million in rural districts.

In Table 1 the incidence of some congenital malformations are indicated partly per 100,000 inhabitants of the average population and partly per 100,000 new-born children.

As indicated in Table 1, the incidence of harelip and cleft palate is higher at birth than in the average population on account of the greater mortality among the deformed children. The frequency at birth is decided by going over a report from lying-in departments consisting of 128,000 children (121,000 born alive).

Isolated cleft palate is, according to Fogh-Andersen (1943), genetically independent from harelip with or without associated cleft palate.

Most cases of harelip (possibly with cleft palate) must be supposed to be hereditary, the most likely manner of inheritance being that of "conditioned dominance," the gene occurring as a dominant or as a recessive gene, according to how many generations ago the mutation in a given case had arisen. It has been imagined that when the mutation causing harelip arises, the heterozygote shows a phenotype which is dominant or intermediary between the normal and the homozygous individuals as regards the malformation. During evolution modifying genes or selected strong allelomorphs develop in the population resulting in the pathological gene in the course of generations becoming recessive. Therefore, in the population we have a mixture of older recessive harelip-genes, arisen many generations ago, and younger genes, arisen few generations ago, which are dominant or intermediate. In man,

TABLE 1. CONGENITAL MALFORMATIONS

	Incidence	
	In the population per 100,000 inhab.	At birth per 100,000
Harelip (and cleft palate)	70	110
Isolated cleft palate	30	40
Club-foot (including non-congenital)	100	80
Congenital dislocation of the hip	150	100
Chondrodystrophy	2	10
Osteogenesis imperfecta congenita	...	2
Cranio-rachischisis	...	100
Anencephaly	0	100
Absence deformities of the upper extremities	15	23
Split hands and ectrodactylism	2	3.3
Defects of radius and ulna	3	3
Amputation of upper arm	0.2	0.7
Amputation of forearm, hand or fingers	8	10
Spontaneous amputation, exogenous syndactyly	2	6
Hypospadia	300	300

today, however, owing to civilization, natural selection acts with less force. Accordingly the possibility of surviving and multiplying for the defective individuals is increasing. Furthermore, the mutation rate and the manifestation of the gene causing harelip must be taken into consideration.

Consequent to all these factors, the incidence of harelip in the Danish population today is about 3,000 patients, a figure which continuously varies, depending upon the interaction of the numerous influences just mentioned.

In isolated cleft palate the manner of inheritance is probably dominance with failing manifestation, there being, however, a considerable admixture of non-hereditary cases.

Considering the frequencies of club-foot (Monberg, 1931; Thomasen, 1941) and dislocation of the hip (Fremming, 1947) it is noticed that the incidences are higher in the population than at birth, because some cases of club-foot may not develop before several years after birth, and dislocation of the hip is not always diagnosed at birth when present.

In deciding the frequency of chondrodystrophy a special method has been used, viz. counting all the cases of the abnormality found in the country. In applying this procedure one can be sure that the material is representative and that no difficulties with regard to the selection and composition of the propositi are occurring. The very same procedure has been used in the investigations concerning aniridia, hemophilia, surdomutitas (congenital and early deafness), tuberous sclerosis, mongolism and deformities of the upper extremities mentioned later.

In 1941 Trier Mørch observed 86 chondrodystrophics in Denmark, and by going through 94,000 births in lying-in departments he found that chondrodystrophy will appear once in every 10,000 births. Only one-fifth of the children survived the first year of life, and the effective fertility of chondrodystrophics surviving the first year of life is considerably reduced. Therefore it must be supposed that the dominant gene causing chondrodystrophy frequently arises through mutation, and the mutation rate is calculated to be 8.5–10 per 100,000; between 1–12,000 and 1–10,000 per individual per generation and 1–20,000 to 1–24,000 per chromosome per generation. As mentioned later, the mutation rate has been calculated for several dominant and sex-linked traits. These rates were found to fall between $1:10^{\div 4}$ and $1:10^{\div 5}$.

Osteogenesis imperfecta presents dominant inheritance and probably often arises through mutation. It is, however, as in tuberous sclerosis, impossible to calculate the mutation rate owing to the great intrafamilial variation, and the considerable difference in the manifestation of the gene causing the disease. Seedorff (1949) investigated 55 Danish families comprising 180 affected individuals, some few suffering from the serious congenital type and the majority from the milder tardive forms, all of which constitute a genetical entity; on the basis of his material he estimated that about one child is born every year in Denmark with congenital osteogenesis imperfecta.

Hindse-Nielsen (1938) found 67 cases of spina bifida in 69,973 new-born children from lying-in departments, and collected 357 patients from

hospitals and institutions throughout Denmark. The death-rate is enormous especially during the first half year of life; this is why the frequency is much smaller in the average population than in new-born; it has not been computed, however.

In anencephaly the prognosis is still worse, the incidence in the population thus being practically zero.

Birch-Jensen (1949) collected material comprising nearly all patients living in Denmark 1943–46 with congenital absence deformities of the upper extremities. The total number of patients was 625. They are equally distributed over the entire country, with no accumulation of patients in remote districts or small islands, where intermarriage is common. For most of them the incidence at birth is higher than in the average population on account of the reduced prognosis *quoad vitam*, thus being accentuated for the more serious malformations such as amputation of the upper arm. About 20 children suffering from absence deformities of the upper extremities are born in Denmark yearly.

Rahbek Sørensen (in press) investigated 27,600 new-born children and found 0.32 per cent suffering from hypospadia; in school children of 7–15 years and probably in the general population the incidence of hypospadia is about of the same magnitude.

While it is comparatively simple to decide the frequency of congenital malformations generally existing throughout life, it is more intricate to compute the incidence figures of the hereditary or hereditarily predisposed diseases of the internal organs. Often it is easier to calculate the morbid risk (see Table 2).

Bartels (1941) investigated a normal group consisting of the families of 500 normal propositi in Copenhagen and comprising 7,144 persons over 14 years of age. The morbid risk in women of Graves' disease was calculated to 0.4 per cent and of non-toxic goitre to 1.1 per cent. The first of these figures, however, is changing very much during the course of time probably depending on environmental factors, in some periods it is essentially higher than indicated above. And the cited frequency of goitre does not hold true in districts with endemic goitre. In the just mentioned material Bartels calculated the frequency of diabetes mellitus in persons over 14 years of age to be 1.7 per cent, and in 1950 Horstmann found 0.4 per cent in a sample (175,000) of the total population.

Søbye (1948) investigated 220 families with essential hypertension and nephrosclerosis, and a normal group of about 2,800 persons, and concluded that the two diseases constitute a genetic entity, that the inheritance is dominant and that the morbid risk in the average population is about 30 to 40 per cent; it means that the chance for old people to get hypertension is very great.

The same holds good of the predisposition to cancer investigated recently by a group of Danish investigators (see, for instance, Jacobsen, 1946; Videbaek, 1947; Brøbeck, 1949; Busk, 1948; Kemp, 1948) who have estimated the morbid risk of cancer on the basis of the proband method using samples of normal persons as propositi, supplemented with experiences from mortality statistics. The Danish Cancer Registry has investigated the incidence of malignant tumors in Denmark (Clemmesen and Nielsen, 1943; Clemmesen and Busk, 1948); the result will not be quoted here, however, because many malignant tumors are not hereditary at all; but a few figures with relation to the aforementioned proband investigations will be reported.

In 1943 The Cancer Registry attempted to carry out a census of all cancer cases under treatment in Denmark and answers were obtained from all doctors and hospitals. In this way, of course, knowledge was not obtained concerning the total number of cases of cancer present in the popu-

TABLE 2. DISEASES IN INTERNAL ORGANS

	Incidence	
	In the population per 100,000 inhab.	Morbid risk per 100,000
Graves' disease	...	400 ?
Non-toxic goitre	...	1,100
Diabetes mellitus	400	...
Essential hypertension	...	35,000
Cancer of all types	(131)	22–29,000
Hemophilia (only men affected)	2	...
Genuine epilepsy	...	350
Familial periodic paralysis	0.8	3
Progressive infantile muscular atrophy: about 1 child is born every year per 1 million inhabitants.		

lation, but 131 cases (including lymphogranulomatosis and leukemia) per 100,000 inhabitants were reported. Of these, 20 cases were breast cancer, 4 cases leukemia and 20 cases uterine cancer. Of the cases of uterine cancer three-fourths were cervical cancer, chiefly caused by environmental factors, and one-fourth or 5 per 100,000 inhabitants were cancer of the corpus, more dependent on a hereditary predisposition.

Andreassen (1943) investigated as far as possible all the hemophilic families in Denmark, 63 families including 205 hemophiliacs, all males, and 74 sure heterozygous females (carriers). Of the 205 hemophiliacs, 81 were living in the country in 1943. The average lifetime of hemophiliacs is about one-third of the normal. The mutation rate per X-chromosome per generation was calculated to about 1 : 50,000.

Fremming in his aforementioned sample investigation found the morbid risk in genuine epilepsy to be 0.35 per cent and in genuine plus symptomatic epilepsy to be 0.46 per cent; he considered the period of manifestation to be 0–29 years.

Helweg-Larsen (in press) investigated all cases of familial periodic paralysis in Denmark and states the frequency to be 0.0008 per cent and the morbid risk 0.003 per cent.

Brandt (1950) found 70 families including 112 cases of infantile progressive muscular atrophy in Denmark during the last 40 years, and 20 new cases in the period 1943–47. He calculates with rough approximation that about one patient with the disease is born every year in one million inhabitants. Eighty per cent of the patients died before they were four years old and only 7 per cent survived their fifteenth year of age; therefore the incidence of the disease in the population is very low.

The incidences of several hereditary eye diseases have been estimated recently (see Table 3).

Møllenbach (1947) investigated congenital aniridia and coloboma. In 1944, altogether 40 patients were observed in Denmark with congenital total defect of the iris. The frequency of partial defects of iris and choriodea, coloboma iridochoroidalis, was in a sample of about 100,000 persons of the average population computed to be about 0.01 per cent, but among 625 mental defectives 12 cases of coloboma were ascertained, corresponding to 0.73 per cent. The total number of cases of coloboma in Denmark would be 1,000–1,100, two-thirds of which would be externally recognizable, and one-third would be fundic coloboma. No transitional cases were found between aniridia and coloboma.

TABLE 3. HEREDITARY EYE-DISEASES

	Incidence	
	In the population per 100,000 inhab.	At birth per 100,000
Congenital aniridia	1	...
Iridochoroidal coloboma	24	...
Congenital hydrophthalmos	8	8
Glaucoma	55	...
Glaucoma intermittens	46	...
" simplex	9	...
Optic nerve atrophy (Leber)	...	3–4 new cases annually
Retinitis pigmentosa	5–20 ?	...
Partial color-blindness		
In males	7–8,000	...
In females	440	...
Total color-blindness	0.3	in an isolate: 1 per 100 inhab.

The frequency of mutation for aniridia is estimated to be about 1 : 100,000, allowing a suitable margin of safety for cases that might not have been recorded.

As regards the primary glaucoma diseases, Westerlund (1947) has conducted investigations.

Recessive congenital hydrophthalmos (congenital glaucoma) was judged to be the cause of blindness in 6–7 per cent of the patients admitted to institutions for the blind, and as blindness is judged to be hereditary in about half of the cases, this means that hydrophthalmos is the cause of blindness in about 13 per cent of the hereditary cases. A total of 121 patients were examined, 36 per cent females, 64 per cent males, and 27 per cent of the cases were unilateral. A number of the unilateral cases were supposed to be "abor-

tive" bilateral cases. Intermarriage in the parents of the patients is found in 10.7 per cent and the parents are first cousins in 5.8 per cent.

On the basis of hospital admission statistics in Copenhagen 1921–1940, the incidences of hydrophthalmos at birth and in the average population have been calculated to be 0.008 per cent for both, which means that 300 patients with the disease should live, and about 6–8 new cases should occur annually in Denmark. The effective fertility of the patients has been calculated to 0.45.

The incidence of primary glaucoma, juvenile and adult, was computed on the basis of 82 cases observed by Copenhagen ophthalmologists and calculated to be 0.055 per cent in the average population. In 13 per cent of the cases familial predisposition was demonstrated, the mode of inheritance is dominance with failing manifestation. Congenital and adult glaucoma must be regarded as genotypically different.

Lundsgård (1944) studied about 100 cases in 20 Danish families of Leber's optic nerve atrophy. The affected males never get affected children or affected descendants in later generations, therefore a Leber gene disappears with every affected male, and the Leber gene in each family has only a limited term of life. The disease must be supposed to arise frequently through mutation occurring in a female, who thus becomes the first ancestress of a new Leber family. Lundsgård observed 19 (18 males, 1 female) new cases in Denmark 1930–39, and because it may be assumed that not all cases are registered, she reckons that at least 3 new male cases occur every year and the frequency of mutation must then correspond to the number of new cases.

The frequency of retinitis pigmentosa in the average population has been roughly estimated to be 0.005–0.02 per cent and for partial color blindness (Daltonism) the incidence has been reckoned to be of about the same magnitude as in Norway, viz. 7–8 per cent in males and 0.44 per cent in females (Waaler, 1927).

Holm and Lodberg (1940) estimated the incidence of total color blindness or monochromosia to be 0.0003 per cent in the average population, but on an island, Fuur, situated in the Limfjord, which has about 1,600 inhabitants and frequent intermarriages, the disease has been common through at least the last four or five generations. Fifteen patients still alive were observed at the time of the investigation, as a result of the high incidence of consanguinity.

The earliest attempts to estimate the incidence of hereditary diseases in the population were made in the field of mental defects and diseases.

Such investigations carried out during the last 50 years were necessary for the genetical studies in psychiatry developing in the first decades of this century, and later they have been of importance to social psychiatry, prevailing at the present time. The older investigations have been supplemented and enhanced recently by Danish investigators (Strömgren, 1938; Fremming, 1947; Borberg, in press; Øster, in press) as indicated in Table 4.

The incidences of the feeble-minded and mentally retarded are calculated on the basis of the investigations on Bornholm compared with Smith's (1930) twin studies.

Øster studied mongoloid idiocy in the island group of Seeland, Lolland, Falster and others with 1,840,000 inhabitants and counted ca. 450 cases

TABLE 4. MENTAL DEFECTS AND DISEASES

	Incidence	
	In the population per 100,000 inhab.	Morbid risk per 100,000
Feeble-mindedness	1,300	...
Hereditary cases	1,000	...
Non-hereditary cases	300	...
Mentally retarded	1,700	...
Psychopathy	3,000	...
Schizophrenia	300	900
Manic-depressive psychosis (both sexes)	...	1,640
In males	...	1,020
In females	...	2,240
Tuberous sclerosis	0.5–1	...
		At birth per 100,000
Mongoloid idiocy	25	150

of mongolism, and on the basis of material from lying-in departments he calculated the frequency at birth. Thus we have an exact census concerning this disease, for continued study of its etiology.

Borberg (in press) investigated all cases of tuberous sclerosis in Denmark during the period 1924–43. He found about 40 cases; 10 cases were in institutions for feeble-minded, 9 in hospital departments for dermatology, 7 in neurological services and 4 in an institution for epileptics. In 1944, 22 patients were observed living in the country, but it is probable that a rather considerable number of cases existed undiagnosed. The disease is inherited as a dominant character with failing manifestation, but consequent to the great interfamilial variability it has not been considered possible to calculate the mutation rate.

At last some frequencies are given in Table 5 concerning various more or less hereditary characters of special sociological significance.

The purpose of Fremming's aforementioned investigation on Bornholm of persons born between the years 1883 and 1887 was primarily to provide figures for the psychiatric morbidity of the Danish average population, but he further investigated the frequency of some other characters among the probands, most of them being more than 55 years of age: Alcoholism occurred in 65 males or 3.4 per cent and in two females; in 1.7 per cent in both sexes. In half of the probands addicted to alcohol the alcoholism was found to be the result of psychic abnormality, generally psychopathy. The total criminal expectation for male probands between 15 and 55 years was found to be 2.80 per cent and for females 0.61 per cent. A little more than half of the criminal probands deviated mentally from the normal, some were retarded or feebleminded, some were psychopaths and others suffered from psychoses. On the whole the criminal frequency was found to be comparatively moderate, owing to the area investigated being mainly rural (Fremming, 1946). The total psychosis expectation up to the age of 55 years was found to be 3 per cent in men and 5.3 per cent in women. The number of persons (490), who at the time of the investigation were mentally abnormal or who during one or more periods of their life had suffered from mental diseases was found to be 12 per cent of the persons who all had survived the age of 10, and of whom nearly all at the time of the investigation were more than 50 years of age. The psychotic probands showed an undoubtedly increased death rate.

TABLE 5. VARIOUS FREQUENCIES

	Incidence	
	In the population per 100,000 inhab.	Morbid risk per 100,000
Alcoholism	1,700	...
Criminality, 15–55 years		
In males	...	2,800
In females	...	610
Total psychosis expectation up to 55 years	...	4,100
Mentally abnormal, evt. periodically, 10–55 years	...	12,000
Gipsies	20	...
Hereditary blindness	30	...
Hereditary deafmutism	20–30	...

Fremming's figures for psychopathy, 3.1 per cent in men, 2.8 per cent in women, are undoubtedly minimum figures; the most common types of psychopaths in men were the weak and impulsive, in women the asthenic, impulsive, sensitive and hysteric psychopaths.

Fremming decided the expectation of schizophrenia to be 0.90 per cent, reckoning with a period of manifestation of between 15 and 45 years.

Furthermore, he found the morbid risk of manic-depressive psychosis to be 1.22 per cent, when reckoning with a period of manifestation from 20 to 50 years. When the calculation is performed with a period of manifestation of 20 to 65 years and using Strömgren's (1935) method, the morbid risk of manic-depressive psychosis was calculated to 1.64 per cent, namely 1.02 per cent for men and 2.24 per cent for women. These figures are probably close to correct and three to four times greater than the figures given by earlier investigators.

The Danish population is relatively uniform. The bulk of it are descendants from a people who came to the country four to five thousand years ago and have formed the main stock ever since.

But of course a certain amount of immigration has later taken place from several countries and races. As a typical example of such small immigrated groups in the population the gipsies may be mentioned.

Bartels and Brun (1943) investigated the gipsies living in Denmark and estimated their number to be 700 to 800, nearly all of whom were members of eight large families. Their immigration into Denmark took place between 1800 and 1850 through Germany. The gipsies form a biologically delimited group within the population and the majority of the gipsies are still maintaining the traditional mode of living of the families, but in the course of three or four generations they will probably have assimilated to a very great extent, if no renewed immigration of gipsies takes place. The gipsies in general, of course, have to be regarded as mentally sound, but certain traits of character, their habits and views on social and moral questions and their outlandish exterior distinguish them so far from the average population. But, as emphasized above, it is to be expected that complete assimilation in the population will occur within about a hundred years if new immigration is avoided.

It is not possible to give the exact figures for the incidence of hereditary blindness and deaf-mutism (congenital and early deafness), partly because the delimination of the two defects from weakness of sight and hardness of hearing, respectively, in many cases are rather vague, and partly because of difficulty in deciding whether a given case is exogenous or endogenous.

The frequency of blindness in the population is estimated to ca. 0.06 per cent and at least half the cases are caused by hereditary factors.

Lindenov made a census examination of the deaf-mutism (congenital and early deafness) in the island group of Seeland, Lolland and Falster, and found about 0.04 per cent, and about half the number were cases of hereditary deaf-mutism, most of them sporadic-recessive deaf-mutism, and only a few cases (less than 5 per cent) heredolabyrinthic deaf-mutism. Retinitis pigmentosa occurred in about 6 per cent of deaf-mutes. The total number of deaf-mutes resulting from consanguineous marriages amounts to about 6 per cent, but for the hereditary cases alone to more than 10 per cent.

TABLE 6. THE CAUSES OF DEAF-MUTISM IN 345 CASES

(176 Men and 169 Women)

	per cent	per cent
Hereditary deaf-mutism		45
Sporadic recessive deaf-mutism	43	
Heredolabyrinthic deaf-mutism	2	
Acquired deaf-mutism caused by		55
Meningitis epidemica	15	
Scarlatina	6	
Other infectious diseases (pneumonia, typhus abd., diphtheria, morbilli, tussis conv., parotitis, influenza, poliomyelitis *et al.*)	18	
Otitis media supp.	6	
Lues cong.	2	
Trauma capitis	4	
Other causes	4	

It must be considered, however, that Lindenov did not find all deaf-mutes in the district examined, therefore the percentages of hereditary deaf-mutism in the population may be estimated to 0.02–0.03.

Lindenov decided with great exactitude the causes of the deaf-mutism in 345 cases as indicated in Table 6.

From the figures in Table 6 it is obvious that the number of cases of deaf-mutism caused by exogenous causes in all probability will be decreasing during coming years. Today it is possible to treat scarlatina, meningitis and other infectious diseases effectively contrary to what was the case only one or two decades ago, and trauma capitis, intracranial hemorrhages in new-born and other environmental factors are much more rare than previously. This is why the proportional frequency of endogenous deaf-mutism, the percentage of hereditary cases among the total number of deaf-mutes, must be expected to increase considerably if prophylactic measures are not taken, which so far has been done only in a very limited degree.

The same holds true as regards other defects and diseases, as for instance blindness and oligophrenia. The exogenous cases are decreasing, the endogenous remaining constant or even increasing as a result of the progress of civilization. Furthermore the possibilities that many patients who suffer from hereditary lesions will live and propagate are improving year by year, and negative eugenic measures are only applied in few countries and even there generally in a rather haphazard way and without any definite plan.

These factors influence the frequencies of the hereditary lesions and the future development and genetic composition of the various human populations essentially. And the only way to follow, control and study the whole body of hereditary lesions in a population is through a permanent systematic and thorough medico-genetic or eugenic registration, comprising all important hereditary affections in the population.

The above review concerning the frequencies of the hereditary lesions throws light upon a human population as a living body, continuously changing in its composition, variable and inconstant, in progressive or retrogressive development, following the rules of natural selection and evolution or doing away with these rules, when the "wild-type" is disappearing, as a result of culture and civilization.

The hereditary diseases are constantly arising through mutation; some of them, anomalies and less severe diseases, persist through many generations, others, the more serious defects and diseases, disappear very fast, after one or a few generations. It is supposed that a certain equilibrium exists between the mutation rate and the elimination of the pathological gene, on the whole keeping the frequency of a hereditary disease unaltered in the population.

In this respect, however, a number of different factors are interacting:

Any disease or any defect is the cooperative result of hereditary and environmental influences, and the same abnormality may be caused by one or several different genes or by non-genetic factors.

Some lesions are chiefly due to heredity, each generally caused by a single pathological gene, arisen through mutation in the past, perhaps many generations ago, perhaps more recently. The acquired diseases on the other hand are principally caused by environmental factors. Between these two extremes lie the majority of lesions, for the production of which both genotypical and paratypical factors may assert themselves; they are dependent on a hereditary predisposition.

Hereditary diseases are monomeric in many cases though not in all, but are often also dependent on modifying genes, and always more or less dependent on the entire gene milieu. The hereditary lesions *sensu strictiori* are generally caused by what have been termed major mutant genes (see, for example, Darlington and Mather, 1949; Mather, 1949). Several hundred such genes have been identified in man, producing definite defects and abnormalities, of course operating on the variable background of the other genes and the environments. The hereditary diseases caused by major mutant genes are as a rule rare, as indicated in the aforementioned tables. A harmful mutant gene of this type can only become at all widespread if it is recessive.

Yet, a very mild defect as color blindness is far from being rare; although undoubtedly an abnormality, it may perhaps be regarded as a result of the human race being in the process of acquiring color vision (Roberts, 1950).

Predispositions to diseases that in a greater or lesser degree are hereditary must generally be regarded as polymeric. They are graded characters dependent on many genes, which, when appearing alone, have but little effect. In some cases, probably, the so-called polygenes and supergenes are in action.

Some of the hereditary predisposed diseases mentioned above, as for instance essential hypertension, are rather frequent. Other diseases of this type, as oligophrenia and cancer, may be caused by several reciprocally independent genes or by polymeric genes and by non-genetic influences. Also the possibility of cytoplasmic or maternal actions and of milk factors may in some cases be considered.

Of other factors affecting the frequencies of hereditary diseases in a population the following may be mentioned:

The mode of inheritance and the manifestation of the lesion, the geographical and social distribution, the possibilities of treatment and prevention, the effective fertility of the affected persons and the effect of consanguinity, of isolates, of selection and selective mating, of differential fertility and of lethal genes.

In conclusion the significance of knowledge concerning the frequency of the defective traits to all studies in and investigations on population problems are to be emphasized.

SUMMARY

Investigations on the frequency of hereditary defects and diseases are of great significance to the study of population problems. The principal methods for such investigations are mentioned. In this connection the importance of a Medico-Genetic Registry is emphasized.

Recent results concerning the incidence of hereditary lesions in the Danish population are reported; the frequency in the average population and at birth and, for some diseases, the morbid risk are indicated.

In Tables 1–5 the incidences are given of congenital malformations, of diseases in internal organs, of hereditary eye diseases, of mental defects and diseases, and of various more or less hereditary characters of special sociological significance. The consequences of the various figures are discussed.

The percentages of the various causes of deaf-mutism are computed in Table 6. On the basis of the figures in this table it is emphasized, that the proportional frequency of endogenous cases for many hereditary lesions is increasing as a result of the progress of civilization.

The significance of knowledge concerning the frequency of the defective traits to all studies in and investigations on population problems is emphasized.

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DISCUSSION

GLASS: Regarding the frequency of color blindness, a recent study by my colleague A. Chapanis and myself brings out a point of general importance I would like to make. We examined between 500 and 600 white school children in one Baltimore public school by means of the Ishihara charts, the American Optical Company charts, and a set of new, still unpublished charts especially prepared by Dr. Chapanis to distinguish between protanopic and deuteranopic types of color blindness. The comparative results reveal that both the Ishihara and American Optical charts overestimate the frequency of color blindness, particularly of the protanopic type. It seems that certain charts are confusing and difficult even for persons of normal color vision and allow a psychological element to enter the records. The point I wish to emphasize is not so much that frequencies of traits may be over-estimated by unreliable methods as that in making comparisons between frequencies obtained in different countries and at different times it is most important to use similar criteria for diagnosis; or, if different criteria are used, to establish by adequate comparisons the differences that result from their use.

KEMP: For the investigations on the frequency of color blindness, Ishihara's tables were used. It would be of very great value if the investigators in the various countries would use uniform methods for diagnosing, not least in the field of psychiatry. As regards mongolism not all cases can be diagnosed in new-born children; the indicated frequency at birth (Table 4) is therefore of limited value.

The frequency, 1.7%, of diabetes mellitus in persons over 14 years of age agrees fairly well with the incidence found by Dr. Joslin in the population total: 1%.

I want to emphasize what already was said in the paper, but omitted in the reading of it owing to lack of time, that any disease or any defect is the cooperative result of hereditary and environmental influences, and the same abnormality may be caused by one or several different genes or by non-genetic factors. Some lesions are chiefly due to heredity, each generally caused by a single pathological gene, arisen through mutation in the past. The acquired diseases on the other hand are principally caused by environmental factors. Between these two extremes lie the majority of lesions, for production of which both genotypical and paratypical factors may assert themselves.

To Dr. Snyder, the speaker wishes to emphasize that it would not be correct to regard the total Danish population as an isolate in the same sense of the word as the small north-Swedish population investigated by Dr. Böök.

BÖÖK: The expected incidence of mongoloid idiocy was stated by Dr. Kemp to be 1 per one thousand births. Whether mongolism is a genetic defect or not is still a matter of conjecture but anyhow it seems probable that the true frequency is somewhat higher. Penrose (1938) gives an estimation of 1:600. In a recent paper (Böök and Reed, 1950) I have discussed the frequency of mongoloid idiocy and came to the conclusion that the true value probably is close to 1:500. It is not always easy to diagnose mongolism at birth and furthermore many of these children die from congenital heart disorders and escape diagnosis. This may account for the differences found in the current literature. I would like to know whether Dr. Kemp agrees with this and also if some studies are under way in Denmark to give better information on this particular point. (Penrose, L. S., 1938, Some genetic problems in mental deficiency, J. Ment. Sc. *84*: 693–707; Böök, J. A., and Reed, S. C., 1950, Empiric risk figures in mongolism, J. Amer. Med. Ass. *143*: 8: 730–732)

KEMP: As I mentioned in my paper, the incidence of mongoloid idiocy at birth was actually observed to be one (later revised to 1.5) per 1,000 new-born children. Not all cases of mongolism can, however, be diagnosed at birth; therefore the true frequency is, as mentioned by Dr. Böök, somewhat higher. It is, however, difficult to estimate the exact figure for this frequency.

WASHBURN: As Dr. Kemp has stated, both heredity and environment play a part in the production of many conditions. However, the relative role of each varies so that it seems quite misleading to include alcoholism and criminality in a list of hereditary diseases. Actually, many of the other items in the list have been produced by disease and dietary deficiency in the mother. The implications of such tables might be clearer if the diseases were divided into groups, listing together: 1) those due mainly to heredity, 2) those where the environment plays a moderate role, and 3) those in which the hereditary factor is very small.

KEMP: The answer to Dr. Washburn's question is already given in my paper, as far as it can be

answered today. Where criminality and alcoholism are concerned, it is, for example, mentioned that "in half of the probands addicted to alcohol the alcoholism was found (chiefly) to be the result of psychic abnormality, generally psychopathy" and that "a little more than half of the criminal probands deviated mentally from the normal, some were retarded or feeble-minded, some were psychopaths and others suffered from psychoses."

THE POPULATION GENETICS OF TWO INHERITED BLOOD DYSCRASIAS IN MAN

JAMES V. NEEL[1]

Institute of Human Biology, University of Michigan, Ann Arbor, Michigan

INTRODUCTION

Until quite recently, investigations of possible genetic differences between the various subdivisions of mankind have involved for the most part the evaluation of the relative frequencies of certain traits of comparatively little or no known adaptive significance. Thus, the extensive studies of the A-B-O and M-N blood types, color blindness, and the ability to taste phenylthiocarbamide, valuable though they have been, have told us little concerning the interplay of selection and mutation in the dynamic processes whereby a human group either maintains itself for awhile in precarious equilibrium or in the course of time becomes different from other groups. The possibility that important selective values may ultimately be shown to attach to the aforementioned apparently superficial traits of course cannot be denied. But I believe it is fair to state that by the large up to the present time we have little exact information concerning the comparative racial distribution and the population genetics of inherited traits of recognized significant positive or negative selective value to their possessors. To be sure, we have been aware in a general way of the existence of genetic differences of adaptive significance. For instance, the depth of skin pigmentation is genetically determined and can reasonably be assumed to have an adaptive value. But we know little about the degree of adaptive significance or even the exact genetics of the situation. The interest attaching to clean cut genetic differences resulting in readily evaluated phenotypes of possible significance from the standpoint of natural selection—the type of situation so dear to the heart of the geneticist—is therefore considerable. In the following presentation I should like to discuss with you two inherited hematological disorders which in recent years have been the object of considerable research throughout the world. Both of these diseases are highly fatal, both are virtually restricted to definite elements of the world's population, and both occur with a sufficient frequency within these elements to raise problems in population genetics that are both complex and baffling at the present time.

[1]This investigation has been supported in part by a grant from the U. S. Public Health Service. It is a pleasure to mention my gratitude to the Anemia Clinic of the Children's Hospital of Michigan, Detroit, Michigan, for the generous manner in which its staff has made both records and clinical facilities freely available. I am also indebted to the Wayne County General Hospital and Infirmary, Eloise, Michigan, and the Michigan Rapid Treatment Center, Ann Arbor, Michigan, for their cooperation in various aspects of the study. It is a further pleasure to acknowledge the hematological assistance of Mrs. Harriett Shapiro and Mrs. Marion Weyrauch, and the case work of Mrs. Catharine Williams and Mrs. Laura Williams.

THALASSEMIA (COOLEY'S ANEMIA)

Mode of Inheritance

Cooley's anemia or thalassemia major[2], the first of the two diseases to be discussed, is a chronic and progressive disorder usually terminating fatally in childhood and characterized by a profound anemia with marked hypochromia, anisocytosis, and poikilocytosis of the erythrocytes, the occurrence of large numbers of erythroblasts in the circulating blood, splenomegaly, the deposition of pigment in the viscera, and an increase in the medullary bone spaces. The disease was first clearly described in 1925 by two Detroit pediatricians (Cooley and Lee, 1925). Almost from the first, it was apparent that the disorder was largely confined to persons derived from the vicinity of the northern shores of the Mediterranean, for which reason the disease has also been called Mediterranean anemia. About the same time that Cooley's anemia was described in this country, Italian physicians (Rietti, 1925, Greppi, 1928) were describing a much less severe hematologic disorder characterized by a mild microcytic anemia, splenomegaly, and slight evidences of increased blood destruction. The same anemia

[2]This anemia and the related condition to be discussed below (thalassemia minor) are known by many names. In the following discussion I shall use the terms thalassemia major and minor, recognizing that there are certain valid objections to this terminology, but feeling that there has not yet been proposed a better alternative nomenclature.

was independently described in this country some fifteen years later (Wintrobe, Matthews, Pollack, and Dobyns, 1940; Dameshek, 1940; Strauss, Daland, and Fox, 1941). Both the mild and severe anemias are resistant to all known therapy. They were soon found to have a familial incidence and further, to be associated in the same family. The currently accepted theory, evolved independently in Italy and this country, is that the mild anemia—which has been termed thalassemia minor—is due to the heterozygous state for a gene which when homozygous produces the severe anemia—which has been termed thalassemia major. (Italy: Gatto, 1942a, b; Chini, 1946; Silvestroni and Bianco, 1946a, b; U.S.A.: Dameshek, 1943; Valentine and Neel, 1944, 1947). The evidence in support of this conclusion is chiefly of three types: 1) With certain possible exceptions, to be mentioned below, both the parents of an individual with thalassemia major have had hematological findings consistent with a diagnosis of thalassemia minor, 2) when all the reported sibships in which thalassemia major has made its appearance are considered, there is a satisfactory approximation to a 3 : 1 ratio, and 3) in the marriage of individuals with thalassemia minor to normal persons, children occur in the ratio of 1 normal : 1 thalassemia minor, while among the siblings of individuals with thalassemia major, thalassemia minor and normal individuals occur in a ratio of 2 : 1. Those interested in a thorough summary of the clinical and hematological data now available concerning these two conditions are referred to the recent extensive review of Silvestroni (1949).

Fawdry (1946), Smith (1948), Schwartz and Mason (1949), and Chini and Valeri (1949) have emphasized the fact that it is possible to select cases of thalassemia major and minor so that there is a continuous spectrum of severity ranging from very mild to extremely severe. While this is undoubtedly so, the vast majority of all cases fall into one or the other of two clearly defined categories, with only a relatively few intermediates. Whenever one of these latter is found, the possibility must be explored that some other medical disorder has been superimposed on what is fundamentally a case of thalassemia minor, particularly an iron deficiency anemia on a dietary or chronic hemorrhagic basis. Thus, my own experience includes a male patient whose hemoglobin level of 9.6 grams per cent was unusually low for thalassemia minor but whose hematological picture certainly did not suggest thalassemia major. But three months after his blood studies, this individual developed gastrointestinal symptomatology leading to the diagnosis of carcinoma of the large intestine. The lesion was probably already present at the time of our hematological studies and exercising a definite effect on the findings. However, I do not mean to imply that there must always be a complicating circumstance for the intermediates—the occurrence of modifying genes capable of accentuating the phenotype of the heterozygote or ameliorating the phenotype of the homozygote is very probable.

The Frequency of the Disease

The disease in this country has been studied chiefly in individuals of Italian extraction. In Rochester, New York, Dr. Valentine and I estimated in 1945 that thalassemia major occurred amongst the Italian element of that city, largely of Sicilian origin, with a frequency of 4.2 per 10,000 births, from which the frequency of thalassemia minor was calculated to be 4.1 per cent (Neel and Valentine, 1945). In a series of 100 consecutive blood smears involving persons of Italian extraction admitted to Strong Memorial and Rochester Municipal Hospitals, there were three certain and two possible cases of thalassemia minor, a satisfactory small-scale confirmation of the results of the calculation (Neel and Valentine, 1947). Recently Silvestroni (1949) and Silvestroni and Bianco (1949) have summarized the results of extensive studies on the distribution of thalassemia minor in Italy. The results of these studies are presented in Figure 1. Although the condition is found all over Italy, there appear to be two highs, namely, in Sicily, where 4.45 per cent of 6,739 persons showed the trait, and in northeastern Italy, around the Po delta, where 10.2 per cent of 7,557 persons tested in the cities of Ferrara and Rovigo were thought to show the disease, although in surrounding communities the incidence was more like 1 to 2 per cent. The correspondence of their estimate based on direct methods with ours based on indirect methods is noteworthy. In dealing with such large numbers of persons, Silvestroni and Bianco employed a screening method which would probably not completely exclude individuals with an iron-deficiency type of anemia, but this is probably not a major source of error. For no other Mediterranean country do we have survey figures such as those from Italy. However, there are clear indications that the disease may have a comparable incidence in Greece, Syria, and Cyprus (Caminopetros, 1938; Fawdry, 1944; Smith, 1948; Banton, 1948). Thus, Banton (1948), in a briefly recorded discussion of a case of thalassemia minor presented

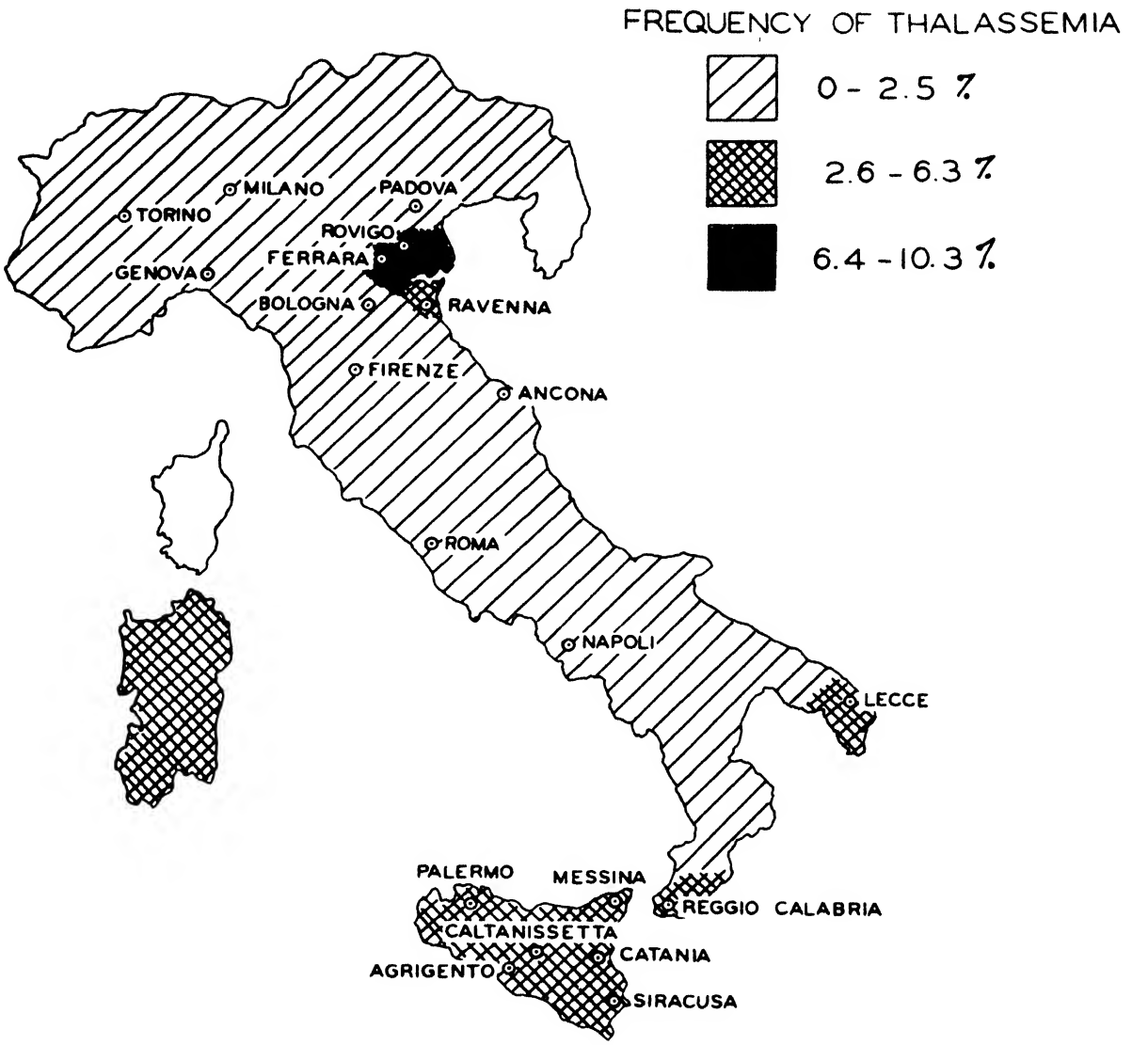

FIG. 1. The distribution of thalassemia minor in Italy, Sicily, and Corsica, according to the data of Silvestroni and his collaborators.

by Rubie (1948), speaks of observing 20 per cent thalassemia minor on Cyprus. Scattered cases of both thalassemia major and minor have also been reported in "non-Mediterranean" Europeans, including two cases in Jews and one in an English child (Bywaters, 1938; Freudenberg and Esser, 1942; Rohr, 1943; Schieber, 1945; Altmann, 1946); in Egyptians (Diwani, 1944; Silvestroni and Bianco, 1948a); in Indians (Mukherji, 1938; Napier, Shorten, and Das Gupta, 1939; Patel and Bhende, 1939; Coelho, 1939; Dhayagude, 1944); in an "Anglo-Indian" (Fairley, 1940); in Chinese (Foster, 1940; Greenblatt, Cohn, and Deutsch, 1946; Scott, 1947; Gardner, 1947); in Negroes (Faber and Roth, 1946; Stiles, Manlove, and Dangerfield, 1946; Schwartz and Mason, 1949; Coffey and Salmon, 1949); in an American Indian (Prouty, 1950); and in Filipinos (Soransky and Regola, 1942; Slaten, 1948). Although a number of these cases fall short of meeting rigid diagnostic requirements, there can be no doubt of the occurrence in non-Mediterraneans of clinical syndromes indistinguishable from thalassemia. It does not follow automatically that all these cases have the same genetic basis, but that at least a portion represent the same disease appears probable. One gets the impression that in non-Mediterraneans thalassemia minor is more ex-

tremely expressed than in persons who by virtue of centuries of genetic exposure may be assumed to have built up a partial genetic immunity. Many of the above mentioned case reports do not include family studies; the inclusion of such studies in future reports would be of great value.

Evidence Concerning Mutation and Selection

In 1947 Valentine and I pointed out that inasmuch as the homozygote with only a few questionable exceptions has always failed to reproduce, then if the frequency of the disease is being maintained through mutation in Sicily, we must postulate a minimum rate of about 4×10^{-4} if the heterozygote is selectively neutral, and even higher rates if the heterozygote is in any way at a biological disadvantage. This was a disturbingly high estimate. Three alternatives to the assumption of so high a mutation rate were listed: 1) that the disease was being eliminated—in which case we had the problem of accounting for its high frequency in the past, 2) that some abnormal genetic mechanism existed resulting in an excess over expectation of thalassemia minor, a possibility for which there was no evidence, and 3) that the heterozygote was in some way actually the object of a positive selection. In this connection, it was pointed out that an increased fertility of 2 per cent in individuals with thalassemia minor would maintain the equilibrium even in the absence of any mutation. Haldane (1949) and Silvestroni, Bianco and Montalenti (1949) have expressed the opinion that the last named alternative deserves especial consideration.

The problem of reaching a decision between a high mutation rate as opposed to selection for the heterozygote may be approached in several different ways:

1. Undoubtedly the most clean cut solution would involve extensive figures on the fertility of individuals with thalassemia minor as compared with individuals without this trait. The demonstration of a 2 per cent reproductive differential would require a rather extensive body of data, subject to a good many qualifications. Silvestroni *et al.* (1950) have quite recently presented preliminary data indicating that in Italy the marriage of two heterozygous individuals with thalassemia minor is more fertile than the marriage of normal with normal, or thalassemia minor with normal. But the mortality among the children of the mating of two heterozygotes was also increased, even beyond what could be expected from the elimination of the resulting homozygous children, with the result that the mean number of surviving children from the three types of marriage did not appear to be significantly different. Theoretically, even in the face of this differential mortality, the fact that the number of surviving children from the mating of two heterozygotes equals that from the other two types of marriage could provide a mechanism which would at least in part offset the effects of negative selection against the homozygote. However, there is absolutely no evidence indicating whether the observed "compensatory fertility," as it may be termed, is a phenomenon of long standing or whether it is, as seems quite possible, a product of modern civilization and so of little significance in establishing the present-day gene frequencies.

2. A second line of attack involves a search for direct evidences of mutation. In Sicily, for instance, the frequency of the gene involved can be readily calculated from the equation $.0445 = 2p(1-p)$, from which $p = 0.0217$, and the frequency of the homozygote, disregarding consanguinity effects in the case of a gene with such an incidence, would be $\overline{0.0217}^2 = .00047089$. The ratio of heterozygote to homozygote would be $.04450000 : .00047089$, or $94.5 : 1$. Since the homozygote fails to reproduce, one in 47.25 thalassemia genes should be eliminated each generation. If this loss is made up in whole or part through mutation, we might expect to find evidences of this, in the form either of isolated cases of thalassemia minor where neither parent shows the trait, or isolated cases of thalassemia major where one parent shows thalassemia minor and the other is normal. However, the occurrence of such apparently isolated cases of what clinically seems to be thalassemia is not *per se* evidence for mutation. There are at least four alternative possibilities, namely 1) the occurrence of hematological conditions clinically indistinguishable from thalassemia major, due to the interaction of the heterozygous state for the thalassemia gene with some other constitutional factor, 2) the inclusion among these apparently isolated cases of some children who with the passage of time and further diagnostic studies might be shown not to have thalassemia major or minor, 3) the occurrence, among the parents, of individuals who although heterozygous for the thalassemia gene are actually phenotypically normal (cf. Neel and Valentine, 1947, kindred No. 17), and 4) the parentage of the child not as assumed. The first possibility will always exist as an alternative to mutation, the second possibility is one which can largely be avoided by the proper selection of cases, the third possibility can be

evaluated when the family of the apparently normal person is available for study, and the final possibility may at present be established in approximately 50 per cent of cases in which it occurs by appropriate serological studies.

Turning now to the literature, we find among three different series of cases the following results: In my own experience with five isolated cases of thalassemia major where both parents were studied, all 10 parents had thalassemia minor, while of six isolated cases of thalassemia minor, one parent was found to have the disease in each case. Smith (1948) found that of 10 isolated cases of thalassemia major, all 20 parents had thalassemia minor, while for nine isolated cases of thalassemia minor, one or both parents also had thalassemia minor in each instance. By far the most extensive data on the point has been supplied by Silvestroni and Bianco (1945, 1946a, b, 1948b) and Silvestroni, Bianco, and Vallisneri (1949). In the first four references cited they report that of eight isolated cases of thalassemia minor, a parent was affected in each instance, while of 32 isolated cases of thalassemia major, both parents had minor in 26 cases, but only one in six instances (1946—families 20, 21, 23, 24, 25, 28). However, five of the cases of thalassemia major for which only one parent appeared to exhibit thalassemia minor appear to have been deceased prior to the initiation of their studies of the family and so not available for critical reevaluation, the diagnosis apparently being based on hospital records. They give no blood data on these cases in their publication. In the sixth case, the findings in the "normal" parent are somewhat equivocal. More recently, in the fifth reference cited above, they have reported the results of studying 220 parents of children with thalassemia major (both "isolated" and "familial" cases): 210 of these definitely had blood findings compatible with thalassemia minor, six had mild but very suggestive findings, three had equivocal findings, and for one parent "the absence of microcythemia was proved without doubt." Serological studies to evaluate the ever-present question of parentage, and examinations of the blood of the parents and siblings of the apparently exceptional parents, do not appear to have been done. It must be concluded that while up to the present there have been reported a number of possible examples of mutation to the gene for thalassemia, there are alternative and equally probable explanations for each case. It would appear that from the genetic standpoint the intensive study of these "exceptional" parents and their families is of paramount importance. Only through such studies will it be possible to reach a decision between the occurrence of mutation and its various alternatives.

3. The third obvious line of attack on the question of how to account for the relatively high incidence of thalassemia consists in an attempt to evaluate on the basis of present medical evidence the "fitness" of the heterozygote. This is an extremely difficult issue. By the large, physicians in this country have felt that thalassemia minor has a definite but ill-defined medical significance, in part because of the not infrequent objective findings of splenomegaly and evidences of increased blood destruction and regeneration, and in part because of such subjective complaints as ease of fatigue. Italian investigators have been inclined to give even greater weight to the clinical significance of thalassemia minor. Thus, Chini and Valeri (1949) in a recent review of the problem write (p. 995): "In numerous cases of 'Mediterranean hemopathic syndrome' (their term for thalassemia minor) we find a *marked hemolytic element.* These cases are more readily recognizable clinically and have been termed 'hemolytic jaundice with decreased red cell fragility' (Rietti, Greppi). The picture is that of the 'Mediterranean hematologic disorder' with anemia of one or the other variety (increased resistance to hypotonic solutions, occasional ovalocytosis, presence of target cells: 'oval-target cell syndrome' of Dameshek). There is marked hyperplasia and erythroblastic anaplasia of the bone marrow, but no erythroblasts are found in the circulating blood and hemolysis is increased. In some cases the hemolytic index reaches values as high as in acholuric jaundice. Jaundice is present, there is marked splenomegaly and intense hemolytic crises may occur." Elsewhere (p. 1001) the same authors write: " 'Thalassemia minor' would seem to include well-defined syndromes, some of which are of marked severity and for which the term 'minor' could hardly seem acceptable" (see also Silvestroni, 1949). In our own experience (Valentine and Neel, 1948), individuals with thalassemia minor have averaged two grams of hemoglobin less than normal persons. While there is undoubtedly a large margin of safety in normal hematological physiology, it is difficult to see how such a departure from the norm can *per se* be of adaptive value to the organisms. The possibility remains that the hematological trait is linked to some as yet unrecognized characteristic of distinct value. Linkages of hematological traits with alterations in apparently unrelated

systems have been recognized in both the guinea pig (Russell, 1949) and the mouse (siderocyte anemia; review in Grüneberg, 1943). In this connection, Silvestroni and Gentile (1945-6) have presented evidence of a "microcytic facies," characterized by a concave nose with sunken root and thickened flat tip, and evidence of a peculiar conformation of the cheek bones, with anterior and lateral flattening of the zygomatic area. As they point out, it is impossible to say whether these are the characteristics of the particular human stock in which thalassemia happens to occur, or whether the thalassemia gene *per se* is responsible for these effects. If the thalassemia gene is linked with a favorable gene or genes, some mechanism is necessary to maintain this relationship. This might conceivably be supplied by a chromosomal inversion.

Regardless of whether it is mutation or selection for the heterozygote which is responsible for maintaining the frequency of the disease—and no decision appears possible at the present time—we are faced with the enigma of its restricted racial distribution. In this connection it might be pointed out that if there is selection in favor of the heterozygote, the racial distribution could be explicable in terms of the appearance in a particular human stock of a mutation, possibly associated with an inversion, which in that particular genetic background (but not in others) was selected for and so increased until a balance between homozygote and heterozygote was established. If, on the other hand, the explanation is in terms of a high mutation rate, we have at the present time no clues as to the reason for its virtual restriction to this one group.

Sickle Cell Disease

Mode of Inheritance

The second of the two conditions which we shall consider is known as sickle cell disease. If blood specimens from a randomly assembled series of Negroes, to whom the condition is largely confined, are treated in such a manner as to lower the O_2-tension, in certain cases the erythrocytes will be observed to undergo bizarre distortions of their shape, with the appearance of one or more fine projections, so that the cells resemble sickles, holly-leaves, etc. In the majority of these individuals the tendency has no known pathological consequences, but some persons with the sickling tendency are the victims of a severe, chronic hemolytic type of anemia, presumably on the basis of increased intravascular hemolysis. These latter individuals are spoken of as having sickle cell disease, whereas those in whom the sickling is accompanied by no pathological consequences are said to have the sickle cell trait. Pauling, Itano, Singer, and Wells (1949) have recently demonstrated that in sickle cell disease the hemoglobin—and probably the globin portion of the hemoglobin molecule—has a different electrophoretic behavior than does normal hemoglobin. In the sickle cell trait two types of hemoglobin molecules are present, namely, normal, and the type present in sickle cell disease. Persons with sickle cell disease regularly exhibit, in addition to the anemia, other consequences of increased blood destruction, such as an elevated serum bilirubin, an elevated reticulocyte count, leucocytosis, and an increase in the medullary bone space. The habitus is typically asthenic. They are subject to hemolytic crises, during which there may be acute abdominal or joint pain, cerebrovascular symptoms, etc. Transfused erythrocytes from persons with sickle cell disease soon disappear from the recipient's circulation, whereas cells from a person with the sickle cell trait have a normal life span (Singer, Sidney, King, and Jefferson, 1948; Callender, Nickel, Moore, and Powell, 1948).

The medical literature contains a considerable discussion of the etiological relationship between sickle cell disease and the sickle cell trait. It was early observed that both conditions tended to occur in the same family, and early genetic studies, failing to make a clear distinction between the trait and the disease, considered both as manifestations of a dominant gene of variable expression (Taliaferro and Huck, 1923), a point of view which has prevailed until quite recently. Several years ago I undertook to test the hypothesis, first outlined in a review article by the present author in 1947, that the genetic situation here was comparable to that which obtains in thalassemia, postulating the existence of a gene which in single dose elicited the sickling phenomenon and in double dose, sickle cell disease. Seventy-two families in which either sickle cell disease or the sickle cell trait were known to be segregating have now been subjected to rather complete hematological and serological studies. Representative pedigrees are shown in Figure 2. The data in support of the hypothesis, which have thus far only been treated in a short note (Neel, 1949) and will be published in detail elsewhere, may be summarized under the same three headings used for thalassemia. 1. A total of 91 parents of cases of sickle cell disease have been studied

for the occurrence of the sickling trait. All but one of these have shown the trait. The possible significance of this exception will be returned to later. 2. Among 58 sibships segregating for sickle cell disease, there were 74 cases of sickle cell disease in a total of 201 children. On the face of it this is a serious departure from a 3 : 1 ratio, but as you all know, the fact that families come to our attention only if there is at least one affected child is a very significant distorting factor when segregation is studied in small human families.

The Frequency of the Disease

The original description of the disease by Herrick in 1910 was based upon observations on a United States Negro male. The first case reports were all concerned with Negro subjects, but during the past 40 years there have crept into the literature at least 26 primary case reports of the sickling phenomenon usually associated with a hemolytic anemia in presumably Caucasian individuals with no *known* Negro admixture (Cooley

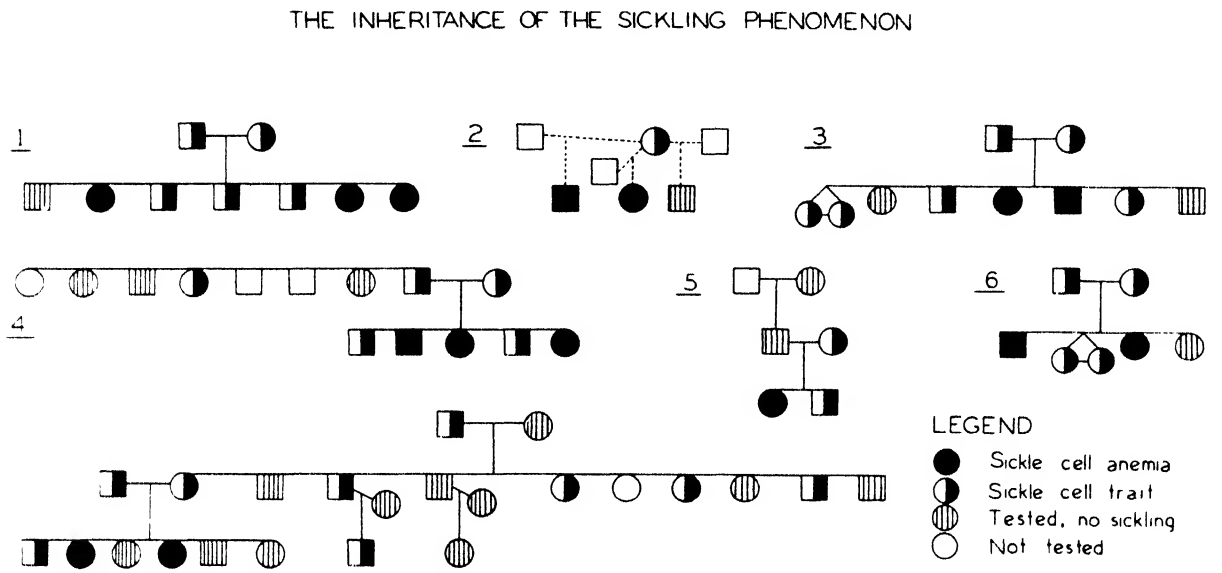

FIG. 2. Representative pedigrees of the sickle cell trait and sickle cell disease in American Negroes.

When allowance is made for this source of distortion, assuming for the moment that ascertainment of the disease in the Negro population studied is complete, the expected number of affected children is 80.8 ± 4.59, the difference between observation and expectation being non-significant. Actually, the assumption of complete ascertainment is at variance with the facts and introduces a slight error into the expected incidence given above; this problem will be treated elsewhere. 3. Finally, among the 94 siblings of children with sickle cell disease the ratio of sickle cell trait to normal has been 60:34, a satisfactory approximation to the expected 2:1 ratio.

The findings of Pauling, Itano, Singer and Wells (1949), with biochemical evidence for a clear separation between sickle cell disease and the sickle cell trait, may be taken as additional data in favor of the homozygous-heterozygous hypothesis. Recently Beet (1949), on the basis of the study of a single large African family, has independently arrived at the same genetic hypothesis. and Lee, 1929; Sights and Simon, 1931; Rosenfeld and Pincus, 1932; Clarke, 1933; Cooke and Mack, 1934; Wallace and Killingsworth, 1935; Haden and Evans, 1937; Johnson and Townsend, 1937; Pontoni, 1939; Greenwald and Burrett, 1940; Vance and Fisher, 1941; Mallory, 1941; Wade and Stevenson, 1941; Morrison, Samwick, and Landsberg, 1942; Ogden, 1943; Canby, Carpenter, and Ellmore, 1944; Woofter, Dick, and Biering, 1945; Altmann, 1945). It is significant for two reasons that of the 22 families involved, 16 have been of Greek or Italian derivation. In the first place, Sicily has historically been a meeting ground for many races. In the second place, there is reason to suspect that some of these cases of what appears to be sickle cell disease may actually be individuals who have received a thalassemia gene from one parent and a sickle cell gene from the other, a situation which leads to a condition medically very similar to sickle cell disease (see below). No cases of sickle cell disease have been reported in Mongolians. Two cases have

been reported in Indians (Berk and Bull, 1943; Wright and Pearson, 1949).

Numerous surveys of the frequency of the sickling trait have been carried out on the American Negro. The results of such surveys are summarized in Table 1. It will be seen that the incidences reported prior to 1932 average somewhat

TABLE 1. THE INCIDENCE OF SICKLING IN AMERICAN NEGROES (EXCLUSIVE OF NEWBORN INFANTS)

Investigators	Number tested	Number positive	Per cent positive
Sydenstricker, Mulherin, and Houseal, 1923	300	13	4.3
Cooley and Lee, 1926	400	30	7.5
Miyamoto and Korb, 1927	300	19	6.3
Wollstein and Kreidel, 1928	150	13	8.7
Smith, 1928	100	5	5.0
Josephs, 1928	250	16	6.4
Levy, 1929	213	12	5.6
Dolgopol and Stitt, 1929	77	4	5.2
Graham and McCarty, 1930	1,500	122	8.1
Brandau, 1930	150	10	6.7
Sydenstricker, 1932	1,800	99	5.5
Total	5,240	343	6.6
Diggs, Ahmann, and Bibb, 1933	3,213	276	8.6
Beck and Hertz, 1935	100	13	13.0
Hansen-Pruss, 1936	100	14	14.0
Cardozo, 1937	1,263	119	9.4
Diggs and Pettit, 1940	406	37	9.1
Tomlinson, 1941	275	18	6.6
Watson, Stahman, and Bilello, 1948	226	18	8.0
Scott, Crawford, and Jenkins, 1948	209	16	7.7
Switzer and Fouche, 1948	1,000	140	14.0
Switzer, 1950	3,066	412	13.4
Total	9,858	1,063	10.8
Neel, unpublished	1,000	91	9.1

lower than those reported since that date, a finding probably to be attributed in part to improvements in the techniques for eliciting sickling, and in part to the inclusion in the later data of the large series of tests of Switzer and Fouche (1948) and Switzer (1950) on what would appear to be a relatively "undiluted" group of Negroes, the Sea Island Negroes of South Carolina. My own findings, also shown in Table 1, are in satisfactory agreement with other results since 1933. There have been relatively few surveys on non-Negro groups in this country, undoubtedly because in view of the paucity of non-Negro cases of sickle cell disease such surveys scarcely seemed worth while. However, Sydenstricker (1924), Korb and Miyamoto (1927), Diggs *et al.* (1933), Cardozo (1937) and Ogden (1943) have between them examined 2,621 Caucasians in the United States, finding only one instance of sickling, this in a 10 year-old Mexican boy described by Cardozo (1937). Da Silva (1945) found no sickling in 120 Brazilian Caucasians; Calero (1946) none in 105 Caucasian Panamanians, while Findlay, Robertson, and Zacharias (1946) failed to detect sickling among 568 British soldiers and airmen stationed during the recent war in West Africa. Wallace and Killingsworth (1935), subsequent to discovering a case of sickle cell disease in a Mexican child, found no further sickling in a random sample of 239 Mexicans, and da Silva (1948) found no sickling in 1,379 Brazilian Indians.

It has been estimated that the ancestry of the average American Negro is approximately one-third Caucasian and Indian, so that the studies in this country on "Negro" populations involve a decidedly heterogeneous group (Herskovits, 1935, 1942; Ashley Montagu, 1944; Meier, 1949). Studies on the incidence of sickling in other such heterogeneous Negro groups have been carried out in various localities in the Western Hemisphere, as summarized in Table 2. The incidence of sickling in these groups is comparable to that observed in the Negroes of the United States.

It is only within the past six years that data have been available on the incidence of the sickling phenomenon in native Africans. These data are summarized in Figure 3. Incidences ranging all the way from below 1 per cent up to 45 per cent have been reported in various groups, with most of the groups studied showing an incidence of between 12 and 30 per cent. The recently published results of Lehman and Raper (1949) in Uganda are of especial interest. They found that among four different, nominally Negro tribes speaking an Hamitic-type language, and presumably with a strong Hamitic racial element, the incidence of sickling varied from 0.8 per cent to 3.9 per cent. Among seven different tribes with a Nilotic-type language, the incidence of sickling varied from 21.0 to 28.0 per cent. Finally, among 11 different Bantu language group tribes, the incidence of sickling varied from 2.0 to 45.0 per cent, with an average of 20 per cent. Their studies involved a total of 4,039 persons.

Information concerning the origins of the Negroes brought as slaves to this country is in many ways unsatisfactory. It seems firmly established, however, that the majority were drawn from the coastal and adjacent areas of West Africa, from

the Gambia to the Niger rivers, with the Congo basin making the next greatest contribution, and lesser numbers drawn from such places as Madagascar and Mozambique (Herskovits, 1933-4, 1942; Klineberg, 1944; Frazier, 1949). Unfortunately for our present purposes, significant studies of the incidence of sickling have been carried out in only one of the above mentioned points of origin, namely the West African Coast. The gap in our knowledge of the Congo region is especially regrettable. The difference between the 9–10 per cent sickling incidence in the United States and the 15 per cent thus far reported in West Africa would indicate that the anthropologists' estimate that the "average" Negro is one-third white and Indian is substantially correct.

Trowell, 1945; Beet, 1946, 1949; Robertson and Findlay, 1947; Raper, 1949; Lehmann and Milne, 1949). Some of these cases are of very dubious validity, being in all probability a combination of the sickle cell trait with an unrelated anemia. In view of the known incidence of the sickle cell trait the number of valid reports is really quite small. Raper (1950) has recently reviewed the literature on sickle cell disease in Africa, and expressed the opinion that the observed paucity of cases of the disease is a real phenomenon and not due to a failure in diagnosis. He advances the hypothesis "that the appearance of sickle-cell anaemia depends, not only on the extent to which the trait is present in a community, but also on the extent to which admixture with other genetic

TABLE 2. THE INCIDENCE OF THE SICKLING PHENOMENON IN NEGROID GROUPS OUTSIDE THE UNITED STATES, EXCLUSIVE OF NATIVE AFRICANS

Locality	Investigator	Number examined	Number sickling	Per cent sickling
Brazil	de Castro, 1934, after da Silva, 1945	86	...	12.8
"	Maia de Mendonça, 1942	406	30	7.4
"	da Silva, 1945	1,130	113	10.0
Central America	Tomlinson, 1945	3,000	246	8.2
Colombia	Mera, 1943	489	46	9.4
Cuba	Chediak et al, 1939, after da Silva, 1945	57	...	5.7
Honduras	McGavack and German, 1944	300	24	8.0
Curaçao	van der Sar, 1949	2,499	...	11.7

Clinical estimates of the ratio of sickle cell disease to sickle cell trait in the general population have ranged between 1 : 1.4 (Mera, 1943) and 1 : 40 (Diggs, Ahmann, and Bibb, 1933). The exact ratio can readily be calculated once the genetic situation has been clarified. If we accept 0.09 as a satisfactory estimate of the incidence of sickling in the American Negro, then $0.09 = 2p(1-p)$, from which $p = 0.047$, and p^2, the incidence of sickle cell disease in this country, is 2.2/1000. The ratio of the sickle cell trait to sickle cell disease is 0.0900 : 0.0022, or, at birth, 41 : 1, with, of course, higher ratios in the population as a whole because of the selective elimination of children with sickle cell disease. In Africa the incidence of the homozygote would be correspondingly higher. Thus, in a tribe where the incidence of the sickling trait is 0.30, $p = 0.167$, and the incidence of the homozygote would be 27.9/1000.

At the present time our knowledge of the frequency and severity of sickle cell disease in Africans is quite limited. A number of investigators have reported cases of the disease among native Africans (Russel and Taylor, 1932; Smith, 1933–4; Reid, 1936; Evans, 1944 and 1945; strains has occurred." Paraphrased in the light of current thought on the genetics of sickle cell disease, this would amount to postulating that the genetic balance of the native African is such that the effect of homozygosity for the sickle cell gene is relatively mild; the disturbance of this balance in the United States by intermarriage with Caucasians and American Indians has resulted in an accentuation of these effects.

This is a very interesting hypothesis, which certainly must be further explored in the future. However, it does not appear to the present author that the evidence for the failure of sickle cell disease to appear among native Africans is as yet as strong as it needs be. Thus, it is still possible that sickle cell disease is just as severe in Africa, and that because of the more rigorous conditions obtaining in the early years of life there, most of the children are eliminated when quite young, either in consequence of a hemolytic crisis or because of intercurrent disease. This possibility is indirectly made the stronger by the evidence (see below) that in Africa as well as the United States the sickle cell gene may have deleterious effects in the heterozygote. Critical data can be derived from a careful consideration of the

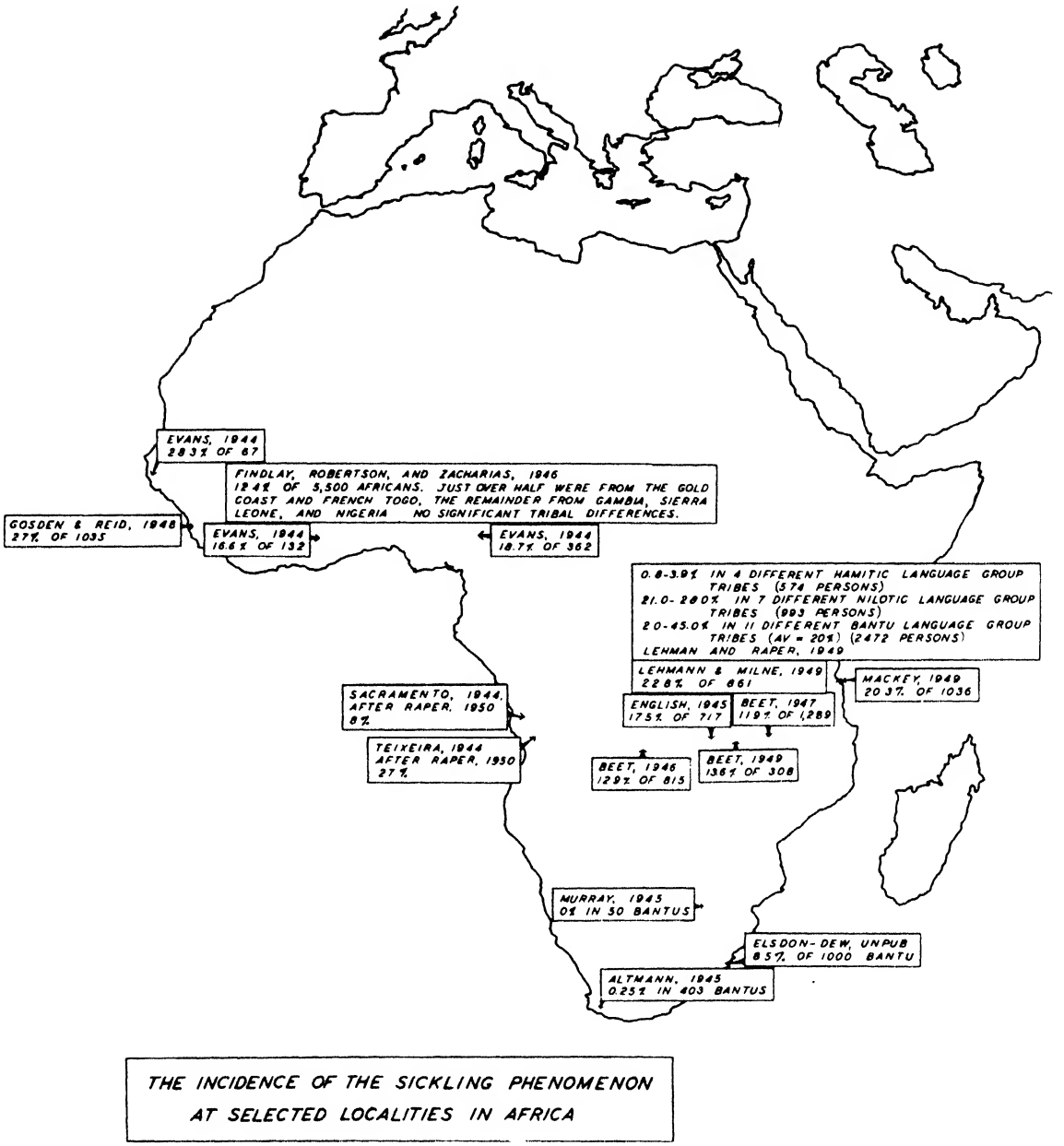

FIG. 3. The incidence of the sickling phenomenon in various groups of native Africans.

offspring of marriages involving two heterozygotes as contrasted with the offspring of the marriage of heterozygous with normal and/or normal with normal persons.

So often the inherited pathological conditions with a simple genetic basis are rarities. Sickle cell disease may be an outstanding exception to this general rule. Thus, if the population of Africa south of the Sahara amounts to approximately 200,000,000 persons, of whom 20 per cent have the sickle cell trait, then, neglecting for the moment the effects of differential mortality, approximately 2,400,000 persons should be homozygous for the sickle cell gene in that one region alone. These facts point to the possible existence of a medical problem of first-order magnitude.

Evidence Concerning Mutation and Selection

The selective disadvantage under which individuals with sickle cell disease in the United

States labor has never been estimated accurately. We are now in the process of working out mortality curves. Individuals with the disease not infrequently die prior to the age of 20. It is a rare event for a woman with sickle cell disease to give birth to a live child (cf. Anderson and Busby, 1949). Men who reach the age of reproduction are less handicapped from the standpoint of procreation, but the depressant effects of severe anemia on physiological functions are so well known as to require no further comment here. We will not be in serious error if we estimate the relative fertility of individuals with sickle cell disease in this country at something less than 20 per cent of normal.

If sickle cell disease is in Africa the same disease that it is in this country, then some very thorny problems in gene dynamics are raised. Thus, in a region with a 20 per cent incidence of sickling, the frequency of the disease should be 12.8 per 1000 births, and the mutation rate necessary to maintain this frequency, assuming the heterozygote to be neutral from the standpoint of natural selection, would be approximately 1×10^{-2} —a truly staggering figure.

Just as in the case of thalassemia, the most logical alternative to the assumption of so high a mutation rate is positive selection in favor of the heterozygote. In Table 3 I have tabulated the age-incidence relationship for the sickle cell trait as seen in some of the more extensive series on United States and African Negroes. In all six series the highest incidence is seen in children, with a decrease in the older age groups. In presenting the data of Diggs, Ahmann, and Bibb (1933) and Switzer (1950), I have omitted those categories of their data which included children below the age of three months, since children of this age do not sickle as readily as older children (Watson *et al.*, 1948). In the data of both these papers those age groups tend to show a lower incidence than older children. The reports from Africa cited in the table do not indicate to what extent newborns are included in the series.

The existence of such a trend, and the inference that there is a differential elimination of individuals with the sickle cell trait, seems first to have been pointed out by Raper in 1949. Mackey (1949) has questioned the validity of the trend, but his own data, which showed no difference between children and adults, were based upon observations on mothers and their children—a circumstance which would appear to limit the value of his findings. An alternative to the postulate of differential elimination of persons with the sickle cell trait is, of course, the possibility that the penetrance of the sickle cell gene is decreased in the older age groups. There are no present data to this effect. Furthermore, since in part at least these series are based upon hospital populations, the apparent decrease in the incidence of sickling in older age groups might mean only that the sicklers are enjoying better health and so are not represented in the series.

TABLE 3. THE RELATION BETWEEN AGE AND THE SICKLE CELL TRAIT IN SOME OF THE LARGER SERIES OF TESTS FOR THE TRAIT IN AMERICAN AND AFRICAN NEGROES

Location of studies	Investigator	Age group	Number tested	Number sickling	Per cent sickling
America	Diggs, Ahmann, and Bibb, 1933	6–20	1,112	108	9.7
		21–50	1,102	96	8.7
		51–	403	28	7.0
	Switzer, 1950	6–20	843	130	15.4
		21–50	1,233	165	13.4
		51–	302	42	13.9
	Neel, unpublished	12–20	147	15	10.2
		21–50	703	67	9.6
		51–	146	7	4.8
Africa	Findlay, Robertson, and Zacharias, 1946	0–5	268	38	14.2
		6–20	881	87	9.9
		21–	1,560	194	12.4
	Beet, 1947	0–5	164	28	17.1
		6–15	160	18	11.3
		15–	965	108	11.2
	Elsdon-Dew, unpublished	0–20	232	24	10.3
		21–50	555	48	8.7
		51–	213	13	6.1

Further data on this important point have been supplied by Evans (1944) who found that among 302 native West African soldiers classified as "fit" the incidence of sickling was 15.5 per cent, whereas among 259 suffering from acute or chronic disease it was 25 per cent. Beet's (1947) findings on hospitalized East Africans are more difficult to interpret, since all his subjects had sought hospital care and there was no control group—within the group studied there were no clear cut indications of particular disease susceptibilities conditioned by the sickling trait.

In the realm of more controlled observations, Dickstein *et al.* (1949) found that the erythrocytes from individuals with the sickle cell trait show an increased resistance to hypotonic saline, and transfusion experiments have revealed a normal life expectancy for cells from individuals with the trait (Singer, Sidney, King, and Jefferson, 1948; Callender, Nickel, Moore, and Powell, 1948).

As in the case of thalassemia, at present we cannot rule out a relatively small selective advantage on the part of the heterozygote; we can only say that no conclusive data exist, the evidence if anything suggesting that the reverse is true. Further detailed studies on the exact medical significance of the sickle cell trait would seem to be highly desirable.

If, now, it is assumed that the heterozygote is selectively neutral and that equilibrium is being maintained through mutation, then in America approximately $\frac{2.2 \times .8 \times 2}{90 + 2.2 \times .2}$ genes, or 1 in 25.7 genes should be a new mutant. It is almost certain that the American Negro population is not in equilibrium in this respect for a number of reasons, but at least we can use the assumption to fix an order of magnitude for mutation. This is a sufficiently high fraction, and the end point of mutation is in this case sufficiently clear cut, that it should be possible to gather critical data on this point. As a matter of fact, one of the considerations directing our attention to sickle cell disease was the hope of finding a genetic situation where if it became necessary to postulate a high mutation rate one could seek direct evidence for the validity of the postulate. As stated above, the place to look for evidences of mutation is in families where a single child has either sickle cell disease or the sickle cell trait, and both parents have been tested for the occurrence of the sickling phenomenon. Thus far we have 23 families falling in the former category and 4 in the latter. In 22 of the 23 families where there occurred an isolated case of sickle cell disease, both parents sickled, but in one instance we appear to have sickling in only one parent. In three of the four families where there is a single child with the sickle cell trait, one parent sickled, but in one family, neither parent was found to sickle. A description of these two exceptional families follows:

1. The Wa kindred (#1619). The proposita was a 14 year-old girl (b. 1936) on whom a diagnosis of sickle cell disease was first made at Children's Hospital, Detroit, Mich., when she was 1 year of age. She has been seen repeatedly at that hospital since the diagnosis was made, always with typical hematological findings, and pursuing a typical clinical course characterized by episodes of joint and abdominal pain. Our examination in December, 1949, revealed an asthenic Negro girl with an erythrocyte count of 2,350,000/mm^3, a hemoglobin of 7.5 grams per cent, a hematocrit of 20.2 per cent, a leucocyte count of 11,200/mm^3, a reticulocyte count of 5.4 per cent, and 100 per cent sickling of the filamentous type in 48 hours. Serum bilirubin was 2.2 mgm. per cent, with .9 mgm. per cent free and 1.3 mgm. per cent combined. She had one sibling, a brother, who had sickle cell trait. The mother's blood could be readily induced to sickle, but the father's resisted all efforts to induce the sickling phenomenon. The patient's paternal grandfather was dead; the paternal grandmother also failed to sickle. The results of serological studies were as follows: proposita—O R_1r M S-positive; brother—A$_1$ R_1R_2 M S-positive; father—A$_1$ R_1r MN S-negative; mother—A$_1$ R_1R_2 M S-positive.

2. The Wy kindred (#1564). The proposita for this kindred was a 6 month-old infant who one month previously, while hospitalized at the Children's Hospital of Detroit because of diarrhea, had been found to have the sickle cell trait. Our own studies revealed an erythrocyte count of 4,730,000/mm^3, a hemoglobin of 11.9 grams per cent, a reticulocyte count of 0.8 per cent, and a leucocyte count of 14,225. Sickling preparation was positive. Except for the leucocytosis, possibly attributable to an upper respiratory infection, these are thought to be normal hematological values.

Neither parent nor any one of 6 siblings was found to exhibit the sickling phenomenon. The results of serological studies on the family were as follows: father—O R_0r M; mother—B R_1r MN; sibling 1—O R_1r (R_1R_0) N; sibling 2—O rr M; sibling 3—O R_1r (R_1R_0) MN; sibling 4—B rr MN; sibling 5—O R_0r M; sibling 6—B rr M; and patient—O R_1r (R_1R_0) MN. It will be noted that sibling #1 presents us with a paternity exclusion on the basis of the M-N reactions.

Before we can accept either of these exceptional cases as an example of the results of mutation, we must inquire carefully into certain alternative possibilities. The first is failure of penetrance, i.e., failure of the gene for the sickle cell phenomenon to find phenotypic expression. If, for instance, penetrance was only 95 per cent complete, these apparent exceptions could be explained. Two lines of evidence bear on this possibility. In the first place, we have tested 22 children of 8 apparently non-sickling sibs of persons with the sickle cell trait. None of these children has sickled, evidence against the possible transmission of the gene by a phenotypically normal individual. Secondly, the agreement with the expected ratios in segregating families is of such a degree as to militate against any very significant failure of penetrance, although anything under 5 per cent or so would be difficult to rule out entirely. A second alternative explanation involves the possibility that the legal father is not the biological father; there is no evidence for this from the serological tests on the two putative fathers. On the other hand, the fact that in both instances it is the father who is the exceptional parent may be of significance. The discovery of a family where it is the mother who appears to be the exceptional parent would have more meaning. Finally, a third alternative is that what clinically appears to be sickle cell disease is a similar phenotype produced by the interaction of a single gene for the sickling phenomenon with unknown environmental or genetic factors. The only such interaction now recognized is between the genes responsible for the sickling phenomenon and thalassemia (see below); there is no evidence that any of the parents investigated has thalassemia minor.

It would appear, then, that we may have some evidence for the existence of mutation to the gene responsible for the sickling phenomenon. However, it would be premature to conclude on the basis of these few cases that we have sufficient evidence that a high mutation rate is the key to the riddle of sickle cell disease. A much more extensive material than now exists will be necessary to determine whether the quantitative relationships are as demanded by theory.

The Interaction of the Thalassemia and Sickle Cell Genes

By way of concluding this paper, I should like to raise two questions. First, is it a matter of chance that we find in such geographical proximity two anemias presenting us with similar problems in population dynamics? Recently, in collaboration with Dr. W. N. Powell and Dr. J. G. Rodarte (Powell, Rodarte, and Neel, in press), I have had the opportunity of studying a family of Sicilian derivation in which both the thalassemia gene and the gene responsible for the sickling phenomenon were segregating. The propositus for the family was an individual with a severe hemolytic type of anemia clinically indistinguishable from sickle cell anemia. Complete blood studies of three generations of this family revealed that one of the parents of the propositus had the sickle cell trait, while the other had thalassemia minor. The propositus had two children, both of whom exhibited thalassemia minor. It is clear from the facts that the propositus sickled and had also transmitted thalassemia minor to his children, that he must have received the thalassemia gene from one parent and the sickle cell gene from the other. This is the first such family studied in this country, but Silvestroni (1944–5, 1946c, 1946d, 1948c, 1949) has in the past five years described under the heading "microdrepanocytic disease" a total of 22 cases from 11 Italian families which in all probability fall into the same category. In most of his 22 cases, all with the same clinical picture as exhibited by our subject, one parent was known to exhibit the sickle cell phenomenon or could be presumed to have done so while the other was known to exhibit thalassemia minor or could be presumed to have done so, but for none of his cases, unlike our own, was the presence of a thalassemia gene definitely established by the progeny test.

There are three possible explanations of this phenomenon. 1) Occasionally, as we have seen above, an individual with thalassemia minor may actually exhibit a rather severe, hemolytic-type of anemia. We might therefore interpret our findings as due to unusually severe thalassemia minor in an individual who incidentally happens to sickle. But while this might explain one or two cases, it would seem to be stretching the long arm of coincidence to explain all the cases so far seen on this basis. There is a further argument against that explanation. A marked difference has been observed between the type of sickling seen in the propositi and in the "sickling" parents, consisting in a preponderance of "holly-leaf" forms in the parent as contrasted to a preponderance of more elongate, "sickle" forms in the child. That difference is one which I have frequently observed between the sickle cell trait and sickle cell disease, and would lead one to feel that an intensified sickling process, such as is never seen in the simple heterozygote, is

concerned in the hemolytic process in these patients. 2) A second possible explanation is that we are here confronted with a case of factor interaction on the part of two independent genes. 3) Finally, we must consider the possibility that these two genes are actually allelomorphs.

There are ways of distinguishing between these three possibilities. If individuals with both the sickle cell and the thalassemia genes only occasionally exhibit the picture seen in our propositus, then weight must be given to the first possibility. If, on the other hand, the severe hemolytic syndrome is a constant feature, then possibilities 2) and 3) are favored. A decision as to which of the latter two is correct is possible from a study of the children of such an individual. If, married to normal persons, such individuals produce normal, sickle cell trait, thalassemia minor, and the hemolytic syndrome in equal proportions, then we are dealing with two non-allelomorphic genes situated on different chromosomes. If, on the other hand, from such marriages only children with thalassemia minor or sickle cell disease result, we are either dealing with allelomorphic or completely linked genes. Partial linkage (permitting less than 50 per cent crossing-over) should result in an excess of persons with thalassemia minor or sickle cell trait, as contrasted to normal or anemic persons. The distinction between allelomorphic and linked genes is extremely difficult in man, particularly when one is concerned, as here, with traits so seldom co-existent in a family.

A second line of attack leading to a decision depends on linkage studies. Snyder, Russell, and Graham (1947) have reported a linkage between the M-N blood types and sickle cell disease. This report needs confirmation. If, now, the M-N blood types and thalassemia should also show linkage, this would place the thalassemia and sickle cell genes within the same chromosome—a necessary step in evidence for allelism, and one independent of the other line of proof outlined above.

At present, we can only say that the bulk of the evidence appears to favor hypotheses 2) or 3). Time and the patient accumulation of evidence will lead to a decision as to which of these latter two possibilities is correct. I am sure we will all agree that the possibility that these two genes are alleles opens exciting paths for speculation.

The Occurrence of These Two Dyscrasias in the Past

The second of the two concluding questions I should like to raise is this: Have inherited blood dyscrasias such as thalassemia and sickle cell disease occurred in significant numbers in various racial groups in the past, and if so, with what consequences? This question has most recently been discussed by Chini and Valeri (1949). In both sickle cell disease and thalassemia major there is very significant bone marrow hyperplasia, in the case of sickle cell disease presumably a work hyperplasia compensating for the increased erythrocyte destruction, in the case of thalassemia apparently primarily due to a maturation arrest in the erythrocyte series. Such marrow hyperplasia may be seen in any chronic hemolytic anemia of early onset (e.g., hereditary hemolytic icterus). In the skull this hyperplasia results in a characteristic "hair-on-end" X-ray appearance. Studies of osseous remains of a variety of now extinct human groups such as Peruvian and Mayan Indians and the "mound builders" of Arkansas have revealed that a sizeable proportion of the skulls show changes very similar to those encountered in the hemolytic anemias (Williams, 1929; Moore, 1929; Feingold and Case, 1933; Wakefield, Dillinger and Camp, 1937). There is some evidence that these abnormal findings were more frequent among the younger age groups (Williams, 1929), from which we may infer either that the associated condition altered the mean duration of life or disappeared with advancing age. The most probable alternative etiology for the skull changes is rickets. Similar changes have been observed in skulls from ancient Egypt and Italy (Adachi, 1904; Caponnetto, 1938, after Chini and Valeri, 1949; Graziosi, 1947, after Chini and Valeri, 1949). Moore (1929) was apparently the first to conjecture that the disease revealed by these osseous changes may have played a significant role in the decline of the racial groups in which it occurred. Far-fetched though this possibility may sound, there is sufficient solid evidence behind it, particularly in the light of our growing knowledge of the possible high incidence of thalassemia and sickle cell disease in certain restricted areas, to warrant serious consideration of the hypothesis.

With these two questions I close this discussion. I feel that I should apologize for having brought you not the completed story which is supposed to characterize symposium presentations, but rather a fragmentary sketch of several situations which fairly bristle with loose ends. Fortunately for the subject in which we are interested, many of these questions can and should be answered in the next ten years.

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DISCUSSION

ANGEL: Osteoporosis occurs in ancient Greeks, less severely than among ancient Egyptians, in early prehistoric times and in the Middle Ages. Is there any chance of distinguishing bony changes resulting from thalassemia from those following severe dietary deficiency, for instance, lack of vitamins A and C?

NEEL: In well preserved material it should be possible to distinguish in some cases between the effects of thalassemia and of dietary deficiency on the skeleton. The effects of thalassemia are primarily an increase in the extent of the medullary bone space. The effects of dietary deficiencies are varied. The most important deficiencies involve vitamins C and D. In both these cases the chief effect is upon the structure of the cortex and epiphyses or sutures, and hence—theoretically at least—rather readily distinguishable from effects on the medulla.

MOURANT: While the pathological conditions discussed by Professor Kemp this morning are rare and cannot on the basis of samples of reasonable size be used for purposes of anthropological classification, thalassemia and sickling are not only sufficiently common to be so used but they show a distribution related to that of the blood groups, as I propose to show, in the case of thalassemia, in my own paper.

GENETIC ANALYSIS OF RACIAL TRAITS (I)

CONCLUDING REMARKS OF THE CHAIRMAN

LAURENCE H. SNYDER

The University of Oklahoma

Previous speakers in the symposium have set the stage for the detailed analysis of racial traits, by outlining the broad picture of man's origin and early development, and of the population units in which he now finds himself. The present phase of the symposium deals with the frequency, extent and genetic determination of various specific characters which may be of racial significance. It is hoped that the three papers presented today, as well as those to be presented during the ensuing two days, may offer the anthropologist and others some first hand information on the actual working materials of the student of human heredity, and on the serious difficulties which handicap field studies in human genetics.

Dr. Böök has called attention to the fact that man and most experimental organisms used in genetic research are quantitatively different in length of time of embryonic development and of life cycle, resulting in phenogenetic complications and difficulties of diagnosis of the genic background of human traits. One other point to which I should like to direct attention is the frequent lack of precision in some writings on human genetics in the use of the words "stock" and "strain." These terms are used with specific meanings by the laboratory geneticist. They imply complete or very nearly complete genetic homogeneity, and are frequently qualified by the term "isogenic." Even in animal breeding, the terms usually connote a group of individuals having a reasonably high degree of genetic uniformity, generally expressed visibly in similarity of color, pattern, conformation and so on.

It is possible to measure genetic homogeneity, and to express the amount in terms of the coefficient of relationships, which gives the average probability, for pairs of individuals chosen at random from a strain or stock, that any given gene will be present in both of them through inheritance from a common ancestor. The coefficient also indicates the average fraction of all genes shared in common by members of pairs chosen from the stock at random, by virtue of common ancestry.

The value of the coefficient is unity for pairs of identical twins, 0.50 for siblings, 0.125 for first cousins, 0.031 for second cousins, and so on. So homogeneous are the individuals of a highly inbred strain of laboratory animals that the coefficient of relationship is well over 0.95, which means that the individual members of the strain are very nearly identical in genotype. Even in breeds of livestock the coefficient may range as high as 0.40 due to inbreeding. Such breeds are properly designated stock or strains in the genetic sense, since there is genetic identity at least in regard to a number of genes which determine the breed characteristics.

The usual use of these terms in human populations is seldom justified. Particularly is it an error to refer to the current descendants of some past ancestor as a strain or stock. Such terms have no genetic meaning when used in this sense. The fact that we have no isogenic stocks or strains of man creates difficulties in genetic analysis of human traits as compared with the analysis of characters of laboratory organisms, and emphasizes the importance of the nearest approach we have to such stocks, namely identical twins. Reference to such twins will be made again later in this summary.

Dr. Böök and Dr. Kemp have pointed out many other practical difficulties in collecting significant genetic data in man, and have presented methods of overcoming some of these difficulties. It is becoming clear that the effective unit for the study of population genetics is the isolate.

More often than not, what appear to be large natural populations are in fact composed of numerous local, and more or less self-contained breeding units (isolates). If each of these units is completely self contained, and there is no intermigration, the gene frequency dynamics of each is determined by its own size and mating pattern. If there is a certain amount of intermigration, the evolution of the whole super-population depends in major ways on the numbers in the individual sub-groups and on the extent of the intermigration.

It is important to recognize that the effective breeding population of an isolate is not necessarily its apparent population size. The effective breeding number is determined by the number of

mating individuals which are progenitors of a subsequent generation.

Populations of human beings numbering in the hundreds of millions have continuous distributions over large areas of the earth's surface. There are, however, countless isolated rural groups which contribute only an occasional emigrant to the outside world. Their apparent populations may each comprise only a few hundred individuals, and their effective breeding numbers may be even smaller. Even in urbanized regions, matings are significantly restricted by geographic distance, social class, religious affiliations and other factors. The mating pattern of modern Europe and America, in fact, is essentially that of a large number of partial isolates. Dahlberg (1947) has roughly estimated, from the frequencies of various types of consanguineous marriages, that the average effective mating number of the quasi-isolates lies somewhere between 400 and 3000. It should be obvious that in earlier centuries the sizes of mating groups must have been appreciably smaller than now. Archeologic evidence indicates that neolithic human communities through Central Europe were commonly composed of only 25 to 35 households, and most sub-human primates appear to live in groups comprising from a dozen to a few score individuals. It seems a rather plausible inference that a great part of primate evolution has been accomplished in populations with very small effective mating numbers.

The importance of the isolate should not blind us, however, to the importance of family studies, twin studies, and the biophysical and biochemical study of individuals.

The principles of sampling as applied to variously-sized sources of supply lead to some important conclusions in human genetics. In large populations, numbering in the thousands, sampling fluctuations are likely to result in only negligible shifts in gene frequencies from generation to generation, while in small populations of a few hundreds or smaller, radical alterations in gene frequencies are to be expected as a consequence of sampling fluctuations alone, that is, even in the absence of selection, mutation or other disturbing factors.

Moreover, since the sample of genes drawn from the supply of any generation will in turn generate the supply from which a new sample will be drawn when the progeny reproduce, it will inevitably happen that the allele which is the less frequent in the supply (the parental generation) tends to have its frequency further reduced in samples (progeny) drawn from the supply. This means that in successive generations sampling fluctuations tend to have cumulative effects. Such change is known as genetic drift. It can lead to the spread of a new mutant gene through a small population, or to the loss of a new allele before it has had a chance to spread appreciably or at all.

Dr. Böök and Dr. Kemp are to be commended for having realized the importance of their native populations as sources of isolates and for having so significantly and successfully exploited the genetic possibilities of such restricted groups. We need more studies of this sort, based on complete ascertainment in specific populations.

Dr. Neel, in his remarkably thorough and critical study of two sets of genes with adaptive significance, has extended the range of the analysis of isolates to the far corners of the earth. He has properly called attention to the "very thorny problems in gene dynamics" raised by the high incidence of the two anemias in various populations. The mutation rates necessary to maintain the incidences at their present levels, in the face of the elimination or reduced fertility of the affected homozygotes, are inordinately high. It would seem that positive selection in favor of the heterozygote is certainly a logical assumption. The possibility that women who lose children as a result of the death of the homozygotes consciously tend to complete their families, thus increasing the percentage of heterozygotes, would appear to be a reasonable alternative or correlative possibility.

The suggestion that the genes for thalassemia and for sickling are alleles raises a most fascinating problem. The accumulation of more data on the families of individuals receiving the sickle cell gene from one parent and the thalassemia gene from the other is urgently to be desired. My own studies indicating that the sickle cell gene is in the same linkage group with the M—N alleles should be repeated as soon as possible, with the further testing of the linkage relations of the M—N genes with the thalassemia gene. The allelism of the genes for sickle cells and for thalassemia seems to me highly probable.

Dr. Neel's demonstration that the heterozygotes for the thalassemia gene and for the sickle cell gene are phenotypically recognizable adds another piece of evidence to the theory that I have always held, and for which I have obtained some evidence in my own laboratory in the case of telangiectasia, that every gene produces some phenotypic effect in single dose, and that with the proper technics of observation, measurement or analysis we shall be able to recognize all these effects.

I was interested in Dr. Kemp's categorical statement that males affected with Leber's optic nerve atrophy never have affected descendents. This recalls the old controversy over Lossen's and Nasse's Laws. Further investigation of this disease is clearly indicated, involving the following of the existing families through further generations and the statistical analysis of the material at hand.

The traits reported on in today's papers are all pathologic in nature, as indeed have been most of the traits studied in human genetics. Yet the significant differences between human populations are to be found in such things as intelligence, social behavior, personality, special abilities, size, features and so on: traits of a non-pathological nature. These facts prompt me to make some observations on human traits in general, and on gene action in particular, which may have some bearing on future possibilities in the genetic analysis of racial traits.

To begin with, it now seems certain that there is no structure or organ, and no physiological process of the organism that cannot be altered, and radically altered, by a single-gene substitution at some locus. Although the demonstration of this principle has not been as easy in man as in laboratory organisms because of the impracticability of controlled matings in man, it has become more feasible to demonstrate it in recent years, by virtue of especially developed statistical technics. There is now available presumptive evidence that more than 100 variations (mostly pathologic) in the skin and its derivatives, more than 100 eye abnormalities, and a comparable number of skeletal anomalies are attributable to single gene substitutions. There is reasonable evidence of single gene determination for a score of blood dyscrasias and for comparable numbers of aberrations in the muscular system, of nervous disorders, and of metabolic and endocrine disturbances. Although the evidence for the single-gene determination of many of these pathological conditions is as yet only presumptive, there is every reason to believe that the effects of single gene substitutions are at least as numerous, varied and far-reaching in man as in the various laboratory organisms which have been so extensively studied.

On the other hand, there is a remarkably small number of non-pathologic variations in man which have been demonstrated to be the results of single gene substitutions. The various antigens which account for the blood groups, the taste-threshold for phenyl-thio-carbamide, and the direction of the fine hair of the forehead practically exhaust the list of normal human characters affected by single genes.

A second important principle to keep in mind in the analysis of racial traits is that the phenotype of man, as of other organisms, is a function both of its genotype and of the environment in which the organism develops. A demonstrated effect of one of these variables does not mean that the peculiarity is not subject to modification by the other. Let me cite an example. During the war much attention was given to color blindness and its possible control. One group of workers reported that color blindness could be cured by massive doses of vitamin A (Dunlap and Loken, 1942).

Now it was entirely reasonable to suppose that color blindness, although thought to be genetically controlled, could nevertheless be alleviated in some fashion. Moreover, in the absence of any other leads, this was a reasonable one, since it was known that rhodopsin was related to vitamin A, and was somehow bound up with the latter's metabolism.

The results were severely criticized by other workers (Hamilton, Briggs and Butler, 1943; Murray, 1942), and vitamin A was finally shown not to be the cure for color blindness that was originally claimed. But it is the conclusions of the two groups of workers that I am here concerned with. The original investigators concluded that since color blindness could be cured, it was obviously not the simple Mendelian sex-linked gene that it had been reported to be. In other words, this conclusion implied that since it could be affected by the environment, it could not have been genetic in the first place. The other group of workers used the same misconceived argument, *but the other way around.* They concluded that they must hold to the original conception that color blindness is hereditary and incurable. This conclusion implies that if the anomaly were in fact genetic, it was foolish to have started out to cure it at all.

A third important principle in analyzing racial differences is that the phenotype of an individual depends on developmental interactions involving the entire aggregate of genes as well as of other genetic material in the cytoplasm. It is reasonable to assume that the effect of a gene substitution at any given locus is influenced by the genes at every other locus.

As a fourth principle I would cite the observation that the effect of a gene substitution can be simulated by the effect of appropriate environ-

mental conditions, and that the resulting phenocopies can be indistinguishable from the effects of genes. In man, certain conditions apparently occur as single-gene effects in some families and as phenocopies in others, due to radiation, infection such as rubella, social environment, and other causes.

Finally, it should be emphasized that most single genes have multiple effects. Particularly is it true that most gene substitutions, in addition to some major action, affect viability either in a plus or minus (usually a minus) direction.

So striking are the effects of single-gene substitutions, and so great is their variety, that it is tempting to suppose that collectively, they play a major role in the determination of individual differences in human populations. We have become increasingly aware in recent years, however, that single-gene differences which result in marked phenotypic variations are not in fact the most common type of genetic variability. The effects of radiation on gene mutation have helped to establish this principle. Radiation results in some mutations having conspicuous phenotypic effects, apparently identical with spontaneous natural mutations; it results in a larger number of lethal mutations; and it produces the largest number, by far, of mutations which only have slight effect on viability. Probably both morphologic and physiologic characters are involved in viability, and there seems to be a general parallelism between the conspicuousness of the visible effect of a gene and the degree to which it impairs viability. The more striking the phenotypic effect, the more drastically is viability reduced. The largest class of radiation-produced mutant genes thus has few if any readily discernible phenotypic effects of the individual gene, although the cumulative effects may be striking. There is ample reason to believe that natural spontaneous mutant genes are also made up largely of those which individually do not have readily discernible phenotypic effects.

Mather and his colleagues (Mather, 1949) have been sufficiently impressed with the importance of the special problems presented by such cumulatively acting genes that they have designated genes of this class *polygenes*. The single genes responsible for conspicuous phenotypic discontinuities are called *major genes*. Major genes are capable of individual identification by the characteristics they produce, and can be assigned to precise loci and specific linkage groups, in laboratory material at least. It is becoming more and more feasible to do the same in human material.

Polygenes, on the other hand, seem to have effects which are quantitatively equivalent and cumulative; moreover these genes cannot be individually identified or assigned to specific chromosomal loci. Their existence must be accepted however, if for no other reason than the effectiveness of selective breeding for almost any continuously variable quantitative character in a genetically heterogeneous population. There is in addition evidence adduced by Mather that polygenes possess the essential characters of classical major genes, namely that they undergo segregation and crossing over.

If then, as seems clear, polygenes constitute the largest class of gene mutations, much of the genetic variability of man and other organisms is contingent upon large numbers of such polygenes, with individually minute, but cumulatively appreciable, effects. Not only most of the genetic variability, but most of the phenotypic variability in man must depend on polygenic differences. This can be inferred from the fact that, generally speaking, natural selection will keep at a low incidence the large discontinuities produced by major genes because of the viability impairment associated with them. This inference is substantiated by observation.

Almost the only discernible single-gene differences which have achieved appreciably high incidences in human populations are those which appear to be approximately neutral as to viability effects. These involve such genes as those for the blood antigens, taste deficiency, color vision, hair whorl and so on. The genes for thalassemia and for sickle cells, as outlined by Dr. Neel, presented exceptions for which we do not at present know the explanation. Of the hundreds of presumptively single-gene abnormalities in man outlined above, no more than a very few have population incidences above one in ten thousand, and the vast majority are very much less frequent than this.

As David and I recently pointed out (David and Snyder, 1950), if two unrelated people were picked at random from any human population, or even one from each of two populations, they might be found to differ in respect to one or another of the blood agglutinogens, and one might be a taster and the other a non-taster. Beyond this it is highly unlikely that any of the observable phenotypic differences between them would be referable to known major genes. And yet these phenotypic differences must be largely genetic, as evidenced by the almost complete physical identity of the members of pairs of monozygotic twins, who have identical intra-pair genotypes.

It must be assumed that the major part of such genetic differences as are involved in the non-pathologic range of human variability is probably determined by polygenes rather than by single major genes. This may even be true for certain pathological traits such as hypertensive disease and neoplasms, and is very probably also true for the genetic differences in disease resistance and susceptibility.

Moreover, Wright (1939) has indicated that the expression of polygenic variability may in general be especially sensitive to environmental exigencies. Recognition of the fact that polygenic differences rather than major-gene differences account for the larger part of human variability has, as David and I have pointed out (1950), vital methodologic implications for research in human genetics, because it sets a limit to the amount of information that we may expect to gain through analyses of single gene differences.

I do not mean to infer that we should cease searching for individual gene differences. It is essential that we continue to develop and refine the statistical methods which many of us have been formulating for detecting major-gene effects in human populations. It is essential that we continue the search for such single-gene variations. Much is to be hoped for along these lines, especially since we are finally learning to put our faith in critical data, systematically collected and assembled, rather than those culled from casual observations which happened to be reported in the literature. I have discussed on numerous recent occasions (Snyder, 1946, 1947 a and b, 1948) the various ways in which such critical data can be useful, even indispensable, in medical practice, in research, and in anthropology, and I will not attempt to go into detail here.

But if the field of human genetics is to break new ground and to make progress along the lines of the analysis of racial traits, it is clear that the traditional atomistic approach must be supplemented by methods which can furnish information on the significance of genetic variability without recourse to the classical single-gene analyses. Such new methods must be actively developed. At present the newer types of twin studies seem to provide a fruitful approach to this type of methodology. Although these studies need considerable elaboration and refinement, they are making significant progress through quantitative comparisons of intra-pair differences in monozygotic and dizygotic twins, studies of separated identical twins, co-twin controls, and concordance studies involving sibs and other relatives. Further exploitation of such methods and the development of new methods for the analysis of polygenic variability are immediate urgent needs.

If we are interested in the genetic analysis of racial traits which are significant on the level of intelligence, personality, and social behavior, we shall have to consider the genetic implications of polygene transmission. For one thing, such transmission would seem less likely to bring about phenotypic differentiation through genetic drift than the transmission of major genes, because the effects of individual polygenes are apparently in large part interchangeable. Even though genetic drift should lead to the accumulation of different constellations of polygenes in different populations, the overall phenotypic result would tend to remain constant since the relative proportions of plus and minus polygenes should tend to be about the same from one population to the next. Even though genetic drift should lead to phenotypic differentiation, this would have little chance of persisting after the populations expanded, unless it had a highly adaptive value. As Dobzhansky and Montagu (1947) have pointed out, flexibility and plasticity of behavioral adjustments are likely to have had a selective advantage over any fixed or stereotyped responses in human intelligence and social behavior.

In summary it may be said that the fruitful pathways for the future study of human traits include the genetic analyses of populations in regard to three kinds of characteristics: normal characters dependent upon major genes, pathological traits determined by major genes but which have for some reason reached relatively large incidences in the population, and traits determined by polygenes. The complete genetic analysis of today includes the study of how the genes act and may involve physical or chemical analyses of development. The difficulties and pitfalls are many, but the pathways have been set, and this symposium is providing evidence that we may hope eventually to reach the goal.

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GENETIC ANALYSIS OF RACIAL TRAITS (II)

BLOOD GROUPS, MORPHOLOGY AND POPULATION SIZE OF THE ESKIMOS

W. S. LAUGHLIN[1]

Department of Anthropology, University of Oregon

Interpretations of a number of anthropological studies on various peoples have been partially vitiated by disregard of the size and stability of the isolate from which the samples were drawn, though the samples themselves may have been adequate for their particular isolates. Many theories concerning racial origins have been based on similarities between breeding isolates of two diverse populations without recognition of the fact that the samples represented only particular isolates extracted from the larger populations. Owing to their limited size and isolation these often have not been as truly representative of the populations being compared as the larger and more stable divisions.

An examination of various studies on the Eskimos provides a useful example of the way in which this source of error has been permitted to distort our interpretation of the physical data concerning them. Evaluation of the genetic constitution and morphological aspects of the Eskimos has been further confused by the accident of historical priority in the study of certain Eskimo groups and the consequent construction of an ideal "Eskimo type." Deviants from this arbitrarily selected type have been considered "mixed" and, as a consequence, have been disbarred from consideration as genuine or pure Eskimos. The resulting bias has distorted not only our understanding of the biological history of the Eskimos, but of their cultural relationships as well.

[1]Original data concerning the Aleuts used in this paper were derived from research sponsored by the Peabody Museum and Department of Anthropology, Harvard University. Funds were provided by the Viking Fund, Inc., the Arctic Institute of North America, the Office of Naval Research. Assistance was given by the U. S. Navy, U. S. Coast Guard, U. S. Army and U. S. Air Force, U. S. Fish and Wildlife Service and the Alaska Native Service. Dr. W. C. Boyd and Dr. A. S. Wiener provided blood grouping sera. Dr. Victor E. Levine provided the data for his blood grouping of the Point Barrow and Nome Eskimos.

Eskimo Blood Groups

Consideration of the blood group data for many geographically separated Eskimo-speaking groups suggests a basic homogeneity underlying the morphologically diverse forms (Table 1). Though there are intriguing variations, most noticeable in the MN types, the larger groups of Eskimos remain distinguished from the Indians and other peoples by the frequencies of their blood groups, types and Rh factors. Beginning with the most widely separated groups, Greenland Eskimos and Aleutian Eskimos, it is seen that there is marked similarity in the gene frequencies of the Nanortalik Eskimos, those having slight mixture with Europeans in particular, and the Aleuts, who also are mixed with Europeans. The effects of European mixture on the frequencies can be seen in comparing the relatively least mixed, Western Aleuts and Greenland Eskimos south of Nanortalik, with the relatively more mixed. In each case European mixture raises the frequencies for group O and lowers those for group A. Additional significance is lent to the similarity of these frequencies from the geographically distant groups when it is observed that they are drawn from populations which are, or were, large and from areas which had relatively high population densities. Thus the total number of Greenland Eskimo, of whom the greater portion were located in southern Greenland, at the time of early European contact is estimated at 10,000, with a population density of 6.34 per 100 km.^{2}. The original Aleut population is estimated at 16,000, with a population density of 64.70 per 100 km.^{2}. At present they number around 1,000 (Kroeber, 1939, p. 135).

Examination of the figures for other Eskimos indicates the general excess of the frequencies of the genes for group A over group O, with varying amounts of group B, generally falling between 2 per cent and 12 per cent. Unfortunately estimates of European admixture are often not indicated or are based on different criteria. In other cases the

TABLE 1. ESKIMO BLOOD GROUPS (LARGER GROUPS)

Group	Investigator	No.	O	A	B	AB	p	q	r	$\frac{D}{\sigma}$
Aleutian Eskimos	Laughlin									
West (Attu-Atka)	1948,	42	45.24	50.0	2.38	2.38	.303	.018	.673	.61
East (Nikolski-Unalaska)	1949	54	44.44	46.30	7.41	1.85	.286	.054	.666	.41
Interisland (Most mixed)		48	58.33	37.50	2.08	2.08	.215	.013	.764	.13
Total		144	49.31	44.44	4.17	2.08	.266	.029	.702	.5
Alaskan Eskimos	Matson and									
Bethel (Kuskokwim)	Roberts 1949	341	36.95	44.87	11.73	6.45	.299	.095	.607	1.00
Alaskan Eskimos	Levine									
Nome Pure	1944	254	43.31	42.52	11.81	2.36	.268	.084	.659	1.32
Nome Mixed		68	44.12	42.65	11.76	1.47	.267	.083	.664	.99
Alaskan Eskimos	Levine									
Point Barrow Pure	1948	329	40.73	47.11	9.73	2.43	.299	.072	.638	1.32
Point Barrow Mixed		172	31.40	54.65	5.23	8.72	.368	.045	.560	1.78
Greenland, West	Fabricius-									
(District of Julianhaab)	Hansen									
1. South of Nanortalik	1939									
(almost entirely pure)		377	36.33	54.63	5.30	3.71	.355	.046	.603	.82
2. Nanortalik (slight mixture										
with Europeans)		419	48.92	44.39	4.29	2.38	.271	.034	.699	.99
3. North of Nanortalik										
(very mixed population)		267	55.05	36.70	5.26	2.99	.223	.042	.742	1.57
Total		1,063	46.00	46.09	4.89	3.01	.285	.038	.679	.57
Greenland, Cape Farewell	Bay-Schmith									
1. Pure Eskimos	1927,	204	41.1	53.8	3.5	1.4	.332	.025	.641	...
2. Eskimos in contact with	1930									
whites		607	54.2	38.5	4.8	2.0	.225	.036	.742	...
3. Civilized Eskimos (Mixed)		101	46.5	27.7	23.8	2.0	.179	.157	.682	1.20
Greenland, Jacobshoven	Freuchen	340	43.5	47.1	7.3	8.7	.287	.048	.659	...
Greenland, East	Fabricius-									
Angmassalik region	Hansen									
(Said to be) Pure	1939	569	23.9	56.2	11.2	8.7	.406	.106	.489	.60

figures represent composite series drawn from different breeding isolates and represent no one particular isolate. All group A Aleuts belong to group A_1. Other Eskimos are also group A_1, where anti-A_1 serum has been used. Exceptions occur where European mixture has taken place.

Turning to the figures for small populations or isolates it is seen that they deviate greatly from those for the larger groups (Table 2). Thus the Polar Eskimo have 12.90 per cent group A and 80.65 per cent group O. Individuals not belonging to group O were considered to be "half-breeds." Consequently Polar Eskimos have been described as being 100 per cent group O in the literature (Heinbecker and Pauli, 1927, p. 283). These figures are of particular interest for they have been cited as being representative of the original condition among Eskimos, the A and B of the other Eskimos being interpreted as possibly due to local mutations (Birket-Smith, 1940, p. 110).

It would be difficult to find a more classic example of an isolated population than that of the Polar Eskimo in northern Greenland. They had been isolated from other humans for so many generations that, when discovered in 1818, they had forgotten their origin and believed themselves the only people in the world. A group of Eskimos from North Baffin Land endured hardships extending over several years in their effort to reach the Polar Eskimo. With a maximum population of 271 and complete isolation it is quite understandable that they should present such an atypical blood group distribution. Owing to the fact that drift operates most rapidly in small populations, it could hardly be expected that such a small group as this, living in absolute isolation for generations, could maintain the same gene frequencies as those found in the larger and more stable populations. It appears evident, therefore, that generalizations concerning the original blood groups

TABLE 2. ESKIMO BLOOD GROUPS (SMALLER GROUPS)

Group	Investigator	No.	O	A	B	AB	p	q	r	$\frac{D}{\sigma}$
Polar Eskimo (North Greenland)	Heinbecker and Pauli									
Thule	1927	57	70.1	15.8	5.3	8.8	.090	.031	.837	8.01
Other Polar Eskimo										
Cape York		24	95.83	4.27	...	...	...	...	...	...
Northumberland Island		12	91.66	8.33	...	...	...	...	...	...
Karma		31	83.87	16.12	...	...	...	...	...	...
Total (including Thule)		124	80.7	12.9	2.40	4.00	.069	.013	.898	9.57
Baffin Island	Heinbecker and Pauli 1928	166	55.4	43.3	0.6	0.6	.248	.005	.745	...
Labrador and Baffin Land	Sewall	143	55.6	44.4	0	0	.253	0	.752	...
Labrador and Baffin Land	1939	56	46.5	53.5	0	0	.318	0	.682	...

(Boyd, 1939; Matson and Roberts, 1949; Wiener, 1943)

of the Eskimos can not be based upon such a small isolate as that of the Polar Eskimo.

The presence of blood group B among the Eskimos may be more cogently interpreted as a manifestation of their more recent Asiatic origin, than of a mutation in the New World. Blood group B reaches high frequencies among the Asiatic Mongoloids and is generally absent among the Indians of North America. Not only are the Eskimos distinguished from the Indians by their blood groups, they are different from all other populations for whom data are available, when the MN types and Rh factors are also employed.

Examination of the MN types for Eskimos shows a generally low n frequency, shared also by the Indians, with higher frequencies where European mixture has occurred (Table 3 and Table 4). The relatively high values of N for the Labrador and Baffin Island Eskimos may also be the result of drift, as well as of mixture with Europeans. In this connection it is interesting to see that some of these Labrador and Baffin Land Eskimos have

TABLE 3. ESKIMO BLOOD TYPES (LARGER GROUPS)

Group	Investigator	No.	M	MN	N	m	n	$\frac{D}{\sigma}$
Aleutian Eskimos	Laughlin							
West (Attu-Atka)	1948,	41	90.24	9.76	...	.951	.049	.64
East (Nikolski-Unalaska)	1949	54	59.26	38.89	1.85	.787	.213	1.38
Interisland (Most mixed)		47	70.21	23.40	6.38	.819	.181	1.23
Total		142	71.83	25.35	2.82	.845	.155	.35
Alaskan Eskimos	Matson and							
Bethel (Kuskokwim)	Roberts 1949	341	47.80	41.64	10.56	...	...	...
Alaskan Eskimos	Levine							
Nome Pure	1944	254	60.63	34.65	4.72	.780	.220	.19
Mixed		68	51.47	42.65	5.88	.728	.272	.27
Alaskan Eskimos	Levine							
Point Barrow Pure	1948	329	59.27	37.08	3.65	.778	.222	1.42
Mixed		172	43.60	47.10	9.30	.672	.328	.91
Greenland, West (District of Julianhaab)	Fabricius-Hansen							
1. South of Nanortalik	1939							
(almost entirely pure)		377	63.63	29.97	2.38	.826	.174	.93
2. Nanortalike (slight mixture with Europeans)		356	64.60	32.05	3.31	.806	.193	.52
Total		733	66.6	30.97	2.86	.817	.184	.92
Greenland, East	Fabricius-Hansen							
Angmassalik region (Said to be) Pure	1939	569	83.48	15.64	.88	.913	.087	.39

TABLE 4. ESKIMO BLOOD TYPES (SMALLER GROUPS)

Group	Investigator	No.	M	MN	N	m	n	$\frac{D}{\sigma}$
Labrador and Baffin Land	Sewall	144	31.2	52.8	16.0	.559	.400	1.0
Labrador and Baffin Land	1939	58	32.8	44.8	22.4	.572	.473	0.7

lost group B. The population densities of Labrador and Baffin Land are 1.73 and 1.62 per 100 km.^{2} respectively and the numbers involved are small.

The Eskimos, like Indians and Asiatics, are 100 per cent Rh positive. Insufficient data are available for generalizations concerning the Rh factors.

In summarizing the blood group data of the Eskimos it appears that the larger populations display an impressive similarity, especially considering the great extent of their geographical range. This may be attributed, in part, to their recent arrival from Siberia, possibly 3000 BC, with subsequent additions, and to the fact that individual communities, though often small, have remained within mating range of each other, with the exception of portions of Baffin Land, Hudson Bay, North Greenland and Labrador, whose frequency of contacts with other groups of Eskimos has been considerably less than that in the larger population centers of western Alaska and southern Greenland.

MORPHOLOGY

Anthropometric studies of the Eskimos have, for the most part, freely compared small and large breeding isolates without any suggestion that the size of the populations was pertinent to the validity of these comparisons. As with the blood groups this has meant that large and stable populations such as those of southern Greenland have been equated with small populations such as those of the Central Eskimo. The latter in addition to being small in their total numbers are subject to a particularly inhospitable environment which at times has drastically reduced their numbers through starvation and put the component groups through bottlenecks to which the larger populations have not been subjected. By contrast a single Aleutian island such as Umnak with 22 coexistent villages could lose the entire population of a single village of 100 Aleuts without any appreciable effect on the composition of the island as a whole. Loss of the same number of people would clearly affect the composition of a smaller group, for example the 432 Netsilik Eskimos of the Central area. The constriction and reexpansion or replacement of these small populations is illustrated in the expiration of the original population of Southampton Island in 1902–03 and the subsequent settlement of a number of Aivilingmiut on the island. Preference for interpretations based on small and isolated groups has apparently been founded on the theory that these represent the unsullied archetypes of an original stage which have persisted into a later period and are thus available for reconstructions. A more realistic view is that these small isolates are precisely the ones which are most quickly affected by drift, constriction and expansion, and mixture.

The Eskimo-speaking population as a whole, from Attu to Greenland, constitutes a relatively homogeneous population with regard to such characters as large head, large face and lower jaw, large relative sitting height, medium or submedium stature, small hands and feet, and a generally Mongoloid physiognomy, particularly noticeable in such characters as the epicanthic fold. The similarity in blood groups, large amounts of group A with varying amounts of group B, has already been alluded to. There is, however, an interesting diversity in head form, a diversity which has received a great deal of attention owing in large part to the fact that most studies have been centered about the measurements of the head and face of adult males. Means for the cephalic indices of groups of Eskimos from Greenland to Attu are shown in Table 5. It will be seen that the heads become proportionately rounder in western Alaska, reaching a maximum in the Eastern Aleuts and declining again in the Western Aleuts and Kodiak Islanders. Similarly, dimensions show that the heads become increasingly broader and lower in western Alaska, proceeding from north to south and out into the Aleutians. The important point to be observed is that there is a gradation in the distribution of these characters, as previously noted by Hrdlička, and that at no point is it possible to draw a line separating one major type from another (Hrdlička, 1930, p. 358). Thus, the mesocephaly of the Central and Eastern Eskimo grades into the brachycephaly of the Western Eskimos without interruption. This polymorphy, manifested primarily in the vault form, has been interpreted in a variety of ways.

Three major premises have been employed in the interpretation of the morphological studies, separately or collectively. First: small isolates may represent an early or original Eskimo type. This premise involves the assumption that small groups are static and ignores the known difference in rates of change between large and small populations. As a consequence the biological history, environmental stressing resulting in contraction of a group and expansion of the survivors, are ignored. Second: the Central and Eastern Eskimo represent the typical or stereotype for the Eskimo. Deviants from these longheaded Eskimos are presumed to represent the effects of mixture with Indians. This second premise has probably been the result of historical priority and the thoroughness of the study of these Central and Eastern populations, a result of approach from Greenland (Kroeber, 1939, p. 157). It has had the important effect of focusing attention on the Central and Eastern Eskimos to the exclusion of the Western Eskimos. Third: the hypothesis of an inland origin, involving derivation from Indians, presupposes that similarities between Eskimos and Indians in physical appearance must occur. This hypothesis of an inland, American origin, was originally based on ethnological theory and was formulated before archaeological researches in western Alaska revealed greater time depth and early Asiatic connections. This third premise has apparently provided the justification for extracting certain isolates from the total Eskimo population for comparison with selected groups of Indians, in order to demonstrate an Indian origin for all Eskimos.

There are three important studies of the Eskimos which have provided the bulk of the data for comparisons with Indians. These have drawn

TABLE 5. TABLE OF MEAN CEPHALIC INDEX

Group	Authority	Males		Females	
		No.	Mean	No.	Mean
East Greenland	Hansen	...	76.9	...	75.2
Angmassalik (E. Greenland)	Hansen (1914)	31	77.8	15	76.5
Angmassalik (E. Greenland)	Poulsen	26	76.52	10	76.29
Southeast Greenland	Hansen (1914)	22	75.7	21	75.0
Southwest Greenland	Hansen (1914)	21	78.1	24	76.8
Greenland	Deniker (1913)	614	76.8	...	...
Smith Sound	Steensby	8	78.06	10	77.40
Labrador	Pittard	8	76.11	6	74.84
Labrador	Duckworth and Pain	11	77.0	5	74.5
Labrador	Virchow	3	75.5	2	72.0
Baffin Island	Oetteking	10	76.2	13	77.7
Southampton Island	Tocher	35	77.2	...	...
Hudson Bay	Birket-Smith	99	77.3	...	...
Coronation Gulf	Seltzer	65	77.26	46	76.24
Coronation Gulf	Jenness	82	77.6	42	76.7
Victoria Island	Seltzer	30	78.30	19	77.79
Mackenzie	Seltzer	48	74.75	40	75.38
Mackenzie	Jenness	4	76.1	...	...
Mackenzie (Koupagmiut)	Boas	12	73.9	6	75.2
Alaska	Boas (1895)	114	79.2	...	...
Nunatagmiut	Seltzer	64	81.39	55	81.18
Nunatagmiut	Boas	11	81.6	5	78.8
Barrow	Seltzer	62	78.55	26	78.12
Point Hope	Jenness	13	78.3	...	...
Kotzebue Sound	Seltzer	30	78.60	8	77.0
Seward Peninsula	Shapiro	40	77.96	...	...
St. Lawrence Island	Hrdlička	63	79.7	48	79.6
Asiatic Eskimo	Jochelson-Brodsky	60	80.8	80	79.7
Marshall (Lower Yukon)	Hrdlička	6	83.3	...	...
Kuskokwim	Hrdlička	174	80.31	...	...
Hooper Bay	Hrdlička	20	81.3	2	81.2
Kulukak	Hrdlička	8	81.7	...	...
Togiak	Hrdlička	4	82.9	...	...
Kanakanak (Bristol Bay)	Hrdlička	...	...	10	84.3
Kodiak	Hrdlička	11	87.15	...	...
Eastern Aleut	Laughlin	17	84.62	17	84.32
Western Aleut	Laughlin	11	82.50	15	81.30

attention to the similarity between various groups of Eskimos such as the Hudson Bay Eskimo and certain groups of Seward Peninsula, with the Cree and Chipewyan Indians of Canada. These comparisons have been made primarily on the anthropometry of the head and face (Shapiro, 1931; Seltzer, 1933; Birket-Smith, 1940). The most recent, and cautious, appraisal of these similarities is that of Birket-Smith, "Therefore, all that can be said at present regarding the relationships between the Eskimos and the Northern Woodlands Indians is that in the regions about Lake Athabaska lives an Indian group whose likeness to the Eskimos seems unmistakable. This, however, is a fact of far reaching importance. It agrees exactly with the opinion I advanced years ago, that the ancestors of the Eskimos once lived in the northern woodlands west of Hudson Bay" (Birket-Smith, 1940, p. 109).

The principal questions which may be posed concerning the validity of the interpretation of these anthropometric similarities can be grouped as follows: 1. Are the groups used for comparison representative of all Eskimos?; 2. Are these anthropometric data in agreement with the more reliable blood group data?; 3. Is the respective time depth of the Eastern and Western Eskimos taken into consideration?

Comparisons between Eskimos and Indians have completely ignored the population centers. It has in each case been assumed that the Eskimo isolates employed for comparisons, represent all Eskimos. This illusion has been maintained by disbarring from serious consideration perhaps half of all Eskimos, namely those of western Alaska, because of their failure to meet the metrical specifications of the Eastern Eskimo stereotype. Thus only those segments of the total Eskimo population have been accorded recognition as genuine Eskimos which conform to this arbitrarily selected stereotype. This, of course, is simply treating the problem of describing the Eskimo population by means of definition rather than by analysis.

The major population center of the Eskimos lies in the west. Kroeber, using the population estimates of James Mooney, for the period of early contact with Caucasians, summarizes the distribution for western Alaska as follows, "Nearly a third of all the Eskimo lived on open Pacific Ocean frontage—27,300 Aleut, Kaniagmiut, Chugachigmiut, and Ugalakmiut, out of 89,700. From the Malemiut south, that is roughly, in Alaska from Bering Strait south, were almost 60 per cent of all members of the stock—53,000 out of 89,700" (Kroeber, 1939, p. 157). These are for the most part roundheaded Eskimo and are broader and lower vaulted than the Central and Greenland Eskimos.

Attention may be called to the study of one group in particular for which there are both anthropometric and blood group data. In his study of the Kuskokwim Eskimo, Hrdlička found these to be roundheaded, large faced, of submedium stature, and with great trunk height. He also observed that those above the village of Bethel were slightly longer headed than those at or below Bethel, in spite of the fact that those up the river were more accessible to mixture with Indians. He pointed out that these Eskimos belonged intimately to the general family of the south- and midwestern Eskimo, "...which at one end connects directly with the present Siberian and St. Lawrence Island Eskimo, and on the other end merges with the natives of the base of the Alaskan peninsula" (Hrdlička, 1933, p. 132). A later study of the blood groups of the Eskimos at Bethel, by Matson and Roberts, shows them to have the blood groups characteristic of Eskimos, an excess of group A over O and the presence of B. These blood group figures immediately distinguish them, like other Eskimos, from all Indians so far typed (Table 1). Additional significance enters the data for these Eskimos who constituted a major bloc of the total Eskimo population. The early contact estimate credits them with a population of 7,200 and a population density of 17.30 per 100 km.^{2}, an amount exceeded only by the Aleuts, the Kaniagmiut, and the Greenland Eskimos.

By contrast it is interesting to note the population figure for one of the studies which has been cited as evidence for the Indian origin of Eskimos. The Caribou Eskimos, comprising four small tribes, provide the bulk of the observations for a study of the Central Eskimos by Birket-Smith. The early contact estimate for the Caribou Eskimos is 700 individuals, with a population density of 0.41 per 100 km.^{2}. It is apparent that the processes of drift, selection and mixture will operate more rapidly in this small isolate. On the basis of numerical representation alone many of these small groups of Central and Eastern Eskimos must be considered peripheral to the major centers of Eskimo population and as such can not be used as the type models for Eskimos as a whole.

Concerning the question of divergent interpretation of blood group data and anthropometric data, it has already been shown that there is an essential similarity in the blood group data for

Eskimos drawn from the larger populations both in the west and the east. On the basis of the available blood group figures it is not possible to class the Eskimos into separate divisions. Greater weight must be attached to blood group data than to anthropometric data owing to the fact that their mode of inheritance is known and that they apply to all members of a group regardless of sex or age. Neither is it possible to support the hypothesis of an Indian origin for Eskimos on the basis of blood group data. As previously mentioned, the group B of the Eskimos indicates an Asiatic origin, and not the result of a mutation in the New World as has been suggested.

The length of time in which the Eskimos have occupied the northern fringe of North America is relevant to the elucidation of the movements of these people and to the past size of their population. There is ample evidence to indicate the arrival of Eskimo groups first in western Alaska with the subsequent movement of some of the groups into the east. Thus, a carbon-14 date for the Paleo-Aleut occupation of Nikolski, Umnak Island, the Aleutian Islands, gives an elapsed time of 3,000 years. By contrast the Eskimos reached their eastern extremity, Greenland, much later. European objects date one site here in the 10th century AD, and the possibility of an Eskimo occupation as early as 500 AD is generally accepted. For the Paleo-Aleuts (a morphological variant of the western Eskimos) to have reached Umnak Island by 1000 BC, an earlier date of arrival on the mainland to the north is necessarily presupposed. Early settlements of western Alaska, at many places on the mainland, Kodiak Island and the Aleutians, indicate the early development of a relatively large population. The variety and wealth of marine animals in western Alaska made possible the elaboration of large populations.

Interpretation of Anthropometric Similarities

Throughout the literature dealing with Eskimo origins and relationships two conflicting interpretations of the evidence may be found. On the one hand similarities between Eskimos and Indians are adduced as evidence of an inland Indian origin of the Eskimos, and on the other hand similarities between these people are adduced as evidence of mixture between them. As a specimen of this point of view we may consider the statement of Birket-Smith, "On turning to the west we find much more heterogeneity. That the *basis* is essentially the same here as farther east is scarcely to be doubted; but evidently there are foreign intrusions. For example, we find an unmistakable increase of the cephalic index among the Eskimos on Colville River, the Asiatic tribes and the tribes in South Alaska, where the population is on the border of brachycephaly. It is probable that this is due to mixing with the surrounding Indians—with whom the Aleut are also associated—and with the Palaeo-Asiatics, both of which groups are markedly brachycephalic" (Birket-Smith, 1940, p. 101). In view of the large size of the western Eskimo populations it is questionable whether their brachycephaly should be explained on the basis of mixture with Indians, while the smaller groups of Central Eskimos who display similarities with the Indians to the south, are corsidered to have been derived from them. Unfortunately there have not been many studies on the western Eskimos and there have been even fewer on the Indians so that arguments for Indian mixture can not be advanced on the basis of particular groups who have had the opportunity of mixing.

The smaller groups are presumably most likely to manifest the effects of mixture. Logically the Eskimo-Indian similarities in the west could also be used as the basis for the origin of the western Eskimos.

Obviously the fact that similarities in one case are used as evidence of origin, and in the other case, as evidence of mixture is a historical judgment and not a scientific judgment. In one case the Indians are awarded the status of contemporary ancestors and in the other are considered adulterating agents. It is unnecessary to resort to either of these interpretations. Recognition of the polymorphic constitution of the Eskimos makes it unnecessary to select any particular isolates as being the most representative of all Eskimos. The variety of morphological types among them may be due to a multiplicity of factors such as original differences in the various groups who crossed Bering Strait at different times, to the various genetic processes which have acted upon these groups since their arrival and, in some cases, absorption of older populations.

Archaeologically we know there are a number of different morphological types, ranging from extreme dolichocephaly to brachycephaly. At least as great a range of physical types exists in the time sequence as exists now in the contemporary geographical distribution. The most extensive change appears to have taken place in southwestern Alaska, Kodiak Island and the Aleutians. In this general area a variety of earlier mesocephalic types have been overlain by brachycephalic types. Judgments concerning the origin

of the Eskimos must also take into consideration the actual sequence of physical types, as well as the contemporary distribution.

One of the interesting results of the analysis of Eskimo-Indian similarities has been the revelation that Indians are in some cases more Eskimo than the Eskimos themselves. A study involving the Eskimos from Smith Sound, Coronation Gulf, Seward Peninsula and the Chipewyan Indians has been summarized as follows, "On the basis of this statistical device, the differences between the pure Chipewyan and the Seward Peninsula Eskimo group appear to be smaller than they are between any of the three Eskimo groups themselves" (Shapiro, 1931, p. 378). Similar observations may be made for many other Eskimo groups. Thus the differences between Eastern and Western Aleuts, occurring not only in the dimensions and indices but also in such genetic characters as the fissural patterns and cusps of the dentition, and mandibular torus (Moorrees, unpub.), are greater than those between selected groups of Indians and Eskimos. It is quite apparent, however, that these results are achieved by extracting particular breeding isolates from the total population and comparing them with breeding isolates similarly removed from Indian populations.

The theories concerning Indian origin of the Eskimos and concerning Indian admixture with Eskimos have been based on the anthropometry of the head. As previously suggested, the fact of continuous gradation in the various features of headform, of which only the cephalic index has here been taken as a sample, appears to indicate that the Eskimos form one geographically varying population. Existing data on the anthropometry of the remainder of the body indicate even fewer geographical variants than occur in the vault form. Additionally, the error of relying upon vault form for determining genetic relationships, may be clearly seen when it is realized that headform was originally invoked to disbar from consideration a major portion of the Eskimo population. Thus, the data from the blood groups, the anthropometry of the head, the anthropometry of the body, and genetic characters such as dentition and mandibular torus (Pedersen), do not permit the division of the Eskimo-speaking peoples into genetically distinct populations.

Conclusions

1. An examination of the physical data concerning the Eskimos demonstrates the fact that conclusions concerning all Eskimos should not be based on conclusions derived only from the lesser breeding isolates. Small populations are most susceptible to rapid changes arising from genetic drift, selection, and repopulation from surviving elements of frequently reduced groups.

2. In reality, the physical data concerning the Eskimos indicate that all Eskimo-speaking peoples constitute one major breeding population. This major breeding population is composed of a morphologically intergrading series of geographical variants.

3. Having assessed the physical constitution of all Eskimos as one major unit, we are then in a position to compare Eskimos with Indians and Eskimos with Asiatic Mongoloids.

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Discussion

Lasker: Laughlin presents evidence that some of the differences in blood group frequencies among Eskimos may be caused by the effects of genetic drift in small isolated breeding groups, but that differences in the cephalic index form a broad gradient over the whole group. Similarly,

Kurulkar and Sanghvi have recently demonstrated that among castes in India, similar to each other in head form and other such traits, the differences in blood groups are considerable. These findings have significance for anthropology for it may emphasize Professor Snyder's remark on the greater importance, for some human problems, of polygenic traits over simple Mendelian traits. Whereas the latter may reflect the effects of small populations, the former may better reflect broad historical relationships.

LAUGHLIN: Though it may not be possible here to use polygenic in its most recently defined sense, certainly those traits which represent the effects of a number of genes may be expected to be more stable than those due to only a single pair of alleles, such as the MN types. That the n frequency should be so uniformly low throughout the New World is an interesting question. The various blood group series should prove to be of great value in future research dealing with small populations, especially where comparable data for larger populations exist and to whom the historical, if not racial, relationship of the small population may be known. At the same time it will become increasingly apparent that more accurate data concerning the size of the groups under consideration, the extent of their interaction with other groups, and time depth information indicating the previous size of fluctuations of size of the groups, is collected.

GENETICS OF THREE NORMAL MORPHOLOGICAL VARIATIONS: PATTERNS OF SUPERFICIAL VEINS OF THE ANTERIOR THORAX, PERONEUS TERTIUS MUSCLE, AND NUMBER OF VALLATE PAPILLAE[1]

J. N. SPUHLER[2]

Division of Anthropology and Department of Zoology, Ohio State University, Columbus

INTRODUCTION

One of the central problems discussed in this Symposium takes this shape: Given knowledge about *form* (whether form be morphological, the result of serological tests, etc.), we wish to make controlled inferences about genetic *relationship* between the populations furnishing the forms. Formal genetics is a science which has the assignment of studying the reverse of this argument: Relationships are controlled and variation of form is observed. Genetics, thus, is uniquely equipped to provide the grammar for statements which translate inferences from observations of form into inferences about relationships. Population genetics is a study which applies such rules.

For population genetics, the Hardy-Weinberg steady state furnishes a theoretical model in which the distribution of gene-controlled forms within a breeding population remains constant over time when certain evolutionary processes are negligible. What appears to be an exhaustive list of these processes has been provided by investigators like Wright, Haldane, and Fisher. Given no increments or decrements from mutation, selection, migration, and genetic drift, the frequencies of human characters under simple gene control (in an ideally large, random-mated population where the genes in question are neither almost universal nor almost absent, and where generations do not overlap in mating) remain constant over an indefinitely large number of generations. This constancy of gene frequency through time, together with a known association of genotypes with phenotypes, permits making controlled inferences about relationships among populations from observations on the frequency of genetic characters in such populations. Operation rates for the above evolutionary processes (or rather the present difficulties in empirically estimating such rates and their interaction) over a large number of generations make the method reliable only for relatively short time slices, say around 1,000 years.

Utilization of models from population genetics in the solution of anthropological problems requires knowledge on the mode of inheritance for characters common in the populations under investigation. Characters provided by serology and sense physiology most clearly meet the strict requirements needed by the argument (see Boyd, 1949, and the papers by Race and by Mourant in this Symposium). In general, the security of the argument from form to relationship is increased directly with the number of independent characters available for insertion in the argument. Here lies one motivation underlying a search for normal morphological characters showing simple modes of inheritance in man.

MATERIALS

Data on three characters are reported: 1) Patterns of the superficial veins of the anterior thorax, 2) absence of the peroneus tertius muscle, and 3) number of vallate papillae. These data were specified on all or a portion of 365 Ramah Navaho Indians studied in New Mexico during the Summer of 1948. Except for a small deficiency of adult males, the 1948 sample is representative on most biological, social and cultural criteria of the total living Ramah Navaho population which numbered about 620 individuals in September, 1948. Both parents were examined in 44 matings, while in 50 matings the male parent, and in 11 matings the female parent, have not been observed. (We plan to study these specific "missing" parents during the Summer of 1950.) The family samples employed in genetic analysis of the three characters in the present paper will be those in which both parents are specified for the character in question. In most cases the characters considered here were not specified on about 50 infants included in the

[1] The field work for this study was part of a larger project on the Human Biology and Public Health of the Ramah Navaho supported by grants from the Rockefeller Foundation, Harvard and Ohio State Universities. The work was done at Zuni Indian Hospital, Blackrock, New Mexico, in collaboration with the Medical Division of the U. S. Indian Service.

[2] Present address: Institute of Human Biology, University of Michigan, Ann Arbor.

general Ramah series. Thus less than half of the available information on Ramah Navaho individuals for the three characters will be used in this paper. Full reports on the total series will be made after completion of our 1950 field season.

General acknowledgement is due the members of the 1948 Ramah project field staff: Gordon Allen, Lyle Boyd, William Boyd, Edward Bruner, Mary Hall, Thomas Hall, Clyde Kluckhohn, Theodore Sadock, and the late Jerry Swenson. Special thanks go to those who have had immediate concern with the problems reported here: Gordon Allen for observing and helping to analyse the peroneus tertius variations, Theodore Sadock for recording the number of vallate papillae, William Schull for analysis of the phlebograms of the anterior thorax, and Helen Spuhler for devoting much time needed for her applied work in human genetics to these affairs.

The three characters have been selected for presentation here for three main reasons: 1) None has been the subject of previous family line nor gene frequency study, 2) all show a satisfactory statistical fit in one or more statistical tests for simple modes of inheritance, and 3) each demonstrates a different set of problems important (and, our experience in the Ramah study would indicate, frequent) in genetical investigations of normal morphological variations in man. Examples of such problems are: a) A common character classifiable into two discrete phenotypes following a simple mode of inheritance with full penetrance, e.g., patterns of superficial veins of anterior thorax; b) a common character classifiable into two phenotypes following a simple mode of inheritance on the qualifying assumption of reduced penetrance and variable expression, e.g., absence of the peroneus tertius muscle; c) a common character classifiable into several discrete phenotypes, e.g., number of vallate papillae.

Patterns of Superficial Veins of the Anterior Thorax

The purpose of this part of the paper is to record the frequency and probable mode of inheritance of two patterns of the superficial veins of the anterior thorax in the Ramah Navaho population. The frequency of the two patterns in the Navaho group is compared with that found in a female white sample from southeastern Wisconsin. (The relative importance of genetic and non-genetic factors in determination of the two patterns is suggested by observations on 7 pairs of monozygotic twins.) Finally, the hypothesis that the two phenotypes are controlled by single autosomal alleles with dominance and full penetrance is shown to be compatible with our preliminary data.

An outline of the anatomical standard for the venous drainage of the anterior thorax (Schaeffer, 1942) is as follows (Fig. 1): The superficial veins of the anterior thorax form a plexus over the entire chest, of which the portion over the mammary gland is called the mammary venous plexus. The lateral thoracic vein drains the mammary plexus while the veins near the median line are drained by the internal mammary vein and its anterior intercostal and superior epigastric tributaries. In the anatomical standard, named by Massopust (1948) the *transverse type*, the superficial veins radiate laterally from the pectoral venous plexus (drained by the internal mammary veins) toward the axillary and costoaxillary regions.

In a second type of drainage of the anterior thorax, called by Massopust the *longitudinal type*, the veins radiate in a fan-like pattern downward and laterally into the breast from the point where the anterior jugular vein turns beneath the sternocleidomastoid muscle. At this lateral turn of the anterior jugular vein, there is a branch which may be traced across the trachea and beneath the cervical fascia to its junction with the anterior jugular of the opposite side. This arch across the trachea is called the jugular venous arch. The superficial veins of the median aspect of the anterior thorax lie, then, roughly parallel either to the longitudinal or to the transverse axis of the body.

Classification as to pattern type is on the basis of the drainage of the mammary region. This point is stressed because it is common to find individuals in whom the venous drainage of the mammary tissue is of the transverse type but in whom the venous drainage of the upper anterior thorax, particularly of the clavicular region, is by way of the jugular venous arch or the anterior jugulars. In both male and female subjects reported here, classification was based solely on the venous drainage of the mammary tissue.

Little is known about the embryonic development of the superficial veins. When the patterns take their definitive shape is unknown. Probably the pattern is laid down by the time the principal veins draining the thorax are functional. If this assumption is valid, then the definitive form of the transverse pattern may be attained as early as the sixth to the eighth week of development since the internal mammaries are functional at that time. The longitudinal pattern, however, probably reaches its final form relatively late in

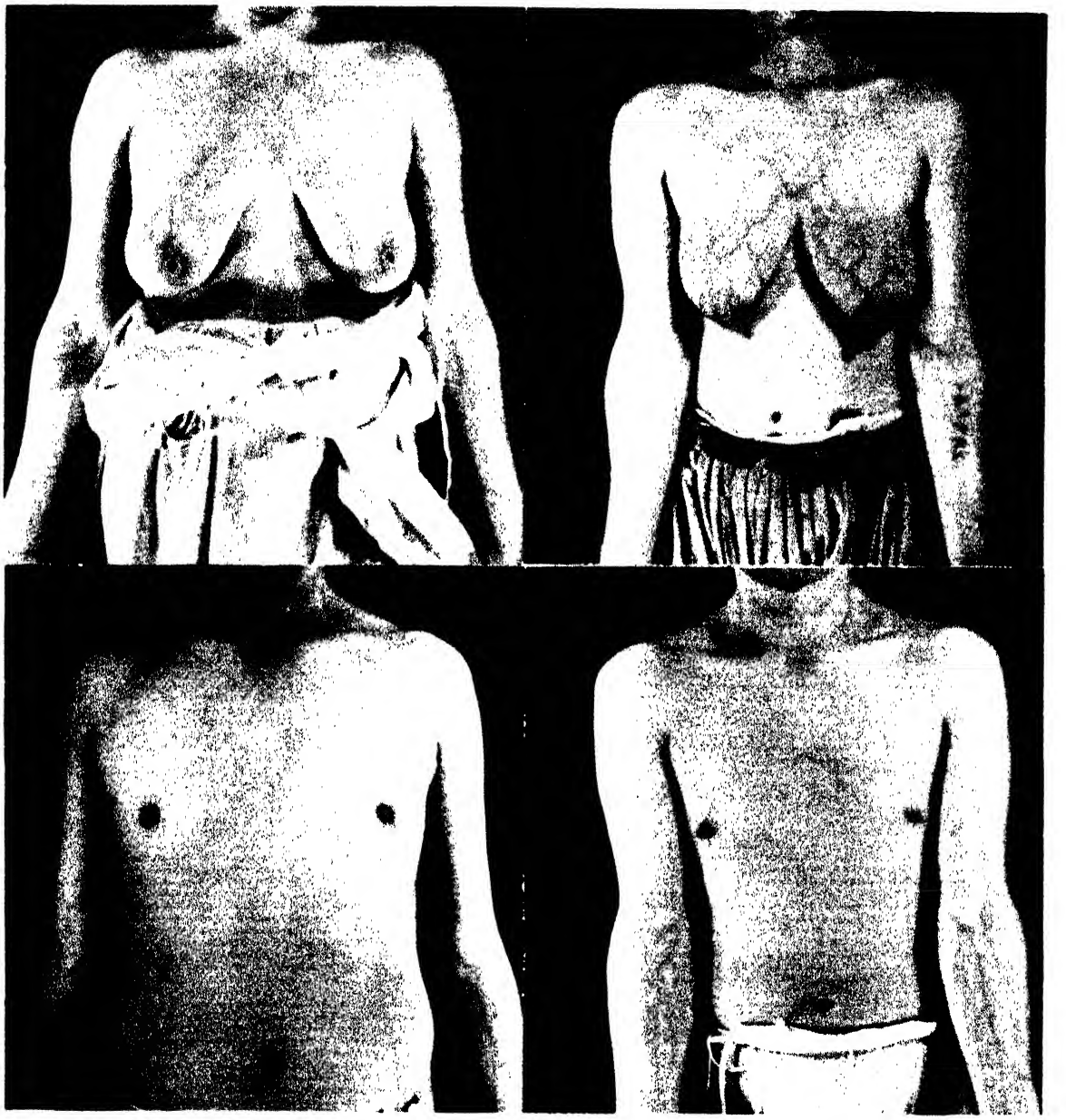

FIG. 1. The longitudinal (left) and transverse (right) patterns of the superficial veins of the anterior thorax in Ramah Navaho Indian females (top) and males (bottom).

embryonic development since the appearance of the anterior jugulars occurs relatively late. The anterior jugulars arise from the gradual organization of small vessels which were tributaries of the anterior cardinals at the cervical level. This difference in time when the patterns are formed may account for the relative constancy of detail in the longitudinal pattern as opposed to the marked variability in detail of the transverse pattern.

The pattern is probably constant once the definitive, general form is reached since at present the only known alterations in the pattern are due to breast tumors. Massopust (1936) has observed the pattern of a pregnant woman from two and one half months of gestation to eleven months after parturition. He finds that the pattern becomes more and more distinct as the time for lactation approaches, with the maximum clarity of pattern

being reached shortly after parturition when the breasts are actively lactating. This is to be expected because of the increased flow of blood to the mammary gland during lactation.

The patterns of the superficial veins of the anterior thorax were recorded by means of infrared photography (see Gibson, 1945, for general techniques). A fairly large negative image is required in order to record fine detail. We used a Grundlack 5 × 7″ view camera with a Wollensak f6.8 lens. Four No. 2 photoflood lamps provided flat illumination of the chest region. A black sheet was used for a background. The image was focused on a ground glass using a Wratten 25 red filter. After focusing, a Wratten 87 filter was substituted and the bellows extension was increased approximately 0.25% of the extension required for visual focus. Eastman infrared sheet film was used with exposure one-half second at f/11. (In later work we found that use of photoflash lamps permits reduction of exposure time with the result that fewer films are ruined due to movement of the subject.) Usually the venous patterns are more easily read from the negative; if prints are made, stress venous detail and ignore flesh tones.

Phlebograms of 273 Navaho individuals have been classified. A pattern was assigned to an individual only if at least one of the larger superficial veins was clearly visible in the phlebograms. One hundred and ninety individuals, or 69.6%, have the transverse type and 83 individuals, or 30.4%, show the longitudinal pattern. A chi-squared analysis indicates that the patterns are not significantly associated with sex ($\chi^2 = 0.0429$, $P = .7\text{–}.8$). Massopust (reported by Schull, 1949) has indicated that the frequency of the longitudinal pattern in white populations, based on a sample of 850 females from southeastern Wisconsin, is about 6 to 10 per cent. Seemingly there is a significant difference in incidence of the patterns between white and Ramah Navaho populations (Table 1).

Our data contain 27 families in which both parents have been classified, comprising a total of 104 parents and children. (Data from 62 families where one parent and one or more offspring have been phlebogramed have not been utilized in the present genetical analysis. Patterns of the missing spouses and certain other offspring will be determined during the Summer of 1950.) Matings in the Ramah sample are non-assortative with regard to the two patterns.

TABLE 1. DISTRIBUTION OF THE LONGITUDINAL PATTERN OF THE SUPERFICIAL VEINS OF THE ANTERIOR THORAX, AND OF RECESSIVE GENE *l* IN TWO POPULATIONS

Population	Author	No.	% long. pattern	Gene freq. *l*
Ramah Navaho	Spuhler, unpublished	273	30.4	.55
American whites	Massopust (Schull, 1949)	850	6.–10.	.24–.32

A test designed by Haldane and Smith (1948) was performed to ascertain whether or not the pattern is dependent on such factors as maternal age or order of birth. If variation of pattern type is under gene control with complete penetrance a birth order effect would be unexpected. Of course demonstration of a birth order effect would not preclude a genetic basis for the character, but would indicate that non-genetic factors account for some portion of the observed variation. The families where variation occurred among the sibships were scored on the Haldane and Smith test. The observed mean was 360 and the expected mean 403.998 with a standard error of ±30.318. The difference between the observed and expected means is less than twice the standard error and it is concluded that birth order does not influence the distribution of the patterns within sibships.

Swed and Eisenhart (1943) have devised a test which permits examination of the hypothesis of randomness (independent occurrence) of the two patterns in parents and offspring. Results of this test show that the pattern of the siblings are dependent on the pattern of their parents, at the 5 per cent level of significance. This dependence is interpreted as being caused by hereditary control of the patterns.

Seven pairs (four male, three female) of white monozygotic twins, ranging in age from 19 to 28 years of age and resident in Columbus, Ohio, were classified with regard to the two patterns. All of the pairs were concordant for the patterns (six pairs were transverse, one longitudinal). Although the size of the twin sample is inadequate, these results are consistent with the hypothesis that the variation in pattern is under gene control.

Given evidence in support of the hypothesis of inheritance of the patterns of the superficial veins of the anterior thorax, appropriate tests for the mode of inheritance may be made. The simplest hypotheses are those of determination by a single pair of alleles. Four different types of single allelic inheritance have been demonstrated in man and a fifth may exist; these are autosomal, sex-linked, incompletely sex-linked, holandric, and possibly hologynic.

Demonstration of both patterns in each sex excludes the possibilities of holandric and hologynic

modes of inheritance. Observation that 30.9 per cent of females and 29.7 per cent of males show the longitudinal pattern indicates a sex-ratio incompatible with sex-linked inheritance (there being no evidence of a differential viability factor). Extensive examination of the pedigrees of families where both parents were recorded fails to support the hypothesis of incomplete sex-linkage unless an unwarrantedly high rate of crossing-over is postulated.

TABLE 2. TEST OF THE HYPOTHESIS THAT THE PATTERNS OF THE SUPERFICIAL VEINS OF THE ANTERIOR THORAX ARE DETERMINED BY SINGLE AUTOSOMAL ALLELES WITH THE TRANSVERSE PATTERN (*L-*) DOMINANT OVER THE LONGITUDINAL PATTERN (*ll*) USING FAMILY DATA FROM THE RAMAH NAVAHO POPULATION

Mating	Number	Offspring				
		Observed			Expected	
		L-	*ll*	Total	*L-*	*ll*
L- × *L-*	12	16	3	19	16.60	2.40
L- × *ll*	13	20	9	29	18.69	10.31
ll × *ll*	2	0	3	3	0	3
Totals	27	36	15	51	35.29	15.71

Table 2 gives the test of the hypothesis that the patterns are determined by single autosomal alleles with the transverse pattern (*L-*) dominant over the longitudinal pattern (*ll*) using Snyder's method (1932, 1943) on 27 matings with 51 classified offspring. All the offspring have patterns consistent with the hypothesis. Without correction for small numbers, χ^2 is 0.430 which for two degrees of freedom is interpreted that the deviation between observed and expected number of recessive offspring would be expected as a chance variation in more than 80 per cent of cases. On the basis of Hogben's familial analysis method (1946) the deviation for recessives is 2.43 individuals with a standard error of ±1.73 and $D/\sigma = 1.4$.

Preliminary analyses of a rather small quantity of data, using pedigree inspection, gene frequency tests, and a twin study, are accordant with the hypothesis that the two phenotypical patterns observed in phlebograms of the anterior thorax are controlled by autosomal single alleles with full penetrance, the transverse pattern being determined by the genotypes *LL* and *Ll*, and the longitudinal pattern by the homozygous recessive genotype *ll*. It requires emphasis that this is a preliminary result. The data are limited and the statistical tests employed are of low power. In the study of human genetics, hypotheses of single allelic mode of inheritance are always suspect until they have been repeatedly subjected to test.

Peroneus Tertius Muscle

The anterior peroneal muscle, *M. peroneus tertius*, is one of four anterior muscles of the leg. It assists in dorsi-flexion of the foot at the ankle, and in elevation of the lateral border of the foot. When present in man, it develops as a fasciculus of the extensor digitorum longus. Arising from the distal third of the antero-medial surface of the fibula, the interosseus membrane, and the anterior intermuscular septum, it inserts, sometimes with a double or triple tendon, on the dorsal surface of the base of the fifth metatarsal and sometimes on the base of the fourth metatarsal. The muscle is usually absent in Old World Monkeys (Straus, 1930; Wells, 1935), but has been reported in 5 per cent of 15 Chimpanzee legs (Loth, 1931) and 30 per cent of 18 Gorilla legs (Straus, 1930). Charac-

TABLE 3. ABSENCE OF THE PERONEUS TERTIUS MUSCLE IN THE RAMAH NAVAHO POPULATION WITH COMPARATIVE DATA FROM 13 OTHER PEOPLES

Population	Author	Number of legs	% absent
Papuans	Nagel (Loth, 1931)	28	0
Japanese, Tokyo	Koganei, *et al.* (Loth, 1931)	308	3.2
Japanese, Kyoto	Adachi (Loth, 1931)	938	4.5
French	Le Double (Loth, 1931)	240	5.8
Japanese, Okayama	Adachi (Loth, 1931)	228	6.1
English	Wood (1907a, b, 1908)	204	6.9
Polish	Posmykiewicz (1934)	1,814	7.1
Alsatians	Schwalbe and Pfitzner (Loth, 1931)	537	8.2
Negroes	Loth (1931)	114	9.8
Polish Jews	Posmykiewicz (1934)	186	10.2
Chinese	Nakano (1923)	84	10.7
Ramah Navaho Indians	Allen and Spuhler, unpublished	608	14.3
Negroes	Vallois (Loth, 1931)	124	15.3
Berbers	Leblanc, *et al.* (Loth, 1931)	106	23.6

teristically present in man, its observed distribution ranges from presence in all of 28 Papuan legs (Nagel, cited by Loth, 1931) to presence in only 76.4 per cent of 106 Berber legs (Leblanc, *et al.*, in Loth, 1931). Frequency of absence of the peroneus tertius muscle in 14 population samples is given in Table 3.

This part of the paper reports the incidence of the peroneus tertius muscle in a sample of Ramah Navaho Indians and discusses the possible role of genetic factors in determining the distribution of this character.

The feet of 306 Navahos were examined by Gordon Allen for presence of the peroneus tertius tendon: 59 individuals, mostly infants, out of the total series of 365 were not recorded for this character during our 1948 field season.

While most workers have obtained data on this muscle from dissecting-room material, the observation was extended to the living by Posmykiewicz (1934). In the Ramah study, Allen found that when the subject stands with toes in sharp dorsiflexion, the tendon of the peroneus tertius (when present) becomes prominent over the cuboid bone just outside the most lateral tendon of the extensor digitorum longus. The tendon cannot be palpated satisfactorily when relaxed; therefore the reliability of our method of observation cannot be checked on cadavers.

The morphology of the tendon is highly variable. Observations were recorded in five categories reflecting this variability: L large, M medium, S small, D doubtful, and A absent. In practice, the dividing lines between these categories were poorly drawn, and even the distinction between present and absent is obscured by the doubtful class. For purposes of the present genetical analysis, the categories large, moderate, small, *and doubtful* have been treated together as *presence* of the muscle.

Table 4 gives the frequencies of the several observational classes. The variation in size is of unknown significance, but a more detailed study of tendons which occur unilaterally might establish an equivalence between some atypical forms of the muscle and complete absence.

The percentages in the right side of Table 4 emphasize two features of the distribution: The muscle is suppressed more often in females than in males, and more often on the right than on the left. The total legs with muscles absent are 24.6 per cent in females and 10.5 per cent in males. This sex difference is significant. The difference between left and right is reversed in the sexes.

An interesting feature of the distribution of the muscle is presented when the data are tabulated to reveal asymmetry. Table 5 shows that 21.3 per cent of the population lack one or both muscles, but about four-sevenths of these individuals are asymmetrical in this respect.

TABLE 4. DISTRIBUTION OF THE PERONEUS TERTIUS MUSCLE BY SEX AND SIDE OF BODY IN 608 LEGS FROM THE RAMAH NAVAHO POPULATION

Sex	Side	Large or moderate	Small	Doubtful	Absent	Present	Absent
Female	Right	90	32	14	34	136 (80.0%)	34 (20.0%)
	Left	94	42	9	25	145 (85.3%)	25 (14.7%)
Male	Right	90	25	7	12	122 (90.2%)	12 (9.8%)
	Left	86	25	7	16	118 (88.1%)	16 (11.9%)
Totals		360	124	37	87	521 (85.7%)	87 (14.3%)

Since 13.1 per cent of individuals have the muscle on only one side of the body, non-genetic factors are obviously important in determination of the character. If genetic factors are responsible for some portion of the observed variation, such factors must have variable expression or reduced penetrance or both. Both presence and absence are sufficiently frequent in our material that inheritance should manifest itself (even in the case of a recessive character) in a significant parent-offspring association. Table 6 indicates such an association is significant in our material at the 1 per cent level ($\chi^2_1 = 10.21$). This in itself is necessary but not sufficient evidence for inheritance of the muscle variation, because parent-offspring correlation is not all genetic in origin (Wright, 1934). Our preliminary data are not large enough to warrant a quantitative estimate which might prove more decisive.

Inspection of the most favorable pedigrees fails to give decisive support for any of the unit-factor modes of inheritance. Likewise no significant results were obtained for the operation of simple genetic factors using methods similar to those of Danforth (1924), Schinz (1945), and Lasker (1947) for an analysis of the degree of correlation be-

TABLE 5. DISTRIBUTION OF THE PERONEUS TERTIUS MUSCLE BY INDIVIDUALS IN 306 RAMAH NAVAHO INDIANS

Sex	Bilaterally present	Unilaterally absent	Bilaterally absent	Total
Females	130 74.8%	26 14.9%	18 10.3%	174
Males	111 84.1%	14 10.6%	7 5.3%	132
Totals	241 78.7%	40 13.1%	25 8.2%	306

tween right and left sides in individuals. Twin data for the peroneus tertius are seemingly not available in sufficient bulk for a genetic study.

Presumptive evidence for the operation of a simple mode of inheritance was obtained by two methods of gene frequency analysis where simplifying assumptions were made by ignoring the complications due to possible differences in expression, penetrance or both.

Inspection of the family material suggests that occurrence of the muscle may be due to a single pair of alleles, *F* and *f*, with dominance in that order, and with variable expression or incomplete penetrance. On this hypothesis (neglecting variations in gene action) the genotypes *FF* and *Ff* would determine presence of the muscle (+) and the genotype *ff* absence (–). Table 7 gives a test of this simplified hypothesis using Snyder's gene frequency method (1932, 1934). The data are inadequate to test the crucial mating (–) × (–) where one individual contrary to the hypothesis was observed. When the observed and expected recessives (–) from the three mating types are compared by the chi-square method (2 × 2 table), χ^2_1 is 0.520 and P = .80 – .90.

Because of the scarcity in our preliminary data of families with both parents recorded for the peroneus tertius muscle, it is desirable to utilize the larger body of information available on sibships, whether or not the parents of these sibships were specified for the muscle. Cotterman's (1937) method for indication of single allelic inheritance in data comprising but a single generation is appropriate.

TABLE 6. PARENT-CHILD ASSOCIATION FOR SUPPRESSION OF THE PERONEUS TERTIUS MUSCLE IN THE RAMAH NAVAHO POPULATION

Observed and expected frequencies are given on the hypothesis of no association. (The left-hand cells include families with only one parent examined.)

	Absent in one or both parents	Present in both parents	Totals
Absent in children	22 (13.8)	15 (23.2)	37
Present in children	36 (44.2)	82 (73.8)	118
Totals	58	97	155

Again consider two alternative characters, the presence (+) and absence (–) of the peroneus tertius muscle, assumed to be determined by a single pair of autosomal alleles, *F* and *f*, with the former dominant. A randomly collected group of sibships, of 2 or more members, may be classified taking 2 sibs at a time as to their composition with regard to the two characters (+) and (–). The number of sib-pairs supplied by sibships of s members is given by ${}^sC_2 = s(s-1)/2$. Letting the frequency of *F* be designated by p and that of *f* by (1 – p), expectations in the 3 classes are given by the sum of the expected proportion of sib-pairs for each type of sib-pair (cf. Cotterman, 1937). Thus in a set of n_2 sib-pairs, the expected frequencies, e, of the 3 classes containing 2 members where 0, 1, or 2 members are dominant (+) are:

$$e_{20} = \tfrac{1}{4}(1-p)^2(2-p)^2 n_2$$
$$e_{21} = \tfrac{1}{2}p(1-p)^2(4-p)n_2$$
$$e_{22} = \tfrac{1}{4}p(4+5p-6p^2+3p^3)n_2$$

An estimate of p may be obtained from the observed proportions of (+) and (–) individuals in

TABLE 7. GENE FREQUENCY TEST FOR SINGLE ALLELIC INHERITANCE OF PRESENCE (+) AND ABSENCE (–) OF THE PERONEUS TERTIUS MUSCLE IN THE RAMAH NAVAHO POPULATION

Mating	Number	Offspring				
		Observed			Expected	
		(+)	(–)	Total	(+)	(–)
(+) × (+)	13	27	5	32	28.09	3.91
(+) × (–)	15	27	14	41	26.67	14.33
(–) × (–)	2	1	1	2	0	2
Totals	30	55	20	75	54.76	20.24

the aggregate of the sibships used in the test. The expected proportions, under a condition of random mating, of (+) individuals is $1 - (1 - p)^2$. Let A and B, respectively, designate the corresponding observed proportions of (+) and (−): then $p = 1 - \sqrt{B}$ and substitution of this p value in the above equations for e provides the expected frequencies of the 3 sib-types. The observed and expected values may then be compared by the χ^2 method. Since the expected values have been adjusted to conformity with the observed values in 2 respects (p and n_2), the probability table for χ^2 should be entered with 1 degree of freedom.

TABLE 8. VALUES OF A AND p INDICATED BY SIBSHIPS OF SIZES 2 AND 3 CLASSIFIED FOR PRESENCE (+) AND ABSENCE (−) OF THE PERONEUS TERTIUS MUSCLE IN THE RAMAH NAVAHO POPULATION

Size of sibships	Total number of (+)	Total number of (−)	Total number of sibs	Gene frequency p
2	58	12	70	
3	33	9	42	
Totals	91	21	112	.567

The information available on sibships of sizes 2 and 3 is given in Table 8 and the calculations are summarized in Table 9. The expected and observed numbers of sib-pairs agree closely, χ^2_1 being 0.055 and $.80 < P > .90$.

In the case of the sib material, a contrary hypothesis, that presence and absence of the peroneus tertius muscle is determined by non-hereditary chance factors, may be tested and rejected by the following argument (Cotterman, 1937): The expected frequencies of sib-pairs possessing 0, 1, and 2 of the (+) characters under this non-genetic hypothesis are, respectively,

$$B^2n_2 = (21/112)^2 \times 77 = 2.71,$$
$$2ABn_2 = 2(91/112)(21/112) \times 77 = 23.46,$$
$$A^2n_2 = (91/112)^2 \times 77 = 50.83.$$

If these values are compared with the observed number of sib-pairs (n_2), that is, 8, 14, and 55, the value of χ^2 is 14.483, which, when n = 1, should be exceeded in less than 1 in 1,000 trials.

Suppression of the peroneus tertius muscle is controlled by the interaction of genetic and non-genetic factors, According to our initial results, a single pair of autosomal genes with reduced penetrance, variable expression or both condition the occurrence of the muscle.

NUMBER OF VALLATE PAPILLAE

The vallate, or circumvallate, papillae in man number from 3 to 14 and are located slightly anterior to the terminal sulcus on the upper surface of the tongue. These papillae are most often of cylindrical shape, 1 to 2 mm. in diameter and about 1 mm. in height. Each papilla is usually surrounded by a fossa; the walls of this fossa contain taste buds and the bottom receives ducts of the serous glands of von Ebner. When the mouth is open wide, and the tongue pulled forward, the number of papillae is easily counted.

Since first named by Cuvier (see Testut, 1922), the vallate papillae have been the subject of several morphological and anthropological studies. Loth (1931) gives a brief summary, incomplete for Chinese and Japanese investigations, of the human and other Primate material. Percentage distributions of the number of papillae in eight populations are given in Table 10.

Aside from a study on Japanese fetal twins by Ogawa (1940), which is discussed below, genetic studies on the vallate papillae have not been previously reported. The number of vallate papillae was determined on 297 Ramah Navaho Indians during the Summer of 1948. (Each papilla is counted, regardless of whether or not it has its individual fossa.) The purpose of this part of the paper is to compare the frequencies of the various number-types among the Ramah Navaho with those of other populations, and to suggest a possible mode of inheritance for the number of papillae.

TABLE 9. SIB-PAIRS CLASSIFIED FOR PRESENCE (+) AND ABSENCE (−) OF THE PERONEUS TERTIUS MUSCLE AND AVAILABLE IN SIBSHIPS OF 2 AND 3 SIBS IN THE RAMAH NAVAHO PRELIMINARY DATA

Observed and expected classes are shown

Number of (+)	Sib-pairs in sibships of 2	Sib-pairs in sibships of 3 in which (+) numbers				Total n_2	Expected e
		0	1	2	3		
0	4	3	1	...	...	8	7.4
1	4	...	2	8	...	14	14.0
2	27	...	...	4	24	55	55.6
Totals	35	3	3	12	24	77	77.0

The distribution of the various numbers in the total Ramah Navaho series is given in Table 11. No significant difference is found between the distributions for males and females. 7-V (seven vallate papillae with V pattern) is the most com-

TABLE 10. PERCENTAGE DISTRIBUTION OF THE NUMBER OF VALLATE PAPILLAE IN EIGHT POPULATIONS

Sample size is given in parentheses at the head of each column

Number of papillae	Chinese Miyashita, 1935	Japanese Kunitomo and Kikuchi, 1935	Ainu Kukita, 1932	European Grabert, 1910	Melanesian Zuckermann, 1912	Herrero and Hottentot Grabert, 1910	East African and Cameroons Hopf and Edzard, 1910	Ramah Navaho Indians Spuhler, unpublished
	(135)	(127)	(5)	(50)	(13)	(49)	(5)	(297)
3	0.7	...	...	...	...	...	...	0.3
4	5.9	...	...	...	...	...	...	...
5	8.2	...	20.0	...	...	2.0	...	4.0
6	18.5	3.1	40.0	2.0	...	10.2	...	2.0
7	17.8	4.7	40.0	6.0	...	18.4	20.0	80.2
8	18.5	13.4	...	8.0	23.0	6.1	...	2.3
9	14.8	21.3	...	16.0	15.4	22.4	...	10.8
10	11.9	29.9	...	16.0	7.7	18.4	40.0	...
11	1.5	11.8	...	14.0	38.5	6.1	...	0.4
12	2.2	7.1	...	10.0	...	12.3	...	...
13	...	4.7	...	18.0	7.7	2.0	...	...
14	...	4.0	...	10.0	7.7	2.1	40.0	...
Totals	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

mon type in the Ramah sample, occurring in 80.3 per cent of males and 79.4 per cent of females.

Ogawa (1940) studied the patterns, angles, and numbers of vallate papillae in 14 pairs of monozygotic and 7 pairs of dizygotic Japanese fetal twins. These were classified as discordant when the between-pair number differed by 1 or more:

	Monozygotic (14)		Dizygotic (7)	
	No.	%	No.	%
Concordant	5	35.7	2	28.6
Discordant	9	64.3	5	71.4

Ogawa concluded that while genetic factors are responsible for much of the variation in pattern (e.g., V and Y arrangements) and size of angle (between the two lateral rows of papillae), nongenetic factors are clearly of primary importance in determining the number of papillae. This last conclusion is based on the assumption that age changes in number of papillae do not occur during the 7th to 9th fetal months. Retabulation of Ogawa's Table 2 (1940, p. 381) indicates (the evidence is regrettably small) that concordance

TABLE 11. NUMBER AND PATTERN OF VALLATE PAPILLAE IN MALE AND FEMALE RAMAH NAVAHO INDIANS

No. & pattern	Males	%	Females	%	Total	%	% in family series range	
3-V	...	...	1	0.6	1	0.3	...	
5-V	7	5.3	5	3.0	12	4.0	4.0	(12)
6-V	2	1.5	4	2.4	6	2.0	2.1	(6)
7-V	106	80.3	131	79.4	237	79.8	80.6	(238)
7-Y	1	0.7	...	...	1	0.3		
8-V	3	2.3	1	0.6	4	1.3	2.4	(7)
8-Y	...	...	3	1.8	3	1.0		
9-V	12	9.1	18	10.9	30	10.1		
9-Y	1	0.8	...	...	1	0.4	10.9	(32)
9-W	...	...	1	0.6	1	0.4		
11-V	...	...	1	0.7	1	0.4	...	
Totals	132	100.0	165	100.0	297	100.0	100.0	(295)

in total number of papillae increases with fetal age in the monozygotic but not in the dizygotic twins. The mean intra-pair difference of the 2 types of twins is:

		Mean intra-pair difference
Monozygotic:	5 pairs, age 9 fetal months	1.40
	6 pairs, age 8 fetal months	1.83
	3 pairs, age 7 fetal months	3.33
Dizygotic:	2 pairs, age 9 fetal months	2.00
	1 pair, age 8 fetal months	6.00
	4 pairs, age 7 fetal months	1.25

A study of the number of vallate papillae in an adequate series of adult twins is required to settle this issue. For the present it is concluded that non-genetic factors are responsible for some, but not necessarily a predominant portion of, observed variations in the number of vallate papillae. The mean intra-pair difference in the 5 pairs of Japanese monozygotic fetal twins 9 months in age (1.40) is small compared to the range in number of papillae in the Ramah family material (5 to 9). The average difference within pairs of all 28 monozygotic twins reported by Ogawa is about one half (2.18) the family-series range.

In our preliminary two-generation data, information is available on 28 matings with 70 children (total of 126 individuals) as shown in Table 14. (Data on 171 individuals from families where one of the parents has not yet been studied are not used in this analysis.) The family material falls into 5 phenotypes with reference to the total number of papillae: that is, an individual may have 5, 6, 7, 8, or 9 papillae. (The patterns of the papillae will be considered in a later report.)

Possible types of hypotheses involving 2 and 3 pairs of multiple factors, and one for 3 multiple alleles, although showing a fairly good fit by inspection of pedigrees, have been rejected temporarily on the basis of gene frequency tests. A histogram for the Ramah family data shows three peaks at odd numbers of papillae, 5, 7, and 9, with sharp valleys at the even numbers, 6 and 8. In part this trimodality accounts for the poor statistical fit of various multiple factor hypotheses. It should be noted that emphasis on odd-numbered papillae types is not characteristic of other populations (Table 10).

The most simple hypothesis showing a satisfactory fit to our preliminary data is that of 5 multiple alleles. On this hypothesis there is the following association of phenotypes and genotypes:

Phenotypes:	Genotypes:
V-5	v^5v^5
V-6	v^6v^6, v^6v^5
V-7	v^7v^7, v^7v^6, v^7v^5
V-8	v^8v^8, v^8v^7, v^8v^6, v^8v^5
V-9	v^9v^9, v^9v^8, v^9v^7, v^9v^6, v^9v^5

Of the 70 children from specified matings slightly more than 7 per cent (5 individuals from 3 matings) are exceptions to the above hypothesis; slightly less than 93 per cent accord with the model for 5 multiple alleles.

A gene frequency test for the hypothesis that the 5 phenotypes are determined by 5 multiple alleles may be made on the assumption that mating is at random for the number of vallate papillae. A 5 × 5 table giving the observed mating combinations indicates that mating in the Ramah population is non-assortative for this character.

Phenotypically distinguishable matings are:

1) V5 × V5
2) V5 × V6
3) V5 × V7
4) V5 × V8
5) V5 × V9
6) V6 × V6
7) V6 × V7
8) V6 × V8
9) V6 × V9
10) V7 × V7
11) V7 × V8
12) V7 × V9
13) V8 × V8
14) V8 × V9
15) V9 × V9

Let the frequencies of the 5 alleles in the population be:

$$p = v^9,\ q = v^8,\ r = v^7,\ s = v^6,\ t = v^5,$$
$$\text{such that } p + q + r + s + t = 1.$$

Except for the mating (1) V5 × V5, where all offspring are V5, the expected proportions of offspring from each type of mating is a function of p, q, r, s, and t, and thus dependent on these gene frequencies in the population providing the matings. The expected proportions of the 5 possible phenotypes, for each of the 15 possible matings is shown in Table 12. A single example will illustrate the construction of this table:

Mating V5 × V6

Mating	Frequency	Offspring	
		V5	V6
$v^5v^5 \times v^6v^6$	$2s^2t^2$	0	$2s^2t^2$
$v^5v^5 \times v^6v^5$	$4st^3$	$2st^3$	$2st^3$

The total frequency of all classes of offspring from matings of the type

V5 × V6 is: $2s^2t^2 + 4st^3 = 2st^2(s + 2t)$.

Hence the expectation of the 2 possible classes

TABLE 12. PROPORTION OF OFFSPRING OF FIVE PHENOTYPES (5, 6, 7, 8, 9) EXPECTED FROM 15 POSSIBLE MATINGS UNDER A SYSTEM OF 5 MULTIPLE ALLELES (v^5, v^6, v^7, v^8, v^9)

Numerators (N) are given for each type of offspring, denominators (D) for each type of mating.

Mating	ND	5	6	7	8	9
$v^5 \times v^5$	N	1	0	0	0	0
	D	1				
$v^5 \times v^6$	N	t	s + t	0	0	0
	D	s + 2t				
$v^5 \times v^7$	N	t	s	r + s + t	0	0
	D	2(½r + s + t)				
$v^5 \times v^8$	N	t	s	r	q + r + s + t	0
	D	2(½q + r + s + t)				
$v^5 \times v^9$	N	t	s	r	q	p + q + r + s + t = 1
	D	2(½p + q + r + s + t)				
$v^6 \times v^6$	N	t^2	(s + t)(s + 3t)	0	0	0
	D	$(s + 2t)^2$				
$v^6 \times v^7$	N	t^2	$(s + t)^2 + st$	(s + 2t)(r + s + t)	0	0
	D	2(s + 2t)(½r + s + t)				
$v^6 \times v^8$	N	t^2	$(s + t)^2 + st$	r(s + 2t)	(s + 2t)(q + r + s + t)	0
	D	2(s + 2t)(½q + r + s + t)				
$v^6 \times v^9$	N	t^2	$(s + t)^2 + st$	r(s + 2t)	q(s + 2t)	(s + 2t)(p + q + r + s + t)
	D	2(s + 2t)(½p + q + r + s + t)				
$v^7 \times v^7$	N	t^2	s(s + 2t)	4r(¼r + s + t) + 3(s + t)²	0	0
	D	4r(¼r + s + t) + 4(s + t)²				
$v^7 \times v^8$	N	t^2	s(s + 2t)	3r(⅓r + s + t) + (s + t)²	2q(½r + s + t) + 3r(⅓r + s + t) + 2(s + t)²	0
	D	2q(½r + s + t) + 6r(⅓r + s + t) + 4(s + t)²				
$v^7 \times v^9$	N	t^2	s(s + 2t)	3r(⅓r + s + t) + (s + t)²	2q(½r + s + t)	2(p + q)(½r + s + t) + 3r(⅓r + s + t) + 2(s + t)²
	D	2(p + 2q)(½r + s + t) + 6r(⅓r + s + t) + 4(s + t)²				
$v^8 \times v^8$	N	t^2	s(s + 2t)	2r(½r + s + t)	2q(½q + r + s + t) + 6r(½r + s + t) + 3(s + t)²	0
	D	2q(½q + r + s + t) + 8r(½r + s + t) + 4(s + t)²				
$v^8 \times v^9$	N	t^2	s(s + 2t)	2r(½r + s + t)	3q(⅓q + r + s + t) + 2r(⅓r + s + t) + (s + t)²	2p(½q + r + s + t) + 3q(⅓q + r + s + t) + 4r(½r + s + t) + 2(s + t)²
	D	2p(½q + r + s + t) + 6q(⅓q + r + s + t) + 8r(½r + s + t) + 4(s + t)²				
$v^9 \times v^9$	N	t^2	s(s + 2t)	2r(½r + s + t)	2q(½q + r + s + t)	4p(¼p + q + r + s + t) + 6q(½q + r + s + t) + 6r(½r + s + t) + 3(s + t)²
	D	4p(¼p + q + r + s + t) + 8q(½q + r + s + t) + 8r(½r + s + t) + 4(s + t)²				

of offspring (V5 and V6) which this mating can produce is:

$$V5 = \frac{2st^3}{2st^3(s + 2t)} = \frac{t}{(s + 2t)},$$

$$V6 = \frac{2s^2t^2 + 2st^3}{2st^2(s + 2t)} = \frac{(s + t)}{(s + 2t)}.$$

Rough estimates for the gene frequencies, p, q, r, s, and t, may be obtained from the observed frequencies of the phenotypes in the total series and in the family series, by solution of a sequence of 5 quadratic equations representing the sums of the hypothetical genotype frequencies associated with the appropriate phenotype frequencies (Table 13). Resulting estimates for the two series are:

Gene frequency:	Total series:	Family series:
p	.055	.047
q	.013	.013
r	.685	.683
s	.045	.017
t	.202	.240
	1.000	1.000

The expected number of offspring of the various sorts from the 6 observed mating types may be estimated by inserting the above gene frequency estimates from the family series (which correspond fairly closely to those of the total series) into the expressions given for the appropriate matings in Table 12. *Neglecting exceptions*, correspondence of the observed and expected numbers is tested in a 3 × 5 table using the chi-square method (Table 14). Without correction for small numbers, X^2 is 10.74, which for 8 degrees of freedom is interpreted as indicating that the deviation between observed and hypothetical results can be explained on a chance basis in more than 20 per cent of cases.

Genetic factors probably account for considerable part of the variation in the number of vallate papillae. A system of genotypes involving 5 multiple alleles has a good statistical fit to the distribution of phenotypes for the number of vallate papillae observed in families of the Ramah Navaho preliminary series.

TABLE 13. OBSERVED FREQUENCIES IN THE TOTAL AND THE FAMILY SERIES OF RAMAH NAVAHO INDIANS SHOWING THE HYPOTHETICAL CORRESPONDENCE BETWEEN THE PHENOTYPICAL AND GENOTYPICAL FREQUENCIES

Genotype	Population frequency of genes	Phenotype	Observed frequencies	
			Total series (295)	Family series (121)
v^9v^9	p^2	V9	.1085	.0909
v^9v^8	2pq			
v^9v^7	2pr			
v^9v^6	2ps			
v^9v^5	2pt			
v^8v^8	q^2	V8	.0238	.0248
v^8v^7	2qr			
v^8v^6	2qs			
v^8v^5	2qt			
v^7v^7	r^2	V7	.8067	.8182
v^7v^6	2rs			
v^7v^5	2rt			
v^6v^6	s^2	V6	.0204	.0083
v^6v^5	2st			
v^5v^5	t^2	V5	.0406	.0578
Totals	1		1.0000	1.0000

DISCUSSION

Differences in genetic characters between human breeding populations may be catalogued in terms of differences in gene frequencies. Statisti-

TABLE 14. TEST OF THE HYPOTHESIS THAT THE NUMBER OF VALLATE PAPILLAE REPRESENTED IN THE FAMILY DATA FROM THE RAMAH NAVAHO POPULATION IS DETERMINED BY FIVE MULTIPLE ALLELES

Exceptions are italicized

Mating	No.	5		6		7		8		9		Total offspring
		Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	
5 × 5	1	1	3	...	0	*2*	0	...	0	...	0	3
5 × 7	2	1	1.40	1	0.10	5	5.50	...	0	...	0	7
7 × 7	19	1	1.74	...	0.25	40	41.01	...	0	*2*	0	43
7 × 8	1	...	0.23	...	0.03	6	4.20	2	4.54	*1*	0	9
7 × 9	2	...	0.046	...	0.006	...	0.904	...	0.008	2	1.036	2
9 × 9	1	...	0.015	...	0.002	1	0.214	...	0.007	...	0.762	1
Totals	26	3	6.431	1	0.388	54	51.828	2	4.555	5	1.798	65

cal models are available to explain change in gene frequency. In theory the process of race formation can be reduced to a single concept—change in gene frequency. Theoretically, then, population genetics provides a method for studying the relationship between, and the history of, contemporary or recently extinct populations. Empirical application of this method presupposes knowledge of a number of characters controlled by simple genotype systems showing fairly constant expressivity and nearly complete penetrance in the range of environments characteristic for human societies. Serology furnishes the best candidates for characters of this sort. Because of limitations in the application of serological techniques (for example to the vast body of data already available from the world's dissecting rooms, and from field observations by physical anthropologists), and the security provided by ever more characters employed in analysis, genetic knowledge on other widely-distributed characters, especially normal morphological variations, is required to supplement, and in some cases to substitute for, the serological data.

A preliminary report on the genetics of three such characters is presented in this paper. None of these characters should be fully trusted for anthropological use until additional work on other populations has been reported. Our work to date indicated that the mode of inheritance for one of them (venous patterns) may be considered fairly well established. Results on the other two should be considered only as suggestive for further research.

One example of the utility of normal morphological variations in a genetical anthropology is found in the problem of the racial affinities of the American Indians. A comparison of the available data on "putative" genetic characters for American Indians with that for caucasoids, negroids, and mongoloids substantiates the general anthropological conclusion that American Indians are more closely related to the mongoloid division of mankind than to the negroids or caucasoids. Table 15 summarizes this information by assigning four ranks to the variation observed in the major groups (see Spuhler, 1950). Rank 1 signifies the lowest numerical values of gene frequencies and phenotypes for the eight characters. Ranks 2 and 3 refer respectively to the lower and higher intermediate values and rank 4 indicates the highest values. In the case of the vallate papillae, the four ranks denote the lowest, low, high, and highest central tendencies in their frequency distribution. The numbers in parentheses following the character names show the number of different population samples furnishing information used in the table. The frequencies in parentheses following the rank orders in the four columns on the right are rough estimates of the gene or phenotype frequencies for the eight characters in American Indians and the three major racial divisions of man.

TABLE 15. RANK ORDERS FOR THE DISTRIBUTION OF GENE OR PHENOTYPE* FREQUENCIES OF EIGHT CHARACTERS IN AMERICAN INDIANS AND THE MAJOR DIVISIONS OF MANKIND

(See Spuhler, 1950, for data)

Character	American Indians	Mongoloids	Negroids	Caucasoids
Secretor factor (9)	1 (.15)	3 (.48)	4 (.6)	2 (.37–.51)
Taste reaction (35)	1 (.14–.30)	2 (.17–.33)	3 (.20–30)	4 (.39–.77)
Venous patterns AT (2)	4? (.55)	?	?	1? (.24–.32)
Color perception (17)	1 (.01–.02)	2 (.03)	3 (.04)	4 (.06–.08)
*Hair whorl (13)	2? (.29)	4? (.32–.40)	?	1? (.13–.20)
*Palmaris longus (17)	2 (.02–.19?)	1 (.03)	3 (.05)	4 (.10–.25)
*Peroneus tertius (14)	4 (.14)	1 (.03–.11)	2 (.09–.15)	3 (.06–.23)
*Vallate papillae (8)	1 (7)	2 (10)	3 (9–11)	4 (13)
Totals	16 – ?	15 – ?	18 – ?	23 – ?

SUMMARY

Preliminary data on the distribution and the mode of inheritance of three normal morphological variations in the Ramah Navaho population, with comparative data on the distributions in other population samples, is presented.

Results of pedigree inspection, a twin study, and gene frequency tests, indicate that the two phenotypical patterns observed in phlebograms of the superficial veins of the anterior thorax recorded by infrared photography are controlled by autosomal single alleles with full penetrance, the transverse pattern being determined by genotypes *LL* and *Ll*, and the longitudinal

pattern by the homozygous recessive genotype *ll*.

Presence and absence variation in the peroneus tertius muscle is controlled by the interaction of genetic and non-genetic factors. There is some evidence that the genetic factors may be single autosomal alleles with variable expression and/or reduced penetrance.

The number of vallate papillae in the preliminary Ramah Navaho data shows a distribution different from that observed in other populations. Some of the observed variation, possibly a major part, is due to the operation of genetic factors. A model of five multiple alleles shows the best statistical fit to the observed distribution in the Ramah family material.

These results are preliminary. It is planned that additional information on 61 matings for the three characters will be completed during the summer of 1950.

Application of the "presumptive" genetics of eight morphological characters is made to the problem of the racial relationships of the American Indians.

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DISCUSSION

LEVENE: I should like to point out that if we apply a suitable test to a large number of different traits to see whether they behave as unit characters, and use say the 5 per cent level of significance, we will make two kinds of errors. In 5 per cent of all cases where the trait is a unit character, our test will lead us to say it is not. Also, if we test enough different traits that are not unit

characters, we will find some for which the test does not contradict the hypothesis that they are. In this second case, we do not know what the probability of error is, since it depends on the true mode of inheritance of the character, but we do know that the smaller the sample, the less its value is in discriminating between different hypotheses.

Since Dr. Spuhler has used Snyder's method of gene frequency analysis, some comments on it are in order. In this method the gene frequencies are estimated from a combined sample of parents and their children. Fisher has shown that treating this as an equal sized sample of unrelated people gives a consistent but inefficient estimate, and Fisher and others have shown how to calculate efficient estimates. Even when the efficient estimates are used, their variance is greater than that for an equal number of unrelated people. Furthermore, the "observed" and "expected" frequencies in Snyder's table are not independent and hence the variance of their difference is not the sum of their variances. It follows that Snyder's original method is useful for a rough comparison of "observed" and "expected" frequencies but that no reliance should be placed on the test of significance. It is to be hoped that a correct test of significance will be found; if so its use will require the original data family by family and not a mere summary.

As to the vallate papillae, without implying that Dr. Spuhler is guilty in this case, I should like to remark that by assuming a large enough series of multiple alleles, one can get a reasonable fit to any short series of data. Because of the nature of the inefficient fitting method used for this data, one would expect the best fit where there are five papillae and the worst fit where there are nine. From cursory inspection of the table this seems to be the case.

STERN: If the allele frequency analysis is applied to different populations having different gene frequencies then a genetic hypothesis can be more validly tested than by analysis of several samples of the same population. Such tests of different populations might be decisive for Dr. Spuhler's interpretations.

SPUHLER: The cautions of Dr. Levene and the suggestion of Dr. Stern are highly pertinent. Conclusions in human genetics on mode of inheritance are secure only when results on adequate samples for tests on twin, pedigree, and gene frequency methods are concordant by efficient statistics in two or more populations. Two kinds of errors from the short history of human genetics illustrate this: a) The multiple factor hypotheses for the ABO blood groups, and b) Sturtevant's experience with tongue curling.

Work planned for this Summer will increase our matings to about 90 and our usable sample size to about 400 on these and other characters. We can use the more efficient methods of estimation in analyses of this larger body of data, but it will be up to Dr. Levene and his statistical colleagues to provide, I hope in the meantime, a correct test of significance.

Five alleles at one human autosomal locus is not an extraordinary number if we are to trust certain serological characters and analogies from laboratory organisms. If we can swallow 8, we should not gag on 5. Regarding the number of vallate papillae, I am worried by the inefficiency of the test of estimation, but not by the genetical propriety of the hypothesis.

Fortunately data are published, especially by the Japanese anatomists, which will permit application of Dr. Stern's suggestion. Someone should test the data on the number of vallate papillae in Chinese and Japanese.

GENETIC ANALYSIS OF RACIAL TRAITS OF THE TEETH

GABRIEL WARD LASKER

Department of Anatomy, Wayne University Medical College, Detroit, Michigan

Despite the influence of exogenous factors, the teeth of man present, in their racial attributes, numerous inborn developmental features. Although inheritable constitutional factors undoubtedly affect the color, the density, the histology, and the pathology of the teeth, I plan to confine my remarks to some of the gross morphological features of the teeth and the jaws which have pertinence for racial and evolutionary studies of man.

Teeth are the one structure of the body where paleontological and genetic studies of man can easily be brought to bear on the same material. The primate fossil record deals with bones and teeth and from these remains inferences are made about other systems and organs such as muscles and brain.

Virtually all fossil forms of primate now known are represented by teeth. The same cannot be said of the remains of any other part of the body. In fact, fewer individuals are probably represented by all other known bony remains than are known from teeth, and this predominance of the teeth (sometimes imbedded in bits of the jaws) is particularly pronounced for the early periods (for example see Gregory, Hellman and Lewis, 1938, and MacInnes, 1943). The preservation of teeth is accounted for by their hardness. Dentine resembles bone but is harder, and enamel is the hardest substance found in the body—it gives sparks with steel (Maximow and Bloom, 1930).

In the living, on the other hand, no part of the skeletal system is available for unobstructed examination except for the parts of the teeth which protrude through the gums. Genetic studies must almost always be made on the living if twin studies or pedigree studies are contemplated. A few pairs of aborted twin fetuses have been collected and studied, and there may be a few skeletal and other remains of known relatives preserved in museums (certain Egyptian mummies, for instance); but neither of these sources promises much material for the study of the genetics of anatomical characters which are more than "skin deep." The X-ray, however, has made possible the analysis of osteological details in individuals of known relationship to each other. So far, its application to genetic studies is limited to some promising beginnings in the investigation of development (see, for example, Reynolds, 1943, and Sontag and Reynolds, 1944) and to studies of congenital anomalies.

In the case of the teeth, it is possible to examine them directly, to X-ray them, to photograph them, and to make casts. The same techniques can be applied to living individuals in family groups, to twin pairs, to skeletons of the recently dead and to the fossils. In a way seldom possible for most characters of anthropological interest, comparable frequency data on a number of dental traits can be collected on populations of living men and collections of skeletal material. As the skull is the part most frequently preserved in the skeletal collections of archaeologists and as fossil teeth are the most frequently recovered remains dug up by paleontologists, there are even occasionally adequate series of teeth for statistical analyses of populations of the kind most likely to be fruitful in phylogenetic studies at sub-specific levels.

In a recent odontological study of the Greenland Eskimo, Pedersen (1949) has produced a model. He has examined both living subjects and skeletal remains and has reviewed the literature in respect to the racial distribution of numerous dental traits. Other important racial studies previously have been published by Hrdlička (1920, 1921, and 1923), Schwarz (1925), Campbell (1925), Krogman (1927), Hellman (1928), Drennan (1929), Muñoz Ribeck (1936), and Nelson (1937–1938). The present paper will discuss the extension of such studies to the analysis of the genetic mechanisms involved.

The advantages of studies on teeth are rather self-evident. As will be seen, however, these are somewhat offset by a number of difficulties. The genetic analyst of dental traits faces many of the same obstacles that hinder similar analysis of characteristics of other parts of the body.

Most obvious to one who would make such a study, for instance, is the problem of determining what constitutes a trait, and of clustering the observations made into a classificatory system that has some meaning beyond convenience in presenting the data. Let us start with a list of some dental traits which have in the past been thought to have some meaningfulness as inherent

constitutional variables in man and the other primates:

- Development
  - Order of eruption
  - Age at eruption
  - Age at shedding of deciduous teeth
- Number
  - Supernumerary teeth
  - Congenitally missing and peg teeth
    - (e.g., upper lateral incisors and third molars)
- Crown pattern and cusp number
  - Supernumerary cusps
    - (e.g., C_6, C_7, paramolar tubercle, and Carabelli's cusp)
  - Cusplets
  - Wrinkles
- Incisor pattern
  - Shovel shape
  - Lingual ridges
  - Dental tubercle
- Enamel line
  - Extensions
  - Nodules
- Root pattern
  - Supernumerary roots
  - "Fused" roots
  - Bent roots
  - "Taurodontism"
- Measurements
  - Crown dimensions
  - Root length
- Maxillary and mandibular hyperostoses
  - Palatine torus
  - Mandibular torus
  - Alveolar hyperostoses
- Tooth spacing
  - Diastemata
  - Trema
- Occlusion
  - Bite and jut
  - Shape of dental arches
  - Prodontism

It will be seen that some of the traits listed pertain to the jaws rather than to the teeth. The reason for their inclusion is that, like those of the teeth, these factors can readily be studied in the mouths of the living. In any case, the line of distinction is somewhat arbitrary: for example, the number, size and shape of tooth roots can be studied on empty sockets following post-mortem loss of teeth, and a gap between the upper medial incisors is equally a characteristic of the bone and of the teeth.

In classifying purely dental traits it is customary to group them according to variations in number and variations in form. However, numerous studies have shown a close relationship between reduced size and total absence of a dental element: thus, lateral incisors or third molars are more frequently peg-shaped on one side and congenitally absent on the other than would be expected if these numerical and morphological traits were independent. The distinction between variations in number and form is therefore somewhat arbitrary.

In classifying teeth it is also customary to deal with different parts of the tooth separately. This also leads to difficulties, however. Thus, if the crown is defined as extending to the enamel margin, variations in the form of the margin will tend to be related to the size of both crown and root, and there will be an inverse relationship between height of crown and root. A similar interdependence is present to the extent that supplementary roots may tend to be related to corresponding supplementary cusps.

Another way in which dental traits are classified is according to the tooth which is affected. This obviously separates observations which might better be grouped together. Anomalies tend to be related to tooth *districts* rather than to the dentition as a whole or to particular teeth, as Dahlberg (1945a) has shown in his discussion of the field concept. A characteristic of a particular tooth, for instance the shovel-shape trait in the upper left medial incisor, is likely to be duplicated in the upper right medial incisor, the upper lateral incisors, and sometimes in the lower incisors. Even classification by types of teeth is not wholly satisfactory, for one may see such intergrading as premolariform or incisiform canines. In comparative studies not even the proper homologies are always beyond dispute.

It is clear that in respect to the teeth the genetic units do not lend themselves to morphological classification in any simple way. In fact, it seems plausible that the same genes influence teeth and other structures as seems to be the case in such anomalies as cleidocranial dysostosis (Rushton, 1938) and hypertrichosis (Keeler, 1935).

Under the circumstances it would seem best to use a purely phenotypic morphological classification. One can take such a list as that set forth above, indicate briefly the possibilities of pedigree studies, note some of the difficulties in observing the characteristic both on the living and in skeletal series, and look for some of the interrelations with other traits.

The data which will be cited in connection with a few of the points just mentioned is based on the examinations of 258 adult white Americans under the age of 29 years and on 12 pairs of twins of comparable age of which at least nine pairs are homozygous. Older individuals are excluded from consideration here because of the prevalence of dental caries, loss of teeth and attrition. Most of the material I shall cite, however, is from published sources and the findings of other students.

Order and age of eruption of teeth and age of shedding of deciduous teeth

Studies of eruption can be made only on children, of course, and although twin studies are practicable (Bachrach and Young, 1927, and Ford and Mason, 1943), other pedigree studies would require a generation and have not been attempted as far as I know. In population studies the order and age of eruption has been worked out on large numbers of individuals. Hurme (1948) has reviewed the literature on more than 93,000 children of Western and Northern European racial stock; other racial groups have been studied by Bean (1914), Drennan (1932), Steggerda and Hill (1942), and Shourie (1946). Schultz (1949) has discussed the situation in other primates. In the case of skeletal material, however, the exact age is usually unknown: each individual can represent only one stage, so large numbers would be needed to show variations in pattern of eruption. Pedigree studies on other aspects of the deciduous teeth would likewise require a full generation's time to investigate and therefore, despite their interest, have not been made.

In the identical twins which I myself have examined, the status of eruption of third molars was somewhat dissimilar in several cases, which shows that longitudinal studies of this problem would be highly desirable. Only 4 of the 8 definitely monozygous pairs for whom the information was available had identical or mirror-image pattern of erupted third molars. The other four pairs were discordant at the time they were examined. Nicolas (1949) reports on an unusual occurrence in which one of a pair of monozygous twins was exchanged with another child at birth. When examined, the true twins both still lacked all first molars but the third individual already had three of them erupted. The true pair also differed from the unrelated child, but were similar to each other, in such dental traits as congenital absence of teeth and shape of the tooth crowns.

However, it is interesting to note that these monozygous twins who were reared apart showed different patterns of carious lesions.

Supernumerary and supplementary teeth

Large-scale surveys of supernumerary teeth are rare. Stafne (1932) found 500 supernumerary teeth in 441 individuals among 48,550 patients who were studied with the aid of complete dental roentgenograms. Pedersen (1949) has reviewed the literature on various racial groups. In my own studies the only indubitable cases were of an extra upper incisor in one individual and of a fourth molar in another. In several other cases the possibility of retained deciduous teeth or of extraction of teeth could not be settled. Euler and Ritter (1939–1940), in reviewing the literature, mention an instance of concordant peg tooth behind the superior medial incisors in a pair of monozygous twins, but they also refer to discordant occurrences in two other similar pairs and in three pairs of fraternal twins.

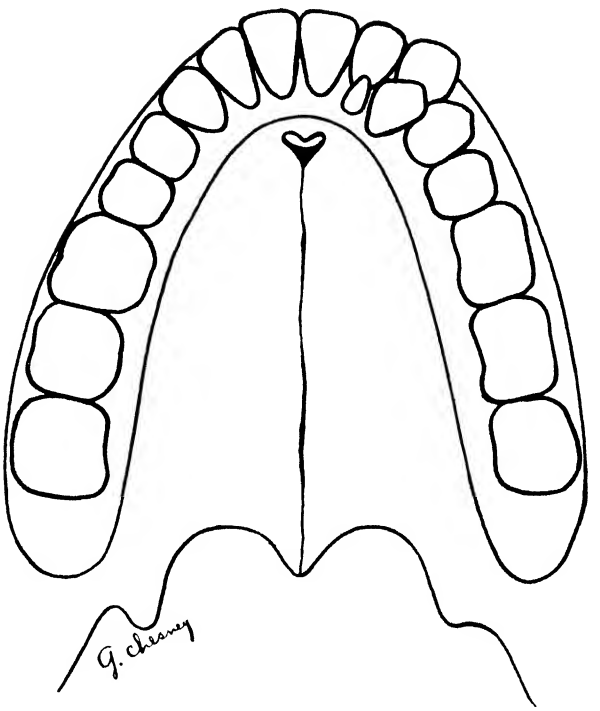

FIG. 1. Supernumerary teeth. Note supernumerary upper canine and incisor.

Congenitally missing teeth

Congenital lack of teeth is important because there is evidence that it represents a series of genetic traits (Keeler, 1935). Accurate estimates of the frequency of congenital absence, especially of third molars, requires that X-ray studies be used to distinguish congenital lack of the tooth bud from non-eruption of an impacted tooth. Impaction of third molars may, of course, also have genetic determinants although identical twins such as the pair reported by Burman (1944) may be discordant. Extraction of teeth also is a source of error which, however, is minimal in young individuals and can be further restricted in the case of living individuals by asking them about it.

Various teeth may be congenitally absent. Third molars, upper lateral incisors and second premolars are most frequently undeveloped; lower medial incisors and first premolars also are not infrequently suppressed, according to Brekhus *et al.* (1944). In my series there were two cases of absence of upper lateral incisors, one case of lack of lower medial incisors, one case of lack of lower first premolars and a case lacking

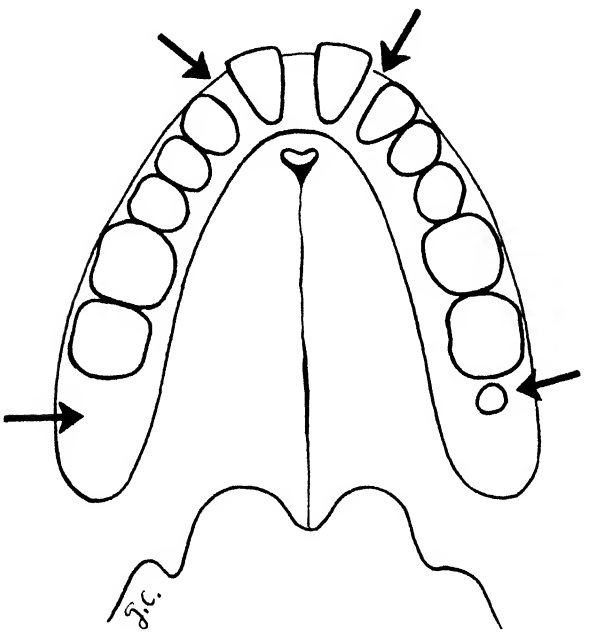

FIG. 2. Congenitally missing teeth. Note congenital absence of upper lateral incisors and one third molar, associated with a third molar on the other side which is much reduced in size.

the lower right first or second premolar. Information in some other cases, especially where back teeth were involved, is inadequate. Some differences are reported in the proportion of different teeth affected in various races (Pedersen, 1949). Nevertheless, suppression of different teeth is not independent: in a recent study by Erwin and Corkern (1949), for instance, at least four individuals in a single family show similar patterns of absence involving all third molar and second premolar teeth in all cases and, second molars, canines, incisors and upper first premolars in some instances. Dahlberg (1937) reported a pedigree in which all lateral incisors and the lower medial incisors were regularly lacking in a large number of affected individuals.

Furthermore, absence of teeth and reduced size are closely interrelated. Absence of a lateral incisor or third molar on one side is sometimes accompanied by a peg tooth on the other. In pedigrees absence and reduction may alternate in a family (Schultz, 1932 and 1934; Montagu, 1940; Mandeville, 1949). In my own series there were eight instances of reduced lateral incisors. Six of these, as well as both cases of total absence of these teeth, were in females. This sexual predominance holds for some other series (Pedersen, 1949). Pedersen noticed that in his series unilateral absence occurred only on the right side. This is also true of some pedigrees illustrated in Keeler's (1935) paper. In my series a unilateral reduced lateral incisor was on the right side in five cases, but in one case the greater reduction was on the left. In two of the cases in my series, according to report, other members of the family have the same condition.

In regard to congenital absence of upper lateral incisors there are abundant data from pedigrees which suggest simple dominant inheritance (Mandeville, 1949), although Schultz (1932 and 1934) suggests that other mechanisms may better explain some pedigrees. The one twin pair with absent superior lateral incisors which I have seen was monozygotic and concordant. Among 42 monozygous pairs studied by Goldberg (1930) one pair showed congenital lack of a lower second premolar on the same side, and one pair showed congenital lack of an upper lateral incisor on opposite sides. The monozygous pair reported by Nicolas (1949) was concordant for congenital lack of the lower central deciduous incisors and for the form of the accompanying diastemas. Euler and Ritter (1939–1940) review some twin studies dealing with congenitally missing teeth including a number of instances of discordance in monozygous pairs. They also note that among 10,000 children Bolder found 340 children with congenitally missing teeth but that only 18 of these had family histories of the condition. There are considerable differences in the frequency of the trait in various populations (Montagu, 1940; Pedersen, 1949); Jöhn (1934) reports that approximately one third of the people were affected in a Swiss community which he investigated.

In regard to congenital lack of third molar teeth, numerous studies indicate that this occurs frequently not only in Europeans, as was formerly emphasized, but perhaps especially in Mongoloids (Goldstein, 1932; Lasker, 1945; Pedersen, 1949). On the other hand, there have been few studies of the genetics of the trait. Among the monozygous twins examined by me, the upper molars had failed to erupt in two pairs and in one of these two pairs of twins the individuals reported that

roentgenograms had confirmed the concordant congenital lack of these teeth.

Number and pattern of cusps

Careful studies of primate fossils by Gregory (1922), Gregory and Hellman (1926–1927) and others indicate the importance in human evolution of the cusp pattern, especially the presence of the so-called Dryopithecus pattern, or some modification of it, in the lower molars. Despite numerous studies of the distribution in racial groups (Hellman, 1928, Goldstein, 1931, Nelson, 1937–1938, and Pedersen, 1949), the inheritance of the number and pattern of cusps has not, however, yet been systematically traced in pedigree studies.

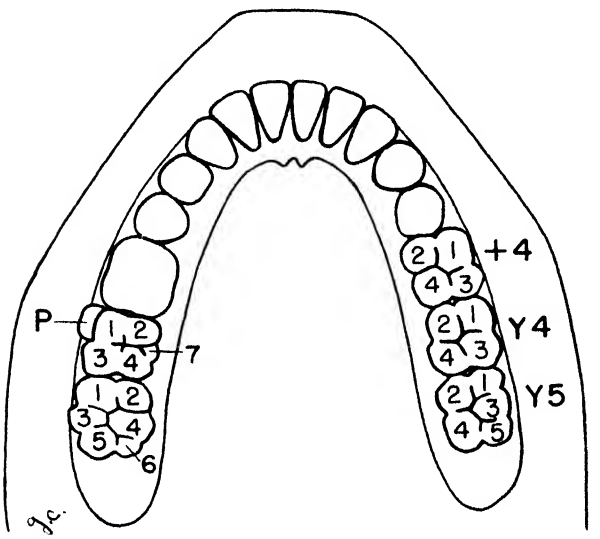

FIG. 3. Number and pattern of cusps of lower molars. Note the plus (+) pattern with no common boundary between cusps 2 and 3, and the Y pattern with cusps 2 and 3 adjacent to each other. Cusp 6 lies between cusps 4 and 5; cusp 7 lies between cusps 2 and 4; and the paramolar cusp of Bolk or protostylid (P) lies adjacent to cusp 1.

Particular supernumerary cusps in the lower molars such as the extra distal cusp—C_6, an anomalous cusp between the lingual cusps—C_7, and the paramolar tubercle of Bolk (1914 and 1916) have been traced in various racial groups and also in fossil man. Dahlberg (1945b and 1950) has collected information on the paramolar tubercle. His data on the Pima Indians, among whom the trait is common, may yield information on the genetics.

The cusp of Carabelli in the upper molars sometimes occurs in paleolithic man (Gorjanovic-Kramberger, 1907; Jeanselme, 1917). It is much more frequent in Caucasians (Dietz, 1944) than in Australians (Campbell, 1925) or American Indians (Muñoz Ribeck, 1936; Nelson, 1937–1938). The infrequency in Mongoloids has been emphasized by Pedersen (1949) who suggests that studies on crosses between Eskimos and whites would afford an excellent opportunity to determine the genetics of the trait. My own study shows an equal frequency of medium or pronounced cases in both sexes (20%) and some trace in 45 per cent of the white population studied. As Dietz (1944) also noted, most cases are bilateral. Nevertheless, in the identical twins who showed the trait there is a difference in the degree of expression. Euler and Ritter (1939–1940) give examples of concordance in monozygous twins. They state that among 126 pairs of dizygous twins, 10 pairs had Carabelli's cusps of similar form and size, four pairs were quantitatively discordant and eight pairs were fully discordant. Other evidence supporting the inheritance of the trait as dominant is said to be presented by Korkhaus (1930a), von Verschuer (1931), and Ritter (1937). Carabelli's cusp is not an altogether simple trait, for, as Gorjanovic-Kramberger (1907) and Dietz (1944) have shown, a pit sometimes occupies the same position. Similarly a buccal pit or groove in the lower molar teeth may be closely related to the paramolar tubercle.

Another feature of the crown which is observed in occasional molar teeth is an appearance of wrinkles on the occlusal surface (Weidenreich, 1937). It remains questionable whether this is a discreet genetic trait. In any case, the condition would be difficult to study as the fine crenelations are rapidly worn off after the teeth have erupted. As a matter of fact, moderate wear may interfere with observations on small cusplets, and more pronounced attrition makes impossible the determination of the crown pattern or even the number of cusps. As fine detail is best exemplified in newly erupted teeth, the most satisfactory pedigree studies of crown patterns would have to be extended over at least a full generation.

Shovel-shaped teeth, dental tubercles, and lingual ridges

In the anterior teeth one of the most conspicuous points of variability in man is in the extent of vertical ridges on the lingual surface. When these occur at the mesial and distal margins of an incisor they give the tooth the appearance of a shovel. Hrdlička (1920 and 1921) noted the high frequency of teeth of this type in members

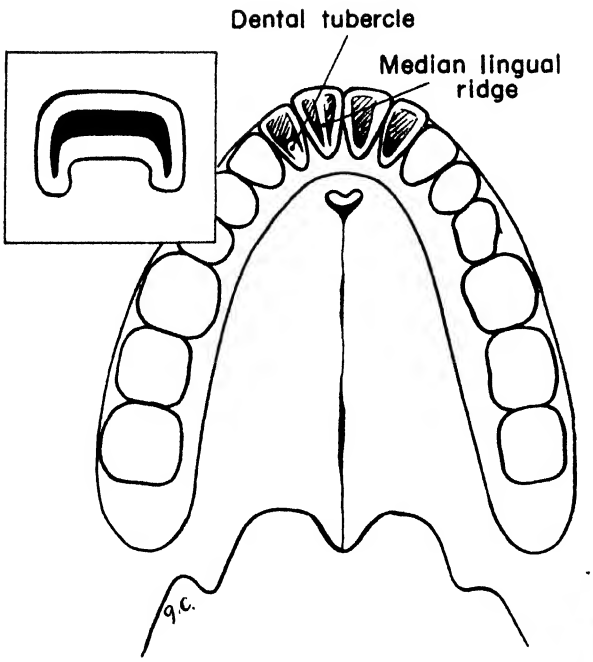

FIG. 4. Shovel-shaped teeth, dental tubercle, and lingual ridge. Note in inset a cross-section or worn occlusal surface of a shovel-shaped tooth of the type shown in the upper left incisors.

of the Mongoloid race, and this has been confirmed by numerous authors (see, for instance, Nelson, 1937-1938, Lasker, 1945, Pedersen, 1949). Similar teeth also occur in occasional whites (de Jonge-Cohen, 1926). The present author found that in both sexes the incidence is 14 per cent among white Americans. Half the population shows some tendency to manifest mesial and distal ridges, however. In this group the trait was usually equally evident in lateral and medial upper incisors, but if it was more pronounced in one than the other, it was more frequently the lateral incisors in which the trait predominated. Despite the occurrence of this trait in fossil man (Weidenreich, 1937), and its variation in the races of modern man, pedigree studies have apparently not yet been undertaken. All the monozygous twin pairs which I saw were concordant in respect to this trait; the degree of expression also tended to be similar.

The dental tubercle, it is said, has nothing to do with the shovel-shape form of incisors, but, in the case of the latter, confluence of the marginal ridges makes difficult the detection of a small tubercle. Despite interest in the tubercle as a possibly primitive characteristic, few except Pedersen (1949) have given figures on the frequency in a population. I know of no pedigree studies.

Median ridges may also interfere with the measurement of the degree of concavity in shovel-shaped teeth. Such ridges themselves have been little studied in human populations.

Enamel margin, extensions and nodules

Pedersen and Thyssen (according to Pedersen, 1949) have classified the types of enamel margins and studied them in various groups of man and in the anthropoids. The enamel margin sometimes extends towards or between the bifurcation of the roots. Enamel nodules or pearls between the roots of molars are reported to occur frequently in the same populations as enamel extensions and are, no doubt, related. Despite Pedersen's (1949) interesting observation that these characteristics are common in Eskimos and rare in whites, comparative studies of the enamel margin

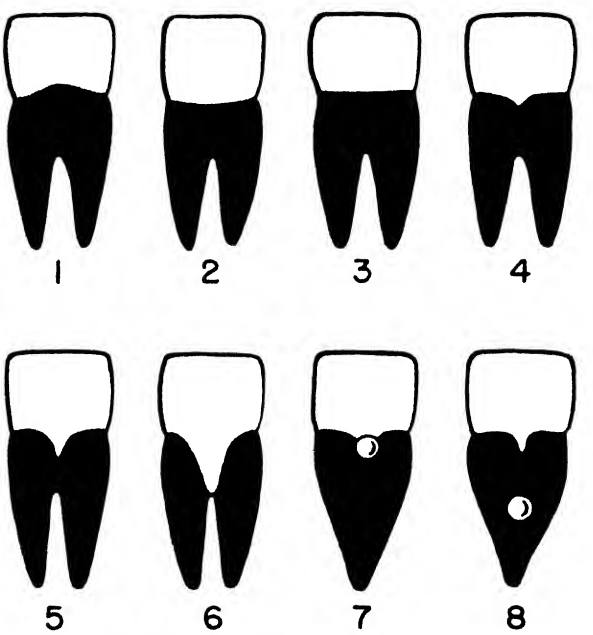

FIG. 5. Enamel margin, extensions and nodules.
1. Margin convex toward occlusal surface.
2. Margin concave toward occlusal surface.
3. Margin straight.
4. Enamel extension toward root bifurcation not exceeding 1.5 mm.
5. Enamel extension over 1.5 mm. but not between the roots.
6. Enamel extension continues between the roots.
7. Enamel nodule or pearl associated with extension. Roots fused.
8. Enamel nodule or pearl separate from extension. Roots fused.

are difficult as they cannot be done on the living. Furthermore, a root bifurcation or groove is a necessary condition for such extensions, so the trait is not independent. As far as I know, pedigree studies have not been made, although some types of defective enamel have been shown to be inherited as a Mendelian dominant (Keeler, 1935).

Supernumerary roots, fused roots, and root form

X-ray studies of tooth roots, although practicable on the living are not completely accurate. Pedersen (1949) points out that roots may be superimposed in the exposure, and that thick bone, as in the mandibular torus, may lead to difficulties of interpretation. In the upper molars supernumerary roots occur under the anterior buccal cusp, and in the lower jaw they may be associated with the paramolar tubercle according to Bolk (1916) although he adds that one may often have the root without the cusp. Pedersen (1949), however, says that in the lower molars an extra root is more frequently disto-lingual. Tratman (1938) has shown that, among 3,083 people studied at Singapore, three-rooted lower deciduous and permanent molars are rare in Europeans, East Indians and offspring of unions between them, but common in such Mongoloids as Malays and Chinese. Frequent occurrence among the offspring of European-Mongoloid unions suggests to him a dominant mode of inheritance. Gabriel (1948) describes a postero-lingual third root appearing concordantly in both lower first molars in a pair of monozygous twins. Goldberg (1930) mentions a similar pair in which there was concordant unilateral occurrence of double-rooted upper premolars. I do not know of any pedigree studies, however.

Pulp cavity

In studies of human phylogeny a great deal of emphasis has been placed on the form and size of the pulp cavity. A "taurodont" pulp chamber is especially marked in some Neanderthal teeth, especially in some of the Krapina specimens (Gorjanovic-Kramberger, 1907; Keith, 1913). Weidenreich (1937) indicates that in *Sinanthropus* taurodontism is less marked. At least moderate taurodontism occurs in various modern groups (Shaw, 1928; Pedersen, 1949; Senyürek, 1949), but the size of the pulp cavity changes after eruption, and it is therefore difficult to make direct comparisons. Furthermore, the taurodont trait is closely related to root fusion. Pedigree studies with X-rays might be feasible but have not been undertaken to my knowledge.

Measurements

Numerous measurements of the teeth have been suggested, but most investigators use the measurements suggested by Martin (1928) as an indication of size. Measurements frequently taken are maximum mesio-distal length, breadth, and crown height. Various indices have also been devised to show the relationship of one dimension to another or the size of one tooth to that of another. Measurement of crown height and tooth length are subject to error caused by occlusal and interproximal attrition respectively. Root height is much subject to modification because of absorption. Dental measurements are difficult on the living, and the use of casts introduces another source of error, although modern casting methods make possible adequate accuracy for most purposes. The numerous studies of tooth size in fossil man and in various racial groups are of considerable interest. Pedigree studies of dental measurements would be practicable and highly desirable. Such traits as reduced tooth size, the inheritance of which has so far been studied only by crude examination, could be better studied by anthropometric methods.

Torus palatinus

Torus palatinus, a bony ridge in the midline of the hard palate, may vary in form, location, and size. Studies on both skulls and living individuals show a high frequency in Ainus, Eskimos, Icelanders, Lapps, and other northern European and northern Asiatic peoples (for example see Waldeyer, 1892, Godlee, 1909, and Hooton, 1918). The evolutionary significance is not clear: few examples exist in early forms of fossil man; among other primates a torus is sometimes found in the Old World monkeys (I have seen a large one in a mandrill); it is very rare in great apes (Woo, 1950).

Although various other explanations of the etiology have been advanced, inheritance seems to play a major role. In 13 pairs of monozygous twins, I (Lasker, 1947) found only one instance of a discordant pair. Pedigrees reported by Godlee (1909), Körner (1910, who also mentions the observations of Carabelli, 1842), Greifenstein and Dieminger (1938), and five families investigated by the present author would seem to suggest an autosomal dominant inheritance in some instances. Not all cases can be explained so simply, however: there are some cases of generation skipping and the greater frequency in females would also be unexplained unless one were dealing with sex-linked dominant inheritance.

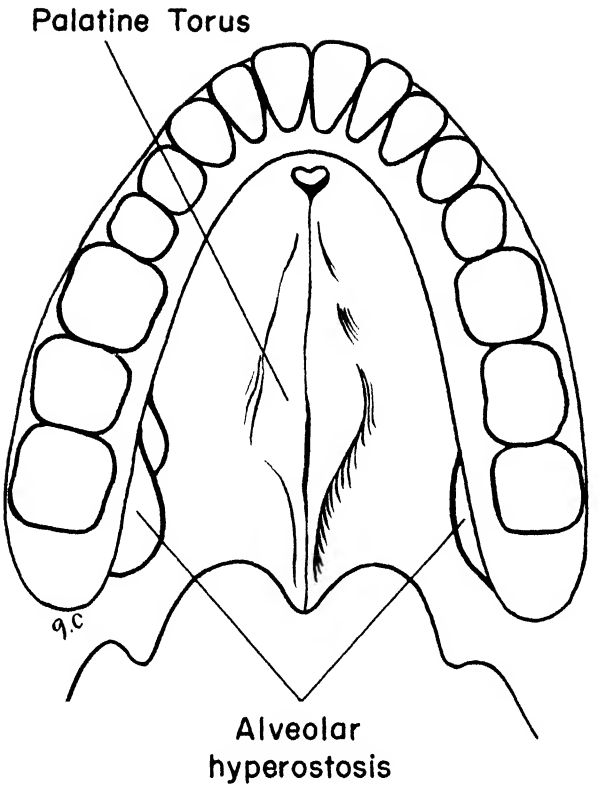

FIG. 6. Palatine torus and alveolar hyperostosis. Note that in this instance the hyperostoses are of the lingual aspect of the posterior part of the maxillary alveolar processes.

Torus mandibularis

Torus mandibularis, a bony prominence on the lingual aspect of the mandible, usually opposite the premolar teeth, has been well described by Hrdlička (1940) among others. He points out that many previous authors have suggested an association between torus mandibularis and torus palatinus. In my series there seems to be little relationship between the two traits. There is no statistically significant association among the males. For the females there is a significant association but of such a low order that it may not represent a common factor of any consequence. Nevertheless, it should be noted that the association is most definite for very large tori and that the two traits are encountered most frequently in the same racial groups. Among 83 male American negroes, 257 male and 154 female Mexicans, and an additional series of 59 white males all examined by the author, no statistically significant associations of the occurrence of mandibular and palatine tori were found. Among American whites and negroes, Woo (1950) found a tendency for the two traits to be associated, but the association was not statistically significant. The evolutionary significance of the mandibular torus was emphasized by Weidenreich (1936) who noted the occurrence of this trait in *Sinanthropus* mandibles. He thought the torus to be characteristic of Mongoloids, but it is also common in Icelanders and Lapps. The genetics have so far not been well worked out. My own findings (Lasker, 1947) suggest a high penetrance because of the tendency toward bilateral symmetry in individuals. The cases of unilateral dominance were shown to predominate more frequently on the right side; this remains unexplained and is similar to the situation reported for unilateral occurrence of reduced lateral incisors.

Alveolar hyperostoses

Bony posterior alveolar hyperostoses have been reported buccally and lingually especially on the maxilla. Knap (1932) says that their occurrence correlates to some extent with that of torus palatinus and that of torus mandibularis. In my series mandibular and maxillary buccal hyperostoses are significantly associated with each other in both sexes. Neither of these traits is significantly associated with either torus palatinus or torus mandibularis in the males, but in the females maxillary hyperostoses are associated significantly with both, and mandibular hyperostoses are significantly associated with mandibular tori. The figures for the χ^2 tests for these associations, however, although they are significant are of an order which indicates that the

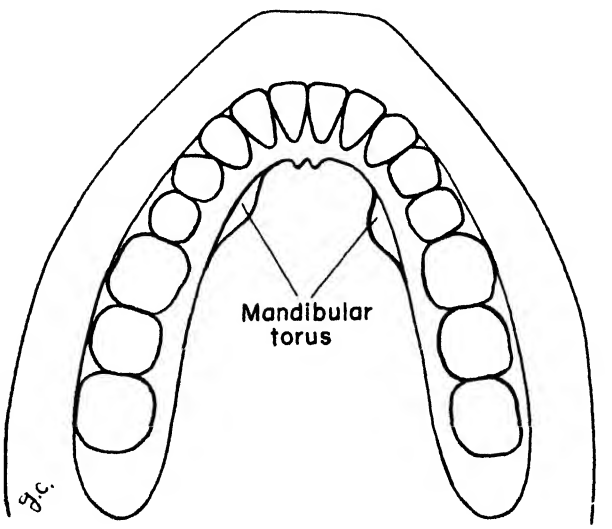

FIG. 7. Mandibular torus.

common factors are unimportant and may merely represent observational inaccuracies or undiscounted age and race differences rather than important common factors in the etiology. Woo (1950) also reports a tendency for torus palatinus and maxillary hyperostoses to be associated. It is not known whether maxillary alveolar hyperostoses have any evolutionary significance. They quite probably have an unequal racial distribution, but pedigree studies seem not to have been undertaken. No cases occur in the monozygous twins which I have studied. Unilateral occurrences are frequent enough to suggest that the genetics of the trait will be difficult to trace.

Diastemata and trema

The diastema is a characteristic of considerable interest in the study of human phylogeny. It is very doubtful, however, whether gaps between teeth which are occasionally found in the human adult are related to the diastemata of the other catarrhines. A number of pedigrees of a space between the upper medial incisors (gat tooth or trema) have been published (see Gates, 1946). The mode of inheritance appears to be dominant. Korkhaus (1930b) reports concordance in four pairs of monozygous twins. The racial occurrence of the trema has not been studied nor does the trait occur in fossil man although the premaxillary diastema is well marked in *Pithecanthropus* IV.

Anteversion of the teeth

Prodontism of the upper incisors, which was popularized as a characteristic trait of the Japanese by American war-time cartoonists, is closely related on the one hand to prognathism and on the other to the form of the occlusion. There are clearly racial differences; but other than the study of Oshima (1937), who gives a mean angle of 81.1° of the medial incisors with the eye-ear plane for adult Chinese, I do not know of any published data.

Malocclusion, crowding and shape of the dental arches

All students of the subject are agreed that crowding and malocclusion are complex traits. There is some disagreement, however, as to the extent to which these characteristics, which are so prominent in modern man, are constitutional. Despite the possible role of nutritional (Price, 1939) and other factors, there would seem to be a considerable genetic influence. Similar patterns of occlusion have frequently been reported in monozygous twins (Bachrach and Young, 1927, Goldberg, 1930, Macklin and Moore, 1936, Braun, 1938, Ford and Mason, 1943, and Lasker and Reynolds, 1948). In one study of triplets (Cohen, Oliver and Bernick, 1942), however, measurements of the dental arches are shown to vary as much in the identical pairs as in some fraternal sets or even as much as in some pairs of unrelated children. It has been suggested (Davenport, 1917) that malocclusions manifesting large teeth and small jaws are caused by disharmonious race crossing, but if that were true one would expect the resegregation also of small teeth in large jaws. Furthermore, empirical studies of race crossing have so far failed to establish a significantly higher frequency of disharmonious types such as would be expected according to the hypothesis.

Discussion

This review has probably suggested to you that, despite the promise of significant findings in respect to a considerable number of characteristics, few attempts have so far been made to study the genetics of dental traits. There are many examples of observations on familial occurrences of dental anomalies besides the examples so far cited. Nevertheless, I think that it is fair to say that genetic studies of the teeth have not kept abreast of racial studies of the teeth. So far there are no published accounts of systematic familial investigations yielding data comparable to those collected from out-of-the-way peoples such as Eskimos and Australian aborigines. The unequal racial distribution of a number of traits suggests that pedigree studies would be very revealing. Today it should be possible to execute genetic studies of virtually all these characteristics. Although such investigations might be launched within a relatively short period of time, it would be a full generation before age-constant data would be available for analysis of the inheritance of such traits as eruption time of teeth, fine details and measurements of the tooth crown, palatine and mandibular tori, form of the occlusion, etc. Nevertheless, in the meanwhile, observations on traits which are less influenced by age, such as number and pattern of cusps and shovel-shaped incisors, could be utilized for genetic analysis. Twin studies on the whole array of traits are immediately possible. The study of only a few of the characteristics I have named, such as variations in the dental roots and pulp cavities, present special difficulties in living populations. Roentgenograms, which are necessary for studies of supernumerary and congenit-

ally missing teeth, would permit at least a preliminary approach to some of these other problems as well.

We have seen that there are a large number of dental traits in which genetic factors are important and in which evolutionary significance is manifest. However, the question arises whether a particular trait occurring in two races of man or in two species of primates is actually homologous. From the point of view of anthropology one might be satisfied with a definition of "homology" which would give the term to similar structures in different forms if the structures had the same generic origin. In the process of natural selection it is, of course, primarily the individual and his phenotype on which selective forces play. Would it not therefore be possible for a species to survive which had a certain advantageous trait phenotypically even though the genetic mechanism for the trait were altered? For example, different families in which there are dental reductions may show different patterns: some members of one family will show peg-shaped lateral incisors; in another family line these teeth will be absent; in a third, all the lower incisors will also be suppressed; and in a fourth, half of the teeth will be congenitally absent. The genes responsible in these four instances are apparently different despite the fact that the anomalies tend to grade into each other. In the case of identical phenotypes it is also conceivable that more than one genetic mechanism is responsible, although this is sometimes difficult to prove in man where genetic experimentation is not possible. If such a situation were to hold for a selectively advantageous trait, especially if the fullest expression were to depend on reenforcement by several genes, it is conceivable that, in the process of evolution, some new genes would substitute for others of similar effect until an essentially like phenotype with historical continuity would have a new genotype. In that case one might consider the structures in the earlier and later forms to be phenotypically homologous but genetypically disparate. In spite of this, such a trait would, of course, have none the less significance for evolutionary studies. For this reason it would seem to me that studies on the exact mode of inheritance and, eventually, location of human genes in linkage studies, will have less direct relevance to fossil man and to other fossil primates, although the very mode of inheritance may be a character of great importance in assessing the interrelationship of populations of modern man and in describing the on-going evolution of the race.

When it comes to the assessment of the value of particular traits for the study of human origins, however, the degree to which genetic factors control their development will be a more important consideration. From this point of view studies of bilaterality and of concordance in twins are of great value. Pedigree studies and studies of the effects of non-genetic factors also contribute to the assessment of the importance of the genetic factors in the development. In such studies the teeth are an ideal material. Not only are they paired structures with, so-to-speak, a co-twin control for each tooth, but fields of increasing susceptibility to genetic influence apparently spread out from key stable teeth as Dahlberg (1945a) has shown.

The time is ripe for a really significant interdisciplinary project on the inheritance of human dental characteristics. There are already sufficient data to indicate that, with the skills now available, geneticists, anthropologists and odontologists can, by relating their studies to a major object of scientific inquiry, jointly bring order into a whole field of knowledge where, until now, we have had only a somewhat bewildering chance collection of small specialized studies.

The teeth are a material rich in the paleontological record, accessible in the living and variable in respect to a large number of genetic traits. Pioneer studies, some of which I have cited, suggest the value of genetic analysis of racial traits of the teeth for the interpretation of human evolution.

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DISCUSSION

GARN: To the other probably hereditary and non-pathological dental characteristics enumerated by Dr. Lasker in his comprehensive paper, one should perhaps add the rare but desirable trait of being caries-free. Obviously the inheritance of this trait can be studied in a carious population, like our own, rather than in a caries-free isolate. So far I have collected a number of pedigrees of individuals caries-free at college age, and have noted that one parent was also caries-resistant in several cases (including my own). In the "caries-free" children under study at the medical-nutrition clinic of Forsyth Dental Infirmary in the last year, there was a predominance of males, despite a predominance of females in the admissions as a whole. This fits well with the evidence that the caries rate is higher in the growing female, and adds the suggestion that the caries-free (or caries-resistant) trait is one with a disproportionate sex ratio. I do not mean to suggest that other factors in the etiology of caries are not important, but rather that some individuals are congenitally resistant to caries, and that this trait may be hereditary, and definitely worth watching in the hope that associated salivary or other factors can be identified.

LASKER: As was mentioned in connection with another matter earlier, one should perhaps deal with those traits which are to a considerable

extent subject to environmental influences separately from those in which hereditary factors are predominant. It is true that I have mentioned such traits as form of occlusion in which environmental factors appear to be significant, but that I excluded a discussion of dental caries. Dental caries is certainly determined by several different factors, some important ones of which are environmental. The influence of fluorine in the drinking water, the diet, the form of the teeth and the chemistry of the saliva are all involved. In such a situation we cannot yet indentify the genetic elements in the observed differences.

OLIVER: It might be well to refer to some work we have done on the genetics of congenitally absent teeth. This work was begun in Minnesota, using patients of the Dental Clinic. All cases had complete oral radiographs; dental casts were made; and oral examinations made. Some publications of the data have been made but we are now working on the genetic data.

Considering now just the upper lateral incisor teeth, approximately 70 per cent of the probands had identical bilateral expression. That is, both sides showed peg-shaped teeth or both teeth were absent. The other cases had only one side affected or had the two sides affected differently.

Parents who have the congenital absence of both teeth tend to produce affected children with that same severe manifestation, but they also have children with the less severe type of defect. Moreover, a parent who has a less severe anomaly of the upper lateral incisors will produce affected children some of whom have the severest defect. Normal parents have children with the defect.

The method of inheritance is not clear with the present analysis. I believe that I am going to describe the trait as due to a dominant gene with reduced penetrance as well as expressivity. Of course it is possible that the reduced penetrance is actually a smaller tooth but the dentist is unable to describe it as not-normal in size. Reduced penetrance seems the logical conclusion to make because of the incidence of the trait among relatives of the probands. Evidence clearly indicates that a sex-influenced inheritance will not explain the observations.

Second prepolars were also studied but the data are not analyzed to the point that I can say much about them. Third molars were ignored, in selecting probands for the study.

LASKER: The previously published accounts by Dr. Oliver and his colleagues are based on a large volume of material. It is therefore of considerable interest that his findings on the inheritance of absent or reduced upper lateral incisors tend to confirm the impression that this condition is inherited as a simple dominant. The fact that this trait is relatively common makes its study particularly desirable from the anthropological point of view. One looks forward to the publication of Dr. Oliver's study and hopes that parallel investigations will soon be undertaken on other populations.

GENETIC ANALYSIS OF RACIAL TRAITS (II)

CONCLUDING REMARKS OF THE CHAIRMAN

SHELDON C. REED

Dight Institute for Human Genetics, University of Minnesota, Minneapolis, Minnesota

At yesterday's meetings we were given a glance at the rather new, and certainly most stimulating, field of medical genetics. I am not sure that the anthropologists recognized many signs of their paternity in yesterday's productions. However, I hope that they were impressed by the great need for more knowledge in medical genetics, for example in regard to mutation rates. Obviously these should be of considerable interest to students of the evolution of man.

Today the speakers combine the disciplines of anthropology and genetics in their training as well as in their papers. To them the hybridization of the two subjects is an accomplished fact. One can predict that they will profit greatly from their ability to cope with both fields.

Laughlin's paper is a convincing example of the usefulness of such simple genetic tools as the blood groups and concepts of population size as developed by Sewall Wright in an understanding of small isolates as racial components.

Spuhler has made a fine contribution to the genetics of normal morphological variations. Because they are variations with little, if any, adaptive value, they are precisely the kind which we need to have in hand by the score. The marker genes of peas, corn and Drosophila were indispensable to the development of the science of genetics. It will be a long time before the "normal" characters of man which we know now are allocated to their proper linkage groups. However, they serve multiple purposes in the meantime. An additional ten or fifteen more genetically well understood normal characters would solve many problems including that of establishing positive paternity, to mention only one item.

I do *not* think it would be meaningful to compare the biting capacity of Gabriel Lasker with that of the much discussed twelve-year-old Eskimo girl or the Minnesota football team. But, as Lasker points out, the teeth are excellent material if comparisons are to be made between fossil and living men and women.

The material covered today was concerned with some genetic characters of Eskimos, American Indians, Caucasian Americans and others. The significance lies not in the details of the work but in that here we have pilot studies in anthropology which have obviously been enriched by the application of concepts and techniques of genetics. This is most certainly just the beginning of a new kind of race biology which will be fun for all concerned.

GENETIC ANALYSIS OF RACIAL TRAITS (III)

THE EIGHT BLOOD GROUP SYSTEMS AND THEIR INHERITANCE

R. R. RACE

Medical Research Council Blood Group Research Unit, Lister Institute, London

I am afraid too much honor has been done me by the invitation to speak at this symposium. I am but a technician, not a philosopher. Very conscious of this I propose merely to present to you facts that may recur to your minds and perhaps be useful in some of your wider deliberations.

A blood group is the outward sign of an antigen situated on a red cell. In recent years the blood group antigens A and B have been separated, purified and analysed. They are lipo-carbohydrate in nature but no chemical nor physical difference has yet been found between the two substances A and B. The presence of a blood group antigen in a sample of red cells is deduced from the behavior of the cells when they are mixed with a serum containing the antibody for that antigen. Little is yet known of the chemical nature of the blood group antibodies except that they are protein and that the fraction of serum protein in which some of them are to be found has been identified. On the other hand a very great deal is known of the immunological specificities of these antibodies. So the determination of blood groups remains for the present a purely immunological problem.

The Inheritance of Blood Groups in General

Landsteiner discovered the ABO blood groups in 1900, but it was a surprisingly long time before they were recognized as inherited characters.

In 1909 Bateson's *Mendel's Principles of Heredity* was published; in it the chapter on "Evidence as to Mendelian inheritance in man" begins with the words "Of Mendelian inheritance of *normal* characters in man there is as yet but little evidence." *Normal* is in italics for there was at that time plenty of evidence of the Mendelian inheritance of abnormal human characters, the first example having been demonstrated by Farabee in 1905, only five years after the discovery of Mendel's writings. Farabee showed that brachydactyly, which he investigated in a large Pennsylvanian family, was inherited as a dominant Mendelian character.

In 1908, however, a paper by Epstein and Ottenberg in the Proceedings of the New York Pathological Society had contained this most pregnant paragraph:

"The coincidence of a brother and a sister, whose bloods were examined, belonging to the same agglutination group, led the authors to enquire whether this blood characteristic, which from the work of Hektoen and Gay seems to be a permanent characteristic of the individual, is hereditary. Hektoen tested a family, and found that the mother and three of the children belonged to group 1, and the remaining child to group 2. The authors tested two families. In the one the mother and seven children were all found to belong to group 2; the father could not be examined. In another family, mother, father, and four children all belonged to group 3. It seemed probably a coincidence that the father and mother were of the same group, but possibly a matter of heredity that the children were.

"Before any definite conclusions can be reached on this point a great deal of careful work must be done, and the authors hope to present further studies later on. It seems, however, from the sharply opposed nature of these blood characteristics that if they are inherited at all they will form a very good example of the Mendelian law of heredity."

And this indeed they did, as von Dungern and Hirszfeld (1910) and Bernstein (1924 and 1925) showed a few years later. The blood groups perhaps provide the best example of all of the basic uncomplicated type of inheritance that Mendel discovered. If the gene is present then the blood group is present. Blood group genes are unusually free from the influence of other genes in the body, and free from the influence of sex, of age, of health and of climate.

During the 50 years following Landsteiner's discovery seven more blood group systems have been discovered, all of them inherited in a Mendelian manner. The eight blood groups, which are listed in Table 1 together with the ability to taste phenyl thio-carbamide, are the only human

TABLE 1. NINE FIXED POINTS ON THE HUMAN CHROMOSOMES

1. ABO blood groups	1900
$A_1 A_2$ subdivisions	1911
2. MN blood groups	1927
MNS subdivisions	1947
3. P blood groups	1927
4. Ability to taste phenyl thio-carbamide	1931
5. Secretion of the ABO antigens in saliva	1932
Lewis blood groups closely associated	1946
6. Rh blood groups	1940
Many subsequent subdivisions	
7. Lutheran blood groups	1945
8. Kell blood groups	1946
9. Duffy blood groups	1950

physiological characters (apart from sex) of which the manner of inheritance is known with certainty.

We do not know all about the inheritance of the blood groups, there are some gaps obvious and doubtless many more unsuspected, but what we do know we know with certainty. This confidence, hardly to be found in biological work outside genetics, is inspired by the happy way in which the work lends itself to statistical treatment. When we can say—if this is the manner of inheritance then from such and such a mating so many of the children should be + and so many −, and we find such agreement as that shown in Table 2, it seems right to be confident of the theory.

The theory on which the expectations in this example are based is that the Rh antigens E and e are Mendelian characters controlled by allelomorphic genes *E* and *e*, each gene capable of expressing itself in single as well as double dose.

If we did not know that these antigens were intimately associated with two other such pairs

TABLE 2. THE INHERITANCE OF THE ANTIGENS E AND e IN 209 FAMILES TESTED WITH ANTI-E AND ANTI-e (FROM RACE & SANGER, 1950)

Matings		Children						
			EE		Ee		ee	
Type	No.	No.	obs.	exp.	obs.	exp.	obs.	exp.
EE × EE	0	0	0	0.0	0	0.0	0	0.0
EE × Ee	7	15	8	7.5	7	7.5	0	0.0
EE × ee	7	15	0	0.0	15	15.0	0	0.0
Ee × Ee	14	33	8	8.25	16	16.5	9	8.25
Ee × ee	80	183	0	0.0	96	91.5	87	91.5
ee × ee	101	246	0	0.0	1	0.0	245	246.0
Total	209	492						

it would only be a gap in our knowledge, it would not invalidate what had been won.

The recognition of the manner of inheritance of a blood group seems to proceed by steps (Table 3). First, owing to the discovery of an antiserum, say anti-X, an antigen X is recognized. The antigen X is shown to be a dominant Mendelian character and the gene frequency of X is established, together with that of the theoretical recessive and purely negative allelomorph x. The blood groups Lutheran and Duffy may be said to be in this stage at present.

The second step is the recognition that there is a little more X antigen in blood homozygous for the gene than in heterozygous blood, and so the

TABLE 3. STAGES IN GENETIC KNOWLEDGE OF A BLOOD GROUP

	XX	Xx	xx
1. anti-X	+	+	—
2. "	+++	++	—
3. anti-x	—	+	+
4. "	—	++	+++

character no longer quite fits the definition of dominance which demands that the character should be as fully expressed when the gene is in the heterozygous state as it is when the gene is in the homozygous state.

Then, the third step, the antibody anti-x is found, and the antigen and gene x become positively detectable and it is realized that had anti-x been found first the antigen X would have been called a recessive character and x a dominant character—at any rate until the dosage effect of anti-x had been recognized, which is the fourth step.

At this stage the use of the word dominant is usually given up—somewhat reluctantly for there is, as far as I know, no single word to replace it, and instead of the two words dominant character a phrase such as "a character depending on a gene capable of expressing itself in single or double dose" has to be used.

The Kell groups are at this stage at present.

The last stage so far recognized is that reached by the Rh genes and by the MNS genes and perhaps by the Lewis and secretion genes (Fig. 1.). At this level it is realized that other detectable allelomorphic characters Y and y are closely associated with X and x, and the problem arises whether the two allelomorphic sites are in one gene, at subloci in other words, or whether they are tightly linked adjacent, but theoretically separable, genes. The two possibilities are

illustrated in Figure 1. The distinction is highly academic and interesting but it makes no practical difference which of the two more nearly approaches the truth.

There is one blood group which is original in its way of inheritance. When Dr. Mourant published his first note on the discovery of the Lewis blood groups he had tested both parents of seven Lewis positive persons and one or other parent was also Lewis positive in all seven families. Mourant said "This is conclusive evidence that the agglutinogen is inherited, and suggestive, but not statistically significant evidence that it is a Mendelian dominant character rather than a recessive." Considering that all other known blood group genes express themselves in single dose this restraint was most praiseworthy and justified when, two years later, the Lewis antigen was shown to be a recessive Mendelian character. The reason why it was not immediately obvious as a recessive is that a recessive character with a high rate of incidence will frequently occur in two generations and so, at first, may appear to be dominant.

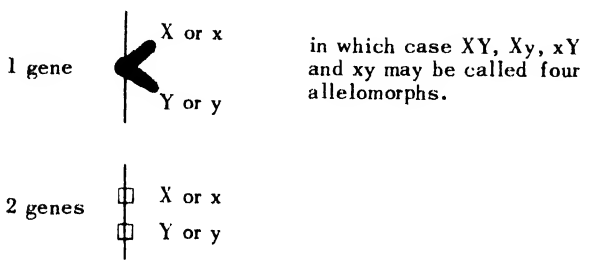


FIG. 1. The Two Possibilities

THE INHERITANCE OF THE INDIVIDUAL BLOOD GROUPS

I propose now to take you on a brief introductory tour round the blood groups. To many of you I will merely be introducing old and familiar friends and to some of you I will be introducing your children, but I hope you will forgive this.

I realize that little can be remembered from the flicker of a slide but hope that the European blood group frequencies which I will show you now briefly, may, when published in the volume of this Symposium, be of some use to you.

The A_1A_2BO groups: the Landsteiner groups

The manner of inheritance of these groups was finally solved by the mathematician Bernstein in 1924. The gene can exist in any one of four allelomorphic forms: A_1, A_2, B or O. The genes combine to make the ten genotypes and six phenotypes shown in Table 4. There are only six phenotypes because we cannot distinguish serologically between certain of the genotypes. Sometimes the groups of other members of the family disclose the exact genotype of a sample. A family tested in my Unit serves as an example (Fig. 2.). The father and the girl twin are of the phenotype A_1 and their genotypes would not be known but for the evidence provided by the genotypes of the mother and boy

TABLE 4. THE A_1A_2BO GROUPS AS DEFINED BY ANTI-A, ANTI-B AND α_1: SOUTH ENGLAND FREQUENCIES

(from Ikin *et al.*, 1939)

Genotypes	anti- A	anti- B	anti- α_1	Phenotypes	
A_1A_1 A_1A_2 A_1O	+	−	+	A_1	34.81%
A_2A_2 A_2O	+	−	−	A_2	9.89%
BB BO	−	+	−	B	8.59%
A_1B	+	+	+	A_1B	2.62%
A_2B	+	+	−	A_2B	0.64%
OO	−	−	−	O	43.45%

Genes	
A_1	0.2090
A_2	0.0696
B	0.0612
O	0.6602

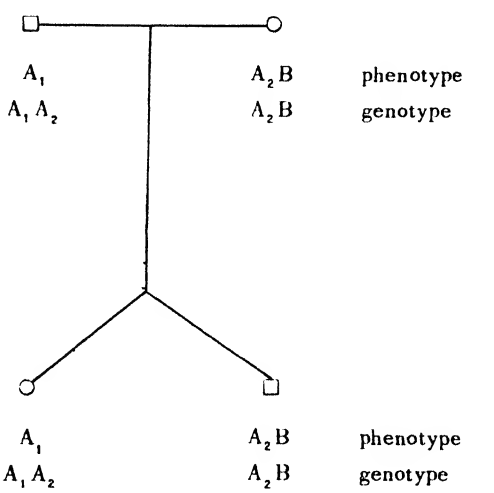


FIG. 2. The inheritance of the A_1A_2BO groups showing how genotypes may be disclosed by phenotypes of relatives.

twin. The boy has received *B* from his mother and A_2 from his father, whose genotype must therefore be $A_1 A_2$. The girl of the phenotype A_1, has no *B* so must have received A_2 from the mother. The genotype of the girl twin is consequently $A_1 A_2$.

It was during the 1914 war that Hirszfeld and Hirszfeld (1919) made the far reaching discovery that different peoples had different ABO distributions. Because of this great addition to the interest of blood groups the results have since been published of hundreds of thousands of tests performed all over the world. The vast material thus provided for ethnological speculation was brought together into one publication by Boyd in 1939.

The MNS groups

The MN system of blood groups was discovered by Landsteiner and Levine in 1927 (1927a and b, 1928). The antibodies anti-M and anti-N seldom occur in human serum; they are made by immunizing rabbits with appropriate human red cells. Anti-S, the antibody that subdivides these groups was discovered in 1947 (Walsh and Montgomery, 1947; Sanger and Race, 1947; Sanger, Race, Walsh and Montgomery, 1948). Anti-S does occur in human serum as a rarity, only about eight examples have so far been found, and immunization of rabbits has not yet been successful in producing it.

TABLE 5. THE MNS GROUPS IN ENGLAND AS DEFINED BY ANTI-M, ANTI-N AND ANTI-S

(based on 1,419 tests)

Genotypes	anti- M	N	S	Phenotypes	
MS MS *MS Ms*	+	−	+	M. S	20.79%
Ms Ms	+	−	−	Ms Ms	7.54%
MS NS *MS Ns* *Ms NS*	+	+	+	MN. S	26.71%
Ms Ns	+	+	−	Ms Ns	22.69%
NS NS *NS Ns*	−	+	+	N. S	7.19%
Ns Ns	−	+	−	Ns Ns	15.08%

Genes	
MS	0.2472
Ms	0.2831
NS	0.0802
Ns	0.3895

In the English there are four different chromosomes MS, Ms, NS and Ns (Table 5). Small s represents the absence of S. An antiserum anti-s has not yet been found but is expected and is being looked for. When anti-s is found the system will be very like Rh and it will be a matter of academic argument whether to place the loci for the two pairs of allelomorphs within the boundaries of one gene or whether to consider them as separate but very closely linked genes. Again the decision will make little practical difference.

The frequencies in England of the genes, genotypes and phenotypes are shown in the table. It will be seen what a useful division the anti-S serum makes within the three groups, M, MN and N previously thought to be homogeneous.

Two pedigrees illustrating the inheritance of these groups are shown in Figure 3. Black represents the S antigen. In the first family the S is attached to the father's M and is segregating with it. In the second family the S is attached to the mother's N and is segregating with it.

The distribution of the MN groups throughout the world shows less variability than the ABO distribution. A notable difference was however found by Birdsell (see Boyd, 1939) in the Australian aborigines, the frequency of the *M* gene being very low in these people. The use of the anti-S serum will probably add considerably to the ethnological value of this system, as the following promising example shows. My colleague Dr. Sanger tested samples of blood from 178 Australian aborigines and 141 New Guinea natives. The MN groups of these two ethnologically distinct people were much the same. The anti-S serum however disclosed a notable difference, as the following gene frequencies show (Sanger, 1950).

	MS	*Ms*	*NS*	*Ns*
Australian aborigines	0.0000	0.2556	0.0000	0.7444
New Guinea natives	0.0522	0.1489	0.0843	0.7146

The P Groups

The P groups were recognized as being somewhat complicated by intermediate forms at the time of their discovery by Landsteiner and Levine in 1927 (1927b). It now seems clear from the work of Henningsen (1949a and b) that there are several allelomorphs of the P gene causing variations in strength of the P positive antigen. But with a reasonably powerful anti-P serum there is no great difficulty in classifying people into

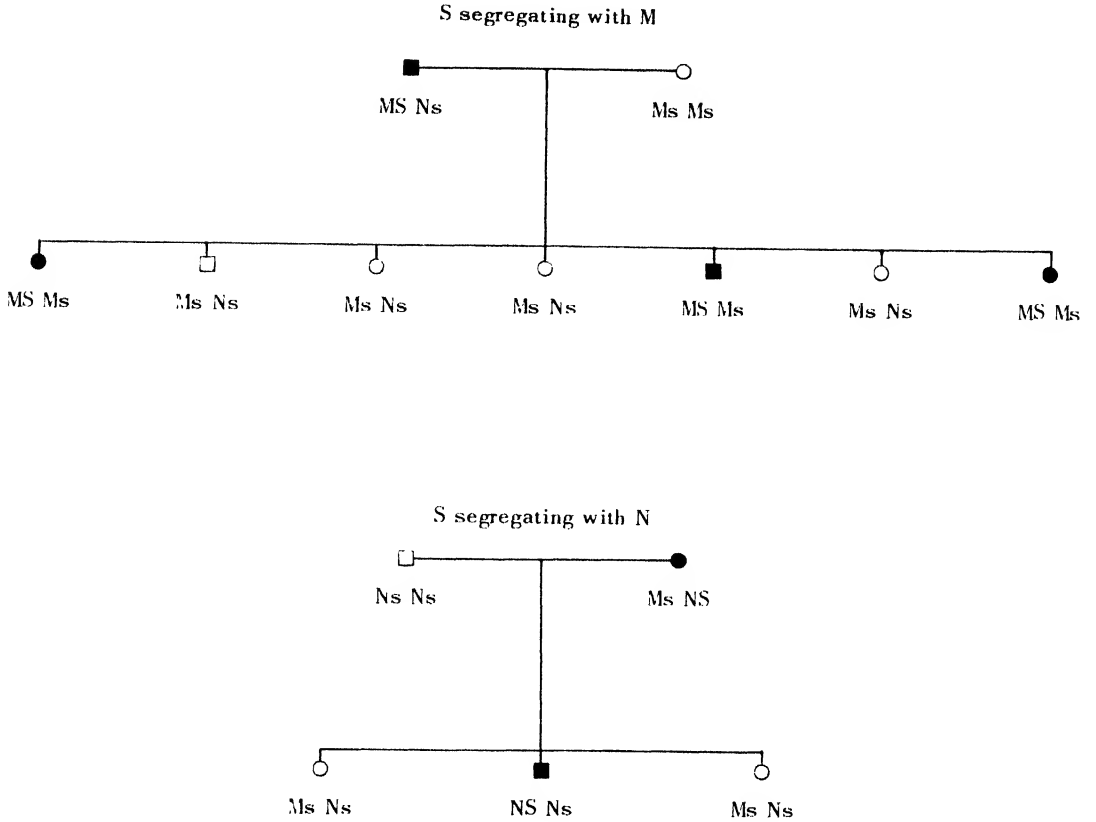


FIG. 3. The inheritance of the MNS groups. Black represents the S antigen.

those with the antigen however weak, P positive, and those without it, P negative.

Table 6 shows the distribution of the P groups found by Wiener and Unger (1944) in New York whites. My colleagues and I have found an almost precisely similar distribution in London (Sanger, Lawler and Race, 1949). The Table shows that marked racial differences are to be found in the distribution of these groups. The negroes not only have a higher frequency of P positive blood, but amongst the P positive negroes there is a higher proportion of the strong P type than is to be found amongst the P positive whites, a fact noted by Landsteiner and Levine in their original paper (1927b).

TABLE 6. THE DISTRIBUTION OF THE P GROUPS

(from Wiener and Unger, 1944)

	Total number tested	P +	P −	Gene *P*	Gene *p*
New York whites	237	176 74.26%	61 25.74%	0.4927	0.5073
New York negroes	73	71 97.26%	2 2.74%	0.8345	0.1655

Landsteiner and Levine (1930, 1931) showed that the P antigen was inherited and that the manner of its inheritance was probably that of a Mendelian dominant character. This has since been amply confirmed by several workers, notably Henningsen (1949b).

The P groups have so far contributed but little ethnological data. Apart from those for Europeans and American negroes the only results I have been able to find are Moharram's (1942) for the mixed inhabitants of Cairo. In testing 1,000 of these people Moharram found 77.5 per cent to be P positive; a distribution very close to that found in Europe.

The Rh Blood Groups

The discovery of the Rh groups by Landsteiner and Wiener in 1940 (1940, 1941), with which must be associated the work of Levine and Stetson in 1939, was the most important advance in knowledge in this field since the discovery of the ABO blood groups at the beginning of the century. The

discovery of a new blood group is always an important event for it defines one more fixed and recognizable point on the chromosomes of man; but Levine, Katzin, Burnham and Vogel showed that Rh did more than this when they demonstrated, in 1941 (1941a and b), that it was the cause of haemolytic disease of the new-born. This of course was of great importance in paediatrics and has revolutionized blood transfusion as far as females are concerned. But it also showed us selection at work, selection against the heterozygote (as Haldane and Wiener were quick to point out); and it showed us one of the mechanisms that could make interspecies crosses infertile. The latter possibility was shown to be more than theoretical when Caroli and Bessis (1947) discovered that a fairly common fatal disease of the new-born mule was in fact haemolytic disease due to anti-donkey antibodies produced by the horse mother of the mule.

TABLE 7. THE Rh GROUPS IN ENGLAND

8 chromosome combinations			36 genotypes, the commonest being		
CDe	R_1	0.4205	*CDe/cde*	R_1r	32.68%
cde	r	0.3886	*CDe/CDe*	R_1R_1	17.76%
cDE	R_2	0.1411	*cde /cde*	*rr*	15.10%
cDe	R_0	0.0257	*CDe/cDE*	R_1R_2	11.86%
cdE	R''	0.0119	*cDE/cde*	R_2r	10.97%
Cde	R'	0.0098			
CDE	R_z	0.0024			
CdE	R_y	but a few found			

Early in 1944 Fisher showed that three pairs of allelomorphic antigens were responsible for the Rh blood groups (Table 7). The three pairs are C and c, D and d, E and e. The genes that give rise to these antigens are known by the same symbols. The relationship between the members of these pairs is one of genetic allelomorphism. That is to say a chromosome can carry the gene for D or d, but not both. The three loci are certainly very close together on the chromosome, some prefer to think of them as being within the boundary of one gene but this makes no practical difference.

Three pairs of alternatives can combine in eight different ways all of which chromosome combinations have now been found. They are shown in the table with their English frequencies and with the shorthand notation in use in England unchanged since 1944.

Finally the table shows the five commonest genotypes. These make up 88 per cent of English blood samples; leaving only 12 per cent to be accounted for by the remaining 31 genotypes. (The frequencies of Table 7 are taken from Race, Mourant, Lawler and Sanger, 1948. For purposes of exposition the third allelomorph at the *C* locus, C^w, has been counted as *C*).

The Rh system seems more complex than other blood group systems only because it is made up of three simple blood groups stuck together. You will realise from Dr. Mourant's paper what a great contribution the Rh groups have made, and are likely to make, to ethnology.

The Lutheran Blood Groups

This system of blood groups was recognized in 1946 (Callender and Race) and the symbols L and l were used. As these symbols later came to be used also for the Lewis groups it was felt that the rather boring subject of notation must be grappled with if confusion were to be avoided. With assistance from the World Health Organization a number of workers (Andresen *et al.*, 1949) interested in these groups were able to meet and agree upon a standardized notation for the two systems (Table 8). The notation has worked well for the Lutheran and Lewis systems in practice and it has been adopted for the newly discovered Duffy system.

TABLE 8. THE LUTHERAN BLOOD GROUPS

Genes		Frequency in England
Lu^a		0.0390
Lu^b		0.9610
Genotypes	**Phenotypes**	
Lu^aLu^a Lu^aLu^b	Lu(a+)	7.65%
Lu^bLu^b	Lu(a−)	92.35%
Antibody		
anti-Lu^a		

The inheritance of these groups is established with certainty (Callender and Race, 1946; Lawler, 1950). The antigen Lu^a is inherited as a dominant character and the fact that we can say so boldly suggests that we have yet a good deal to learn about this antigen. For example we do not yet know whether the red cells of a homozygote Lu^aLu^a react more strongly with the serum anti-

Lu^a than do red cells of the heterozygote Lu^aLu^b. If we knew that they did we could hardly use the convenient term dominant.

The only people, other than Europeans, whose blood has been tested with the anti-Lutheran serum are the Australian aborigines and the New Guinea natives. Dr. Sanger tested 178 aborigines and found all of them to lack the antigen, as did 141 New Guinea natives.

The Kell Blood Groups

This system of groups was discovered in 1946 (Coombs, Mourant and Race). The antibody, anti-K, of which many examples have now been found is usually, though not always, in the incomplete form. It is a most dangerous antibody; though fortunately rarer it is perhaps more dangerous than anti-Rh in causing transfusion reactions and haemolytic disease.

The frequencies are shown in Table 9. An intellectually most satisfying addition to the knowledge of these groups was made in 1949 when Levine, Wigod, Backer and Ponder found and recognized the antibody anti-k. At first this antibody appeared to agglutinate the blood of everyone except the person in whose serum it was found, but testing was continued and, at a total of 2,500, five other examples of negative blood had been found. The frequency suggested that the serum contained anti-k and this was proved when all the negatives were found to be positive with anti-K.

The Kell antigen was shown to be inherited by means of a gene capable of expressing itself in the heterozygous as well as the homozygous state (Sanger, Bertinshaw, Lawler and Race, 1949). When anti-k was discovered it was clear that had it been found before anti-K then the antigen K would have appeared to be, and would have been labelled, a recessive character.

TABLE 9. THE KELL BLOOD GROUPS

Genes			Frequency in England
K			0.0522
k			0.9478
Genotypes	Phenotypes		
	anti-K	anti-k	
KK	+	−	0.27%
Kk	+	+	9.90%
kk	−	+	89.83%
Antibodies			
anti-K			
anti-k			

Testing the family of one of the rare anti-k negative donors provided the beautiful pedigree shown in Figure 4.

The Lewis Blood Groups

This system was discovered by Mourant in 1946. The anti-Lewis antibody, now called anti-Le^a, agglutinates the blood of 22 per cent of English people. The corresponding antigen is called Le^a.

Two surprising discoveries were subsequently made; the first when Andresen (1947) found that the antigen Le^a, unlike all other known blood group antigens, is inherited as a recessive character; the second when Grubb (1948) found that Lewis positive, that is Le(a+) people, are salivary non-secretors of the ABH group substance (Table 10).

In 1948 Andresen found an antiserum anti-Le^b which agglutinated blood containing the antigen Le^b, allelomorphic to Le^a. That about 6 per cent of samples are agglutinated by neither anti-Le^a nor anti-Le^b shows that there are other allelo-

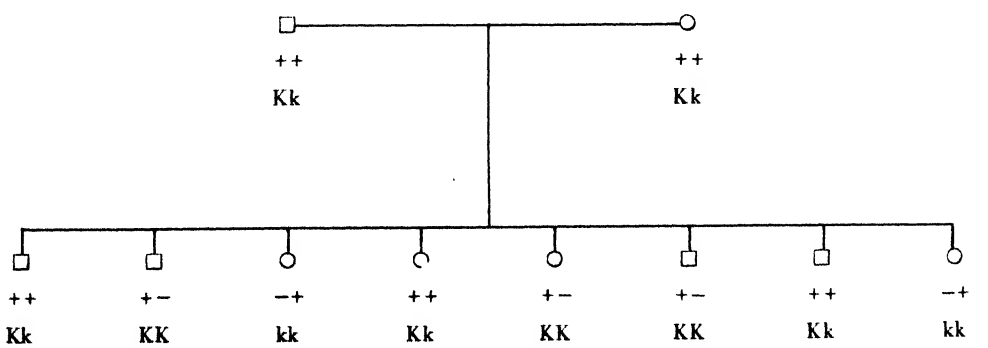


FIG. 4. A family showing segregation of the Kell genes. The + and − signs show the reactions with anti-K and anti-k respectively. (From Levine, Wigod, Backer and Ponder, 1949.)

TABLE 10. THE LEWIS BLOOD GROUPS

Genotypes	anti-Le^a	anti-Le^b	Phenotypes	Frequency in Europe	Secretion in saliva of ABH antigens
Le^aLe^a	+	−	Le(a + b−)	22.04%	probably all non-secretors
Le^aLe^b	−	+	Le(a − b +)	about 72%	nearly all secretors
Le^bLe^b	−	+			
?	−	−	Le(a−b−)	about 6%	nearly all secretors

morphs not yet completely identified. Anti-Le^b sera have the peculiar property of agglutinating appropriate red cells when they belong to group O or A_2, but not agglutinating red cells when they belong to group A_1 though they are genetically Le^b.

Anti-Le^a is fairly widely available but anti-Le^b is a somewhat rare serum. The Lewis groups for this reason are usually considered as but two, Le(a+) and Le(a−) depending on the reactions with the one serum anti-Le^a.

The two families in Figure 5 illustrate the characteristic inheritance of a Mendelian recessive character. That the antigen Le^a is inherited as a recessive character is now beyond doubt, but the genetic basis of the third allelomorph, which we may call Le^c, and of the association with salivary secretion remains to be worked out.

From an ethnological point of view it is, as far as we know, a matter of indifference whether a group of people have been classified for ABH secretion in their saliva or for the Lewis groups of their red cells. Although the genetic control of the secretor distinction was discovered by Schiff and Sasaki as long ago as 1932 very little

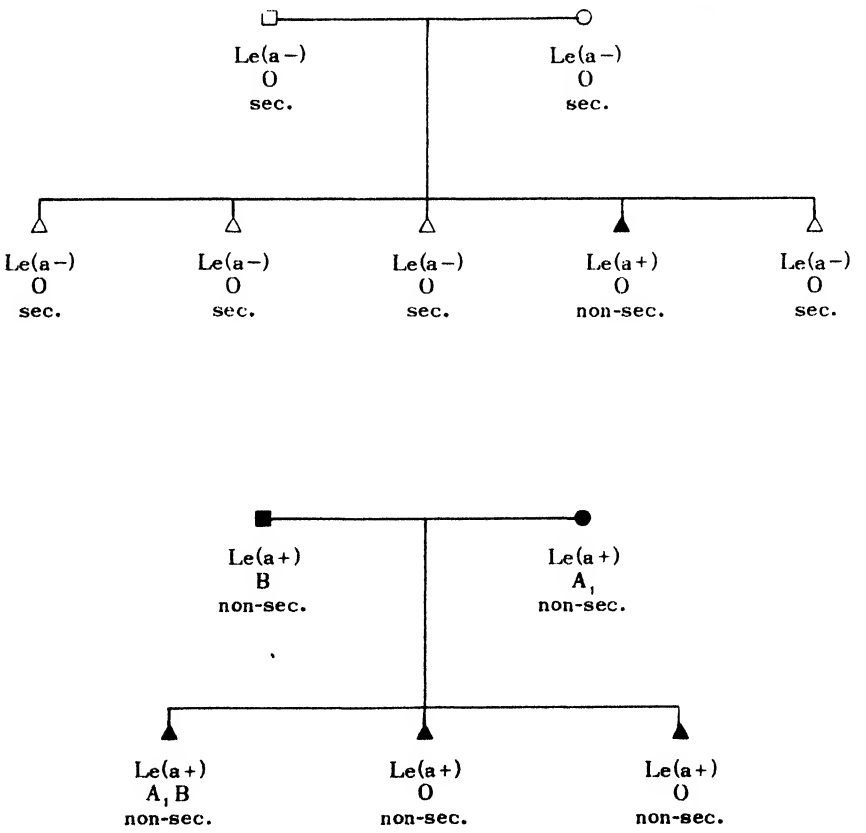


FIG. 5. Two families illustrating the recessive inheritance of the Le(a+) antigen (black) and showing the association between this antigen and salivary secretion. (From Race, Sanger, Lawler and Bertinshaw, 1949.)

ethnological work has been done on samples other than European. The most striking variation was that observed by Matson and Piper (1947) when they did not find a single non-secretor in testing 79 Ute Indians of Utah. In Cairo (Moharram, 1943) and in Japan (Susuki, 1936) the distribution is the same as that found in Europe.

The Duffy System

This system of blood groups was discovered by Cutbush, Mollison and Parkin in 1950.

The antibody which enabled the new blood group antigen to be recognized was found in the serum of a man suffering from haemophilia who had had several blood transfusions during the previous 20 years. The form of notation designed for the Lutheran and Lewis system was adopted for the new groups; it is shown in Table 11 together with the frequencies found in England.

TABLE 11. THE DUFFY BLOOD GROUPS

Genes		Frequencies in England
Fy^a		0.4102
Fy^b		0.5898
Genotypes	Phenotypes	
Fy^aFy^a Fy^aFy^b	Fy(a+)	65.22%
Fy^bFy^b	Fy(a−)	34.78%
Antibody		
anti-Fy^a		

The Duffy blood groups are certain to play an important part in the genetics of Europeans amongst whom the groups Fy(a+) and Fy(a−) are both large.

Cutbush and Mollison (1950) demonstrated that the groups were inherited by means of two allelomorphic genes Fy^a and Fy^b; Fy^a in single or double dose causes the presence of the recognizable antigen. This conclusion was strongly supported by the work of Race, Holt and Thompson (1950).

The Duffy groups promise to be of use in ethnology, for Cutbush and Mollison tested samples of blood from 47 Indians from Pakistan and found only four to be Fy(a−).

The discovery of this latest and sparkling system came as a great encouragement. For, in spite of the huge sieve of the transfusion laboratories of the world, no new blood group system had been found for four years and it was beginning to seem as if the limits of discrimination of the available techniques had been reached. But now it seems that if we could miss Duffy for so long there is no reason why many other nugget systems may not be awaiting the prospector.

The "Usefulness" of the Various Systems

The more and the larger the divisions into which a blood group system splits a population the more useful is it in genetic work and to some extent in ethnological work also. For example, a blood group which divided a population into 99 per cent negative and 1 per cent positive would be little use in genetic work because so few people would have the positive character. It would be but little use in ethnology for if a different racial group had even twice the frequency of the antigen, or lacked it entirely, many hundreds of samples would have to be tested to demonstrate the significance of the difference between the two peoples.

A convenient way of comparing the usefulness of the different systems of blood groups is to sum the squares of the phenotype frequencies. A figure is obtained which represents the percentage of failures to distinguish between two random samples of blood in a given population. Table 12 shows the results of summing the squares of English phenotype frequencies. It may surprise you that the MNS system is as useful as Rh with all its subgroups; when anti-s is found the MNS system will be the most useful of markers of the chromosomes of Europeans.

TABLE 12. THE "USEFULNESS" OF THE VARIOUS SYSTEMS, AS MEASURED BY THEIR ABILITY TO DISTINGUISH BETWEEN TWO RANDOM SAMPLES OF ENGLISH BLOOD

(from Race and Sanger, 1950)

Rh	19.5%	failures
MNS	20.0%	failures
A_1A_2BO	32.8%	failures
Duffy	53.8%	failures
P	61.5%	failures
Lewis	64.8%	failures
Kell	81.7%	failures
Lutheran	85.4%	failures

However well a blood group splits up any one population it is, of course, no use in ethnological work if it shows no geographical differences. As knowledge of a blood group grows its powers of racial discrimination, at first unsuspected, tend to become apparent. For example, in the early days of Rh West Africans and Indians could scarcely be distinguished by these groups. The

discoveries of the subgroups enabled Rh to make a clear distinction between these peoples.

The Serological Independence of the Eight Blood Group Systems

All of the eight blood group systems are serologically independent of each other. A group O person, for example, is as frequently group M as a group A person; an Rh positive person as frequently Kell positive as an Rh negative person; a Duffy positive person as frequently Lutheran positive as a Duffy negative person (Sanger and Race, 1949; Bertinshaw *et al.*, 1950; Race, Holt and Thompson, 1950).

The Genetic Independence of the Eight Blood Group Systems

Genetic linkage between the ABO, MN or P groups was shown by Wiener (1943) to be improbable. In my Unit we are at present analysing somewhat extensive family data involving all eight blood group systems and we have not yet found evidence for linkage between any of them, nor do any of them appear to be sex linked or partially sex linked.

It is quite possible therefore that in the eight blood groups systems we have markers for eight of the 23 autosomes of man.

Evidence of Selection affecting Blood Groups

The ABO groups

There is evidence which is difficult to ignore that selection is markedly affecting the ABO groups. In 1925 Hirszfeld and Zborowski in a study of the literature observed that the incidence of A children was lower in the mating of mother O × father A than in the mating of mother A × father O. Levine (1943) collected more figures which showed the same disturbance and recently Waterhouse and Hogben (1947) have taken up the problem. The latter authors collected from the literature the results of 12 series of family investigations which they considered to be trustworthy. The results of the counts on O × A matings were as shown in Table 13. It will be seen that there is a deficiency of children when the mother is O and that the deficiency is entirely due to the shortage of A children.

Waterhouse and Hogben calculate that this deficiency is very highly significant and represents a foetal death rate of eight per cent of A children, or three per cent of all conceptions.

TABLE 13. THE ISSUE FROM MATINGS O × A

(Collected from the literature by Waterhouse and Hogben, 1947)

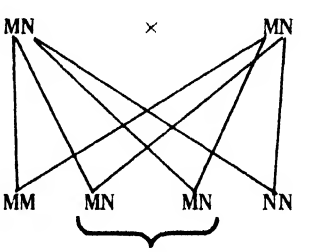
	Mother O	Father A	Mother A	Father O
Total families	209		244	
Total children	686		835	
Mean	3.28	Mean	3.42	
O children	301		320	
A children	385		515	

The MN Blood Groups

In 1939 Taylor and Prior working at the Galton Laboratory on the inheritance of the MN groups noticed that in the families which they had tested, and those reported in the literature then available, there was a significant excess of MN children from the mating MN × MN. Table 14 shows that 50 per cent of the children of such matings are expected to be MN. In 1943 Wiener collected from the literature the results of 616 MN × MN matings and found that 58.4% of the 1,827 children were MN. Wiener is of the opinion that the excess is entirely due to errors of technique, but such a gross rate of error seems incompatible with the figures for MN tests on unrelated random persons published by most of the workers involved. Such tests constantly show the correct number of MN persons. In favor of Wiener's explanation is his own average of 51.3 per cent MN children.

It seems that this problem deserves still more consideration, for if even a part of the excess is

TABLE 14. THE ISSUE OF MATINGS MN × MN



expected	25%	50%	25%
observed		58.4%	Wiener's collection from the literature. 616 families, 1,827 children.

true, and not due to errors of technique, it would show in a direct way the phenomenon of the heterozygote being favored by selection. Favoring of the heterozygote has been shown to be one way in which a balanced polymorphism can be maintained.

The Rh Blood Groups

Selection must be affecting the Rh groups. When a child dies of haemolytic disease one Rh positive (*D*) gene and one Rh negative (*d*) gene is withdrawn from circulation. If uncompensated this should result, as Wiener (1942) and Haldane (1942) pointed out, in a reduction in the frequency of the rarer of the two genes, that is the Rh negative (*d*), if we are considering an American or English population. This could result in a gradual decrease of the Rh negative gene from generation to generation. In order to explain the high frequency of the Rh negative gene still present in European people, both Haldane and Wiener suggested that such people were descended from a cross between a race predominantly Rh positive and a hypothetical race predominantly Rh negative. But of this I will say no more for Dr. Mourant will be speaking on this subject in his paper.

Hogben (1943) and Fisher and his colleagues (Fisher, Race and Taylor, 1944) think on the other hand that the Rh polymorphism is of the balanced type. If this view is correct then there must be some compensation for the drain on the Rh negative genes. Hogben suggested mutation and Fisher the selective survival of Rh negative children in families with haemolytic disease in which the father is heterozygous.

The Kell Blood Groups

The Kell positive gene *K* can be the primary cause of haemolytic disease of the newborn and it is presumably exposed to the same perils at the teeth of selection as is the Rh negative gene, *d*. In the case of Kell it is the antigenic gene *K* which is less frequent than its allelomorph *k*. Since each eliminated child is of the genotype *Kk* it is the gene *K* which, if there is no counter selection, is presumably being reduced in frequency.

I have, rather apprehensively for the subject is one of immense difficulties and pitfalls for the inexpert, mentioned this impact of selection on the blood groups. In weighing the facts that blood groups have to offer to the vast study of the origin and evolution of man, I assumed that you would need to know how much evidence there is of the pruning of these groups by natural selection.

If there is pruning by selection, I personally am inclined to believe that there is compensation by counter selection; for there are one or two hints which are difficult to ignore that the blood group polymorphisms are balanced ones.

I have in mind the often quoted work of Vĕrzar and Weszeczky (1921) who tested the blood of certain gypsies, a people of Hindu origin who have lived in Hungary for several hundred years, and found that they had the blood group distribution of the modern Hindus which was quite unlike that of the surrounding Hungarians with whom the gypsies had not intermarried. I hope Dr. Sanghvi will criticise this evidence.

I also have in mind the more recent work of Hart (1944) who found that in the rural population of Ulster, in Ireland, the donors with English names have the English distribution of blood groups although it is more than 400 years since their ancestors settled there.

In conclusion I may express the hope that there will before long be an immense amount of ethnological blood group data for your consideration. Boyd's compilation includes 73 pages of tightly packed ABO results alone. Perhaps increasing interest and increasing availability of antisera may soon result in the adequate plotting of the distribution on the face of the earth of the other seven blood group systems; though one also hopes that by that time the available results will seem even more incomplete than they do now, owing to the lining up of still newer groups.

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DISCUSSION

KEMP: I wish to call attention to the blood-types A_3, A_4, A_5, A_x, ...and N_2. The frequency of A_3 is about 1 pro milli, the other types are very rare and probably not spread in the total population, being either rather new mutation or having a tendency to disappear again during the generations.

MOURANT: (In reply to question referred to AEM) While the MN groups do not appear on present evidence to show the same kind of wide and rapid variations in frequency as do the ABO groups, they do vary considerably. Over most of Europe and Africa M is only slightly in excess of N but M increases in eastern Europe and is in great excess in southern and south-eastern Asia up to and including Java. Somewhere east of Java there is a rapid change from very high M to a very high N, and N maintains high frequencies throughout the Pacific area and Australia. M is high in all the aboriginal populations of the American continent.

SANGHVI: In connection with the distribution of blood group P, a mention might be made of the addition of data of three endogamous groups of people from Bombay to the existing very scanty material. Interesting enough, the difference in the distribution of two of these three groups is as large as reported for American Whites and American Negroes. It might be further mentioned, that these data form a part of a more extensive study of six endogamous groups of people in Bombay. During the course of the study, ABO, A_1A_2, MN and Rh blood groups, taste reactions to phenyl-thio-carbamide and color blindness of the red-green type were studied for all the six groups in addition to the blood group P studied for three of them. A sample of 200 unrelated individuals was examined from each of the four endogamous groups and a sample of 100 individuals, from each of the remaining two. Physical measurements mostly concerning head and face were examined for five out of six groups. The results of this study are reported in the Annals of Eugenics (*15*: 52–76: 1949).

The second point is regarding the illustration of Vérzar and Weszeczky regarding the comparison of the distribution of ABO blood groups in "Indians" studied by Hirszfelds, with their distribution of Gypsies in Hungary. It is not possible to say from the paper of the Hirszfelds (Lancet, *2*: 675: 1919), which castes and tribes were examined by them. It is known that the Indian troops in Macedonia during the first World War included Gurkhas, Garowalis, Rajputs, Jats and Kumaons. Labor Transport Corps were composed chiefly of scheduled caste persons from different parts in India. It is therefore, likely that their sample of "Indians" contained a mixture of some or all of these groups. In the study mentioned above, a significant difference was found in the distribution of ABO blood groups among some of the endogamous groups. The sample of "Indians" of Hirszfelds subsequently called "Hindus" by Ohenberg (J. Amer. Med. Ass., *84*: 1393: 1925) may probably be composed of such varying groups. The illustration should therefore be looked upon with this limitation.

WARREN, K. B.: Editorial note: A comment was made by Dr. A. S. Wiener to the effect that the

question is still unsettled as to the exact nature of the Rh locus. Although Dr. Wiener did not submit his discussion for publication, the following reply by Dr. H. B. Glass is published herewith.

GLASS: I am sure we can agree with Dr. Wiener that the question whether the Rh genes form a series of multiple alleles or represent multiple loci is still unsettled, and further that until it has been conclusively proved that there is more than one Rh locus, it is best to adopt the simplest hypothesis, namely, that there is only a single one. I would like to point out, however, that a considerable body of evidence has now accumulated in the study of the genetics of other organisms, as well as the human species, to support the view that replication of a particular locus to form a series of duplicate loci, either in tandem or inverted order, is quite a common genetic occurrence. More than that, it is the only known way in which altogether new types of genes can arise in evolution and transcend the mutational limits of the existent loci. I mention only a few examples out of many: In *Drosophila melanogaster*, the loci Star and asteroid interact like alleles, but, as E. B. Lewis has shown, they cross over (about 0.01%) upon occasion and so must lie in distinct portions of the chromosome. Our chairman, Dr. Oliver, will possibly wish to say something about the similar situation involving the "alleles" of lozenge in the same species. Laughnan has recently demonstrated crossing over between "alleles" at the anthocyanin *A* locus in maize, and Yu and Chang have observed crossing over between parts of the *R* flower color locus in cotton. Furthermore, a parallel to the scheme of three adjacent Rh loci proposed by Fisher is to be found in the human species, for two forms of colorblindness, deuteranopia and protanopia, are apparently determined by adjacent loci which do not seem to interact, although no crossing over has ever been observed to occur between them. The evidence is therefore such as to compel us to keep an open mind regarding the alternative Rh theories. We must go on looking carefully for cases of crossing over in those particular families, of the back-cross type, in which crossing over could be detected if it were to occur. The great majority of reported families throw no light on the question, inasmuch as crossing over could not be detected in them if it did occur.

THE BLOOD GROUPS OF THE PEOPLES OF THE MEDITERRANEAN AREA

A. E. MOURANT

Medical Research Council, Blood Group Reference Laboratory, Lister Institute, London, England

INTRODUCTION

The distribution of the ABO and Rh blood groups in most of the countries north of the Pyrenees and the Alps has been the subject of much investigation and study. The broad outlines have been known for some years and further advances in knowledge will depend on intensive studies of those remote areas where the picture has not been confused by recent large-scale mixing of populations.

The data for the countries surrounding the Mediterranean Sea are much less complete even for the ABO groups, and still less so for the Rh groups, but recent investigations into the latter have yielded data which, though patchy, are highly suggestive. It has thus become worth while to bring together all the available data and to see whether any underlying regularities can yet be glimpsed, or any suggestions of correlation with the data of anthropology or with historical movements of peoples. It must be emphasized that most of the conclusions reached can as yet only be regarded as tentative; only in a few cases are the numbers of persons tested sufficiently large to enable the suggested correlations and contrasts to stand the tests of statistical significance. They may however be a valuable guide to the directions in which further research is likely to be fruitful.

It will help in focussing our ideas if we regard the Mediterranean basin as a great melting pot with streams of human life flowing towards and through it from the surrounding land masses. The streams, to change the metaphor, are colored by their blood groups but the ABO groups give us a very limited palette. The Rh groups with their great variety enable us to make much finer distinctions and even to trace one stream after it has mingled with others, but only in parts of the picture has the dark varnish of the ages been removed allowing us to appreciate these more delicate tints.

Most of the data on the ABO groups have been obtained from the paper of Vallois (1944) and the compilations of Boyd (1939), Elsdon Dew (1939) and De Hoyos Sainz (1947). The frequencies of the Rh groups and a certain amount of ABO data are contained in a large number of papers listed among the references. Specific reference to individual papers is not in all cases made in the text of this paper.

THE BLOOD GROUPS OF THE PEOPLES OF EUROPE AND AFRICA

Before studying in detail the blood groups of the Mediterranean peoples we must therefore consider in broad outline the blood group distributions of northern and central Europe and of Africa south of the Sahara Desert.

Northern and central Europe can be divided into three main zones on the basis of the distribution of the ABO blood groups. East of a line running down the Baltic Sea and across central Germany to the head of the Adriatic Sea is a region of high B frequencies. West of this line is an area of high A frequencies, while in the extreme west, in Scotland, Ireland, and Iceland, O frequencies are high and B still low though slightly higher than in the high A zone. Over the whole area Rh frequencies are almost uniform with about 40 per cent each of CDe(R_1) and cde(r) chromosomes.

In Africa south of the Sahara, blood group distributions again appear to be relatively simple with, in general, A highest in the south, B in the center and O near the coasts. As in Europe, Rh frequencies vary little though they differ completely from those found in Europe, with cDe(R_2) about 60 per cent and cde(r) about 20 per cent.

THE ABO GROUPS IN THE MEDITERRANEAN AREA

In the Mediterranean area the distribution of the ABO groups is complex and is best followed, on the European side at least, by distribution maps of the three genes concerned (Figs. 1, 2 and 3).

The east European zone of high B is continued into the Balkan Peninsula excluding Greece. B is also high in most of Asia Minor, Syria and Palestine.

West of the Adriatic Sea and in Greece, A frequencies are mostly high and in general higher

THE DISTRIBUTION OF BLOOD GROUP GENE A IN THE MEDITERRANEAN AREA.

The lines connect points of equal gene frequency. The numbers represent percentages.

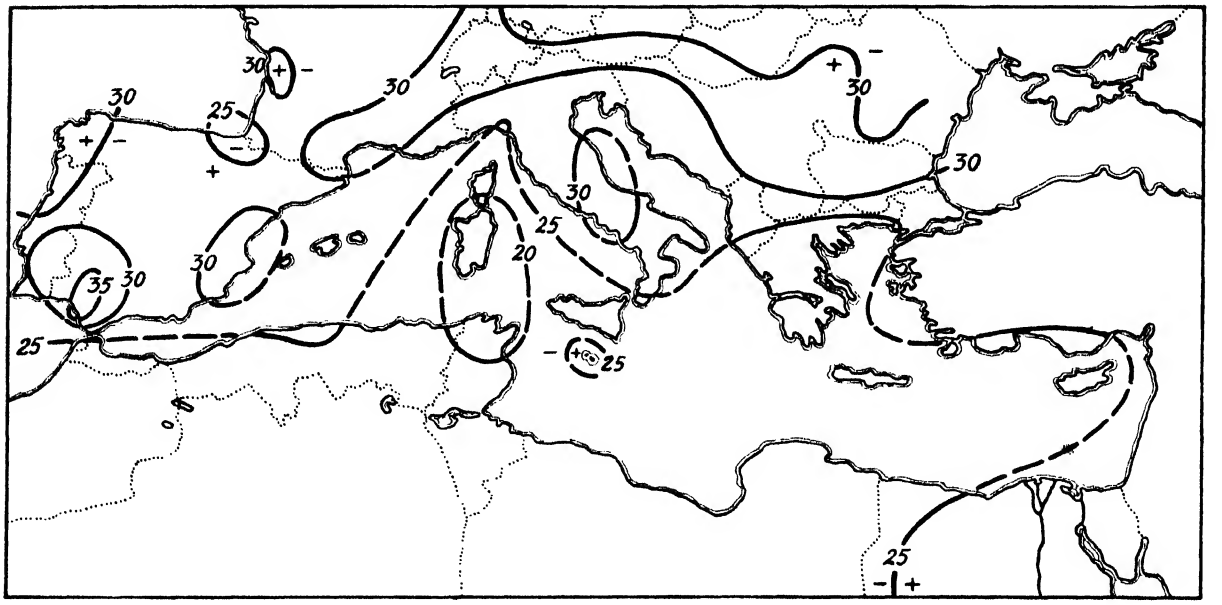


FIG. 1. The distribution of blood group gene A in the Mediterranean area.

than in northern Europe. Gene frequencies of A exceeding 30 per cent are found in patches in Italy, Spain and Portugal, and along a band following roughly the line of the Alps. Similar high frequencies are found in Scandinavia, but have not been found in Asia; and in Africa have been found very rarely, and only in frankly Negroid peoples. Thus the high A peoples of Europe, wherever they may originally have come from, are to be regarded as essentially European and *sui generis*. Had less been known of African blood groups, the presence of high A frequencies in Andalusia and especially in Cadiz, just opposite the coast of Africa, might have suggested an African derivation. We know, however, that very high A frequencies are reported in the aboriginal Guanches of the Canary Islands and De Hoyos Sainz (1947) has in fact suggested a connection between them and the population of the extreme south of Spain.

There is no single zone of high O frequency in the Mediterranean area but a number of isolated populations show a combination of high O and low B, similar to that of the Scots, the Irish and the Icelanders. Such are the Basques, the Sardinians, the Cretans, a few Berber tribes in north Africa and, rather to the east of the region, the peoples of the western Caucasus. The Basques differ from the other high O peoples both of the Mediterranean region and of north-western Europe in their extremely low B frequency which is the lowest in Europe.

In north Africa, apart from Egypt, the mixed nature of the people and the tribal organization and nomadic habits of many of them make it almost impossible to represent their blood distribution completely by means of a map.

Egypt shows a very high B frequency. The scattered observations on populations in the remainder of north Africa, from Libya to Morocco, have been discussed by Elsdon-Dew (1939) who classified most of them as Libyans, with average gene frequencies A = 21 per cent, B = 12 per cent, O = 67 per cent, and Berbers, with an average of A = 25 per cent, B = 11 per cent, O = 64 per cent. There is a well defined group of Berbers with gene frequencies very near A = 20 per cent, B = 5 per cent, O = 75 per cent, figures closely similar to those of the high O peoples of Sardinia and the islands of north western Europe; the tribes concerned are described as Berbers of Beni Qunif; Douiret from near Tatahouine, Tunisia; and Toureg of Tamanrasset, Hoggar.

The Rh Groups in the Mediterranean Area

There are many gaps in our knowledge of the circum-Mediterranean distribution of the ABO groups; within those gaps it is probable that in some cases highly aberrant ABO distributions will be found; but none of the gaps is so wide that we cannot make a plausible guess at what it holds. When we consider the Rh groups, on the other hand, much of the map might well be labelled "Here be dragons." Were the Rh groups in the Mediterranean basin as uniformly distributed as in northern Europe or in Negro Africa, the existing data might suffice for us to interpolate over the whole area. On the contrary there are wide variations in Rh frequencies, so that many more observations are needed before a complete map can be drawn.

It is however possible from a consideration of three populations, the Italians, the Basques and the Sardinians, to erect a provisional framework within which most of the known Rh distributions of the Mediterranean can find a place.

In Italy the Rh data for Milan and for Naples show a picture almost identical with that found all over northern and central Europe. Such differences as exist are in the direction of a slight excess of the CDe(R_1) chromosome. The ABO frequencies found in Italy are likewise typical of the areas to the north.

The Basques have the highest cde(r) frequency in the world, together with a low cDE(R_2) and a fairly high CDe(R_1) frequency. Thus both ABO and Rh groups show that this population stands apart from all the rest of Europe in that its genetic constitution is incompatible with anything more than a limited interbreeding with the surrounding populations. The other physical features, the language, and the traditions of the Basques are in accordance with this conclusion, and the writer and his colleagues (Chalmers, Ikin and Mourant, 1950) have suggested that the Basques represent the relatively unmixed descendants of a stock which occupied much of Europe in Palaeolithic times and which throughout the greater part of the continent interbred with invaders from Asia who were mainly D positive, the ancestors of the Basques thus being the main contributors to Europe of the d gene. It must however be noticed that besides the commonest Rh chromosome, cde(r), the Basques show a marked excess of CDe(R_1) relative to cDE(R_2) as compared with northern Europe.

THE DISTRIBUTION OF BLOOD GROUP GENE B IN THE MEDITERRANEAN AREA.

The lines connect points of equal gene frequency. The numbers represent percentages.

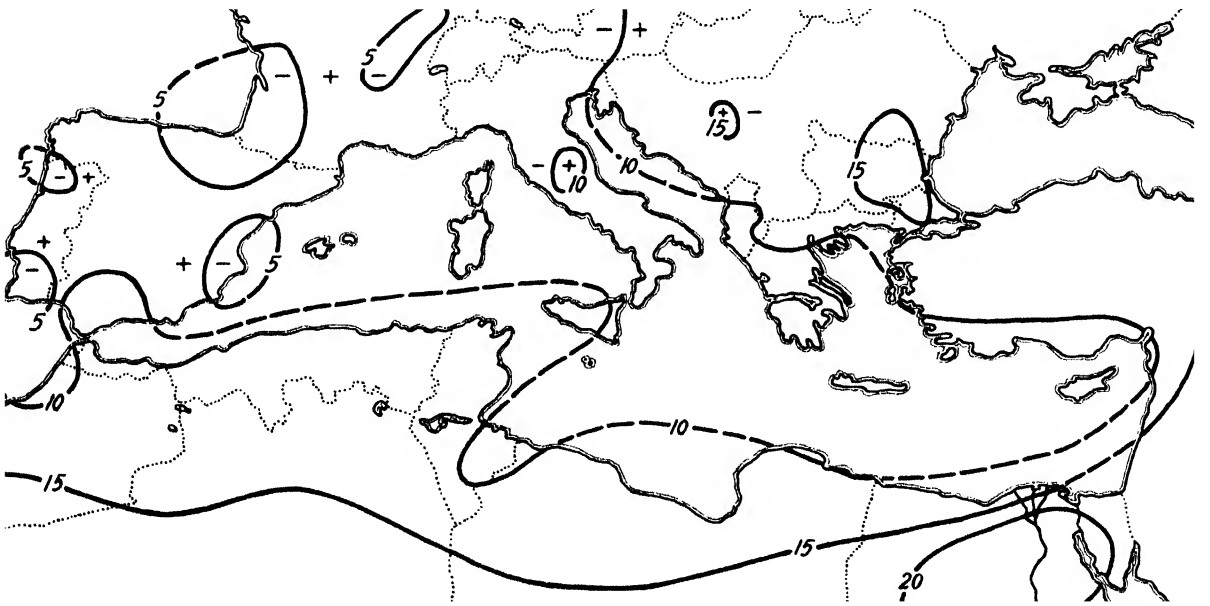


FIG. 2. The distribution of blood group gene B in the Mediterranean area.

THE DISTRIBUTION OF BLOOD GROUP GENE O IN THE MEDITERRANEAN AREA.

The lines connect points of equal gene frequency. The numbers represent percentages.

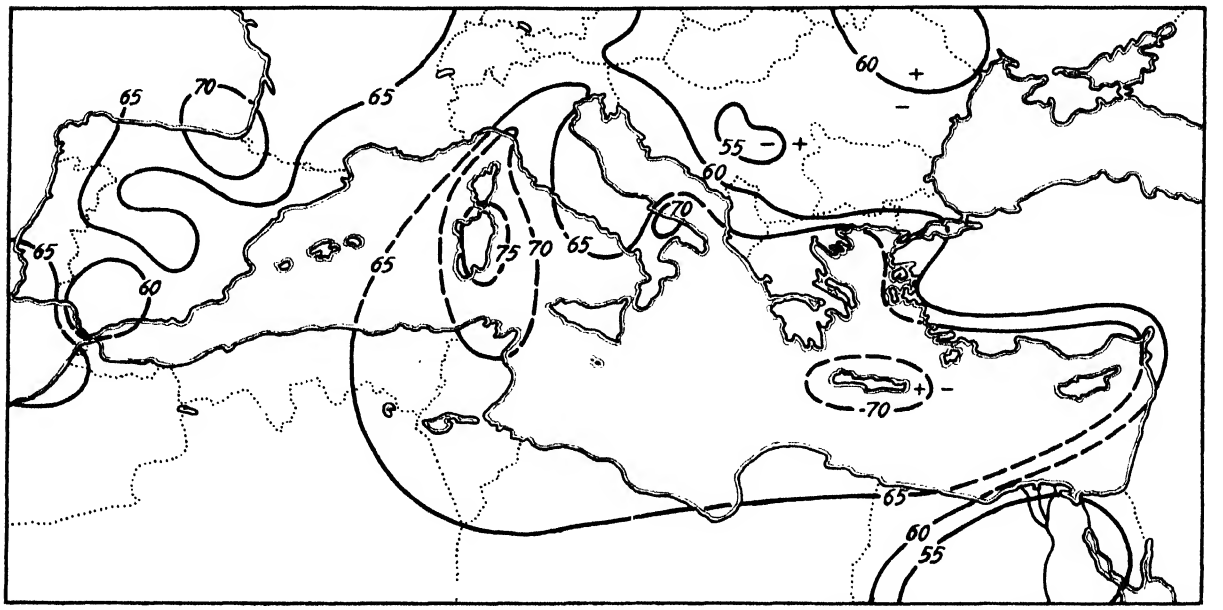


FIG. 3. The distribution of blood group gene O in the Mediterranean area.

In Sardinia an Rh distribution is found which is unique as far as Europe is concerned both in the lowness of the cde(r) frequency and in the high frequency of CDe(R_1). The cDE(R_2) chromosome is slightly less frequent than in northern Europe. Once again aberrant Rh and ABO distributions are found in the same population. Sardinia with a very high O frequency resembles Scotland, Ireland and Iceland in its ABO distribution but Iceland and Ireland certainly and Scotland probably share the north European Rh distribution. Sardinians differ from Basques not only in having an extremely different Rh distribution but in having a somewhat higher B frequency. Incidentally, Sardinia also shows a very high M frequency.

Catalonia has been shown (Race, Lawler, Bertinshaw, Grifols Lucas, Grifols Lucas, Ibarz Roqueta and Oppenheimer, 1949) to have a typical northern European cde(r) frequency but a much higher CDe(R_1) than northern Europe. This is readily explained if the Catalonians are mainly a blend of the stocks represented by the Basques and the Sardinians, that is to say, if the Rh positive stock which combined with the primitive Rh negative race was principally the high CDe(R_1) stock which we seem to be finding all over the Mediterranean basin, and only to a lesser extent the one with lower CDe(R_1) and higher cDE(R_2) which combined similarly north of the Alps and Pyrenees. That this is not the complete story is shown by the fact that A is higher in Catalonians than in Basques or Sardinians.

If indeed the ancestors of the Basques were almost exclusively cde(r) the presence of a proto-Sardinian component must also be the explanation of why in the modern Basques themselves the ratio of CDe(R_1) to cDE(R_2) is so much higher than in the peoples to the north. Here too is the probable reason why the populations of Milan and Naples though almost identical in their Rh composition with the northern Europeans show a slight excess of CDe(R_1).

Next to the Sardinians the isolated population of Ferrara near the mouth of the River Po has in common with the Galicians the lowest known cde(r) frequency in Europe. Its gene composition could be derived from a suitable combination of Sardinians and of northern Europeans or of Milanese. The people of Ferrara have however an Rh composition almost identical with that found by Wiener, Sonn and Belkin (1945) and by Prasad, Ikin and Mourant (1949) for the people of India. The ABO frequencies of the Ferrarese, which we

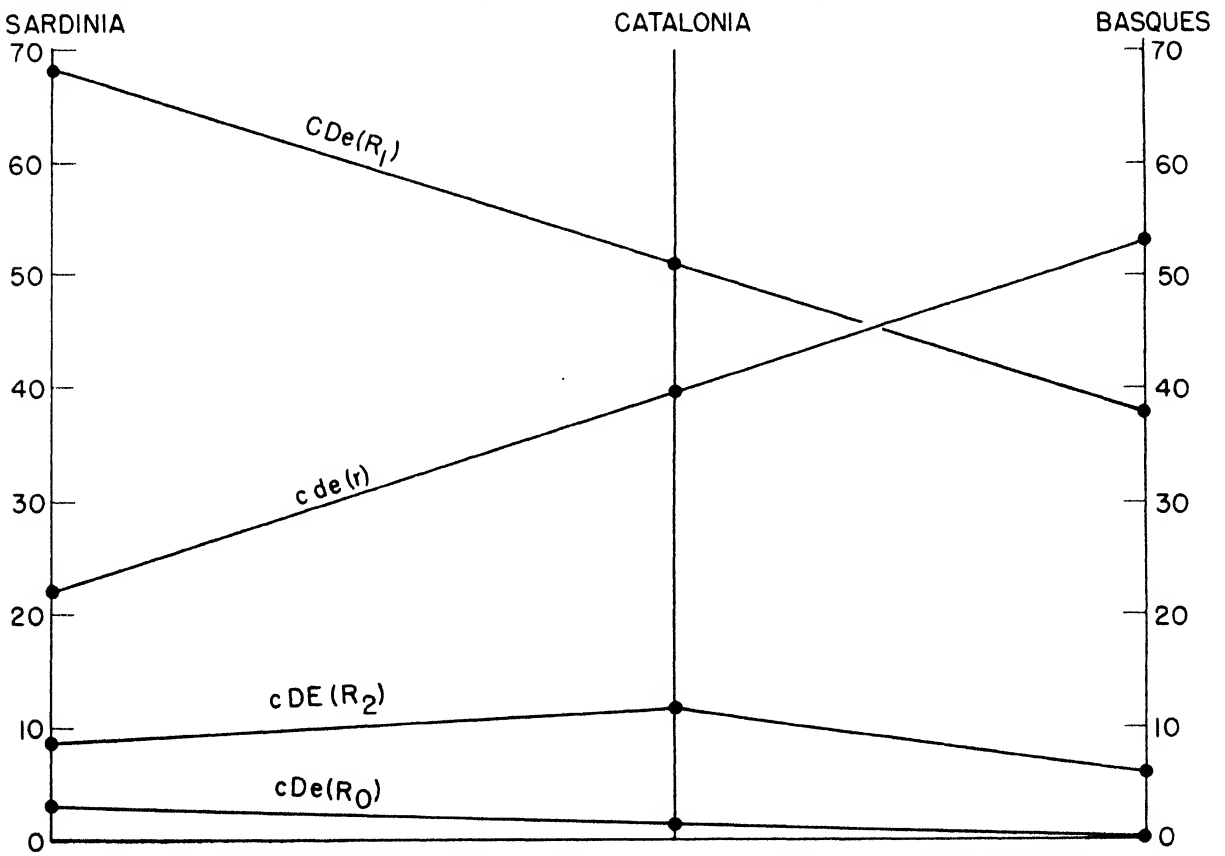
unfortunately do not know, would be a most valuable clue to their affinities since the very high B frequencies found in India are widely different from anything known in Europe.

Using the Rh groups alone we are in fact making the problem appear too simple. So long as only three chromosome combinations, cde(r) CDe(R_1) and cDE(R_2) have frequencies above five per cent in any population subjected to analysis, and so long as the frequency of cDE(R_2) remains less than that found in northern Europe, almost any Rh constitution that we are likely to meet can be synthesized approximately from a suitable mixture of the three stocks already mentioned. Speculation can only be controlled by using other blood group systems, especially ABO, at the same time, and by finding that any given hypothetical mixture is only present in a situation which appears reasonable on the basis of historical or demonstrable prehistoric movements of population or of their present geographical relationships. For instance, Morganti, Panella and Cresseri (1949) have produced historical evidence that there has been immigration into Ferrara from the east.

When we find cDe(R_0) frequencies exceeding the normal 2 to 3 per cent of Europe it is necessary to call upon another source of supply which can hardly be other than the Negroes with 60 per cent of cDe(R_0). There is now practically no population which we cannot readily synthesize in imagination but if we need to bring in all four combinations of chromosomes repeatedly our whole theoretical structure must be suspect.

Three populations living in or near the Mediterranean area have been found to possess relatively high cDe(R_0) frequencies; the Egyptians, the Arabs of Iraq and the Galicians of north-west Spain.

The Egyptian Rh distribution can be derived from that of the Sardinians together with a negro admixture. This hypothesis is strongly supported, at least with regard to the negro contribution, by work now in progress which shows an almost continuous change along the Nile Valley from



Rh CHROMOSOME FREQUENCIES (per cent) IN THE WESTERN MEDITERRANEAN.

FIG. 4. Rh chromosome frequencies (per cent) in the western Mediterranean area.

Egyptian to Negro. Moreover, the relatively high B frequency of Egyptians may have some connection with even higher B frequencies found in central Africa. The Rh constitution of the Arabs of Iraq lies between that of the Egyptians and that of the Latvians of east central Europe. The negro element in Egypt and Iraq is moreover easily explained by the progressive assimilation of negro slaves which is known to have taken place.

The Galicians are near enough to the Sardinians to leave little doubt as to the main source of their Rh genes. Their 7 per cent of cDe(R_0) chromosomes can however hardly be other than of negro origin. As only 97 persons were tested the slight excess of cde(r) and cDE(R_2) unaccounted for by such a mixture may be due to sampling errors but if confirmed on larger numbers would require a northern and possibly a proto-Basque contribution.

We have now considered all the circum-Mediterranean populations for which full Rh statistics are available. Two other populations, the Indians and the Jews, appear to bear some relation to the peoples of this area. Chown, Peterson, Lewis and Hall (1949) have determined the full ABO and Rh groups of 3,000 of the inhabitants of Manitoba, Canada, and classified them according to their European or other country of origin, Hebrews being classified separately. The northern and central European nations show almost completely uniform Rh gene frequencies together with divergent ABO frequencies. The Hebrews, agreeing closely in this series with Poles and Ukrainians in their ABO groups and especially in their high B frequency, differ from all the others with regard to Rh. In a highly mixed emigrant population such as that of Canada one cannot be sure of getting a true sample of any European stock but the good general agreement of the findings of Chown and his colleagues with what is known of the blood groups found in the countries of origin of the peoples concerned is a cause for confidence in his Hebrews being a representative sample of European Jews. Their Rh constitution is a typical Mediterranean one. They have a cDe(R_0) frequency higher than has been found anywhere in Europe except in Galicia though considerably lower than in Egypt and Iraq. This can hardly be other than the result of a negro component, probably received through Egypt. Otherwise they appear Mediterranean with a considerable added population component of the central and north European type. The latter is clearly the result of proselytization and intermarriage in recent centuries and the writer must confess his surprise at finding the Mediterranean stock not only distinctly recognizable but predominant.

Closely agreeing observations on the Rh groups of Indians by Wiener, Sonn and Belkin (1945) and by Prasad, Ikin and Mourant (1949) suggest a near relationship between northern India with 10 per cent of D-negatives on the one hand and Europe and the Mediterranean basin on the other. Southern India with only about 2 per cent of D-negatives is much nearer to eastern Asia in this respect.

It was suggested by Chalmers, Ikin and Mourant (1949) that the Indians were the descendants of a mainly D-positive population other members of which, mixing with a mainly D-negative race akin to the modern Basques had given rise to the present population of Europe. This hypothesis is supported in a broad sense not only by the Rh distribution of the Indians but by their ABO and MN groups which are a culmination, in high B and M frequencies, of the general European trend. The present paper shows however that the situation is much more complex than we supposed. In particular central and northern Europeans have a higher cDE(R_2) frequency than either Basques or Indians, while in Europe itself, in the Mediterranean basin, we find close parallels to the Indians in both Rh and MN though not in ABO groups. As was suggested by Chalmers, Ikin and Mourant (1950), if Indians represent one of the main stocks contributory to modern Europe, we still have to seek, probably to the north east, a source for the abundance of cDE(R_2) chromosomes.

Mediterranean Anaemia

The abnormality of the red blood cells, giving rise to the condition known as Mediterranean anaemia, or thalassaemia, appears to be mainly confined to populations of Mediterranean origin. The condition is inherited as a Mendelian dominant, the heterozygotes having a mild anaemia while the rare homozygotes suffer from a severe and usually fatal disease, Cooley's anaemia. The distribution of the condition in continental Italy and in Sicily has been studied in detail by Silvestroni and Bianco (1949). They find frequencies of about 10 per cent in Ferrara and the neighbouring town of Rovigo, and of about 5 per cent in most parts of Sicily. In most other parts of Italy the frequency is about one per cent. Most of the positive persons found in Rome come from Sicily and Sardinia, but no local investigations were done in Sardinia. It will be seen, however, that a high frequency of Mediterranean anaemia was found in natives of just those parts

of Italy, namely Ferrara and Sardinia, where a high frequency of R_1(CDe) was found by other workers.

A survey of the distribution of this condition in other Mediterranean lands would probably yield valuable data and it would not be difficult to combine it with a blood group survey. At the same time a search should be made for another haematological abnormality, the sickle-cell trait. This also is inherited as a Mendelian dominant and many workers consider that only the homozygotes show clinical symptoms. The condition is almost wholly confined to Africa and its frequency varies from about one per cent to 40 per cent in different tribes. It might be a useful additional index of the presence of a negro element in Mediterranean and other populations.

Throughout the Mediterranean basin we find a similar distribution recurring but with evidence of dilution with other neighboring stocks. Perhaps the most interesting of the latter is the negro component which appears at both ends of the basin. In the east the Semitic speaking peoples including the Jews of Europe have received it along the Nile or the east coast of Africa. The Galicians in the west must have received it along the Atlantic coast and further research will probably demonstrate this stream of migration more fully in other parts of the Iberian peninsula.

Wide variations of ABO frequencies have been recorded for populations whose Rh groups have not yet been tested. It is impossible to predict the results of such testing but certain peoples are likely to yield results of special interest. The very high A frequencies found in the inhabitants of Cadiz and in the Guanches of the Canary Islands, and the peculiar skeletal features of the latter, call for full Rh and MN testing of these populations. The Berbers with their high O frequency will surely prove to be related to one of the similar peoples in Europe, the Sardinians, the Basques or the north Atlantic islanders. Each of these has a different and readily recognizable distribution of the Rh groups. The Libyans, too, demand investigation, and ultimately when the difficult problems of organization have been overcome an examination of the nomads of the Sahara should connect the Mediterranean area with negro Africa along a continuous front. As to what will be discovered it is idle to speculate, as it is regarding the Rh groups of the inhabitants of the long stretch of coast from Naples to Cairo. Whatever is found is sure to throw fresh light on the relationships and movements of mankind

TABLE 1. Rh CHROMOSOME FREQUENCIES IN THE MEDITERRANEAN AND RELATED PEOPLES EXPRESSED AS PERCENTAGES TO THE NEAREST INTEGER

	Egypt	Iraq	Canadian Jews	Sardinia	Ferrara	Milan	Catalonia	Basques	Galicia	England	Latvia	India
CDe(R_1)	49	44	53	67	53	45	49	38	56	42	42	57
cDE(R_2)	9	15	12	9	12	13	11	7	11	14	18	10
cde(r)	24	27	27	22	25	38	38	53	25	39	35	25
cDe(R_0)	17	11	5	2	3	3	1	0	7	3	1	4
Cde(R')	0	2	3	0	6	1	0	1	0	1	2	4
cdE(R'')	0	1	0	0	2	0	1	0	2	1	1	0
CDE(R_z)	0	0	1	...	...	...	0	0	0	0	0	0

These figures are based on the papers listed in the bibliography. In most cases chromosome frequencies have been recalculated by the author of the present paper.

CONCLUSIONS

We may sum up the ABO distribution by saying that B is high in the east of the area, and A and O in a somewhat patchy manner high in the west. As in some other areas of continental dimensions, the Rh groups seem to vary less than the ABO and a very clear Mediterranean distribution of Rh groups emerges of which the extreme type is found in Sardinia. The important work of Morganti, Panella and Cresseri (1949) in this island has indeed served as a point of reference in the whole of the present study. It might have been expected that in an island the rather extreme ABO, MN and Rh distributions would prove to be the results of random fluctuations of gene frequencies in a small and isolated population. On the contrary, however, had we not the actual results of the observations carried out in Sardinia it would have been necessary to postulate a primitive Mediterranean race with almost precisely such an Rh distribution.

in what is beyond dispute the most important area in the world from the standpoint of history.

SUMMARY

Blood group A shows high frequencies in the European lands bordering the Western Mediterranean and in Greece. Group B has a high frequency all around the Eastern Mediterranean. The Sardinians, the Basques and certain Berber tribes in North Africa have a high O frequency. The Rh blood groups of the Mediterranean lands differ considerably from those of Northern Europe. Two main strains can be recognized, typified by the Basques with high cde(r) and the Sardinians with high CDe(R$_1$). These, together with a north European and a negro strain, are sufficient to account for the Rh groups of all the Mediterranean populations yet examined.

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DISCUSSION

BUZZATI-TRAVERSO: I wish to comment on some points in Dr. Mourant's paper. (1) First, regarding the occurrence of a peculiar dialect in the province of Bergamo and its correlation with a high r frequency, I think that one cannot rely on such coincidence to draw conclusions on the origin of such population. In fact, approximately the same gene frequency occurs in the provinces of Brescia and Torino (according to Morganti's summarizing paper), where the local dialects do not show any phonetic peculiarity. (2) In connection with such high frequency of r in the neighborhood of the Alps as compared with the low frequency of the same gene in Southern Italy, I wish to call attention to the interrelationships between the distribution of gene frequencies and demographic factors, since it seems to me likely that the cline in r frequencies throughout the Italian peninsula might be brought about by the higher fertility of Southern populations and by their corresponding migration towards Northern regions. (3) In connection with the peculiar distribution of blood groups in Sardinia, I would like to stress that the *m* gene has a frequency of 0.75, as compared to 0.55 of other Italian populations, and that this fact might be of importance if taken into consideration together with the high frequency of thalassemia minor. (4) Concerning the point raised by Dr. Dobzhansky on the validity of Darlington's

theory of the genetic component of language, I would like to point out that in respect to the threshold value of 68 per cent O gene frequency chosen by this author to discriminate between populations having the "th" sound in their language, Italy represented an exception, as it was considered to have just that frequency. The maps shown by Dr. Mourant, however, show that Italy shows a lower frequency of O group, and therefore this might be considered as evidence in favor of Darlington's ideas. I would like to add, however, that I have tried to check such theory on the population living in the province of Belluno, the dialect of which has a typical "th" sound. A sample of some thousand individuals gave a gene frequency for O of about 62 per cent, this not being in accord to the said theory.

MOURANT: (1) If indeed the slightly higher r frequency in Bergamo above that found, for instance, in Milan, is significantly so, it is not surprising to find that the increased frequency extends beyond the present limits of the Bergamasque dialect as it does beyond those of the Basque language. It would be most interesting to know whether any or all of the very high r areas also show significant deviations in their ABO frequencies. I do not however regard the coexistence of a high r frequency and a peculiar dialect and physique in the Bergamo region as anything more than a hint to guide future research.

DOBZHANSKY: It may be useful to clarify here an issue which, I believe, is a purely semantic one. The blood group distributions in the Mediterranean area can be described as resulting from mixture of racial "elements" approached by the present inhabitants of Sardinia, the Basque Country, and Africa. These "elements" may easily be mistaken for the "primary" or "pure" races of classical anthropology. In Dr. Mourant's usage, there is however no implication of any such assumption of race purity in bygone days. The "elements" are simply the extreme points in a multi-dimensional surface of gene frequencies. Ancient human populations were polymorphic, just as the modern ones are, although the genetic variance has probably grown in recent times owing to greater mobility of populations and their consequent mixing.

MOURANT: I am entirely in agreement with the speaker. In the title of my communication I deliberately applied the term "Mediterranean" to the area and not to the peoples so as to avoid any implication of identification with a race or races in the sense of the older anthropology. I do not regard the "elements" which I have used in my attempted analysis as anything more than rather extreme but transient integrations in a constant process of mutation, selection, genetic drift and interbreeding. I shall endeavor in revising my paper for publication to correct any suggestion that these "elements" have any absolute connotation.

KEMP: The blood-types are rather constant, and probably no certain exceptions from their regular inheritance are known. But still during generations it may be supposed that new types arise through mutations such as A_3, A_4, etc. and a long time ago type A and B are supposed to have arisen through mutation from type O.

MOURANT: The presence of all the groups A, B, and O among the great apes, and of A-like and B-like antigens in a variety of mammals, suggests that these groups may have been present in the human stock from the beginning. I personally support the suggestion of Boyd and others that this was so, and that the present distribution is mainly the result of local genetic drift at a time when man was a rare animal. This does not exclude the possibility that a very small amount of mutation is taking place between the three major genes, as well as mutations from O or A_1 to A_2, A_3, and A_4; or that there is a slow selection on a geographical basis. The almost complete limitation of A_2 to European, African and South East Asiatic populations suggests that the A_2 gene is also an ancient one; though in this case again, selection in relation to the geographic environment might account for the distribution.

HUNT: I think that not only simple genetic traits, but complex morphological features, may have differential potentialities for survival in a population. In man, where the history of a racial group is unknown, this may be an important source of error in the anthropometric study of living populations.

MAYR: The analysis of the geographical distribution of blood groups provides a magnificent means for the study of the history of human populations. Dr. Mourant has applied this method most effectively to reconstruct the migrations of peoples in the Mediterranean area. If the blood group genes are not neutral, but represent another case of balanced polymorphism, as appears now possible, the usefulness of this method will be particularly great to demonstrate migrations in the recent past before selection has had an opportunity to change the ratios too drastically.

MOURANT: A full consideration of the effect of selection on blood group frequencies would require a paper to itself. The effect of hemolytic

disease in eliminating the D gene in most countries which have both D and d genes is well known but it is probable, as suggested by Fisher and by Wiener that this is compensated, at least in part. There is probably a similar selection against the A and B genes in favor of the O gene due to direct effects of maternal immunisation. Hemolytic disease due to the Rh factor is accompanied by a selection of A and B and against O. The mechanism of the latter effect is unknown but its existence as shown by the statistics of numerous workers is beyond doubt. The Kell gene (K) is also being selectively eliminated. There ought soon to be plentiful data available for the calculation of the magnitude of the above effects but not perhaps for the size of any compensatory effects.

In addition to selection related solely to the blood group distribution in the population there may be selective influences of the external environment on the blood groups, especially perhaps on the MN groups as Dr. Race has just suggested. Much more information on the whole subject could probably be obtained by large-scale testing of populations and families.

Until such information is available some reserve must be maintained in using blood group data as evidence of population movements and mixing which may have taken place more than about one thousand years ago. There is considerable evidence that blood groups can be used almost unreservedly for tracing events in the last few hundred years, and strong indications such as those detailed in my paper, that they can apply to happenings in a much more distant past. If further work shows that the different blood group systems give consistent results this will be strong evidence for the slowness of any selective action. On the other hand anthropological evidence may serve to show that selection is acting much more strongly in some blood group systems than in others.

MONTAGU: Dr. Mourant has called his paper "largely speculative." If it may be so described I think we would all agree that the more we have of such speculation the better. In America "speculation" is frowned upon, so that to make Dr. Mourant feel more at home I should like to tell him of a "speculative venture" carried out by Dr. W. C. Boyd and myself in 1944 or 1945. We were interested in discovering where Rh-negative may have originated. We therefore drew up a "weather-map" of the genic distribution of Rh-negative. The resulting isogenic map led us to conclude that Rh-negative originated in Southwestern France. We conjectured the period at about 50,000 years, and the population probably a Neanderthaloid-like (!) one. I hope there are no Basques here, but I think you will agree that we were remarkably close to the facts in our "speculation." If we can do this sort of thing with the distribution of serological characters, I believe it will be generally agreed that they are not without value in the attempt to reconstruct something of the genetic history of man.

MOURANT: I am most interested to hear that Dr. Montagu and Dr. Boyd had independently concluded that the climax of Rh-negative frequency should be sought in Southwestern France. Somewhat later, on different grounds, namely their ABO blood groups and their physical anthropology and language, I had suspected that the Basques might represent the high Rh-negative population postulated by Haldane and by Wiener and I had made arrangements to obtain specimens of their blood, but before I actually received the specimens which proved my assumption to be correct I became aware that Etcheverry had already shown it to be true in 1945; but his work remained unknown to most English-speaking workers until 1947. Vallois and other workers have stated that both the Basques and certain inhabitants of the Dordogne show a considerable skeletal resemblance to Cro-Magnon man. Not all anthropologists would agree to this precise attribution.

SANGHVI: A word might be said about the column "India" in the table of the Rh chromosome frequencies. Our study of the distribution of Rh factor in Bombay, mentioned by Dr. Mourant (1945, Nature, Lond. *155*: 427) constituted a sample of 100 individuals of which only two were Rh-negative. One of these Rh-negatives was among the 14 Parsees and one was among the 11 Indian Christians. All 70 Hindus in the sample, which consisted mainly of Marathas, were Rh-positive. Our later work (1947, Ind. J. Med. Sci. *1*: 45) on the distribution of Rh factor in Parsees, Indian Christians and Marathas with a sample of 200 individuals each, showed eight per cent Rh-negatives among Parsees, six per cent among Indian Christians and 1.5 per cent among Marathas.

The situation has however completely changed by our subsequent study (1949, Ann. Eugen. *15*: 52–76) mentioned at the end of the paper read by Dr. Race. Among the six endogamous groups belonging to the Hindu community, the range of variation is from 12 per cent Rh-negative among one endogamous group to 1.5 per cent among another. On the basis of this study it might be stated in a general way that the future studies on the distri-

bution of genetical characters of the people of India, should take into careful consideration the endogamous groups.

MOURANT: The Indian Rh chromosome frequencies quoted in my paper are based on the only two studies of Indians using several anti-Rh sera, those of Wiener, Sonn and Belkin (1945) and of Prasad, Ikin and Mourant (1949). In the latter paper we made it clear that we were aware of the great heterogeneity of the population of India and quoted previous observations showing wide variations in the frequency of the Rh-positive and Rh-negative groups. I am at present collaborating in further studies in which much fuller details, including those of caste, are being recorded.

TORTORA: Over a random population of 1,006 people studied in the Department of Obstetrics and Gynecology of the University of Naples, we found 8.7 per cent of Rh-negative. We are now extending our research to the different provinces of Campania. The results will be presented at the next meeting of the International Society of Hematology in Cambridge, England. As concerns Sardinia, according to the data collected by Morganti (in press) there is a significant difference in the Rh-negative distribution between the two provinces of Cagliari and Sassari. The Rh-negative distribution in Cagliari is almost the same as in Naples and Sicily. It must be referred to the different ethnical constitution of these two provinces.

MOURANT: I am interested to see how the observations of Dr. Tortora and numerous other unpublished observations on Rh groups in Italy, recently sent to me by Dr. Morganti of the Institute of Human Genetics at Milan, give general support to my suggestion of two main stocks having contributed to the present population of Italy.

THREE GENERAL TYPES OF RACIAL CHARACTERISTICS

WILLIAM C. BOYD

Boston University School of Medicine, Boston, Massachusetts

Earlier papers given at this Symposium make it quite clear that most anthropologists would prefer to be able to base their classifications of mankind into races on hereditary characters inherited in a known manner. Characters which are clearly not inherited and are due solely to accident, or to environment, such as cultural traits, will not appeal to the physical anthropologist. For unless the traits we use are physically inherited, any racial classification based upon them may only too likely prove to be impermanent, shifting structures built upon foundations of sand. What is characteristic of a race today should also be characteristic of its descendants some generations hence, allowing only for mixture with other races in the meantime.

One reason the physical anthropologist wants a classification based upon inherited characteristics is that he hopes his classification will tell him something of the history of the human species. Morant (1939) said that "the main aim of physical anthropology is to unravel the course of human evolution and it may be taken for granted that the proper study of the natural history of man is concerned essentially with the mode and path of his descent." It may well be doubted that all taxonomists would agree that this is the sole reason for wanting a sound classification, but it is certainly true that the problem of human evolution intensely interests most anthropologists.

Interest in human evolution has in the past led to a great preoccupation with ancient human remains, such as skeletons and skulls, for these are best preserved, since they are hard, and can often be measured with a high degree of precision. Other writers have noted, however, that the form of the bones and their external characteristics are affected by the muscles attached to them, and Washburn (1945) has pointed out how the absence of one or more of the usual attached muscles may result in the absence of one of the characteristic features of a bone. In such a case, clearly, we are left wondering if that feature of the bone is really inherited. What the organism inherits is a developmental scheme, including the growth of the bone and the attached muscle. The bone responds to the attached muscles by altering in a characteristic way.

It has further been pointed out that it is altogether probable that the final morphological features of any organ or bone are the end result of the action of a number of different genes, acting in a given environment. And in many cases it seems certain that environmental factors, such as the calcium and vitamin content of the diet, do affect the final result considerably. Neel (1950) has pointed out how a human gene producing the blood condition called thalassemia produces also characteristic alterations in many of the bones. R. A. Fisher (1950), in his work on the genetics of poultry, obtained from poultry breeders a considerable number of chickens bearing dominant genes (Fisher, 1930). Most of these were identified by external features, such as comb shape, distribution of feathers, etc. Nevertheless Fisher found, apparently without exception, that all these genes affected also the skeleton of the bird, in some cases slightly, in some cases markedly. Some of the skeletal changes produced were so great that a paleontologist, presented with the skeletons but with no other data, might have given two different specimens the rank of different species, or at least different races, although they differed only in that one possessed, while the other did not, a single or perhaps a double dose of a single gene.

Our knowledge of the genetics of skeletal structure in man is even less satisfactory than it is in poultry. It may be asserted pretty safely that no single human bone, or bony structure, has been shown to be controlled by a single known gene. Genetic analysis of skeletal features in man is still something for the future.

Before we undertake to suggest how such analysis could be carried out, we may pause to consider the question which a student might possibly ask us: Why do you want to know the exact genetic mechanism of skeletal features, if you are convinced—and I suppose we should admit that by and large we are convinced—that they are somehow really inherited?

There are a number of reasons why we prefer to know the exact genetic basis of the features we use for classification.

a) In the first place, unless we know the mechanism of inheritance, we can never be really sure

that a certain feature X, occurring in population A, is the same as the seemingly identical X which we observe in population B. They may be caused by different genes or combinations of genes. And it may be that individuals of population C, although not exhibiting the X character, nevertheless do possess on the whole five out of the six genes required to produce X, and are therefore constitutionally very similar to those members of population A which do have the X characteristic.

These principles could be illustrated by a number of examples. Alvord (1947) in analyzing two unrelated families, both of which displayed in some of their members syndactyly or zygodactyly, or both, concluded that a number of genes was involved, and that the mechanism of inheritance of the abnormality was not necessarily the same in the two families. In addition, rather marked differences in the expression of the gene (or genes) were found, so that some phenotypically normal members could transmit zygodactyly or syndactyly or both, and polydactyly could be transmitted through an individual who was non-polydactyl but was zygodactyl, and so on.

b) Another reason for knowing the genetic mechanism is that it makes possible accurately quantitative comparisons between different populations. This is not usually possible from phenotypic frequencies alone. Suppose we have two genes, A and a, the first dominant over the second. If we find the percentage of the A-appearing type in one population to be 19 per cent, whereas in another it is 91 per cent, we might be inclined to say that the A character was 4.8 times as common in one as in the other population. But the A-appearing group included both the genotype AA and Aa. The gene frequencies are calculated very simply. In the first case the percentage of aa (the recessive) equals 81, and

$$\text{the frequency of a} = \sqrt{.81} = 0.90$$

Consequently, the frequency of A = 0.10.

In the second case,

$$aa = 0.09, \text{ the frequency of a} = \sqrt{.09} = 0.3,$$

and the frequency of A = 0.7

Consequently the true relative frequencies of the A gene in the two populations are 0.7 and 0.1, giving the ratio $\frac{0.7}{0.1} = 7$, a value considerably greater than estimated from the phenotypes alone.

Thus it is easy to see that a map of gene frequencies, rather than phenotypes, might enable us more easily to draw sound conclusions as to geographical distributions of the characteristic, and thus provide a better foundation for speculation about its distribution in earlier times, and so give us some guide to the evolution and formation of the present races.

In addition to quantitative comparisons of two related races, a knowledge of gene frequencies enables us to compute the degree of mixture which an originally "pure" race has undergone. Thus Boyd and Boyd (1949) found in the Navaho a percentage of blood group A of 23.3, while Allen and Korber (1935) found 26.4. If we assume that the difference is due to white mixture in the Indians studied by Allen and Korber, we may compute from the gene frequencies for A that p = 0.124 and 0.148 (if we assume the whites involved had a typical frequency of p = 0.281) and that the Indians of Allen and Korber had

$$\frac{0.148-0.124}{0.281-0.124} \times 100 = 15.3\% \text{ white mixture.}$$

The genetic analysis of racial characters has proved easier in some cases than in others. We may consider three general types of racial characters. We begin with those easiest to analyze, without intending to imply that they are of any greater value than others which are at present more difficult.

1) Genetic analysis of useful racial characteristics was first accomplished in the case of the blood groups. The greater ease in achieving this may be accounted for by various facts. The classical blood group genes, at least, exhibit complete penetrance and uniform expressivity, in all known environments. Each gene produces at least one distinct antigen. Reagents were naturally available (in normal human blood) to detect two of these three antigens. This enabled all individuals to be classified into one of four groups,—the familiar ABO blood groups.

It soon became evident that blood group O was serologically (with reagents then available) simply the absence of A and B, and group AB consisted of individuals whose erythrocytes contained both. The idea that A and B were dominants was soon thought of, although the theory of two independent pairs of factors, *A, a* and *B, b*, proposed by von Dungern and Hirszfeld (1911), was not correct, and Bernstein's (1925) theory of triple alleles, *A, B, O*, when proposed and tested, proved to be correct. It is interesting to recall that Bernstein (1945) was led to try the hypothesis of triple allelomorphs, not because he was especially interested in blood groups, but because he wanted to find an example of an inherited trait in man

which demanded multiple alleles to explain it. After experimenting rather unsatisfactorily with certain recorded human traits, he turned, more or less by chance, to blood groups, and found the example he was seeking. The theory was tested not only by family studies, but by statistical studies of populations.

From the principle of random mating, it is easy to show (see Wiener, 1943, and Boyd, 1950) that if the blood groups are inherited as a pair of independent factors, as supposed by von Dungern and Hirszfeld, then this relationship should hold between the frequencies of the various groups:

$$\overline{O} \times \overline{AB} = \overline{A} \times \overline{B}$$

(the bars above the group symbols show that frequencies, not percentages, are being used.) Tests made on reliable data from various populations show that this relationship is far from satisfied.

At the same time Bernstein pointed out that a statistical test of his theory, based on the same data, did indicate that his theory of three alleles fitted the data, for it was found that in no case did D/σ exceed the value of 2.000, which it might do by chance, in otherwise reliable data, once in twenty times.

Analysis on the M, N blood types was not difficult (Landsteiner and Levine, 1928), and when the more complex Rh types were discovered, genetic analysis kept pace with successive discoveries, so that contemporary theory can account for all the facts known at present.

In retrospect, it may be said that one of the conspicuous features, which made genetic analysis of the blood groups easy, was the all-or-none effect of the genes, so that scoring individuals and families for genetic study simply involved writing pluses or minuses, without any measurement.

The genetic analysis of certain abnormal human traits preceded that of the blood groups, and Farabee (1905) showed, by study of a large Pennsylvania family, that brachydactyly was inherited as a Mendelian dominant. Since then many other characters have been studied, and the work of investigators such as Böök (1950) and Kemp (1950), presented at this Symposium, shows how such characters may be analyzed. Nevertheless, in certain cases some doubt remains about the genetic mechanism, or penetrance or expressivity are incomplete, thus complicating the picture. In any case, all of these abnormalities, with the exception of thalassemia and sickle-cell trait, discussed by Neel, are too rare in all populations to be of much use to the anthropologist. To demonstrate convincing racial differences, prohibitively large population samples would have to be examined.

2) The second general type of hereditary character is one which clearly divides a population into two major groups, but not quite as sharply as do blood grouping reagents. A good example is furnished by the ability to taste phenylthiourea, often called phenylthiocarbamide, and usually abbreviated to PTC, and ability to taste related compounds.

About twenty years ago Dr. A. L. Fox (1932) had occasion to prepare a quantity of PTC. As he was putting the compound into a bottle, some of it was dispersed into the air as dust, and another occupant of the laboratory complained of the bitter taste of the dust. This surprised Fox, who had been much closer to the scene of operations and had of course inhaled more of the dust, for he had perceived no taste. He was so convinced that the stuff was tasteless that he sampled some of the crystals directly, and found them as tasteless as chalk. The other chemist, nevertheless, tasted some of the crystals and found them to be intensely bitter. In an attempt to settle the argument which followed, other people were called in to taste the crystals, but they, too differed in their reactions. Some found PTC to be tasteless, and others found it bitter. Snyder (1932) and Blakeslee (1932) studied the inheritance of this taste ability, and came to the conclusion that the lack of ability to taste PTC and related compounds is inherited as a simple Mendelian recessive. Thus originated the discovery of another human gene pair, which we may designate as *T*, for "tasting," and *t*, for "non-tasting."

Tests of various populations revealed racial differences in the proportion of tasters. They also revealed sex differences which in some populations were quite marked. Certain groups of people, such as the American Indians, seem to consist of nearly 100 per cent tasters, although in other ethnic groups, as among the men in Wales, less than 50 per cent may be tasters.

It is of interest to anthropologists to speculate on the possible evolutionary significance of such a gene pair. Fisher, Ford, and Huxley (1939) tested the chimpanzees in the London zoo, and found that they too could be divided into tasters and non-tasters. This might suggest that the gene pair has been in the primate stock for a long time, and it also raises the problem of how both genes have been retained, since in the great time which has elapsed since our ancestors and those

of the chimpanzee split off the family tree it would have been expected that one of the members of the pair would have been eliminated by selection or genetic drift, or both. It may be remarked here that some explanation is generally needed for the presence of more than one allele at a locus in a population. Most genes are probably what Haldane designates as "transients," that is, they are either on the way up to 100 per cent frequency, or else they are on the way to zero. Nevertheless, polymorphism due to the presence of gene pairs and alleles is common in human populations. No less than six different mechanisms could, at least theoretically, operate to maintain polymorphism in a given case (Haldane, 1950). One of the easiest explanations to understand for the persistence of polymorphism is the possession by the heterozygote of a selective advantage over either of the homozygotes, and Fisher, Ford, and Huxley (1939) proposed this as an explanation of the persistence of both *T* and *t* in man and the chimpanzees. It is not known whether this is the true explanation.

Summaries of the racial incidence of the "taste" ability have been given by Parr (1934), Strandskov (1941), Gates (1946), and Boyd (1950).

Falconer (1947), who published the extensive data of Fisher, has shown that the sex difference in frequency of tasters, at least in the English population, is due to a sex difference in taste thresholds, and not to a difference in incidence of the two phenotypes in male and female.

The distinction between taster and non-taster, even when PTC solutions are used in the right concentrations (and PTC seems to make the sharpest distinction between tasters and non-tasters of all the substances whose taste is controlled by this gene pair) is not always absolute. If thresholds are plotted for a large sample, the curve is clearly bimodal, but some individuals occur at all the intermediate points. By use of different concentrations of PTC, different technics, or different taste substances, we may convert these intermediates at will into "tasters" or "non-tasters." This does not matter much in anthropological investigations, but it can be disturbing to the geneticist. It would seem that the tasting gene may show various degrees of expressivity in different individuals, or else modifying genes may operate. Which, if either, of these applies is not known. It may be worth while to observe that I have tested one family which appears to consist almost exclusively of such intermediate tasters.

It is true that we may obtain a bimodal curve, with a certain number of intermediates, if we plot the degree of expression of most other hereditary traits, even when we are sure that they are determined by a single gene pair, and the present author (Boyd, 1946) has shown that this can be done even for the blood groups, particularly when certain reagents are employed. But there seems to be a difference, doubtless not qualitative, but perhaps quantitative, between the two cases. By use of the proper reagents, all persons tested for blood group antigen A, for example, could be put without question into the category A_1 or A_2 (the much rarer A_3 and A_4 were not encountered). But in the case of PTC some doubt often still remains with certain individuals. This is really more the sort of result generally observed in genetics, and the blood groups constitute a fortunate exception. In other cases (Glass, 1943), however, the geneticist has no difficulty in distinguishing all possible homozygous recessives from all possible homozygous dominants, and even from all possible heterozygotes. The M, N blood types and the Rh system offer examples of this in man. This feature helps give them their unique anthropological usefulness. But in the case of PTC tasting, it does not seem that the perfect method of distinguishing even all non-tasters from all tasters has been found. Also, the subjective element involved makes this a more difficult trait to study, not to speak of the linguistic difficulties that may arise in some cases.

In connection with the possible evolutionary significance of the tasting gene, we may note that PTC, and probably most substances of this class, are anti-thyroid drugs, some of them of considerable potency. One of them occurs naturally and is found in considerable amounts in cabbage and turnips. However, tests on patients with goiter (Harris, Kalmus, and Trotter, 1949) do not reveal any difference from the normal in the frequency of tasters.

In view of the fact that practically all the genes investigated in lower organisms have pleiotropic effects, we must expect to find examples of this in man, and it might well be that the selective advantage of the *Tt* tasting type (if it is true that there is one) is totally unconnected with the ability to taste. Dr. L. C. Dunn (1950) has suggested that if tasters and non-tasters, from a reasonably homogeneous population in which members had on the whole the same life expectancy, were arranged according to age, a higher proportion of tasters should be found in the higher age groups, due to the differential elimination of homozygous non-tasters. Homozygous tasters might be eliminated too,

but since they are outnumbered about two to one—in our population—the net effect would be an increase in the ratio of tasters to non-tasters as the subjects tested got older. Whether the selective advantage, if it exists, of the heterozygote is great enough to be detected by such a method is unknown, but it should be tried.

We may conclude that the mode of inheritance of ability to taste PTC is known in its main outlines, but that a few details remain to be worked out. The trait, while anthropologically useful, thus falls in a less satisfactory category than do blood groups. However, it can hardly be doubted that further work will fully resolve the residual difficulties.

3) It does not appear that any other racial character has been as well analyzed as taste for PTC, so we may now turn to traits of the third, and more difficult class. Attempts have been made to analyze many racial characters, and we shall consider the results of some. We may first state some requisite conditions.

a) The character must be one which is all-or-none in expression, or else one which permits individuals possessing it to be divided into well-defined, fairly distinct classes, so that the individual's constitution can be recorded and codified. The differences must be clear and definite enough for different observers independently to classify the material and obtain substantially the same results.

b) The character, or its various grades, must segregate fairly sharply in families, so that genetic hypotheses can be tested against family data.

c) For the character to be anthropologically useful, its various grades must be identifiable in more than one population.

Spuhler (1950) has presented the results of family studies on three traits which appear to meet these conditions,—phlebograms of the anterior thorax, presence or absence of the peroneus tertius muscle, and the number of vallate papillae on the tongue. In all three of these cases he obtains good statistical fit with genetic hypothesis, although to explain the last example he is obliged to postulate the action of five alleles with increasing dominance going up the series. Spuhler's work is of a refreshingly new sort in anthropology, and if substantiated by the results of later investigations, will provide us with three new sets of genes for use in racial classification. In the opinion of the present author, it is precisely more of this sort of work which is needed.

At the same time, some of the possible pitfalls which yawn in front of the investigator of such new traits should be pointed out. It has been remarked that by assuming enough multiple alleles we can explain practically any sort of family data, and there is some truth in this, although from the example of the blood groups we may see that one could distinguish, in well studied populations, between multiple alleles and independent pairs of factors. It does not mean, however, that such theories should not be proposed and tested. For example, we know that the classical blood groups in man are inherited by a series of three, or probably four or more alleles, and that the Rh types are explainable by the assumption of eight or more alleles. In Drosophila even larger series of genes capable of occupying a given locus are known. The various possibilities can nearly always be worked out, if adequate family and population studies are available. In man, one is deprived of the great advantage of being able to make test matings at will, and the length of the generation is inconveniently long, compared to Drosophila. But progress has been made, and will continue to be made, in human genetics, especially as more properly trained workers begin to devote their time to it.

Another and somewhat more subtle error is possible. If one examines family material for a large number of traits to see if some simple Mendelian hypothesis will account for the results, some will fail to fit, and some will fit, within our standard levels of statistical significance. But some might fit by accident. And the larger the number of traits tested, the more likely this is, with limited material. This difficulty cannot be got around by altering the level of statistical significance required. The situation is somewhat similar to that in linkage studies, where, if we test for linkage between enough pairs of characters, we shall observe in one in twenty such tests, on the average, an apparently significant degree of linkage, purely by chance. In testing for fit to a theory of inheritance, there is the difference that we test, using Snyder's method, the goodness of fit of expected and observed categories in the children, and do not know how often we get such a fit by chance. In both situations there is a simple remedy: examine further family data, preferably from a different population. It is most unlikely that the same indication of linkage will be found again, by chance. If it is found, it is probably real.

Earlier workers have attempted the genetic analysis of other morphological characters, in-

cluding the cephalic index. But it is obvious that the cephalic index, which is a simple ratio, cannot reflect all the differences in cranial bone structure, many of which are almost certainly determined by genes the nature of which we know nothing. But it is not impossible that we could explain the shape of the skull and its component bones (supposing no environmental effects such as hard cradles and dietary deficiencies), if we studied also the attached muscles, and patiently identified units which were apparently acted on by one gene or genes, and not affected much by genes controlling other parts. (Of course we should always keep in mind the possible effects of a gene on almost any part of the body.) Such analysis would be difficult, but it is probably not impossible.

Some have warned us of the possible role in human inheritance of the "polygenes," using the word more or less in Mather's sense, or at least in the sense of multiple genes, any one of which has individually less effect on the phenotype than may be produced at times by the normal variation between genetically like phenotypes. Dr. Snyder, in his summary of the papers presented here on June 12, also mentioned polygenes. But I know from personal inquiry that Dr. Snyder did not mean, to paraphrase Dante, *Lasciate ogni speranza, i poligeni sono entrati!*

Before we say the shape of the head is controlled by polygenes, chiefly or alone, and that the situation is thus forever too difficult to analyze, we should exhaust the possibilities that it is the composite result of the action of a number of perfectly good genes. Permit me to make a somewhat fanciful illustration.

Suppose our investigator is dealing with a simple, relatively spherical organism. Suppose this organism possesses, on one side, a simple rather rigid blue foot, on another side a similar foot which is red, and on a third side another which is yellow. Different individuals or races might difier in the length of these feet. If our investigator were color blind he might attempt to characterize the various organisms by determining the diameter of the smallest sphere which could be circumscribed around each one.

Now, if the length of the feet of this creature could assume in each case only one of two definite values, the length being controlled in each case by the action of two allelic genes, then a number of the concentric spheres, which correspond to our cephalic index, could be the same, although in some cases the blue foot would be long, in others short, and so on. By using the device of the concentric sphere, and measuring something which is merely a net result of the length of the three feet, our investigator has pooled the individual variation of the feet, and got something which, although it has the advantage of simplicity, cannot easily be analyzed genetically, although the cause is just the action of six genes acting three at a time,—a situation which we deliberately chose as very simple.

Of course it might turn out that our organism possessed, not three, but thirty, or even three hundred, feet. And the length of each foot might be affected by any one or two of a series of some six to eight allelic genes. In such a case we might find genetic analysis of the "size" of the creature absolutely impossible. Yet this would not constitute an example of the action of polygenes, in the sense in which Mather uses the word. But it would be resistant to genetic analysis. Obviously, most rapid progress will be made if we measure or observe features which are controlled by relatively few genes. Sometimes a clue to genes acting in this fashion may be made from mere observation. It is hard to resist the impression, for instance, that facial characters and family resemblances are not dependent upon too many genes, or at least not on genes in very many of the 24 chromosomes. Otherwise the random shuffling which chromosomes (and eventually genes) undergo in inheritance would render it the exception, rather than almost the rule, for a child to be the "spitting image" of one of its parents or even an ancestor several generations removed. Of course the popular mind tends to exaggerate the degree of similarity, and to overlook differences, but the similarities are still often striking.

As an example of a guess which may eventually prove to have a sound genetic basis which is basically simple, we may mention body build. It has long been known that tall, linear individuals, and also short stocky persons, tend to run in families. Nor is this all the story. Human physiques can be classified, at least roughly, into types. The most fashionable method of describing body build at present is the method of "somatotyping" developed by Sheldon (1940). In this system each physique is given a rating, on an arbitrary scale, of the various amounts of three components, supposed to be basic, of body build. The details can be found in Sheldon's writings. It does not seem that Sheldon has yet concerned himself much with the problem of how these components behave genetically, as shown by the fact that a method of classifying female physique has not yet been presented fully to the public. Naturally, unless we can identify the same thing in the mother which we find in the

father, we can never get far in trying to find the mechanism of inheritance. In any case, it is not likely that there is just one gene for each of the seven grades of endomorphy, ectomorphy, and mesomorphy, nor is it to be supposed that Sheldon holds any such naive view. The actual genetic mechanism is likely to be different from this, and possibly more complex. But one thing which this new work does suggest, and which many have suspected all along, is that basic body build, as we see it at a given age in a given environment, may be profoundly affected by certain genes having large effects. The identification of these genes may not be impossible, and remains as a challenge for the future.

Certainly one may say that, until a genetic mechanism which determines the various somatotypes, in men and women, has been worked out, the breakdown of human physique into graded amounts of just three components is no better founded scientifically than the old Greek analysis of all substances into four "elements": air, water, earth, and fire. It is to be hoped that one or more of the proponents of the somatotyping school will soon begin studies on the hereditary basis of constitution.

As an example of a morphological feature which might prove simpler to analyze, and desirable to know about, we might take the shape of the nose. There can be little doubt that several genetic factors are involved, but we do not yet have sufficient information to tell us how many there are, or how they act. One also wonders how environment affects their expression. It has been suggested by Davies (1932) and by Thomson and Buxton (1923) that the shape of the nose is altered rapidly by the action of selection. Some clues to genetic effects have been found. Dr. Washburn (1947) informs me that the breadth of the nose is correlated, roughly at least, with the distance between the upper canines, and that if, for example, gorillas, chimpanzees, pygmies, and Europeans are arranged in order according to one characteristic, they will be found to be in the same order in regard to the other. Fischer (1926) has stated that in general the high European type of nose seems to be dominant over other types, and Salaman (1911) has supposed the narrow "Ashkenazic" ("Sephardic"?) types of nose, and also the "North European" nose, to be dominant over what he calls the more characteristic Jewish nose. Others have postulated that the "Armenoid" nose, supposedly originating on or near the Iranian plateau, is a dominant type, although it is possible that some writers on this subject have confused the phenomenon of dominance, which can be perfectly real, with the purely imaginary phenomenon which Laughlin (1948) has christened "genophagy." (This is the supposed replacement in a population of recessive genes by dominants, even though random mating in the population has already produced genetic equilibrium.) It is clear that the genetic analysis of noses has not progressed very far.

In order to make much further progress with this characteristic, it would be necessary, first of all, to devise some classification of nose form which could be coded and recorded. As an example of a nose classification which might serve as a starter, we might cite the classification proposed in Martin's (1928) *Lehrbuch der Anthropologie*. Martin considers first the nasal index, which varies somewhat with sex, but not as much as might be feared. This index varies considerably with race, and Martin gives a table of its values for various populations. But he also points out that the nasal index does not by any means tell us the whole story about a nose.

In the first place, some races, such as the Bushmen, have very concave noses, and the appearance of the nose is lower and broader than the nasal index suggests. In the second place, the shape and position of the nostrils must be considered. Martin gives fifteen ideal types of nasal profile, which we might use to begin with. But the fleshy lobes of the nose can also vary. Look at it any way you like, a good many types of nose are possible. But let us suppose that we have set up a classification into which we can fit any nose we come across.

The next task of the investigator, and one which strangely has often been ignored, is to find out, from a study of embryology and early development, how his classifications and his various types correspond with the actual facts of morphological development. Martin gives this question scant attention. But it may be confidently expected that investigation of the subject would enable the original "exhaustive" classification, which at first may have seemed so impressive but is often actually only superficial, to be emended, and a better and revised version, giving information of more fundamental importance, would result.

Now the student has the problem of trying to find out how many genes, acting in what way, determine, together with forces from the rest of the face, plus other environmental factors, the shape of the nose. The student will look for characters which segregate. For purposes of

orientation, he will examine a large number of families, and tentatively record certain characteristics, or certain developmental trends, which he thinks may be unit characters. At first this will be largely a matter of guess work. The observed data will be compared with the results predicted from various Mendelian mechanisms of inheritance, starting with hypotheses which are simple, and gradually working up to more complex mechanisms, as Spuhler did in the case of the vallate papillae of the tongue. Then there must come the period of accumulating sufficient data to prove or disprove each hypothesis, and of replacing discarded hypotheses by new ones. The idea of single gene pairs, with one of them dominant, recessive, or neutral, will be tested first for each feature believed to be a unit character. There can be few readers who do not know how to differentiate a dominant from a recessive gene, providing penetrance and expressivity are good. With a dominant gene, if enough families are studied, we shall find that parents without the character always produce offspring without it, whereas parents with it often, but not always, produce children with the character. A very common recessive may at first look like a dominant, since it will appear in several generations. Matings between parents both of whom display a character must always give offspring with it, if it is a recessive, but exceptions will be observed if the character is a dominant. The mating, heterozygote × heterozygote, for example, will produce 25 per cent of offspring, on the average, lacking the dominant character.

If a population can be divided neatly into two categories, one with and one without a character, studies of family material, if properly analyzed, will enable us to determine if the character we are recording is determined by a single gene, and thus test the simplest hypothesis about the genetics of the situation. Eight different methods have been proposed by various workers. They are 1) the "direct" or "a priori" method of Bernstein, 2) the "sib" method of Weinberg, 3) the method of "empty sib series" of Lenz, 4) the "sib method" of Fisher, and Mather, 5) the "proband method" of Fisher, 6) the "percentage affected" method of Haldane, 7) the direct estimation of segregation ratios of Haldane, and 8) the "Hogben method." The mathematics of these methods is summarized by Ludwig and Boost (1940). Some are more efficient than others, and some more laborious to calculate. The method of "maximum likelihood," as used by Hogben, seems to be the best statistical method of detecting rare recessive genes.

When the inheritance of a character is complicated, it is not always easy to decide whether its heredity is due to several gene pairs acting simultaneously, or to the action of a series of allelomorphic genes. Either may make a considerable number of genotypes and phenotypes possible. Sometimes mathematical calculations enable us to reach a decision. Consider two characters, X and Y, and let those who have X be represented by X+, and those without it as X-, and so on. Bernstein (1925), and Wiener (1943) pointed out that a necessary, but not sufficient, condition that the genes be independent is that

$$(X-Y-)\,(X+Y+) = (X+Y-)\,(X-Y+)$$

If the genes are not independent, but allelic, the left side of the equation could be greater than the right. But in the case of alleles, the frequency of the X+Y+ type cannot exceed 50 per cent. Also, $\sqrt{(X-)} + \sqrt{(Y-)}$ must be greater than or equal to 1. If the left hand side of the above equation is greater than the right, but the frequency of X+Y+ is greater than 50 per cent, then the characters X and Y are probably complex characters determined by a single gene, each of which, however, produces more than one effect. Examples of this in human inheritance are found in the Rh series of genes.

Family studies also help one to decide if alleles are involved. For example, if we think all the genes involved in the determination of a character are alleles referable to a single chromosome locus, we may examine the offspring of homozygous recessives. They cannot produce more than two classes of children, since they contribute only recessive genes all alike. If more than two types result, the hypothesis that all the genes are alleles must be abandoned.

Finally, when some hypothesis fits all the data from a large number of families, we have identified a gene, which we may label with practically any letter or combination of letters we choose.

Once a single gene is identified, the task of identifying others which may be alleles or which may have related effects becomes easier, but is by no means ended. One would predict that a number of genes would be required to account for the various possible noses, but the number might not be any greater than the series of genes now needed to explain the Rh system.

At each stage of the work statistical methods would be applied, both to the family data, to twins and sib pairs, and to population data. These

methods are already known to working geneticists, and are well described elsewhere.

Unless the mode of inheritance of nose form is very complicated, and unless incomplete penetrance and wide variations in expressivity, plus perhaps marked environmental effects, make the interpretation of data impossible, a determined attack on the problem should eventually give results. It can readily be seen, however, that it is likely to be some time before the genetic analysis of this racial trait is on a firm enough basis for us to use the results with the same confidence we display in making use of serological data.

We mightrefer in passing to attempts to analyze the inheritance of skin color. Davenport (1913), for example, devoted considerable time to this problem, but without complete success. He proposed a theory of the action of two sets of genes, without dominance, but cumulative, which seems a good beginning, but to be in need of some elaboration still. The theory is flexible enough to fit a wide variety of facts, but it does not seem enough to fit all the observations. Of course in skin color the effect of the environment, as in tanning, greatly complicates the problem.

In general, it is more difficult to analyze characters which vary with the age and sex of the individual. If sex linkage is involved, this may be an additional complication. But students cannot always be choosers, and if we wish to make a full study of racial traits, and wish to have the requisite knowledge to enable us to use them in the same quantitative way we can use blood group genes, we shall have to attempt such analyses. Unless we can carry them out, racial differences will in the future not be defined much in terms of the skeletal and morphological features used in the past, but future anthropologists will depend more and more on characters which have been analyzed, and the science of anthropology, in its progress, will by-pass the older morphological lanes. Which will happen will depend largely on the energy put into genetic analysis of the various sorts of racial traits, and on how intrinsically difficult the various traits prove to be.

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DISCUSSION

DUNN: I should like to revert to a suggestion which I made on Monday, namely, that one way of estimating the adaptive value of any gene is to compare the age distribution, fertility, fecundity and other elements determining its survival in the population, of individuals homozygous and heterozygous for it with those with the normal or other allele. In the case of taste blindness, it would be very simple to record the age of every subject. One could then construct a life table of tasters as compared to taste blinds and this could be done for many common and accurately scored genic differences. The adaptive value of blood group factors could be tested rather easily.

BOYD: I think that is an excellent suggestion and shall include it in the final version of my paper.

HUNT: In considering the inheritance of morphological features of the nose, embryology may be invaluable. The nose may be regarded as the outcome of the interaction of rostral segments, of processes such as the nasofrontal and maxillary. Even the field concepts which have so successfully been applied to the dentition may be of use in dealing with the entire nose and face.

BOYD: I agree.

MOURANT: It is most important that more markers should be sought and found for the human chromosomes. A promising field lies in physiological and biochemical characters such as tasting of phenylthiocarbamide. For instance, to name an even more toxic substance, dangerous to use in large surveys, one person out of four fails to smell hydrogen cyanide, a proportion suggesting a balanced polymorphism. Rare disadvantageous conditions involving the presence of recognizable abnormal urinary constituents may be paralleled by common PTO non-pathological variations in the urine, a field at present under investigation in the Department of Professor L. Penrose at University College, London.

BOYD: I agree that it is most important.

GENETIC ANALYSIS OF RACIAL TRAITS (III)

CONCLUDING REMARKS OF THE CHAIRMAN

C. P. OLIVER

University of Texas, Austin, Texas

The order of presentation of the papers in the program today has paralleled the procedure in the study of human genetics. Dr. Race has traced the history of the discovery of variant types, in this case the blood types. He has explained the genetic mechanism involved with respect to each blood type, and has presented data on the phenotypic frequencies and gene frequencies in at least one population.

After we know the method of inheritance for a trait and the distribution of the alleles in a population, we become interested in a comparative study of gene frequencies in this and other populations. Dr. Mourant has shown how this can be accomplished even though difficulties arise. Widely separated areas to the south and the north of the Mediterranean area have different blood type patterns easily distinguishable. The populations between the two main centers, on the lines of movement of people so that intramarriages might occur, present a more difficult problem. Isolated populations may supply the information necessary to determine the relationships.

If the number of genetic traits, or subdivisions of traits, available for the study of populations can be increased, the student of human biology will be more able to differentiate people into related but genetically dissimilar groups. He therefore seeks other usable traits for the study. Dr. Boyd has emphasized this need and has at the same time added a word of caution. The genetic mechanism and the possible effects of environmental factors have not been determined for many traits which are recognized to have a hereditary basis. Until these points are determined, the traits can not be used in racial studies with the relative ease of the blood groups.

The blood groups of man are well suited to the study of population differences and similarities. It has been relatively easy to work out the method of inheritance of the groups. Different observers can agree exactly as to the serological classification of any subject, as Dr. Boyd stated. Most of the genotypes can be determined exactly and it is possible to arrive at a reliable estimation of the gene frequencies in each population.

Eight main human blood groups have now been reported. Some of these have been discovered so recently that their use is not yet very widespread. Dr. Race has reported their methods of inheritance, as so far determined. The frequencies of the allelic forms of the genes have been determined for the population in England. Agreement is found between hypothesis as to inheritance and observations among groups and family histories. All of this has been clearly presented in Dr. Race's paper. The eight blood groups vary as to their availability for genetic studies. With some of the blood groups, an antibody has been found so that the presence or absence of one antigen can be determined but it is not possible to differentiate the heterozygote from one of the homozygotes by known serological tests. Sometimes the differentiation can be made by the study of family histories.

If it is at all possible, the investigator wants to be able to recognize the heterozygote. This genotype may on occasion prove to be a stumbling-block in genetic studies. It may be responsible for differences of opinion among workers on the relative phenotypic frequencies of some traits in separate populations. What a gene does under one set of internal or external environmental conditions may not be the same as that observed under different conditions. It is known that in some experimental organisms the dominance of a gene can be changed. For example, a mutant eye color, Punch, in *Drosophila melanogaster*, which behaves as a dominant in that the presence of one gene causes the trait, can be completely suppressed by adding a modifying gene to the genotype. The result is a normal-type eye. Another gene, which in homozygous form causes abnormal wings but which ordinarily can not be detected in a heterozygote, can be made to manifest itself if that heterozygote carries a gene which acts as modifier. Normally this modifier has no recognizable effect on the wing. If in human populations one group has a modifying gene which is not present in the other, the populations may differ phenotypically and yet not differ widely in gene frequencies in so far as the "primary" pair of alleles are concerned. The environment itself

may be the factor which influences the dominance between a pair of alleles. We should not expect this phenomenon to cause much trouble in population genetics but we must keep the general principle in mind.

So far the commonly used blood groups have not shown any evidence of an effect by modifiers. As new blood groups are added to the studies, though, we can expect to encounter some of the genetic phenomena found with experimental organisms. Two or more of the pairs of genes may produce some effects in common. In fact the Kell and the Rh types are both responsible for hemolytic disease. The relationship between the Lewis blood group and the Secretor, ABO, type is of definite interest. The possibility that the latter two are in an allelic series requires more checking. The known allelic series in some of the blood groups suggest the need for us to keep in mind that in some organisms series of alleles behave contrarily to the expected good and predictable behavior of multiple alleles as based upon earlier knowledge.

In some of the discussions, references have been made to series of alleles in Drosophila, maize and cotton. I want to add a little more about one series in Drosophila because of the several interesting phenomena associated with them. They show what might be encountered in any organism. The alleles are sex-linked. The first detected mutant at the locus was named "lozenge" because of the modified eye structure. At least ten alleles are described in the series, all recessive to the non-mutant or wild-type of *Drosophila melanogaster*. All of the alleles affect the structure of the eye because selection has been made upon this basis. They also affect other body parts. All except one allele causes modification of the pigment of the eyes, absence or anomalies of the pulvilli used by the flies in crawling on smooth surfaces, and abnormalities in the claws. All affect the internal reproductive structures, from abnormal shape to absence, in homozygous females. Deficiencies in certain of the structures lead to reduced fecundity and viability. Flies lacking pulvilli, for example, have difficulty emerging from pupal cases and trouble crawling away from the sticky food. Most of them die because they can not crawl away from their moist food, lacking the foot structures to make it possible. If this strain of flies is raised on very dry food, their viability is not reduced; at least they lived for the periods tested. Incidentally, this mutant type of eye has been found in another species of Drosophila and here also the pigment, pulvilli and genitalia were affected.

The ten alleles do not produce exactly the same phenotypes. Some affect all of the characters more strongly than do the other alleles. One allele may affect one character strongly and the other traits to a lesser degree. The alleles in various heterozygous combinations also show different degrees of interaction or dominance. To take just one example, two of the alleles cause total effect on all characters and are phenotypically indistinguishable. Yet they behave differently in compound with other members of the allelic series. The heterozygote lz/lz^{ss} shows a blending of traits or, for some, the dominance of lz^{ss} except for abnormal genitalia which is completely defective. The lz/lz^{s} heterozygote, however, shows heterosis, a reversion to or toward the non-mutant type, except for the abnormal genitalia.

Alleles, as they are usually defined, may even lack the simple chromosomal relationship which has usually been assigned them. Crossing over occurs between some alleles, but with a very low frequency. The alleles in the lozenge series apparently are distributed at three closely associated loci. A mutant gene at one of the loci will interact with a mutant at either of the three loci on the homologous chromosome.

Allelic series of genes have made possible the recognition of genic differences among populations where one pair of alleles had proved to be unsuitable for that purpose. This has been true with the Rh series and also with the MN series, as the authors of the papers reported today. The widely separated racial groups of Africa, below the Sahara, and of Northern Europe differ to a recognizable degree in the incidences of Rh positive and Rh negative groups. A greater difference occurs, though, in the gene or chromosomal type frequencies. The African members have a high frequency of cDe(R_o) whereas the European has a high frequency of CDe(R_1).

Complexity arises in the region between the two main centers; that is, the Mediterranean area. Dr. Mourant has described the pattern so well that it seems unnecessary to repeat his data. The need to study isolated groups of any area is emphasized by the report on the Mediterranean area. Basques have a very low B frequency and an extremely high cde(r) frequency. This isolate and Sardinia with its characteristic gene frequencies make possible plausible interpretations of the origin of other groups in the area.

Isolates are changing now and obviously did in the past. Migrations may cause the break down of one group where intramarriages by force or by peaceful means have occurred. New isolates may be formed by a portion of the conquering group,

or a small group of the population being pressed may cut itself off from the main population. The result may be that within time three groups isolated culturally are formed. Interbreeding units may also be formed by colonists who have migrated to another country and have kept their groups isolated from their neighbors. Approximately one hundred years ago colonists from Germany settled in three close areas of Texas. The people kept their old cultures and intermingled very little with other settlers of the state. Marriages in the area occurred principally only among members of the group. Family records collected in genetic studies show the intermarriages within the group. Many of the families are represented in more than one kinship of the genetic histories. The isolate is now beginning to break down. The younger generation is leaving the group and is bringing other peoples into their cultural group.

Human geneticists have been slow in increasing our knowledge about hereditary traits in man. Dr. Boyd has reminded us of this short-coming and has requested the aid of geneticists in adding to the number of traits which can be used in population genetics. It is always embarrassing to a geneticist to have to admit that often we have only a very crude estimate of the frequencies with which many of our hereditary traits occur in our population. Little effort is being made to correct this paucity of data. Some investigators are studying expressivity for certain conditions and attempting to determine the causes of such variations. The progress, though, is slow and the need is great.

The PTC taste deficiency has been used in studies of racial groups. Even though variations in threshold reactions are as yet genetically unexplained, the technique can be repeated and the testing of populations should be made. Individuals do not respond alike to the chemical. Some persons can not taste a 0.2 per cent concentration of the substance. Others can taste a 0.05 per cent or lower concentration of PTC. Investigations of family groups, among the racial groups, show that the genetic mechanism for the threshold differences can not be easily explained. Individuals who are tasters also vary as to whether they have a very bitter or only slightly bitter taste reaction to the chemical. Two heterozygotes, shown by pedigree analysis to be *Tt*, who taste a 0.05 per cent concentration sometimes differ as to whether the taste to them is very bitter or only slightly bitter. Family records have been collected in which both parents get a very bitter taste of 0.05 per cent concentration, and also in which both parents report only a slightly bitter taste. Both sets of parents produce children in both the very bitter and slightly bitter taster groups. There is still considerable work to be done on this trait in man but with as much as is known the trait can be used in the study of populations.

The gauntlet has been thrown to human geneticists. It is our privilege to determine more accurately the genetics of human traits, the more complex as well as the simple. If we can judge from the discussions of the past few days, the geneticists are aware of the scarcity of accurate data and the need to develop our knowledge about our traits so that a better analysis of human populations will be possible. Since isolates are beginning to lose their identities, it is necessary to use such information as we have to study the phenotypic and the gene frequencies in these populations. We can only hope that increased efforts by many workers will bring forth traits as well known genetically and as easily used by various workers as are the blood groups at this time.

RACE CONCEPT AND HUMAN RACES

HUMAN RACES IN RELATION TO ENVIRONMENT AND CULTURE WITH SPECIAL REFERENCE TO THE INFLUENCE OF CULTURE UPON GENETIC CHANGES IN HUMAN POPULATION

CARLETON STEVENS COON

University Museum, University of Pennsylvania, Philadelphia, Pennsylvania

INTRODUCTION

From the first appearance of life on earth until the Pleistocene period, the number of species of plants and animals progressively increased. Although the rate may have been variable, the effect was cumulative. No species lived in a vacuum; each had its part to play in the total ecological system. Between the plants and the animals of land, sea, and air, the complexity of these relationships must have increased with the numbers of species. Then, with the Pleistocene, appeared man.

Man brought with him something new, stemming from something old; a genetic capacity for cultural living. Uniquely among the animals he made use of fire, and learned to produce it at will. With his coordination of hand, eye, and speech organs through an expanded and elaborated central nervous system he further learned to make and use tools, kill animals, cook meat and coarse vegetables, make clothing, houses, and aids to transportation such as boats, sleds, and snowshoes. By means of these cultural achievements he was able to grow in numbers and to occupy all of the continents except Antarctica, and to live in every kind of environment.

Since the recession of the last ice man has learned to grow plants and to breed animals in captivity. He has greatly increased his use of fire, and added to it the control of other chemical principles such as the explosion of unstable substances and the release of atomic energy. With the expansion of man, the other animals dependent on the same terrain for their livelihood have decreased both in absolute numbers and in numbers of species. This decrease has proceeded geometrically when plotted against time, like the human increase which caused it.

What, then, of the evolutionary progression which manifested itself in an increase of ecological complexity? This may be conceived as having shifted to a new level in the regional diversification of man, and in the human division of labor within regional populations. All human populations have not shared this growth of cultural complexity to an equal degree. For various historical reasons, of which geographical limitation is the most obvious and most easily explained, some groups of people were still living, at the dawn of the twentieth century, in the same general cultural situation in which the ancestors of all human beings participated during most of the latter part of the Pleistocene.

Among such culturally archaic peoples the division of labor, which marks this new evolutionary level, is limited almost entirely to biologically dictated lines of cleavage. These separate many of the activities of men from those of women, of children from mature adults, and of mature adults from the very old. In parts of the world where agriculture, animal husbandry, and hand industry have been practiced for several thousands of years, another kind of division of labor has arisen, that between men practicing different occupations, trades, and professions. This division still follows biological lines to a certain extent. Most of the skilled, full-time trades are the concern of men, while women keep to a diversity of minor skills which they can practice in the time left over from the care of children and household duties. Which man follows what trade is only in a minor sense dependent on biology; the choice of occupations is culturally determined.

It is generally believed that the possession of a capacity for cultural living, and the increasing exercise of this capacity in terms of cultural complexity, have prevented human beings from splitting up into a number of genera and species. Although this point is subject to debate and disagreement, no one can deny that carpenters have failed to develop chisel teeth, and bakers paddle-shaped hands. Few could further disagree with the following premises: that the possession of various cultural items has enabled human beings to move into and inhabit certain extreme environments in which they could not have survived had

they come empty-brained and empty-handed, that the fact that their cultural equipment let them stay there at all exposed them to selective influences which they could not otherwise have undergone, and that the racial differences of their descendants thus require a cultural as well as a climatically selective explanation. Most would, I believe, admit that culture in the form of easier chewing requirements has had a permissive influence in the evolution of the jaws, teeth, and face, or that the recorded changes in the size of the human brain are in some way associated with increases in cultural complexity.

How modern races may have arisen in association with the cultural and climatic phenomena mentioned above is the subject of a recent book, entitled *Races*, in which Garn and Birdsell have joined me in exposing ourselves to the critical eyes, tongues, and typewriters of our colleagues (Coon, Garn and Birdsell, 1950). There seems to be little need to repeat those heresies here. The purpose of this paper is to explore a little further than was possible in that book some of the ways in which the culturally controlled activities of human beings can have had something to do with changes in the gene counts of various characters in different populations. As a concrete example I give the well known increase in dark hair in the total population of England owing to the expansion of the local population of the Midlands with the industrial revolution. As another I shall steal from my colleague Birdsell his example of the introduction of blood group B in northern Australia by Malay trepang fishermen. This could never have happened if the Malays had not had ships nor the Chinese a weakness for dried sea-slugs.

Returning to generalizations, we are interested in the capacity of a population as a whole to survive in its environment with the aid of its cultural equipment, at moments when the population is small enough and the externally selective influences strong enough to provide optimum conditions for genetic change. We are further interested in the capacity of such a population to increase in numbers, to push out or absorb other populations, and to change the proportions of certain gene frequencies within its own genetic pool, in response to cultural changes.

Many if not most of the phenotypical differences between categories of people which we conveniently label as races must have a genetic basis. The same is true of many other differences hidden from the naked eye, which fall more strictly into the physiological realm. These include capacities for resisting diseases and psychological capacities for group living. Energy, the ability to initiate action, the capacity for leadership, the capacity for teamwork under difficult situations, the capacity for aesthetic performances which will tide over group disturbances; these may have been more important from the standpoint of the evolution of man as a cultural animal than his stature or the shape of his skull.

Our primary interest is the study of how culture influences genetic changes in populations, but this study is possible only if we concern ourselves with individuals, for the genetic capacities of population depend on the separate capacities of the members of the group. These are of two kinds: the person's own culturally channelled ability to produce living offspring, and his ability by cultural means to influence group survival even if he himself fails to reproduce. It is this second capacity, most easily illustrated in our society by the celibate priest or nursing sister, that makes the group more than a collection of individuals.

What, in this paper, do we mean by culture? We mean the totality of human activities which involve the use of the hands, eyes, speech organs, and higher centers of the brain. We include all of man's voluntary activities directed toward his outer environment, including things and people. We include the subject matter of material culture, social anthropology, and aesthetics. Two procedures are possible. One is to review all categories of human behavior at all known times and places, picking out pertinent examples. Another is to move in terms of the strictly biological aspects of the problem, and to select examples of pertinent cultural behavior which fit into this framework. The second seems the more practical.

Here are the items picked on this second basis. (1) The selection of mates. (2) The ability of the mated female to produce offspring. (3) The ability of the offspring to reach the age of reproduction. (4) The reproductive longevity of the individual. (5) The ability of the individual to influence group equilibrium and group survival.

I. The Selection of Mates

Human opportunities for mating may be divided into two categories. The first is habitual, normal, socially approved mating, usually designated as marriage, which accounts for the great majority of sexual relations in all societies. The second is the temporary or irregular sexual experiences outside the marital bounds which nearly all human beings in all societies at one time or another enjoy. Both are involved in the genetics of populations and both are culturally controlled.

Concerning the first type of mating, I have already summarized this material in an earlier work, from which I quote (Coon, 1948, p. 602–603). The choice of spouses in any given social system follows one universal principle: the ideal or preferred mating is one which under normal circumstances will produce the minimum of disturbance to all persons in any way concerned. All marital codes forbid marriage of a man with his daughter or a mother with her son. Such unions would obviously produce conflicts within the family. Were a widower to marry his daughter she would be placed in the position of mother to her brothers, sisters, and herself, and grandmother to her own child; the whole system of relations in the family would be confused. It is a characteristic of codes and systems of law that there be no exceptions, no extenuating circumstances. This must be so or they would not work.

"Brother-sister marriages are disadvantageous for another reason. Wholly aside from the debatable biological results of such close inbreeding, human beings need to establish working relationships with people outside the immediate family, for purposes of sharing, and to have friends over the hill in case of famine. Then again, if half a dozen families are living together in a band and sharing food, the young people see each other every day and establish close personal adjustments. The boys and girls are all good friends and playmates. If suddenly the boys of a certain age grade go through a puberty ceremony, and then one of the boys marries one of the girls, her relationship to all of the other boys undergoes an abrupt change. She cannot be as friendly with all of the boys as she was before. Such habits are hard to break. It is far less likely to cause trouble in the camp if she marries someone in another camp whom she has seen but a few times at ceremonies, rather than every day, and if each boy in the camp brings in a comparative stranger from outside. Then the girl builds up her adjustment to her new husband and has none with his classmates to break. But one must not go too far afield for a wife; she must if possible have been brought up with the same language, the same general set of customs as the groom's sisters, or she will cause too much disturbance among the other women and perhaps among the men with her outlandish ways. If you find that among one tribe of people it is the custom to marry the mother's brother's daughter and in another the daughter of the father's brother, study the whole picture of how these people live, how they get their food, what is the seasonal work calendar of the men and of the women, who stays together at what time of year and for how long—and you will see that the rules which regulate marriage make sense. But remember, if there is a choice between two or more equally efficient sets of rules, the one selected may be simply a historically governed choice, like that of driving on the right or left. It matters less which side you choose than that you do it the right way."

Most marriages, then, take place between pairs of individuals belonging to closely similar but separate biological families, and similar but separate economically determined communities. The men from A take their wives from B, and vice versa. Often more than two communities are involved, but in any case the genetic pool is small, and genealogies repetitive. The system provides for the maximum variability of genetic combinations within these narrow bounds. This type of mating is particularly characteristic of people living in a hunting stage, and particularly significant for our inquiry, since no matter who we are or where we come from, each of us comes from a long line of hunters from whom most of our genetic structure is derived.

Among many agricultural peoples the communities are larger, and matings take place within the village. In such cases the girls are often secluded by the time they reach puberty, so that their interaction with the boys of their own age is reduced before marriage age. Ordinary village girls are seldom given to outsiders in marriage because relations between villages are in the hands of the village leaders or landowners, who marry within their own class among the families of the chiefs of other villages.

Among the camel-breeding desert Arabs, it is the custom for the young man to marry his father's brother's daughter. If someone else wants to marry her, he must first induce the legal potential spouse to yield. No one has calculated how many of these parallel cousin marriages actually take place in a given tribe, but they are probably frequent. The physical anthropologist knows that the Bedawi, with his narrow jaw and hawklike nose, is inbred. This inbreeding is based on sound cultural motivation. The kinship unit, in which all members are bound to avenge each other's deaths or losses of property, must be kept small and well integrated; this is important to people who live in small mobile groups and who spend much of their lives fighting over water and grass.

Arab society is a mosaic of interrelationships between a large number of economically interdependent but genetically isolated groups. The blacksmith, for example, is no kin to the other members of the camp. If raiders kill off his hosts

they leave him in peace, for everyone needs metal tools and weapons and no one can afford to kill the smith.

Beside the smiths one may list the Sloubbies, workers in wood and leather, and desert guides, the merchants camped with their customers and the agents of camel jobbers, who do likewise. No outsider marries or harms any of these. Now in such a system, if any of the various endogamous groups happens to have come from elsewhere, and to possess racial characters different from the rest, these characters will be maintained, and may in fact become symbols of class differentiation.

In India the caste system carries this ethnic division of labor to its extreme. Opler and Singh (1948) have described an Indian village of 1,400 inhabitants in which members of 26 distinct endogamous castes reside, and in which the services of a number of persons of other non-resident castes are required from time to time. Since the different castes have originated from different regions, a genetic differentiation must be assumed.

Another framework in which the division of labor in a society may be laid out is the class system. Here the accent is more on prestige, wealth, and authority than on occupation. Travellers and anthropologists have frequently noted differences in appearance between the upper and lower classes in stratified societies. The royal families of Hawaii and Samoa were noted for their great stature and bulk; Ibn Saud is a foot taller than most of his subjects. Bernal Diaz commented on the fair skin and fine features of Montezuma. The early conquerors of Bogota noted a similar difference between the nobles and serfs in what was to become the capital of Colombia. In our southern states before 1865, a distinct racial difference could be noted between landowners and their slaves.

As a rule marriage regulations keep social classes pretty much apart, but there are nearly always exceptions. Among the Kurds of Iraq and Iran, who, like Arabs, are parallel-cousin marriers, a brave young man who has shown himself worth ten men in battle, will be taken into the aristocracy. He will be given the daughter of a nobleman in marriage, and his children will belong to their mother's group. This reminds one of the familiar theme in European folklore, about the wayfaring stranger who slays the monster and marries the king's daughter, succeeding his father-in-law on the throne. As we have already pointed out in the case of village chieftains, in all societies in which a class system prevails, it is normal for members of the upper crust to marry persons of equal status from other groups, as exemplified by the royal marriages of Europe before World War I.

In societies in which, owing largely to geographical isolation, the royal house can find no neighboring potentates of equal rank with whom to exchange marital partners, its members may resort to close inbreeding, and even brother and sister marriage, as in Egypt, in Incaic Peru, and among the Azande. In such instances, when descent is matrilineal, the women of the highest class may take commoners as husbands, as in the case of the Natchez of the lower Mississippi valley at the time of the first European contact. The genetic effect of this on the class structure would of course be one of levelling.

In a patriarchal kingdom where monogamy is not required, the king may create a harem of several hundred young women, some of whom are but temporarily his wives. These ladies are, for the most part, the daughters of chiefs from the corners of the kingdom whom his majesty wishes to keep in order.

The harems best known to the western world are those of the Turks as they existed before the days of Mustafa Kemal; in these Circassian and Georgian girls were greatly in demand, and many pasha's sons married Caucasian slaves. That the Ottoman Turks have changed genetically during the last five centuries, as a result of their widely practiced outbreeding, and the absorption of local peoples, is more than likely.

Habitual matings in different societies may be monogamous, polygynous, or polyandrous, or any combination of the three side by side. Where marriage is polygynous one man alone has the legal opportunity of fertilizing two or more women, reducing the number of possible genetic combinations in the group. Where it is polyandrous, the woman has access to two or more husbands, thus, all else equal, increasing the possible genetic combinations, except for the fact that most co-husbands are brothers.

It should be clear that normal, habitual matings in human societies serve more than one purpose, just as most human organs have more than one function. The number of marital partners assigned to each individual depends largely on economic factors. In most societies each man needs a fully active wife, and vice versa. One is reminded of the story of the Indian in the northwest who took a young wife when his old one was too feeble to work, and who could not understand why the missionaries tried to break up his family. Among the

Ona of Tierra del Fuego, a young man may marry a widowed mother along with her daughter; both need to be fed. Among the Riffians a younger brother may inherit the wife of his deceased older brother, even when the woman is already twice his age and he already has a satisfactory younger wife. Among some Australian tribes the older men, who receive the finest cuts of meat from the younger hunters, get the young girls who have just ripened for marriage, while the young man just past initiation, who has a harder time finding food, may have as his first wife an older woman who knows the local ropes, and who can bring in more vegetable food and slow game than a young girl, newly arrived from another food-gathering territory.

Marriage customs have been known to change in response to cultural changes in other departments of life. Probably the best example of this is in the Old Testament. In the tribal days before the conquest of Canaan the children of Israel, who were pastoralists, followed the Arab system previously described. When they settled down as farmers in Palestine they developed large economically self-sufficient households with slaves, both Israelite and non-Israelite, and gers, or resident foreigners. The father of the family and his sons married among the women of the household, whatever their origin or provenience. Later, in the time of Deuteronomy when the position of Israel was critical and ethnic unity was essential, both the old patrilineal inbreeding and the later outbreeding were forbidden; the emphasis was on marrying Israelite women some kinship distance away.

We now come to the second kind of human mating, the temporary or extracurricular. Among most of the food-gathering peoples, whose standard marital arrangements we have already discussed, there comes, usually once a year but in some cases less frequently, a time of abundance, when a whale has washed ashore, when the cactus fruits are ripe, or when certain moths are laying their eggs by the millions in one place. Several neighboring groups who at other times live apart come together to share this bounty, and at the same time indulge in fun and games. The merriment includes a letdown of ordinary incest barriers, other than those between father and daughter, mother and son, sister and brother, and the like. Couples disappear into the shrubbery, and spermatozoa seek unaccustomed channels. This sexual outlet is not confined to simple food-gatherers, but finds its counterpart in many more complicated societies.

Another custom is that of lending one's wife to the honored guest. In Australia the stranger establishes his totemic affiliation to everyone's satisfaction, and is given the woman most suitable under the existing regular mating system. Among the Eskimo, the principal host renders a wife. Among the Lapps, mutual agreements made in advance regulate this. Here again exotic sperm is available. Probably, in most instances in most cultures, the stranger is only comparatively strange; he may fall within the existing genetic range, but exceptionally he does not. Witness blood group B among the Australians and the sons of explorers among the Eskimo.

Still a third device for escaping marital bonds is the custom of permitting promiscuity among adolescents before they settle down to marriage. This is best recorded for Polynesia, Micronesia, and Melanesia, and was also discovered in Central America by some of the early Spanish explorers. Among the Choroti young women were encouraged to have relations with a number of lovers. Eventually a girl's father gave her a piece of land as a dowry. Her masculine admirers built her a house on the land, and then she announced her choice from among the suitors. Some of the rejected lovers then hanged themselves from the house-frame, and their bodies furnished the meat for a bridal feast. At least, that is what the early accounts tell us. At any rate, it is commonly agreed that few children result from this period of promiscuity. Why this should be will be discussed in the next section.

Pre-columbian America has supplied us with other instances of unusual matings. The Tupinamba, who lived where Rio de Janeiro now stands, were warlike people, and brought home many captives. These captives were eventually killed ceremonially, but sometimes a year or two intervened between capture and execution. During this time the prisoners had intercourse with the young women of the village. The Aztecs, whose appetite for sacrifices was nearly insatiable, also used captives from distant villages, and again the victims were given access to young women during the period of deification before the grisly ritual. The privileged victim, like the honored guest, may have introduced new genes into the victorious population, as slave women have in many countries throughout recorded history.

In conclusion to this lengthy discourse on human mating, one may say that by and large the selection of spouses closely follows the social pattern concerned, providing definite limitations on the availability of sexual partners. Each indi-

vidual normally has the chance to copulate with several members of the opposite sex during his or her lifetime, nearly always avoiding parent-child and brother-sister unions, and fostering the spread of mutations within a limited circle.

While the selection of spouses follows the social pattern of a people, the social pattern itself follows other elements of their culture, notably their consumption of energy per capita and in single operations, their efficiency of transportation, the extent of their trade, and the degree of political stability which they are able to impose over wide areas. Under the Roman Empire veterans from Gaul and Britain could settle in Syria. Under the Arab caliphate Persians from Shiraz were induced to found Jerez, and Spain must still produce their genes as well as their wine. What has happened to the genetics of man in the New World since the days of Columbus, if we consider it in terms of changes of methods of transportation alone, needs no explanation. The tens and even hundreds of millennia during which our ancestors were hunters and gatherers provided optimum cultural opportunities for racial differentiation; which the ages of gunpowder, coal, gasoline, and atomic energy are reversing. To live in the modern world, we need other kinds of adaptation to which race may contribute its genetic share; not for particular environments and cultures, but for the climate and culture of a single, if unstable world.

II. The Ability of the Mated Female to Produce Offspring

Our next consideration is, what is the result of human matings? Do some women bear more children than others? Do some men sire more than their share? Statistics are notoriously lacking except for modern western society, where we know that differences do occur. A brief review of the facts about conception may be in order, even for biologists. Dr. Edmond J. Farris, of the Wistar Institute, Philadelphia, has been carrying on research in this subject for a number of years, and has made it possible for hundreds of childless couples to have offspring. In his book, *Human Fertility, the Male*, and in patiently answering my questions, he has given much help in this stage of the inquiry.

The human female ovulates once in each menstrual cycle, some 85 per cent of the time. Usually the ovaries alternate, so that if one tube is blocked, ovulation will occur once in two months. Most women ovulate between the eleventh and sixteenth day of the menstrual cycle, with the thirteenth the commonest. The ovum is available for a period of between two and twelve hours, according to different authorities. The sperm cell may retain its fertilizing power in the uterus and tubes for a period of 12 to 24 hours after copulation. This means that on only 12 days a year is fertilization possible.

What are the chances that a woman will conceive on any one of the 200 or so opportunities in her lifetime? Granted that she receives the sexual attention of some male or males during most of her reproductive life, much depends on the man. In Dr. Farris's random sample of 643 men, 30 per cent were incapable of producing offspring without medical assistance, and of the remaining 70 per cent only 39 per cent were rated as highly fertile.

The most significant fact about fertile men is that even they cannot produce fertile semen day after day. Highly fertile men fall below the critical level on the third day; less fertile men on the second. A highly fertile individual can recover enough sperm in six hours but most men require five days of sexual rest to recharge their procreative batteries. Therefore, even if a man is highly fertile, he has less than a 44 per cent chance of fertilizing his wife if he has intercourse with her every day after the end of menstruation; by the eleventh to sixteenth day, when ovulation is most likely, his sperm will be inadequate.

What cultural conditions permit the male to rest at the right moment? Obviously, some occupation that will separate him and his wife and keep him away from other means of sexual satisfaction. Among hunting peoples, and all of our ancestors were hunters during the critical period of human evolution, men leave the camp or village for days at a time after game. In Australia this is routine. Among the Ona described by Lucas Bridges (1949) the hunter leaves his wives and children and comes back several days later, if he is lucky, with a guanaco.

Thus human beings living on the simplest known level of cultural complexity fulfill the requirements of the organism for reproduction. Sedentary agriculturalists, at first glance, would seem less favorably situated. However, we need an ethnographic Dr. Kinsey to explore this subject. Among slash and burn farmers where the bulk of the agriculture is in the hands of the women, the men have a habit of going on hunting trips during times of the year when they are not needed in the village. Sometimes the hunting trip becomes a war party. In any case sexual abstinence is the rule on these expeditions, and the women receive the men enthusiastically on their return, especially if they

have been successful. Such happy reunions would seem optimum for conception.

Who else absent themselves from home for five days at a time or more? Camel nomads, and all other kinds of pastoralists where the men take the animals out for grazing. Fishermen and sailors. Although sailors are not noted for their continence, their sexual excursions are by necessity infrequent, and an adequate rest period in most instances seems probable. Itinerant specialists, like blacksmiths, tinkers, and entertainers; well diggers in Morocco who leave their families in the city or in their home territory of the Draa valley when they go out for work elsewhere; Hindu traders in Baluchistan who visit their wives in India only once or twice a year; the Aztec far-travelling merchants described by Bernal Dias.

At any rate, Dr. Farris has made it clear that frequency of intercourse is not positively correlated with fertility, but in a sense the reverse. This helps explain why oriental monarchs with hundreds of wives have so few children per wife. Dr. Farris' evidence also gives us a means of evaluating the relative potential chances of fertilization in different segments of a society which vary in occupations and other habits. On this basis alone we find a strong possibility of genetic shifts in and between human populations which vary in ways of making a living.

The age at marriage may again have significance. Once the male has reached his peak of fertility, at about 18, he levels off, and his spermatozoa count remains reasonably constant as long as he is able to have intercourse. If as he grows older his frequency of intercourse becomes less, then the rest periods would become longer and his fertility at any one instance increase. The young woman married to a graybeard may thus have a better chance of fertilization than if she had been given to a newly initiated young man. On the other hand it is essential that she be mated as soon as possible after reaching sexual maturity, since her fertility curve is not a flat one; if she does not bear a child during her late teens or early twenties she may be unable to later.

Several years normally intervene between menarche and full sexual maturation in the female. In societies which permit a period of sexual license for young people, as in parts of Polynesia and Micronesia, few children result from this adolescent intercourse. In some of the Polynesian Islands the girls wash themselves out with seawater, immediately after intercourse. In Yap, as the Harvard U. S. Navy expedition discovered, young women scratch the head of the cervix with leaves in an attempt to produce abortion, and also insert a poultice into the cervix (Hunt *et al.*, 1948).

Some of these practices render the young women infertile after marriage. In Ulithi (Lessa, 1950) gonorrhea is the chief culprit, while several kinds of infection are responsible in Truk (Goodenough, personal communication). It is no wonder that the populations of these islands are declining. Contraception and abortion, especially the latter, are no novelties, nor are they confined to western civilization. They are cultural practices which must be reckoned with in any study of fertility.

So must celibacy. It is a commonplace of anthropology that only in a complex society like ours can one find bachelors and old maids. This is not exactly true. Among most hunters and gatherers, everyone gets married sooner or later. However, among the Maidu Indians of California there was a class of celibate males who specialized in feather working, needed for the production of ceremonial objects. Berdaches among some of the southwestern Indians and "soft men" among the Chukchi were apparently individuals not suited for the rigorous life required by an adult male in those cultures. By failing to reproduce these men were unable to pass on whatever genes, if any, made them soft.

Quite different is the case of the celibate shaman or priest, common in many Indian tribes or nations of Middle and South America. In the old world, of course, a number of religions, including some branches of Christianity, provide for the sexual continence of specialists who at least on the more primitive levels have unusual emotional qualities. These men heal persons of both sexes and all ages at all hours. Marriage conflicts with this way of life. If the capacity for trances, visions, and other spiritual powers is inherited, the celibacy which culture imposes on many of them must reduce the frequency of whatever gene or genes may be responsible for this kind or these kinds of personality. The number of spiritual leaders needed may thus be kept to its optimum level.

What else can influence fertility? It has recently been claimed that diet is a factor. Drs. Carlson and Hoelzel, in a recent paper of which the only report I have seen is a press release by the dean of scientific reporters, William Laurance, show that inbred rats are least infertile when fed a diet rich in proteins and fat but also containing roughage. The diet of simple hunters and gatherers, including roots and wild seeds, berries and fruits, is rich in roughage. If this experiment means anything for man, it means that again our ancestors

over their long period of development had the maximum chance of fertility, while in the more complex cultures a considerable area of variation is possible. However, no one has proved that this applies to man at all. It is purely inferential. Dr. Farris is sceptical.

Disease can influence fertility, not only by its direct effects on the reproductive organs, but also by rendering the patient unattractive and unmarriageable. Two villages come to my mind, one in Morocco and the other in Iran. In each village there is one bachelor. In the first, the man is a stonecutter, the strongest man in the village. As a child he was infected with a local variety of spirochete which destroyed his external nose. No girl would marry him, and no father could force his daughter to do so. In the second, the man is a deaf mute. Unable to work, he lives on charity. It is unlikely that either of these men, however fertile, has ever produced or will ever produce offspring. Each of us can probably remember some such unfortunate celibate in our own native places.

Deliberate mutilation, which is certainly a cultural factor, can affect fertility. Castration, widely practiced in the higher civilizations of the old world, in some places so recently that man-made eunuchs may still be seen, has had the effect of limiting the introduction of alien genes into local populations, since the victims are usually foreigners. No one ordinarily castrates a member of his own community. Since most eunuchs are harem guards, it further restricts genetic variability. The Romans had a practice of inserting metal rings into paired holes in the foreskins of slaves, with presumably the same result. Among some Australian tribes, the practice of subincision, or slitting the lower portion of the penis, must lengthen the journey of the spermatozoa from the customary 180 mm. to at least half again that distance and correspondingly reduce the chances of fertilization. Since every male in the group undergoes the operation, its effect must be simply to reduce the birthrate in general. Ordinary circumcision, which is very widely practiced, can be a factor insofar as in the absence of sanitary methods the infant's penis often infects, and this infection may cause deformity or death. Many American missionary doctors are constantly faced with this problem, and some perhaps may have pertinent information.

The female organs are also mutilated in many societies. Removal of the clitoris is common. In some islands of Polynesia girls of the upper class have their clitoris constantly manipulated until it is stretched to a length of three or four inches. Among the Somalis parents have their daughters' labiae minorae sewn together at puberty, and leave the task of unlacing to the girl's husband, or to a barber under his direction. Tampering with the clitoris cannot seriously affect fertility unless it does so indirectly in influencing desire; the Somali practice at least keeps the girl from abortion and infection before marriage.

Several other factors may have something to do with fertility; these include fatigue, fear, the use of drugs, and temperature. Dr. Farris has shown by experiments on football players that extreme muscular fatigue has no effect on the fertility of the semen. It may, however, limit sexual desire in that the tired man prefers slumber to intercourse. In such a case, fatigue from long hours in the fields may provide the farmer with the seminal rest periods that the hunter and herdsman get by absence from home. It would not equally affect the sedentary skilled craftsman in the oriental or mediaeval city.

Fear, Dr. Farris finds, does not affect masculine fertility. It may, however, affect his desire for intercourse. Despite all that has been said to the contrary, Dr. Farris finds no lowering of fertility from the use of alcohol. It cannot be denied, however, that a certain amount of drinking may release inhibitions and promote extra-marital intercourse. Drinking is part of the ritual life of many simple agricultural peoples. Drinking to excess may have the same immediate result as fatigue or fear.

The effect of other drugs upon fertility has not, as far as I can determine, been adequately studied. Tea and coffee apparently make no difference. Quat is said to cause a leaking of seminal fluid. With cocaine, opium, hashish, etc., the field for investigation is open. One suspects that whether or not these drugs reduce the quantity of spermatozoa in a single ejaculate, they do affect the frequency of intercourse, and the frequency of intercourse has been shown to be an important factor in conception.

One other culturally imposed situation may materially lower the fertility of the male. That is the practice of raising the temperature of the testes to 41°C., or 105.8°F. MacLeod and Hotchkiss (1941) found, in an experiment with six men, that when the temperature of the testicles was raised from 40.5° to 41.0°C., the subjects were sterilized for periods varying from 22 to 55 days. The easiest way to raise the temperature of the testes to 41°C is to take a very hot bath. We were told in the Victorian period that too fre-

quent bathing was the downfall of the Roman aristocracy, and perhaps the Victorians were correct.

Hot baths are commonly taken by all the peoples of the Middle East, from Morocco to Pakistan. These are built on the Roman model. The ordinary working man is often able to bathe once a week, usually on Thursday, preceding his day of rest. The rich man may attend the *hammam* more frequently. From Norway to Greenland, and over much of aboriginal North America, steam baths are the rule. This type of bath, in which water is thrown on hot stones, and the bather lashes himself with birch rods, is best known to the western world as the Swedish or Finnish bath. The Japanese in particular take notoriously hot baths. It would not require very much research to find out what effect, if any, hot bathing can have on different populations or segments of populations.

It is clear that even while working on this speculative level we have uncovered abundant evidence to show that human reproduction differs profoundly from that of wild animals in that it is culturally controlled. Not only do economics and political convenience dictate the choice of a mate; work habits and warfare, conviviality, attempts to alleviate human sorrows, and efforts to keep clean may all have something to do with who produces how many offspring, if any. The chances for differential selection between individuals, groups of individuals within a population, and populations, are wide. Genetic differences between individuals, groups within populations, and populations, which may arise through mutation, mixture, and migration may well become accentuated or reduced according to historical circumstances, and history is a record of man's cultural experience.

III. The Ability of the Offspring to Reach the Age of Reproduction

Once the child has been born, it is immediately faced by its parents' decision as to whether or not it shall be allowed to continue living. Among some tribes the child is destroyed if the mother is still nursing an older sibling, and among others, some of the baby girls are killed. In both such instances scarcity of food is the guiding motive. In the latter, polyandry is a natural result, with the effects which we have already seen. Many peoples destroy twins, as in the famous attempt made on the lives of Romulus and Remus. All of these practices have the effect of keeping the population down, and the last mentioned, of course, of reducing the incidence of the gene for bearing twins.

Children are far less liable to the hazards of war and occupation than adults. If the camp is raided the chances are good that they will be taken captive, even if their parents are killed. The principal hazard that faces them is that of disease. This can be illustrated very simply. In Iraq in 1948 an expedition of which I was a member excavated a significant number of skeletons from two layers, 10th century Arabs and Achaemenians of the 5th to 3rd centuries B.C. In both series the number of infants and adolescents was high, but in the Achaemenian series the burials of preadolescents outnumbered those in the Arab series two to one. Why? The Achaemenians were invaders from the Iranian highlands. They were not used to drinking contaminated Euphrates water. Just the adjustment to this source of water, which would wipe out a European or American colony in short order unless boiled, must have played a strong role in selecting the genes of the Mesopotamian population. The racial composition of the rural districts of the Mesopotamian portion of Iraq has not changed since Sumerian times. It could not. The foreigners could not survive.

In 1898 Lucas Bridges, the son of the Reverend Thomas Bridges, missionary to the Yaghans, entered Ona-land in northern Tierra del Fuego. He made friends with and lived among the Ona, one of the most primitive peoples to survive upon the earth until that time. They never numbered more than a few thousands. By all the rules, they were due to die off, as the white man invaded their country with his sheep, rifles, rum, and diseases. In northern Ona-land this took place. But in southern Ona-land, which became Lucas Bridges' home, he was able to persuade these guanaco-hunters to work for him as shepherds at a white man's wages, and to keep them from drinking, and from being shot. By 1922 he had succeeded in converting a truly primitive people to a way of life in which they could compete with the white man on his own level. In 1922 measles struck, and again in 1929. These two bouts killed off 70 per cent of the Indians. If measles vaccine had been available to these people at those two times, the historical process might have been reversed.

This kind of selection, by immunity to disease, has been very important in the relations between white and Indian in North America as well. Stearn and Stearn (1945) have shown how much of the depopulation of the North American Indian before the whites reached them in numbers was due to

disease brought by the whites but advancing ahead of them. Indians who have established an equilibrium after reaching their lowest point have again increased, but these increases are again qualified by the pressure of whites who have filled in the land left empty. It would be interesting to see what would have happened if the whites had let a few centuries elapse between their infection and their occupation. In Mexico, Guatemala, Peru, and Bolivia, where the Indians lived in large, agricultural communities, the Spaniards with all their diseases were unable to dislodge them. In this respect the Indians were comparable to the Mesopotamians. This tendency of large, well-adjusted agricultural populations to possess a survival advantage over invading foreigners, and of invading foreigners who come from large agricultural populations over numerically smaller, more primitive peoples, can be a potent mechanism of evolution.

Other factors beside disease influence the chances of the child to reach the age of reproduction, but disease is so much more important than the others that it will suffice as an illustration. And disease, intentionally or otherwise, is culturally controlled.

IV. The Reproductive Longevity of the Individual

Our child has been begotten, born, and reared to an age suitable for marriage. The mere fact of its having lived so long makes it the product of a chain of selection. Its chances to reproduce now depend on a number of other factors, some of which have already been mentioned, and of which its span of life is one. Generally speaking, the length of life of the average individual in a population is a function of culture. The simpler the culture the shorter the life, the more complex the longer. All else equal, the longer the life span in the male, the greater the chance for reproduction. In the female the effective life-span for breeding usually ends before forty. Survival of the female past this age is still biologically effective, however, in that by her skilled efforts she may prolong the lives of her husband and children.

Choice of occupation may affect longevity. Hunting has its hazards, since the hunter may fall off a cliff, drown while crossing a stream, or die of thirst or exposure. Fishermen and sailors may be lost at sea, miners smothered and crushed by earthfalls. The smith may be kicked by a horse, or have a hot rivet dropped on his head. The young man who has learned a skilled trade may leave the village for the city, where he will rear his offspring. Selection in migration on an occupational basis is a well known cause of genetic change.

Warfare, too, is a mechanism of selection. No matter what the cultural pattern, some men are more eager for combat than others, and all are not equally exposed to enemy action. During the last war the Commandos and the Rangers, all volunteers, suffered heavier casualties than the regular infantry. In societies which are typically warlike and in which many young men are killed from each age group and each generation, selection against their type of personality is inevitable. If a society is stratified into classes, including warriors and drones, the result is obvious. The warrior is attractive to women, but he has less time to put that attraction to genetic use than the quiet man who stays at home. In most of the social systems of which we know in our own time, selection acts against the rash and the brave, so that the meek truly tend to inherit the earth. However, if we examine the most primitive surviving societies and project ourselves back into earlier times, it is possible to conceive a cultural situation in which human groups are very small, and in which every man may be equally exposed to enemy action, the enemies including ferocious animals as well as other men. Under these conditions the brave and the bold will have a higher survival value than the meek. During the history of man the individual survival value of the warrior temperament may have been reversed.

V. The Ability of the Individual to Foster Group Survival if not his Own

Whether or not the warrior succeeds in reproducing, his very death may turn the scales of victory, and increase the chance for survival of the group which he had died to defend. In this sense he puts himself in the position of the celibate priest whose capacity to perform ritual at the right moment has pulled the people together and given them the united strength needed to override a threatening crisis. It is possible that most societies need only a certain number of such powerful personalities as the warrior and the priest, and that the cultural mechanisms which may inhibit their reproduction have in themselves a social value.

Like the woman who cares for her family after menopause, the hero continues to affect his people after death, since he becomes a revered ancestor and a symbol to be invoked in times of stress. So

also with the saintly man, who may even affect the birth of children from the grave. A tomb may be erected over him, and childless women make pilgrimages to his shrine, thus giving their husbands time to rest and recover their powers of fertilization.

Finally, one must not forget the geniuses who invented the bow and arrow, the potter's wheel, writing, and all of the other great innovations through the steam engine, the airplane, the telephone, and the atomic bomb, who whether or not they have reproduced themselves, have profoundly influenced the reproduction of others, and hence the history of races. Gordon Childe was right. Man Makes Himself.

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DISCUSSION

ANGEL: (Answering criticism of Dr. Coon's *general* thesis that longevity increases with transition from simple to complex societies.) There is evidence for this thesis from the ancient world. Mean age at death of Greek skeletal remains rises from about 33 in early prehistoric times to about 40 in Classical to Roman times. Interpolating infant and pre-adult deaths from cemetery statistics suggests life expectancy increase from about 17 to about 21, a low value even after the increase.

When you mention in relation to human physical evolution such things as the capacity for leadership, or for aesthetic performance as priest or shaman, how definitely do you consider these to be inherited? Is it a fair restatement to say that society might modify hereditarily unusual, but not specific, temperaments in unusual, but not uniform, directions?

COON: Thank you very much for the added information on longevity. I will also agree that your restatement on the inheritance of personality factors is much safer.

BRITTON: What is the justification for saying that increase in life expectancy of man is referable to increasing complexity? Do not medical advances have quite a part in this matter? Also, does not increasing complexity of life mean increasing irritability and instability, and the latter, or greater instability, lead perhaps to earlier death rather than longer life?

COON: I include medical advances in my definition of complexity. Concerning the second half of your inquiry, I have no information.

HUNT: I should like to amend a few of Dr. Coon's remarks concerning Yap. The modal age of first conception in Yap women is 18 years, not 27 years.

Contraceptive measures are not used in Yap, although women may keep leaves in the vagina during menstruation. These leaves are not employed as cervical diaphragms during sexual intercourse.

Although the use of hot baths may have some limiting effect on the production of spermatozoa in men, it is also true that the Japanese, who frequent such baths, are among the most rapidly increasing groups in the world. In my opinion, these baths may not be overwhelming factors in the limitation of human reproduction.

The same argument may be true of another limiting factor in human reproduction: intestinal parasites. Severely infested populations, as in Egypt and Java, are nevertheless highly fertile.

One of the most detailed studies of demography in non-literate societies is the work of Krzywicki. In his book, *Primitive Society and its Vital Statistics*, he concludes that hunting and gathering societies tend to be relatively infertile. The number of pregnancies per woman tends to increase with the adoption of agriculture and a sedentary mode of existence. This evidence is not conclusive, but it tends to contradict Dr. Coon's contention of a greater fertility among peoples at the simplest levels of human subsistence. The reasons for this difference are not yet clear.

COON: If you will read my paper as it stands revised for publication you will see that I have altered it to accord with your oral statements made at the meeting. I did not say that contra-

ceptive measures are used in Yap. You yourself stated that they used leaves for abortion.

I did not state that people living at the simplest levels of human subsistence are more fertile than primitive agriculturalists.

MONTAGU: It should perhaps be mentioned that it has long been well known that elevation of the temperature of the testes inactivates spermatozoa. This is so only during the period of temperature elevation. It would be difficult to conceive of hot baths having anything to do with the reduction in libido or fertility—as witness Japan.

COON: The effect of hot baths on human fertility in the male as stated in my paper was determined by the authors of the monograph quoted by actual experimentation on two young men. Nothing was said about libido. Infertility was determined by actual count of sperm cells in the ejaculates of these two subjects, after their testes had been subjected to the temperature specified. If Drs. Hunt and Ashley Montagu do not accept this, I suggest that they find some way to conduct similar experiments and thus enlarge the series.

SOME IMPLICATIONS OF THE GENETICAL CONCEPT OF RACE IN TERMS OF SPATIAL ANALYSIS

JOSEPH B. BIRDSELL

Department of Anthropology, The University of California at Los Angeles, California

PART I. INTRODUCTION

This symposium stands as testimony to the need for revitalizing racial anthropology. A history of this field would reveal that it has suffered in a sense from its own virtues. On the one hand, it developed its descriptive techniques to a higher level of refinement than most of the other natural sciences. On the other, its concentration of effort upon a single organism, man, resulted in a self-imposed isolation which has seriously retarded its conceptual development. As a natural consequence of this involution, the field has scarcely been aware of the ground-swell created by the development of the new systematics. Racial anthropology is not bankrupt, but it will require assistance in bridging the awkward gap between its descriptive phase of development and the new analytical phase lying ahead. The problems of human evolution and racial differentiation are essentially population problems, and their solution will be advanced by borrowing techniques of analysis from the vigorous field of population genetics.

To proceed to the goal of a genetical anthropology, we must start with a genetical definition of race. That formulated by Professor Curt Stern (1949: p. 558) can serve as point of departure. In his terms, a race is "a genetically more or less isolated division of mankind possessing a corporate genic content which differs from that of all other similar isolates." It is an explicit imperative of such a definition that the proper unit of study is a population, or an isolate. Historically it was but natural that racial anthropologists, viewing each man as an organic unit, should have commenced by using the individual as the unit of study. This approach resulted in an impressive waste of effort to characterize races in terms of the mean or average man in a racial group, and to describe the variability of the total population in terms of deviation from this abstraction. A creditably early acceptance of the necessity of controlling the sampling factor in descriptive data carried the attendant disadvantage that statistical techniques became confused with the goal of research. Attracted by the specious beauty of exact measurement, the search for biologically meaningful measurement was ignored. The raising of the concept of the probable error to a fetish status perpetuated the individual as the unit of study long after it should have been replaced by the population.

It is implicit in Stern's definition that the analysis of the corporate genic content shall be a synthesis in terms of the varying frequencies of the alleles at numerous genetic loci. Classical genetics has elaborated more dependent theory in this area than racial anthropologists are now prepared to utilize. The more complicated area of the evolutionary dynamics of populations has seen much exploratory work performed by such eminent scientists as R. A. Fisher, J. B. S. Haldane, Th. Dobzhansky and Sewall Wright. Their work, along with that of many others, has succeeded in giving a mathematical definition to certain of the processes important in racial differentiation. Thus, insight has been gained into the ways by which new genotypes become established in some or all members of a population. The dynamics of such changes have been investigated commonly by utilizing mathematical models which, through the use of simplifying assumptions, are able to provide approximate answers to difficult questions involving a complex system of variables. In much of this research time is the primary variable. The time calculus which has been developed in recent decades to explore the dynamics of evolution has yielded most rewarding results, and its ideas are basic to an understanding of genetical anthropology.

This time calculus contains latent implications concerning relationships between populations in space, but it makes little use of the concept of space as a primary variable. But a genetical definition of race of necessity carries broad implications concerning the importance of space as an analytical variable. The evolutionary processes inherent in racial differentiation occur in space, are affected by spatial relationships, and to some degree are dependent upon space. Despite the important exposition by Huxley (1939) on the use of clines as an auxiliary method in taxonomy, population geneticists have neither fully exploited the properties of space in their con-

ceptual formulations, nor in their analytical techniques. It is the purpose of this paper to point out in a very preliminary and uncertain fashion further specific types of analysis in which space is the primary variable. These exploratory steps are necessarily halting in character and their tentative nature will be evident. Even so, I am confident that approaches of this type to the analysis of the problems of population genetics can ultimately lead to the development of a mature space calculus.

The body of this paper is divided into two sections. The first is concerned with the suggested operation of genetic drift in certain human gene series, and a preliminary formulation of the possible use of the concept of drift as an analytical tool in human population genetics. The second section represents an attempt to investigate certain phenomena involved in gene flow on a very simple level through the utilization of gene flow models in genetic space. Applications of the method to human data are given by way of illustration. All data have been drawn from the aboriginal populations of Australia. A portion has been derived from my own field work, the remainder from the research of many other investigators. All of the illustrative materials are subject to more searching analysis than time allowed here, and hence, if necessary, to rectification in later publications.

The illustrations to be presented in subsequent sections require a brief account of the racial framework used as an analytical background. Summarized very briefly, my data disclose the presence of three major racial groups on the Australian mainland. These basic elements represent three major phases of migration coming from the mainland of Asia. All elements are blended in varying proportions regionally to form the present aboriginal population.

The earliest type of *Homo sapiens* to cross Wallace's line into the Australasian area was the Oceanic Negrito. The date of this migration may be placed tentatively as early in the Fourth Glacial Period. The type persists in mixed but recognizable form among the 12 nuclear tribes of the tropical jungle region in northeastern Queensland. The extinct Tasmanian aborigines were also part negritic in their racial composition. Other more attenuated traces of this early substratum are found in marginal regions of the mainland. Using the living Andamanese as a basis for reference, the negritic migrants may be characterized as of very short stature, dark skin color, woolly hair form, moderate round-headedness, low nasal relief, and a very short and narrow face. Head hair was but little affected by baldness, and graying occurred late in life. The ear is negroid in size and shape. The general impression is that of an infantile type. There is every reason to believe that these Negritos represent an early extension of the African Negrillos into Asia and the offshore islands.

The second major racial group to penetrate the continent of Australia represents an archaic form of Caucasoid. They have been named Murrayian owing to their presence in least mixed form in the Murray River drainage and the marginal coastal regions to the south and east. This group may be considered as having reached Australia sometime during the mid-portion of the Fourth Glacial Period. The Murrayians are short in stature, relatively lateral in general body build and show a significant tendency toward obesity. Their unexposed skin color is relatively light. Hair form ranges from wavy to straight, baldness shows an unusually high incidence, and both body and facial hair are excessive. The cranial vault is characterized both absolutely and relatively by great length and low height, while breadth is narrow. Brow ridges are large and nasian depression is characteristically deep. The upper face gives an impression of massiveness but the mandible, while broad, is relatively shallow. The nose is unique among living races in being both very wide and high in relief. Ears are extremely long and broad, and their lobes are unusually large. Teeth reach a maximum size among living races. The general facial impression is that of a coarse and rough-hewn caucasoid type. The Murrayian race is most closely related among living peoples to the Ainu of Hokkaido and Sakhalin. In more extended terms it may bear some relationship to the terminal Pleistocene populations of Europe.

The third and last major racial element to enter Australia has been called the Carpentarian because of the distribution of the nuclear population around the shores of that Gulf. Their time of arrival lies between the latter portion of the Fourth Glacial Period and the early part of the Recent Period. They are characterized by their tall stature and notable linearity in body build. Skin color is very dark and this, combined with the type of body build, has led to the unjustified belief that they bear a genetical relationship to the full-sized Negroes of Africa. Hair form is wavy to straight, and both the body and face hair is scanty. Carpentarians show little tendency toward baldness, but the graying of head hair

occurs unusually early. Head proportions are characterized by a moderate absolute length and height combined with extreme narrowness. Consequently the breadth-height and the cephalo-facial indices are extremely high. Brow ridges are large and nasian depression is deep. The nose is short, broad and low in relief. The ear is undistinguished both as to size and form. The teeth are large, prognathism is marked, and the chin of the mandible ill developed. In their general appearance the Carpentarians are extremely primitive, generalized, and non-caucasoid in appearance. They are most nearly related to the dark-skinned, linear racial substratum evident among the aboriginal tribes and low caste peoples of India. They represent a fourth major racial group equivalent in status with the caucasoid, mongoloid, and negroid groups.

Birdsell (1948) has presented this racial schema in somewhat greater detail. Tindale and Birdsell (1941) gave a preliminary description of the negritoid tribes of North Queensland. Birdsell and Boyd (1940) have given a preliminary survey of the blood groups and the blood types in Australia. Throughout this paper wherever tribal names are utilized, they have been taken from the excellent tribal map published by my field collaborator, Norman B. Tindale (1940), whose contribution in this field has provided a powerful tool for the regional analysis of Australian populations.

Part II. Inter-Isolate Fluctuations Suggestive of Genetic Drift in Human Populations and Possible Uses of the Concept of Drift as an Analytical Approach

Genetic drift is one of four evolutionary forces which operate to produce changes in the gene frequencies in populations. It produces evolutionary changes in a random and hence in an individually unpredictable way. Its very nature suggests that the process of drift may confuse racial analysis, that in any case it can hardly be expected to illuminate it. Drift is claimed to be of some importance in human evolution during the entire Pleistocene, so that it is deserving of examination, before summary rejection as a nuisance factor.

Drift is a concept which applies particularly to populations whose effective breeding size is small. In a stabilized population the character of the population pyramid will remain relatively constant. Hence it may be anticipated that the size of the effective breeding population will be directly correlated with the size of the genetic isolate. It will be shown later that in aboriginal Australia the tribe approximates the genetic isolate, and averages about 500 persons in size. *A priori* such populations should prove especially suitable for demonstrating the possible presence of drift in man. Drift might be expected to operate throughout Australia, but its effects should be most marked in areas where the size of the effective breeding population is the smallest. Most coastal tribes in Australia are situated in regions with relatively high annual rainfall, which occurs with a moderate degree of reliability. In contrast, the desert portions of the interior are characterized both by reduced rainfall, and by a marked increase in its variability. It is generally agreed that in populations which fluctuate markedly in size in a cyclical sense through time, the effective breeding size is nearer the lower limit of the population than its upper limit. My own data, and that of other field workers, can be broken down into tribal series in the central desert and still yield a modest degree of statistical reliability. For most other areas in the continent it is necessary to be dependent upon less revealing pooled tribal data. For these reasons the arid wastes of central Australia may be expected to show the effects of random genetic drift more clearly than other portions of the continent.

Figure 1 is an outline map of Australia upon which have been superimposed hachured areas representing sections depicted in later maps in this paper. The area keyed with the letter (A) represents the central region which is to be surveyed in the maps shown in Figures 2 through 6.

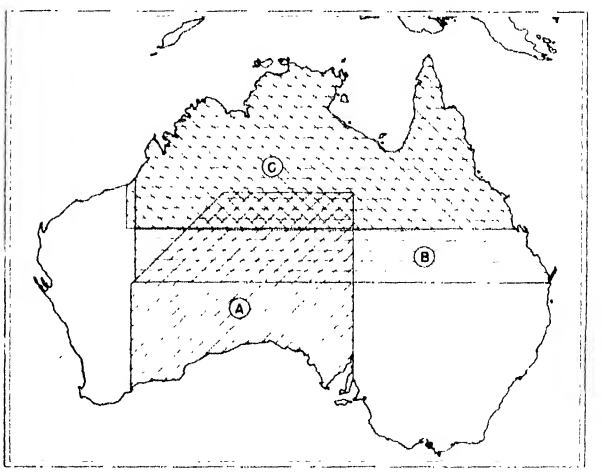

FIG. 1. Areas represented in subsequent maps: (A) Figs. 2 through 6, (B) Fig. 7, (C) Fig. 12.

The region is bounded on the south by the arid coast of the Great Australian Bight, and on the north approximates the northern boundary of the territory of Central Australia. The eastern limit falls along the eastern boundary of that territory and its projection southward to Spencer's Gulf. The western boundary is irregular and is placed to include those tribes for which sufficient data are available for the purpose of analyzing drift. A total of 42 tribes are included totally or partially within the region under consideration. Owing to the nature of tribal sampling, only pooled data are available for the tribes of the coast and its immediate hinterland. The upper two-thirds of the map contains 17 tribes for which individual series are available. Three of these series are based upon my own data, the remainder on the data of various workers from the South Australia Museum. From the nature of drift, it may be anticipated that its results will show most clearly in that portion of the map where data have been analyzed upon a tribal basis.

There are no clear-cut rules for identifying the effects of random genetic drift. Models based upon time calculus have shown that the process can be expected to tend toward fluctuating deviations in frequencies which may ultimately produce fixation in one of a series of allelic genes and the complete loss of all the others. For genetical data in a spacial context, drift may be visible in those areas where extreme fluctuations in gene frequencies occur which cannot be attributed to one or more of the following causes: mutation, hybridization, or natural selection. The operation of the latter forces is difficult to identify and define with certainty in human materials today. *Thus drift at best, can be no more than suggested in terms of broad probabilities.* The identification of the effects of drift in either isogenic or isophenic maps will be to some degree dependent upon the size of interval between the isogenes or the isophenes.[1] The smaller the interval between two such contours the greater the sensitivity that will be reflected in the topographical surface created by the contour system. Should the interval between contour lines be too great, areas influenced by genetic drift may not emerge visibly from the general level of the topography. If the group interval is too small, the topographic surface of the model may be blurred by variations produced by sampling errors. In the maps in this section, group interval values between contours have been chosen so that the total range of variation for all data now available for aboriginal Australian groups would be represented by about seven or eight isophenes or isogenes. This basis for establishing group interval size is an attempt to maintain roughly equivalent sensitivity in the data for various traits. These standards may require changes later, but their present use will not vitiate the broad implications which follow here.

[1]Just as an isogene is a contour line for equal gene frequencies, so an isophene represents a locus of points of equal phenotypic frequencies or values.

A. Isogenic map for the blood group gene I^A

In central Australia the blood group alleles are represented only by two genes I^O and I^A. The gene I^A equates with the gene I^A_1 since the allele I^{A_2} seems absent from the continent. A single isogenic map, shown as Figure 2, serves to represent the distribution of both alleles. The gene frequency for the allele I^A for the entire continent ranges from a minimum of .121 to a maximum of .488. The isogenic group interval has been set at .05, thus creating 8 isogenes to cover the range of data. Isogenic contours, based upon gene frequency data for population units, are necessarily an abstraction. The contours are generalized to present a clear visual pattern. Contour construction involves some degree of subjective interpretation; but despite these theoretical difficulties, the over-all configuration of a contour system adequately reflects regional variations in gene frequencies. Interpretation of isogenic topographic surfaces is less dependent upon the given location and direction of a specific line than upon the slope, or gradient, revealed by the over-all configuration of the surface. *Areas of significance are determined by the nature of the slopes themselves; by rates of change in gene frequencies rather than by absolute values of gene frequencies at any given point.*

The isogenic map for the gene I^A is primarily characterized by three outstanding topographic features. The first of these is a peak area of restricted nature in which the isogenic frequencies exceed .45. The area centers in the Pitjandjara tribe, keyed as (1), but extends north into the Pintubi (2) and thence northeastward into the Jumu and Ngalia tribes. A series of 99 Pitjandjara have a gene frequence of I^A of .488. I have presumed that some hordes of this tribe may exceed a gene frequency of .50, and this purely hypothetical maximum has been shown in the accompanying map. If the Pintubi, Jumu, Ngalia and Pitjandjara tribes are pooled, the .45 contour line then rests upon a combined series of 178 individuals.

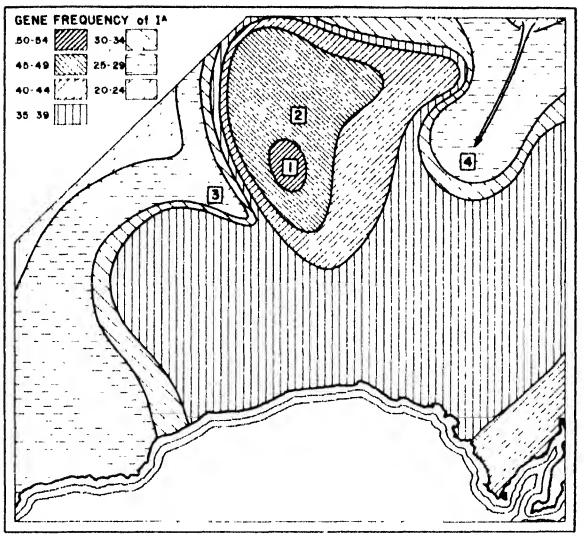

FIG. 2. Isogenic map for the gene I^A.

Adjacent to the Pitjandjara on the west is the tribal territory of Ngadadjara (3). A series of 67 of these tribesmen gives a gene frequency of .277 for I^A. Thus the crossing of a single tribal boundary involves a decrease in gene frequency in excess of .20. The compressed contours shown on the map in this region do not adequately represent the extreme gradient necessary to achieve so drastic a change in gene frequencies. The probability of such a shift in gene frequency being caused by sampling errors alone is beyond chance limits. The chi-square method, for one degree of freedom, gives $\chi^2 = 7.45$; P is less than .01.[2]

A third noteworthy feature is the presence next to the Pitjandjara peak of a deep trough extending in a northerly direction. The isogenic gradient between these two major regions is so steep as to represent another veritable escarpment in the topographic surface. This depression, which slopes gradually toward the northern coast, is best outlined by the .30 isogene. Aranda (4) tribal data totaling 224 individuals is the primary evidence for the existence of this southerly salient. It is improbable that a difference such as exists between the Pitjandjara and the Aranda gene frequencies is due to sampling alone. The chi-square calculations, with one degree of freedom are: $\chi^2 = 17.11$; P is less than .01. Thus the primary features of the map are determined by the gene frequencies for three tribal populations which differ significantly. The remaining data, while secondary in importance, satisfactorily determine the position and direction of contour lines surrounding the Pitjandjara peak, the Aranda trough, and the Ngadadjara depression.

An interpretation of the significance of the contoured surfaces shown in the map in Figure 2 depends upon features characterizing the distribution of the gene I^A beyond its immediate boundaries. Broadly, the northern portion of the continent, in which the Carpentarian racial element predominates, shows low frequency for the gene I^A. Southern Australia and the marginal coastal districts, in what is essentially Murrayian territory, are characterized by higher frequencies. These general trends indicate that the Murrayians introduced relatively high frequency for the gene I^A into Australia, and were followed by Carpentarians who showed considerably reduced values. This seemingly simple situation is complicated by the occurrence of the highest frequencies for this allele in the desert regions. There the populations can be described taxonomically only as a hybrid group in which the Murrayian and Carpentarian genetic contributions are roughly equivalent. The high frequencies observed in and around the peak area and even more widely within the contour line of .35 value cannot be attributed to hybridization between Murrayian and Carpentarian elements. Hybridization may be excluded as the force responsible for the Pitjandjara peak.

Other evolutionary forces must be roughly evaluated. Little data are available for the rates of mutation at various loci in man. The more extensive information available for other organisms does not seem to provide an adequate explanation for the violent local fluctuations in gene frequencies for I^A shown in Figure 2. The area contained above the .30 isogene corresponds broadly to the region of minimum rainfall on the Australian continent. Selection, operating through some now unknown means, cannot be ruled out as contributory cause, but it need not be postulated as the only operative force.

The probabilities seem high that the Pitjandjara peak for I^A is a partial consequence of the operation of drift in an area where the influence of this evolutionary factor might be expected to obtain a maximum value. Consequently, it is of interest that while the highest frequencies are limited to the Pitjandjara tribe, the isogenic contour line of .45 value actually includes four tribal territories. The portion of the topographic surface lying above the .40 isogene includes three more

[2]Although in this, and certain other cases, I have used simple tests for significance, I am not certain that deviations in values on a topographic surface are best tested by this method to evaluate the true sampling errors.

tribes, or a total of seven. This broad peak area may be interpreted in three ways. The first alternative would be to explain the observed gene frequencies as a result of drift occurring simultaneously and in the same direction in all seven of the affected tribal populations. This would presuppose a consistency in the direction of gene frequency changes which does not characterize drift. Another simple explanation would hold that extreme drift had occurred in one tribal area, probably that of the Pitjandjara, and that its influence had been spread via hybridization to the adjacent tribal populations. Or drift, hybridization and selection may have operated simultaneously or at different times in any of several combinations. In any case, the Pitjandjara peak may serve as an illustration in man for the initial phases of emergent gene flow emanating from an area where high frequencies for a given allele may have been attained partially through the operation of drift.

The Aranda trough is subject to a different type of interpretation. Topographically, this region is no local depression, but rather a tongue-like extension of the low values for the gene I^A which characterize areas further to the north. The observed contours are most easily explained as representing a population thrust from regions to the north to the present Aranda domain. The escarpment rising to the west of this trough indicates that the Aranda are not yet in genetic equilibrium with their westerly neighbors, and is highly suggestive of a relatively recent date for the Aranda migration southward. Linguistic and other cultural data for the Aranda tribe tend to substantiate this view.

The minor trough represented by the Ngadadjara series is more difficult to interpret. No data are available for the tribes immediately to the west of this region; hence it is not known whether the low values of the Ngadadjara represent a localized depression or a trough-like extension, such as seen for the Aranda. In the former case, drift would seem the most likely explanation, operating in this case to reduce the values of the gene I^A, as those for I^O increased. On the other hand, the desert regions to the west are so sparsely populated as to suggest that migrating peoples could move through this region very rapidly. Hence, the Ngadadjara might represent a tribal group who came in across the desert to their present locality from regions further to the north. Fortunately other data, including the gene M^N, tawny hair, and supernumerary distomolars, show this tribe to fit into the local cline system smoothly, so that drift is the more probable cause for low I^A values here. It seems asking too much for selection to have produced the bipolar tendencies inferable from the observed changes in I^A frequencies in the adjacent Ngadadjara and Pitjandjara isolates.

The extreme fluctuations observed in the value of gene frequencies of the allele I^A in the central desert of Australia are reminiscent of similar peaks in other regions of the world. Even higher frequencies for the allele I^A have been reported for the Algonkin-speaking Blackfeet and Blood tribes of the Great Plains of North America. Drift in part may again explain the origin of the very high gene frequencies observed. Similar values for this gene have been observed in the marginal regions of the island world of Polynesia, where drift should be operative.

The concept of drift may serve to explain the appearance of peak frequencies in areas characterized by small effective breeding populations, although selective forces cannot be eliminated as causal agencies in the present state of knowledge. On the other hand, the very fact that such wide deviations can occur points out the hazard of attempting comprehensive racial interpretations on the basis of varying gene frequencies in the alleles at a single locus. Anthropologists, who have been disturbed in the past by the incompatibility between the isogenic contours for the blood group alleles and the distribution of races as conventionally defined on a broad taxonomic basis, have clearly been expecting too much, too early, in genetical anthropology.

B. Isogenic map for the blood type gene M^N

The map shown in Figure 3, which represents the isogenes for the blood type allele M^N, is based upon less extensive data than the preceding one. The total range of variation in the gene frequency of M^N for the continent of Australia lies between .617 and .985. This over-all range has been divided into isogenic contour intervals of .05 value, hence the total known variation in M^N for Australia can be described by seven contour lines. Both the maximum and minimum gene frequency values occur in the region mapped here, in groups which are separated by only four intervening tribal boundaries.

This map shows a single major topographical characteristic, the dual peaks enclosed inside the .95 contour line. This feature is based upon a series of 99 aborigines, divided between three tribes as follows: 34 Nangatadjara (keyed as no.

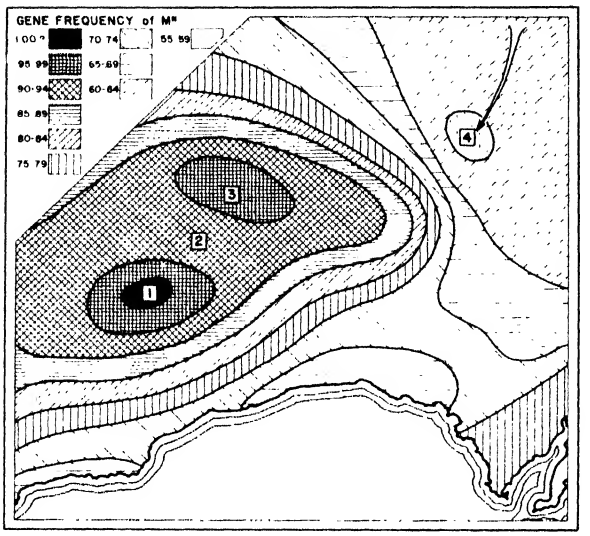

FIG. 3. Isogenic map for the gene M^N

1 on the map), who have a frequency of .985 for M^N; 32 Mandjindja (2) with a frequency of .922; and 33 Ngadadjara (3), with a frequency of .970. The M^N frequency for the three pooled tribal populations is .960. The variations in the gene frequencies among these three tribes is non-significant in nature, owing to the small size of the samples, but for mapping purposes, I have chosen to ignore this limitation and have presented the Nangatadjara and the Ngadadjara as representing dual peaks exceeding .95, and contained within the over-all isogenic line of .90. If statistically more conservative procedures were followed, a single peak based upon the isogenic line of .95 value would circumscribe all three tribal areas.

Another feature of interest in this map is less dramatic in nature. It consists of the broad belt of tribes to the northeast lying below the .65 isogenic line. Evidence is based primarily upon a series of 137 Aranda, and more diffused data for adjacent regions, which give a valid definition to this general area of low frequencies for the gene M^N. The Aranda sample yields a frequency of .617, which is the lowest yet found for an Australian tribal group, but this may be exceeded in the future when more extensive field work has been undertaken.

The interpretation of the primary features shown in the isogenic distribution of M^N is similar to that for the gene I^A. Here the peak areas contained with the .95 isogenic contour, whether represented as a single or a dual eminence, can perhaps best be explained as a consequence of drift. Both the Murrayian and the Carpentarian nuclear areas are characterized by gene frequencies for M^N which are substantially below the value of .95, so hybridization offers no explanation for the occurrence of the high values observed in the Western Desert. Nor does the process of mutation provide a more satisfactory answer. Unlike the distribution of I^A, M^N in its pattern shows no consistent change in terms of aridity. Unless selection can be shown capable of producing marked fluctuations within a few limited isolates, in man, as shown here, it is not attractive as a sole explanation. The configuration of the isogenic contours for the entire continent, which cannot be shown in the present map, suggest that this region of peak values represents a disturbance in an otherwise consistent topographic surface. Drift seems most likely to have been at least a contributary force.

Drift, as in the case of I^A, seems likely to have produced very high gene frequencies for M^N in a restricted region, covering at most no more than three tribal areas. These heightened gene frequencies appear to have spread outward in all directions by intertribal hybridization in an incipient pattern of emergent gene flow. It will be noted that in the Nangatadjara domain, a small area has been suggestively enclosed in an isogenic contour with a value of 1.00. This is a schematic representation of the probability that one or more hordes in this tribe may actually have been so influenced by drift that the allele M^N has become totally lost. This probability can be confirmed only by a much larger series than is now available.

In this map, as in the preceding one, the Aranda seem to represent the apex of a southerly movement of populations. Here the evidence for such a thrust is less clear. Note that the peak area for the gene M^N lies further to the south and west of the Aranda than did the Pitjandjara peak for I^A. This change in spatial relationship has an important bearing upon the slope values for the topographic surface between the peak and the Aranda region of low frequencies. There is, of course, no *a priori* reason to believe that an isogenic topographic surface based upon a gene at one locus need resemble that based upon a gene at another locus, unless the two loci are so closely linked as to impede crossing-over. The *I* and *M* loci are known to be not linked. The use of such isogenic topographical surfaces to detect tribal migrations is dependent upon a number of variables beside the over-all configuration. Gradients are determined both by the distances between the populations concerned and

the differences between their gene frequency values. Ideally, the differences between frequencies should be high and the distances short. These conditions obtained in the isogenic map for I^A, and the Aranda thrust was well defined; less extreme conditions occur in the case of the gene M^N, hence, while the migration of the Aranda is suggested, its delineation is by no means so sharp.

C. A model showing the general inapplicability of the concept of drift to phenotypic characteristics of multifactorial inheritance

In preceding sections, it was shown that under favorable conditions, random genetic drift seems to influence allelic gene frequencies in human populations. The peak areas for I^A and M^N are evidence to this point.

Workers in racial anthropology have for nearly a century amassed data descriptive of human populations in terms of metrical measurements. It has frequently been suggested that from a genetical point of view such metrical data are useless for purposes of racial analysis. This summary opinion is open to some doubt. For example, if multifactorial traits are less affected by random drift than unifactorial traits, then the former may be more useful than the latter in preserving records of racial relationship over longer periods of time. For instance, it can be confidently stated that in Australasia the presence of spirally curled hair, with various degrees of curvature in the helix, serves as a better marker-trait for the presence of negritic genetic elements than have most of the serological genes to date. Even if a unique marker-gene for the negritic component were to be discovered in the future, the operation of random genetic drift, by tending to produce fixation in some cases, and losses in others, might cause errors in an evaluation of the negritic contribution. On the other hand, spiral hair form, as well as other multifactorial traits in both the fields of morphological observations and metrical measurements, may be relied upon to suffer less distortion from the operations of drift. It is important that we recognize that multifactorial phenotypic traits may ultimately prove especially valuable for certain purposes of analysis.

Approaching the problem from a somewhat different point of view, racial analysis remains in great need of the early identification of more loci at which series of alleles determine phenotypic characteristics in a unifactorial manner. To date, genetical anthropology owes most of its progress to the investigations of serologists. Anthropologists must reevaluate their existing techniques and data to see whether or not they can contribute to the progress of genetic racial analysis. We have too easily assumed that the classical metrical and morphological data in our field are all of complicated, multifactorial nature. This assumption needs reexamination. In any case, drift may be so important in small populations that a trait cannot be properly interpreted in analysis unless the level of complexity of its genetic bases is in part known.

The various types of models devised by research workers are valuable in determining approximate trends in dynamic situations which are dependent upon a complex of variables. They frequently serve to give clarifying, if approximate, answers to rather difficult questions. For example, we may ask: "How does drift vary in its impact upon the phenotypic expression of multifactorial traits as the number of loci involved in the mode of inheritance increases?" Even though it seems obvious that drift will have less influence on a phenotypic characteristic determined by many loci than it will upon a unifactorial trait, a simple mathematical model will provide both confirmation and more information as to how the variables interact. Using human stature for purposes of illustration, let us make the following simplifying assumptions:

1) At each postulated locus, there will occur two alleles which give an intermediate character expression in the heterozygote.

2) The gene action increasing stature is additive.

3) The absolute additive effect for each allele at every locus will be inversely proportional to the total number of loci involved in stature. Thus the numerical additive effect of every positively acting allele will be equal to the total human range in stature, divided by twice the number of the loci influencing phenotypic stature. If the total range in man is presumed to fall between 140 and 180 cm., giving an over-all range of 40 cm., then, if stature is determined by a pair of alleles at a single locus, the phenotypic stature of the two homozygotes would be 140 cm. and 180 cm. respectively and that of the heterozygote would be 160 cm. In this instance, each positively acting allele would give an additive effect equal to 40 divided by (2×1), or 20 cm., per allele. If stature is presumed determined by similar alleles at two loci, then each positively acting allele would have a contributing effect in the phenotype of 10 cm. increase in stature; for four loci,

each positively acting allele would add but 5 cm., cumulatively to stature, etc.

4) It is assumed that at each locus the initial frequency of each allele will equal .50. Thus each of the two alleles involved will have an equal chance, or a probability of P = .5, of reaching fixation, and a similar chance of being lost, if drift proceeds to its limits.

5) Let the process of random genetic drift commence in the model and continue until complete fixation of one or the other allele occurs at all of the postulated loci. For the present, the factor of time will be ignored.

For the purposes of our analysis, we are interested in the probability that drift will produce by fixation and extinction phenotypes which reach the extreme limits of the stature range; namely, 140 or 180 cm. This probability takes the form of a simple binomial: $(\frac{1}{2}F + \frac{1}{2}L)^N = 1$. Here F is the symbol for fixation, and L the symbol for loss. One-half represents the probability of the event occurring in each case. The exponent N represents the number of loci involved in producing the phenotypic expression of stature. For instance, where a single locus is postulated, it is inevitable that if one allele reaches fixation, the other must be lost. Thus, under this assumption the probability of reaching either the maximum or minimum phenotypic value of stature would equal $(\frac{1}{2} + \frac{1}{2})^1 = 1$, or certainty. If it is assumed that two loci are involved the binomial expansion becomes $(\frac{F^2}{4} + \frac{FL}{2} + \frac{L^2}{4}) = 1$. In this instance but two of the three genotypic categories represent extreme statures: the first term represents the case in which both dominant alleles become fixed; the third term is representative of the condition in which both dominant alleles become lost. Thus, for two loci, the chance for random genetic drift producing either extreme of stature is: $P = \frac{1}{2}$.

A more generalized expression can be constructed to express the probability that genetic drift will succeed in producing either extremes of phenotypic stature. Since the probability of the positively acting alleles at all loci becoming fixed is equal to $(\frac{1}{2})^N$, and it is equally probable that all such alleles will become lost, the probability for both events equals: $P = \frac{2}{2^N}$. Thus the probability of drift producing the extremes of phenotypic stature is equal to $\frac{1}{4}$ for 3 loci, $\frac{1}{8}$ for 4 loci, $\frac{1}{16}$ for 5 loci, and $\frac{1}{32}$ for 6 loci.

In this simple model, it has seemed wise to ignore those combinations of fixation and loss which do not reconstruct the extreme possible ranges of stature. Their inclusion would increase these probabilities, but this error is perhaps counterbalanced by the omission of the time factor. In a general way, the length of time involved for complete loss or fixation would vary directly as some function of the number of loci involved.

This simple model has served to provide the approximate answer required by our initial question. Although complex multifactorial phenotypic traits may become drastically modified in their mean values by the operation of drift, the probability of this occurring is small as compared to those traits which have a unifactorial basis of inheritance. This conclusion may be restated in a more important form for purposes of analysis, if selection is considered not to have produced the inter-isolate mosaic pattern occurring in Australia. Metrical and morphological characteristics in man, which show violently fluctuating mean values in a random pattern from one isolate to another, beyond that expected from sampling error, then may have a genetically relatively simple mode of inheritance. This statement is not intended as a rigorous formulation, but merely to point to a type of spatial analysis which may result in the useful salvaging of some existing anthropometrical and morphological data. Its use is dependent upon the primary ordering of such data in terms of tribal populations or some other group which approximates the genetic isolate. Control must be exercised to minimize the effect of random sampling errors, but the current anthropological procedure of combining data from many isolates into a single pooled series, in order to minimize the value of the probable errors, serves only to destroy the microgeographical variations in traits which are the outward symbols of the processes of evolution. Research design in racial anthropology must have as a primary goal the collection of statistically adequate data for each genetic isolate, with the isolates ranging continuously through space.

D. Isophenic map for stature

The isophenic contour map for stature is shown in Figure 4. It is based upon extensive data, so that sampling errors may be considered minimized. The total range of stature among Australian populations is from a minimum of 155 cm., to in excess of 173 cm. The use of two centimeter group intervals between contours results in nine isophenes being used to express the total range.

The genetic bases for phenotypic stature are generally considered to be multifactorial, and the trait further shows some environmental plasticity. The isophenic configuration for the topographic surface revealed in this map is noteworthy only for its general complacency. The surface slopes smoothly and regularly from low values in the southwest toward high values in the northeast. There are no local regions reflecting steepened gradients and no tribal areas set off as either peaks or depressions. The irregular meandering of the contour lines of 167 and 169 cm. is without significance for this discussion.

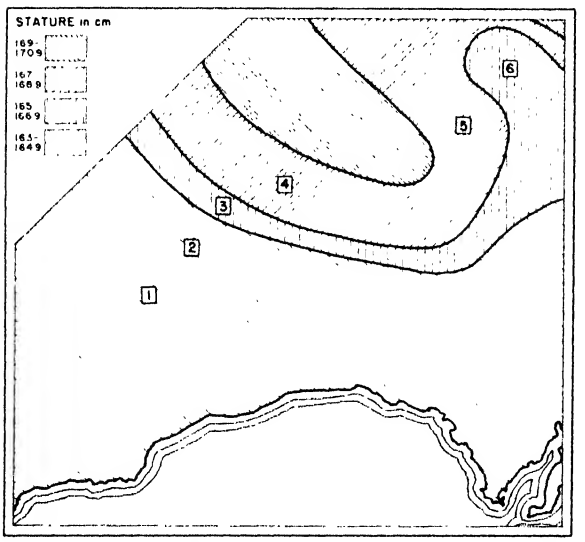

FIG. 4. Isophenic map for stature

The group interval between isophenes has been chosen so as sensitively to reveal drift. The keyed numbers on the map, ranging from 1 through 6, refer respectively to Nangatadjara, Mandjindja, Ngadadjara, Pitjandjara, Aranda and Iliaura tribes respectively. In the two preceding maps, the first four of these tribes were characterized by extreme fluctuations in gene frequencies, reflecting the possible operations of drift in this area. It is noteworthy that the isophenic map for stature reflects a smooth, even cline through this series of four contiguous tribes, and gives no indication of any phenotypic alterations due to the operation of drift. The Iliaura, in another instance, will be found responding to drift, but here show no evidence of the process. Thus the predictions provided by the simple, preceding model anent the relationship between drift and multifactorial phenotypic characters seem well borne out in the case of stature.

Turning to the Aranda, the isophenes for stature reveal no uneven relationships suggestive of a recent population movement into their area. This lack of disturbance in the contour surface may be primarily ascribed to the very low gradient extending from north to south for this feature, in itself probably a consequence of its multifactorial nature. Thus some multifactorial phenotypic traits may prove less sensitive in revealing localized population movements than do single factor characters, unless unique marker-traits such as negroid hair form are involved. Nonetheless, the very lack of sensitivity which may be expected with multifactorial traits saves them from being unduly disturbed by such local processes as drift, and may make them more valuable in certain aspects of racial analysis in revealing relationships between populations widely separated by either space or time.

E. Isophenic map for total facial height

The hypothesis has been advanced that phenotypic traits dependent upon multifactorial genetical bases are unlikely to show the effects of drift, and conversely that those traits which do reveal extreme fluctuations in their mean values from one isolate to another may in some cases theoretically be expected to be phenotypic expressions of relatively simple genetic modes of inheritance.[3]

Figure 5 shows the topographic surface for total facial height. The maximum range for Australian aborigines as established to date is from a minimum of 110 mm. to a maximum of 123 mm. An isophenic contour group interval of 2 mm. has been chosen, yielding a total of seven isophenic lines to express the total range of variation. This results in a contour system considerably less sensitive in recording local group fluctuations than that adapted for stature in the preceding map; hence one which should de-emphasize the effects of random drift as they operate on phenotypic facial height.

The outstanding feature of the isophenic configuration for total facial height consists of two areas of depression. The more westerly one, occurring in the territory of the Mandjindja and Pitjandjara tribes, (1 and 3 respectively), has been represented as a dual depression. The mean

[3]For example, with reference to the latter, their phenotypic expression need not be unifactorial in its genetic basis, but possibly determined by a limited series of genes at several loci, provided that a small number of genes are disproportionately important in determining the phenotypic expression. Complex multiple allelic systems may also at times fall in this category.

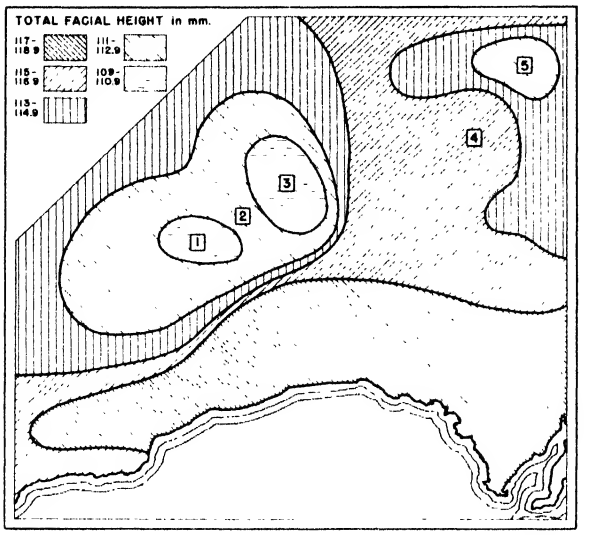

FIG. 5. Isophenic map for total facial height

facial height for the former tribe is 110.5 mm., for the latter, 110.2 mm. The Ngadadjara, who lie between these two, has been sampled by two different workers, who obtained mean total facial heights of 111.1 and 111.3 mm. The consistency of these two small samples has inclined me to favor the visual device of a dual depression in this area, but it must be confessed that the mean values for all three tribes lie within the error of sampling. Hence this dual depression might have been more conservatively represented as a single one. The eastern area of low values, in the tribal territory of the Iliaura, represents a mean value of 111.7 mm., and this population is clearly surrounded on all sides by other groups with greater facial height.

The interpretation of this configuration is again dependent upon data for all parts of the continent. The basic Murrayian populations of the southeastern portion of Australia show mean values ranging between 120 and 123 mm. The northern coastal populations, in which the Carpentarian racial element is preponderant, show mean values fluctuating about 118 mm. The generally used, but unproven, doctrine of the intermediacy of hybrids would lead one to expect that the desert tribes considered here should show metrical values for total facial height somewhere between 119 and 121 mm. The means for the area mapped, however, lie below this expected value in all cases, and are far smaller in the areas of depression. It is clear that means for this trait are less than that to be expected from hybridization. The factor of mutation again does not seem a likely explanation for the observed variations. There is a temptation to correlate the lowered mean total face height values for this desert region with some force of natural selection related to extreme aridity, but such an interpretation might be premature as well as based upon inadequate data. It again would fail to explain the localized depressions characteristic of the region, unless the coefficients of selection in man are much higher than usually postulated. Selection should not be ruled out as a contributary factor in this case, but the very localized, extremely low values encountered can better be explained as originating in the operations of drift.

The observed variations in total facial height have been identified as probably produced by drift by the elimination of other evolutionary forces and, hence, in a sense, by default. There are, however, several subsidiary considerations which suggest that this may prove a proper identification. In the first place, the westerly area of depression occurs among tribes which have been shown by previous genetical analysis to have been apparently susceptible to the operations of drift. Secondly, the extremely localized character of these depressions, coinciding as they do with tribal populations, fulfills the expectations as to the random character of the process of drift operating on the isolate as a unit. Finally, there is evidence from another portion of the continent which indicates that phenotypic total facial height shows a rather peculiar pattern in inheritance.

Phenotypic characteristics based upon complicated multifactorial inheritance are the basis for the expectation that hybrids should show values intermediate between the parental extremes. The inheritance of total facial height is an exception to this generality. In the jungle covered plateaus behind Cairns, there exists a bloc of tribes characterized by the survival of a large negritic element. These miniature aborigines represent a population to which the Negrito and the Murrayian components have contributed about equally. Five small regional samples of adult males from this area show mean total facial height ranging from 114.40 ± 1.01 mm. for 21 males to an average of 118.96 ± .93 mm. for 22 individuals. Pooling all five samples, the number measured reaches 97 adult males and the mean value for total facial height lies approximately between 116 and 117 mm. This figure, which will be assumed to approximate 116.50 ± 1.00 mm., may be contrasted with a series of 66 adult male white Australians whose average total facial height is 123.62 ± .50 mm. Following the expectation that hybrids should show intermediate values

between the parental extremes, it might be anticipated that first generation hybrids between Australian whites and these aborigines should approximate 120 mm. for this trait. A series of 25 hybrids, all adult males, representing the primary crosses between these two parental populations, show a mean value of 117.38 ± .75 mm. for total facial height. The F_1 hybrid average lies very close to the aboriginal mean value and far removed from that of the Caucasoids. In fact, the hybrid average falls within the range of the mean for the five regional aboriginal series. The F_1 hybrids deviate from the whites by 6.2 mm., or 6.9 × P.E., well beyond sampling errors; they differ from the aborigines by 0.9 mm., or 0.7 × P.E. clearly within errors of sampling. The hybrids differ from the shortest faced aboriginal sample, 22 men with a mean of 114.40 ± 1.01 mm., by but 3.0 mm., or 2.4 × P.E., a doubtfully significant deviation. I suggest that this deviation from the expectancy of intermediacy may be a consequence of a relatively simple genetical base of inheritance. For example, the observed situation could be explained if at one of the loci involved there existed a dominant gene for shortness of facial height which exerted a disproportionate effect in determining the phenotypic characteristics. In such a case, the other alleles of these loci, and genes at other loci might have relatively little effect in modifying the phenotypic value.[4] Such a genetical basis of inheritance would be consonant with the above F_1 hybrid data, and also with the marked regional fluctuations in the Western Desert which may be attributed to the process of drift.

The evidence relating to total facial height, both with regard to its regional distribution, and as to its behavior in primary racial crosses, by no means proves that this phenotypic characteristic is, in fact, genetically simple in its inheritance. But it is highly suggestive that this may in time be proved true. I am less concerned with this particular tenuous hypothesis, than with the broader implication of the analysis. This instance has been used to indicate that spatial distributions of metrical traits in terms of isolates are in themselves important, both in defining the limitations of characteristics ordinarily used for racial analysis, and for grading them according to their sensitivity to distortion under the impact of localized evolutionary forces. There remains the added advantage that areal analyses may suggest that a number of conventional metrical measurements are in fact inherited on a moderately simple genetical basis. In those instances the way is paved for further intensive genetical analysis of such traits. I do not agree with those who would completely discard the descriptive data gathered in the past by the anthropologists who have preceded us. Some, perhaps even much, of this data may lend itself to profitable salvage operations.

[4]Pedigree analysis of the data will be undertaken later to test this and other possible hypotheses.

F. The isophenic distribution of supernumerary fourth molar teeth

The preceding sections have been concerned with the presentation of evidence for the possible operation of drift at two genetic loci in man, and the application of this concept has been suggested to phenotypical metrical traits. Morphological characteristics in the phenotype also show extreme regional fluctuations in frequency among contiguous isolates. Similar types of spatial analysis may point to those morphological traits whose inheritance follows rather simple genetical patterns. The supernumerary fourth distomolar tooth has been chosen as an example for this analysis.

The racial incidence of fourth molar teeth varies in different populations, but in all groups the trait appears to be rare. Among Caucasoids, it has been observed in only a fraction of a per cent in very large series of living individuals. The trait has been recorded for various Mongoloid populations, and again the frequency is low. It is more common in Negroids, among whom the occurrence approximates 1.0 per cent. Australian aborigines show an average frequency in crania between 1 and 2 per cent, the highest racial frequency for this trait. New Caledonians and Tasmanians may have a similar frequency, and since all three populations contain the same Murrayian substratum, such frequencies of fourth molar teeth may ultimately prove useful as a racial-marker. Broadly, the incidence of supernumerary distomolar teeth varies inversely with the frequency in which the third molar teeth are reduced in size, malpositioned, or congenitally lacking.

The literature reports 16 Australian aboriginal crania characterized by one or more fourth molar teeth. But 11 of these cases can be localized as to their place of origin. My own data on the living provide eight additional instances for the characteristic. The frequency of this trait cannot be accurately estimated among the Australians. Campbell (1925) observed but five cases in a series of approximately 600 crania examined in

Australian museums. More than twice as many instances have been reported from the far less extensive collections of European institutions. There is some evidence that crania possessing fourth molar teeth, because of their unusual rarity and interest, were sent in disproportionate numbers from Australia to Europe at the turn of the Century. Thus the frequency calculated from Australian collections may be too low, while that based upon European series of crania correspondingly too high. An estimated frequency of expressed fourth molar teeth lying between one and two per cent may be taken as a fair approximate evaluation. This range is probably a minimum estimate, since there are no data for correcting for the number of crania in which the mandible is lacking, in which ante-mortem tooth loss distorts the frequency, or post-mortem damage and destruction of the alveolar region obscures the true incidence.

As in other racial groups, fourth molar teeth among the Australians show a wide phenotypic range of expression. Of the 16 crania which have been adequately described, five are characterized by the bilateral presence of supernumerary distomolars; four cases in the maxilla, and one case in the mandible. One of these crania is of unusual interest; in addition to the bilateral expression of fourth molars, it also shows the presence of a fifth right maxillary molar.[5] The 11 crania which show only a unilateral expression of tooth express the character in the maxilla in ten cases, and but once in the mandible. Of the maxillary cases, six occur in the left side, four on the right. The single mandibular instance affects the right side. Sexual differences in the expression of this trait are difficult to evaluate. But eight of the 16 available crania have been sexed; five were classed as males, three as females. In terms of sexual sampling factors in cranial collections, there is little basis for judging the significance of these frequencies.

My own data based upon living adult male aborigines show in all eight instances, a unilateral expression of the character. Seven of these cases are in the maxilla, and but one in the mandible. The fourth molar tooth occurs unilaterally on the left side of the maxilla in four cases, and on the right side in the remaining three. The single mandibular instance was on the right side.

Supernumerary distomolar teeth vary widely in the number of cusp elements present, and in the over-all size of the tooth. There is little reason to doubt that these two apparent variables are closely and directly correlated. The eight cases from my data showed the number of cusps ranging from two to five and crown modules ranging approximately from six to 12 mm. There were two cases each of supernumerary molars having two and three cusps. In four cases the tooth was quadricuspite and in one case five cusps occurred. The last instance, a mandibular supernumerary molar, is of particular interest. This fourth molar element was fused to the third molar tooth just anterior to it on a broad front so that in appearance it seemed to be a nine-cusped molar tooth with an estimated length of 20 mm., and perhaps 12 mm. breadth. The compound nature of this tooth was shown by the deep fissure separating the posterior five-cusped element from the anterior four-cusped third molar element.

The available sample of 24 cases in which one or more fourth molar teeth were present is admittedly small, but a brief summary of the range of expression will be useful later. The maxillary occurrence of the trait is more frequent than the mandibular in the ratio of 21 to 3. A unilateral expression exceeds the bilateral in the ratio of 19 to 5. Although the differences are probably not at the level of significance, in the maxillary cases both series of living aborigines and the combined cranial series showed a slight excess for the expression on the left side as compared to the right: in crania the ratio was 6 to 4; in the living 4 to 3. The relative sexual frequency of the fourth molar tooth cannot be estimated owing to a lack of proper sampling information.

The data as they stand suggest a very complicated situation anatomically which might be interpreted from several opposing points of view. The genetic basis for the appearance of this supernumerary distomolar tooth might be theorized as consisting of a multi-allelic series, or in even more complex multifactorial terms. This complicated view would be held by those who prefer to believe that the widely varied phenotypic expression, in terms of differences in number, cusp count, size, and region of origin, are all primary expressions of separate genes. But even in this approach to the data, there would be no genetical basis to explain the differences between a bilateral expression, on the one hand, and either a right or left-handed unilateral expression on the other. These variations in the trait must be considered in any case as consequences of variable genetic expressivity.

[5] This is the only case of its kind in man that I found in the literature, but others probably have been reported.

Opposed to this complicated approach to the matter, it can with equal logicality be considered that all the variations of expression in site of occurrence, size, and cusp pattern of these supernumerary distomolar teeth may be due solely to the variable expressivity of a single gene. This alternative explanation could be defended with ideas now current in both the dental and genetical literature that many, and perhaps most, dental characteristics may be determined by genes which exert field effects through a complicated series of physiological interactions in growth, rather than being caused by genes which produce specific localized expressions in the phenotype. In the form in which the data had been presented there is no basis for objectively choosing between these two extreme hypotheses for the genetic nature of fourth molar teeth.

We are not concerned here with an evolutionary interpretation of the significance of the fourth molar tooth. Early authorities tended to view the trait as having broad phylogenetic significance; but in more recent years, these implications have been rejected, and the trait is now considered as an anomalous expression without atavistic implications. Supernumerary distomolars occur among other primates in frequencies which range from very low values to those considerably in excess of any reported for human populations on a broad sampling basis. Whatever its genetic basis, the trait is recurrent throughout most of the primates.

Passing note should be taken that the situation concerning fourth molar teeth is more complicated than described above. A number of authorities, including Shaw (1931), and Campbell (1925), have expressed an opinion that the so-called "Dellae" or fourth molar pits, are in some genetic way related to the expressed fourth distomolar teeth. These pits range from faint depressions to rather large fossa, and are situated on the alveolus immediately posterior to the third molars. The suggestion has been made that these fourth molar pits are related to the development of fourth distomolar teeth in the sense that they are a consequence of the development of tooth germs for the latter which have not completed their growth, so that the alveolar border has grown up and around them, leaving a resultant area of depression. If this proves true, the genetic expression of a tendency toward supernumerary molar teeth will prove more complicated than described in the preceding section, and the estimated frequencies for the occurrence of this trait have grossly underestimated the true values. The frequency of these fourth molar pits in various racial groups has not been accurately described in the literature, nor can they be observed in living individuals. Hence they must here be ignored of necessity. Nor can the significance of the existence of supernumerary paramolars be considered at this time.

I have stressed the idea that an analysis of spatial relations may frequently yield important information concerning the genetical complexity of a given trait, or category of traits. Figure 6 illustrates a map based upon the isophenic frequency

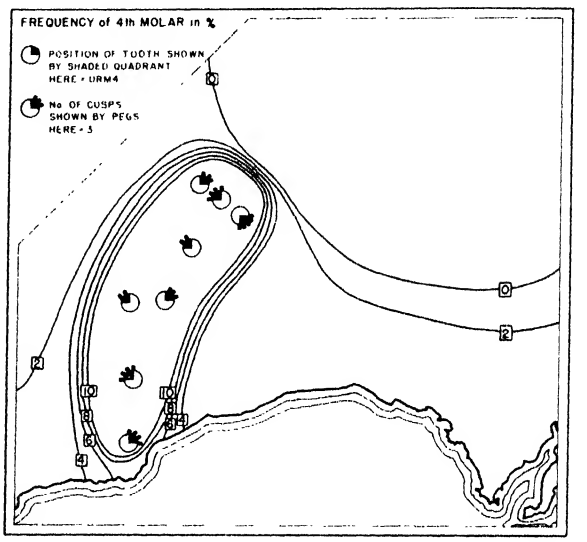

FIG. 6. Isophenic map for fourth distomolars

of the occurrence of supernumerary fourth distomolars among living Australian aborigines. My data provided but eight cases from among approximately 900 adult aborigines. A minority of this series must be excluded owing to excessive tooth loss, particularly in those regions where white settlement, and hence diet, is the longest established. My total series is drawn from an estimated minimum of 200 tribal areas, so it is the more remarkable that all eight cases were concentrated in a belt of five adjoining tribes. Of these three occurred among the Ngadadjara, one in the Mandjindja, two in the Nangatadjara and one each in the Tjeraridjal and Ngadjunma tribes extending toward the south coast. A total series of 74 adult males, whose teeth were in sufficiently satisfactory condition to be expected to show the occurrence of these supernumerary molar teeth, were measured from these five tribal areas. The occurrence of eight such cases in this sample indicates an expressed frequency of the trait of about 11 per

cent for the five tribes under consideration. The true frequency for the trait, if allowances were made for unobservable fourth molar pits, and the well-formed but unerupted fourth molar such as occasionally occur, would be certainly appreciably higher. A total of only 13 female aborigines from the same tribal areas were measured but disclosed no instances of fourth molar teeth. These sexual differences in observed frequency are not significant.

The isophenic contours in Figure 6 are based upon group intervals of 2 per cent. The five tribes with the eight observed cases have all been included inside the 10 per cent isophenic line. The expressed frequency for the trait may possibly vary considerably within the belt of affected tribes. For example, the most northerly tribe, the Ngadadjara, revealed three cases of fourth molar teeth among only 18 adult males. This corresponds to an expressed tribal frequency of approximately 17 per cent. The next tribe to the south, the Mandjindja, showed but one instance among 25 males. This corresponds to an approximate frequency of but 4 per cent. Available data are unfortunately too scanty to allow refined estimates of the true frequency of expression of this trait in its area of concentration. Since the overall frequency has been estimated as about of one to two per cent for the rest of Australia, four isophenic contour lines closely encircle the area in which the phenomena have been found concentrated. There are little data for the exact placement of the remaining contour lines, those corresponding to two per cent and 0 per cent respectively. However, the scientists on the various expeditions sponsored by the South Australian Museum have measured and observed more than 260 adult males, and 130 adult females from the area mapped here. Dental examinations were made of each individual and it is significant that no cases showed the presence of fourth molar teeth. These data suggest that the expression of this trait is either absent, or but present in a very low frequency, in the region contained north of the isophenic line labeled 0 per cent frequency. Included in these data were 51 men and 24 women from the Pitjandjara tribe, which abuts against the full northern boundary of the Ngadadjara, who in my data show the highest observed frequency. It is clear that a very steep gradient must exist along the boundary between these two tribal populations.

Figure 6, like some of the preceding maps, is characterized by dramatically steep cline gradients around restricted local tribal populations. Interpretation of this isophenic topographical surface seems quite clear. There is no known source from which such high expressed phenotypic frequencies could have been obtained via the process of hybridization; this factor may be eliminated from consideration. Known mutational processes can hardly account for the observed high frequencies limited to these five tribes. Selection of the necessary magnitude is difficult to postulate for a region where the environment does not difier dramatically from the rest of the arid interior of Australia. Genetic drift remains an evolutionary mechanism which can plausibly explain the phenomenon.

An acceptance of genetic drift as the evolutionary force producing this extreme increase in the locally expressed frequency of fourth molar teeth proffers some interesting genetical implications. Earlier two extreme hypotheses were presented to account for the genetical basis of this anomalous dental trait. The first considered the genetic cause as a complicated series of multiple allelic, or even multifactorial genes. The second hypothesized a single factor trait which, through field action in an indeterminate series of complex physiological events, produced widely varying degree of expression. The observed areal distribution of fourth molar teeth shown in this bloc of tribes makes the choice between these alternate hypotheses very clear. The first hypothesis demands that the various multiple genes postulated as responsible for the anomaly be independently heightened in frequency by drift in this single circumscribed area. One needs no mathematical model, however simple, to realize that this would be a most improbable concatenation of events. The alternate hypothesis, since it requires that drift operate so as to increase the frequency of a single gene in this local region, clearly is to be preferred on the basis of probability.

To my mind the data justify a tentative acceptance of the hypothesis that a single gene is responsible for the supernumerary fourth distomolar in all its various forms of expression. There is no evidence to indicate its mode of inheritance. Even though the expressed trait is but a part of an ill-defined growth complex, its value is greatly enhanced as a racial discriminant since all its forms appear to fall into a single genetic category. It justifies a reformulation of the method of collecting new data for future use so that the full range and frequency of the various forms of expression can be further defined. Pedigree and gene frequency analyses will be required. The rarity of the trait in most available populations, together

with the wide range of expressivity, unfortunately suggests that at the best these may prove laborious, and at the worst impossible, tasks.

It may prove feasible through some other form of analysis ultimately to demonstrate that the extension or contraction of the dental lamina, relative to its normal position in cases where the third molars in man erupt functionally, is a field phenomenon controlled by a relatively simple set of allelic genes. The malpositioning of lower wisdom teeth might be explicable in terms of directional deviations upward of the posterior portion of the dental lamina, resulting from genetic factors controlling mandibular size. The field reduction in molar size and cusp number from first through third, observable in both jaws in modern populations, may express a genetically imposed distal tapering of the lamina. Genetical research centering about modifications in the form and positioning of the dental lamina would be pregnant in its racial implications.

G. A summary of the possible use of the concept of genetic drift as an analytical tool

A single recurrent theme, the importance of spatial relationships, has run through the preceding discussion of the Australian distributions of the blood-group gene I^A, the blood-type gene M^N, the metrical traits of stature and total facial height, and the morphological characteristics of supernumerary fourth molar teeth. These data have been utilized to illustrate a general analytical principle which is of more importance than specific conclusions with regard to any given trait. Analysis of space relationships is dependent upon the field collection of data in such terms that the observations are obtained for contiguous human isolates. The requirements of spatial coverage and of the elimination of sampling error are directly opposable to each other in most practicable research designs. In the past, anthropologists, to minimize the sampling error in their data, pooled their series so broadly as to blur the minor variations in space which build up the topographic surface of an isophenic or isogenic map in sufficient detail to make a plausible interpretation possible. This procedure has been as disastrous in its way as the earlier historical tendency to ignore the nature of sampling variations, for it distorted the very aim of good research design. Ideally, present field research in racial anthropology should be designed to obtain statistically significant samples from series of isolates continuously distributed through space. If available time and funds impose limitations it is better to risk the inclusion of some sampling errors than completely to destroy the meaningfulness of spatial variations in the data.

The reader may have noted that in the preceding four analyses where drift seemed to be operative, it occurred repeatedly in four adjoining tribes, the Nangatadjara, the Mandjindja, the Ngadadjara, and the Pitjandjara. This is not due totally to an artifact inherent in the data themselves. While the first three tribes represent the only isolates adequately represented in my own data, that generously offered for my use by the various workers of the South Australian Museum contained 12 additional tribal populations. Among the latter groups, aside from the Pitjandjara, drift seemed only to have occurred in one instance, that for total facial height in the Iliaura tribe. One may interpret the clustering of the affected tribes to indicate that while drift over a long period of time may be expected to occur widely and essentially randomly throughout such areas as the arid interior of Australia, that at a given horizon in time its impact may be strongly localized in certain restricted regions.

The desert interior may be characterized as uniformly receiving less than 10 inches of mean annual rainfall. Tindale (1940) has pointed out that the rains in this region are of summer monsoonal nature, and that local droughts are inevitable and recurrent. He records that the longest continuous drought in a single area in Central Australia occurred in the region southwest of Alice Springs, lasting from 1919 through 1930. This major climatic catastrophe followed closely on the heels of a shorter drought period, from 1914 through 1917, centering in a region about the Musgrave Range, slightly further to the south. The former drought did not affect the whole country of the interior, but was particularly severe around Lake Amedeus, and was strongly felt as far east as Hermannsburg Mission. He records that those natives who were unable to travel, or who traveled in wrong directions, were the principal sufferers. Thus some of the eastern hordes of the Pitjandjara tribe were seen at Hermannsburg Mission in 1929, when they were in a critical physical condition. Other members of the same tribe, who had retreated from the Lake Amedeus area either by choice or accident toward the southwest, not only did not have to leave their tribal country, but did not seem to have suffered insuperable hardships. They lost but few children, and when seen again in 1933, they were found to be in a thriving condition. These observational data are meager, but they are suggestive of the

causes which may have operated to concentrate the apparent aspects of random genetic drift in the four tribes previously mentioned. It should be recalled that this very region not only receives minimal rainfall, but that the reliability of precipitation here is at a very low level for the entire continent. The present data seem to show that climatic accidents, such as localized droughts, may produce accelerated changes due to genetic drift. In earlier times a survey might have found the overt manifestations of drift localized in some other areas. All Australian tribes fall within classification of small effective breeding populations, but those of the dry interior stretches seem subject to climatic disasters which cause considerable cyclical fluctuation in population size, particularly through the elimination of children. Hence there the size of the effective breeding population tends to be nearer the minimum density this country can sustain in times of climactic crisis than the maximum. Drift would be expected to be more extreme among such desert populations.

The concept of genetic drift has in the past complicated the racial analysis and interpretation of such simple characteristics as the blood groups and the blood types. Material from arid Australia, based upon tribal populations, have been used to illustrate that in certain instances drift may possibly serve the purpose of a discriminatory analytical tool. It is suggested that spatial analysis, based upon continuously distributed genetic isolates, or their population equivalents, may be useful tentatively to identify those metrical measurements and morphological observations which have relatively simple genetical modes of inheritance. If the distribution of the traits through space are such that extreme fluctuations in their isolate frequencies produce steep and localized gradients in the clines of the resultant topographic surface map, and if the other evolutionary forces of hybridization, mutation, and natural selection can reasonably be excluded from having been influential, in such instances drift may operate visibly upon the frequencies of characters genetically simple in their inheritance. Total facial height among metrical traits and supernumerary distomolars among morphological characters seem to answer the requirements and hence tentatively may be considered of relatively simple genetic origin. It may be anticipated that in those traits in which the genetic basis for transmission is complicated, the effects of drift upon the genes contributory to their total phenotypic expression will not appear visibly in the isophenic contour surface. Stature among central Australian tribes seems to fall into this category. It should be emphasized that the use of drift to make tentative identifications of metrical and morphological traits which may prove simple in their ultimate mode of genetic transmission is merely preliminary to a systematic and intensive pedigree and ultimately gene frequency analyses which will be required for the full genetic definition of such traits. Use of the concept of drift as an analytical device is only supplementary to normal genetical procedures, and its real function lies in its use to salvage racial data existing in classical anthropology.

While hybridization and mutation can be reasonably discarded as unimportant in producing the observed mosaic patterns in arid Australia, the evolutionary forces of selection and drift are more difficult choices. In human evolution, selection is undoubtedly of primary importance, whereas drift may have had only passing effects. But this is not the question here. The issue is whether the above inter-isolate fluctuations may be attributed in part or all to drift. Unfortunately no instance of selection has been demonstrated by human population genetics and hence no coefficients have been calculated to weigh the probabilities involved in a decision. If very high coefficients are ultimately confirmed as operative on man under these Australian conditions of environmental stress, then drift must be rejected. Man differs from classical laboratory organisms in several aspects which indicate caution in extrapolations from existing genetical data. Man's intelligence provides for flexibility in response to stress, and his culture offers some degree of insulation from the environment. He is warm-blooded, and the period between generations is prolonged. I would not minimize the importance of selection, but the instances cited from Australia seem from our present knowledge attributable to drift with a modest degree of probability. In any case, fluctuations of this inter-isolate nature must be analyzed to control and interpret anthropological measurements and observations.

PART III. THE GENE FLOW MODEL: A SYNTHETIC EXPERIMENTAL METHODOLOGY FOR HUMAN POPULATION GENETICS

The concept of space as an important variable in genetical analysis is emphasized throughout this paper. I propose to use data from aboriginal Australia to create certain simple models to help define the nature and dynamics of gene flow through populations continuously distributed in

space. It must be considered a purely exploratory venture, in which the basic assumptions have been drastically simplified owing to our present general ignorance of the detailed data for, and the dynamics of, inter-population relationships. The general concept of gene flow can be introduced via the illustrations of the introduction of the blood group gene I^B into Australia.

A. The recent infiltration of the alien blood group gene I^B into Australia

One of the clearest and simplest services offered by a genetic analysis of race is the delimitation of the area influenced by a relatively recent infiltrating gene, or genetic elements, into a previously undisturbed series of populations. The spread of the blood group gene I^B into Australia represents this situation. Figure 7 is a map showing the area of penetration of the gene I^B along the northern coast of Australia. The area covered by this map is indicated in Figure 1 by the hachured region designated by the letter (B). The area penetrated by the gene I^B is defined by 21 individual aborigines possessing the blood group phenotype B or AB, whose tribal origins are known. Seventeen of these individual cases are from my data, three from Simmons, and one from Phillips. The three cases reported by Simmons all come from the Alawa tribe on the Hodgson River, a tributary of the Roper River in Northern Territory. They may represent non-random sampling for this region, but the other cases seem representative within the limitations of the relatively small series available.

The area influenced by I^B begins in the west at the Roper River and extends along the southern coast of the Gulf of Carpentaria in a narrow band approximately 75 miles in width, and about two tribal territories inland from the coast. Its southern boundary extends deep into the base of Cape York Peninsula and then turns abruptly northward, remaining on the western side of the Great Dividing Range until the tribal territory of the Kokokulunggur is reached, where it crosses the mountains to reach the Pacific coast. Thus on the eastern coast, the belt of penetration of the gene I^B only reaches the northern limit of the rain jungle refuge area and does not impinge upon the 12 nuclear tribes in which the negritic substratum survivals are the strongest.

The entire flow pattern of the gene I^B is based upon a sample of but 21 individuals; consequently it seems wise to indicate those data which assist in defining the outer limits of this infiltration. Commencing at Port Hedland on the northwestern coast of Western Australia, (lying outside the western boundaries of this map) and extending to the northern coastal boundary between that state and Northern Territory, Simmons and Gay separately have tested the blood groups of 321 full blooded aborigines and found the gene I^B completely absent. Simmons and his co-workers have further typed 211 aborigines between this point on the coast and the Roper River to the east as detailed below. The Tiwi tribe on Melville and Bathurst Islands offshore from Port Darwin in Northern Territory is represented by 108 samples in which I^B is lacking. A series of 55 Ingura tribesmen from Grotte Eylandt, lying northeast of the mouth of the Roper River also showed this gene to be absent. I^B was not found among 48 aborigines from the coastal districts of the mainland. A further sample of 54 natives from the interior of Northern Territory revealed three individuals of the phenotype B or AB. They were all members of the Alawa tribe and have been included within the hachured area in Figure 7. These data suggest that the gene I^B is either absent from the region listed or at most occurs only in a very low frequency.

South of the belt depicted as representing the outer limits of the gene I^B, there are other series which serve to confirm the maximum extent of genetic penetration. Thus in Central Australia, Cleland has tested 260 aborigines without finding a single individual carrying this gene. Further east, at the base of Cape York Peninsula, Birdsell tested 33 individuals with the same results. Finally, the extreme eastern boundary of the penetration area seems adequately defined by 110 individuals from the region just to the south in the tropical forest area, tested by Birdsell, all of whom lack the gene I^B. Thus, within reasonable sampling limits, the outer boundary of the area penetrated by the gene I^B seems reasonably well-defined, with the possible exception of the coastal stretch between the Roper River and Port Darwin.[6]

The penetration of the gene I^B into Australia has resulted from transient contacts between the aborigines and two culturally and racially different alien populations. Cape York Peninsula has largely been influenced by hybridization with the Papuan populations of the Torres Strait Islands, while the remainder of the area affected has received its quota of I^B from late prehistoric

[6] Complete bibliographic references for Cleland will be found in Birdsell (1940); for Simmons, Graydon and co-workers in R. T. Simmons, J. J. Graydon and J. Avias (1949); for Gay in R. K. Gay (1942); and for Phillips in Phillips, G. (1928).

and historic Malay fishermen. Evidence indicates that the dugout canoe-using Papuans from the islands in Torres Strait voyaged as far down the east coast of Cape York Peninsula as the Pascoe River. On the west coast of the Peninsula physical trade contacts with the Islanders extended no further than the Pennefather River. These points are shown on Figure 7 by the solid arrows embracing Cape York Peninsula. The dotted arrows (X) and (Y) represent the maximum postulated extension of Papuan contact and are based upon data related to the diffusion of cultural items from these people rather than upon historical evidence of contact. In a sense they are improbable limits of maximum range of physical, and hence genetical, penetration by these Islanders.

My data for the I^B influenced area consists of 220 aborigines. Sampling procedures in the field were such that it was impossible to obtain a random distribution throughout this entire region. The tribes from the tip of Cape York Peninsula along the east coast as far south as Princess Charlotte Bay are poorly represented. The groups bordering the eastern and southern coast of the Gulf of Carpentaria likewise have been too inadequately sampled to allow calculations of the actual frequency of the gene I^B in these areas. In an area beginning at Princess Charlotte Bay and extending south nearly to the line representing the maximum penetration of the gene I^B data allow the calculation of approximate gene frequencies. This area is enclosed in Figure 7 within a broken dotted line. For a series of 65 aborigines, of whom 39 belong to the blood group O, 17 to group A, and 9 to group B, the frequency of the gene I^B falls between .08 and .09. If this value is compared with gene frequencies from the nearest region tested in New Guinea, it is, found to be surprisingly high. Simmons and Graydon (1945, and v.v. 1946) have tested a total of 128 Papuans from Daru Administrative District, the sample nearest Cape York Peninsula. The gene frequence for I^B in this randomly sampled population is .17. Another series totaling 100 individuals, from the same workers, in the Kikori Administrative District, northeast of the Fly River, gives a frequency of .20 for the same gene. In terms of the simple equations for hybridization, these values indicate that the aborigines along the east coast at the base of Cape York Peninsula in Australia should contain about 50 per cent Papuan genes through initial hybridization and subsequent gene flow. Both the overall taxonomic considerations and the cultural

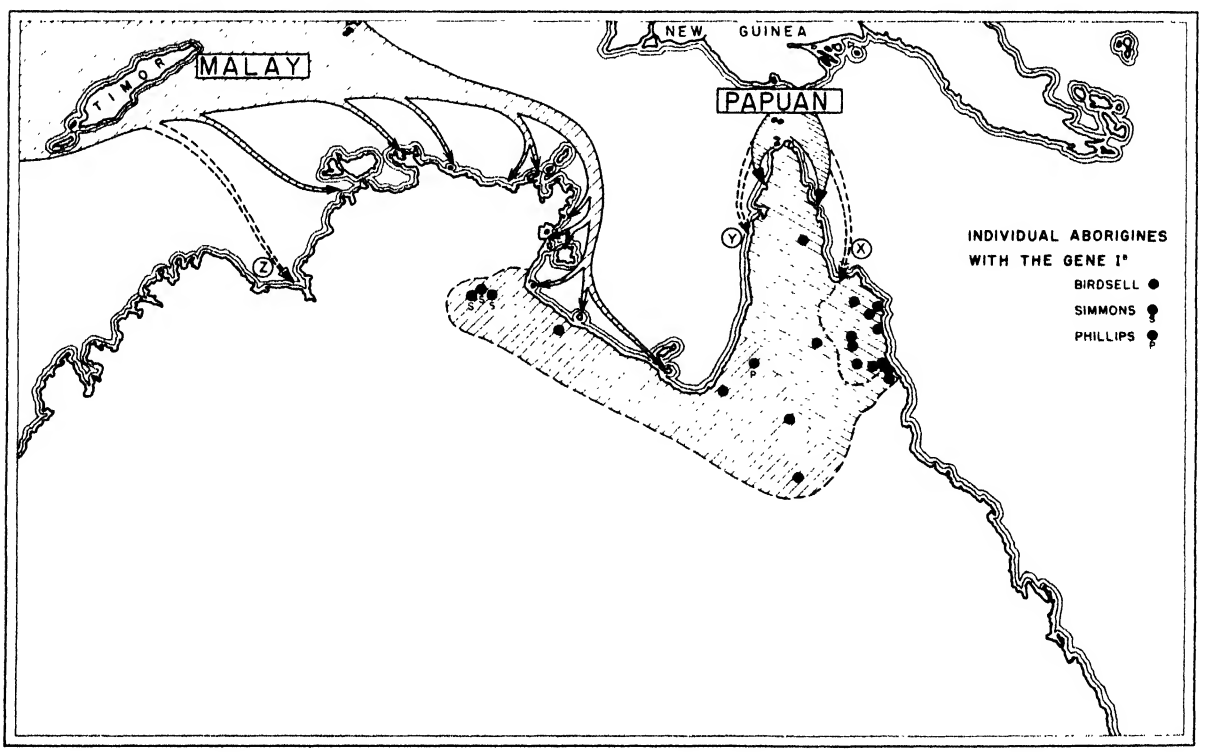

FIG. 7. Map showing area of recent penetration by the alien gene I^B.

evidence suggest that this estimate of Papuan genetic influence is far too high. Here, as in so many other areas of the world, where the frequency of the gene I^B seems to be a relatively recent introduction, its frequencies are too high to be explained by hybridization alone. Other evidence suggests that the frequencies for this gene may be increased in some way by the operation of selection.

There is no evidence to determine how early Papuan influences became important in Cape York Peninsula. Such genetic infiltration was dependent upon the existence of the dugout canoe, so the earliest possible date would extend backwards about 4,000 years. The general configuration of the distribution of the gene I^B is suggestive of a shorter period of contact, possibly no more than 1,000 years in duration. Until evidence from archeology provides a definitive time measure, no more accurate estimate will be available.

A second alien racial group, the Malays of Indonesia, were responsible for the introduction of the gene I^B along the southern coast of the Gulf of Carpentaria. There is evidence for the presence of Malay fishing fleets in early historic times, ranging from Port Darwin in Northern Territory on the west, as far east as Sweer's Island in the southeastern corner of the Gulf of Carpentaria. Each year these fleets sailed from Timor on favorable monsoonal winds to fish for bêche-de-mer in the waters of Australia, returning when the winds shifted. Historical data indicate the greatest points of Malay concentration were Arnhem Land, Groote Eylandt and the adjacent mainland as far south as the mouth of the Roper River. Malay contact did not extend to the eastern shores of the Gulf of Carpentaria. McCarthy (1939) suggests from the indirect evidence of trade materials that Malay contact may have extended as far west as the region around the mouth of the Victoria River, shown on Figure 7 by the dotted arrow labeled (Z). The gene I^B is absent from stretches of coastal Northern Territory which are known to have been subject to Malay contact. The question arises as to the probable cause of discrepancy between the historical and the genetical data. Blood group sampling for the region north and west of the Roper River are not yet adequate to exclude the possibility of a very low frequency of the gene I^B in these regions. This is true even in the relatively compact island samples from the Tiwi and the Ingura tribes. It applies even more pertinently to the intervening coastal mainland. On the other hand, Warner (1932) found that the tribes to the east of the Goyder River and north of Groote Eylandt were unusual among Australians, being jealously possessive of their women, and insisting upon strict monogamy. In this region the Malays may have been prevented from establishing effective genetical contact with the native women. Hence, for this area, the apparent absence of the gene I^B may in time prove real, but more intensive sampling will be required for proof.

Timor was the point of departure and return for the bêche-de-mer fleets and it was known that the crews were derived from various Malay dialectical groups. They may have been recruited widely throughout Indonesia. The limited archaeological and historical evidence available suggests that the Malayan fishermen may not have begun their annual visits to the northern coast of Australia earlier than 500 to 1,000 years ago. Data unfortunately do not allow even an approximate calculation of the regional frequency of the gene I^B, as introduced from Malay sources. The pattern of distribution suggests that Malay genes have penetrated as far as the base of Cape York Peninsula, there to interdigitate with the gene I^B introduced from Papua. Thus a single alien gene present throughout and continuous territory in Australia can clearly be shown to have been derived from two racially different sources of foreign contact.

The distribution of gene I^B represents the incipient stages of normal flow resulting from hybridization. If the data were more extensive, the flow pattern might be analyzed profitably in greater detail by model methods. Even so it is instructive to compare the actual area influenced by Malayan and Papuan contacts, as demonstrated by simple genetical analysis, with that previously postulated by earlier workers. Some writers have believed that Malay contacts have left their mark upon the aboriginal population along the entire northern coast and indeed, far down the eastern margin of the continent. These ideas were based upon ill-defined and non-specific traits, including superficial impressions of skin color, as well as linguistic vocabularies. The range of Papuan genetical influence has been similarly overestimated, using the occurrence of crisp, spirally curly hair as the primary criterion. Papuan influence has been claimed for regions as far west as Melville and Bathurst Islands, and as far south as the New South Wales coast. The high frequency of helically curled hair in the jungle area of North Queensland has been incorrectly quoted as evidence of prehistoric or historic Papuan influence. The distribution of the gene

I^B serves to clearly delimit the extent of penetration of both Papuan and Malay genetical influences on the mainland of Australia, and thus serves a valuable function in correcting erroneous attributions from the earlier literature.

B. The Australian tribe as a genetic isolate

The preceding exercise in defining the limits to which aboriginal populations have been influenced by the gene I^B from two alien sources, is based upon the simplest interpretation of spatial distributions. Inferences from this map are largely overt and provide little help in the evaluation of population dynamics. I propose to use data from aboriginal Australia to create simple models which simulate the processes by which genes flow through populations continuously distributed in space. This formulation is tentative in nature.

Aboriginal Australia is in many ways an ideal area in which to apply gene flow models. The entire population obtained its substance from a hunting and collecting economy. Such continental uniformity is unique. Material culture varied but little throughout Australia, and the minor deviations which are recognizable modify man's relation to man, rather than offering any increased efficiency in the exploitation of the natural environment. It is important for our purposes that the low level of social organization attained in Australia was constant and nowhere permitted the successful governing of large groups of people. Existing authority was diffuse, and informally exercised through a gerontocratic council of elders. Direct authority hardly operated outside of the extended family group. The marital restrictions imposed by the class systems of the aborigines are of little importance to our present problem.

The concept of gene flow refers to the spread of genes through populations, the interchange of genes between isolates via hybridization. It will be usually detected, and its pattern of flow evaluated, through the observation of one or more marker-genes. The rate of gene flow may be defined as the distance in space which specific genes traverse in a constant unit of time. *For meaningful measurement normal geographical space, and hence distance, must be replaced by the concepts of genetic space and distance which are evaluated in terms of a population unit, the genetic isolate. These concepts will be applied in later portions of the paper.*

The genetic isolate is the basic unit used for the construction of gene flow models. *An isolate may be defined as a population which forms a more or less closed group, so that its members are less likely, than is expected by chance, to exchange genes with members of another group.* (See Stern, 1949, among others.) If the population pyramids are uniform from group to group and constant through time, isolate size will be directly correlated with, but larger than, the effective breeding population. The isolate may prove easier to identify as an entity than the latter, and hence will be used as a basis for model construction. There are but two units of social organization in Australia which might be expected to approximate the genetic isolate: the horde, and the tribe.

The horde, or the local group, is equivalent to an extended family. It represents the primary land owning unit in Australia. Throughout the continent it may be characterized as exogamous, patrilineal and patrilocal. Expressed more simply, a man takes his wife from outside his local group, she lives with him, and their children belong to his horde. Inevitably in each generation 50 per cent of the total horde gene pool is introduced from other hordes outside of its boundary. Due to this rapid influx of genic materials the horde does not closely approach the concept of the genetic isolate. This is fortunate since the literature contains but scanty data on the size, number, location and boundaries of Australian hordes.

In Australia hordes are grouped into more complex social units, which have been called tribes by the anthropologist and layman alike. More pertinently, their existence as a discrete social entity is recognized by the aborigines themselves. A tribe consists of a group of hordes which are united by speaking a common linguistic dialect, and possessing a similar culture. No form of authority exists to bind the tribe into a single cohesive unit. The tribe owes its existence to subtle forces of internal cohesion. Significant among these is a common genetical or socially attributed line of descent. Although the aborigines may have had no knowledge of physiological paternity, and occasional inter-tribal marriages and instances of ceremonial license did occur, these are exceptions to the forces which made for intra-tribal cohesion. It cannot be doubted that *the Australian tribe fulfills the essential requirements defining the genetic isolate.* This assumption is basic for all subsequent pages.

The population characteristics of the Australian tribe must now be evaluated. Tindale (1940) has listed 574 aboriginal tribes for the continent. At the time of discovery Radcliffe Brown (1930) has estimated that the total aboriginal population of

the continent represented 251,000 natives as a minimum, and more probably exceeded 300,000. These figures are the best available, for no accurate census of a native Australian tribe seems ever to have been taken prior to the disruptive influence of acculturation. Single tribes have been estimated as varying in their total populations from the low value of 100 persons upward to perhaps as high as 1,500. If Brown's minimum estimate of 250,000 aborigines is divided by Tindale's total of 574 tribes, an overall average of 437 individuals per tribe is obtained. Using the former's higher, and probably more accurate, estimate of 300,000 aborigines, the mean value is 523 persons per tribe. These are approximate figures, but they indicate that it will be safe to assume that on the average, and in a purely statistical sense, the aboriginal tribes of Australia had a population approximating 500 individuals. It is probable that in a long time span, tribes grow and decline in population. There is some evidence that the exigencies of inter-tribal warfare occasionally caused the remnants of a decimated tribe to be absorbed by another. Likewise, there are indications that a tribe which succeeded in expanding its population tended to differentiate into several new tribal groups. It must be assumed that in a statistical sense these two opposing tendencies balanced each other out.

In establishing a theory for gene flow through contiguous populations, some consideration must be given to the structuring factors present in the space traversed. If no social organization existed the genetic transfer which characterizes the flow might be presumed to operate through series of family units in space which was essentially amorphous and unstructured. The aborigines do not show this condition, but on the contrary, group themselves in broader, socially defined, population units. Since the Australian tribe is held together by the forces of internal cohesion, we must presume, and it is clearly a safe assumption, that both cultural and genetical contacts between the hordes of a given tribe are more frequent and of greater intensity than between hordes belonging to different tribes. Intra-tribal relationships must be more intensive than inter-tribal relationships, otherwise the tribe could have no reality as an entity. In these terms one can visualize gene flow as analogous to the diffusion of a liquid by osmosis through the semi-permeable membranes of a cell-structured space. *Tribal boundaries in Australia are the primary barriers to gene flow.*

As a corollary, it is assumed, for convenience, interaction between the hordes of a tribe will be at such a level that genetic panmixia is obtained so rapidly that actual time required may be ignored. These assumptions both err toward the extremes, but are made to simplify the concept of gene flow. Panmixia is not attained instantaneously within the confines of a tribal area, and it is equally clear that tribal boundaries operate as barriers to gene flow only in a relative sense.

My field collaborator in Australia, Mr. Norman B. Tindale, Ethnologist of the South Australian Museum, has published (1940) a map showing the distribution of aboriginal tribes. For the first time there is now available a detailed map giving individual tribal boundaries for the whole of Australia, (excepting a relatively small region in the northwestern coast and interior). This map has provided an analytical tool of great potentiality for space analysis and I acknowledge my deep indebtedness to my colleague for its publication. From his broad field experience, Tindale has noted that there is a high degree of correlation between tribal boundary limits and geographical and ecological boundaries. Mountain ranges, divides, rivers, general ecological and plant associational boundaries, microclimatic zone limits, straits and peninsulas often furnish clear-cut and stable lines of tribal demarcation. In the desert, the distribution of clusters of hordes around a few permanent waters is equally evident, and in many instances waterless tracts effectively delimit tribal boundaries. Other seemingly waterless regions possess tree-root water resources sufficient to maintain human communities which have become adapted to the utilization of such specialized water sources. Tindale has commented on the general inverse relationship which exists between the size of a tribal area and the amount of its mean annual rainfall. Throughout the central arid region of Australia, where annual rainfall averages less than 10 inches, tribal territories are uniformly large. For the Pitjandjara tribe, 60 square miles of land is required to support a single aboriginal. This compares with the average population density for the entire continent calculated by Radcliffe Brown (1930) as one person per 12 square miles of area. Coastal regions, especially those along the north and east borders of the continent where rainfall is relatively high, are marked by the occurrence of many very small tribal territories. In such favorable areas the population density may attain values as high as one aboriginal for every two

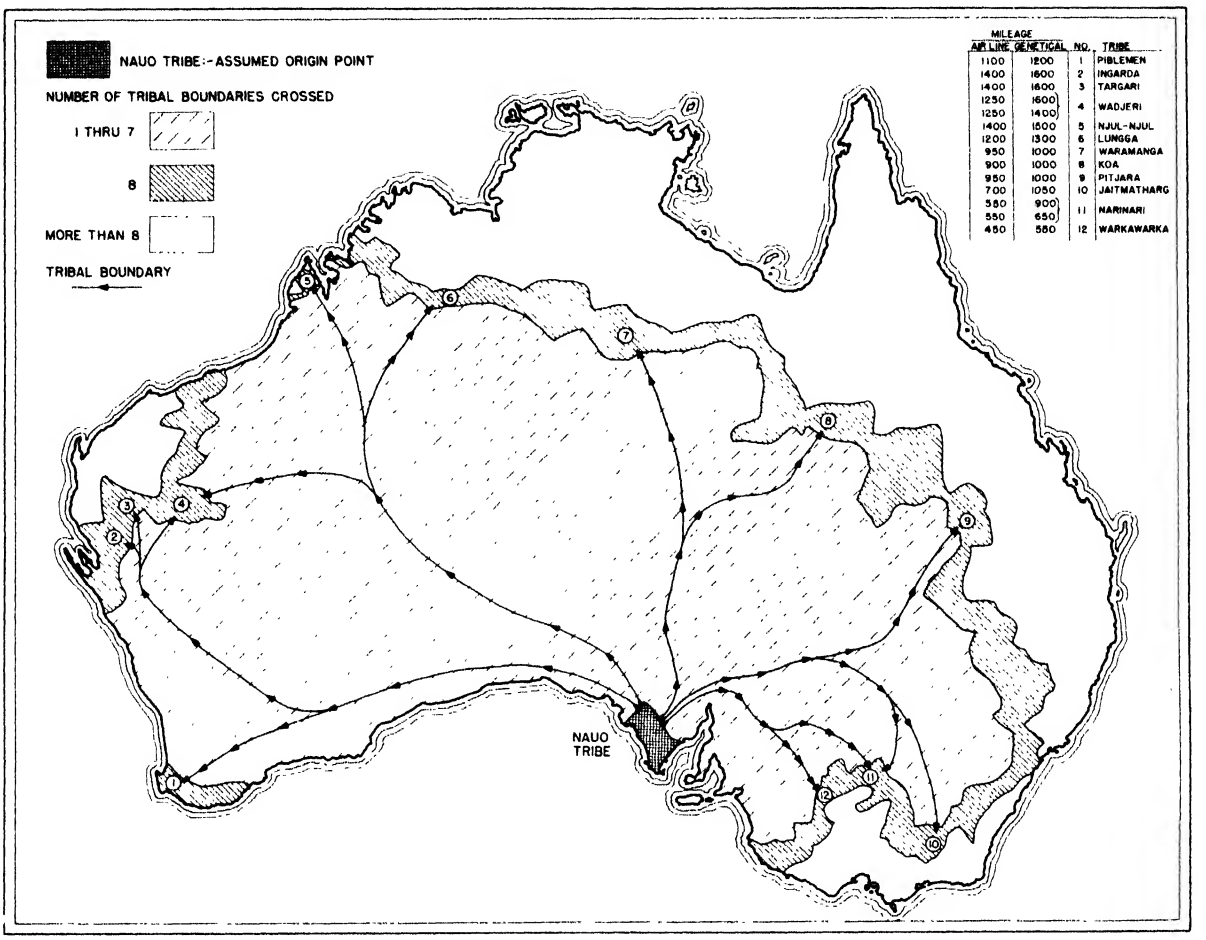

FIG. 8. Map showing differences between genetic and geographic distance and space.

square miles of tribal territory. The country at the mouth of the Murray River supported two natives per square mile, a maximum density for the continent.

C. The concept of genetic space

Spatial analysis is ordinarily conceived in terms of some absolute unit of metrical space. The cultural uniformities for the entire continent of Australia are such that the tribal populations approximate the genetic isolate, and hence *the tribal area represents the unit of genetic space. Tribal boundaries represent the basic barrier to gene flow.* Available population estimates allowed the calculation of the average tribal population throughout Australia as approximating 500 persons. Wide divergences from this mean do occur, but however large the standard deviation may be, it must be assumed not to introduce any systematic error which would seriously distort the flow models. The high degree of inverse correlation between the area of the tribe and the mean annual rainfall indicates that in this context genetic space will be characterized by a coordinate system which deviates widely, and in varying amounts, from the usual metrical units of geographical space. Thus for Australia the basic unit of genetic space must be equated to the tribal area.

Figure 8 represents a map used to illustrate simply how the concept of genetic space in Australia differs from that of geographical space. It was presumed that an alien gene was introduced into the tribal territory of the Nauo, located on Eyre's Peninsula on the southern coast of the continent.[7] The process of gene flow proceeds outward from the Nauo until the introduced genes have been spread across eight tribal boundaries

[7] This particular tribe was chosen as an origin point merely to present a certain configurational pattern, and any other tribe would have served the purpose nearly as well.

in all directions. The outer hachured periphery represents the locus of all tribes lying eight boundaries distant from the Nauo. This belt is usually one tribal area in thickness, but in certain instances it is two, or even three, in breadth as a consequence of the peculiar traits of genetic space.

A glance at Figure 8 reveals that the band of tribes eight boundaries distance from the Nauo individually vary greatly in their geographical distance from the origin point. For example, the Piblemen tribe in the extreme southwestern corner of Australia (and keyed No. 1 on the map) is approximately 1,100 miles air-line distance from the Nauo. In contrast the Warkawarka tribe (12) is but 450 miles air-line distance from the center of genetic disturbance. If the air-line distance is replaced by the mileage necessary for the actual flow of the genes from the Nauo to these tribes, the distances increase respectively to 1,200 and 550 miles. Nor is this the most extreme comparison possible, for the Ingarda (2) and the Targari (3) are both 1,400 miles air-line distance from the Nauo, and about 1,600 miles ground distance. Thus some tribes, three times as far away from the center of genetic flow as others, may be more easily affected by gene flow owing to the variable characteristics of genetic space. *Genetic distance is an undefinably variable function of geographical distance, and must replace the latter in problems involving gene flow.*

For illustrative purposes routes of minimum genetic distance have been drawn between the Nauo tribe and 12 tribes located eight boundaries distance from the former. The arrowheads located on these pathways indicate where a single tribal boundary has been crossed. Several points of interest emerge. The shortest genetic distance from the Nauo to the tribes labeled 1, 2, and 3, on the map coincides in each case through the first four boundaries crossed, and then each individually diverges widely to reach its ultimate destination. A similar condition is encountered in the gene flow pathways to tribes labeled 4, 5, and 6.

These paths of genetic flow illustrate another feature. The configuration of genetic space is such in some instances that a tribe can be reached with equal efficiency by two divergent paths of flow. The Wadjeri (4) of Western Australia demonstrate this condition. One pathway of flow is primarily through the southern coastal tribes and then turns abruptly to the northwest. An equally efficient path of flow goes deep into the western desert region in a northwesterly direction, ultimately to turn sharply west to reach the Wadjeri. The Narinari (11) show the same condition in a less extreme fashion. It is a characteristic of genetic space that the shortest distance between widely separated isolates need not coincide with the shortest geographical distance, and it may in certain configurations be reduplicated by totally different pathways of flow.

As an unjustifiable simplifying assumption, it has been considered in constructing the map in Figure 8 that all barriers to gene flow of a geographical or ecological nature could be ignored. Tribal boundaries have been presumed here to act as the only barriers to flow. In the present model the barrier influence of the Flinders Range, which extends northward from the head of Spencer's Gulf, has been totally disregarded. Later it will be shown that this particular range exercised considerable inhibiting effect upon gene flow. In reality those tribes lying eight boundaries distant from the Nauo toward the east could only have been reached by a roundabout route of flow far to the north of the pictured pathways. Under these conditions the eastern terminal tribes would have been even closer to the Nauo in terms of geographical distance.

The concept of genetic distance as applied in Figure 8 has important interpretive consequences. Considered in terms of the rate and ease of gene flow, the great, forbidding, arid desert spaces of the central portion of the continent represent freeways, rather than obstacles, to gene exchange between distant populations. Life in such areas is admittedly drastic, but as long as the isolates are continuous through such a region, gene flow can occur at its normal rate and quickly traverse great geographical distances. In contrast, the compact tribal domains in the densely settled and well-watered coastal areas of Australia represent the regions more difficult for genetic penetration, both in terms of the rate of gene flow as measured by geographical distance, and in terms of the magnitude of over-all genetic impact. Along the coasts tribal boundaries occur much closer together in geographical space, and hence barriers to gene flow are encountered more frequently. These observations apply specifically only to Australia, where the entire population is on a hunting and collecting basis of subsistence, and where navigable coastwise watercraft were unknown. The concept of genetic space obviously becomes more complicated in other regions of the world, but its broad principles, when modified to correspond to local conditions, may be presumed applicable elsewhere.

D. The distribution pattern of an ancient gene flow entering Australia from the north

Reference was made earlier to the presence of three separate racial elements contributing to the present aboriginal populations of Australia. These were, in the order of their migrations outward from Southeastern Asia, the Oceanic Negritos, the Murrayians, and the Carpentarians. This last racial group reached the Australian mainland either late in the Fourth Glacial Period or early in the Recent, but no evidence exists to provide a more exact date. If the two earlier racial elements are considered together, the penetration of the Carpentarian peoples into Australia may be considered to represent the intrusion of alien genes impinging upon the resident populations. Since our data referred to living populations, this genetic infiltration was ancient in point of time. Enough millennia had elapsed since the arrival of Carpentarians in Australia so that their genetic influence has permeated most of the continent, but with decreasing intensity from north to south. Only those populations marginal in nature, or distant from the point of entry, have escaped genetic modification. I propose in subsequent sections to test by means of gene flow models two hypotheses concerning the point of entry of the Carpentarians in Australia. To evaluate the success of these models in a predictive sense, I have constructed a map shown in Figure 9 which gives a subjective estimate of the relative contribution attributable to the Carpentarian element throughout Australia. The data utilized in the construction of this map are entirely independent of those used to control the gene flow in the models. The materials available include the author's measured series of approximately 1,000 aborigines coming from the entire southern and eastern coastal regions of the continent and their respective hinterlands. Large additional series covering the interior have been made available to me in raw data form through the generosity of the South Australian Museum and its various scientific workers. Extensive additional anthropometric data, both published and unpublished, have been useful for estimates concerning the northern portion of the continent. Photographic data have been utilized wherever possible for regions not otherwise covered. Distribution of the total data available is such that with the exception of the western and northern coastal stretches of Western Australia, sampling reliability may be considered adequate for the present purpose.

The estimates used in constructing the map in Figure 9 are primarily subjective in nature. They were made on a broad taxonomic basis with certain marker-traits utilized to evaluate the Carpentarian contribution as it varied regionally. The pre-Carpentarian population, consisting of negritic and Murrayian elements, has been considered as a single unit in contrast to the incoming Carpentarian peoples. This earlier substratum varies in its composition regionally: the tribes of southeastern Australia are predominantly Murrayian in their characteristics and contain but a minor negritic element; on the other hand, the nuclear tribes of the Cairns tropical forest area contain so high a negritic contribution that there it must be reckoned as equal to the Murrayian. In neither of these regions is there any phenotypic evidence for the presence of the Carpentarian element. The marker-traits utilized to identify these racial elements were given earlier under the descriptive summary. The basis of my estimate for the distribution of the Carpentarian component is highly subjective, and I am cognizant of its limitations, but I believe that as an over-all configurational pattern it will ultimately be verified by genetical techniques.

The pattern of distribution indicates a concentration of the Carpentarian contribution in its highest frequency, a value estimated to average about .90, in the coastal region of Northern Territory.[8] A second belt, in which the Carpentarian contribution is estimated as .70, envelopes the whole remainder of the northern coastline from Kimberley region on the west to the eastern shoulder of Cape York Peninsula. Populations within both zones are preponderantly Carpentarian in their derivation. A third belt, shown by the vertical hachuring, extends from the west coast, broadening through the arid center of Australia, and narrowing down to emerge on the east coast some distance above the jungle refuge pocket. These populations appear to display roughly balanced contributions from both the Carpentarian and the pre-Carpentarian components. A fourth zone, in which the Carpentarian contribution for the first time is a minority, with estimated frequencies averaging .30, commences broadly on the west coast to extend across the southern interior of the continent as a narrowed band before expanding into the upper Darling drainage. Thence, it breaks through the Great Dividing Range to penetrate the eastern coastal lowland for some

[8] It may be noted in passing that the off-shore islands of Melville and Bathurst to the west and Groote Eylandt to the east are estimated as showing lower values. I have no explanation to offer at this time for the deviation in these estimates of the island populations.

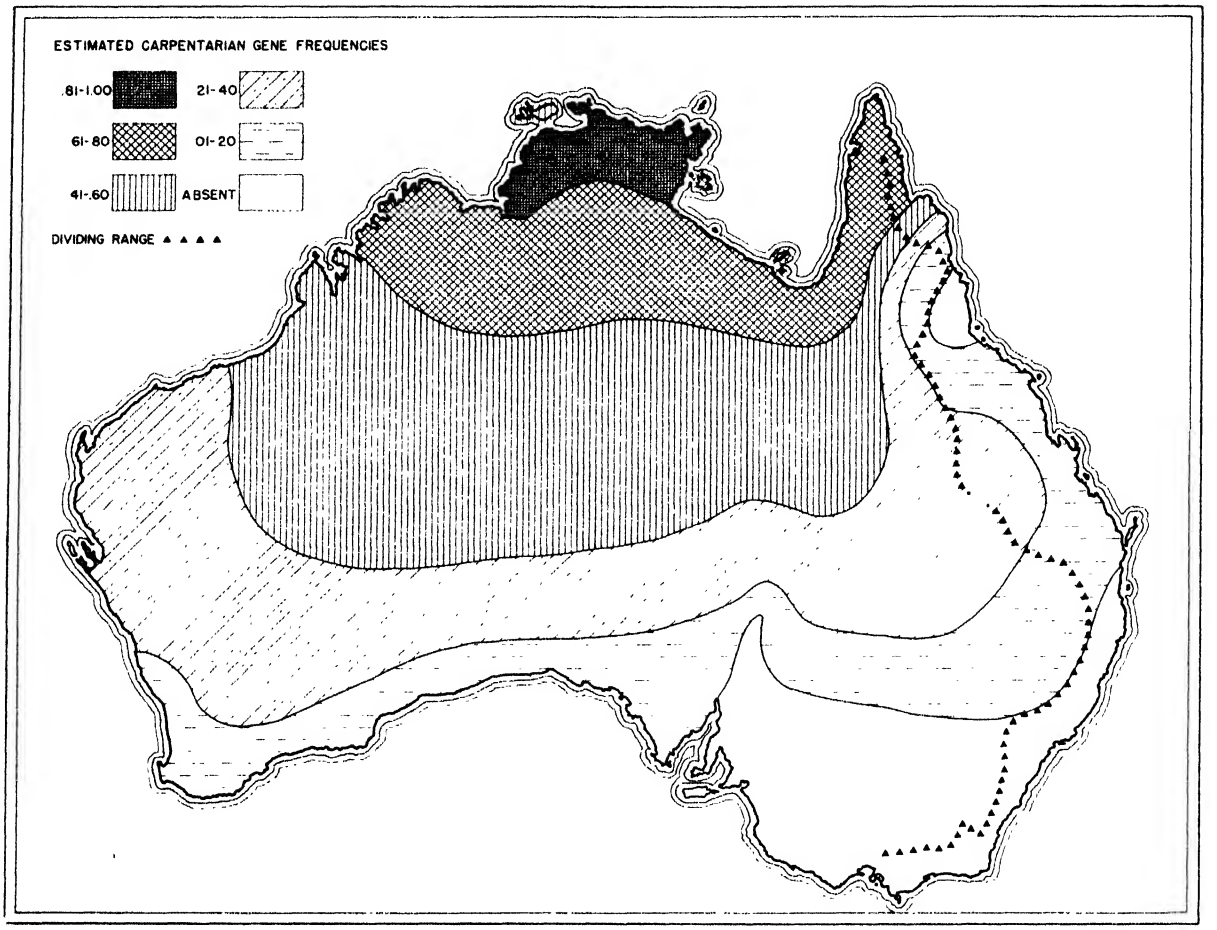

FIG. 9. Distribution pattern of the Carpentarian element in recent aboriginal populations, based upon a subjective taxonomic evaluation.

little distance before turning northward along the western flank of this extensive mountain range to reach the eastern coast at Cooktown. A final belt, in which Carpentarian contributions are estimated as averaging but .10, includes the whole southern coast of the continent as far as Spencer's Gulf, where it is sharply restrained by the northwardly trending Flinders Range. It then descends slightly to cross the greater Murray drainage system in an easterly direction, until it meets the Dividing Range. There it turns abruptly northward, crossing the mountains to terminate on the eastern coast near Brisbane. Note that to the north, the refuge area on the tablelands behind Cairns is excluded from its influence. Thus the various zones wrap themselves around this tropical jungle area in successive layers.[9] The unhachured areas of the continent represent pre-Carpentarian elements, that is, populations comprised only of Murrayian and negritic components, uninfluenced by the last migrants to Australia. There is no phenotypic evidence for the penetration of Carpentarian influence into the whole of the southeastern portion of Australia, extending as far north on the eastern coast as the northern boundary of New South Wales. Equally important for racial analysis is the absence of Carpentarian traces from the negritoid populations around Cairns. This subjective synthesis of the distribution of Carpentarian genetic elements in Australia is submitted with full recognition of its weaknesses and sources of error, to be used as a basis for predicting the success of the gene flow models presented later.

[9] In addition to the physical evidence, there are some linguistic data which suggest that this condition obtains.

E. Basic assumptions utilized in constructing gene flow models

Two different regions of entry have been postulated by various authors for the migrants into

Australia. The weight of opinion has favored the Torres Strait gateway. This hypothesis presumes that at the time man reached continental Australia, sea level approximated its present position, and the date would hence be post-Pleistocene. The other and less favored theory considers that migrating peoples entered Australia broadly on a northern front which coincides with the outline of the Sahul Shelf. A eustatic lowering of sea level corresponding to the Fourth Glacial Period is implicit in this idea. I propose to test the correctness of these hypotheses by the use of models for gene flow.

Three of the four primary assumptions necessary for the construction of a model of gene flow have been discussed in preceding sections.

Primary Assumptions.

1) *The tribal population and area may be identified as approximating the genetic isolate on the Australian continent.*

2) *The barriers to gene flow in Australia are represented by the tribal boundaries.* It is presumed that the time required to attain a panmictic state within a tribal area is relatively short as compared with the time required for effective gene flow across a boundary into the next tribal territory.

3) *The rate of gene flow over long periods of time is constant across all tribal boundaries.* It is necessary for purposes of simplification to assume that fluctuating relationships of amity and enmity may be considered randomized throughout Australian inter-tribal contacts.

4) *The genetic mass is a constant for all Australian tribes.* The concept of genetic mass is simple, and involves no more than the number of individuals in a tribe, multiplied by two, the number of alleles carried per person at a given locus. In problems involving gene flow, if the population size varies from one isolate to another, some corrective factor must be introduced into the model. As explained previously, in Australia it has been assumed that the average value for the tribal population approximates 500 individuals. Thus each tribe is given an equal weighting in a statistical sense in the model.

It is clear that the above primary assumptions will not be true in a rigorous sense when applied to an individual tribe. For the purposes of model construction, they need not be true for a single tribe, or any small number of tribes, provided that in a statistical sense they represent central tendencies which hold for broad areas of genetical space. These assumptions vitiate an attempt to construct a gene flow model for a limited number of tribes, whereas, owing to the non-systematic nature of deviations away from them, they are presumed safe to use for predictive purposes in genetic space involving hundreds of isolates.

These primary assumptions assist in reducing the total number of variables involved in gene flow to a manageable total. Even so, there are certain other problems involved in the process which remain intractable if uncontrolled. Below are listed a series of secondary assumptions which are convenient to make in the present developmental state of the gene flow methodology. There is reason to believe that intensive investigation of the characteristics of gene flow in genetical space may allow these assumed constants to be replaced later by some form of controlled variable.

Secondary Assumptions.

1) *It is assumed that the present regional pattern of population densities has persisted unchanged from late Fourth Glacial times to the present.* This assumption is clearly without foundation and certainly incorrect in detail. Nevertheless, until some basis is found for predicting how population densities have varied in Australia in terms of climatic changes in the time interval concerned, such an assumption must be made.

2) *It is assumed that the process of gene flow has proceeded solely on the basis of inter-tribal hybridization.* Thus, the migration of populations and the processes of natural selection, genetic drift, and mutation, are explicitly excluded. This simplifying assumption is necessary now, but there is no reason why it need be continued as model construction becomes elaborated.

3) *It is assumed that the phenomenon of gene flow proceeds in such fashion that the advancing frontier of a recently introduced gene will tend to maintain itself as a smooth contour in genetic space.* It can be shown by models constructed for the purpose (but not included here owing to a lack of time and space) that forces tending to produce equilibrium are operative on the front of gene flow. Thus a projecting salient in the advancing gene flow front is subject to restoring forces which tend to eliminate it. In the same fashion,

a recess or niche in the front of flow is subject to a set of equilibrium forces which operate to restore a smooth contour.

F. Spatial gene flow model no. 1 based upon a Cape York Peninsula entry of Carpentarian genes into Australia

A gene flow model may be defined as a dynamic construct whose purpose is to demonstrate the areal pattern of gene flow at various stages through a series of designated isolates under conditions imposed by a series of explicit assumptions. The purpose of such a model is to provide one reconstruction, among the many possible, for probing and tentatively evaluating the processes involved in evolutionary change. As an analytical device such a model represents a high degree of abstraction, and it contains all the weaknesses inherent in such historical methodologies. Its validity, in the sense of probabilities, can be no better than the assumptions upon which it is based, or the rigidities utilized for its simplification.

At their present level of development spatial models of gene flow can be used only to provide approximate answers to simple questions in the field of population dynamics. The present model is designed to answer the question "In terms of the configuration of its estimated contribution to the existing populations of aboriginal Australia, can the Carpentarian element have entered the continent via the tip of Cape York Peninsula?"

The map in Figure 10 shows the completed model, which is based upon Tindale's tribal map (1940). Before drawing conclusions from its distributional pattern, the steps necessary for its construction must be examined. At the time represented in the model, the early phases of the post-glacial period, the Australian aborigines can be assumed to possess no water craft competent for coastwise travel. The dugout canoes now found in coastal Arnhem Land can be shown to result from recent Malay contacts, while around the tip of Cape York Peninsula similar watercraft have been introduced at a relatively late date from the Torres Strait Islanders. All inter-tribal interactions were terrestrial in nature.

The model commences operation with the introduction of Carpentarian genes into the domain of the two tribes which today occupy the tip of Cape York Peninsula. All of the assumptions described earlier in this paper are presumed to be operating. Thus panmixia is attained within a given tribal territory relatively instantaneously, while the tribal boundaries themselves represent the real barrier to gene flow. In the next stage of development, the Carpentarian genes are allowed to infiltrate those tribal territories lying immediately adjacent to the first tier of tribes, where the alien racial element was initially introduced. At the completion of this stage, the Carpentarian genetic contribution is allowed to flow to a third tier of tribes abutting against the second tier. In this fashion the construction of the model proceeds, tier by tier of tribes. In this first model a contour line is drawn to represent the completion of the gene flow front in each instance after five successive tribal tiers have been penetrated. Figure 10 shows five such contour lines, and hence the model has been allowed to proceed until 25 tiers, that is five groups of five tribal tiers each, have been infiltrated from the point of entry on Cape York Peninsula. Tribal boundaries are so irregular in their detailed relationships that a conscious subjective effort was made to keep the front of gene flow smoothly contoured. Thus occasionally, where two tribes abut against each other on only a very narrow line of contact, genetic infiltration is not presumed to occur until a broader front for tribal interaction is established. This type of subjective control is exercised so that its influence will be randomized in an extensive pattern of flow.

If genetic space were featureless and drab, it could be assumed that gene flow occurs with equal facility in all directions across tribal boundaries. But actual land surfaces are characterized by a changing topography and the land itself supports a widely varied flora. These, and other complicated variables, must be introduced in some fashion into models for gene flow if they are in any way to approximate a plausible reconstruction of population dynamics. In Australia, mountain ranges represent the most dramatic topographic feature of the continent. The flora ranges from a true wet, tropical jungle to brush-covered, waterless deserts. Since the Australian flora sensitively reflects climatic differences in its distribution, the flora may be taken as an indicator of the climatic variables. These topographic and ecological features have dramatically influenced the direction and rate of gene flow. Primitive man, especially on a hunting and collecting level of culture, sensitively responds to such inhibitors.

The influence of such barrier effects on gene flow may be estimated in two different ways. The first and simplest, but perhaps the less useful method, would be to ignore them in the construction of the flow model, and subsequently to estimate their influence by comparing the final contour of

the unimpeded gene flow front with that attained in the actual population. I have rejected this approach on the grounds that two-dimensional gene flow will be too complicated in most instances to allow the separation, and hence the proper evaluation, of independent topographic and ecologic continuous populations will be explained in detail in the second model presented, and will be passed over here. It may be noted that such barriers are indicated in Figure 10 by the heavy crosses enclosed between parallel lines. The numerals in the squares correspond to the number of tribal

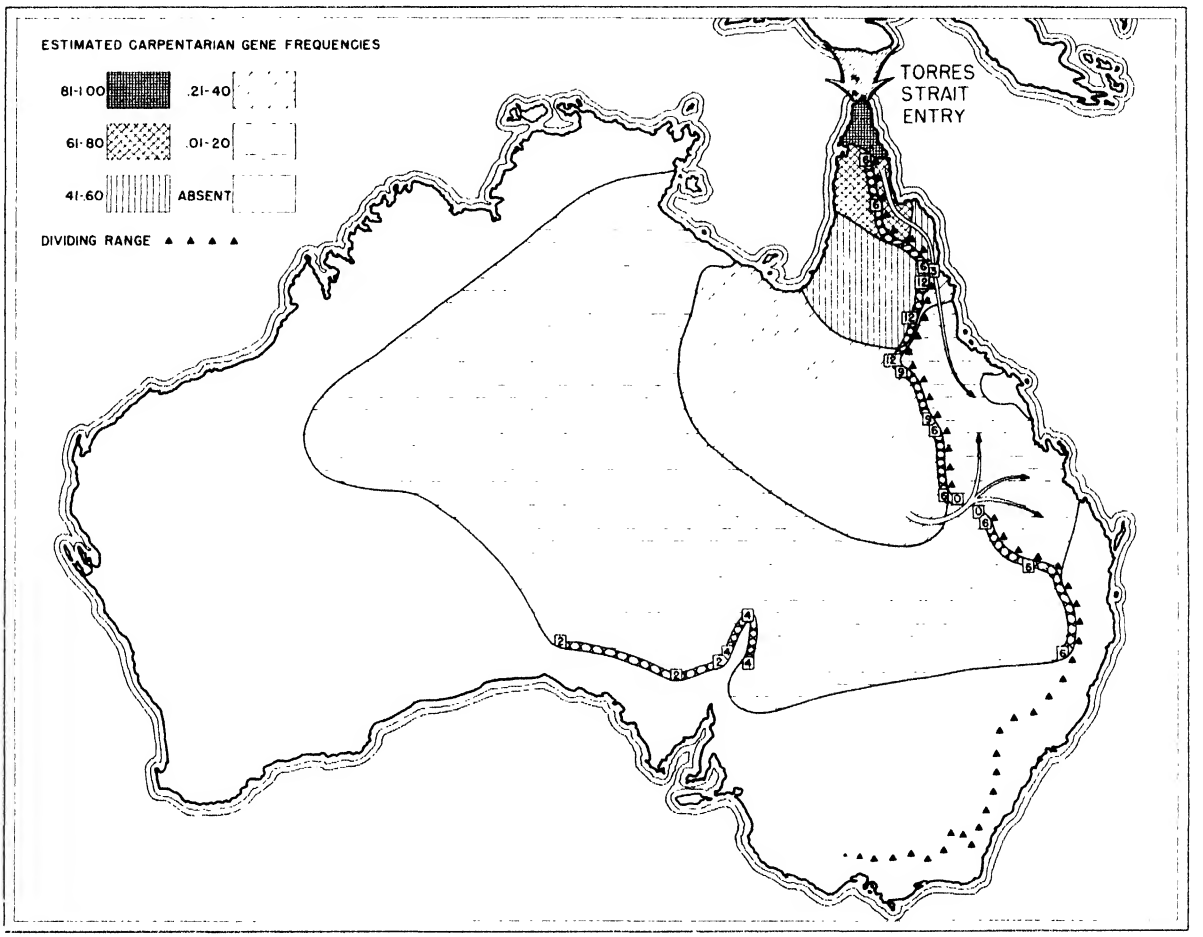

FIG. 10. Gene flow model no. 1, based upon the Torres Strait entry into Australia.

barriers. In the models here illustrated another approach has been chosen; namely, *the extent of observed penetration is utilized to provide a direct estimate of the effectiveness of topographical and ecological barriers in inhibiting gene flow.* Such inhibitory effects must be measured in some consistent unit, and I have measured this influence in terms of the number of tribal boundaries crossed in the unimpeded gene flow as compared to the number of crossings which must be inhibited at the barrier to produce the desired result. This method of evaluating the barrier effect of various features which influence the spread of genes in boundary crossings inhibited by the specific feature. With one exception, the values of these barriers to gene flow were determined in the second model, and were simply applied to the present model so that the gene flow might be controlled comparably in the two instances. Thus the Great Dividing Range, which begins at the south in central Victoria and extends along the eastern coast nearly to the tip of Cape York Peninsula represents the most important topographic barrier in Australia. It consists of a virtually unbroken chain of uplifted and steeply dissected tablelands, punctuated here and there by towering mountain peaks.

These mountains would not have seriously impeded the gene flow entering the continent across Torres Strait since the direction of flow is parallel to its long axis. This is true as far south as the Cairns rainforest region. At that point on the eastern coast where the wet jungle begins, a barrier value, equal to three tribal boundary crossings inhibitor effect, was inserted to slow the flow of Carpentarian influence as the edge of the jungle was reached. That portion of the Dividing Range lying behind the Cairns tablelands was given an inhibitor effect of 12 tribal boundary crossing units, and subsequently diminishing values were introduced as gene flow proceeded to the south. This represented but a formal exercise in this model since the spread of Carpentarian genes proceeded relatively rapidly down the eastern coastal plains.

The model was stopped after the 25th tribal boundary had been crossed in order that the frontal contour correspond to a line of unimpeded flow approximating the estimate of maximum Carpentarian penetration in the upper Murray drainage system. At the time gene flow ceased, it will be noted that the negritoid tribal regions had become completely overrun by the advancing gene front and that along the eastern coastal plain only a small pocket in central Queensland remained intact and free from Carpentarian elements.

The map depicting the conclusion of this first model of gene flow, shown in Figure 10, has been hachured with five different types of symbols to give a visual impression of the approximate density of the Carpentarian component as estimated to occur regionally. *It was assumed that these alien genetic contributions continued to flow ceaselessly into Australia at Cape York Peninsula until the model flow was stopped.* This simple assumption is but one of a number which might have been utilized without seriously changing the character of the configuration. For the sake of visual simplicity I have presumed that a cline drawn from the point of entry to any portion of the most advanced front of gene flow where no topographical or ecological barriers had intervened, could be represented in a linear fashion. This assumption is technically incorrect[10] but it will not importantly distort the frequency distribution shown by the model. Thus the area at the tip of Cape York Peninsula, which represents the first five tiers of gene flow, is finely cross-hatched and may be considered to show an average frequency value of Carpentarian component approximating .90. The next area with lighter diagonal cross-hatching represents an estimated frequency of about .70. The remaining types of hachuring correspond to regularly decreasing frequencies estimated for the Carpentarian component in Australia by means of this particular model.

If the resultant gene flow shown in the first model is compared with that estimated in Figure 9, where the distribution is based upon over-all taxonomic considerations, it quickly will be seen that the two configurations are totally dissimilar. Figure 9 shows the maximum estimated Carpentarian frequency centering in Arnhem Land on the north central coast of Australia. Model no. 1 finds the highest concentration at the tip of Cape York Peninsula. Perhaps the only point in which the model agrees with the estimate occurs in the southern limit of gene flow in the Murray Valley drainage and this is an artifact resulting from the decision to limit the flow when the boundary in this region coincided approximately with the subjective estimate. Otherwise, the two distributions show little in common. Even if the model flow had been allowed to proceed through another five or ten tiers of tribal boundaries, the similarity would be no greater in the end. In such a case, low Carpentarian frequencies would have resulted in Western Australia and Northern Territory, but this meaningless increase in similarity between the over-all limits of gene flow could not induce correspondence between the widely varying frequencies for Arnhem Land and the regions which are critical in estimating the success of a model. This apparent gain would have been more than counter-balanced by the inundation of the lower Murray Valley by the Carpentarian element, a region where its influence is lacking.

The inundation of the Cairns tropical jungle area by Carpentarian gene flow is another point in which the model fails to correspond with reality. But here, by the addition of approximately ten more tribal boundary units inhibitor effect, this

[10] Such a cline, seen in profile, would only approximate a linear condition at the end of gene flow when all genetic isolates concerned in the model had attained a panmictic equilibrium; then the linear cline would become horizontal as a limiting case. The nature of the true cline, when seen in profile, would vary markedly with the initial assumptions concerning the gene flow, and with the length of time through which the gene flow had been allowed to proceed. It can be shown by other models, not introduced here, that in a juvenile or youthful model stage of gene flow the cline profile will tend to be convex curve, bulging downward. As the age of the model increases the profile will take on an S-shaped curve until in senescence the profile shows a complex, convex outline bulging upward. In spite of this complicated situation, it seems reasonable to assume a linear cline for illustrative purposes. If selection is operative, the situation becomes even more involved. At a later date models will be published which explored this phase of the gene flow problem.

critical region could have been kept free from Carpentarian influence. Perhaps the only success demonstrated by the model is to be found in the central region of coastal Queensland lying to the east of the Dividing Range. It was assumed that unimpeded flow of genes could occur through a low point in the range in Pitjara tribal territory. The flow spreading out from this pass yields an estimate of Carpentarian frequencies averaging .10 on this coastal plain, a value not too distant from that shown in the taxonomic estimate.

The first gene flow model is totally unsuccessful. Its degree of failure is so marked that no reasonable alteration of the assumptions used for simplification could bring it into alignment with the configuration shown in Figure 9. I submit that, even with the obvious imperfections of the methodology as it exists today, *this model invalidates the hypothesis that the Carpentarian racial group entered Australia via Torres Strait.* This purely spatial judgment is the more valuable since it carries a time implication. This component could not have obtained its present distributional pattern if it had entered Australia after the establishment of normal sea levels in early post-glacial times.

This unsuccessful model carries latent difficulties which are worth a brief examination. In terms of the concept of genetic mass, it is clear that a portal into Australia but two tribal territories in breadth makes stringent demands in one of two possible directions. It was assumed that migration *per se* could be ignored, and that gene flow was solely a consequence of intertribal hybridization. This first model shows a rapidly expanding frontier as gene flow continues through the later tiers. It is a characteristic of genetic space that such a configuration of tribal territories makes exorbitant demands upon the rate of gene flow from New Guinea into Australia. If the basic assumption is modified to the extent that the entry of Carpentarian genes into Australia is largely a consequence of migrations instead of hybridization, then equally heavy demands are made in terms of the number of migrants involved. A tremendous number of Carpentarians must have rafted their way across Torres Strait to have provided the necessary genetic mass needed to obtain the flow pattern. Either of these assumptions, or a third possible one which would recognize an intermediate condition in which both factors were operating, require such frenzied sexual or migratory activity at the Torres Strait portal as to fall outside the bounds of reasonable postulates. This model of spatial gene flow can be discarded with no regrets.

H. Spatial gene flow model no. 2 based upon a Carpentarian entry into Australia over a broad Sahul Shelf front

The second model of gene flow is based upon the assumption that Carpentarian component entered Australia broadly across the entire front of the now sunken Sahul Shelf. A map showing the completed model is given in Figure 11. Aside from the different portal, the same basic assumptions are operative in this model that were utilized in the Torres Strait version. The heavy, unilaterally-barbed arrows designate the outer limits of the Sahul Shelf; gene flow is assumed to have proceeded uniformly into Australia between the limits thus established as long as flow proceeded in the model. The westerly arrow terminates in the tribal territory of Bagu, the easterly terminates at the tip of Cape York Peninsula. It is assumed that gene flow occurred equally across all points of what are now the shorelines of the Australian continent. The nature of existing data demands this erroneous assumption. But when the subsurface topography of the Sahul Shelf is better known, it may be possible to modify it through the creation of a controlled variable to approach conditions as they may have existed in reality. This model is more important than the first one, and hence its stages of construction will be presented in greater detail.

The same principles are utilized here as in the preceding case. The first tier of gene flow introduced the Carpentarian element into tribal territories along the entire coastal portion between the two delimiting arrows. The second and third tiers of gene flow proceeded uneventfully, and at the end of the latter a contour was drawn to represent the front of flow. At the end of the fourth tribal boundary crossing it proved necessary to insert the first topographical inhibitor barrier factor. Its value was predetermined as equivalent to 6 inbars[11] and it was placed on the summit of the Great Dividing Range, extending from the tribal territory of the Atjinuri in the north to that of the Koko-imudji in the south. A value of 6 was chosen since at the end of the

[11]The expression, "inhibitor barrier factor equivalent to X tribal boundary crossings in model gene flow" is too cumbersome for continued usage. With an apologetic glance toward those who rightly resent the unnecessary introduction of new terms, this complicated phrase in subsequent portions of this paper will be replaced with "X inbars." Shorthand notations of this type, while esthetically offensive, are commonplace in modern scientific vocabularies; e.g., clo, erg, dyne, etc.

tenth tier of flow, Carpentarian influence could have penetrated the eastern coast of Cape York Peninsula in the vicinity of Princess Charlotte Bay by indirect flow around the northern end of the mountain range. At the same time a 12 inbar topographical factor was inserted along the summit of the Great Dividing Range between the Koko-imudji territory in the north and that of the Warungu tribe in the south. This enhanced inbar value is justified by the more rugged characteristics of the Divide in the latter region. A profile-section through the base of Cape York Peninsula from the Gulf of Carpentaria on the west to the Pacific Coast on the east shows a gradual rise in the terrain as one proceeds from the Gulf toward the headwaters of the numerous rivers draining to the west. Further eastward the rising land becomes increasingly rugged, and in their upper reaches, the rivers are deeply entrenched in a highly dissected land form. The upper slopes of the Dividing Range are granitic in nature and are relatively sterile in flora. Crossing the divide to the eastern slope, dense tropical jungles range to the top of peaks such as Bartle Frere and Bellenden Ker, both of which attain altitudes of nearly 5,000 feet. In the descent from the crest toward the eastern coast first the Herberton Plateau is reached, at an average elevation of 3,000 ft., and subsequently the lower-lying Atherton Plateau which has an average altitude of about 2,000 ft. From the eastern rim of the latter a steep escarpment drops precipitously to the narrow coastal plain. Both plateaus, the eastern slopes of the divide, and the coastal plain are primarily covered by dense shelter jungles. This climax, high-canopied forest is inter-digitated with belts of eucalyptus savannah. Rainfall varies from 50 inches annually at Atherton to a maximum of 143 at Innisfail. But two months in 12 are relatively dry. Mammalian fauna

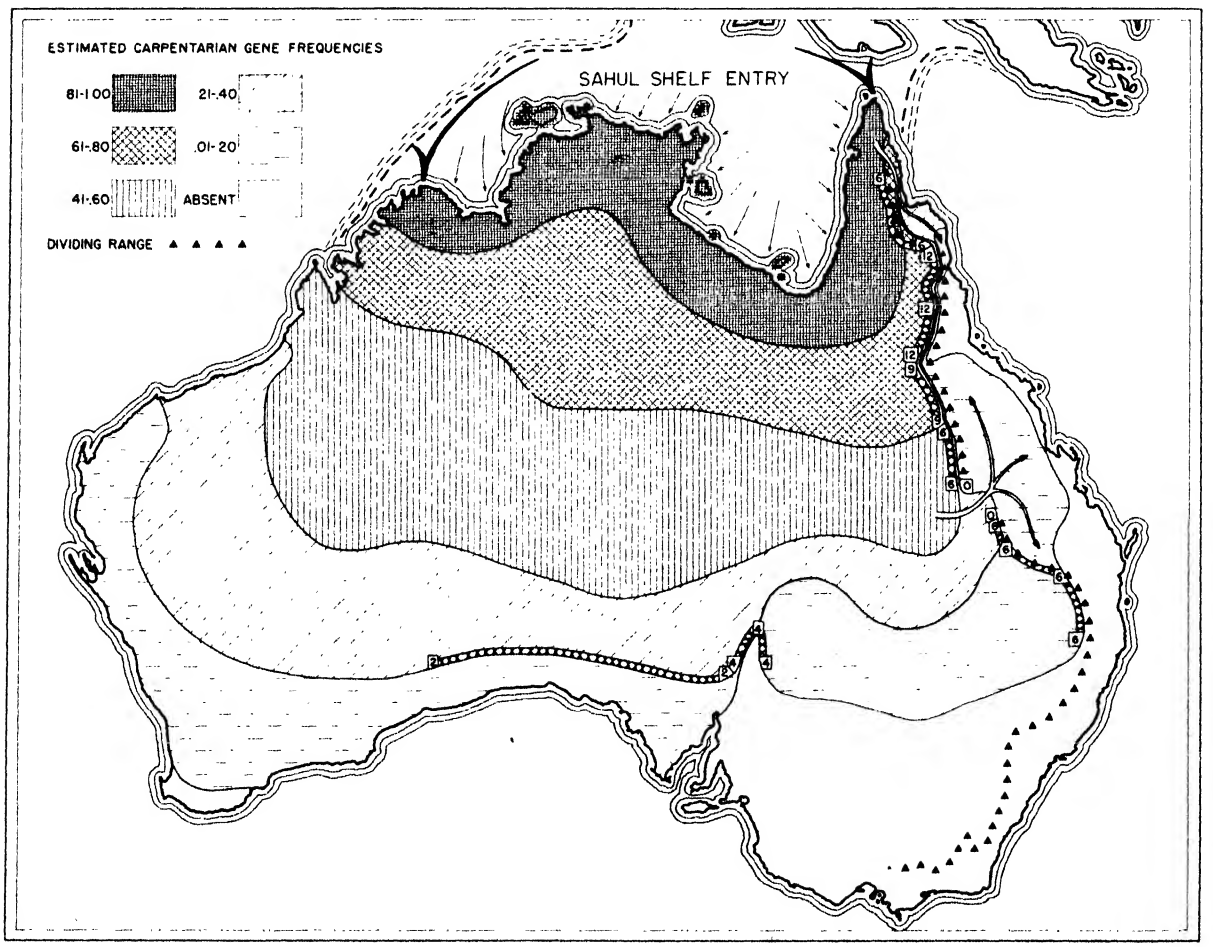

FIG. 11. Gene flow model no. 2, based upon the Sahul Shelf entry.

in the rain-forest is scanty, and aboriginal food chiefly consists of roots, nuts, fruits and seeds. It is difficult to exaggerate the ecological barrier presented by a transition from open grassland into a dense jungle of this type. As the ecological difference is reinforced topographically by a continuous mountain range, the 12 inbars assigned for this stretch does not seem unreasonable. It must be emphasized again that *in the case of ecological and topographical barriers the gene flow model is used to evaluate their inhibiting effects, as measured by the number of inbars required to attain certain localized terminal gene flow patterns.*

The extension of the gene flow pattern to the fifth tier requires no further artifacts to control the pattern. However, at the end of the sixth tier, which is mapped as a contour line, a 6 inbar topographical factor was established for that portion of the Great Dividing Range extending between the Warungu and the Mian tribe in the south. At the end of infiltration of the seventh tier, a new factor has been introduced into the model, that of an accelerator. Tindale, (1940) comments that among the tribes clustered in the Boulia region of central Queensland, tribal fragmentation seems to have occurred. This implies a breaking up of normal tribal populations into smaller units, so that, to keep genetic mass constant, I have been compelled to assume that in this area two of the small tribal areas are equivalent to one normal isolate in terms of gene flow.[12]

The seventh tier of flow also reached the territory of the Aranda tribe in the central interior of Australia. This tribe appears to be in the process of differentiating into three sub-tribal units, the East, West, and South Aranda. To approximate the maintenance of a constant genetic mass the East and West Aranda were treated as equivalent to a single tribal population, while the South Aranda were also considered so equivalent. It was additionally necessary to insert a further topographical factor equivalent to 6 inbars on the Dividing Range beginning at the Mian tribe, and extending south to the territory of the Jagalingu.

The eighth and ninth tiers of tribal infiltration proceeded uneventfully, and an enclosing contour outlines the front of the latter. It should be noted that the former involved gene flow through the Bedengo tribe: its domain is an ill-defined region lying midway between Eighty Mile Beach on the Indian Ocean Coast of Western Australia and dry Lake McKay on the boundary between Western Australia and Central Australia. This region appears to be the most sparsely inhabited in the entire continent, and the Bedengo tribe is unknown anthropologically. The frequency of their tribal interactions with surrounding isolates is unknown, and I have been reluctantly forced to assume them equivalent to those in the remainder of the continent. I suspect that data will ultimately prove them to be somewhat isolated in terms of their social interaction, and hence in terms of gene flow. When more knowledge is available, it may be necessary to introduce inbars around the boundary of this tribe for ecological reasons.

At the end of the tenth tier of gene flow, the topographical 6 inbar factor originally imposed between the Atjinuri and Koko-imudji along the Great Dividing Range was removed, and from this stage on it ceased to influence gene flow in this model. With the termination of the eleventh tier of flow the tribal territory of the Pitjara was reached. It lies astride the Great Dividing Range at its lowest point, and its members are in contact with isolates on both sides of the divide. To attain the desired configuration of gene flow for the Carpentarian element on the eastern coastal plain of central Queensland, shown by the trident arrow in Figure 11, it has been necessary to assume that this low-lying region presents no topographical inhibitor to gene spread. This assignment may be considered a measure of the effectiveness of this tribal area as a pass between the great interior plains of the continent and the coastal side of the divide. At the same stage, a topographical, 6 inbar factor was imposed on the Great Dividing Range just south of the Pitjara, extending from the tribal territory of the Konabula as far south as was needed to complete the pattern of terminal flow. It will be noted that the value assigned this barrier is of little diagnostic use in evaluating the real inhibiting influence of the Great Dividing Range in this region, since the flow of the model terminates but four tiers later, and hence offers no adequate test for this particular mountainous stretch.

The termination of the 12th tier of gene flow, traced as a contour line on the map, requires the introduction of two new barriers, one topographical, the other ecological in nature. The Flinders Range of mountains extends from the head of Spencer's Gulf in South Australia northward approximately 100 miles toward the arid center.

[12]While I suspect this assumption is conservative in nature, I have hopes that later work may test its validity.

The aborigines at the northern tip of this range, the Wailpi tribe, are regarded from observational materials to be entirely pre-Carpentarian in their genetic constitution. Hence an inhibitor sufficient to keep the model flow excluded from this region has been inserted, and its value on both sides of this range amounts to four inbars. Since this model is now approaching its terminal flow, this may prove to be a minimum inbar value rather than a definitive estimate. The ecological barrier inserted corresponds to the northern boundary of the great Nullabor Plain which represents the approximate northern boundary of the Mirning and Wirangu tribes. This barrier effect was rather arbitrarily extended along the northern boundary of the Pankala tribe to the base of the Flinders Range. The Nullabor Plain is a massive limestone formation arising some miles inland from the coast and extending unbroken and waterless northward another 75 to 100 miles. The author empirically observed that the Mirning and Wirangu tribesmen do show slight evidence of modification by Carpentarian influences, but not so great as would have been expected had flow continued unimpeded across their northern boundaries. Some cultural data to exist would suggest the validity of this ecological barrier, which has been set at two inbars. The thirteenth tier of genetic flow occurred without novelty. At the end of the fourteenth tier, the ecological barrier just previously imposed along the Nullabor Plain was lifted and at the fifteenth and terminal tier of flow, Carpentarian elements extended to the limits shown by the boundaries pictured in Figure 11.

As in the case of the first model, it has here been assumed that a cline drawn from any point on the Sahul Shelf portal to the unimpeded margin of terminal gene flow would be linear in nature. In regions where inhibitor barriers intervene, the cline profile would show a stepped effect. This assumption, as stated earlier, is almost certainly in error, but it is a reasonable simplification required to achieve the visual impact necessary for an easy evaluation of the model. Five contour lines have been drawn showing the terminus of gene flow at the end of 3, 6, 9, 12 and 15 tiers. Each of the belts so outlined have been hachured according to the system used in Figures 9 and 10, and estimates have been made of the approximate frequency of the Carpentarian component using the assumption of a linear cline structure. Here, as in the first model, it has been considered that Carpentarian element continue to infiltrate constantly across the entire Sahul Shelf entry as long as gene flow was continued in the model.

A comparison between Figure 9 in which the over-all distribution of Carpentarian gene frequencies has been estimated on a taxonomic basis, and the second model of gene flow, shown in Figure 11, indicates that the latter corresponds to the original prediction to a surprising degree. Minor discrepancies are observable, but the configurations are so similar that this model must be classed broadly as successful. In both the empirical map and the model, the area for maximum Carpentarian contributions has a similar focal point. A discrepancy is to be noted in the model. Maximum frequencies, estimated at .90, range across the entire Sahul entry, whereas the empirical estimate limits this value to the salient coastal region of Northern Territory. This discrepancy is not in itself of great importance, but it will be referred to later as a direct consequence of the uncompensated for characteristics of genetic space. Let it be noted here briefly that the introduction of an alien genetic component under Australian conditions along a coastline which is convex seawards has a different result than if the coastline had a concave conformation on its seaward aspect.

Comparing the two configurations from the other extremity, the areas into which no Carpentarian influence has penetrated, the general similarity is again marked. This parallelism, however, is a construct of the model. Gene flow was terminated after 15 tribal boundaries had been crossed to obtain a correspondence in the model to the distribution shown in the empirical map in the upper Murray drainage system, where flow is unimpeded. In a similar sense the failure of Carpentarian genetic influence to penetrate the North Queensland tropical jungle, and the Flinders Range, was a direct consequence of choosing inbar values to attain this end product in order to evaluate the influence of these topographical barriers by dynamic methods. Close agreement is, however, independently obtained along the eastern coast of Queensland in that unimpeded gene flow through the Pitjara gap in the model corresponds rather closely to that postulated from observational data. Turning to the extreme southwestern corner of the continent, it will be seen that the model is deficient here, in that the outer terminal flow of the Carpentarian element fails to reach Cape Leeuwin. The discrepancy would have disappeared had the model been allowed to flow through the 16th tier of tribes. This difference is well within the error of the methodology, but it will be noted later by an independent method of assessment that this discrepancy may have real significance. The

four zones lying between the two extremes discussed above correspond so closely that the observable differences may be a direct consequence of a single assumption, namely that a cline from the point of entry to the uninhibited terminal flow can be represented as linear.

One other area of mild disagreement between the model and the taxonomic map deserves brief discussion. In Figure 8 in the region surrounding the refuge area of North Queensland, the contour lines sweep around its outer periphery in such a fashion as to present narrow, enveloping belts projecting northeastward from each of the major zones contoured. A cline profile from the southeastern corner of the Gulf of Carpentaria to the center of this refuge region would be relatively smooth and show only a minor stepped effect. In the second model, however, the artifice of creating a single barrier equivalent to 12 inbars on the summit of the Dividing Range produces a cline showing a dramatic stepped effect. I have sufficient reliance in my empirical data, and the estimates based upon them, to believe that the distributions shown in the taxonomic estimate are closer to reality than those represented in the model, which is a result of over-simplification. Cultural observations for other regions of Australia suggest that, even where the Great Dividing Range is a less rigorous topographic obstacle than it is here, plains-dwelling tribes shun, in fact culturally abhor, leaving their familiar terrain to establish contact with those tribes living in the more mountainous regions. The model might be profitably revised by replacing the single 12 inbar factor on the top of the range with a series of perhaps four barriers each of three inbar value, commencing where the westerly draining rivers reach higher ground and from there erected at regular intervals until the top of the divide has been reached. This simple alteration in the artificial inhibitors used in this region would bring the second model into close conformity to the taxonomic pattern mapped in Figure 9.

As the fabricator of this genetical Frankenstein, I must frankly admit to being appalled by the success of the second model. I can only state that Figure 9, in which the over-all and admittedly subjective estimate of the frequency of Carpentarian component is shown, was formulated in its essential pattern more than ten years ago, upon the completion of field work in Australia. There was no glimmer in my mind at that time that a model of gene flow might be devised for purposes of testing and prediction. The taxonomic map and the successful model are totally independent creatures.

For the assurance of the reader, let me further profess a feeling of bewilderment that the numerous and highly varied assumptions utilized in constructing the model have not distorted the distributional results beyond possible recognition. These assumptions have been necessary to simplify the model to a point where it could become practicable, but it appears to me that however approximate their nature, they cannot have exerted too warping an influence in any systematic direction. It is desirable that each of these assumptions be independently tested further for refinement and possible verification. I intend to explore each as fully as existing data allow. For my own part, I am now inclined to regard them as applicable in a broad statistical sense to the special circumstances obtaining in Australian aboriginal populations. Even in its present experimental and highly abstracted form the methodology of the dynamic gene flow model is worth intensive development and progressive refinement as a significant instrument of analysis in human population genetics.

A momentary digression will illustrate one form of refinement I have in mind which affects the interpretation of gene flow patterns in genetic space. Somewhat earlier it was stated that the configuration of a coastline, that is whether it was concave, straight or convex on the seaward side, influenced the manner in which introduced genetic elements flowed into the interior. Figure 12 gives a concrete illustration of these differences as applied to the northern coastline of Australia. The region chosen, keyed as (B) in Figure 1, represents a large portion of the Sahul Shelf portal and has been divided for purposes of analysis into two sections. The first of these, shown by the map lettered "A" in Figure 12, represents a coastal section lying between the Fitzmaurice River on the west and the Roper

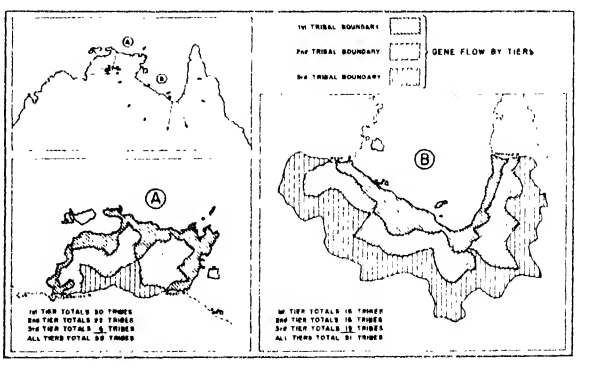

FIG. 12. Models illustrative of effects of coastline shape on gene flow in genetical space.

River on the east. This coastal land is strongly convex toward the sea, and it will be used to demonstrate the focusing effect of this configuration in terms of genetic space. The second portion, labelled (B) in Figure 12, begins on the west at the Roper River and extends along the southern and eastern shores of the Gulf of Carpentaria, being bounded on the east by the Holyrod River. This coast is strongly concave in relation to the Gulf, and will be used to demonstrate how this configuration acts as a diffusor of gene flow in genetic space, as compared to a convex coastline.

These two sections will be used as independent models for limited gene flow. It is assumed that alien genes in each instance are introduced to the coastal tribes as the first tier of gene flow. Massive hybridization between the alien elements and the resident populations is presumed for purposes of clarification, resulting in the introduction of alien genes in the frequency of .50 into coastal isolates. Hybridization then ceases and gene flow proceeds to the second tier of tribes. An "end-plate" effect is assumed to exclude gene flow laterally across the boundary rivers. This is justifiable since if hybridization occurred also beyond the limiting rivers, as it would in reality, lateral gene flow would hence be completely reciprocal, and produce no changes from that shown in the model. In the final phase of the model gene flow proceeds to the third tier of tribes where it terminates. To illustrate the differences inherent in these two configurations of genetic space, the area of gene flow is sealed off from all other disturbing forces until a panmictic condition is attained in each model. Post-panmictic Carpentarian gene frequency in the area (A), enclosed by the convex coastline is .26. The corresponding frequency for the concave coastline area (B) is .16. Utilizing different assumptions concerning the initial frequency of introduced genes in the first tier of coastal tribes does not alter the ratio between the panmictic gene frequencies in the area (A) as compared to (B). To express the situation in different terms, the frequency of the alien Carpentarian genes in the first instance is 65 per cent higher than that obtained in the second, totally as a result of this particular configuration of genetic space.

The characteristics of genetic space become clarified by examining the number of tribal isolates present in each tier of gene flow in the two models. For the convex coastline, the first tier comprised 30 tribes, and gene flow proceeded thence to 22 tribes, and then flowed into a terminal tier of but six tribal areas. This has had an effect of focusing the total gene flow into a smaller number of genetic isolates. Expressed in another way, 500 alien alleles per locus per isolate were introduced into each of an initial tier of 30 coastal tribes and were required to spread to a panmictic terminal condition in a total of 58 isolates. In the second instance, the concave coastal tier of tribes numbered but 16. Gene flow proceeded from these to a second tier of isolates also numbering 16, and thence to a terminal tier of tribes totaling 19. In this instance, the genetic mass of 500 exotic genes per locus initially introduced into each of 16 isolates ultimately spread through a total of 51 when terminal panmixia was reached. By comparison this concave type of coastline results in the flow of genes through space in such a fashion that they tended to *diffuse* or spread out thinly rather than to *focus* or pile up, as they approached the last tier.

These conclusions apply to specific portions of genetic space in Australia, and cannot be indiscriminately applied to human populations in other areas. These supplementary models have been utilized to demonstrate that one of the areas of discrepancy between the second flow model and the taxonomic estimate, as shown in Figures 11 and 9 respectively, is but a resultant of the simplicity of the model. If the characteristics of the genetic space along the northern coastline of Australia had been taken into consideration in the construction of the Sahul Shelf model, the zone showing the maximum concentration of the Carpentarian component in the model would have closely approximated that of the taxonomic estimate. It is possible to illustrate the same focusing and diffusing effects using idealized models rather than the particular tribal areas chosen for Australia. I find a certain comfort in the fact that this apparent discrepancy would disappear if the characteristics of genetic space had been given the full weighting in the construction of the successful model.

If the essential correspondence in distribution between the Sahul Shelf model and the taxonomic estimate is to be granted, then it may seem worthwhile to list some of the inferences to be derived from this exercise. The primary hypothesis under test, that the Carpentarian contribution to the modern aboriginal population entered Australia via the Sahul Shelf seems established. The time implications of the spatial analysis indicate that the Carpentarian entry occurred prior to the submergence of the Sahul Shelf, a time which

can be reasonably fixed by other considerations as late in the Fourth Glacial Period.

The secondary assumption that gene flow has proceeded only via the processes of inter-tribal hybridization now deserves reevaluation. By *excluding* migrations, some information has been derived concerning their nature. Ample evidence exists in cultural materials to show that migrations have occurred, and they must be presumed to have continued throughout the period under consideration. The essence of the reconciliation between this basic assumption and the observable data is that migratory movements of tribal populations within Australia have not been important in advancing the front of gene flow *systematically* in any given direction. Rather, the influence of migrations seems to have been *randomized* along the entire front of gene flow, save where ecological or topographical barriers intervene. The second model demonstrated that the present distribution of Carpentarian influence in Australia *could have been attained* by the process of inter-tribal hybridization alone. Migrations, which we know to have occurred, in general merely extended the front of the flow more rapidly. They have not been important factors in determining the direction of flow. Without pushing this inference too far, the evidence seems small consolation for that school of historical reconstruction in anthropology which would tend to explain all changes in genetic constitution of regional populations in terms of massive migrations.

The Sahul Shelf model, as compared with that for Torres Strait, provides a sufficiently broad region of entry so that very high rates of gene flow need not be postulated to attain the terminal flow pattern. The characteristics of genetic space in the Sahul model are such that the first tier of infiltration involves 58 tribal areas. In each successive tier the number of tribes genetically penetrated diminishes. Thus, the terminal boundary of the flow pattern appears extensive in terms of geographic space, but it is a highly focused front in terms of genetic space. This condition is diametrically opposed to that obtaining in the first model, and it has the advantage of requiring a comparatively low rate of gene flow over the portal area to attain the model distribution.

The concept of genetic mass allows a further evaluation to be made between the taxonomic distribution of the Carpentarian component estimated in Figure 9 and the second gene flow distribution mapped in Figure 11. Tindale (1940) tabulated 574 tribal populations. (About 25 of these are so little known that it was necessary to omit their tribal boundaries from his map.) By using a prior assumption that tribal populations average 500 persons, it may be calculated that the total genetic mass at a given locus consists of 549,000 genes in the entire aboriginal population. By approximate methods the contribution of the Carpentarian racial element to this total genetic mass can be calculated. The procedure is as follows: first, taking Figure 9, the taxonomic estimate of Carpentarian distribution, it is assumed that on the average those tribes contained within the area corresponding to estimated frequencies between .81 and 1.00 had an average frequency of .90. This value is then multiplied by the number of tribes contained within the area to obtain the total Carpentarian gene mass for this zone. The same procedure is utilized for the other four zones, through which Carpentarian frequencies diminish in an orderly fashion. The sixth zone, in which Carpentarian genes are estimated as being absent, obviously has a frequency of zero. A summation of the values shown for these six belts indicates that the Carpentarian element has contributed 39 per cent of the total genetic mass of the aboriginal population. By reciprocal process for the pre-Carpentarian populations, it can be shown that the Murrayian and negritic elements together have contributed 61 per cent of the total aboriginal genetic mass. The sum of two values obviously should, and does, equal unity.

The same procedure for calculating genetic mass may then be applied to the Sahul Shelf model. Here the relative contributions of the Carpentarians to the total genetic mass of the living aborigines is calculated as 42 per cent, leaving a value of 58 per cent to apply to the combined Murrayian and negritic elements. These simple methods in evaluation provide a quantitative expression for a degree of correspondence between the second flow model and the taxonomic estimate. The values are surprisingly close considering the rude methods utilized, but if a correction were made to the model to take into account the genetic space characteristic of the northern coastline, their similarity would become even closer. Hence an approximate estimate that the Carpentarian racial element has contributed about 40 per cent to the genetic mass of aboriginal Australia seems reasonable.

The implications of this estimate are of some interest in reconstructing population dynamics in this region in late Fourth Glacial times. Let us take two limiting assumptions. For the first, it will be presumed that the Carpentarian migrants

were sufficiently advanced culturally so that in competition with pre-Carpentarian peoples on the continent, none of them succumbed to the stresses of population pressure. If such a population of comparatively unmixed Carpentarian peoples were available on the Sahul Shelf, submergence by rising sea level would have driven them across the northern "shoreline," representing the present continental boundaries. It will be presumed that they became established successfully on the mainland by displacing the earlier population. The consequent over-population was compensated for by elimination of Murrayian and Negritic peoples. The stringent situation outlined above still requires that the Carpentarian populations originally numbered 120,000 persons to have effectively contributed 40 per cent to the present total aboriginal genetic mass. No existing evidence suggests that the Carpentarian migrants did possess any tangible cultural advantage.

The second limiting assumption involves somewhat less straining. The situation is generally similar to the preceding case, save that the Carpentarians are assumed to possess no *cultural* advantage which would confer differential survival values upon them as a group. Since the pre-Carpentarian population within the present boundaries of the continent may be presumed equivalent to that found today, namely 300,000, a 40 per cent contribution of incoming Carpentarian genetic mass requires an original population of 200,000 Carpentarian migrants to have reached the Sahul Shelf. The combined populations totaling 500,000 persons, were reduced to the present equilibrium numbers by *pro rata* elimination among both groups.

These rough approximations suggest that between 120,000 and 200,000 Carpentarian migrants would be required to have attained the Sahul Shelf had hybridization alone been the evolutionary process by which the Carpentarians had spread throughout the mainland. Even during the maximum eustatic lowering of sea level in the Fourth Glacial Period, there remained many difficult water gaps between the Sunda and Sahul Shelves. The magnitude of these water barriers, of which there were more than a few, were at a minimum not less than 20 miles in extent and probably exceeded this value in some cases. Watercraft available in terms of the basic tools utilized by such peoples could have been no better than primitive bark canoes or poorly fabricated rafts. Neither show notable sea-worthiness. A migration of the proportions suggested by either of the limiting figures provided above seems unacceptable. Even if the period of migration were extended over several millennia, as it may well have been, so massive a movement of peoples represents a logistic problem beyond the realms of reasonable probability. I therefore reject the implication that the Carpentarian distribution in Australia has been derived by the process of hybridization alone.

Some other evolutionary process beyond hybridizing must have been at work to have produced the results observable in Australia. Neither the concepts of mutation or drift have meaning in this situation. There remains a high probability that the penetration of Carpentarians into Australia was assisted by some form of selection. Even if a modest population of Carpentarian peoples gradually trickled across the various water gaps to reach the Sahul Shelf, and though their total numbers may have reached tens of thousands of individuals, this is still far below the required minimum values. The observed results in Australia can be obtained only under the influence of selection differentially favoring the survival of the Carpentarian racial types as compared to the earlier populations. The time span available for the operation of selection may be estimated as between 15,000 and 25,000 years, depending upon which geological time scale is followed. Even these blurred datum points suggest that high coefficients of selection may have been involved. Its value could perhaps be approximated, but until the primary data are more refined, I am not tempted to calculate it.

The concept of selection as applied to the Carpentarian racial element fits admirably into the frame of reference postulated by Coon (1950) in his stimulating work on the principles of race formation. Two attributes of the Carpentarian racial type are especially suggestive as having selective value in the conditions prevailing in aboriginal Australia: the extreme linearity of their body build and their heavy pigmentation. Both features present adaptive advantages in the essentially hot, dry climate which prevails now, and doubtless did also in former times, in northern and central Australia.

The probability that selection assisted hybridization in producing the pattern of gene flow observed in the Sahul Shelf model requires a reinterpretation of the latter. Throughout the preceding discussion the Carpentarian gene flow was referred to in a unitary sense, as though the total corporate genic content of that race had diffused *in toto* into the earlier population. If hybridization *alone* operated to produce gene flow, then the

total genotype might spread as a whole through isolates. This simple condition will seldom obtain, however, and strict usage requires the limiting of the concept of gene flow to a single marker-gene, or more broadly to cover the reciprocal aspects of flow of allelic series of genes.

In these terms, the bases for the subjective taxonomic estimate of the Carpentarian distribution shown in Figure 9 must be reevaluated. The phenotypic characteristics of the Carpentarian race have been defined in terms of the populations of northern coastal Australia. The terminal limits of its distribution have been evaluated through metrical and morphological data, backed by visual impressions, used to determine which pre-Carpentarian populations reveal traces of genetic "disturbance," as reflected largely in body build, relative hairiness and skin color. These may be the phenotypic expressions of genes at a moderate number of loci, and the visual impact may be heightened by the manifold expression of some of the genes involved. Thus it is quite possible that the genes producing linear body build may find expression in correlated changes in reduced head breadth, and increased cranial breadth-height and cephalofacial indices. In the intermediate zones, where Carpentarian and pre-Carpentarian contributions approach equality, it has been observed that phenotypes vary appreciably from one isolate to another and the impression is one of genetic chaos. It is clearly impossible to evaluate the contribution of the Carpentarians in terms of the total phenotype, and hence by implication, total genotype. The taxonomic estimate, of which the pattern is mapped in Figure 9, must be considered to have been based upon visually important manifestations of a few marker-genes for the Carpentarian race, presumably genes which have flowed at roughly similar rates under the dual impetus from selection and hybridization. *It is hence improper to regard either the taxonomic estimate, or the flow pattern of the Sahul Shelf model as representing the diffusion of the total Carpentarian genotype;—at most they are representative of the averaged pattern of a few marker-traits for the Carpentarian component. All previous text material and map legends should be reinterpreted in this light.*

Dynamic gene flow models carry detailed time implications, even though they are expressions of space as the primary variable. It would be of considerable interest to interpret the meaning of the successful model in terms of the time required for various phases of gene flow. The fact that 15 tiers of flow were required for this model might suggest that the total elapsed time divided by 15 would yield the length of time required for each tier of flow. This interpretation of the model is specious, and the temptation must be resisted. The dynamics of gene flow, even with simplifying assumptions in the number used here, are too complex for such neat equations. When the complicated interrelationships between time and gene flow are more thoroughly explored, then approximate time interpretations will be possible.

If the preceding inferences derived from the Sahul Shelf model of gene flow seem based on inadequate data, let me attempt to put them in their proper perspective. I have not been concerned here primarily with the detailed analysis and reconstruction of population dynamics in Australia as a substantive exercise or even as an end in itself. Such ideas have emerged as consequences from a type of space analysis. While they have a modest probability of approximating reality, I do not press for their validity. My concern is rather to present a type of analysis which is dependent on genetic space, and to suggest in a tentative fashion the type of implications concerning population dynamics which may result from this approach. Australian data have been used to give more concrete form. The many imperfections in this presentation are recognized, but formulations of this kind may prove valuable as refinements are introduced, and as basic assumptions are verified or modified. This methodology is complicated even under the simple circumstances presented in Australia. An application of these principles to areas of more complex data must be done in a most guarded and cautious fashion. But even with these explicit reservations, I am confident that new approaches such as this are important if the forces which have produced human evolution are to be comprehended in any detailed sense.

I. The phenotypic distribution of tawny hair

The preceding model illustrated how ancient genetic infiltration may have changed the aboriginal population in most of Australia. Dramatic population changes may result from other causes. Frequently evolution results from genetic changes of localized origin which then spread throughout the remainder of the gene pool. A case of this type of transient polymorphism seems illustrated in Australia by the diffusion of tawny hair color.

Tawny, or so-called blond, hair has long been noted among the aborigines by various writers,

but they have not explained its regional pattern of occurrence and its evolutionary significance. The earliest account, quoted by Carmichael (1878), is that of the Italian Benedictine missionary, Bishop Don Rudesindo Salvado, who landed on the western coast of Australia in 1846. He noted that the natives in a district somewhat north of Perth often had hair so fair that it would have been envied by a native of northern Europe. Schulze (1891) briefly commented that among the Aranda the hair color normally was dark but in rare cases it was fair. Spencer and Gillen (1899) reported that the hair was jet black in color in males, although the use of red ochre occasionally made it appear a more brownish hue. In some instances a real dark-brown tint was found. Now and then among the children a decidedly lighter hair color occurred, which was confined to the tips and rarely reached the roots. In adulthood the hair of such individuals usually, but not always, assumed the normal dark color. Thomas (1906) referring to the above description, stated that of 12 hair specimens in his possession, none of them approached jet black in color, and one aboriginal woman, 20 years of age, had hair which ranged from fair to sandy at the tips. Spencer (1928) provided a more accurate description, stating that even flaxen-colored hair tips occurred among occasional children, particularly among the girls. But fair hair was never characteristic of any tribe or community as a whole, and it darkened with age.

Hrdlička (1926) briefly examined two small groups of natives while traveling across the Nullabor Plain. He described a minority of the children in which the tips of the hair approached the dull yellow color of crude sheep's wool, or that of tow. He concluded that the condition was not albinistic, since these individuals showed no other indications of that abnormality. In his opinion the lusterless tow hair looked as if it had been bleached, but repeated inquiries among natives and whites discouraged this view, although red ochre used as hair dressing possibly caused rust-black discoloration. He erroneously inferred that the condition was generalized occurring in all parts of the continent. Hrdlička recognized the interesting nature of this phenomenon, but offered no explanation.

Griffith Taylor (1926, p. 2388) gave the first detailed description of the phenomenon and a partial account of its regional distribution. His comments are worth quotation:

> The writer in 1924 made a brief study of the aborigines along the West Australian coast at Carnarvon, Hedland, Wallal, and Broome, without noticing any very special features. On returning from Broome via Hedland on the railway to Marble Bar, he was told that he would meet fair-haired, even golden-haired, types in the interior after leaving Nullagine. The writer journeyed by car from Marble Bar to Meekatharra; and as the attached map shows, he encountered tawny-haired aborigines all through this country along the borders of settlements.
>
> At almost every station on this journey of about 1,000 miles, one found that about half of the women had tawny hair. Among the boys and girls it was still more common, but as they became adult, the boys' hair became much darker—until it was a dark brown with a reddish tinge (the color in the rest of Australia is almost uniformly black). In several examples the adult women's hair could be called yellow-brown, but generally the color was tawny or brown. The ends of the hair were always lighter than the roots of the hair, so that the living hair has a lighter appearance than that of the severed specimen.

Taylor advanced several improbable explanations for tawny hair. He quoted with apparent approval the suggestion of Hickson, a former medical man in Tasmania, that the hair of the extinct Tasmanians, when thoroughly clean, was a golden-brown color, and concluded that the tawny aborigines may have inherited their unusual hair color from a submerged negritic stock. Again, noting that unusual cold has been known to blacken the white and yellow hair in rabbits, he postulated that the intense heat of the desert may have affected the aboriginal hair, causing it to turn brown.

Campbell, Gray and Hackett (1936, p. 247 et seq.) did extensive field work among the isolates where tawny hair shows maximum frequencies. Among 225 males for which color could be estimated, 84 showed "black" hair, 141 "brownish-black" hair. Corresponding figures for 115 females were 35 and 80 respectively. Among the younger men, six had "medium-brown" hair color, while the younger women had an additional three with "medium brown" and three with "a mixture of brown and straw" colors. "From these tables it will be seen that the predominant hair color of these aborigines varies from dark brown to black." For beard color, 148 males were "black," nine showed lighter shades. Among 171 men, 113 had "black or dark-brown," 58 "light" chest hair. For 37 women the fine down on the chest was "light," in two it was "black or dark brown." Hair color on the forearm in 215 males was "black" in 160 cases, "light" in 55. For 54 females, but 17 were "black," 37 "light." Eyebrow hair color was "black" in practically all individuals, where graying was no factor. Pubic hair was almost universally "black" in both sexes: four males

showed "brown," three females "light" colored hair in this region. These data indicate regional body variations in frequency of the lighter tones of hair color, which most commonly are found in head hair, least often in beard, eyebrow and pubic hair. Sexual differences are marked only in body hair on the chest and forearm, where the terminal hair of men is usually "black," while the vellus of women is most commonly "light."

Miss Daisy Bates (1939, p. 107), who long ministered to the spiritual needs of the aborigines in the southwestern corner of the continent, had perhaps the most novel explanation for the origins of the tawny-haired aborigines. She said:

> I also found traces of types distinctly Dutch. When Pelsart marooned two white criminals on the mainland of Australia in 1627, these Dutchmen had probably been allowed to live with the natives, and it may be that they and their progeny journeyed far along the river-highways, for I found these types as far out as the headwaters of the Gascoyne and the Murchison. There was no mistaking the flat heavy Dutch face, curly fair hair, and heavy stocky build.

During field work in the years 1937–1938, the author measured and examined 287 "full-blooded" aborigines from within the area where tawny hair occurred. Hair samples were obtained for all of these individuals. An additional 454 hair samples with full documentations have been made available to me through the generosity of the scientists of the South Australian Museum. The following data are based on a subjective analysis of hair color and hence the following tentative conclusions are subject to revisions at some future date when I have completed an objective analysis. Within these limitations certain generalizations are safe.

The tawny hair described by earlier writers is far more widespread than reported. Figure 13 shows the trait extending over about one-half of the total area of Australia. Among the aborigines the light-colored hair is affected by the phenomenon of progressive pigmentation, as in European populations. It is lightest during the years of infancy and childhood, and prior to adolescence begins to darken. But tawny-haired children in growing to adulthood never show the degree of pigmentation characteristic among normally dark-haired aborigines. This important difference, which was noted by Taylor, means that although tawny hair as an expression is less noticeable among the adult, it can still be distinguished phenotypically from the so-called "black" hair found elsewhere in Australia. The tips of the hair are lighter colored than the roots, but this sun-bleaching is a by-product of being genotypically tawny-haired, and is not the cause of the phenomenon. Similar effects may be noted among the Europeans of mixed pigmentation. My data suggest no significant differences in the sexual incidence of tawny hair, but the progressive darkening of the hair occurs more slowly among females than among males, and only women retain the lighter forms of tawny hair into adulthood. The most striking cases of blondness have been noted in female children, but the length at which hair is worn may be a contributing factor here. Sexual differences occurring in the course of aging may result from hormone mediation. Both skin and eye color show considerable variation among aborigines, but I have not noted that these are correlated markedly with tawny hair. If later analysis does prove differences to exist between tawny-haired and dark-haired aborigines in skin and eye color, they will be slight in amount.

Hair color is usually considered to result from the presence of two types of pigments. The first and most obvious of these consists of granular melanin. The various degrees of brownness in human hair correlate with the amount of granular melanin present, so that the lightest ash-blond color represents one normal extreme, black the other extreme of the range. Apparently diffused through the cellular structure of hair is a red-gold pigment which seems responsible for the various degrees of goldness and redness observable in human hair colors. When it is absent, all the melanin tones of brown are ash tones, and its presence in small amounts results in golden tones in the hair. Moderate to pronounced amounts of this pigment, if not masked by dense granular melanin, produce the various tones of red hair found in Europeans. The wide variety of hair colors observable in a population of mixed pigmentation is suggestive that the granular melanin and the diffused red-gold pigment may be genetically independent of each other.

Among tawny-haired aborigines, it is hence surprising to find that both pigment series are diminished in color value. This is noticeable when hair samples are examined by transmitted light, as opposed to reflected light. Light-haired individuals show a remarkably low value for the granular melanin of the hair, even among adults. This is in striking contrast to the darker color of normal aborigines, where the melanin values are high, although not reaching the human maximum. At the same time (with a few exceptions which will be omitted in this tentative analysis for the sake of simplification), the red-gold component of hair color has been reduced to its minimum, so that the tawny hair is distinctly ash rather than golden in color. Hrdlička's comparison

of such hair to the color of crude sheep's wool and his emphasis upon its lusterless appearance are well taken. Whatever genetic action may be responsible for tawny hair, it has markedly reduced the amount of both the granular melanin and the red-gold pigment.

been mapped as follows: the core regions for both tribes have been shown with a phenotypic frequency of 100 per cent; and a narrow band with a phenotypic frequency ranging between 90.0 and 99.9 per cent has been inserted between the two regions of maximum value.

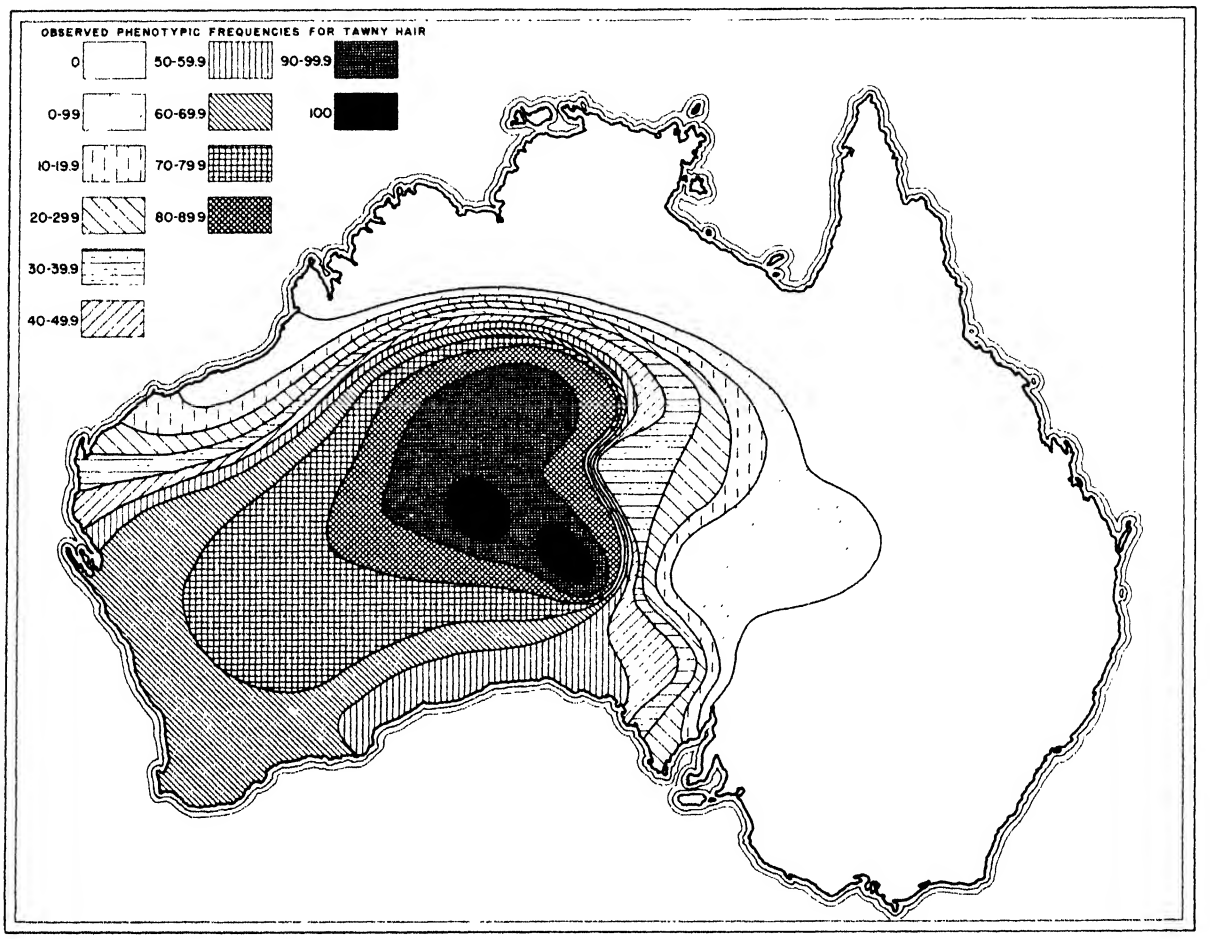

FIG. 13. Isophenic distribution of tawny hair.

The phenotypic frequency distribution of tawny hair among aborigines is shown in Figure 13. All data are based upon hair samples, including subadult and adult groups of both sexes since at all age levels prior to graying the tawny-hair phenotypes can be distinguished from those normal for aborigines. The largest tribal sample is that of the Pitjandjara for whom 118 specimens are available. In this population, 117 individuals showed tawny hair. Among the Jangkundjara, adjoining them on the east, all 43 individuals are tawny. Pooling both isolates, one person shows dark hair, 150 tawny hair. This individual occurred near the intertribal boundary, so that this situation has

Three tribal populations, 68 Ngadadjara, 22 Pintubi, and 22 Ngalia, are characterized by phenotypic values in excess of 90 per cent of tawny hair. Four isolates show phenotypic values ranging from 80.0 to 89.9 per cent. They are the Walpari with 33 individuals, the Kukatja with 37, the Mandjindja with 36 and the Anmatjera with 24 persons of all ages. A single series of 42 Nangadadjara represents the only isolate with values between 70.0 and 79.9 per cent. Upon the descriptive evidence presented by Griffith Taylor (1926), the widely-spaced vertical cross-hachured area which includes the last tribe, has been extended to the west to include much of the yet unsampled

desert north of the mining town of Laverton. Two other tribal samples are important in determining isophenic contours of lower values. A sample of 35 Iliaura are tawny haired in 40.0 per cent of cases and 67 Aranda in 41.7 per cent.

The tribal samples quoted above determine the primary configuration shown on the map. Series of pooled isolates provide the data for the southern and western coastal stretches. This reduces the efficiency of the data for plotting purposes, but since the natives in these districts are nearing extinction, no more adequate series can be anticipated for further definition. More information is needed from the interior region lying between Laverton and Derby in Western Australia, and along the northern periphery of the tawny hair distribution. I have undertaken steps to obtain further samples to define these critical areas more adequately. Despite the gaps in the data, I have confidence in the reliability of the general configuration for the distributional pattern for tawny hair.

Three features in the isophenic topography pictured in Figure 13 deserve comment. The most striking and best documented of these is the great escarpment separating the nuclear region lying above 80 per cent from the low-lying area below 40 per cent to the east. The reality of this abrupt step depends primarily upon the incidence of 86.5 per cent found among the Kukatja and the contrasting frequency of 31.7 per cent for the Aranda, their neighbors to the east. A chi-square test, with one degree of freedom, applied to these figures shows: $\chi^2 = 28.79$; P less than .01. Hence the observed difference far exceeds sampling error. Earlier isogenic maps for the M^N and I^A also emphasized a steep gradient in the cline structure of this region. These three independent analyses point to a relatively recent migration from some point to the north bringing the Aranda to their present location. The presence of tawny hair among the Aranda would seem due to gene flow from the high frequency areas to the west.

A second feature of interest in the topography is the asymmetrical extension of high values from the peak region in a southwesterly direction toward Cape Leeuwin. An interpretation of this ridge will be offered later. This feature is based upon sufficient data from isolates to define the clines in this region.

The third topographical feature is the steeply descending gradient lying along the entire northern boundary of the distribution. Its existence is based upon scanty direct evidence and more extensive negative evidence. The exact positioning and degree of steepness are open to future rectification, but there can be little doubt about its general characteristics. When properly established values have been determined for this sloping northern boundary it may prove possible through model manipulations to infer what evolutionary processes have been instrumental in slowing the rate of gene flow for tawny hair into the northern section of the continent.

Two phenotypic categories of tawny hair color can be subjectively distinguished with some accuracy among adult aboriginal hair samples of both sexes.[13] The first and most common type is characterized by moderate values of melanin and an absence of red-gold pigment when viewed by transmitted light. Its appearance by reflected light is a lusterless, dark medium brown. A less frequent phenotype shows a lower value for melanin, and the same absence of the red-gold pigment. In reflected light such a sample appears a darkish, light brown to medium brown in color value. Complete reliability in subjectively distinguishing between these two phenotypic colors cannot be claimed, but a competent observer should be able to distinguish between them in a great majority of instances. The range of phenotypes to be noticed among sub-adults, who are passing through the various phases of progressive pigmentation, is considerably wider.

The distinction between tawny hair as a phenotypic category and normal hair color in Australia, combined with the existence of two identifiable phenotypes among tawny-haired aborigines suggests that tawny hair may be a unifactorial genetic trait of mutational origin. Based upon the overall characteristics of the phenomena, I suggest as a hypothesis for test purposes that tawny hair is due to a partially dominant gene in which hormone mediation is mildly expressed. Unfortunately I have for pedigree analysis but a limited number of aboriginal families from the area where tawny hair is prevalent. Ten families, in which both parents were measured, yield a total of but 19 children. There are six families in which one parent is normally dark haired, and the other tawny haired. These matings produced 13 children, all of whom were tawny-haired phenotypically. The four remaining families represent matings between tawny-haired individuals. Three of these families had five tawny-haired children. The fourth family yielded but a single child, with normal, dark aboriginal hair color. These data are

[13] This claim does not deny the continuous nature of variation with tawny phenotypes, but refers to what seem subjectively to be modal tendencies within this distribution.

so meagre that they are offered with some apology. The children resulting from these matings, however, show phenotypes which are consonant with the hypothesis that tawny hair is the phenotypic expression of a partially dominant gene.

The identification of two tawny phenotypes suggests that a gene frequency analysis based upon the hypothesized partially dominant gene would be of interest. In those areas where tawny hair is relatively rare, most individuals have the phenotype which may be designated dark-tawny. Thus among 63 adult Aranda, with a frequency of 28.6 per cent for the total tawny phenotype, the dark-tawny phenotype occurs eight times as frequently as the lighter form, which will be called the light-tawny phenotype. As the total phenotypic frequency of tawniness increases in passing from a peripheral to the central portion of the distribution, the light-tawny phenotype becomes relatively much more abundant as compared to dark-tawny. Thus among the Pitjandjara, where 65 adults show a frequency of 98.5 per cent for the combined phenotypes, the ratio between dark- and light-tawny has risen to 5 to 4. Throughout the area of distribution there exists a tendency for the light-tawny phenotype to increase disproportionately as the total phenotypic percentage rises.

If the assumption that tawny hair is produced by a partially dominant gene is valid, then the dark-tawny phenotype represents the heterozygous, the light-tawny, the homozygous dominant expression. Hence, normally dark-haired aborigines must be homozygous for a recessive gene allelic to the gene for tawniness. Seven tribal populations are represented by adult hair samples series ranging in number from 21 to 65 persons of both sexes per isolate. The ratio of light-tawny to dark-tawny phenotypes seems constant for both males and females, hence the sexes have been pooled for test purposes. Chi-square tests for the probability that the observed frequencies deviate from expected hypothetical phenotypic frequencies, as calculated by the Hardy-Weinberg law, were made on these seven varying populations. In five cases the observed frequencies do not deviate significantly from those expected by the hypothesis of a partially dominant gene. Two tribal populations show deviations of doubtful significance. Thus in all seven instances there is no case where the deviation of observed phenotypic frequencies from the calculated frequency is beyond the sampling range. I am constrained to point out, however, that using a more sensitive test, summing all seven boxes by the additive property of chi-square, does reveal that when considered together the deviations from expectancy are significant.

The latter test does not disprove our hypothesis of a single partially dominant gene for tawniness, for certain factors must be given their proper weighting. The phenotypic identification of all three color variants not only contains the errors inherent in subjective evaluation, but was further handicapped in that the hair samples were examined as they were received from the field. There has been no time to wash such adhering materials as thin films of red ochre, dust, and other general grime from the specimens. When the samples have been properly cleaned and objective methods have been utilized to determine the phenotypic identification, the observed frequencies may lie closer to the calculated frequencies than they now do. Additionally, the chi-square tests were based upon frequencies calculated using the Hardy-Weinberg law. Some portion of the deviation occurring between the observed values and the calculated values may arise from the fact that the populations sampled are not in genetic equilibrium. Random drift has been suggested as operating in this region. The intrusion of the Aranda suggests that hybridization between tribes has not yet produced panmixia. Finally, it is probable that the dramatic spread of tawny hair over half of Australia has resulted from the operation of selection which in some way favors the bearers of the gene for tawny hair. For the sake of clarity let me state emphatically that this does not imply any selective advantage in tawny hair as a phenotypic trait, but I cannot escape a belief that some phase of the genic interactions basic to the expression of this hair color must be advantageous in a physiological sense. Since this stringent environment is primarily characterized by aridity and widely fluctuating diurnal range of temperature, the unidentified force of selection postulated as operative may confer some physiological advantage in these environmental terms.

Neither the pedigree analysis nor the gene frequency tests are adequate to substantiate the hypothesis that tawny hair is in fact an expression of a partially dominant gene slightly influenced by hormone mediation. On the other hand, in view of the meager data available, such analyses could not prove definitive. For my part I accept the hypothesis as undemonstrated, but the data are suggestive that with more extensive materials available for test purposes it may be confirmed.

There can be no doubt that tawny hair is the phenotypic expression of some mutant gene.

Mutations to blondness among dark haired and heavily pigmented populations are more common than generally realized. In addition to the Australian evidence, at least four other regions in Oceania have been affected by similar, but not necessarily identical, genic mutations. Ulithi, in Micronesia, is a case to point. Through the generosity of Professor William Lessa of our Department, I have received hair samples from approximately 400 inhabitants of this atoll, nearly the total population. Infantile blondness is fairly common among this mixed mongoloid population and shows some interesting aspects. Unlike tawniness among Australians, here the hair is golden rather than ash in tone. Geneological data allow pedigree analyses, and it appears that the Ulithian mutant behaves in inheritance as a recessive. This conclusion is highly tentative, but this gene is either unlike that found in Australian populations, or its genic background is so dissimilar that it both differs in its phenotypic expression and in its apparent mode of inheritance. Juvenile blondness has been reported for three other regions. Eastern New Guinea contains populations where the phenomena may be similar to that found in Australia. In the Loyalty Islands blondness occurs among children. Finally, in the Lau Islands of the Fijian group, infantile blondness has been reported among the aboriginal populations. Thus the tawny hair found in Australia is not an isolated instance and it must be considered that repeated mutations, possibly involving different loci, have occurred among the dark-skin peoples of the Pacific world.

J. The postulated genotypic distribution for tawny hair

If the hypothesis that tawniness is the expression of a partially dominant gene is acceptable as probable, but not proven, there is some justification in converting the phenotypic distribution for the trait in Australia into a map showing the frequencies for the postulated gene. This has been done in Figure 14. If this partially dominant gene is represented by Ty, and its recessive normal allele by ty, then the hypothetical genetic system can be expressed as a binomial: $(Ty + ty)^2 = 1$. It follows that the phenotypic frequency of tawniness, combining both light- and dark-tawny phenotypes equals $1-ty^2$. Thus a parabolic relationship exists between the phenotype frequencies of tawniness and its gene frequency. The nature of this relationship considerably alters the details of the configuration for the postulated gene frequency distribution map. These relationships can be seen in the insert figure in the upper right-hand corner of Figure 14. Thus a phenotypic incidence of 99 per cent for combined tawny phenotypes and but one per cent recessive dark phenotype, gives a gene frequency for tawniness: Ty = .90. A decrease in phenotypic percentage for tawniness to but 75 per cent corresponds to a drop in the gene frequency to .50.

A comparison of the isogenic with the isophenic map reveals a number of changes. The high, broad, topographic ridge extending from the nuclear area of high frequency in the phenotypic peak area to the southwestern corner of the continent has disappeared, and in its place there remains only a very low and concavely contoured cline extending between these two points. This feature still requires explanation in later sections, but the deflation of its proportions makes it less difficult. Again, the steep escarpment cutting north and south between the Kukatja and Aranda shows a considerably reduced gradient as compared to that present in the phenotypic distribution. The stepped nature of the clines running east and west through this region are still sufficiently marked to justify the presumption that the Aranda represent relatively recent migrants to their present area. The same smoothing tendency evident in the isogenic map applies to the gradient along the northern margin of the distribution. Here too, the isogenic contours have reduced the cline steepness. In summary, the topography of the isogenic map is less extreme in its gradients than the isophenic map. It may be concluded that phenotypic distributions frequently distort regional differences. The degree of warping will depend upon mode of inheritance and genetic complexity of the trait.

The tawny hair distribution covers about one-half of the geographic area of Australia, an impressive pattern of emergent gene flow. Proper perspective is obtained, however, through the calculation of the genetic mass of the postulated gene Ty for tawniness. Methods previously described show that Ty represents only seven per cent of the allelic mass at this locus for aboriginal Australia. The tawny-haired phenotype is well established, and apparently is spreading rapidly, but as its flow has occurred primarily through isolates in desert areas, its impact has an exaggerated appearance. If white colonization had not destroyed the aboriginal way of life it is possible that in future millennia Australians

would have evolved into a unique human group, characterized throughout the continent by the combination of dark skin and tawny hair color.

K. An emergent gene flow model for tawny hair

The spatial distribution of the frequency of the postulated gene for tawniness is representative of frequency.[14] The process of gene flow was allowed to proceed in orderly fashion through ten tiers of tribes. The first tier is considered to represent the establishment of the trait by an effective rate of mutation in the isolate of origin. Thus flow across the Pitjandjara boundaries falls into the second tier of the process. Ten tiers of flow were chosen as a compromise estimate to reconcile

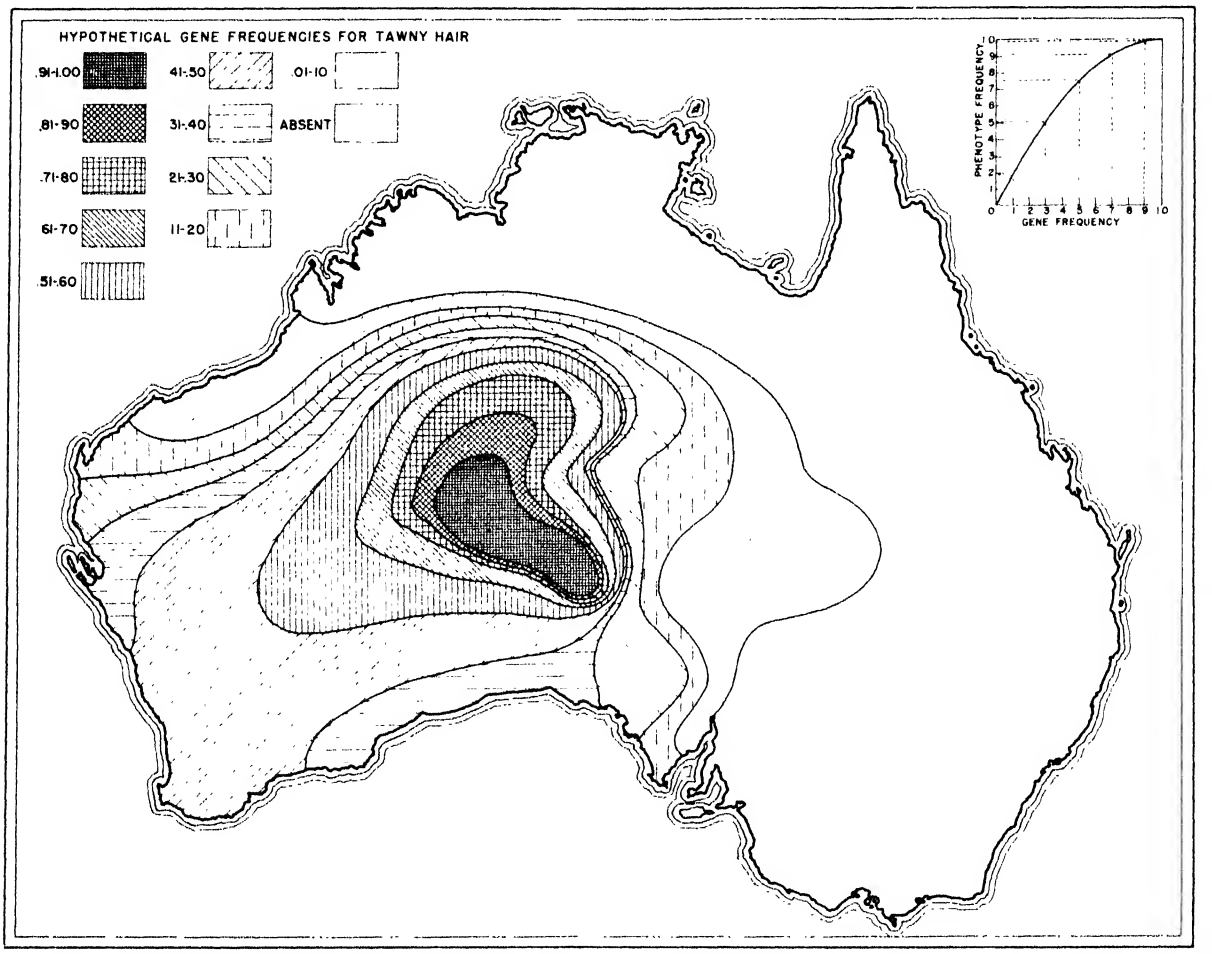

FIG. 14. Isogenic distribution for tawny hair based upon the hypothesis of a partially dominant gene.

a rare event in human evolution, emergent gene flow in the process of creating important phenotypic, and possibly physiological, changes in the population of an entire continent. To provide a basis for comparison, a gene flow model is pictured in Figure 15.

The same basic assumptions have been utilized here as in the earlier models. The point of origin of the trait was presumed to lie in Pitjandjara tribal territory, assuming that the trait would originate in an area now showing maximum two opposing tendencies noted in the flow development. The pattern of flow developed too slowly from the center toward the southwestern corner of Australia and too rapidly toward the northern shores. Termination after ten tiers of flow gave an eastern boundary differing from the observed pattern by but a single tribal unit, and carried the unimportant advantage

[14] There is little to choose between the Jankjunkara and the Pitjandjara, save that the latter are represented by a larger series and are situated nearer to the center of the distribution.

that cline values could be interpreted in round numbers.

The flow pattern impinged upon only two topographical and ecological barriers. Both of these had been previously tested in the Carpentarian Sahul Shelf model. The first barrier encountered consisted of the waterless Nullabor Plain lying parallel to the coast of the Great Australian Bight. Here values to inhibit the flow pattern were inserted to allow the terminal frequencies to correspond with observed values among the Mirning and Wirangu. At the end of the third tier of flow three inbars were inserted across the southern boundary of the Ngalea tribe where it abuts against Mirning territory. After the fourth tier of flow, this ecological barrier was extended by inserting two inbars on the southern boundary of the Wonggai tribe to the west of the Ngalea, and also along the southern boundary of the western half of Kokata territory, which lies just to the east of the Ngalea. After the fifth tier of flow this barrier was extended by inserting one inbar both along the southern boundary of the Murunitja tribe, to the west of the Wonggai, and also to complete the remaining southern boundary of the Kokata tribe. All inhibitors along the Nullabor Plain stretch on the southern coast were simultaneously lifted at the end of the sixth tribal boundary crossed by the gene flow pattern.

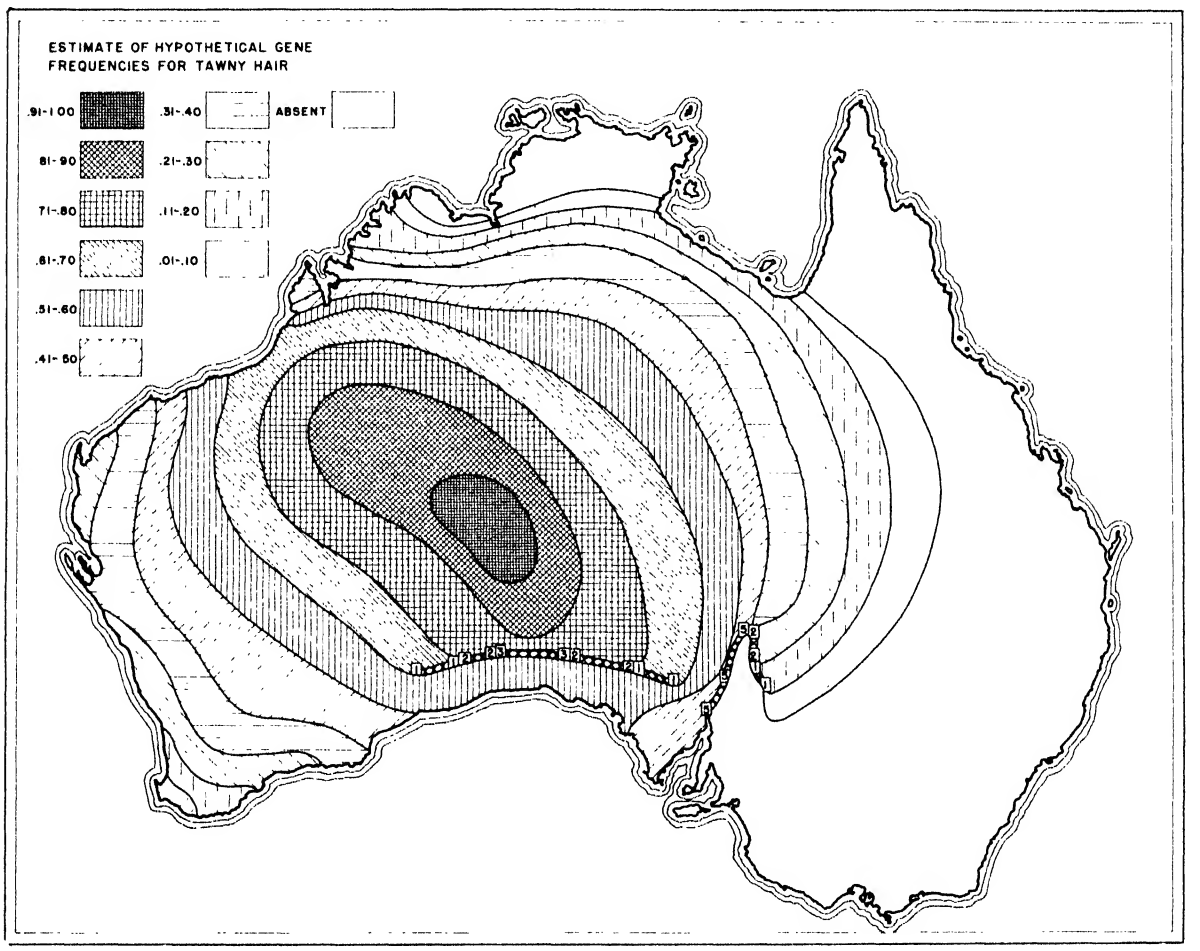

FIG. 15. Gene flow model for tawny hair, assuming the Pitjandjara to represent the origin point of emergent flow.

The second barrier zone, in this case a topographical feature, consisted of the Flinders Range extending northward from the eastern side of Spencer's Gulf. At the end of the sixth tier of gene flow, five inbars were inserted along the western flank of the Flinders Range, to exclude tawniness from this region. In the later stages of gene flow further inhibitors of two and one inbar value are required along the eastern side of the Range to

prevent gene flow from sweeping in from that direction. In this terminal stage of flow, the inbars have scanty diagnostic value. The Great Dividing Range did not enter this gene flow pattern, since its final stages barely lapped at its base.

This model for tawny hair has provided an independent check on the impeding effects exerted on gene flow by the Nullabor Plain and the Flinders Range. Both features have been evaluated previously in the flow model utilizing the Sahul Shelf gateway. A comparison between the separate evaluations is suggestive. In the Sahul model the desired results were obtained from two inbars operative across the entire Nullabor Plain and extending beyond it in the east to join the foot of the Flinders Range. In the present model, to achieve the desired phenotypic observations for tawny hair, inbars ranging from three down to one were utilized. The pattern of these inhibitor units, centering with a maximum where the Nullabor Plain is most formidable, produces more plausible results, which correspond more closely to the ecological nature of the obstacle. In addition, a model which tests the barrier value of a natural feature in the early phases of its flow, should produce more accurate inbar values than models whose flow meets the obstacle only in its waning phases. Even so, the similarity shown in these totally unrelated tests is startling.

The Flinders Range showed four inbars on both flanks in the Sahul model since the flow impinged on the barrier from the north. The flow for tawny hair reached the Flinders Range from a westerly direction, and hence presents its maxima on this side, with declining inbars ranging south along its eastern face. The latter, by the spent nature of the flow, are too low in value. The maximum of five inbars may be taken as more nearly representative for the entire barrier in the second model. This corresponds closely to the value of four inbars necessitated in the Sahul Shelf model to obtain the proper phenotypic distribution. Again, the agreement between the inbar values as ascertained by the two model tests are uncomfortably close. The maximum value of five inbars shown in the tawny hair model is preferred for the same reasons given for the Nullabor Plain.

The inbar is a constant, in an abstract sense, from one model to another. This may be reasoned from the basic assumption utilized throughout, that inter-tribal relationships, both social and biological, are uniform across all isolate boundaries. Thus, it is tempting to accept the similarity in values obtained for both the Nullabor Plain barrier and the Flinders Range barrier in two independent tests as significant. This correspondence would appear to validate the immediate utility of gene flow models for the evaluation of topographical and ecological barriers in impeding gene flow. I am inclined to delay acceptance of this useful and pleasant idea.

Even if the basic concept is granted to carry constant value, grave difficulties and uncertainties arise if this equivalence is transferred to the *interpretation* of barrier values. Inhibitor factors used in these models contain an implicit time value. Time is clearly a function of the gene flow depicted by such model methods, but its relationship to the model is established through a complicated series of variables which are latent in the methodology. It will be recalled that earlier the cline from the point where flow originates to one of its unimpeded margins was described as varying markedly both with the age phase of the model flow and with the assumptions utilized in the construct. Until enough models have been manipulated to adequately test and define the inherent variables of the methodology, I must warn against facile acceptance on an interpretive level of the time constancy of inbars between independent models.

L. Some dynamic aspects of the flow pattern for tawny hair

A tentative analysis of some aspects of population dynamics in Australia may be based upon a comparison between the gene flow model shown in Figure 15, and the isogenic map for tawny hair shown in Figure 14.[15] This comparison is made graphically in the map shown in Figure 16. The inner boundary line conforms to the observed distribution for tawny hair, while the outer boundary depicts the pattern expected from model flow through ten tribal tiers. The arrows between these two boundaries are evaluations of the differences of their attainment in terms of genetic space. All arrows point inward, and their negative sign indicates that inbars are required to make the model terminal flow conform to the observed boundaries. The patterning of these implied inhibitors is suggestive. At the extreme eastern tip of the observed range one inbar is required, well within the range of the error of the method. The adjoining values on both sides of two and three inbars respectively, may likewise be disregarded at this stage of interpretation. The

[15] If the comparison is made instead with the *isophenic* distribution, Figure 13, the results are generally similar.

uniformity of remaining inbars may be of some importance. Along the entire northern portion of the observed distribution four and five inbars are necessary for reconciliation of the two patterns. This value amounts to one-half of the total genetic space through which the model was allowed to flow, and hence may be significant.

sulting human vacuum. In prehistoric times similar slow migratory movements may have resulted from the decimating influence of severe localized droughts. Since the well-watered coastal hinterlands would have been immune to such climatic catastrophies compared to the arid interior, a generalized, randomized movement of populations

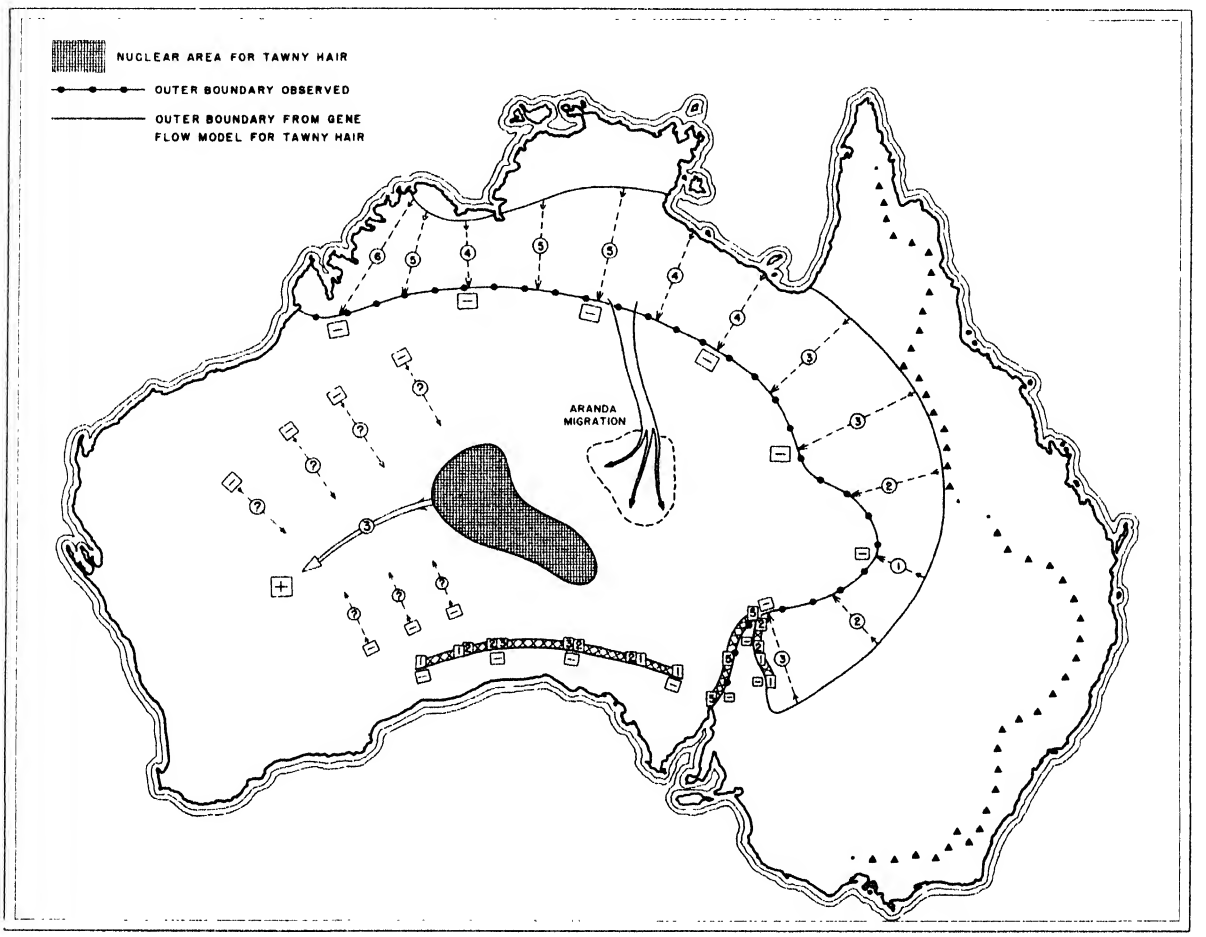

FIG. 16. Dynamic map for tawny gene flow based upon a comparison between Figures 14 and 15.

Evaluation of the evolutionary processes involved in this region of uniformity would be premature, but certain ideas suggest themselves. A similar result could be reproduced if a consistent and systematic southward migratory movement had occurred among Carpentarian peoples entering along the entire Sahul Shelf portal. The migratory thrusts must have been randomized along the entire front to produce these results. In historic times it has been observed that as tribal populations die out or leave their domain owing to the inroads of acculturation, groups still leading a nomadic life gradually drift in to fill the resulting human vacuum. In prehistoric times similar slow migratory movements may have resulted from the decimating influence of severe localized droughts. Since the well-watered coastal hinterlands would have been immune to such climatic catastrophies compared to the arid interior, a generalized, randomized movement of populations from the north toward the interior of Australia may have been the resultant.

Other factors might explain the observed pattern of inhibition. If gene flow across a tribal boundary was not completely reciprocal, as assumed earlier, for cultural or other reasons, then the observed type of deviation might result. If the net flow from north to south exceeded the reverse flow, an unbalanced condition might obtain. The inbars along the northern boundary in Figure 16 seem to require very large difference in the rate of reciprocal flow, and hence the latter is unlikely to be a sole explanation.

A third cause could be postulated. It was suggested earlier in the discussion of the distributional pattern for tawny hair in Australia that its spread seems to require some positive force of natural selection. It could be postulated that the inbars along the northern boundary represent a regional shift from positive to neutral selection, or even to a negative selection. Mean annual rainfall gradually increases when one proceeds from the center toward the north, and the clines for this climatic factor lie parallel to the northern boundary for tawny hair. Even so, this shift in climate does not seem sufficient to account for a sufficient change in selection to cause the observed differential. Or finally the suggested pattern of inhibition may be a consequence of a palaeoclimatological shift which could not be included in these models. These speculations are all premature and a choice need not be made among them now. They have been inserted here only to indicate that spatial gene flow models offer interesting ultimate potentialities in the analysis of population dynamics.

Figure 16 indicates two regions in which recent migratory movements can be identified. A 3-pronged arrow coming down from the north into the central portion of the continent symbolizes the population thrust of the ancestors of the Aranda. Its reality seems confirmed independently in three different analyses. Another arrow will be noted emerging from the nuclear area and swinging in an arc toward the southwest. The plus sign at its head indicates that it symbolizes an acceleration in the flow of genes in that direction. The numeral three encircled in its midshaft region is an estimate of the number of tribal units crossed by this accelerating force. Its existence has been suggested by internal evidence resulting from the comparison of Figure 15 with Figure 14. The gene frequencies observed in the extreme southwestern corner of the continent in the model of gene flow are too low, as compared to those observed from the raw data, implying the flow to the southwest has somehow been accelerated. The simplest explanation lies in the migration of groups from the arid center toward the southwest. The successful Sahul model of flow for the Carpentarian racial elements also showed a deficiency in this area equivalent to two tribal boundary units crossed. Again, despite the close correspondence in the values three and two respectively, it seems unwise to stress the similarity. I should prefer to conclude that, since the two models do indicate the same trend of acceleration, migrations in this direction represent a modest probability, but that it would be premature to measure the accelerating force.

A belt of inwardly directed arrows occurs to either side of the arrow representing acceleration to the southwest. These have again been derived from internal evidence. They represent apparent inhibitor forces operative in the direction of the arrows, as shown by the minus sign appended to their base. No attempt has been made to estimate the inbars represented. Until more data have been obtained for the central portion of Western Australia and until the gene flow methodology has been greatly refined, they must remain on a purely suggestive basis.

Comparisons between observed distributions and flow models, when the methodology of the latter has been sufficiently refined, may provide bases for the evaluation of the evolutionary forces which have produced the spatial patterning. It is not too much to hope that ultimately the contributions of hybridization and migration, selection, mutation and drift may all be identified and their relative influence approximated through appropriate model analyses.

SUMMARY

This paper has stressed the implications of the genetical definition of race in terms of certain aspects of spatial analysis. Two broad approaches have been utilized. The first of these is based upon the concept of genetic drift as a possible analytical tool. Examples are given to indicate that drift may affect human populations under Australian conditions. Utilizing the idea that multifactorial phenotypic expressions might be expected to be less affected by drift than genetically simple traits, which should respond more dramatically, illustrative examples from metrical and morphological data were presented. Total facial height was observed to show an isophenic distributional pattern suggestive of a simple genetical mode of inheritance. This contrasted markedly with phenotypic stature, which showed a complacent cline topography. Supplementary evidence in the form of F_1 hybrids between aborigines and Europeans offered some substantiation, and suggested that this metrical phenotypic trait might be importantly influenced by a dominant gene for reduced facial height. In another instance, the frequency of the observed occurrence of fourth distomolar teeth was mapped. A distributional pattern emerged for which drift provided the most plausible explanation. By implication, the highly varying expressions of this morphological trait were considered to be caused genetically by a unit factor, probably causing the backward extension of the dental lamina.

A different approach to spatial analysis, experimental in essence, was presented in a crude form by the gene flow methodology. In spite of the discouraging number of basic assumptions required for simplification, it offered promise in the future. Even within the present limitations, such analyses indicated that the Carpentarian element entered Australia by the Sahul portal, prior to the subsidence of the Shelf, and hence in the waning phases of the Fourth Glacial Period.

A possibly important by-product of the gene flow methodology was an evaluation of the influence of various topographical and ecological barriers in impeding gene flow. This end was achieved through model manipulation, so that terminal flow in the region of the barriers was made to conform to observed data. Values for the inhibiting factors obtained from the successful Sahul Shelf model found independent corroboration to a startling degree of similarity in the tawny hair model. It was pointed out that these similarities could not, at this time, for technical reasons, be regarded as establishing their equivalence on an interpretive basis.

A third model of gene flow was used to explore the distribution of tawny hair color among Australian aborigines. Observational data for the distribution of this trait were presented in isophenic contours, as well as in postulated isogenic contours. Evidence was presented which suggests, but by no means proves, that this phenotypic character may be the expression of a partially dominant gene whose expression is slightly influenced by hormone mediation. Confirmation of this hypothesis awaits further data. A comparison between the model for ideal gene flow for tawny hair and the observed pattern of distribution on an isogenic basis carried implications for population dynamics in Australia, which, in themselves interesting, are at this time too ill-defined for acceptance. They are suggestive of the future possibilities of this approach in identifying and perhaps even evaluating the influence of such factors as migration, unbalanced reciprocal gene flow across tribal boundaries, various aspects of positive and negative selection, and identification of the effects of palaeoclimatological changes.

The Sahul Shelf and the tawny hair models implied that the observed distributions of these two categories of traits could best be explained by invoking selection as the responsible evolutionary process. Drift, mutation, and hybridization, taken singly or together, did not seem to explain their spatial patterns. Selection in a positive sense here seems confirmed as a causal agency with a high degree of probability.

These two methods of utilizing the concept of genetic space for purposes of racial analysis, and hence the evaluation of evolutionary processes, by no means exhaust this type of approach. One of our gifted graduate students, Mr. William Womble, has independently developed an extremely interesting methodology based upon different principles. While I do not feel free to discuss his formulation in detail, it can be said that it promises, for the first time, a means by which natural taxonomic units on a sub-specific level can be identified with a high degree of objectivity. This much desired goal is attained by flexibly integrating large numbers of independent isogenic and isophenic distributions into a single, highly expressive, and fruitful synthesis. His preliminary results will be published within the next few months and should add a powerful method of analysis to the natural sciences.

The reign of tyranny which sampling calculus has exerted in racial anthropology is drawing to an end. A calculus based upon time has proved its value in this, and the broader field of population genetics. Already its theory has run far ahead of its applications to problems of human evolution. Space calculus has received little attention since Huxley's important contributions to the subject. It has been the purpose of this paper to point to the need of the further development of a space calculus, to stand alongside of time calculus, and ultimately for the two to be blended into a single, powerful research instrument.

ACKNOWLEDGEMENTS

In this paper, whose purpose is the emphasis of space as a primary variable in the methodology of population genetics, data derived from the Australian aborigines has been used for illustrative purposes. Limitations of space and time have precluded proper and full acknowledgment of all the bibliographic references utilized in an indirect or oblique fashion throughout this presentation. I am aware of my indebtedness to these unmentioned sources and plan detailed acknowledgment in subsequent publications on a substantive plane.

I am especially indebted to the many workers who have made their raw data pertaining to the Australian aborigines available to me. I have utilized serological data provided by Professors J. Burton Cleland, T. Harvey Johnston, and H. H. Woollard, for the Central Desert portion of Australia. Dr. R. K. Gay provided blood group data for the northern coast of Western Australia.

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DISCUSSION

BRITTON: I hope I do not seem picayune, especially after Dr. Birdsell's very fine, provocative paper, but I would like to ask three simple technical questions: (1) May one properly consider simply the mean tribal group of 500 in deriving the results; and what was the tribal population range involved? (2) In dealing with the matter of a few mms. only, say an eighth of an inch or so, in facial length difference, the method and technique of actual measurement become very important. How were these data determined? (3) As a benighted or naive medico, may I ask what elements are involved in the term "genetic drift"? Is there the least inherent suggestion in it of implication or involvement of the transmission of acquired characteristics?

BIRDSELL: (1) As stated earlier, estimates of the range of tribal population size vary from the extremes of 100 to 1,500 persons. It has been necessary to assume, as I have explicitly done, that the calculated mean tribal population of 500 persons can be utilized for the construction of these preliminary models. Available data suggest no systematic deviations which would statistically invalidate this assumption when applied to large numbers of isolates.

(2) Total facial height is measured with a standard sliding caliper between the landmarks of nasion and menton. The measurement on the living is subject to considerable personal equation, due to the difficulty of accurately locating nasion. My own variability in identifying nasion, (that is the sagittal point on the fronto-nasal suture), approximated ± 1.00 mm. as determined by dissection on a small series of cadavers. Field controls exercised during work in Australia indicated a comparable over-all range of variability, and an estimate of error a small fraction of this value. As previously pointed out, my measurements for the Ngadadjara tribal sample averaged 111.1 mm., those of the Australian workers 111.3 mm. This high degree of correspondence was taken to indicate comparability in techniques and to justify utilizing the two sets of data conjointly.

(3) Regardless of its other faults, there is nothing Lamarckian about the concept of genetic drift. It refers to the effects of non-random sampling in producing changes in gene frequencies in very small breeding populations.

CAIN: Dr. Birdsell's very interesting paper raises the question of genetic drift as an explanation for otherwise apparently inexplicable irregularities in gene frequencies. Sewall Wright describes genetic drift as the cumulative effect of sampling errors in a population, and has shown that its effect will be most noticeable in rather small populations. He has emphasized on several occasions that it cannot proceed very far against even a moderate degree of selection. Fisher has shown that even a one per cent selective advantage is amply sufficient to bring a particular allele to fixation; such an advantage may be very difficult to detect in practice. Recently, Wright (*Evolution*, December, 1948) presented a detailed study of the inter-relations between population size, low selection coefficients, and drift.

Several speakers have already emphasized the very complex relations between the genotype and phenotype. As is well known, what is usually called "the effect" of a gene is only the most conspicuous one of many. The effects of the same gene can differ in different genotypes. That the effects produced in a heterozygote are not necessarily intermediate between those in the homozygotes is clearly shown in examples of balanced polymorphism, where the heterozygote is superior in selective advantage to both homozygotes.

Further, the intensity of selection in natural populations cannot be assumed to remain constant. There is good evidence that in at least some pairs of alleles (or other alternative genetic systems) one member is favored at certain seasons, but is at a lower advantage than the other during the rest of the year, so that their relative frequencies change very appreciably. Since no two summers, winters, wet seasons, or dry seasons are wholly alike, the cyclical changes in frequency may be very irregular, perhaps even to the point of appearing random. Dr. Birdsell has pointed out the possible consequences of very severe selection during times of drought in the tribes he has studied.

When one considers the complexity of pleiotropic effects seen in all alleles that have been adequately studied, and their modifications in different genotypes, it seems extremely unlikely that the selection coefficients of all the activities of any one gene should be effectively neutral. When, on the other hand, one considers the complexity of the changing selection pressures produced by the changing environment, it seems

equally unlikely that if any particular gene were by chance to be effectively neutral, it could possibly remain so for long. No one can deny categorically that genetic drift can occur, but after these considerations its importance in evolutionary processes must seem very small indeed.

There is, however, a second objection, the essence of which is contained in Charles Kingsley's remark that to prove that no water-babies exist you must see no water-babies existing, which is not the same thing as not seeing water-babies. There is a very real danger that when no obvious selective influences can be found to explain a particular variation in gene frequency, the investigator will conclude that therefore drift must be acting. A similar argument was used by some authors in denying the selective advantages of many differences between species and might be paraphrased (rather unfairly) as, "We see no selective advantages in all these species differences, therefore, there are none," which does not follow. Students of gene frequencies may easily fall into the same error by declaring, "We see no systematic influences determining these frequencies, therefore, they are random." In every case the action of drift and of selection must be proved, not assumed. But it would almost seem that while in some particular instances selection can be shown to be the determining cause and drift therefore be ruled out, it would be extremely difficult, if not impossible in any case, to rule out selection entirely, leaving drift as the only possible explanation.

In general, it is much better to carry on the analysis if the material permits than to say that because all attempts to demonstrate selection have failed, therefore, drift must be responsible. It is possible that in modern man (against whom many selective forces that may be presumed to have acted in the past now no longer operate) may be promising material for investigating drift, provided that the effects of migration and of severe but intermittent local selection can be ruled out. But, in general, one must avoid using drift as a blanket explanation to cover all difficult cases.

BIRDSELL: One may agree completely, as I do, with the detailed arguments so cogently advanced by Dr. Cain, and yet proceed rather differently in an analysis of human materials. The issue is not whether selection *or* drift has been more important in evolution for the former is undoubtedly the primary process. Our question is this: In human groups with a favorable type of population structure can drift in the light of present knowledge always be precluded as a contributory cause of observed inter-isolate variation?

The existence of the current disagreement between Fisher and Wright may be taken to indicate that water-baby-wise the non-existence of drift has not yet been proven. Without claiming man as exempt from the usual processes of evolution, it should be noted that human populations may be expected to respond to evolutionary forces in ways which differ quantitatively from the responses of invertebrates, such as intensively studied Drosophila. Man is a warm-blooded, long-lived mammal. He is unique in possessing a culture which has both partially shielded him from, and allowed him to modify the consequences of, the selective forces inherent in the natural environment. In extrapolations based upon data from other types of organisms such differences must not be underrated.

Strange as it must seem to geneticists, the concept of natural selection operating on man as a powerful evolutionary force has only very recently been reintroduced by anthropologists. The pain of the idea is such that it is by no means universally accepted. To date, no single instance of the operation of selection has been incontrovertibly demonstrated in human population genetics, although a number of instances have been imputed. *The implication*, derived from Dr. Cain's position, *that where the processes of hybridization and mutation can be reasonably precluded, all human inter-isolate variations must result from selective forces, seems both extreme and premature at our present level of knowledge.*

Dr. Cain's discussion raises a second issue, the problem of indeterminacy. The field of population genetics contains problems essentially indeterminate in terms of existing data. This is especially true of human population studies, and these difficulties will remain unresolved for many years. Are the interests of science best served by withholding all opinions and decisions until these can reach a level approximating absolute truth, or does advance proceed most rapidly when workers are willing to hazard their opinions on a tentative basis, in terms of very crude probabilities? In my own case, the latter position is the more congenial. Australian aboriginal tribes show a population structure favorable for random drift due to sampling in small local populations. I believe the examples quoted earlier in this paper may with reasonable present probability be attributed at least *in part* to the operation of drift. When and if evidence accumulates to make this position untenable, these tentative opinions can be rectified without regret.

Sewall Wright (*Evolution* 2, no. 4, 1948, p. 285) expresses these ideas more clearly:

This indeterminacy was unfortunate but it seems likely that more progress will be made in analyzing the difficult problems of the genetics of natural populations if all possibilities are treated symmetrically and any indeterminacy is brought clearly into view rather than concealed by an approach from the point of view of advocacy of any single factor, even one of such undoubted importance as selection.

DOBZHANSKY: Dr. Birdsell, Dr. Cain, and myself agree completely that adaptation through natural selection is an agency of paramount importance in organic evolution. This applies to human evolution as well as to that of any other living species. Studies on the adaptive significance of human genetic traits are indispensable for elucidation of the evolutionary history and of the evolutionary perspectives of our species. The question at issue is whether selection is the only agency of importance in the evolutionary process. In the past, numerous evolutionary theories were published by authors who favored some one factor as the sole active force in evolution. Some believed that evolution is caused by mutation; others regarded selection omnipotent; still others believed that evolution occurs through hybridization. Nobody, to be sure, believed that evolution is caused by genetic drift alone. The great contribution of Sewall Wright to evolutionary thought has been his showing that evolution is caused by interaction of several forces, genetic drift being one of them, and that the relative importance of these forces varies from time to time and from species to species. This view has been challenged particularly by R. A. Fisher, who regards the role of genetic drift negligible and as cribes all changes in gene frequencies exclusively to selection. It follows from this belief that all human traits, including PTC tasting and blood group variations, are adaptive, whether or not their adaptive significance has been ascertained by experiment or observation.

I submit that we are not justified in assuming adaptive significance of any traits without evidence. The problem just can not be settled by dogmatic pronouncements of any authority, no matter how eminent. It may well be found tomorrow that the heterozygotes, *Tt*, for the phenyl-thiocarbamide tasting gene in man, are superior to the homozygotes, *TT* and *tt*, in some respects. Nothing would surprise me less than to find that the O-A-B-AB blood groups in man are adaptive in some environments. But we simply do not know the adaptive significance of most human genetic traits, and it is just as wrong to assume that all of them are adaptively neutral as to believe that they must be either deleterious or harmful. Under the circumstances, we should consider both the possibility that the distribution of a given trait is governed by selection, and that it is produced by genetic drift. The genetic drift hypothesis is valuable as a guide in research. It should be tested by data on population size, reproductive biology, social structure, and migratory habits of the species under study. Indeed, Dr. Birdsell has collected and ably presented such data for the Australian aboriginal tribes which he studied. If Dr. Birdsell would have taken on faith that the traits which he described must be governed by selection, the above information would not have seemed relevant or important. Summary rejection of the hypothesis of genetic drift narrows the vision of a student of evolution. It is just as fallacious as rejection of the importance of selection which was fashionable in some circles of biologists in the early years of the current century.

It should be made clear that selection and genetic drift are not alternatives, but very often cooperating agents. In the same population, some genes may be favored, or discriminated against, by selection, and other genes may fluctuate in frequencies owing to drift. The same gene may be selected at some times, and it may drift at other times. As Dr. Cain rightly emphasized, the selective values of a gene are far from constant. This clearly means that we should not jump to conclusion that any trait of known adaptive value in some environments can not be subject to drift in other environments or at other times. Vice versa, a trait neutral under some conditions may not be neutral in others. Things are just not that simple! Perhaps most interesting are the interactions of selection and drift in the evolutionary process. Sewall Wright has pointed out that conditions most favorable for progressive evolution may be found when the process is not dominated by any one agent but rather when several agents cooperate. Nobody doubts the importance of selection in evolution, but a system entirely controlled by selection is too rigid. Genetic drift alone results eventually in extinction rather than in evolution, but interaction of selection and drift may give rapid evolutionary progress.

Dr. Birdsell has discovered certain peculiarities in the geographic distribution of some traits in Australian aboriginal tribes which can be accounted for by the hypothesis of genetic drift; the distribution of other traits in the same populations suggests selection rather than drift. In my opinion, further studies on these tribal populations may reveal facts of utmost interest for understanding of human evolution.

HUNT: The mechanism of genetic drift may be relatively prevalent in man because of his cultural recognition of kinship. In the Pacific islands, particularly, it is quite likely that migrant groups of people were often closely related, and therefore unrepresentative samples of their parent isolates. The continuous emergence of new isolates in the migrations of primitive man, as a result of the movement of kinsmen, might easily account for random losses and accumulation of genes of a kind subsumed under "genetic drift."

I should therefore be less reluctant than my genetical colleagues to invoke genetic drift to explain kaleidoscopic variations in isogenes among closely related and neighboring human isolates.

The problem of defining human racial variants is complicated by the culturally imposed isolating mechanisms in man. At the present time, many geographic areas are inhabited by sympatric endogamous human groups which are genetically and morphologically distinct.

In the fairly recent past, the number of such sympatric isolates was considerably less than it is now, and many such groups today can be referred mainly to an ancestral region of the world. Such is the case, for example, with groups such as the American Negroes, who usually have some preponderance of African ancestry.

I should like to propose, therefore, that for purposes of sheer nomenclature, we define most of the races of modern man as geographic variants at a time level prior to the invasion of their racial homelands by Europeans. This time level in anthropology is rather ineptly called the "ethnographic present." This proposal is nothing new, and is only a slight variation on the proposals of other racial systematists as far back as Blumenbach in the 18th century.

If our basic geographic stocks were considered as Caucasoid, Mongoloid, African Negroid and Oceanic, human groups for the grossest purposes of nomenclature would be classified into zoogeographic subspecies in harmony with taxonomic procedures on other well-recognized polytypic species of animals. This device would in no way affect the evolutionary study of human speciation, however.

A CONSIDERATION OF THE CONCEPT OF RACE

M. F. ASHLEY MONTAGU

Department of Anthropology, Rutgers University, New Brunswick, New Jersey

In this paper I propose to present a summary of the modern view of the nature of race in general and of human races in particular. Such a summary will necessarily have to consider the mechanism of the origin of human races as well as the concept of race as such. Let us begin with the latter first.

PART I

THE CONCEPT OF RACE

The history of the concept of race has been dealt with by numerous writers (Topinard, 1879; Hankins, 1931; Hogben, 1932; Huxley and Haddon, 1936; Finot, 1906–1944; Snyder, 1939; Count, 1950). It is our task here to consider the modern concept of race. While it would not be altogether irrelevant, even within the framework of this Symposium, to discuss the political and social concepts of race, I shall touch but briefly upon these, and largely devote my attention to a summary and discussion of the concept of race from the biological viewpoint, as seen by the geneticist, the zoologist, and the anthropologist. A presentation of the views of representative workers drawn from each of these fields may help us to arrive at a unified view of what most of us could agree should be meant by the term race.

Waddington (1939) has pointed out that "If we try to derive a concept of race which will be relevant to all characters of a man, the attempt is a complete failure. Segregation and recombination has gone so far in most sections of the human population that it is impossible to summarize an individual by any description less complete than a specification of his whole genotype."

The fact of genotypic variability, particularly in human populations, determines certain ineluctable consequences. These may be set out as follows:

1. Race is a concept which can apply only to populations. It cannot be applied to an individual, but only to a population of individuals. From this it would follow as a corollary that
2. Race is a statistical concept, or a concept which can be arrived at only as a result of a comparative statistical analysis of the genotypically determined traits of populations. From this it follows as a corollary that
3. Race is both a comparative and a relative term in that it compares some condition or conditions in a population with, and attempts to relate that condition or conditions to, all other populations of the species. For example, the "white race" is so called because certain populations are comprised of individuals who possess a "white" skin in comparison with the skin color exhibited by other populations not so characterized. All populations and all individuals possessing a white skin color are by virtue of the possession of that skin color believed to be more closely related to each other than to the members of other populations not possessing white skin color. And so on with respect to most other characters.

The fact that race is a relative term in more than one sense constitutes a danger against which one must be on one's guard. The relativity of race also relates to the investigator. For it is he who will select the traits the frequency distribution of which will determine his races. It is possible to define races, as Dunn and Dobzhansky (1946, p. 101) have done, as "populations which differ in the frequencies of some gene or genes," or as they have done in the same work, as "populations which differ in the relative commonness of some of their genes" (Dunn and Dobzhansky, 1946, p. 108). A difference then in a single gene would be sufficient to constitute a racial difference. For example, various human populations differ in the frequencies of the blood groups A, B, AB, and O, and in the frequencies of the various Rh types. The North American Indians have little or no B or AB (with few exceptions). In this they differ from almost all European, Asiatic, and African populations. In respect of the low frequency of the genes for the blood groups B and AB then, the North American Indians are racially different from these other populations. With respect to the recently discovered gene R^z in the Rh series, this is now known to be extremely rare in the populations of Europe or of European origin. It

[1] Part II of this article is reprinted from a volume in press, *Introduction to Physical Anthropology*, published by C C Thomas, Springfield, Illinois.

occurs, however, in from three to six per cent of Asiatics, American Indians, and Australian aborigines. The even more rare gene R^Y may occur only in certain Mongoloid groups. Here, again, there are obvious differences in respect of the frequency distribution of these genes. Among the Basque people some 30 per cent are Rh negative, almost twice as many as are known in any other population. In respect of their high frequency of Rh-negative genes the Basque people are relatively significantly different from all other populations.

Here is where the meaning of race as a relative concept should become clear. In the first place, populations differ from one another relatively, *not* absolutely, in respect of the frequency of one or more genes. Races, then, are definable in the distribution of certain genes. From the genetical standpoint, therefore, populations can only be defined as races *in particular relation to or in respect of* the gene or genes in the frequency distribution of which they differ from other populations. As Haldane has put it, "A race is nothing homogeneous, but a collection of very various individuals who have something in common which can only be accurately described in terms of ... statistical methods" (Haldane, 1942, p. 195).

This is a very different conception of race from that which until comparatively recently prevailed among most zoologists and anthropologists, who were accustomed to thinking of races in terms of absolute phenotypical differences rather than in terms of relative differences in the frequency distribution of traits or genes. In passing I should like to draw attention to a notable exception among anthropologists, namely to Sir William Flower who, in 1885 wrote, "It is more by the preponderance of certain characters in a large number of members of a group, than by the exclusive or even constant possession of those characters, in each of its members, that the group as a whole must be characterized" (Address delivered at the anniversary meeting of the Anthropological Institute of Great Britain and Ireland, 27 January 1885; Flower, 1898). Thinking in terms of absolute differences led to implications of distinctive homogeneity or identity, separateness, and therefore discontinuous and substantive difference. The distribution and genetic analysis of particular traits in human populations thus far investigated indicates that all living mankind's genes have been drawn from a common pool, and suggests likeness rather than difference, or better it suggests variation in likeness. This suggests the necessity of underscoring the point that when we speak of populations which differ in the frequencies of some gene or genes, we are referring usually to variation of the same things, and not, as is sometimes assumed, to variation of different things. In the study of the population genetics of the human species we are concerned with the study of the variation of likeness rather than of difference.

> "Where order in variety we see,
> And where, tho' all things differ, all agree."
>
> Pope

More accurately stated in the words of a geneticist, L. H. Snyder (1948, p. 586), "Among the findings emerging from the study of population genetics is the conclusion that human populations differ genetically one from the other almost entirely in the varying *proportions* of the alleles of the various sets and not in the *kinds* of alleles they contain.

"The manifold combinations of traits which in turn derive from manifold combinations of genetic and environmental influences result in the almost infinitely diverse range of human individuality—a range which we are just beginning to comprehend."

The inference from the evidence that all mankind draws its genes from a common gene pool renders the conclusion inevitable that all living mankind constitutes a single species, the species *Homo sapiens*. This conclusion, arrived at upon a genetic basis, is in agreement with the conclusion reached by all students of the morphology of man. This is perhaps more than a happy coincidence for, as Simpson (1944) has pointed out "morphological species" are inferences of the "genetic" species actually existing in nature.

In palaeoanthropology the morphological species concept will largely remain the only one which can be used as a yardstick owing to the obvious difficulty of using the biological definition, a definition involving the criterion of crossability or reproductive isolation. What then is a species? I quote Mayr's (1942, p. 120) short definition:

> "Species are groups of actually or potentially interbreeding populations, which are reproductively isolated from other such groups."

Dobzhansky (1944, p. 252) defines species in sexual cross-fertilizing organisms as "groups of populations which are reproductively isolated to the extent that the exchange of genes between them is absent or so slow that the genetic differences are not diminished or swamped." By contrast: "Races are defined as populations differing in the incidence of certain genes, but

actually changing or potentially able to exchange genes across whatever boundaries (usually geographic) separate them."

A species, then, is a group of populations. The group is the species, the populations are the races. The group as such is reproductively isolated from other such groups, being either actually unable to exchange genes with other similar groups or capable of doing so under conditions which do not affect the specific integrity of the group.

A race is one of the group of natural populations comprising the species. Such natural populations differ in the incidence of one or more genes and are usually more or less separated from one another by geographic boundaries. To the extent to which they are geographically separated gene exchange is more or less limited, but under all conditions they remain potentially capable of interbreeding with one another.

One anthropologist has offered a definition of race in which the phrase "ethnic group" replaces the term "race," as follows: "An ethnic group represents one of a number of populations comprising the single species *Homo sapiens* which individually maintain their differences, physical and cultural, by means of isolating mechanisms such as geographic and social barriers. These differences will vary as the power of the geographic and social barriers, acting upon the original genetic differences, vary. Where these barriers are of low power, neighboring groups will intergrade or hybridize with one another. Where these barriers are of high power, such ethnic groups will tend to remain distinct or to replace each other geographically or ecologically" (Montagu, 1945, p. 43).

Curt Stern has recently (Stern, 1949, p. 558) defined a race as "A genetically more or less isolated division of mankind possessing a corporate genic content which differs from that of all other similar isolates."

As it stands it would be difficult to distinguish what there is in Stern's definition of a race which would not also hold good for the definition of a species. What Stern's definition lacks is the operative *differentiam* which distinguishes a race from a species, and this, surely, is the degree of actual or potential isolation. Reference to this is insufficiently sharply made in Stern's definition. Furthermore, the use of the phrase "division of mankind" as equivalent to a race is confusing because this is a phrase which is used by some anthropologists to refer to the major divisions of mankind into which most races naturally fall. Finally, the statement that a race possesses "a corporate genic content which differs from that of all other similar isolates," rather confusingly suggests what the author does not intend to convey, namely, that races differ from one another in a large body of gene differences. Though this is not what Stern means by the word "corporate" that is what it can be taken to mean. If that is so then the word "corporate" is an unhappy one.

Stern's definition could be rewritten in the following form: A race is a more or less isolated population of the species *Homo sapiens* which differs from other populations of the same species in the incidence of one or more genes.

Now, as Dobzhansky and Epling (1944, p. 138) have stated, "A race is not an individual and not a single genotype, it is a group of individuals, a population, in which many different genotypes occur. It would be equally fallacious to define a race as a group of individuals having a given gene allele or a given chromosome structure in common. Since in most species there are many variable genes and chromosome structures, and since different genes and chromosome structures are capable of forming a variety of combinations, an individual or a population might belong to one 'race' so far as the gene *A* is concerned, to a different 'race' with respect to the gene *B*, to a still different 'race' with respect to *C*, etc. To be sure, the ideal of genetic analysis is to be able to describe each individual in terms of gene and chromosome variants which it contains. But the race concept is a tool for the description not of individuals, but of subdivisions of species. We propose to define races as populations characterized by differing frequencies of the variable genes and chromosome structures. Ideally, all variable genes and chromosome structures would have to to be taken into account to describe a given race. At the present level of knowledge this ideal is unattainable. The description of races may become more and more exact as knowledge grows."

Clearly distinctions drawn between human populations on the basis of a difference in the frequency of a single gene must be interpreted with caution. Such a difference may be significant or it may not.

In 1936, J. S. Huxley and A. C. Haddon published their well-known book, *We Europeans, A Survey of "Racial" Problems.* In this work they showed that the popular and scientific views of "race" no longer coincided. "The word 'race', as applied scientifically to human groupings, has lost any sharpness of meaning. Today it is hardly definable in scientific terms, except as an abstract concept which *may*, under certain conditions, very

different from those now prevalent, have been realized approximately in the past, and *might*, under certain other but equally different conditions, be realized in the distant future.

"In spite of the work of the geneticist and anthropologist there is still a lamentable confusion between the ideas of *race*, *culture* and *nation*. In this respect anthropologists themselves have not been blameless, and therefore the deplorable amount of loose thinking on the part of the writers, politicians and the general public is not surprising. In the circumstances, it is very desirable that the term *race* as applied to human groups should be dropped from the vocabulary of science. In part, it represents merely the taking over of a popular term, in part the attempt to apply the biological concept of 'variety' or 'geographical race' to man. But the popular term is so loose that it turns out to be unworkable, and the scientific analysis of human populations shows that the variation of man has taken place on lines quite different from those characteristic of other animals. In other animals, the term *subspecies* has been substituted for 'race.' In man, migration and crossing have produced such a fluid state of affairs that no such clear-cut term, as applied to existing conditions, is permissible. What we observe is the relative isolation of groups, their migration and their crossing. In what follows the word *race* will be deliberately avoided, and the term (*ethnic*) *group* or *people* employed for all general purposes" (Huxley and Haddon, 1936, pp. 82–83).

In his essay "The concept of race" in *Man Stands Alone*, Huxley (1941, p. 126) writes "it would be highly desirable if we could banish the question-begging term 'race' from all discussion of human affairs and substitute the non-committal phrase 'ethnic group.' That would be a first step towards rational consideration of the problem at issue." It is of more than passing interest to note here that Huxley's grandfather, T. H. Huxley, in his essay "On the methods and results of ethnology," published in 1865 and reprinted in *Man's Place in Nature*, similarly refused to use the terms "stocks," "varieties," "races," or "species" with reference to man "because each of the last well-known terms implies, on the part of its employer, a preconceived opinion touching one of those problems, the solution of which is the ultimate object of science; and in regard to which therefore, ethnologists are especially bound to keep their minds open and their judgments freely balanced."

My own usage of the phrase "ethnic group" has its origin in the suggestions of Huxley and Haddon. I cannot wholly agree with their interpretation of the biological facts, nor with their statement that: "Nowhere does a human group now exist which corresponds closely to a systematic sub-species in animals, since various original sub-species have crossed repeatedly and constantly" (Huxley and Haddon, 1936, p. 108). In the biological sense Huxley and Haddon do seem to deny the existence of human races. Since I believe that I have been classed with those scientists who deny the existence of human biological races, advantage may be taken of this opportunity to point out that in my book on "race," I state at the very outset that "In the biological sense there do, of course, exist races of mankind. That is to say, mankind may be regarded as being comprised of a small number of groups which as such are often physically sufficiently distinguishable from one another to justify their being classified as separate races" (Montagu, 1945, p. 2). What I did attack and deny the existence of in nature was the "omelette" conception of race held by many of the older anthropologists, and the popular conception of race which is still with us. The anthropological process of race-making by averaging the characters of a group, of knocking the individuals together, giving them a good stirring, and then serving the resulting omelette as a "race" is the concept of race which I found wanting and rejected.

Certainly in 1936 most anthropologists were still in the pre-genetical phase of their development. Reference to some of the leading texts of the period will indicate how ill-informed most anthropologists were with respect to the elementary principles of genetics. Their interest was largely focussed on the study of complexes of characters and their distribution, instead of upon the mechanism of inheritance and transmission of separate traits. As Dobzhansky pointed out (1941, p. 359), "the difficulty... is that... the concept of race as a system of character averages logically implies a theory of continuous, rather than of particulate germ plasm. Such a concept is obviously outmoded and incapable of producing much insight into the causative factors at work in human populations. Although the genic basis of relatively few human traits is known, it seems that following up the distribution of these few traits could tell us more about the 'races' than a great abundance of measurements."

I doubt whether there are today any anthropologists who would not wholeheartedly subscribe to these statements. This was scarcely the case ten years ago, and the credit for bringing about this change must go to such workers as Huxley, Haldane, Hogben, Muller, Wright, Dobzhansky, Mayr, and possibly one or two irreverent critics of the anthropological conception of race.

I believe it is now obvious to all students of raciation, that is of race formation, that the origin and evolution of races is largely a problem of ecology and population genetics. The student of anthropology interested in these problems will have to undergo a very different type of training from that which has been customary up to the present. In the field of physical anthropology we have today very few men who have been adequately trained in genetics and mathematical analysis or ecology. Time will doubtless see a substantial increase in their number.

It is to be hoped that the physical anthropologist interested in any aspect of race will always remain interested in human beings. It is sometimes forgotten that man is a highly organized social creature, a creature of a socialization process which frequently causes him to mistake his prejudices for the laws of nature. The layman understands by the word "race" something very different from what the scientist understands. The layman's conception of "race" is so emotionally weighed down with false meanings that any attempt to modify it would seem to be met by the greatest obstacle of all, the word itself. Based as it is on unexamined facts and unjustifiable generalizations, some of us have felt that the term should be dropped from the vocabulary, at least until the scientific meaning of the term is generally understood. Some thirty years ago the psychologists were faced with a not dissimilar problem. The meaning of the term "instinct" had become so injected with false meanings, that it was generally agreed among psychologists to drop the term altogether from their vocabulary. This was done, and such non-committal synonyms as drive, urge, or need, were substituted. There can be few psychologists who would not agree that this has been greatly to the advantage of psychology (Barnard, 1924).

I, for one, suggested the use of the phrase "ethnic group" (Montagu, 1945) to replace the term "race" as a simple means, among other things, of causing people to think twice before using the term "race" or not to use it at all unless they could give good reasons for doing so. To what extent such ends are desirable and to what extent they have been achieved by this means everyone will judge for himself.

The biologist is likely to take an oversimplified view of the problems here involved, and to dismiss such attempts at re-education of the layman as unsatisfactory. By substituting one phrase for an agreedly confused term, he will say, one solves nothing. It is quite as possible to feel "ethnic group prejudice" as it is to feel "race prejudice." This, I think, is to miss the point. The phrase "ethnic group" is not a mere substitute for the term "race," the grounds upon which it is offered constitute a difference in viewpoint which significantly differentiates what the phrase stands for from what the term stands for. In the social context in which the term "race" has been and often still is used, the phrase, "ethnic group" serves as a challenge to thought and as a stimulus to rethink the foundations of one's beliefs. Some scientists have felt that the use of the phrase "ethnic group" was an avoidance of the main issue. On the other hand, most students of human nature would take the view that such a usage constitutes a more realistic and more effective approach to the problem of lay thinking on this subject, than the method of attempting to put new meaning into the old bottle of "race." This is the view of the group of experts who constituted the Committee on Race which convened at Unesco in Paris 14–16 December 1949, and drafted the Statement on "Race" which is shortly to be issued to the world. It is a viewpoint, I submit, which deserves serious consideration.

For the layman the term "race" closes the door on his understanding. The phrase "ethnic group" opens that door, and it functions to serve to keep that door open. The contemporary layman's conception of race is akin to the eighteenth century retardative concention of "phlogiston," and the nineteenth and early twentieth centuries psychologists' conception of "instinct." For the same reasons as these terms were dropped, namely, that they corresponded to nothing in reality, the scientist ought to assist the layman to drop his conception of "race." On realistic psychological grounds the contention here is that this cannot be adequately achieved without dropping the term which enshrines that conception.

Huxley and Haddon (1936) urged that "the term *race* as applied to human groups should be dropped from the vocabulary of science," because "the variation of man has taken place on lines quite different from those characteristic of other animals." "In man, migration and crossing have produced such a fluid state of affairs that no such

clear-cut term, as applied to existing conditions, is permissible. What we observe is the relative isolation of groups, their migration and their crossing."

In other words, the exchanges of genes between the breeding populations comprising the human species has been and increasingly continues to be more rapid and fluid than in any other animal species. Hence, sharp and clear-cut application of the term "race" to such rapidly changing groups is not permissible.

It seems to me that here, as elsewhere, in Huxley's writings, there is concealed a conception of race as "pure race." While Huxley and Haddon are at pains to point out that such things as pure races do not exist, nevertheless their conception of race in man sets up an arbitrary degree of purity to which very few human populations could conform. And if they don't conform, according to Huxley and Haddon, they are not races. Without prolonging this discussion, I think it will be generally agreed that in the genetical sense and in the morphological sense in spite of much admixture many races of man are today distinguishable by the same criteria and in pretty much the same way as are races of any other animal. Crossing between different human populations has almost certainly occurred at different rates and frequencies in different populations, and in modern times the process of race making and of race mixture has proceeded before our very eyes as in Hawaii and in the Americas. So that, surely, there is one thing that we can say about race mixture, and that is, though races may to some extent lose their former character as a consequence of race mixture, they become a part of whatever population they are incorporated in. It may be a population that is a race in process of becoming, such as the Hawaiian and the North American Neo-American population. If races are incipient species nations could be regarded as incipient races (Keith, 1949), but only if they maintain their boundaries long enough! In any event, admixture does not mean loss of identity as a race, as Huxley and Haddon imply, but simply change of identity as a race or population. A much mixed population may be a race in precisely the same sense as a long-isolated population which is in genetic equilibrium.

When one understands the nature of man's migrations and crossings, one can understand something of his tremendous variability—a variability which has been claimed as unique by many biologists (Darwin, 1872; Haldane, 1935, 1949; Huxley, 1942, 1947, 1949; Trembley, 1949), but which has been denied as exceeding or even equalling that of many other animal groups by one physical anthropologist (Schultz, 1947). However this may be, the point is that the great variability of any human population, no matter how mixed it may be, does not constitute a sufficient reason for denying it racial status. Most human races are probably much mixed and within limits certainly exhibit a high degree of variability in many of their physical traits. The mixture which such populations represent is usually of relatively old standing and, unless we know its actual history practically impossible to resolve into its original contributing elements. The tendency is strong, therefore, to think as it were unconsciously of such populations as "pure." Many modern populations are also mixed, but they show a tremendous variety of types—types which collectively do not satisfy the requirements of any scientific conception of a race, and which individually are traceable to well-known different racial stocks. The population of the United States is a good example of such a mixture. It should be obvious that the "mixture" represented by the ethnic groups comprising the population of the United States is a very different kind of mixture from that which is characteristic of older isolates. In the latter there has been a sufficient time for exchanges of genes between the component hybridizing groups throughout the breeding population. In the United States different ethnic groups are relatively slow in exchanging genes with other ethnic groups, there has not been a sufficient amount of time for social and other barriers to be broken down between them. We have, then, the phenomenon of a population in the United States which is mixed only as a nation, but not as a race. Mixed only insofar as it is made up of a number of different ethnic groups and persons of other national origins, but which is not a population the component elements of which have interbred upon any large scale for any considerable period of time. Were such conditions ever to be fulfilled under the further conditions of adequate isolation there can be no doubt that a novel race of man would appear in America comprised of all the elements which had entered into its formation. New types have, of course, appeared in America as a result of crossing between the members of various racial stocks, as for example White and Negro, but the resulting offspring do not constitute a race because they do not maintain themselves long enough as a separate isolate, but continue to form part of the larger polymorphic population with which, at a variable rate, they exchange genes. The population of the United States is not a race but a

nation made up of the members of many different racial groups and persons of mixed racial origins who largely maintain their genetic distinctness owing to the existence of social barriers and the very short period of time which has been available for their inevitable breakdown and the free flow of genes across such barriers. In the light of such considerations the juxtaposition of such statements as the following can be somewhat misleading: "Thus, blue eyes are very common in most parts of the United States but rather rare in most parts of Mexico. It is this and similar differences which make it possible to say that the inhabitants of the United States are in general racially distinct from the inhabitants of Mexico. Races can be defined as populations which differ in the frequencies of some gene or genes" (Dunn and Dobzhansky, 1946, p. 101). These statements, quoted from Dunn and Dobzhansky's admirable little book, could be interpreted to mean that the inhabitants of the United States constitute a population which *as a race* is distinct from the Mexican population or race. What the authors actually mean to convey is that the racial elements which have entered into the constitution of the two populations are to some extent different. Hence, there are differences in the frequencies of certain genes which each of them exhibit. Now, this brings us to a critical point with respect to the genetical definition of race as offered by Dunn and Dobzhansky. The population of the United States does not constitute a race, nor does that of Mexico, yet quite clearly these two populations differ from one another in the frequencies of some gene or genes. A definition which can also be applied to a population which is not a race is not necessarily defective if in the light of the realities of the situation there is good reason to believe that such complex populations as those of the United States and of Mexico are actually composed of a number of different racial elements. In such instances the term race is not applicable to the population as a whole, which is properly speaking a nation, but rather to each of those more or less genetically distinct elements within it which at one time were geographically separate populations and which may continue to be more or less separate populations within the larger complex population. The recognition of these facts would suggest that a viewpoint such as that represented by Huxley and Haddon (1936) is insufficiently analytic, erecting arbitrary criteria, such as "fluidity," which would make it impossible to apply the term race to any but allegedly "pure races." It would be pertinent to inquire what the degree of "fluidity" must be between the inhabitants of any geographic area before they cease to become races. How homozygous must a population be before it qualifies as a race? Perhaps we can best answer this question by turning now to a consideration of what zoologists have to say on the subject of race.

The Zoological Conception of Race

It is interesting that on the first page of his book *The Species Problem*, G. C. Robson (1928, p. 3) writes, "At the present time there are signs in evolutionary studies of a renewed interest in the study of variation and race-formation in relation to habitat and mode of life. Herein the species is of less importance than the 'race' or the 'colony'." In spite of this statement Robson nowhere in the whole book offers a definition of race! I have found this to be a peculiarity of a disproportionately large number of zoological textbooks. Again, in their joint work Robson and Richards (1936) have an excellent discussion of race, but no explicit definition of race. The term subspecies is, however, recognized as equivalent to the term race as customarily used by ornithologists and mammalogists. Subspecies is defined as a major subdivision of a species, being a distinct geographic entity having a distinct geographic range. It is, however, pointed out that race is often used for a smaller unit not of the same dimensions as the subspecies. "Local race" and "local forms" are terms used in this way. Clearly such a hierarchy of local or geographic groups does not exist within many species, and this is the principal reason why "the boundaries of the various groups would be difficult to draw and there would be some confusion of terminology." This is, of course, the familiar problem of the physical anthropologist.

Many zoologists recognize that "subspecies themselves are far from being elementary" (Sumner, 1917), that, indeed, in numerous cases they are composite groups constituted of a number of distinguishable local types. Intense localization in segregated populations is known to result in similar groups; such groups have been described by many observers, particularly in land snails (Robson and Richards, 1936), in rats found in different houses in India by Lloyd (Lloyd, 1912), between communities of ants found in different nests (Alpatov, 1924), and in races of *Partula* found on a single tree (Pilsbury, *et al.*, 1912), not to mention numerous other cases. Forty years ago Semenov-Tian-Shansky (1910) proposed the

name "natio" for such "besondere kleine lokal geographische Einheiten." The terms "microraces," "microgeographical races" (Dobzhansky, 1937), "microsubspecies" (Huxley, 1940), and others have been used for such local groups.

The tendency of characters to change gradually and continuously over large areas is today recognized in the concept of character gradients or *clines* (Huxley, 1942, p. 206). Such character or geographic gradients are very evident in man, and since it is likely that they are environmentally adaptive, such clines in man should receive more attention than they have in the past.

In *The New Systematics* (1940) Huxley writes: "The term subspecies should be reserved for natural groups of the same general nature as species, but exhibiting a lower degree of morphological differentiation and/or reproductive isolation" (p. 36). Huxley adds that "the essence of a subspecies should be that it is a form with a definable geographical range and distinctive characters" (p. 37). How many distinctive characters, it may be inquired? In practice we know that morphologically it need have none, and genetically or physiologically it need have no more than one, as in certain physiological races. It has been shown that in many phyla—and it is probably true of all—there exist groups which are of specific rank, as well as others which are of subspecific rank, in all but the accepted morphological sense. There may be ecological barriers, including different food habits, and different breeding season, the barriers may be psychological, or due to a physiological inability to cross (Thorpe, 1940). There is some evidence that there may exist at least one such physiological race in man, namely, Andean man who lives at an elevation of from three to five thousand meters (Monge, 1948). This altitudinal Andean population physiologically differs very markedly from sea-level man. It is adapted to an oxygen deficiency, which is seriously disordering and often fatal to sea-level man. Athletic prowess and inurement to fatigue is extraordinary in Andean man. Monge writes, "However paradoxical it may appear to one not well grounded in the biology of the matter, it is indubitable that at the high altitudes of the Andes rest is not the adaptive procedure but rather exertion" (Monge, 1948, p. 63). "There is no longer a white race, biologically speaking, in the high altitudes," writes Monge. "There exists instead an ethnic type differentiated from the rest of the world's human varieties. We call this type the Man of the Andes...." (Monge, 1948, pp. 38–39).

Apart from the fact that Andean man presents a possible illuminating example of the mechanism of race formation in man, it is of pertinence to point out here that on the basis of morphological characters alone it would never have occurred to anyone to distinguish Andean man from the men of the coastal or plains level. It is probable that certain morphological changes have occurred in Andean man in adaptation to conditions of life at high altitudes. Such morphological differences are found in "altitudinal races" of birds. The tendency of such birds is to be larger and generally darker than those races of the same species living at lower levels (Mayr, 1942, p. 196). Similar changes may occur in altitudinal populations of man. But just as there is no evidence for "altitudinal races" of birds there is none for altitudinal populations of man which would indicate whether their morphological or physiological differences are merely phenotypical or have a genetic basis. It has long been known that in plants the most striking morphological changes occur in valley plants which have been transplanted at high altitudes without any corresponding genetic change (von Naegeli, 1884; Clausen *et al.* 1940). The terms "habitat races," "habitat forms," "ecotypes," and "ecophenotypes," have been most commonly applied to such groups. Where a doubt exists concerning the genetic basis of the phenotypic difference it would by definition—at least by genetic definition—be incorrect to speak of such groups as races. Andean man may represent a physiological race or a population in process of becoming such a race, but until its genetic differentia, if any, are demonstrated, such populations are better described as "habitat types" or "habitat populations." Such considerations lead to the cautionary principle that no population should be described as a race in the absence of good evidence that there is a genetic basis for the characters upon which a racial distinction is being erected. It needs, perhaps, to be emphasized that the phenotypical plasticity of man is considerable. Man is a species which is characterized by a genotype which is capable of a very wide range of phenotypical variation. It is therefore all the more necessary to be on one's guard against falling into the error of mistaking phenotypes for races. This is an error into which anthropologists, as well as others, have frequently fallen.

The Physical Anthropological Conception of Race

Physical anthropologists, with few exceptions, largely work with the morphological conception of

race. This is not to say that they are unaware of the promise of the genetic approach to the study of race in man. The viewpoint has been most recently expressed in a textbook of anthropology, in which the author (Hoebel, 1949) writes, "There has been some recent insistence upon a 'genetic theory of race' in which analysis of races is to be in terms of genes, not morphology. The time will come when it will be possible to describe races in terms of gene components, but that time is not yet here. For the present, we shall continue to use physical traits for diagnostic purposes, taking care to isolate culturally conditioned traits from genetically determined ones. Only the latter are to be treated as racial." This is a reasonable and realistic viewpoint. It is, however, open to the possible criticism that the attitude which it represents realizes the viewpoint of an earlier age rather than that of the present, and encourages the adherence to older methods while insufficiently encouraging attention to the new.

The viewpoint referred to is also illustrated by a remark of Howells that "To anthropology, the problem of race is still one of endeavoring to classify and delimit these breeds of man almost entirely through external characteristics, though the contributions of specialists in tangent fields promise to be helpful" (Howells, 1940). Washburn (1944) writes that: "Racial classifications are made by men who are trying to understand human anatomy." "Racial classification is an anatomical concept and is useful for anatomical purposes" (pp. 692, 702). Washburn states clearly what the physical anthropologist tries to do. He writes, "It is impossible to consider each of the two billion persons in the world. Therefore some system of sampling is necessary. It happens that mankind does divide into great groups so that a relatively small number of individuals may substitute for the entire group. One Bushman looks more like the next Bushman than either looks like a European or Mongolian. There is a great variation in each group. Races intergrade and mix. Nevertheless, at present there is no other practical method of obtaining some superficial acquaintance with what mankind is like from a physical point of view. The racial classification is a *simple sample system* which allows a student to become familiar with the superficial characters of two billion people in a remarkably short period of time.

"Existing races are the products of evolution, and a second aim is to determine the relations of various races to fossil men and ultimately to other primates.... An understanding of comparative human anatomy is essential. Since fossils consist of bones and teeth only, knowledge of these parts is particularly important. Studies of the different proportions of the body are best carried out according to biometric methods. Genetics, particularly of the blood groups, is playing a larger and larger part in studies of the living" (Washburn, 1944, pp. 693–694).

The morphological emphasis here is in the last sentence tempered by a reference to the increasing importance of genetics in "the living." Now, it should be clear that while morphological studies of extinct and living populations or their representatives will always remain necessary in physical anthropology, analysis of such populations or their representatives must increasingly call upon the assistance of modern conceptions of genetics and systematics as exemplified in such works as those of Dobzhansky (1944), Mayr (1942), Huxley (1940, 1942), Simpson (1944), and Boyd (1950). The conceptions developed in these and similar works are applicable to all the levels at which the physical anthropologist studies race and raciation in man, whether living or extinct. I believe that the majority of contemporary physical anthropologists would subscribe to this view. It is or should be evident that it makes a substantial difference in terms of results and understanding whether the problem of race and racial classification is approached in terms of morphology or in terms of morphology *and* genetics. Morphology at best can give us good descriptive results, and in this sense it has often been said that almost all that the physical anthropologist can do is to describe populations. The use of the conceptions of modern genetics and systematics renders possible the more exact analysis of what is described.

The study of man's morphology will always remain a fundamental task of the physical anthropologist in the study of race and raciation, and it can never be supplanted by purely genetical or systematic studies. The phenotype must first be described before it can be genetically or systematically studied—but it *must* be genetically or systematically studied; otherwise the anthropologist will be in danger of continuing to mistake phenotypes for races. In a book entitled *Races* (Coon, Garn, and Birdsell, 1950, p. 112) by three physical anthropologists, precisely this mistake is committed and, what is more, enshrined in their definition of race. They write "a race is a population which differs phenotypically from all others with which it has been compared." They add, "If we know the genotypical differences as well, we can add these to the list."

Surely, this definition had been more soundly written as "a race is a population which differs *genotypically* from all others with which it is compared." If phenotypes are to remain the criteria of racial studies and races are to be defined by such criteria the confusion which has so long characterized such studies is hardly likely to be reduced. A population may differ phenotypically but not genotypically from one or more other populations with which it is compared. Microraces or habitat populations are examples of populations showing phenotypic differences without underlying genotypic differences.

It seems to me that the definition of race offered by these three anthropologists would take for granted what required to be proven, that is, if it be agreed that fundamentally race is a matter of gene frequency differences. Certainly many phenotypical traits make their appearance in the same form in all environments, and it is these that our authors have in mind in their definition of race, such traits as skin color, hair form, and nose form. Certainly, also, classifications of mankind on the basis of such phenotypes are possible. These authors write: "In attempting to classify human races we are obliged by the nature of the evidence and by our means of interpreting it to rely almost entirely on the former method [i.e., classification by phenotypes]. We are dealing with the whole man, in his adult form. We do not know how much of what we see and describe is inherited, and we may never know" (p. 111).

I suggest that we *do* know that a great deal of what we see and describe is inherited. What we don't know is the mechanism of inheritance. Our task as physical anthropologists, surely, is to find out what this mechanism for various traits may be. We already understand this mechanism for several physiological traits, such as the secretory factor, PTC-tasting, the serological factors, and a few others. There is no reason why we should not in time discover the hereditary mechanics of most morphological traits. We shall make no progress this way if we continue to concentrate our energies upon the description of phenotypes. In this connection the law of diminishing returns long ago put a period to the usefulness of this approach both to the classification and the tracing of genetic relationships.

The authors write: "To determine genetic relationships between groups of people we need more than descriptions of their present forms; we need historical evidence in the form of skeletons, sculpture, paintings, etc." (Coon, Garn, and Birdsell, 1950, p. 111). I suggest that we need more "etc.," the "etc." being the study of the genetics of particular traits and the distribution of the genes determining these traits in populations of man. The authors have made a valuable and suggestive attempt to make an ecological analysis of the physical traits of different races and habitat populations of man. They have provided good suggestive evidence of the adaptive nature of most of these traits. Research leading to their genetic analysis in the light of modern genetics and the new systematics is surely the next step in the physical anthropologist's approach to his perennial problem: the problem of how man, in all his forms, got to be the way he is now. For the problem of racial classification cannot be resolved until the problem of the mechanism of race formation—the genetics and systematics—of race has been solved. It is to this problem, the problem of the mechanism of race formation to which we may next address ourselves.

Part II

The Mechanism of Race Formation

Whether we think of the earliest types of man as arising from a common ancestral stock or from several different stocks, ultimately makes very little difference to our understanding of the differentiation of mankind. If they originated from different ancestors and were different to begin with, some of them must have met and interbred and produced hybrids who, in turn, did likewise, and some of the results of these mixtures may have given rise to existing races of mankind. A strong case could be made out for this polygenic (polyphyletic) theory of the origin of the races of mankind, but not quite as strong as that which can be made out for the monogenic theory which postulates the origin of the races of mankind from a common ancestral stock. One of the principal objections to the polygenic theory is that the living races of man so closely resemble one another in all their physical and mental characters that it would be difficult to conceive of them as having originated from distinct lines by a process of convergence. Also while it makes it more difficult to account for the existing differences, the monogenic theory seems to be more in accord with the facts, and with the evolutionary processes involved in the production of other races of living creatures.

Our present knowledge is not by any means adequate to provide an entirely satisfactory explanation of the mechanisms of racial differentiation in man. Much basic research will have to be

carried out before that becomes possible; but by utilizing the findings of geneticists on other animal groups as well as on man it may be possible to obtain some idea of the nature of the probable mechanism or processes involved in the evolution of the races of man. We may begin with the following postulates:

1. The original ancestral human population was genetically relatively heterogeneous.
2. By migration at different times away from the original ancestral population, individual families or groups of families became dispersed over great distances.
3. Some of the groups thus dispersed became geographically isolated from one another, and remained so isolated for more or less considerable periods of time.
4. In all these isolated groups the following factors came into play as conditions leading to evolutionary change:
   i. *Natural selection*
   ii. *Mutation*
   iii. *Isolation*
   iv. *Genetic drift*
   v. *Hybridization*
   vi. *Sexual selection*
   vii. *Social selection*

Natural Selection

By natural selection is meant the preservation through the action of the environment of such variations as arise and are beneficial to the organism under its conditions of life. Because they adapt the organism to those conditions such variations are called adaptive. Under the selective action of the physical environment those individuals who are lacking in the necessary adaptive characters or qualities tend to die out while those who possess them survive and procreate. Natural selection may, then, be regarded as the creative force which out of the raw materials of mutation determines not only which organisms shall survive, but also which among the many millions of possible organisms will in fact arise.

Darwin's own definition of natural selection may be given here. It is from the introduction to *The Origin of Species*, 1859, page 5:

"As many more individuals of each species are born than can possibly survive; and as, consequently, there is a frequently recurring struggle for existence, it follows that any being, if it vary however slightly in any manner profitable to itself, under the complex and sometimes varying conditions of life, will have a better chance of surviving, and thus be *naturally selected*. From the strong principle of inheritance, any selected variety will tend to propagate its new and modified form."

Judging from its distribution it is practically certain that skin color is an adaptive character, that is to say a character which has adaptive value. In man, with few exceptions, darkly pigmented skins are geographically distributed in high temperature-sunlight-humidity regions, lightly pigmented skins in regions of lower temperature-sunlight-humidity conditions.

The marked geographic gradients shown by pigmentation in warm-blooded lower animals have been subsumed in Gloger's rule. This rule states that melanin pigmentation tends to increase in the warm and humid parts of the species range. High humidity together with high temperature favors the selection of black pigmentation (eumelanins), while aridity with high temperature favors the selection of the reddish, yellowish- and reddish-brown pigments (phaeomelanins). The phaeomelanins tend to be reduced under cooler conditions even if arid, as do the melanins under extreme cases such as the polar regions. The maximum depth of pigmentation is found in humid and hot climates, the minimum in arctic climates. Heat and aridity, as in subtropical deserts, tends to select yellowish- and reddish-browns, while lower temperature and aridity, as in steppes, tends to select greys and grey-browns (Huxley, 1942; Mayr, 1942).

With the exception of color varieties which do not occur in man such as greys and grey-browns, and allowing for the shifts which have occurred as a consequence of migration, these relations between climate and skin color would seem to apply equally to man as to lower animals.

It may be that the broad nose of the Negro and the narrow nose of whites also represent adaptive characters. The work of Thomson and Buxton (1923) suggests that air at higher temperatures is breathed more easily through a broad than through a narrow nose.

Populations living in regions of extreme cold, such as those of the Arctic Circle, Siberia, Alaska, and Greenland, tend to be relatively short, and well padded with fat. They present a surface area which is less than that exhibited by populations which have been long resident in regions of high temperature. The latter would appear to be built to radiate as much heat as possible—the former as little as possible. Flat padded faces, flattish noses, and "double" upper eyelids—the epicanthic folds—appear to be adapted to protect the exposed and vulnerable face and eyes from cold (Coon, Garn, and Birdsell, 1950).

The action of natural selection varies under different conditions, and the rate at which it operates depends upon the character or quality involved. Thus, for example, where inherited lack of immunity to certain diseases such as sleeping sickness, malaria, and tuberculosis, is involved, natural selection would operate very rapidly, and those lacking immunity to these diseases would in a relatively short time tend to die out, while those possessing some degree of immunity would tend to survive.

The gradual dying off of individuals possessing a white skin in a tropical humid climate, so that only those with a dark skin remained, would probably take a very considerable amount of time. There is, however, no direct evidence that in this particular respect, such a differential action of natural selection ever occurred in the development of man.

It must be observed here that in addition to its creative action in the preservation of progressive adaptations, natural selection also operates in favor of those individuals who are already preadapted. Preadaptive traits predispose individuals to take advantage of the environment into which, by chance, they may be thrown. It may be, for example, that the broad nose of Negroids is such a character, that in a particular environment already existing persons with broad noses were able to adapt themselves to the conditions of that environment so efficiently that any other form of nose would have been at a disadvantage in comparison, that hence the broad nose persisted. Natural selection expressed itself here in the preservation of a preexisting character which was probably characteristic of all or most Negroids to begin with. It is unnecessary, therefore, always to assume that if a character or quality has survived another character or quality not as well adapted to the conditions of the environment must have died out.

The survival and diffusion of mutations has, to a large extent, been dependent upon natural selection, and since it is quite certain that mutation has played a considerable role in the evolution of man, it goes without saying that natural selection has played an equally important role.

The evidence points to the fact that natural selection has been the principal arbiter of man's evolution. Unfortunately, what is involved in the process of natural selection has not always been too clear to many writers on the subject. Ever since the publication of Darwin's *On the Origin of Species by Means of Natural Selection, Or the Preservation of Favoured Races in the Struggle for Life,* in 1859, most writers have dwelt on the "struggle" aspect of natural selection while altogether omitting to consider its very important cooperative aspects. Since 1859 a great deal of evidence has been accumulated which renders it quite clear that cooperation is an indispensable part of the "struggle" for existence (Bernard, 1911; Burkholder, 1949; Deegener, 1918; Drummond, 1894; Emerson, 1946; Espinas, 1878; Geddes and Thomson, 1889; Haldane, 1935; Holmes, 1948; Huxley and Huxley, 1947; Kropotkin, 1902, Leake, 1945, Miller, 1949; Nasmyth, 1916; Patten, 1920; Reinheimer, 1913, Wheeler, 1927; Wheeler, 1943; Simpson, 1949). If, instead of thinking, as the social patterns of the nineteenth century suggested, of "struggle" as the ruthless competition between individuals for survival we think rather of "struggle" as endeavor or drive to survive we shall be nearer the truth. Involved in process of the endeavoring to survive there are cooperative as well as competitive elements. The distribution of adaptive characters throughout a group is achieved by cooperation as well as by competition. Organisms possessed of certain selective advantages need the cooperation of their fellow organisms in order to be preserved. If natural selection secures the differential survival or perpetuation of different genotypes, then quite clearly cooperation is an integral part of the process without the action of which the survivors could not long be preserved. It is the cohesive effect of natural selection as represented by its cooperative aspect which secures the perpetuation of the species. It should be fairly evident that no animal group could possibly survive without the cooperative aspect of natural selection to sustain and integrate it. Competition without the cohesive effects of cooperation is powerless to preserve anything. "Favoured races" are not preserved by conflict but by cooperation. By cooperation is meant the support which animals give one another in the struggle for existence. As Kropotkin put it in his great book *Mutual Aid,* "If we resort to an indirect test, and ask Nature: 'Who are the fittest: those who are continually at war with each other, or those who support one another?' we at once see that those animals which acquire habits of mutual aid are undoubtedly the fittest. They have more chances to survive, and they attain, in their respective classes, the highest development of intelligence and bodily organization."

These are most important ideas for the reader to grasp, since the principle of the struggle for life has, in the past, been greatly overemphasized,

while the principle of cooperation has been unwarrantably neglected. Natural selection favors the cooperative as opposed to the disoperative struggle for survival. As Burkholder has recently stated, "The most important basis for selection is the ability of associated components to work together harmoniously in the organism and among organisms. All new genetic factors, whether they arise from within by mutation or are incorporated from without by various means, are accepted or rejected according to their cooperation with associated components in the whole aggregation."

The unfortunate habit of thinking in terms of the struggle for existence, by means of which, it is believed, the fittest are alone selected for survival while the weakest are ruthlessly condemned to extinction, is not only an incorrect view of the realities, but is a habit of thought which has done a considerable amount of harm. Only by omitting any reference to such an important evolutionary force as the principle of cooperation, and by viewing evolution as a process of continuous conflict between all living things can man be led to conclude that survival or development depends upon successful aggression. Omitting important facts and basing their arguments on incomplete and false premises the tough Darwinians, but not Darwin himself, could only arrive at false conclusions. In 1944, a group of distinguished biologists resumed the principle of cooperation in the statement that the probability of survival of individual or living things increases with the degree with which they harmoniously adjust themselves to each other and to their environment (Leake, 1945). So far as man is concerned it is particularly necessary to remember as Haldane (1935) has said, that "in so far as it makes for the survival of one's descendants and near relations, altruistic behaviour is a kind of Darwinian fitness, and may be expected to spread as the result of natural selection."

Mutation

Mutation defines the condition in which a particular gene undergoes a permanent change of some sort, resulting in the appearance of a new form of an old character. Mutations of genes for some characters have almost certainly occurred independently at different rates, and have affected different characters. Thus, for example, in one isolate, mutant genes may have appeared and ultimately become scattered throughout the population, as for instance, may have been the case in the original production of "black" skin color among Negroes.

If we assume that "white" was the primitive skin color of man, then in one isolate mutant genes resulting in a brownish skin color may have appeared, while in still another isolate mutation in the direction of a yellowish skin may have occurred, and by subsequent mutation "black" skin may have made its appearance. However, it is possible that these skin colors were already in existence among the earliest groups of man. In this connection it is of interest to note that chimpanzees present some, at least, of the varieties of skin color found among the living groups of *Homo sapiens*. In different geographic races of these animals individuals are encountered that are completely black or brown skinned, and others in which face, hands, and feet, may be black and the remainder of the body white or brown. But nothing like the kind of variability in skin color that occurs in man is encountered in any nonhuman primate. There can, therefore, be little doubt that mutation has played some part in providing the raw materials for the great variety of skin colors seen in man.

Mutation of hair-form genes to yield the present variety of hair form would give a better, and probably more accurate, picture of the manner in which such problems may be discussed and investigated.

Thus a genetically relatively heterogeneous population from which groups have migrated and become isolated from one another, may by random variation in gene frequencies, and the change in the expression of genes themselves, produce new gene combinations which differ from group to group and thus serve to define the differences existing between such groups. This random variation or recombination together with the occurrence of mutation may be considered as the primary or basic conditions for the evolution of all animal forms. That these processes have played such a fundamental role in the evolution of mankind appears to be a justifiable inference from the facts.

Quite as important are those factors which act upon the shifting pattern of the genetic apparatus and influence its course. There are the secondary factors, such as environment, natural selection, hybridization, sexual, and social selection, inbreeding, and so on, factors which have been unremitting in their action upon the primary one, though the character of that action has been very variable.

Here it is principally desired to emphasize the fact that in the character of the action of gene mutation, we have positive evidence that variation is a natural process which is constantly

proceeding in all human groups. But while in man variation brought about by mutation has probably been very great, it has in many discussions too often been permitted to overshadow the variation which has been produced by the action of the secondary factors. Mutations not anthropologically significant occur frequently in man. It is also probable that over long stretches of time more significant mutations occur in one or another human group. But where we know so little the concept of mutation must be used with extreme caution, for it is one which is readily abused, since almost everything can be "explained" by an appeal to mutation.

It should be clear that while mutation presents the raw materials of evolution it does not tell us how that evolution comes about. We know that mutations occur, the real problem is to discover how they (the mutant genes) become differentially distributed, increasing in one group and not in another. If we find that skin color in man has largely arisen as the result of mutation it still remains necessary to explain why some skin colors became localized as, for example, white in Europe, yellowish in a large part of Asia, and black in Africa. Kinky hair, like most other characters, is due to the interaction of several genes (no one knows how many). In order to become established in a population there must be some agent which brings the mutants together and thus ensures their perpetuation. What this agent is we do not know, though it may be strongly suspected that it is selection of some sort.

Bearing these facts in mind, it may then be safely said that some of the physical differences existing between the living varieties of man probably represent the end effects of small gene mutations fitting harmoniously into gene systems which remain relatively unaltered. It is unlikely that the number of genes involved in these differences exceeds more than a very small proportion of the total number carried by each member of the group.

Persons in whom such mutations occurred—for mutations occur in individuals, not in groups—would have to reproduce if the mutation is to survive. Now, an important point to grasp here is that early populations of man consisted of very small breeding groups, much as among the food-gathering and hunting non-literate peoples of today. In such small groups a mutation, if it possessed some selective advantage, could establish itself very rapidly, in the course of several generations. Such a mutation might become distributed through the whole or only through a portion of the population. In the former case, we would have an isolate distinguished by a unique character for which every member was homozygous; in the latter case we would have a situation ready for the further operation of selective factors. Through the agency of limiting factors or social selection those possessing the mutant character gradually become separated from those not characterized by it, and a new group buds off, as it were, from the old, to form a more or less distinct geographic race. This we know to occur in all other forms of life which have been studied, and there is no reason to believe that the same processes have not occurred in the case of man, though definite evidence for this is wanting.

In environments where life is not easy, and the struggle for survival determines the maintenance of small bands rather than large ones, such budding-off of isolates is a perfectly natural process.

Isolation

By isolation is here meant the separation of a group from all other groups of the same species, so that breeding takes place largely or entirely within the isolate. Under such conditions small breeding groups may tend to become relatively more uniform; the genes tend to become evenly distributed, and the process thus defined becomes temporarily genetically stable, and a type of man distinguishable, in some one or more characters, from all others may thus become established. That isolation is a cause of differentiation has already been remarked. "This" as Julian Huxley says "is due to the nature of the evolutionary process, which proceeds by the presentation of numerous small mutative steps, and by the subsequent incorporation of some of them in the constitution by selection, or in some cases by Sewall Wright's 'drift.' The improbability of the mutative steps being identical in two isolated groups, even if they be pursuing parallel evolution, is enormously high" (1942), hence the fact that no two isolates are ever alike.

It is in this manner that geographically or otherwise isolated groups have doubtless been the source of novel types of mankind, but it should not be supposed that any group of man has ever been completely isolated throughout the whole course of its history. Here, of course, the element of time enters. There can be little doubt that some groups of man have, in the course of their history, been isolated for considerable periods of time, but sooner or later contact is generally established with some other group, and interbreeding occurs. The introduction of new genes for a time produces

a certain amount of heterozygosity, and results in a greater variability of the group. If, after such intermixture, the group continues to breed in isolation, the genes are distributed within the population and the latter once more returns to genetic equilibrium. The group will now be different in genotype (in the type of its genes, i.e., in its heredity), and may or may not be different in the appearance of its members, in its phenotype. Whether the group will show any phenotypical difference among its members will depend upon the numbers involved in the original crossings, and upon the characters possessed by each of the mating groups, as well as upon whether marriage is random or otherwise with respect to certain traits.

Genetic Drift

It has already been pointed out that throughout the greater part of his history the numbers entering into the constitution of the various breeding populations of man appear to have been very small. Peoples at the lower hunter stage of cultural development at the present day rarely if ever attain a breeding population size of 1,000. According to Krzywicki's survey (1934) tribes numbering more than 500 individuals were a rarity among the Australian aborigines. Such tribes were at least reproductively partially separated from other tribes.

In such partially isolated populations another factor comes into play. This is the 'accident' of the *breeding structure* of small populations which renders it possible for particular mutant genes or gene combinations to survive. Under such conditions genes for traits which are 'neutral,' that is, which possess neither a positive nor a negative adaptive value, may spread throughout the particular population. The blood groups probably represent such neutral traits. The smaller the population and the more isolated it is the more likely is it that a mutation will become fixed in all its members and its normal allele lost. On the other hand the mutant gene may be completely extinguished, and the mutation wholly disappear.

This accidental increase or decline of mutant genes, resulting in spontaneous random variations in gene frequencies, has been termed *genetic drift* or the Sewall Wright effect. As a result of genetic drift populations commencing with similar genetic structure when more or less isolated from one another, even though they continue to live under similar environmental conditions, will in the course of time come to exhibit certain differences. In this way the accident of genetic drift may produce non-adaptive divergence. Given the inherent variability of the genic system the determining factor in genetic drift is isolation. Isolation may then be regarded as in itself a cause of evolution.

Random local differentiation as a consequence of genetic drift has undoubtedly played an important role in the evolution of man, but on the whole not nearly as important a role as natural selection, for it seems certain that most of the characters of the geographic races of man have some adantive value.

An index of the amount of random differentiation in a species for a single approximately neutral or non-adaptive gene is given by its frequency distributions in the various populations of the species, as, for example, in the blood groups.

In less isolated larger populations genetic drift is of limited importance, owing to the more extended and intensive opposed action of selection.

Hybridization

By hybridization is understood the crossing of individuals differing from one another in one or more genes or characters.

Two kinds of hybridization may be distinguished, (a) the sexual process in general which produces gene recombinations which serve as raw material for selection, genetic drift, etc., this is generally referred to as Mendelian recombination, and (b) intercrossing of distinct populations. Both types of hybridization have played important roles in the evolution of mankind.

Hybridization between populations leads towards the disappearance of racial distinctness, except insofar as it produces intermediate racial groups on geographic boundaries, or within a larger population. It is precisely such intermediate groups which under conditions of geographic or social isolation will develop as geographic races. In short, two of the most important processes in the evolution and diversification of mankind have undoubtedly been isolation and hybridization followed by isolation. This is likewise true of most living organisms. It is to a very considerable extent through hybridization that the whole great process of phenotypical change occurs. When two groups of somewhat different genotypes mix, there is an exchange of genes to form completely new combinations or systems of gene pairs. Numerous dominant genes for which the other parent is recessive are supplied to the hybrid, so that characters or qualities which would not normally be expressed appear, and establish themselves. It is to this kind of rearrangement of genes,

to heterosis, that the phenomenon of hybrid vigor is believed to be due, that is, the condition, as a result of hybridization, in which the offspring exceed both parents in size, fecundity, resistance or other adaptive qualities. In the history of man's progress hybrid vigor probably played an important role in infusing new strength into long isolated groups, and in enabling them to adapt themselves to changes in environment.

When it is stated that hybridization is an important process in the diversification of mankind, it should also be obvious that it is one of the most important processes in the unification of mankind, for hybridization always leads to a union of the characters of the hybridizing populations in the resulting hybrid population, and to intrapopulational variation. It is only when a newly formed hybrid group becomes isolated that the new pattern of genes is able to establish itself as in some respects a unique population.

The American Negro is an example of the simultaneous differential action of both processes. On the one hand social barriers effectively limit his biological participation in the reproductive structure of the white population, and on the other hand a relatively small number of individuals of Negroid ancestry are continually trickling into the ranks of the white population. That it is no more than a trickle is largely a consequence of the asymmetric sexual relations which prevail between the two groups, the only relationship (covertly) allowed being between white men and Negro women.

By hybridization there is not simply produced a mixture of genes between different populations, but what is vastly more important the new combinations of genes thus produced expresses itself in a new pattern, something so significantly unlike anything which has appeared before as to justify being called a new type. The American Negroes, for example, exhibit a number of such new types, and such types are also to be seen in the numerous offspring of crosses in Hawaii and elsewhere in the world. To keep to the example of the American Negroes, there are three possible ways in which the African Negroes introduced into America might have produced a new ethnic group or groups: (1) by being freely permitted to marry with members of the white population, so that all differences between Negro and white would eventually have been completely eliminated through the more or less equal distribution of their genes throughout the population, with the resultant emergence of a new Negro-white ethnic group; (2) by white men mixing with Negro women, which has almost wholly been the case in America, so that while the white population remained relatively unchanged, the Negro population underwent modification in the direction of the white type; and, (3) by segregation of the mixed individuals as a separate breeding isolate from the relatively unmixed Negro population.

It is quite probable that in the evolution of the geographic races of man such processes have been more or less continuously at work. Factors such as sexual and social selection may have played a more or less consequential part in the evolution of the varying types of man, the tendency in the past, however, has been for many biologists to overemphasize the importance of the first factor and to neglect the second.

Sexual Selection

By sexual selection is meant the process of selecting mates on the basis of a preferred standard of beauty or other desirable quality, so that in the course of time the sexually preferred type would become the dominant one in the group, and perhaps cause the non-preferred type to become a separate isolate, or even to die out.

For example, in a group in which kinky hair was preferred to straight hair, the straight-haired individuals would find fewer and fewer mates, until the gene for straight hair ceased to exist altogether, or the kinky-haired would mate with kinky-haired, and straight-haired with straight-haired, and thus two distinct types would be formed. The preference of dark Negro males for lighter females in America is an illustration of the manner in which sexual selection operates to maintain the phenotypic variability of the Negro skin. The preference of brunets of one sex for blonds of the other, and vice versa, is an illustration of how sexual selection serves to maintain a balanced distribution of such types. Since the differentiation of human groups could, at least in part, be brought about through the sexual selection of traits possessing no survival value, that is, no adaptive value, this is a possible factor to be considered in any discussion of the evolution of man. It is, however, difficult, if not impossible, to evaluate the part that sexual selection has played in the history of man's evolution. When we turn to non-literate societies for enlightenment upon this point we find that in such societies everyone usually marries, and there is little or no evidence of sexual selection. It is unlikely that conditions were otherwise in early human populations, and a doubt may legitimately be expressed as to its importance in the past. In the recent period, however, there can be

no doubt that sexual selection has played an important role, nor can there be any doubt that it will continue to do so in the future.

Social Selection

By social selection is meant the regulation of breeding by artificially instituted barriers between socially discriminated individuals or groups within a population, so that mating occurs between individuals preferred by such social standards, rather than at random. Under such conditions strong isolating mechanisms are developed which, in the course of time, may produce considerable modifications in a population. Where, as in America, there are a variety of colored populations, black, brown, and yellow, social barriers more or less successfully tend to keep these groups separate from one another and from the white population. In this way such barriers act as isolating mechanisms akin to natural physiographic isolating factors, which have a similar effect in maintaining the genetic differences between isolated groups.

We may suggest, then, in broad outline, the means by which the evolution of human groups has occurred. Commencing with a single genetically relatively heterogeneous population from which small groups have separated and become more or less isolated from one another, it is possible to conceive how by the action of selection and intrinsic changes in the character of genes and their action (mutation) new combinations of genes may be preserved and distributed throughout a group and thus serve to differentiate it from others. The selection may be either natural, social, or sexual, or any combination of these. As in all other animal groups we may suspect that natural selection has played the most significant role in the differentiation of mankind. Our suspicion needs critical observations to support it. These are, at present, lacking. They must be gathered. Studies must be instituted to determine the adaptive value of certain traits. Skin color is one of the most obvious of such traits. What is the adaptive value of the different skin colors under different environmental conditions? Temperature, ultra-violet radiation, humidity, and aridity? To what environmental conditions is each skin color best adapted?

It has been said that the broad-cheeked faces of the Mongoloids living in the high steppe lands of Asia are well padded with fat. Whether this is so, in fact, remains to be determined. It has, however, been suggested that such a face is very well adapted to tolerate the strong cold winds which blow in these regions. This is an example of the kind of problem which abounds in anthropology, and which for the want of the necessary facilities for research goes begging. The application of thermocouples to the cheek regions of representative samples of Mongoloids and non-Mongoloids ought to be sufficient to tell us whether the Mongoloid face is more likely to be resistant to windy insults than the non-Mongoloid.

Brachycephaly, in some populations at any rate, seems to have some adaptive advantage over dolichocephaly. But what this advantage may be future research alone can tell us. With a progressive increase in stature, there has been a progressive tendency to maintain the infantile headform in the adult at a cephalic index of about 81.0 (Abbie, 1947).

Skin color, head form, face form, eye color, hair color, hair form, and nose form, are a few of the more obvious traits the adaptive value of which has yet to be determined. Until this has been done it will not be possible to arrive at a clear understanding of the manner in which these traits have been evolved.

In addition to natural selection and mutation another important evolutionary factor is that of genetic drift or the random variation in gene frequencies which tend to occur in partially isolated small populations. In such populations this process is essentially complementary to the action of natural selection, and hence may result in the establishment of non-adaptive gene combinations. It has already been remarked that the frequency distributions of the blood groups give every indication of having been produced in this way. It is likely that other traits have been established in the same manner. Studies in the size of prehistoric populations, populations being understood to be breeding units, and in the demography of living nonliterate peoples are therefore very necessary. The demographic number and the genetically effective population are not the same things. The latter, the breeding unit, is always smaller. In dealing with man at any stage of cultural development it is generally observed that demographically a hierarchy of populations obtains. Some being larger than others, occupying larger territories, and some being more effectively isolated, so that exchanges of genes between populations, as well as accidental gene losses, may vary considerably in rate, number, and kind. The isolating barriers may be geographic, sheer distance, or social. These are matters which call for more detailed study than they have yet received. We have good evidence that the breeding populations of man in prehistoric times were

small, rarely if ever exceeding one thousand individuals. For example, it has been estimated that the population of England and Wales in the latter part of the Old Stone Age was not more than a few hundred individuals (Fleure, 1945). Occasionally we have direct evidence of hybridization between diverse populations such as the paleoanthropic Neanderthaloids and the neanthropic types of Mount Carmel. For the rest basic data are wanting and are urgently in need of collection.

Hybridization can easily be overemphasized as a factor in the evolution of man, but it can also be underemphasized. The problem in which we are primarily interested is to discover how the diversity of races arose in the first place. When we speak of hybridization between races we thereby state that this diversity already exists. It tells us nothing concerning the process of initial diversification. Hybridization, however, can be evoked to explain partially, at least, the origin, of some intermediate types which may eventually become distinct races. On the other hand, there is always the possibility that the intermediate types arose by the same mechanisms as the parent types. Clearly, then, the concept of hybridization is one which must be used with great caution, since by its misuse it becomes a simple matter to create all sorts of so-called "secondary races" out of "primary races."

There can be little doubt that hybridization has played an important role in the evolution of man, but the extent of that role is a problem which calls for the kind of investigation which has scarcely yet been undertaken. The fact that in the course of man's history intersterile species have not developed would strongly suggest that hybridization between geographic races of man has been the rule. The divergent variability encountered in mankind as a whole would thus be due to the ensuing simple gene recombinations. This crossing and criss-crossing of human races has been visualized as a reticulum or network, and has been called reticulate evolution. As Huxley points out, man's history of progressively increasing "migration and crossing has led to a progressive increase of general variability.

"Man is the only organism to have exploited this method of evolution and variation to an extreme degree, so that a new dominant type in evolution has come to be represented by a single world-wide species instead of showing an adaptive radiation into many intersterile species. Doubtless this is due to his great tendency to individual, group, and mass migration of an irregular nature, coupled with his mental adaptability which enables him to effect cross-mating quite readily in face of differences in colour, appearance, and behaviour which would act as efficient barriers in the case of more instinctive organisms" (1942).

The whole problem of sexual selection as a factor in the evolution of prehistoric populations remains uninvestigated. It has been indicated that there is good reason to believe that its role has probably been overestimated.

In short, much fundamental work needs to be done before we shall understand the mechanism of ethnic differentiation. The little, however, that we know of man's evolutionary history appears to conform to the conclusion established by Sewall Wright that the potentialities for rapid evolution are greatest in a large species which is separated into partially isolated groups. Such partial discontinuities favors diversity by local adaptation and also by genetic drift and the establishment of non-adaptive combinations. The fact that the discontinuities or isolates are only partially so renders considerable the variance of the total diversity potentially available to the species as a whole (1933).

Increase in the availability of this variance has proceeded at an increasingly more rapid rate within the historic period. Dobzhansky (1944) has pointed out that the merging in the human species of small population groups in a more or less freely interbreeding whole may be regarded as one of the most important of recent evolutionary events. This process today is being markedly accelerated by the increasing facility of contact between populations or segments thereof.

As the evidence accumulates the distinctive differences between "genera" and "species" of fossil man become less and less marked, just as they do for non-human primates. We begin to suspect that all known forms of man, fossil and living, existing at any one time level belong to a single polytypic species.

A polytypic species has been defined as a group of actually or potentially interbreeding natural populations which is reproductively isolated from other such groups. The actual or potential interbreeding populations are usually more or less separated by geographic barriers, so that an appreciable amount of geographic variation in characters is encountered. Such populations are the polytypes, subspecies, or geographic races which together comprise the species.

Quite clearly the whole of mankind comprises a single polytypic species consisting of a large number of geographic races. Exact knowledge con-

cerning the number of human geographic races, their distribution, and rate of gene exchanges between them, is virtually completely wanting. The data which will lead to such exact knowledge remain to be collected.

The racial variability which mankind exhibits is of the kind which in a large number of other animal groups is known to be peculiar to small geographically partially isolated populations. Groups or populations which do not occur together, which exclude each other geographically, are termed *allopatric*. Populations which occur together, whose areas of distribution overlap or coincide, are termed *sympatric*. Man is essentially a member of a sympatric polytypic species. Partial reproductive separation of small populations maintained by geographic barriers are necessary conditions in the production of the observed differences. As Dobzhansky (1944) says, "Racial differences cannot persist if races come to inhabit the same territory, for in such a case the races, lacking reproductive isolation, would exchange genes, the differences between them would gradually be erased, and finally they would fuse into a single variable population." Now that the world has, indeed, become "the same territory" the amalgamation of all varieties of man into a single variable population is but a matter of time. If, then, we are to understand the manner in which these geographic races came into being before this process is completed we cannot too long delay the initiation of the necessary investigations.

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DISCUSSION

ANGEL: We must be careful not to stretch the use of ethnic group beyond the wide number of meanings which it already has, and which do not cover the concept of race as physical anthropologists use it. An ethnic group may include a majority of immigrant and unrelated individuals from diverse biological origins.

MONTAGU: I quite agree with Dr. Angel. But I should like to point out that the phrase "ethnic group" is a noncommittal one. It is a "suspense account" phrase. Whether the persons comprising the group are related or unrelated, it says, is a question demanding solution. The answer cannot be taken for granted. When the term "race" is uncritically used most of the answers are taken for granted. And that is what ought to be discouraged. What we ought to encourage is the asking of questions, and I am suggesting that by the use of the phrase "ethnic group" this is more likely to occur.

BRITTON: Is there any really good reason for throwing overboard the term "race"? Misnomers creep into every branch of science, but are often retained for their historical or other value. In medicine the term anoxia does not really signify without oxygen, the word asphyxia without pulse; yet these are retained in medical usage.

MONTAGU: There is no reason to jettison any term merely because it does not accurately describe the facts. In medicine and science there are many such terms, but they are usually emotionally neutral. The term "race" in popular usage is emotionally heavily loaded and full not only of unsound but of dangerous meanings. It is in the name of "race" that millions of human beings have been murdered and millions of others are held in degradation. I suggest that the phrase "ethnic group" is not a mere substitution of one term for another, but that it introduces a new conception to the layman by means of which it becomes possible to assist him to understand what scientists mean when they use the term

race. Because man is uniquely the *cultural* animal, it may be suggested that the phrase "ethnic group" is a uniquely appropriate phrase by which to describe his sub-divisional groupings. The phrase ethnic group embraces the term race in its strictly scientific meaning, and is also available for use in connection with groups not quite so easily definable. When a term, such as "race," as it has been customarily used by the layman has done as much human and social damage, as has the term "race" it seems to me that the term itself constitutes the greatest impediment to getting the layman to understand what the scientist means when he uses it.

COUNT: Dr. Montagu presents two things: the proposal that we substitute the term "ethnic group" for "race" by making the former exactly synonymous with the latter by fiat; and a statement of his conception of what a race is.

The first proposition must be settled in terms of expediency. Unless it is preceded by a satisfactory clarification of what race is, I confess I fail to see the relevancy of its being discussed in a symposium devoted to the problems of the origin and evolution of man; it seems to me, that is, a not particularly relevant digression from the topic at hand; therefore I shall not debate it. On the other hand, his definition or description of "ethnic group" is relevant. Unfortunately, however, the definition does not, as far as I understand it, lend itself to being synonymized with "race." That is not to say, of course, that the concept of an "ethnic group" would not be useful in its own right.

It would be more relevant and profitable, I believe, in this particular symposium, to thresh out the concept of race itself before proceeding to the more strictly and narrower semantic matter. In the sense used by the older taxonomists, we should no longer speak of "defining" a race at all. To "define" means to delimit, to draw a boundary around. Today we know how fruitless it is to select a list of traits and assign to a race so defined all individuals who meet those specifications, while excluding all others who do not. As a matter of logic, this procedure originated as an inductive method of discovering what "race" itself is, but repeatedly, at some subtle point in the procedure, it has turned deductive, and immediately has become sterile.

No matter how we may redefine the concept of race today, we still have to start with taxonomy; with the phenotype; with what we can see. Thereupon, however, we find that human genetics is still far from the point where it can underwrite any traits of man that are definitely diagnostic of any race. (This is true even of blondism.) But I think we can nevertheless go so far as to theorize that a race is to be thought of as a sort of polarization or focalization of genetically transmissible traits. This would mean that, even without geographic migration and hybridization, we should find a population in which a portion of it manifests most intensively the processes of mutation which are differentiating out the given "race"; while more marginally there are individuals who are no less a part of the same population, as far as ancestry goes, than the most diagnostic of the individuals in it, yet who are less mutant.

This population may be contiguous to another or to several others, in which like processes are going on; and between any two populations there will be transitions *but no actual boundaries*. (This may be read in a geographic sense or in only a sense of genetic populations, as one pleases.) This set of possibilities complicates, to be sure, any diagnosis of an individual; for we now are forced to distinguish in any atypy those cases which manifestly are the result of hybridization and those which are more "pure-bred" but are (to borrow Keith's term) demonstrations that their race is not yet pandiacritical (if it ever will be).

As of the mid-twentieth century, we seem to be on the horns of a dilemma. Races undoubtedly exist, even if only a very few individuals in this world belong to no more than one of them. Races are genetically determined, yet we cannot place our fingers on any single phenotypic trait which is exclusively diagnostic of some particular race; still less can we make even a tolerably complete list of the traits which together are diagnostic of race. And yet, we must go on studying man and his races; the taxonomist cannot go into a state of suspended animation until the geneticist has finished his work. He must still continue to work with phenotypes—and hope that his most careful judgments will some day be justified by the geneticist. The sooner, of course, the happier. He will also be quite ready to revise his evaluations, and even discard them, in the light of genetic findings.

MONTAGU: I think that Dr. Count has made some excellent points. I should, however, like to point out that no attempt has been made to synonymise the phrase "ethnic group" with the term "race." It is a misunderstanding to assume that the phrase "ethnic group" has been suggested as either a synonym or a substitute for the

term "race." I am merely suggesting that, where there is no doubt, we continue to use the term "race," but that where there is any doubt whatever we, as scientists, use the phrase "ethnic group." And I am suggesting that in popular usage it were better that the term "race" be dropped altogether, because it has, as it were, been so badly compromised, and because, as Korzybski has pointed out, terms which are confusedly used make for misunderstanding. The phrase "ethnic group" represents a concept which differs from what is implied in the term "race." It is a concept which implies that groups of men exist, but that we know very little about them; that we should like to find out what we can, and that possibly we might find that some of them actually are races in the scientist's understanding of that term, and that some of them are not. In other words "ethnic group" is the phrase which hangs a question mark upon the problem which those who customarily use the word "race" take it for granted has been solved. "Verbal habits," as Ogden and Richards have remarked "overpower the sense of actuality even in the best of philosophers."

MAYR: More important than the terminology is the concept of race. Race like other taxonomic categories was formerly typologically defined and all the insidious implications of the popular concept of race are associated with the typological race concept. It implies that every individual of a race conforms to the "type" of that race and that the characters of such an individual are therefore, "predictable." This is false concept. Like other taxonomic categories, race is now defined statistically, as a population or group of populations. The obliteration of racism depends on the popular acceptance of this new race concept.

MONTAGU: I'm afraid that the elimination of racism will depend on much more than the popular acceptance of the statistical conception of race. Before we ever reach that desirable condition of acceptance much spade-work will have to be done, many questions raised in the minds of those who bandy the word "race" so freely today. As a question-raising device calculated to secure the end which Dr. Mayr has in view, I am suggesting that the phrase "ethnic group" is worthy of serious consideration. Once you get people asking "What do you mean by 'ethnic group'"? you've made, in my opinion, great progress, for everyone, of course, knows, or rather takes for granted that he knows, what is meant by "race." We want to teach people the truth about what they understand about race. To show them where their beliefs depart from the truth, and if you can get any term to raise the question rather than obscure it, I believe you are making a contribution toward the elimination of racism, and meeting the problem much more efficiently head-on, than by continuing to use the compromised word "race."

ANTHROPCLOGICAL MAPS OF THE NORDIC COUNTRIES

BERTIL LUNDMAN

University of Uppsala, Uppsala, Sweden

I would like to say something about the anthropology of the nordic countries. Anthropologically, these countries are probably the best known in the world; furthermore, because of their history and geographical location, there is relatively little mixture, and therefore their racial conditions are of considerable general biogeographical interest.

The various nordic countries and peoples, however, have not all been studied with equal thoroughness. Norway has been investigated most thoroughly, Sweden and Esthonia almost as well, and Denmark least. I will summarize briefly the most important investigations made in the different countries.

In Sweden, four annual classes of soldiers have been measured: 1897-98 (Fürst and Retzius, 1902) and 1922-23 (Linders and Lundborg, 1926). Furthermore about 15,000 persons in Central Sweden have been measured by myself (most of this material was published in the paper of Lundman, 1945).

In Norway, an annual class of soldiers was studied in 1921 (Bryn and K. E. Schreiner, 1929); and several others were studied in northern Norway around 1920 (A. Schreiner, 1929). Earlier, beginning around 1879, investigations were made by Arbo, then Larsen, and lastly Bryn—mostly of soldiers (see Bryn, 1929).

For Denmark, only some less extensive studies are available, most of them published in the *Meddelelser om Danmarks Antropologi* (Copenhagen, 1907—).

In Finland, Westerlund studied 5,000 soldiers in 1899-1900 (Westerlund, 1900, 1902). Measurements are also available for 8,000 adults of both sexes, taken in 1930 by the Finnische Akademie der Wissenschaften. The best bibliography of published works to date is found in Löfgren (1937). A comprehensive survey of the entire country is still lacking.

In Esthonia, a considerable amount of work was done by Aul from 1930 to 1939, of which brief reviews were published (Aul, 1936). Latvia also has been investigated (Backman, 1937), but no extensive surveys have been published. Finally, the Lapps have been described by several explorers (short summary in Lundman, 1946b), but here also we lack a more detailed anthropological survey.

For the territory as a whole there are only two short papers in Swedish (Lundman, 1940a, 1946a), of which the latter is the more technical and contains a lengthy bibliography. Scheidt's studies contain additional material but do not include Finland and the Baltic countries (Scheidt, 1930).

From the data at my disposal I have prepared several maps. It is not easy to combine the material of different investigators into a unified report, since the anthropometrical methods and the division of localities followed by different authors are not always identical, and in the older publications even the statistical methods are sometimes not reliable. These earlier studies cannot be overlooked, however, because they often reflect the older and more original conditions. In addition, long-term changes in the geno- and phenotypes of the various populations can sometimes make the situation more complicated. On the whole, however, the findings of the different authors agree very well.

Figure 1, summarizing the data on stature, is based on observations made on over a million men, since in this case extensive military statistics could be utilized. In our territory average height has increased 7–8 cm. during the last century (Lundman, 1940b); but the differences between the districts have remained practically the same, and show scarcely any correlation with the differing economical conditions. It is evident that the stature is greater in Scandinavia than in the bordering countries, but that the interior of Scandinavia shows somewhat smaller statures than the outlying districts of the peninsula. A very definite boundary line runs across the economically and geographically unified Finnish lake-plateau.

Figure 2, which presents the data on cephalic index based on material from over 180,000 persons, shows a lower index, with practically no exceptions, in Scandinavia than in the bordering countries. Again in this case, the interior of Finland is fairly uniform. Unfortunately, the data available for Denmark are very meager.

For the distribution of eye colors, extensive data are available for all the Scandinavian

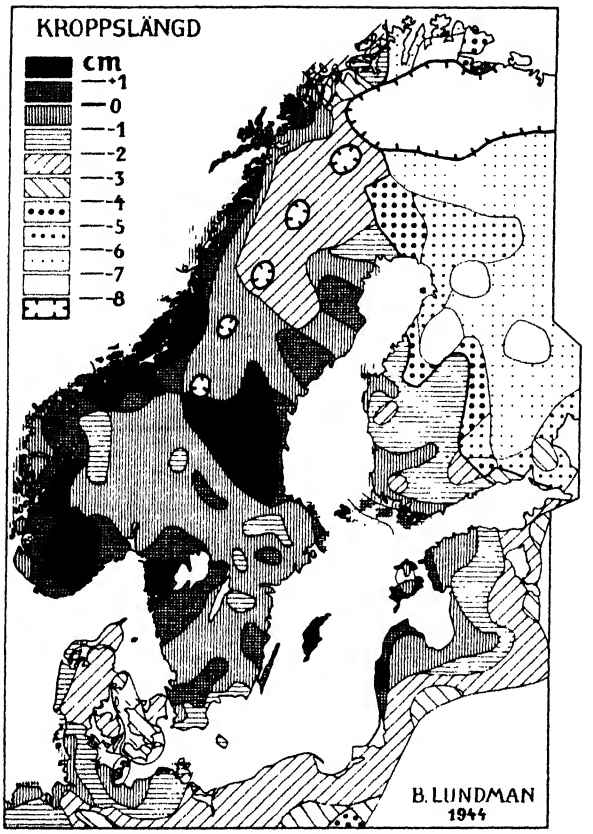

FIG. 1. Stature of adult men. From Lundman, 1945.

countries. The material is shown in Figure 3, where 100 per cent stands for light eye color. This material is sometimes misleading, however, since percentages are based on the distribution of colors rather than on the averages of intensities, the error being relatively large for small numbers of brown eyes. Moreover, in many places these investigations were made without color charts. Although Sweden and Norway are the most extreme in percentage of light eye color, there are a few small islands in the interior where the proportion of darker color is relatively high. All of Finland on the other hand, appears to be very uniform.

In addition, I have prepared two other maps (Figs. 4 and 5), one on the vertical index of the head and one on the percentage of the blood-group gene *q*. These cover the entire continent, since the material from our region is frequently inadequate and up until now Europe as a whole has practically never been mapped. On both maps, Scandinavia is fairly uniform, with a sharp boundary running through the Baltic Sea. The groups of Lapps, which are here of little interest to us, show very peculiar proportions: east-European high skulls in the south and low skulls in the northeast, even though the blood-group distribution is Scandinavian in the south and east-European in the northeast.

The material for other racial characteristics—for example, face and nasal form—is not sufficiently comparable to be mapped for our entire region.

In considering the results of the three first maps, we find a clear confirmation of the old opinion that in Scandinavia (with the exception of some littoral districts) we encounter the tall, dolichocephalic, and blond northern race in its greatest purity. A similar comparison has already been made by De Geer, although he based his study on less extensive and less reliable material (De Geer, 1926, 1928). This region is girded by almost converging isorithms for a stature that lies 1 cm. below the Scandinavian mean, a cephalic index of 80.0, and 7 per cent brown eyes (Fig. 6). A few insignificant enclaves and exclaves do not change the general picture. Of these, the largest exclave—that for lighter eyes in Friesland and Schleswig-Holstein—is indicated on Figure 6.

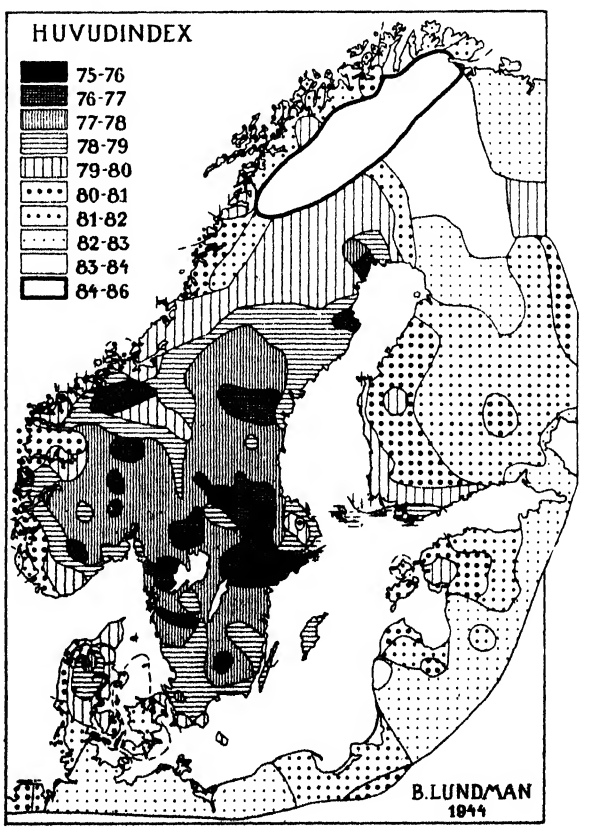

FIG. 2. Cephalic index (men). From Lundman, 1945.

As already mentioned, east of the Baltic Sea the cephalic index and percentage of *q* rise, and stature and heads become shorter simultaneously, but the eye colors remain almost as light. This is the territory of the east-Europid (or east-Baltic) race, which, because of their very different stature, I have divided into two subraces, namely, the Tawastid (or west-Finnish) in the west and the Savolaxid (or east-Finnish) in the east.

The gradually diminishing stature, increasing brachycephaly, and greater number of brown eyes toward the southwest (together with constancy in brachycrania and very low percentage of *q*)

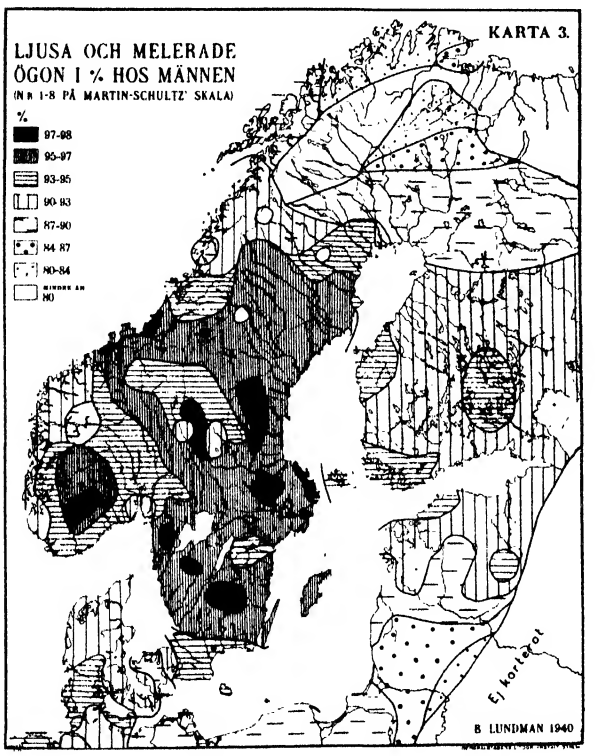

FIG. 3. Color of eyes (men). 100% = light eye color. From Lundman, 1940b.

are due principally to an "infiltration" of the Middle European Alpine race, which, however, hardly becomes strong enough in our district to show dominance anywhere. In order to make this clearer, I have drawn a schematic diagram (Figure 8) across central Scandinavia and Finland. This requires no explanation.

Disregarding the Lapps, because they have no special interest for us here, we have only to explain the islands of darker eye color in the interior of Scandinavia, shown on Figure 3. For the other racial characteristics considered here, the pres-

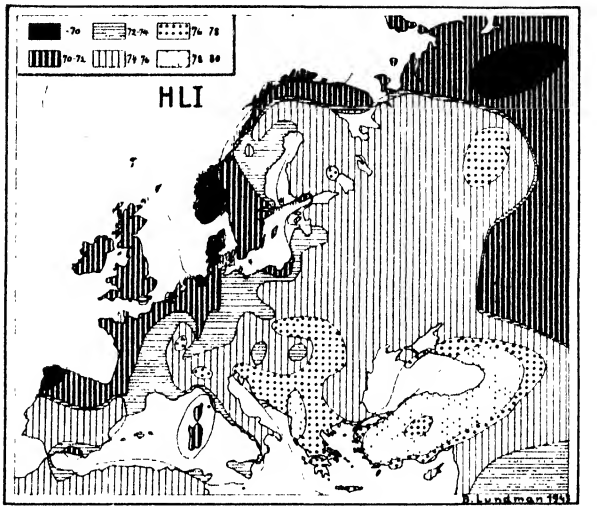

FIG. 4. Vertical index of skull. From Lundman, 1943.

ence of such islands is not indicated. If these regions had not been investigated thoroughly, this apparently isolated occurrence of somewhat greater incidence of brown eyes (approximately 12 per cent as compared with 3 per cent in the surrounding area) might be questioned. Local investigations (Lundman, 1945) show, however, that, among other things, face and nose are much broader here, and the hair is darker. These traits date back to relicts of the ancient paleoatlantid race—in other words, to one still strongly cromagnoid pre-stage of several present west-European races, among others the northern race (Lundman, 1949).

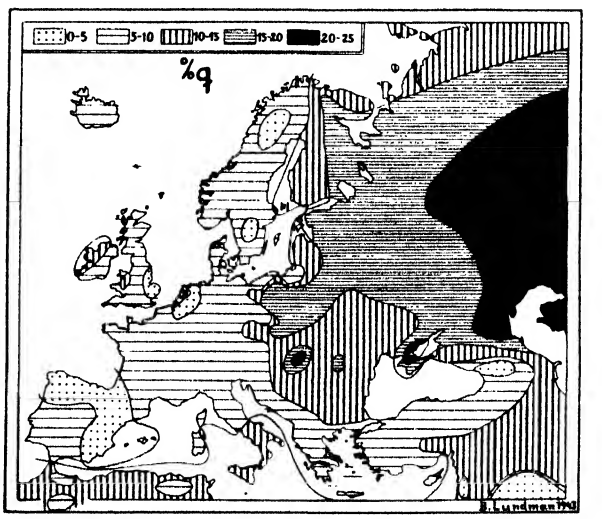

FIG. 5. Blood-group allele *q*. From Lundman, 1943.

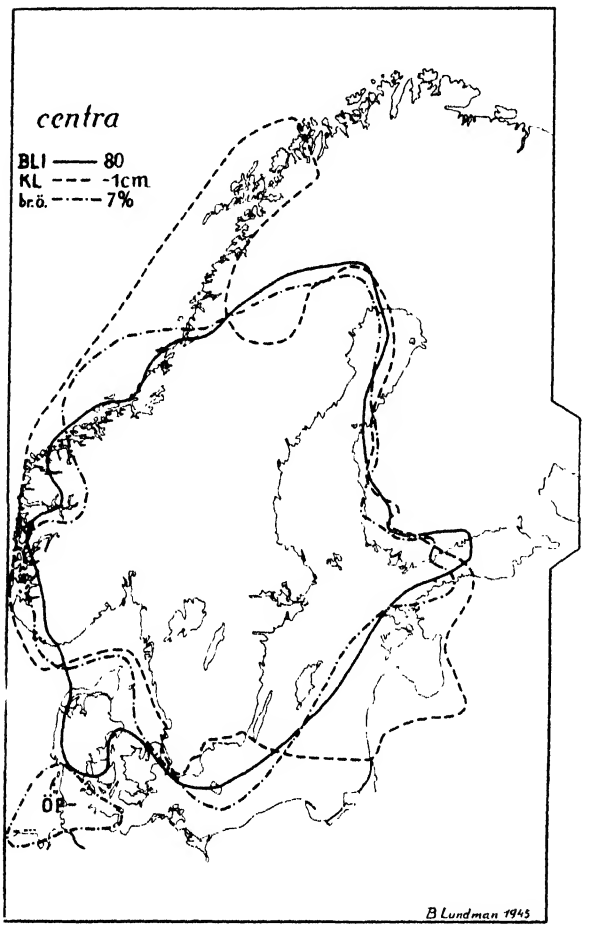

FIG. 6. Nucleus of northern race. Within the lines, the cephalic index (BLI) is under 80, stature (KL) is less than 1 cm. under the Swedish-Norwegian mean, and brown eyes are less than 7% (i.e., light and mixed eyes more than 93%). From Lundman, 1946a.

The lesser contrasts in stature in central Scandinavia may be considered as various subgroups or stocks of the northern race (less dissimilar than those in Finland), from southwest to northeast: the southwest Scandinavian (which is rather polymorphic, however, with the aforementioned "alpine tendencies" in certain outlying districts); the central Scandinavian; and the Troendic (this last stock more mixed in the north). This assumption is supported by observation of the regionally varying incidence of smaller differences (not noted here) in hair and eye color, form of face, etc. Unfortunately, it is difficult to establish these entirely objectively.

Thus we see how from a fair degree of stability has developed a situation similar to what is found in populations of wild animals and plants. Deviations from various racial characteristics appear on the graphs in more or less pronounced form, the lines for several characteristics running almost parallel or, again, intersecting one another (see Lundman, 1946a). It is practically impossible to find a relatively large territory that is wholly uniform; but with some degree of subjectivity, a certain classification can be worked out. Consideration of many more characteristics than those here re-

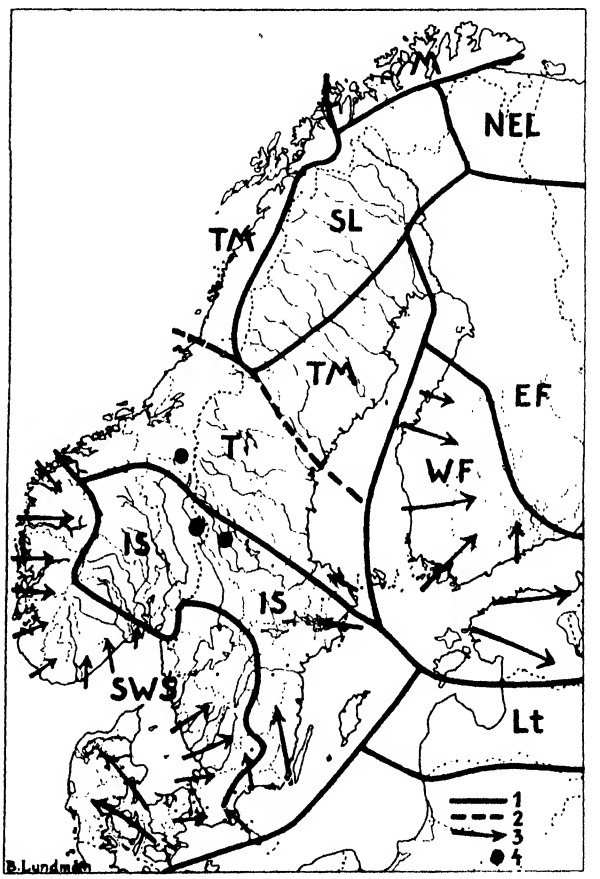

FIG. 7. A few important clines and boundaries in the nordic countries. (Similar maps in Lundman, 1940a and 1946a.) 1 = boundaries of population stocks. 2 = boundaries of their subdivisions. 3 = clines; arrows point toward regions with relatively pure stocks. 4 = stronger infiltration of paleoatlantid race. SWS = southwestern Scandinavian population stock. IS = central Scandinavian stock. T = Troendic; TM = more mixed regions of same. SL = southern Lapps. NEL = northeastern Lapps; M = the population in Norwegian Finnmark, which is strongly mixed with Norwegians, Lapps, and Finns. WF = western Finnish population stock. OF = eastern Finnish population stock. Lt = Latvian population stock.

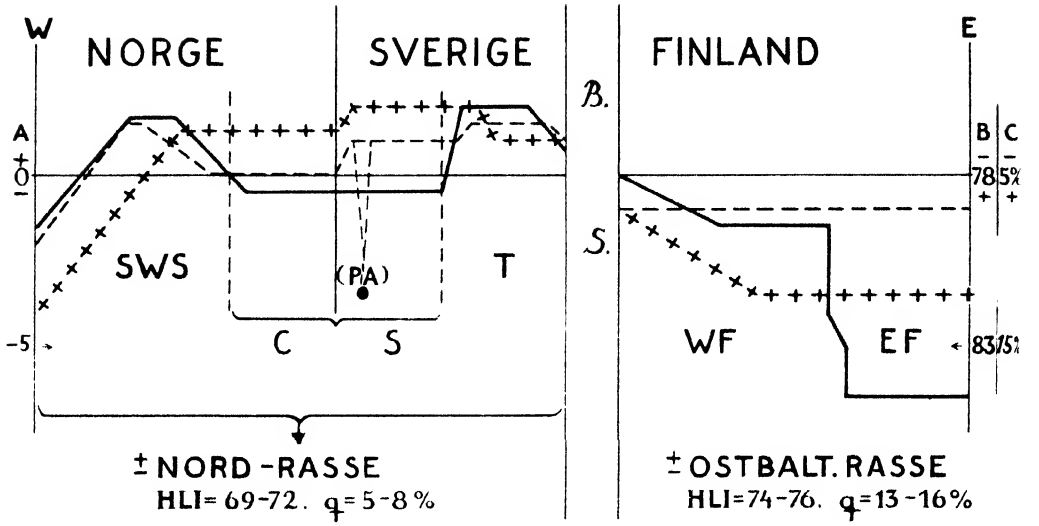

FIG. 8. Schematic diagram across Central Scandinavia and Finland. Thin, horizontal line: baseline for KL (= Scandinavian average, see text; scale at left, A); for BLI (= 78.0; scale at right, B); and for number of brown eyes (= 5%; scale at right, C). The more nordic values are above this line, the less nordic values below; 1 cm. KL = 1 unit BLI = 2% brown eyes. Solid curve = KL. Broken curve = BLI. Crosses = % brown eyes. PA = paleoatlantid enclave. The other abbreviations—SWS, CS, T, etc., indicate the population stocks (see Fig. 7). B. S. between Sweden and Finland = Baltic Sea, Eastern Sea.

corded is of course desirable. Detailed knowledge of hereditary traits would certainly help our interpretation. But a real "hereditary map" for all of Scandinavia still remains very remote, and becomes steadily more difficult because of the continually increasing shifts in populations.

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POPULATION SIZE AND MICROEVOLUTION IN GREECE

J. LAWRENCE ANGEL

Baugh Institute of Anatomy of the Jefferson Medical College, Philadelphia, Pennsylvania

The following chronological study was suggested by the work of Dobzhansky (1941, 1947), Wright (1931, 1948), and others on the genetic (and hence ultimately morphological) effects of fluctuation in size, segmentation, and interchange within a population or reticulum of populations. The present data come from a single small area and cover a span of at least 5,000 years. But they are far from perfect. The samples of each successive batch of generations are too small and too selected by soil conditions and other accidents of preservation. Skeletal materials are influenced by only some of the genes determining morphological and physiological distinctions between groups in recent man and would be a most risky basis for conclusions as to variability and intergroup relationships if not supported by archaeological and historical evidence. We are limited entirely to phenotypes, and breakage makes comparisons uneven even with phenotypic trait frequencies. Because of their rigid artificiality morphological types hardly compensate for this. And, inevitably, there can be no precise knowledge of population size or of factors like age distribution, death rates, differential fertility, mating systems, etc., which affect the size of the breeding population.

But in spite of these limitations we can use much the same sort of broad association between interacting demographic factors as is open to the palaeontologist, only on smaller and more controlled scales of time and space. Huxley, for example (1942, pp. 353–356), stresses the primacy of mixture and recombination in producing variability as a major source of the reticulate kind of evolution important in man. The significance of Huxley's observation on this point is scarcely appreciated at present by social scientists. But the present data appear to fit.

Data for change in population density derive from many findings of archaeologists (cf. Blegen, 1941, and current reports in *Hesperia*, etc.), inferences of historians (Bury, 1913; Larsen, 1938; Tarn, 1930; Tod, 1927), extrapolations from partial censuses (Gomme, 1933; Sargent, 1924), and recent census reports (Epstein, 1944, pp. 988–998; Michalopoulos, 1932, p. 22; Stephanos, 1884, pp. 440–450). From these it is possible to be sure of direction of change (growth or shrinkage) between the rough central points of the periods used. But in spite of modern historians' careful weighing of ancient exaggerations it is impossible to be sure of exact densities or of relative massiveness of migrations.

The area and chronological subdivisions depend on the skeletal material used for microevolution. This consists in 708 adult skulls (70% males), about 200 skeletons, and 37 living males from an area centered around the Isthmus of Corinth, and including Boeotia, Attica, Corinth, Argolis, and adjacent Arcadia. A few skulls from the Ionian islands and from northeastern Greece have been included, but locally specialized series from Submycenaean Cephallenia and from recent monasteries and villages in eastern Thessaly have been excluded. This material was repaired and studied during about 15 months in 1938 and 1949 through the support and help of Harvard University, the Guggenheim Foundation, the Viking Fund, the American School of Classical Studies, Jefferson Medical College, the University Museum, and many people of Greek, American, and other nationality. To all of these I am most grateful.

This 8,000 square mile block of territory generally contained at least a half dozen breeding units, most unified in periods of free sea contact. The geographical and cultural unity at most periods must have approximated that of modern Scandinavia.

Eleven chronological subdivisions are used, approximating 400–500 years, or about 15 generations apiece. By necessity the earliest (from well before 3000 to 2000 B.C.) and the Medieval periods are much longer. The samples are too small and partly too imprecisely dated to allow breakdown into breeding group series and shorter periods. This inclusiveness of the period samples, normal in any study of this sort, adds intra-group variety to inter-group and chronological differences. Hence the breeding units' inner genetic instabilities can be separated only subjectively from the amount of local differentiation. Chronological instability within a period matters only when there is a big change from 15 to 20 generations.

Variability of 18 selected characters can be measured fairly accurately by the Sigma Ratio (Howells, 1941). But heterogeneity, in the sense of mixture in one population of unusually contrasting individuals, can be estimated only subjectively and with the help of artificial morphological groupings or "types." All these reservations are vital, since the purpose of this study is to juxtapose chronologically change in population density and change in variability as well as in average structure. This juxtaposition, against its historical background, is outlined in a period by period summary.

The Neolithic and Early Bronze Age combined sample (N:44) expresses the population of the first settlers. These sedentary farmers and fishermen, with perhaps a few travelling traders, represent two distinct populations of Near Eastern derivation, and probably European Mesolithic, Danubian, and "Corded" Neolithic wanderers who may have followed trade-routes southwards. The first settlements were small and culturally self-contained villages. The dozen skulls of that date suggest marked intergroup differences. But it is possible that like the inhabitants of Neolithic Khirokitia in fourth millennium South Cyprus the people of each Greek Neolithic village may have been low in variability and centered on a homogeneous type. The Early Helladic culture is more uniform. And small samples from near Athens and Corinth show at least a normal range of heterogeneity and differ clearly from each other. Obviously the total variability is raised and would probably remain above normal even if corrected for the extra long time span.

The Middle Bronze Age starts with destruction of Early Bronze Age sites at about 2000 B.C. apparently by invading settlers who introduced the Greek language, probably came from far to the east, and brought in a new but by no means uniform physical type. This is the last archaeologically recorded major addition to the population. There may have been some shrinkage of population before this. And the invaders seem to have formed a large and linguistically dominant minority. It is not surprising to find variability and heterogeneity at their climax although all the material (N:36) comes from Argolis. This was a time of rapid culture change, accelerating population growth, and other minor intrusions; for instance that of Minoan technical experts. Hence the effects of heterosis and of recombination should reach successive maxima, both because of the actual invaders and the start of breakdown of local isolation.

The Mycenaean period in the 15th to 12th centuries B. C. sees the end of population growth and the fruition of cultural (and political?) unification ending in Greece's first taste of problems of urbanism, overcrowding, and a technological revolution (ironworking). Village isolation must almost have disappeared: Attic and Argolid samples are indistinguishable. The population seems to have grown greatly, but was probably mostly rural, with small "cities." Thus one would expect an approach to panmixia. And the Mycenaean sample (N:71) shows a smooth blend, having a fairly wide range between extremes but low variability and marked overall homogeneity.

The Early Iron Age (Submycenaean-Protogeometric-Geometric periods) starts with archaeological reflections of the socioeconomic results of spread of ironworking and new religious ideas, emigrations, and southward and eastward shifts of whole tribal units of Greeks. Dorian and other hill tribes moved into or through the area long after the Bronze Age intrusion of the Achaeans. And the Aeolic, Ionic, and Doric emigrations to less settled territory across and beyond the Aegean continued the move started in late Mycenaean times. This population change may have exceeded absolutely that of the Middle Bronze Age and in addition there may have been some exchange of population with the colonized areas. But the relative change must have been only a fraction of the earlier one because of the larger Mycenaean than Early Helladic population. Presumably there was some depopulation, as well as a most interesting series of social changes. But as in later phases of invasion there was a limited razing of cities and no sharp break in cultural continuity. Burial and religious customs changed, the skill of writing was lost, and overseas trade was broken. But ceramics still continued in almost the identical direction and rate of change of late Mycenaean times. The skulls (N:46) show increase in heterogeneity, judged subjectively, but the slight increase in variability is not statistically significant: invasion and selection by emigration were not enough to raise it to a high level. Inter-site differences seem less than intra-site heterogeneity at the beginning of the period, except for the marginal and insular Cephallenians (N:40). These contrast very strongly with their Isthmian area contemporaries by having developed in isolation a special variant of the pre-Greek population norm. But there is no way to compare their deviation at this date with that in earlier or later times.

The Classical population almost certainly exceeded that of the end of the 19th century and equalled over half modern density. Imported food allowed relatively large urban concentrations through immigration from countryside and from foreign coastal towns (Tod, 1927). But this influx was steady and probably not massive enough to affect population norms much except by social stratification. The sample (N:99) shows the same kind of "panmixed" homogeneity found also in contemporary Egypt (Pearson and Davin, 1924), or in modern European towns. Variability is scarcely above "normal" and intergroup differences seem slight. Averages return toward Ionic Greek norms of the Bronze Age.

In Hellenistic times (Alexander to Hadrian) many social factors worked to allow increase in disease, to reduce both the concention rate and fertility to a point which finally was not balanced by immigration. Thus from the Mithridatic Wars and Sulla's conquest of Athens in 87 B.C. until almost the time of Hadrian there was real decrease in population (Larsen, 1938; Tarn, 1930, pp. 92–94). The sample (N:108) shows a rise in variability and in local distinctiveness. And there is a swing away from Classical averages and beyond the norms of the Early Iron Age. This is hard to explain by immigration.

The ecological fortunes of the area were very changeable during imperial Roman times (Hadrian through Justinian) (Larsen, 1938). In spite of increasing aridity, deforestation, soil erosion, and exhaustion of natural resources (except quarries) the Greeks achieved prosperity and some population increase during the second century A.D. But the invasions of the Third, late Fourth and Fifth centuries A.D. (Herulians and Goths, Visigoths, Huns and Vandals) plus serious epidemics and earthquakes neutralised this as well as the late Third century recovery under Diocletian. And although the earliest Byzantine revival of culture under Justinian is an important episode in the growth of Christianity, this revival ended in 588 with incursions by "Avars" and later by Slavs (Davidson, 1937). And the population was held down by a major outbreak of bubonic plague in 531. Thus the Roman period was one of sharp increase and irregular decline in population density, with great fluctuations in unity. There was some Roman colonial immigration. But local isolation increased and urban populations shrank faster than rural ones. The sample (N:82) maintains the Hellenistic levels of variability and inter-site distinctions and continues the trend away from Classical toward modern Greek morphology.

The over-inclusive Byzantine-Medieval period starts with occupation by small bands of Avars and of Slavs in a phase of declining population and cultural readjustment marked by the plague outbreak of 747. The ancient city planning and sewage systems had largely broken down. Yet by 1100 A.D. there had occurred enough economic recovery for the area to be worth conquest by and to support successively Norse, Frankish, Aragonese, Albanian, and Venetian conquerors or colonists who handed their feudalism on to the Turks in the mid-fifteenth century. The population was checked as much by epidemics as by exploitation. And as elsewhere in Europe this was a time of peasant communities, tiny cities, and monasteries, with strong local isolation. Apparently breeding units were larger than in Neolithic times. And occasional retreat to refuge areas may have maintained some mixture among the subject population. But it is natural to find in the sample (N:70) a continuing raised variability and increasing local diversity.

The same or deteriorating ecologic conditions held throughout the Turkish occupation, except that endemic plague and malaria may have been more severe. And early census estimates show fluctuations around a very sparse density (Stephanos, 1884, pp. 440–450). The sample (N:49) is biased by coming only from Attica. But the high variability, decrease in skull size, negroid nasal features, and return toward a pre-Greek norm may be real effects of contacts with Aegean islanders plus Moslem areas and of selection by disease, following the Medieval absorption of Slavs, Albanians, and others.

A marked improvement started in the 19th century, with accelerating population growth, almost no new immigration, and by 1900 much emigration. But the sharp drop in variability is explicable best by the short time span, since local differences are still clear as at the present day. It is possible that local inbreeding with population reduction during the Turkish occupation was enough to restrict variation more than since prehistoric times.

So far as it is safe to generalize (Table 1) periods of expanded population show low variability but not, till modern times perhaps, approaching the stability of many non-literate groups. Periods of shrinking of population and relative isolation of groups show raised variability. And possibly periods of isolation after

TABLE 1. MEAN SIGMA RATIOS OF 18 CHARACTERS IN MALE CRANIA FROM CIRCUM-ISTHMIAN GREECE TO SHOW VARIABILITY IN RELATION TO ESTIMATED POPULATION SIZE

Period	Neolithic and Early Bronze	Middle Bronze Age	Mycenaean or L.H. III	Early Iron Age	Classic	Hellenistic-Roman
Approximate dates	a. 3300–2000	2000–1500	1500–1150	1150–680	680–300	300 B.C.–120 A.D.
Approximate period length in years	1300	500	350	470	380	420
Mean sigma ratio	111.9	122.3	99.1	105.0	103.9	110.4*
Mean N (maximum N)	14 (24)	16 (21)	26 (42)	23 (27)	47 (64)	54 (72)
Estimated population density per sq. kilom.	0–5	(10)	(25)	(20)	35 ?	32 ??
Relative increment from outside sources	V. massive	Massive	Slight	Submedium	Slight	Submedium
Intrusive groups	Neol. peasants "Carians" Northerners	Greeks and Islanders ?	Experts and Adventurers	Hillmen	Slaves, traders, artisans	
				Emigration		
Cultural unity	None	Beginning	Strong	Lapse	Average	Lapses

Note: 100.0% is Sigma Ratio norm (Howells, 1941) for cranial series of "average" unmixed populations from a single area and archaeological period. Values exceeding those of the preceding period by more than 2 × standard error are underlined, by 1.70–2.00 × standard error starred*. This notation is used in other tables also.

massive invasion show heterogeneity and high variability. In the long historical view there seem to have been frequent flows either of highlanders or of islanders and coast-dwellers into this whole area around the isthmus of Corinth. Hence after the settling of pre-Greeks and Greeks, such intrusions as those of Dorians, Romans, Slavs and Albanians or of East Mediterranean slaves, metics, and Roman colonials were simply relative spurts in this process which must have kept genic and phenotypic variability high throughout. But the internal dynamics of assimilation and use of this variation are of greater importance than the mere fact of invasions. This is a rugged and ecologically isolating area (though small) in which change in population size combined with such selective factors as disease, emigration, warfare, or social frustration and in the presence of fluctuating mixture could be expected to allow small evolutionary changes. In such changes invasion seems less important (cf. Mylonas, 1946) than selection and size of breeding unit.

The mean change between periods (Table 2) as measured by diameters, indices, and type frequencies is highest in prehistoric and Turkish to modern times and lower in the intervening period of larger populations. Hence very broadly, and with certain statistical reservations, we can observe an inverse relationship between population growth on the one hand and variability and speed of change on the other. A considerable part of this increased variability and speed of change in early prehistoric times and in the past millennium springs from long time intervals sampled with small series. But sample size does not serve as an adequate explanation. And the hypothesis that variability and speed

TABLE 2. MEAN PERIOD TO PERIOD CHANGES IN MALE CRANIA FROM CIRCUM-ISTHMIAN GREECE IN RELATION TO GROWTH OR DECLINE IN POPULATION SIZE

	Neol. & E. B.-Mid. Bronze	Mid. Bronze-Mycenaean	Mycenaean-Early Iron	Early Iron-Classic	Classic-Hellenistic
Difference in 13 diameters as % of mean of each	2.45%	1.49	1.21	1.04	1.05
Difference in 5 indices	1.31%	.79	.56	.89	.92
Difference in frequency of each type (both sexes)	12.12%	10.99	10.30	6.95	5.04
Lapse between period centers	750 years	425	410	425	400
Change in size of population	Slow growth	Fast growth	Static or decline	Fast growth	Decline

TABLE 1 (*continued*)

Period	Roman Imperial	Medieval	Turkish	Recent	Living	Cephallenia Submycenaean
Approximate dates	120–600	600–1400	1400–1800	1800–1900	1939	1270–1070 B.C.
Approximate period length in years	480	800	400	100	1	200
Mean sigma ratio	109.1	109.4	105.8	95.7*	92.2	105.0
Mean N (maximum N)	43 (59)	35 (50)	23 (25)	96 (99)	37	21 (29)
Estimated population density per sq. kilom.	25 ??	18 ??	10	21	55	(25)
Relative increment from outside sources	Slight	Medium	Slight	V. slight	None	Slight
Intrusive groups	Colonials (and Goths, etc.)	Slavs, Albanians, Franks and Venetians	Islanders, Moslems	Islanders	Emigration	Hillmen
Cultural unity	Average	Weak	V. weak	Average	Average	Strong

of microevolutionary change vary inversely with breeding group size seems a reasonable one, in agreement with the theories and experiments of Wright and Dobzhansky.

But even more striking than these fluctuations related to population size is the observation that the absolute rate of change (and hence degree of change) is very slow indeed (cf. Haldane, 1949), suggesting a strong genetic as well as ethnic continuity from Mycenaean times onward. This is remarkable in a country as often invaded as Greece. It may be a function of ecology plus a critical optimum population size as well as an established cultural ability to absorb intruders selectively.

The actual changes found are of no vital interest here, except as related to the mechanism producing them. They may be summarised as follows (Table 3): (1) broadening in skull base and vault (ca. 3%) in prehistoric and recent times; (2) decrease (ca. 3%) in skull length since Classical times; (3) increase (ca. 3%) in skull base length since the Middle Bronze Age; (4) broadening of jowls (9–10%) preceding facial broadening (ca. 3%); (5) steady increase in size of nose, up to 8 to 9 per cent accompanying height increase of the upper face; (6) decrease in depth of chin (ca. 8%) accompanying increase in frequency of overbites and perhaps related to chin prominence; (7) marked increase in body size (almost 4%) from prehistoric to Classical times (Table 5); (8) increased depth of pelvis and other skeletal changes in proportions (Table 5). There are other small probable changes still to be tested, such as increased droop of orbits and nasal saliency. And the pattern of morphological types (Table 4) swings from a generalized Mediterranean predominance

TABLE 2 (*continued*)

	Hellenistic-Roman	Roman-Medieval	Medieval-Turkish	Turkish-Recent	Recent-Living
Difference in 13 diameters as % of mean of each	1.20	1.37	1.97	2.04	1.41
Difference in 5 indices	.69	1.28	1.02	1.58	1.27
Difference in frequency of each type (both sexes)	4.67	6.25	3.33	5.82	10.06
Lapse between period centers	450	640	600	250	90
Change in size of population	Decline	Sharp decline	Sharp decline	Growth	Fast growth

TABLE 3. SELECTED MEAN MEASUREMENTS AND INDICES OF MALE CRANIA FROM CIRCUM-ISTHMIAN GREECE TO SHOW GENERAL PHYSICAL CONTINUITY OF THE POPULATION AND CERTAIN SPECIFIC PATTERNS OF CHANGE

Period	Neolithic and Early Bronze	Middle Bronze Age	Mycenaean or L.H. III	Early Iron Age	Classic	Hellenistic-Roman
Approximate central date	2500 B.C.	1750	1325	915	490	90 B.C.
Vault length	185.1	185.9	185.6	185.0	186.7	184.4*
Maximum breadth	139.6	142.6*	140.2	141.4	140.7	142.5
Auricular height	117.4	118.6	116.1*	116.1	116.3	116.1
Minimum frontal breadth	96.3	96.4	95.8	95.9	96.8	96.7
Base length (bas.-nas.)	100.8	98.7	99.3	100.5	101.6	101.2
Base breadth (bicondylar)	114.2	120.6*	122.0	125.6*	124.4	123.5
Face breadth (bizygomatic)	128.2	132.6	130.5	132.0	131.6	131.1
Jowl breadth (bigonial)	93.7	96.8	99.6	99.2	103.4	100.9
Min. breadth jaw ramus	31.1	30.5	30.7	32.5	32.2	31.9
Chin height	33.5	31.0	33.1*	33.1	32.8	31.5*
Upper face height	70.2	68.6	68.4	68.6	69.0	69.7
Nose height	50.2	49.3	49.7	50.6	50.8	50.8
Nose breadth	24.0	24.1	23.9	24.2	24.7	24.8
Cranial (l-br.) index	75.7	77.2	75.8	76.5	75.5	77.4
Length-height index	73.5	73.0	72.0	72.5	71.4	72.3
Fronto-parietal index	69.2	67.2	68.2	67.7	68.7	68.0
Upper facial index	54.7	52.3	52.5	52.0	52.4	53.4
Nasal index	48.0	48.2	48.4	47.7	48.6	48.8
Mean N	14.0	15.7	26.4	23.1	47.4	53.7
Both sexes:						
Definite overbites	5.0	25.0	4.0	11.4	11.4	23.1
Prominent chin	41.7	21.7	47.8	22.2	41.8	65.2

in a Dinaroid and Alpine direction. These changes form overlapping and correlated groups of responses to multiple and interacting causes.

With the growth of culture, ethnic and biological blending, and population expansion from Middle Bronze to Mycenaean and Early Iron Age to Classical times there occurred improvement in diet and living conditions (cf. Angel, 1946; Michell, 1940). This is reflected in increased length of life, decrease in osteoarthritis and presumably other diseases, and undoubtedly much of the observed body size increase which in turn brings about heterogonic changes in limb proportions, pelvis, and skull base length (cf. Thompson, 1946, p. 283; Huxley, 1932). Thus these changes are largely or entirely non-evolutionary, though selection might act on the new phenotypes produced by dietary or other environmental factors.

Intrusions from isolated populations in mountains or islands could conceivably have introduced more lateral than linear body and

TABLE 4. PERCENTAGE FREQUENCIES OF MORPHOLOGICAL TYPES AMONG CRANIA OF BOTH SEXES FROM CIRCUM-ISTHMIAN GREECE TO SHOW TREND AND FLUCTUATIONS IN MICROEVOLUTIONARY CHANGE

Period	Neolithic and Early Bronze	Middle Bronze Age	Mycenaean or L.H. III	Early Iron Age	Classic	Hellenistic-Roman
Approximate central date	2500 B.C.	1750	1325	915	490	90 B.C.
Type C: "Alpine"	15.9	11.1	15.5	23.9	12.1	17.6
Type E: "Mixed Alpine"	2.3	16.7	8.4	13.0	10.1	14.8
Type F: "Dinaroid"	11.4	8.3	5.6	15.2	9.1	13.9
Type D: "Nordic-Iranian"	11.4	33.3	11.3	19.6	27.3	22.2
Type B: Mediterranean	29.5	8.4	22.5	19.6	20.2	11.1
Type A: Basic White	29.5	22.2	36.6	8.7	21.2	20.4
N	44	36	71	46	99	108

Note: These types are selected by matching standardized photographs (Angel, 1946, etc.) and hence are too rigid to express effects of continual recombinations except most arbitrarily. They may clarify degree of heterogeneity in the population. But they can apply strictly only to this Greek population, must be used with caution, and will be replaced by a more functional and less phenotypic analysis when this is worked out.

TABLE 3. (*continued*)

Period	Roman (Imperial)	Medieval	Turkish	Recent	Living	Cephallenia Submycenaean
Approximate central date	360 A.D.	1000	1600	1850	1939 A.D.	1170 B.C.
Vault length	182.9	182.7	182.3	180.2	179.8	188.5
Maximum breadth	142.2	140.5	138.0	140.9	145.1	138.9
Auricular height	116.3	118.0	115.8	116.4	118.6	115.4
Minimum frontal breadth	98.1	98.1	96.4	97.4	98.4	96.6
Base length (bas.-nas.)	101.9	101.8	100.5	102.3	...	102.2
Base breadth (bicondylar)	124.0	123.2	...	...	...	...
Face breadth (bizygomatic)	133.8	132.4	128.5	132.1	134.0	129.6
Jowl breadth (bigonial)	100.9	105.2*	...	...	102.2	...
Min. breadth jaw ramus	32.2	32.9	...	...	...	...
Chin height	30.2	31.6	...	...	(29.5??)	29.8
Upper face height	70.9	71.3	69.9	72.1	71.6	65.3
Nose height	51.9	52.0	49.7	52.6	53.3?	47.6
Nose breadth	25.0	24.5	24.7	24.8	25.3??	24.5
Cranial (l-br.) index	78.0	76.9	75.6	78.2	80.7	73.7
Length-height index	73.3	74.6	74.1	75.7	...	70.8
Fronto-parietal index	69.0	69.5	69.9	69.1	67.8	70.4
Upper facial index	53.1	54.2	54.2	54.6	53.4	50.0
Nasal index	48.3	46.8	49.8	47.3	(47.4??)	51.7
Mean N	43.1	34.6	22.6	95.6	37	21.0
Both sexes:						
Definite overbites	33.3	37.5	...	...	50 ca.	...
Prominent chin	21.4	47.6	...	...	...	...

skull form factors for historical reasons (Angel, 1946, and unpublished data on Neolithic Cypriotes). These would explain the shift in type frequencies and in skull vault and perhaps face breadths. But we do not know with certainty, from any extra-Greek sample, the phenotypes of any one of the archaeologically or historically identified intrusive groups. And extrapolation from the effects of an invasion, even when some of the peripheral populations are known, is most dangerous.

It is possibly more plausible to argue that from 1500 B.C. onward all such changes were mainly microevolutionary and intra-group. This certainly seems to be true of the striking jowl-broadening and increase in respiratory region with vertical shrinkage of masticatory part of the facial skeleton. Recombinations following mixtures in periods of reduced population would provide genic materials for such changes, in a situation where breeding groups had a reticular or intermittent contact with one another.

TABLE 4. (*continued*)

Period	Roman (Imperial)	Medieval	Turkish	Recent	Living	Cephallenia Submycenaean
Approximate central date	360 A.D.	1000	1600	1850	1939 A.D.	1170 B.C.
Type C: "Alpine"	17.1	15.7	12.2	22.4	45.9	12.1
Type E: "Mixed Alpine"	14.6	4.3	8.2	8.7	10.3	15.0
Type F: "Dinaroid"	25.6	18.6	20.4	27.2	13.6	0
Type D: "Nordic-Iranian"	14.6	21.4	18.4	16.5	2.7	10.0
Type B: Mediterranean	13.4	24.3	28.6	16.5	13.5	27.5
Type A: Basic White	14.7	15.7	12.2	8.7	13.5	37.5
N	82	70	49	103	37	40

But it seems easier to explain these and the breadth changes by supposing in addition some selective factor (such as disease) or genic reinforcement from repeated small intrusions, or both.

These hypotheses of internally generated or externally caused microevolutionary change are both simplified when we examine the mechanics of the face. Thus only two gene complexes, plus environmental changes, need be hypothecated to produce the observed results. One might determine a marked degree of overbite, whose expression might be further encouraged by dietary change. This would allow downward overgrowth of the upper face and nose, and inhibit vertical versus anterior growth of the chin region. A second gene complex might reduce sphenoid and squamous temporal growth to shorten the skull vault, shifting the pull of occlusal muscles relative to the chewing plane and through this influencing the arch of the nasal bridge and that part of the glabellar and orbital morphology which depends upon chewing stresses. Actually the changes in nose size and form seem to depend on more influences than these. And this is pure speculation, which can be checked in part by future full analysis of all the data.

But against a background of relative genetic stability in an area where intrusion, mixture, and recombinations kept the variability high, the data presented suggest strongly that microevolutionary changes were promoted by the alternation between phases when the population was segmented, changing in size, and relatively sparse, and periods when it approached nearer to a single breeding unit and was relatively dense. It is noteworthy that changes in measurements and in type frequencies do not follow a completely direct path from ancient to modern times, but rather a fluctuating or spiral one. This is what we would expect if new tendencies from intruders, from recombinations, or from genic loss, occurring in several of the network of breeding units at a time of isolation, high total variability, and perhaps raised selective forces (disease, etc.), should become more widely spread during a phase of expansion and increasing panmixed homogeneity. Here we must rate as of major importance the selective effects of disease and of differential fertility (cf. Thompson, 1942, pp. 47–60) either of rural or urban populations, or of slaves, outsiders, and citizens in the class system. We know almost nothing about these factors except that the infant death rate was very high, as indicated by cemetery statistics, that epidemics were feared, and that malaria and later bubonic plague were endemic scourges. But even without strong selection working in a still unknown way, several repetitions of the population fluctuations noted *could* account both for major trends and the otherwise inexplicable slight fluctuations.

The fact that skeletal data from Greece can be made to fit the well-tested hypotheses of Dobzhansky, Wright, and Huxley does not prove that changes in size of breeding unit plus genetic recombinations were the determining forces in microevolution in circum-Isthmian Greece. For a

TABLE 5. CHANGE IN STATURE AND IN BONY PROPORTIONS AMONG GREEK MALE SKELETONS

Period	Prehistoric (Neol.-Myc.) a. 3300–1150	Early Iron Age 1270–680	Classic-E. Hellenistic 680–150 B.C.	L. Hellenistic-Roman 150 B.C.–1600 A.D.	Turkish 1600-x
Stature (Pearson fml.)	159.7 cm.	162.3	165.6#	165.9#	166.9#
Brachial index	75.8	75.1	76.8	76.8	(78.9)
Crural index	83.2	82.0	82.4	82.0#	(81.6)
Humero-clavicular index	49.5	47.7	47.5	46.2	(48.0)
Humerus shaft flatness	78.2	77.8	80.7	81.2	80.9
Femur: platymeric index	77.7	77.5	79.2	83.1#	87.4#
Femur: pilastric index	105.6	104.1	104.8	108.7	112.7#
Tibia: cnemic index	66.5	68.0	67.7	69.5	72.1#
Pelvis: inlet index	(78.5)	83.3	84.5	86.6	(87.0)
Sacrum: ht.-br. index	108.9	101.1	105.0	93.2#	(91.8)
Lumbar curve index	96.7	97.9	98.1	99.2	(99.8)
Talus: l.-ht. index	57.5	57.3	60.6#	59.2	...
Mean N (maximum N)	15.7 (26)	13.2 (25)	15.9 (22)	12.4 (19)	12.6 (35)
Estimated dietary level	Fair	Improving	Good	Fluctuating	Fair

Note: Statistically significant differences from the preceding period are underlined, from the earliest period marked #.

closer approach to proof we would need good samples from each site dated to a much shorter span of generations—material which will never be available. But even without this, the data on mixture, microevolution, population size, diet, health, patterns of family life, and longevity in their relation to cultural change are of critical interest for a study of human social biology (cf. Angel, 1946).

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RACE CONCEPT AND HUMAN RACES

CONCLUDING REMARKS OF THE CHAIRMAN

L. C. DUNN

Department of Zoology, Columbia University, New York

At the end of this discussion of the concept of race, I think we may fairly ask: why do we need a concept of race? Surely, it is of greater importance than to furnish a classification system, or to enable us to put each human being in his place. The primary scientific purpose of getting a reasonable idea of what race is, is to serve as a guide and stimulus for future research; and the purpose of this research is not only knowledge but *understanding* of how our species has evolved and is evolving today; and in the light of this understanding to make some guesses as to where it is tending, as a species. Race formation, whether we like it or not, is an inevitable stage in the evolutionary process by which bisexual organisms keep in harmony with their surroundings. As long as their breeding follows the normal pattern of random mating within a group of limited size, merely the limitations in the number of possible mates produces the partial isolation which, if it is long continued, tends to produce differences in gene frequency and hence leads toward race formation. Race, like many biological concepts which involve time, can be understood and used only as the processes underlying it are understood.

If a race concept is necessary, then it is chiefly as a working hypothesis of the ways in which human populations are constructed and of the manner in which they interact and change. Race is certainly not always and everywhere the same. The traditional "races" of Europe are certainly very different taxonomic categories from the "races" which at different times peopled the Americas and Oceania. Moreover, the same concept, if defined as a fixed category, could hardly be profitably used to characterize the population of the same locality at different times. Races change as periods of isolation and inbreeding alternate with periods of expansion and migration and mixture. Consequently race as a noun cannot have a fixed or exact meaning, but only a broad and general one, whereas "racial differences" or "racial mixture" and other adjectival uses convey a real meaning without ambiguity if one thinks of "racial" as referring to the relative and often characteristic frequencies, within a group, of a given collection of genes.

Race, as a biological problem, lies in the domain of physical anthropology and one of the benefits to be derived from discussing race is to get a clearer definition of the problems of physical anthropology. Definition is often the first step in the solution of a problem and definitions have offered peculiar difficulties in the study of man, with the result that problems of central importance in anthropology, such as those of heredity, had first to be solved where they presented themselves in the clearest form as in animals and plants. Physical anthropology has come to bear to the study of man much the same relationship that zoology bears to the study of animals, and now it runs the same risks. Zoology is what remains when physiology, cytology, experimental morphology, genetics, and other recent specialties have been subtracted from it. What remains is classification, phylogeny, anatomy, etc., and these tend to be sterile when separated from the actively growing parts. Physical anthropology also tends to become a holding company and suffers from this rather inactive status; but I think we can see distinct signs that racial studies are infusing new life into it and I believe it has a bright future.

Race as a social problem is a different matter with which I believe we are not here concerned except in so far as the notorious misuse of the word for political purposes has impeded research on the racial analysis of man. Such terms as "race degeneration" and "race suicide" are hybrids deriving in part from biological and from social and political vocabularies. Since they are more frequently expressions of opinion than of fact, they tend to disappear as rational and scientific concepts of race develop.

The usefulness of an idea of race depends on how much one learns by using it. In this sense, the new race concept may have a wider scientific influence than on anthropology alone. Several ideas derived from work with human groups have already proved fruitful in genetics and general biology. For example, Wahlund's assumption of

social and geographic isolates was followed by Sjøgren's proof of their existence in respect to juvenile amaurotic idiocy, and by Dahlberg's extension of the idea to isolates of other kinds together with methods of calculation. These isolate-forming agencies involving economic, religious, and cultural factors of all kinds were peculiar to man and could hardly have been derived from studies of other animals.

However, independently of these, Wright, by relating in a general theory population size and breeding structure, had already reached views about isolate and race formation for which the human material provided actual examples.

The studies of human polymorphism of which the foundations were laid by Weinberg, Bernstein, and Hogben, and which now can be pursued with the methods developed for medical purposes, will tend now to lead the way in population genetics. One of the great advantages of man as material for population genetics is that population size is or can be accurately known.

Many examples of the new spirit in racial studies have been presented at these meetings and especially in today's sessions.

Birdsell with new data covering a large part of a whole continent has shown a unique example of a population of 300,000 divided into breeding units of 500 each, with effective breeding sizes of 200 or less, just the situation pictured by Wright as that favorable for evolutionary change, since under these conditions drift may supplement selection. The models which he has set up constitute a theory of race formation and change in Australia which is a necessary first step in understanding not only this but other areas of more complex history. One must first imagine such models in order to determine the type of data required to test such hypotheses.

Professor Coon has utilized some of the unique properties of human groups, i.e., their cultural diversities, as operators which may in the future change the racial composition of our species. Although he drew most of his examples from simpler cultures, the question is clearly raised whether in our complex culture the racial process will not be greatly accelerated in both directions. Because of the longer life span of members of complex cultures, are not these likely to inherit the earth while many races go the way of the Tasmanians?

Professor Montagu has brought the idea of race itself under sharp scrutiny and it is profitable to ask—are there races of men comparable to those of animals and plants? I think we should recognize that even as species has a different meaning in bacteria, lower plants, self-fertilizing plants, and crossfertilizing plants and animals, so race also will vary somewhat from one to the other—but one aspect of each group is common or universal, that is, the differences in gene frequencies and this is seen as the fundamental peculiarity.

CONSTITUTION

THE CONSTITUTIONAL MODIFICATION OF MENDELIAN TRAITS IN MAN

STANLEY MARION GARN

Forsyth Dental Infirmary for Children, Boston; Harvard University, Department of Anthropology

The early writers on evolution conceived of the evolutionary process as a change in the distribution of continuous variants. Assuming, for instance, that the extreme degree of expression of a variant might be advantageous or disadvantageous to the organism, they visualized evolution as a shift in the distribution curve, as the result of natural selection.

But in transferring the study of evolution from an armchair status to an investigative science, continuous variants did not prove entirely satisfactory for experimental study. Such variants were subject to environmental modification, and they presented difficulties in experimentation, in analysis, and interpretation. Therefore traits were selected for study that could be attributed to changes at a single pair of loci. By emphasizing such traits, and investigating the appearance of new traits, mutation came to be stressed; interest was aroused in factors influencing the mutation rate, and in the role of mutation in evolution. Understandably evolutionary mechanisms were advanced by some authors that stressed mutation, and in effect denied selection as a major factor in evolution. To anthropologists whose interests were concerned with continuous variants, the prospect of explaining some aspects of human evolution appeared dim.

In recent years, a number of physical anthropologists have abandoned their preoccupation with taxonomy based on the head and face, and have concerned themselves with variations in human physique, and with their behavioral and functional correlates. During the same period of time, medical investigators have become interested in a number of variable traits which are little influenced by ordinary environmental changes and which seem to bear on survival. The possibility that some of these, as well as physiological traits and variations in known monogenic traits that affect survival, are related to differences in physique has opened an interesting field of investigation.

To the anthropologist is given the job of investigating such relationships, and his present techniques are fairly suited to the work. The interpretation of the relationships, the explanation for correlations between physique and biochemical traits, or the explanation for the interdependence of physique and the degree of expression of monogenic traits lies beyond his technical and theoretical equipment, and requires the assistance of other specialists.

Hereditary Traits Affecting Survival

Workers in medical genetics have investigated a large number of hereditary traits that affect survival. The majority of those reported, like the blood dyscrasias, skeletal abnormalities and enzyme blocks are "abnormalities of kind," yet there is considerable variation in the degree of expression and in the time of appearance, even in siblings. While some of the variance can be attributed to differences in fetal nutrition, growth gradients, and the like, the major portion of the variance has been ascribed to the rest of the genetic makeup of the individual, "constitutional differences," or the "residual heredity"; that is to say, individual differences not yet defined.

More recently attention has been directed toward the blood constituents, apart from the respiratory pigments. The serum concentrations of some of these constituents are normally distributed in the population at large, yet individuals whose serum concentrations fall in the upper tail of the normal curve may be especially prone to certain disorders. Thus these constituents are variable traits, disadvantageous to the organism in the extreme degree of expression, and are of especial interest to the student of evolution because of the large amount of investigative research now devoted to their study.

Two such constituents are presently of interest, cholesterol and uric acid. Men whose serum cholesterol exceeds a defined upper limit are more likely to develop atherosclerosis (Boas,

Parets and Adlersberg, 1948), and in like manner men whose serum uric acid concentration is in the upper portion of the normal curve are more likely to develop gout (Neel, 1949), though it should be emphasized that the serum concentration is by no means the only factor in the development of either disorder.

Recent investigations have shown that high serum concentrations of both cholesterol and uric acid are inheritable, and the mode of inheritance has been studied (Adlersberg, Parets and Boas, 1948; Stecher and Hersh, 1949; Smyth, Cotterman and Freyberg, 1948; Smyth, Stecher and Wolfson, 1948; Neel, 1949). Thus, the serum concentration of some individuals is at the upper end of the normal distribution curve because they have inherited the genic factor for hypercholesterolemia, or hyperuricemia. However, there are individuals whose serum concentrations approximate hypercholesterolemia or hyperuricemia by the *usual standards* who are not members of a hypercholesterolemic or hyperuricemic family, and conversely, some individuals in such a family may fall slightly short of the accepted limits of 305 mgm. percent of cholesterol, or 6.0 mgm. percent of uric acid, even correcting for age [as is necessary in cholesterol studies (Keys, Mickelsen, Hayes and Miller, 1950)] or correcting for sex, as is necessary in uric acid studies (Smyth, Stecher and Wolfson, 1948). The question immediately arises as to whether these cases should be attributed to irregular gene action, or whether such cases can be accounted for in terms of other variables affecting the serum concentration of these constituents.

Physique and Biochemical Traits

At the Coronary Research Project, Massachusetts General Hospital, Dr. M. M. Gertler and the author have explored the relationships between various serum constituents, including cholesterol and uric acid, and a number of likely variables, including physique. Although the literature had led us to expect that the intake of cholesterol-containing foods, the intake of certain other foods, or total caloric intake might correlate positively with these constituents, physique alone showed significant correlations, and the other variables did not. This finding was true both in a control series of healthy men, and in young men with coronary artery disease (Gertler, Garn and Sprague, 1950; Gertler, Garn, and Levine, 1951).

Though caloric intake, cholesterol intake, weight, stature and metabolic rate were not found to be correlated with serum cholesterol concentration (or that of several other lipids), cholesterol showed a significant positive correlation of 0.26 ± .08 with endomorphy- the "first component" of the somatotype (Sheldon, 1940) and a negative correlation of 0.18 ± .08 with ectomorphy, the "third component." It is possible to state that these correlations were not only independent of diet, but also were independent of controllable fat, since low-fat weight-reducing diets are not capable of effecting permanent alterations in the serum cholesterol concentration, a finding originally contained in a report a decade ago (Turner and Steiner, 1939) and subsequently confirmed by other workers. Hence it would appear that the relationship between physique and cholesterol operates through the endogenous cholesterol metabolism.

Since the correlations given above are relatively low (at or below ± 0.30), it may be of interest to illustrate the magnitude of the physique-associated differences, by sorting the group tested into four rough groupings. Dividing the men, therefore, into 51 with endomorphic dominance, 34 with mesomorphic dominance, 34 with ectomorphic dominance, and 27 mid-range physiques with no clear dominance, the endomorphs showed the highest mean cholesterol, 234.6 ± 6.6 mgm. percent, and the ectomorphs showed the lowest mean cholesterol, 207.8 ± 6.0 mgm. percent. These findings are in agreement with an earlier study that reported a higher mean cholesterol concentration in pyknics (Gildea, Kahn and Man, 1936) and may further illuminate the findings of workers interested in relationships between biochemistry and behavior (McQuarrie, Bloor, Husted and Patterson, 1933).

The same pattern emerged in the relationship between physique and serum uric acid concentration, with a positive correlation between endomorphy and serum uric acid, and a negative correlation between ectomorphy and serum uric acid. Again dividing the series into the rough groupings described above, the dominant endomorphs had a mean serum uric acid concentration of 4.87 ± .12 mgm. percent, and the dominant ectomorphs had a mean serum uric acid concentration of 4.34 ± .13 mgm. percent. Thus it again appeared likely that there was a relationship between physique, and the serum constituent.

The utility of such a finding can perhaps be made clearer by pointing out that the serum uric acid concentration in the healthy endomorphs, described above, approximated that in the young men with coronary artery disease, the concentra-

tions being 4.87 ± .12 for the healthy endomorphs, and 4.80 ± .23 for the patients. Since we have shown that the serum uric acid level is elevated above the normal in these patients (Gertler, Garn and White, 1951) it is obvious that physique-associated differences may equal or obscure differences between normal individuals, and those with specific disorders. This point will be enlarged upon subsequently.

Again, it may be pointed out that blood pressure itself shows a correlation with physique; both the systolic and the diastolic blood pressure was highest in the endomorphs, and lowest in the ectomorphs. Thus in any normal distribution, a higher proportion of endomorphs would exceed the acceptable standards set by life insurance examiners, and military screening boards.

These findings bear on the general problem of "norms," and are of especial interest to workers interested in the inheritance of hypercholesterolemia, hyperuricemia, and hypertension. If there are physique-associated differences, as we have shown, it is important to decide whether the same "norms" should be used in defining hypercholesterolemia, hyperuricemia, and hypertension for all individuals, both in general studies, and in family-line analysis. It appears reasonable to redefine the "norms" for different physiques, just as different norms are used when age, or sex appears to influence the results. It would appear that these physique-correlated differences represent one source of variability in the normal distribution of certain biochemical traits, and are likely to be a source of error in investigating the inheritance of traits that are defined as serum concentrations in excess of a fixed value. An ectomorph with a serum cholesterol concentration of 290 mgm. percent is a very likely "genetic carrier" of hypercholesterolemia, even though the usual definition requires a concentration of 305 mgm. percent or higher.

Physique and Morphological Traits

Morphological and physiological traits also vary in the degree of expression, and some of them are covariant with physique. That this should be true of traits involving muscular development, fatty deposition, or elongation is perhaps obvious, for these variables are necessarily employed in any description of physique, whether it assumes discontinuous or continuous variation. On the other hand, within a population, it can be shown that maturation, whether defined as bone age, tooth age, or age at menarche, is related to physique in that the larger, broader or more mesomorphic children are relatively advanced over their fellows (Cattell, 1928; Reynolds, 1946). This association is somewhat less subject to the criticism that the same criteria are being rated twice, and then shown to be covariant. It indicates that genetically-determined differences in growth rate may also find expression in physique or body build, an interpretation that has also emerged from studies of early-maturing and late maturing species.

At the Forsyth Dental Infirmary for Children we have had the opportunity to follow the growth and development of children with various occlusal disharmonies. In certain families in our series a number of siblings are affected by the same type of occlusal disharmony, but the genetically-determined peculiarity is more marked in those siblings who depart most from the modal physiques, and is less marked in those siblings whose physiques are more common in the population. (Note: this statement should not be taken as to apply to all orthodontic problems, but only to certain genetically-determined disharmonies.) It can also be shown, by the use of indices of body-build, that children referred by the orthodontic department exhibited a different distribution of physiques from children selected from the clinic at large, though this is methodologically somewhat less satisfactory than the evidence obtained from sib studies. The reason for an association between physique and the development of occlusal disharmonies is not immediately evident, and while differences in growth rate appear to distinguish certain of the sub-groups among the orthodontic patients, these differences may simply be associated with physique differences, and not causally related to the dental problems. In fact, the elucidation of the relationships between growth and physique may help to place the study of physique differences upon a firm footing.

Physique and Human Evolution

The demonstration of correlations between physique and the degree of development of certain genetically-determined traits adds to our knowledge of the possible role played by physique in evolution, and racial differentiation. Firstly, physique is subject to selection, and in a given environment a particular physique may have adaptive value. Secondly, genetically-determined characteristics may achieve a maximum degree of development in particular physiques, and therefore be most subject to selection in those physiques. Lastly, it is possible to view some of

the evolutionary changes in the hominid line as possible functions of a general change in physique, rather than as independent changes in unrelated morphological characteristics. The more that is known about physique correlates in man, the better able anthropologists will be to interpret the meaning of racial and geographical differences in physique.

That physique itself may have adaptive value is frequently stated, although it is somewhat easier to suggest why a particular body size or body build is advantageous to a mammalian form other than man. Generally speaking, a larger or more muscular primate may have an advantage over its fellows, and this was probably true during the early stages in human evolution, though the development of complex techniques and organizations undoubtedly lessened the premium attached to strength and speed. When men entered into climatic zones presenting problems of heat regulation, certain physiques were better suited to these zones than were others, with the result that selection pressure favored certain physiques. In general a physique permitting efficient temperature regulation in a given climate has adaptive value, as has been pointed out (Coon, Garn and Birdsell, 1950).

The relationship between physique and the development of certain morphological and biochemical traits bears on that class of traits that do not seem to have adaptive value unless well developed. It has been pointed out elsewhere that if a trait has adaptive value, and if it is best expressed in organisms of a particular size, then selection will favor both the trait and size (Simpson, 1949, p. 157). The example may be extended to say that if a trait is advantageous, and if it reaches maximum expression in certain physiques, then both the physique and the trait would be favored. Conversely, if a trait is disadvantageous, and if either the degree of expression or the age at appearance varies with physique, then selection will tend to remove those physiques showing either the maximum expression of the trait, or the earliest expression of the trait.

As an example of such a trait, disadvantageous to the individual and associated with physique, one may give coronary artery disease. Dr. M. M. Gertler and the author have shown that the majority of a group of 97 men who experienced myocardial infarction prior to the age of 40 were mesomorphs (Gertler, Garn and White, 1951), and that these men are unlikely to attain the minimum replacement number of offspring prior to their demise. Thus in a late-breeding human population, mesomorphs with the genetic predisposition to coronary atherosclerosis would have fewer offspring than other men with the same genetic predisposition.

In discussing the role of physique in selection and in human evolution, it is perhaps pertinent to note that the characteristics of the more extreme "paleanthropic" fossils include many seemingly related to general muscularity, and that with a general reduction in mean muscularity, the excessive development of some of these characteristics would no longer be found (an observation first made to me by Dr. S. L. Washburn). If we assume, as we have previously, that conditions may have favored great muscularity during the early Pleistocene (and later in some areas), and that the development of cooperative hunting bands skilled in lore and technology reduced the advantage derived from great strength and endurance, then one could anticipate a general shift to a lower mean musculature, with a consequent reduction of these type characteristics. It is possible to view the somewhat more linear characteristics of the "progressive" Neanderthaloids of Mt. Carmel in this light, as well as the differences between the Upper Palaeolithic and Mesolithic populaces of Europe, and some of the more gracile Neolithic peoples.

The Problem of Physique Correlates

Though it is possible to demonstrate a wide variety of behavioral, biochemical, and morphological correlates with various aspects of physique, it has been suggested that further investigations of such relationships will be unprofitable unless the descriptive method of somatotyping, and the somewhat vague "components" of physique are further delimited by factor analysis, or the proportions of various tissues are stated. A somewhat similar argument has been advanced in metabolic studies, yet at the present time oxygen consumption and surface area correlate highly, and attempts to relate metabolic activity to internal surfaces, the proportions of various organs or tissues, or "the active protoplasmic mass" have not been successful (Kleiber, 1947). So far, the proportions of various tissues (including blood volume and muscle mass) in various somatotypes have been investigated, and the findings may be useful in medical studies, yet it is not likely that further fractionation will, by itself, explain the physique correlates. Similar doubts arise in making the transfer from Sheldonian "components" to "factors" (Tanner, 1947).

It is evident that the most important studies to be made are those relating physique to its genetic determinants, for only in this way is the investigator likely to uncover the causal nature of the correlations. The assumption is made at present that there are a large number of genetically-determined factors responsible for the development of physique, and that these factors also affect the rest of the organism. Thus correlations between behavior, growth, serum cholesterol or other factors and physique, are due to pleiotropism. It may be assumed that the correlations that have been found between physique and certain traits represent cases where the effects of several genes are cumulative, both on the physique and on the trait concerned. Hence, the rationale of using physique as a guide to constitutional factors, and the assumption that it may provide some help in the detection of hereditary traits.

At this stage in our knowledge of human heredity, the "rest of the genetic makeup of the individual," or "the residual heredity," which helps to determine the degree of expression attained by a genetic potential, cannot be isolated or defined. Physique, on the other hand, is at least a partial expression of the constitutional makeup of the individual: it can be defined, it can be measured, and it can be evaluated by a number of methods. Through correlations with other variables it can help to illuminate some problems in genetics and evolution. But there are two operations to be performed; it is necessary to discover what correlations exist (and that is the work of the anthropologist), and it is necessary to know why they exist (and here is an invitation to the geneticist).

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DISCUSSION

ANGEL: (In reference to Dr. Sheldon's comment that American somatotypes covered a wider range than those of other ethnic groups and seemed to change in offspring of immigrants.) It seems clear that mixture has raised the total variability of the American people just as it did in ancient Greece and other centers of civilization. Furthermore, dietary change, through heterogonic growth effects resulting from a simple increase or decrease in stature, must change body build at least in some degree.

GARN: Variance may be large in a population such as ours, as the result of the mere presence of groups with different physique distributions, even if reproductive isolation were maintained.

DUNN: Have measurements of cholesterol and uric acid been applied to any pairs of twins in your study? It seems to me this would be the

most practical way of testing the hereditary nature of the variance in both the biochemical constitution and somatotype at the same time.

GARN: We have not had the opportunity to study lipid metabolism in either monozygotic or dizygotic twins. We located a pair of dizygotic twins for study, examined one, but the other died of a myocardial infarction before we were able to see him. I am not sure whether Kornerup's study (in Denmark) contains the material you seek (Kornerup, V. Familiaer Hypercholesterolaemi og Xanthomatose: Denmark, 1948).

LASKER: First, would Dr. Garn think of the physique as being influenced by all the genes? In that case there might be some 20,000 to 50,000 genes involved in the physique of each individual, according to Spuhler's estimate.

In the second place, Dr. Garn's concept of constitutional modality as being the center region of the somatotype triangle may be somewhat ethnocentric. The three angles of such a triangle are by no means fixed. The triangle merely represents gradients. It therefore can portray certain differences in body build and even, perhaps, a rough estimate of variabilities in build, but it can hardly indicate modality except in reference to the specific population which has been sampled.

GARN: In regard to Dr. Lasker's first question, it may be assumed that a great many genes affect physique in its various aspects; how many is obviously not known (nor is the number of genes in man for that matter).

To the second question, it is true that our present description of physique variations was based on studies of "European whites." However the point is that the most extreme physique deviations are to be found among certain peoples in very different and harsh environments. The suggestion is offered that those physiques have a selective advantage in such areas; perhaps if the environments were changed those groups would gradually shift toward the "mid-range physiques." Some of the secular changes reported by Meredith and others support this idea.

MONTAGU: May I ask Dr. Garn whether he had any particular writers in mind when he referred to selection being denied by some writers as a factor in evolution? May I also ask Dr. Garn why if, as he said, the somatotype system is not in itself a typology he continually referred to types? Finally, may I ask Dr. Garn why it is, if there was selection for body types, as he suggests, such a large variety of body types are found to be present in almost all ethnic groups?

GARN: 1. Add the word "major" before "factor" in the sentence concerned. I was referring to the geneticists who suggested "systemic mutations" and "macromutations" to account for periods of (apparently) rapid evolution, thus giving selection a back seat.

2. I divided the series described into four groups or "types," for the purpose of illustrating the trends shown by the correlations. The names used are simply labels for physiques having certain characteristics in common.

3. If I understand Dr. Montagu's idiom correctly, he asks why—if physique is adaptive—the range of physique is approximately the same in Whites, Mongoloids, and Negroids. This is presumably due to the fact that these three headings each include a number of different local or geographical races. But the geographical races themselves often show wide divergences in both modal physique, and in the distribution of physiques. If one contrasts Eskimo with Dinka, or Tuareg with Ona, the differences are striking. It is the geographical race that may be subjected to environmental selection.

CONSTITUTIONAL ASPECTS OF JUVENILE DELINQUENCY

CARL C. SELTZER[1]

Harvard University, Cambridge, Massachusetts

INTRODUCTION

This work is a sequel to one aspect of an extensive investigation of juvenile delinquency conducted by the Glueck Research in Criminology, Harvard Law School. As anthropological consultant, this writer was responsible for the morphological aspect of the work, the analysis of the data and their interpretation (Glueck and Glueck, 1950).[2] In this paper there has been an attempt to extend the scope of the analysis as it relates to personality and behavior.

THE MATERIAL

The interpretative analysis is based upon a comparative study of the physical characteristics of a group of approximately 500 male juvenile delinquents and a matched group of non-delinquents (Seltzer, 1950). The subjects ranged in age from 9 years, 4 months to 17 years, 9 months. Owing to the fact that the two series were matched in pairs (each delinquent with a non-delinquent) with respect to similarity in age, socio-economic background, intelligence quotient and national origins, it was possible to make direct comparisons between the delinquents and non-delinquents as groups. The basic data were derived from measurements and observations taken from standardized "somatotype" photographs of the individuals enlarged to roughly one-half the actual size of the living subjects. In the morphological comparisons between the delinquents and the non-delinquents the following areas were emphasized: (1) gross bodily measurements, (2) anthropometric indices, (3) bodily disproportions, (4) masculine component, and (5) somatotypes.

Very briefly, detailed analysis of the anthropometric measurements disclosed the existence of a number of statistically significant differences between the two series. These differences revealed the delinquents as having a superiority over the non-delinquents in gross dimensions of the shoulders, chest, waist and upper extremities. More specifically, the delinquents showed larger breadth of neck, wider shoulder dimensions, greater breadth of chest, a larger distance between the nipples, both a deeper and broader waist, and a greater breadth of the forearm and upper arm. In one instance, the breadth of the face, the delinquents were significantly smaller, although they also exhibited a tendency towards narrower hips and smaller lower extremities. With respect to height and weight, no significant differentiation was indicated between delinquents and non-delinquents.

These data clearly emphasize the absence of any evidence of physical inferiority in gross body size on the part of the delinquents. However, it should be pointed out that the size of these differences between the two groups is not very great and accordingly does not indicate any *substantial* superiority in gross size of the delinquents over the non-delinquents. What is important about these metric differences between the two groups is that they seem to form a meaningful pattern which portrays the delinquent as a more masculine and mesomorphic physical specimen than the non-delinquent. The picture of the delinquents with greater lateral breadth of torso, with more exaggerated tapering from the shoulders to the hips, with a heavier development of the arms, and with smaller faces and heads anchored very firmly on the wide shoulders, is one which tends to approximate the typical masculine form.

Although the delinquents and non-delinquents differ but slightly in gross body size, they are strikingly dissimilar in the matter of bodily proportions. Comparison of the two series with respect to indices of bodily proportions showed far more striking differentiation not only in the magnitude of the differences but also in the far larger frequency of significant differences than was the case in the measurements of size. Out of a total of 36 indices studied, 80.6 per cent of them were statistically significant mean divergences.

In those indices which deal exclusively with "lateral" dimensions, the delinquent group was found to have, relative to the width of their hips, deeper chests, broader chests, greater breadth

[1] Anthropologist to the Hygiene Department, Harvard University; Research Fellow in Physical Anthropology, Peabody Museum, Harvard University.

[2] The author wishes to call attention to the fact that in this paper "delinquents" is defined and limited by the selection process made by the Gluecks, and all conclusions in connection with "delinquents" and "delinquency" are referable to that definition.

between the nipples, wider shoulders, and greater waist breadth than the non-delinquents. The delinquents displayed narrower faces relative to shoulder breadth, chest breadth, and nipple breadth. They also had smaller calf dimensions in relation to the width of the thighs, waist, chest, and shoulders. The depth of the chest relative to its breadth and to the width of the shoulders was shallower in the delinquents than in the non-delinquents. With respect to the neck, the width when considered in relation to the depth was greater in the delinquents, while the reverse was true for the waist where the depth relative to the breadth was greater in the delinquents than in their law-abiding counterparts.

In those indices in which the "lateral" dimensions are related to stature, the greater laterality of body build of the delinquents over the non-delinquents was strikingly prominent. This was clearly apparent in the height/$\sqrt[3]{\text{weight}}$ ratio, as well as by the fact that relative to stature the delinquents had broader necks, chest, shoulders, waist, thighs, and upper extremities. They also evidenced greater depth of chest and waist relative to stature than did the non-delinquents.

The above differences in body proportions between the two groups were not to be regarded as mere chance divergences, for they reflected well-defined and comprehensive body type differences between the delinquents and non-delinquents. The most conspicuous feature was the comparatively greater strength of the mesomorphic element among the delinquents. There was also evident a marked deficiency among the delinquents of the ectomorphic or linear element, and conversely its comparatively greater strength among the non-delinquents. The fact that the analysis of the measurements and indices seemed to indicate that the mesomorphic and ectomorphic components were the dominant components of the delinquents and non-delinquents, respectively, made it difficult to assess clearly the relative status of the endomorphic element. All that could be said on the basis of these data was that there was a suggestion of a somewhat greater endomorphic strength among the non-delinquents.

It was interesting to note that the results of the analysis of variance of these metrical figures supported these findings. In both measurements and indices, the delinquent group was more homogeneous than the non-delinquents. The delinquents, on the one hand, showed a strong predominance of the mesomorphic element, while the non-delinquents, with their strong ectomorphy and relatively greater endomorphy reflected through the more extreme body ratios and gross measurements, were perforce more heterogeneous.

The comparison of the two juvenile groups, with respect to body disproportions, also emphasized the basic differences existent between the delinquents and non-delinquents. Out of a total of 10 disproportions selected for analysis, 7 were found to be significantly more frequent among the non-delinquents than in the delinquents. This occurred in the following disproportions:

Stature tall for body weight
Faces broad for width of chest
Hips broad for width of shoulders
Chests narrow for stature
Chests shallow for stature
Chests narrow for width of hips
Chests shallow for width of hips

The degree of strength of the masculine component when studied in the two groups revealed significant differentiation between them in frequency and grade of the more feminine-like physique. Weakness of the masculine component was in far greater evidence in the non-delinquents than in the delinquents. It occurred almost four times as frequently in the control group as in the delinquents. The conclusion was obvious that the delinquents were more masculine in physique than the non-delinquents.

Intensive consideration was given to the question of the somatotype analysis. Two complementary methods were used, the first involving an over-all inspectional somatotype rating of the subjects "as is" into 13 categories, and the second a matched-pair comparison between the delinquents and non-delinquents for relative component strength. The two methods had the advantage of serving as independent checks against each other, and as it turned out, the results obtained were the same by both techniques.

In brief, the results of the somatotype analysis affirm the delinquents to be absolutely and relatively more mesomorphic than the non-delinquents. The delinquents were also decidedly weaker in ectomorphy than their counterparts in the control group. The question of endomorphy, however, was somewhat more complicated. The data indicated that although the frequency of extreme endomorphy was much more common among the non-delinquents, that by and large the relative endomorphic strength of the delinquent was greater than in the non-delinquent. This appeared to clarify the problem of relative endomorphic strength which arose in the analysis of the bodily ratios or indices.

The comparison of the two groups in somatotype categories showed a number of statistically significant differentiations. The delinquents, relative to the non-delinquents, manifested an excess of extreme mesomorphs, an excess of mesomorphs, an excess of endomorphic mesomorphs, a deficiency of extreme endomorphs, a deficiency of extreme ectomorphs, a deficiency of ectomorphs, and a deficiency of mesomorphic ectomorphs.

A comprehensive view of each of the juvenile groups portrays the delinquents as being predominantly mesomorphs of one sort or another, with about equal representation of ectomorphs, endomorphs, and balanced types all in decidedly subordinate frequency. The non-delinquents, on the other hand, display a somewhat greater preponderance of ectomorphs over mesomorphs, while the endomorphs and balanced types in these juveniles, are only in minor representation although in equal frequency.

It is important to indicate that, throughout the somatotype analysis, the magnitude of the differences between the delinquents and non-delinquents, as well as the uniformity of the results by both methods, were very impressive. They are all the more significant in that independently they served to confirm the findings previously derived from the measurements and indices.

This, in brief, is a summary of the more significant findings derived from an analysis of the morphological material. These are the factual data on which are based the speculations and interpretations contained in the discussion to follow.

Discussion

The role of physique as a prime manifestation of the "constitution" of the human organism is axiomatic. Not only does it provide the basic framework through which the individual functions, but its importance is more far-reaching in that the individual's physique is, in the main, biologically inherited, genetically determined. Body-build being thus "a product of influences emanating from the germ plasm" is therefore a constitutional determinant in personality formation. The extent of its significance in shaping personality is most cogently expressed by Kluckhohn and Murray (1948):

> "... biological inheritance provides the stuff from which personality is fashioned and, as manifested in the physique at a given time-point, determines trends and sets limits within which variation is constrained. There are substantial reasons for believing that different genetic structures carry with them varying potentialities for learning, reaction time, for energy level, for frustration tolerance. Different people appear to have different biological rhythms: of growth, of menstrual cycle, of activity, of depression and exaltation.... Personality is also shaped through such traits of physique as stature, pigmentation, strength, conformity of features to the culturally fashionable type, etc. Such characteristics influence a man's needs and expectations."

Certain personality traits, themselves, are the product of one's biological inheritance, albeit the extent of their development and expression is environmentally influenced. This being so, knowledge of body build or more particularly any demonstration of consistent relationship between physique and personality characteristics may throw light on inherent predispositions towards special types of behavior which tend to manifest themselves in a given physical, social, and cultural environment. The nature of the evidence derived from such demonstrations of relationship between physique and personality is essentially statistical. All that can be said is that an individual with a particular type of body build is *more likely* to exhibit certain personality traits (and hence behavior patterns) than an individual of another body build form. In dealing with normal individuals, the relationship is rarely a one-to-one relationship except when confronted with the most extreme types. The most satisfactory interpretations, however, apply to group analyses. In this realm, broad generalizations with respect to personality and behavior can be deduced with considerable confidence from evidence of body build structure.

In this monograph we are concerned with a comparative study of the morphological characteristics of juvenile delinquents and comparable non-delinquents. The results of this investigation show clearly and unequivocally that the delinquents are differentiated in physique from the non-delinquents. Significant differences were noted between the two groups in every morphological aspect studied, in gross measurements, anthropometric indices, bodily disproportions and masculine component, as well as in somatotype. The differences between them are in many instances substantial, but even more important they are consistent. These differentiations can hardly be characterized as random divergences or ascribed to chance sampling.

In view of these findings the pertinent questions which arise are: (1) Do the delinquents show evi-

dence of physical inferiority as compared with the non-delinquents? (2) Does the nature of the physical differences between the delinquents and non-delinquents suggest personality trait differentia for the two groups? (3) If so, how do these personality factors operate in the development of such socially deviant forms of behavior as criminal delinquency? (4) To what extent may we regard such criminal behavior as resulting from constitutional predispositions inherent biologically in the individual?

The answer to the first question can be presented briefly. If we define physical inferiority as representing smaller gross size, more fragile skeletal structure, weaker musculature, and less masculinity, then, from the data on hand, there is no evidence that the delinquents are physically inferior to the non-delinquents. If anything, there is a tendency for the reverse to be true. Of the sixteen gross measurements considered, the delinquents display larger mean dimensions in eleven instances. In body weight, for example, the delinquents are on the average almost three pounds heavier than the non-delinquents. However, the differences are on the whole quite small and certainly do not reflect any substantial superiority in gross size on the part of the delinquents. On the other hand, in skeletal structure and muscularity the delinquent series displays considerably more ruggedness, massiveness, and hardness than the non-delinquent group. This may be seen in the consistently greater degree of mesomorphy in the former series. As far as masculinity is concerned, we have already noted the fact that the delinquents are more masculine in physique than the non-delinquents.

Our data give no support to those who characterize juvenile delinquents as stunted, underdeveloped, defective, and constitutionally inferior biological organisms. As far as our material is concerned, the delinquents as a group are in physical structure *normal* individuals. They are no less normal than other juveniles of the same socio-economic category, although the possibility remains that they may be somewhat less well-developed than juveniles of a higher socio-economic level.

The answer to the second question, which is concerned with the association of physical characteristics to personality traits, is a much more complicated matter. However, the results of other investigations with respect to disproportions, masculine component, and somatotype serve to throw light upon the significance of our own findings.

To begin with, body disproportions have been demonstrated by this writer to be associated with a definite syndrome of personality traits (Seltzer, 1946). From an analysis of the body proportions of a group of "normal" young men investigated by the Grant Study of Harvard University, it was found that individuals possessing certain disproportions had a greater frequency of those *dominant* personality traits that indicated greater sensitivity and complexity of the personality, and a lesser capacity for making easy social adjustments at the personal level. Some of the traits which went with the disproportions were:

"unstable autonomic functions
mood fluctuations
sensitive affect
bland affect
inhibited
self-conscious and introspective
motivations towards physical science
cultural
ideational
verbalistic
asocial"

On the other hand, the young men with a deficiency of body disproportions had abundant traits suggestive of vitality, directness, relative insensibility to fine influences, good integration, and ease in making social relationships at the personal level. A few of the traits most associated with the non-disproportionate individuals were:

"vital affect
practical organizing
humanistic
pragmatic"

The application of this knowledge to our juvenile study leads us to a set of most interesting results. Since the data indicate that our delinquent group shows decidedly fewer disproportions than the non-delinquents, then it would appear that the delinquents have a relatively greater frequency of those traits indicating vitality, directness, relative insensibility to fine external influences, the pragmatic trait, and sociability. Following the definitions of the trait groupings as given in the Grant Study material (Seltzer, 1946), the delinquents should tend to be more frequently "characterized by vitality and richness of affect. They show a spontaneous force and energy which depends upon voluntary effort of the higher ego functions. Such boys show richer verbal expression, greater animation of facial expression, and a more arresting tone of voice... (they) lack

deep interest in any subject matter. They are not theoretical, speculative or scholarly. Their interests are more practical, and in their course work they are better in organization than in analytical or creative work. They describe an interest in managing or organizing and find their satisfaction in the sense of accomplishment, of 'getting things done'. They do not strive after 'higher values and are essentially pragmatic in their outlook...(they) are essentially practical in outlook, and are not concerned with an ultimate purpose and value of life.... The practical considerations of getting ahead in life outweigh intrinsic interest in work, cultural values, philosophical speculation or special reform...(they) have a dominant interest in people, and (are those) for whom a knowledge of people and a desire to do work which will bring them into contact with people is an outstanding feature of their personality."

Our non-delinquent series, because of the more disproportionate nature of its physiques, should be characterized by a relatively greater frequency of those traits indicative of sensitivity and complexity of the personality, and a lesser capacity for making easy social adjustments at the personal level. According to the Grant Study definitions of this syndrome of traits, the non-delinquents should distinguish themselves from the delinquents in the greater frequency of those individuals "who show manifestations of instability in the functions which are generally conceded to be governed by the autonomic nervous system. Included are boys who show either periodic excessive anxiety or an undue amount of chronic anxiety as well as those subject to such symptoms as tremulousness, blushing, increased perspiration, palpitation and functional disturbances of the urinary and gastrointestinal systems...(they) create the impression of being sensitive, subtle in their thinking, inclined to aestheticism which makes difficult their acceptance of the usual values and adjustment to the realities of life... have a strong degree of conscientiousness and who frequently have doubts about doing things which they condone intellectually. They frequently describe a strong sense of responsibility, have difficulty in freeing themselves from their early moral attitudes.... A lack of spontaneity and freedom and a degree of stiffness in manner are characteristic...(they) are highly aware of their own thoughts and subjective feelings. They tend to pay more attention to what is going on within themselves than do more natural and outgoing boys. They also have a heightened sense of being observed by other people, even though they know this to be untrue. In consequence, they are self-conscious and cannot behave with directness and ease in social situations...like to deal with ideas.... They tend to be theoretical or analytical...(they) experience a high degree of tension in social situations, and are embarrassed, reserved, and awkward in manner.... A sense of social insecurity and a lack of confidence are frequently described, which are most marked in social situations.... (In addition there is a) group for whom social life, intimate friendships, and an interest in people are relatively unimportant. Such young men are satisfied with their own company and in the extreme are considered the 'lone wolves'."

Although the body build complex referred to as weakness of the masculine component is found to be on the whole relatively infrequent in our juvenile series, nevertheless it occurs far more often in the non-delinquents than in the delinquent group. Its significance in terms of personality may be derived from a previous study of this author in which the masculine component was demonstrated to be associated with certain aspects of the total personality of the individual (Seltzer, 1945). To quote from this study:

> "Considered as a group, the individuals with weakness of the masculine component exhibit a characteristic pattern of traits which form a consistent and harmonious picture. Briefly summarized, these less masculine persons may be described as having, in general, an aversion to strenuous exercise and sports, particularly those involving bodily contact. They are apt to be low in physical fitness for hard muscular work and often poor in muscular coordination. In the realm of personality structure, they present an affect which is more frequently sensitive and seldom the type which is described as 'vital.' In the autonomic functions, they show a strong tendency to possess manifestations of instability in the functions which are dependent on the vegetative nervous system. At the level of the basic personality, they appear to present higher frequency of cases of individuals whose personality structures are 'less-well integrated.' With respect to the question of motivations, they are inclined towards the 'ideational' and 'creative and intuitive' traits, while showing an infrequency of 'practical organizing' and 'physical science' characteristics. In social traits, they are apt to be more frequently 'shy' and 'asocial', and in the purposive and controlled functions 'self-

conscious' and 'inhibited'. At the attitude level, they fall more frequently in the 'cultural' grouping and are less prone to the 'humanistic' and 'pragmatic' traits than the strongly masculine category."

What is striking here is that the pattern of traits which are associated with weakness of the masculine component is in many respects very similar to the traits suggested by the disproportions. Thus, the evidence of both disproportions and weakness of the masculine component support the delineation of the non-delinquents as being more sensitive and complex in personality structure than the delinquent group. The new evidence is not to be regarded solely as confirmatory but rather as additive information since the individuals with weakness of the masculine component are not likely to be those who possess many disproportions.

On turning to the personality implications of the somatotype, we find that Sheldon and his coworkers have articulated a temperament classification to his system of body build organization (Sheldon, 1942). Three primary components of temperament, viscerotonia, somatotonia, and cerebrotonia, are recognized by Sheldon as being equivalents of the three morphological components. Viscerotonia, the temperamental counterpart of endomorphy, refers essentially to the strength of the element of sensuality (except sexual sensuality) and is manifested by a number of externally observable characteristics. Prominent among these external characteristics are relaxation, externalized emotional warmth (extroversion of affect), and strong appetites, such as appetites for foods, for social companionship, and for physical comforts. Other traits pertinent to this component are evenness of emotional flow, tolerance, complacency, easy communication of feeling, need of people when troubled, and an orientation toward childhood and family relationships.

Somatotonia, which corresponds with mesomorphy on the anatomical side, is a complex of traits associated primarily with the "functional and anatomical predominance of the moving parts of the bodily frame" and in which the activity of the voluntary muscles is persistently a driving force. Somatotonia is, therefore, expressed by assertiveness of posture and movement, love of physical adventure, need for energetic outlets and exercise, love of dominating, lust for power, love of risk and chance, bold directness of manner, physical courage for combat, competitive aggressiveness, psychological callousness, freedom from squeamishness, and extroversion of action. Other important characteristics of this component of temperament include insensitiveness to inhibitory suggestion, spartan indifference to pain, need of action when troubled, and an orientation towards goals and activities of youth. The "natural leader" is necessarily high in somatotonia.

The third Sheldonian temperament component, cerebrotonia, is distinguished by tension, unrelaxability, together with an internalization of response in general—introversion of both feeling and action. When this component is very predominant, the individual is hyperattentional, overattends to all stimulation and is oversensitive to inhibitory influence. Some other traits characteristic of cerebrotonia include restraint in posture and movement, love of privacy, emotional and vocal restraint, sociophobia, poor sleep habits, substitution of cerebration for direct action, need of solitude when troubled, and orientation towards the later periods of life (Sheldon, 1942).

The extent of relationship claimed by Sheldon between his somatotype and psychotype components is marked by correlations at the high level of about + .80, based on data on a series of 200 young academic men. Unfortunately, independent confirmation by other investigators of this very high degree of association at all component levels is not yet available. Partial confirmation, however, has been found for a limited aspect of the integrated complex (Seltzer, Wells and McTernan, 1948). This independent analysis of the relationship between the somatotype and psychotype showed an especially frequent occurrence of *dominant* cerebrotonia where the somatotype *dominance* was ectomorphic. The degree of relationship below the level of component dominance was not investigated nor were other components apart from the third studied. Nevertheless, all things considered, there is presumptive evidence of close relationship between the somatotype and temperament components when they are in a state of dominance. But more particularly for our purpose here, where we are dealing with group comparisons, the general association between the somatotype components and the constellation of temperamental traits is presumably valid. Inferences that we may draw in this connection can be considered with confidence.

In the analysis of the somatotypes, one of the outstanding findings was that the delinquents were absolutely and relatively more mesomorphic and decidedly less ectomorphic than the non-

delinquents. Since mesomorphy is associated with somatotonia and ectomorphy with cerebrotonia, then our delinquents must be characterized by strong somatotonic traits and a relative infrequency of cerebrotonic traits. In comparison with the non-delinquents, then, the delinquent juveniles should be distinguished by more assertiveness, competitive aggressiveness, forcefulness, psychological callousness (insensitive to inhibitory suggestion) adventurousness and extroversion. They should be singularly deficient in those cerebrotonic traits which mark a large segment of the non-delinquents, such as tenseness, restraint, sensitiveness to inhibitory influence, sociophobia, and introversion.

As far as the endomorphic component is concerned, we recall that although instances of extreme endomorphs were more common among the non-delinquents, by and large the endomorphic strength of the delinquent was greater than in the non-delinquent. Translated into their temperamental counterparts, this would suggest that there is a small element, more frequently found in the non-delinquent group, who are true viscerotonics characterized by externalized emotional warmth, relaxness, love for food, comfort and companionship, tolerance, complacency, and amiability. On the other hand, among the delinquents there is to be found (in greater frequency) a group of mesomorphs (endomorphic mesomorphs) whose somatotonia is tempered with varying elements of the viscerotonic traits.

It appears, now, that we have answered the question previously posed, namely: whether or not the nature of the physical differences between the delinquents and non-delinquents suggested personality trait differentia for the two groups. The analysis of the measurements, indices, disproportions, masculine component, and somatotype clearly indicates important personality divergences between the two juvenile series. The picture that emerges is clear-cut, consistent, and harmonious. To state the matter over-simply, the delinquents appear to be "normal" individuals who are rich in vital energy, aggressiveness, physical courage, but particularly insensitive to inhibitory impulses. Relative to the non-delinquents, they are simple, uncomplicated, "thick-skinned" persons whose maturity of appearance and spontaneous drive together with a love for domination and power makes them "natural leaders" in their group. In contrast, the non-delinquents consist of more sensitive and complex personalities. They are more frequently characterized by considerably more tension and restraint than the delinquents. Especially sensitive to inhibitory influences, they tend to seek privacy and substitute cerebration for direct action. They are the "thin-skinned" individuals who are sensitive to social and cultural forces in the environment much as the seismograph is sensitive, geared to record the most minute tremors. Or, they may be thought of as having more antennae to pick up and transmit even the smaller atmospheric impulses to a sensitive internal system.

The reference to the delinquents as "normal" individuals is essentially morphological. As we have shown before, there is no evidence that they are defective, underdeveloped, biologically inferior human animals. Our data, therefore, do not support a contention that the delinquent group is replete with pathological or near pathological personalities. We would rather believe that the delinquents, as a whole, are "normal" individuals possessing a characteristic pattern of personality traits at the motivational and biological level which makes them more readily activated than others against our present standards of social conformity.

It should be emphasized that our descriptive designations of the personalities of the juveniles do not pretend to assert here or anywhere in this monograph that the personality traits are in whole or in part characteristic of every individual in the particular group. The associations are suggested on a statistical basis only. That is to say, for example, that the delinquents with a certain complex of morphological features are *more prone* to possess a definitive pattern of personality traits than the non-delinquents whose physical characteristics are consistently divergent from their law-breaking counterparts.

With these matters understood, we may then proceed to speculate as to the manner in which these personality factors of the delinquents may operate in the development of the socially deviant form of behavior known as criminal delinquency.

Kluckhohn and Murray (1948), in their brilliant thesis on a conception of personality, state:

> "Personality is the continuity of functional forces and forms manifested through sequences of organized regnant processes in the brain from birth to death. The functions of personality are: to allow for the periodic regeneration of energies by sleep; to exercise its processes; to express its feelings and valuations; to reduce successive need-tensions; to design serial programs for the attainment of distant goals;

to reduce conflicts between needs by following schedules which result in an harmonious way of life; to rid itself of unreducible tensions by restricting the number and lowering the levels of goals to be attained; and finally, to reduce conflicts between personal dispositions and social sanctions, between the vagaries of anti-social impulses and the dictates of the super ego by successive compromise formations, the trend of which is towards a wholehearted emotional identification with both the conserving and creative forces of society. Understanding a personality requires following its development through time, study of the processes of differentiation and integration, knowledge of the personality's endowments."

Attention is called particularly to the reference by these authors to the following functions of personality: tension reduction, self-expression, reduction of conflicts by scheduling, reduction of aspiration tensions, and the reduction of conflicts by social conformity and identification. It is obvious that the manner in which the more mesomorphic and hence more somatotonic juveniles express these functions of personality within their cultural setting has important bearing on their socialization and behavioral patterns.[3]

Kluckhohn and Murray stress the fact that the organism is primarily concerned with the reduction of one kind or another of need-tensions, and further that the process of reduction of these tensions gives the individual his satisfactions. The formula, tension → reduction of tension, they point out, is a katabolic process in which energies are released. Let us see, then, how this principle applies to what we know about our juvenile delinquents. The data indicate that the juvenile delinquents are decidedly more mesomorphic and hence more somatotonic than the non-delinquents. The need-tensions of individuals so constitutionally predisposed are by Sheldonian definition numerous and intensive. And, in contrast to the cerebrotonics, they are principally *positive* need-tensions. Somatotonics are primarily distinguished for their need for expression of physical energy, the need for domination of things and persons, a love of risk and chance, a need of action when troubled, and as a result of viscerotonic influence they may well have a secondary need for people and comfort. The need-tensions of somatotonics lay special emphasis on katabolic actions—release of energy—rather than on the anabolic restoration of energies. In these somatotonics the "ego-dominated" and "id-dominated" impulses are paramount.

In the reduction of these need-tensions, the somatotonic juveniles perforce express their reduction by action in contrast to cerebration. The "thick-skinned" somatotonic mesomorphs are especially insensitive to the needs and desires of other personalities. The finer and more subtle impulses and stimuli present in the surrounding milieu do not appear to penetrate their consciousness as readily as in other types. Because of their *high* threshold of awareness (afferent sensory nervous system), they are not constantly buffeted inwardly by social sanctions or special pressures within society which might act to inhibit their strong motor responses. In other words, somatotonics being by nature less restrained, less inhibited, and freer from inner conflict are more active and aggressive. The simple fact of greater aggressive activity of these individuals, exposes them more frequently to the commission of anti-social acts, especially when there are those persons among them who have not learned to express their impulses in socially acceptable ways. Accordingly, one of the forces operating to make the mesomorphs the largest contributors to juvenile delinquency is the fact that they reduce their tension through activity which may either by chance or design be channelized into socially unacceptable behavior.

The non-delinquents, on the other hand, who are more ectomorphic and hence more cerebrotonic, do not reduce their tension primarily through physical activity. These "thin-skinned" cerebrotonics are "superego dominated" and characterized by physical and mental inhibition, and by emotional restraint. They are specially sensitive to impulses in the environment and to the needs and desires of other personalities. They are marked by a high sense of awareness and attention, resulting in a mental over-responsiveness and often an apprehensiveness about everything. Sheldon has said "in a psychological sense he is naked to his environment, overexposed, and oversensitized." Owing to their *low* threshold of awareness, they are constantly being agitated by external environmental impulses which combined with their inner emotional conflict results in strong inhibition to motor activity. Whatever the responses, they are likely to be sudden, acute, often too rapid, and poorly sustained. Tension reduction in these cerebrotonic ectomorphs tends to take the form of withdrawal into privacy, sociophobia, absentmindedness, day-

[3]In this section we have drawn heavily for terminology and argument on Kluckhohn and Murray, (1948), and to some extent on Sheldon (1942).

dreaming, fantasy, procrastination, and physiological overresponse particularly of the autonomic nervous system.

We must remember at all times that the individuals we are dealing with are juveniles, and not adults, and consequently they are still in the process of being completely socialized. Socialization of somatotonic adolescents, we venture to state, is apt to be less rapid and less complete owing to their more uninhibited, aggressive, and energetic behavior. However, when mesomorphic somatotonics do become effectively socialized, particularly in adulthood, these individuals become stable, steady citizens, with strong conformist coloring (Sheldon, 1942; Seltzer, 1945, 1946).

We recognize, of course, that not all delinquency is due to a failure on the part of persons to learn to express their impulses in socially acceptable ways. Criminality is "sometimes rejection of existing institutions, sometimes the active assertion of socially prohibited responses." Somatotonic mesomorphs with their strong tendencies for being energetic, reckless, ambitious, spontaneous, undirected, and insensitive to the needs and desires of others are likely to be impatient with certain cultural constraints and existing institutions, especially when they interfere with their attainment of immediate "mode pleasures." Since these individuals are especially oriented toward the goals and activities of youth, and to the more immediate attainment of power, recognition, money and status, they tend readily to brush aside existing social restraints which may act to interfere with their impulsive activity. The net result is the commission of more anti-social acts than is evident for cerebrotonic ectomorphs. The latter, striving for "end pleasures" and content to secure their goals in a later period of life bend readily to their inhibitory impulses. Being overladen with a heightened need for and dependency upon the approval of others, these "superego-dominated" individuals shun socially deviant forms of behavior except in those cases in which socialization is so severe and so anxiety-laden that they respond by rejecting existing cultural goals and socially approved means of reaching them. Thus, the function of personality through self-expression, taking the form of reckless, energetic activity on the part of the mesomorphic somatotonics, contrasts sharply with the action system of the cerebrotonic ectomorphs who are more likely to take refuge in fantasies and in the construction of programs to be attained in latter periods of life.

The role played by scheduling in the reduction of conflicts, as far as its influence with respect to delinquency is concerned, is not absolutely clear. Sheldon has designated "resistance to habit and poor routinizing" as one of the outstanding traits of the cerebrotonic. Its antithesis, routinized and organized scheduling of events and programs, they claim is about equally viscerotonic and somatotonic. The point may be made, perhaps, that this latter capacity of somatotonics (especially when associated with a good measure of viscerotonia) allows them to plot and organize anti-social acts more readily than cerebrotonics.

The nature and level of aspiration tensions is obviously intimately associated with the culture of the society in which individuals live. Kluckhohn and Murray have pointed out that American ideologies have "encouraged a high level of extrovert aspiration for every individual," which is contrary to the normal tendency to reduce this level after failure of achievement. We have already shown that our mesomorphic somatotonics have by nature a high level of extrovert aspirations which is strongly reinforced by the ideology of the culture in which they live. Accordingly, the reduction of the aspiration tensions in these individuals through socially acceptable means cannot fail to be incomplete and result in much frustration and dissatisfaction. Since they tend to reduce their tensions through activity, then it is not surprising that they are more prone to do so wittingly or unwittingly by delinquent or anti-social behavior. Cerebrotonic ectomorphs, on the other hand, are not by nature as highly geared to *extroverted* aspirations and extroverted action. In these individuals reduction of their aspiration tensions may give full play to their introverted characteristics and is more often channeled off into varying forms of daydreaming, fantasy, and the like, as well as to overtly passive conformity.

We finally arrive at the last question to be discussed. To what extent may we regard delinquent behavior as originating from constitutional predispositions inherent biologically in the individual? Let us first consider the matter of general human behavior. Human behavior is the functioning of the personality of the individual in the external environment. Since the personality of the individual is the "product of inherited predispositions and environmental experiences," then the manner in which the personality functions is dependent on the individual's own biological impulses, variably modified by culture and specific situations, and the interests (overt and covert) of

other individuals and society. The role played by inherent biological factors has been exemplified by those studies which show a general statistical relationship between physique and personality traits. Since the relationship between physique and personality traits is thought to reflect inherent biological factors influencing general human behavior, then by the same token there are inherent biological factors which are in part responsible for delinquent behavior. This must be so since our data indicate clearly the existence of physical differences between delinquents and non-delinquents. These differences, by their very nature and magnitude, are not referable to racial or environmental factors which may pertain between the two groups beyond the selection process.

The conclusion, that there are inherent biological factors which are in part responsible for delinquent behavior, must not be taken to imply inherent criminality in individuals or the existence of fixed criminal anthropological types. But rather that the biological differences of delinquents reflect their possession of certain complexes of *normal* basic personality traits which under certain circumstances make them more readily activated towards the commission of anti-social acts. These personality traits or their combination are by no means the exclusive property of delinquents, but they are to be found *in greater frequency* in the delinquent population than in the non-delinquents.

It should be noted that we do not believe that all delinquents without exception are normal individuals with a certain complex of personality traits in comparatively greater frequency than in the law-abiding population. We recognize that among the delinquents there must be a small pathological group whose traits and impulses are so extreme and abnormal and so beyond voluntary control that they lead inexorably to delinquent or criminal behavior.

Although for the purposes of this study all the delinquents have been lumped together regardless of the nature of the offense committed, it is recognized that an analysis of the data on an offense basis is a necessary sequel to this investigation. In this connection, it is reasonable to predict that when this is done salient morphological differences will be ascertained between offense groupings of the delinquents. The logic for this projection is based on the principle of relationship between physique and personality and behavior. Variations in offense behavior should be correlated with variations in frequency distributions of morphological types.

Throughout, we have been constantly aware that the physical correlates found with delinquents are referable to the commission of anti-social acts *as defined in our society at the present time.* We recognize the fact that the definitions of anti-social acts are variable according to society, culture, and historical period. Whether or not an act is considered a crime, depends not only upon the nature of the act but also upon the attitude of society towards it. In our American society, anti-social acts are extremely heavily weighted on the side of offenses against persons and offenses against property. This fact has a direct bearing on the nature of the morphological types of our delinquents. Thus, the mesomorphic emphasis of our delinquents is a reflection of the accent in our society at the present of what it considers to be an anti-social act. If there were to be a radical change in American culture in its definitions of acts against society, for example, where ideological principles and practices would be considered the dominant overt acts against society, then it can be presumed that a quite different crop of physical types would fill our penal institutions. In other words, the physical types represented in our delinquents are in part referable to the anti-social acts as defined in our society at the present time.

In conclusion, the results of this investigation shed new light on the understanding of the juvenile delinquent. It appears from the evidence on hand that the delinquent may be conceived as a biological product as well as a product of the environmental forces about him. Although delinquents are physically different as a group from non-delinquents as a group, there is no implication of fixed criminal anthropological types, inherent criminality or criminal personality. The biological differences of delinquents are rather a reflection of their possession of certain complexes of normal basic personality traits which under certain circumstances make them more readily activated towards the commission of anti-social acts as defined in our society.

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DISCUSSION

HUNT: Dr. Seltzer's point that the morphological variants of man who take up crime may vary with time and culture is well taken. A small study of mine on criminals in Yap showed that natives with histories of incarceration from 1946 to 1948 were not significantly different from the other males in my series of somatotype. It is interesting, however, that all convicts whose mesomorphic ratings were in excess of 4 were found guilty of violent crimes against persons. In view of Dr. Sheldon's opinion that somatotonia carries a potentiality of physical violence, the association of criminal predilections and body build become very important. Many of us will certainly look forward to Dr. Seltzer's future investigations along such lines.

MONTAGU: I should like to ask Dr. Seltzer whether he has considered the possibility that the differences in physique in the delinquents may not have been the result of the delinquents' behavioral habitus rather than of their constitution. Being a delinquent is associated with a great deal of stress and strain. It has recently been shown that emotional stress and trauma are frequently productive of nutritional disturbances which are capable of bringing about remarkable bodily changes (B. F. Sieve, 1949, "Vitamins and Hormones in Nutrition. V: Emotional Upset and Trauma," Amer. J. Digestive Diseases *16*: 14–25). Such stresses and strains are also capable of acting upon the body through the neurohumoral system. I wonder what Dr. Seltzer's opinion would be in this connection?

(Editorial note: Dr. Seltzer did not wish to make any reply to this comment.)

SHELDON: Dr. Seltzer's findings appear to be well borne out by my own, which were published last year in a volume called *Varieties of Delinquent Youth*. In my study 200 youths were followed closely in Boston for a period of eight years. This study was running concurrently with the Glueck study, on which Dr. Seltzer has just now reported. However, our 200 were differently selected. The Glueck subjects were all taken from two of Massachusetts' most advanced "reform schools" for boys. Therefore they were, for their age, comparatively hardened or at least unusually persistent young "criminals." Our 200 were not all persistent criminals. Only a comparatively small number of them had been sufficiently troublesome to warrant their being sent to the reform schools from which the Glueck subjects were recruited. Most of our 200 were either feebleminded, or were primarily medical delinquents, or primarily psychiatric delinquents. When the mental, medical and psychiatric weaklings had been weeded out of our group (in the statistical analysis), a residue of less than ten per cent remained. This residue appeared to constitute a "hard core of primary criminality" and its description will be found to tally most remarkably with the material Dr. Seltzer has presented today (See *Varieties of Delinquent Youth*, pp. 671–718, and p. 744).

C. O. WARREN: Dr. Sheldon in his comments on your paper has pointed out that your findings appear to be well borne out by his own. He goes on to say that the group of delinquents you have studied constitute something less than ten per cent of the group he calls delinquent. Speaking as an outside observer, it seems to me that two questions should be raised: 1) The definition of "delinquency" needs clarification in the context of this discussion, for it makes a good deal of difference whether your studies are based upon a specially selected group of particularly belligerent delinquents (as Dr. Sheldon's comments imply) or with a group particularly chosen to represent a characteristic sample of delinquency; 2) only in the latter circumstance would you be justified in stating that "delinquents are physically different as a group from non-delinquents as a group." Merely on the grounds of what I have heard today, I am inclined to doubt that this statement is supported by your evidence. Rather, it seems to me, you have shown that a group of particularly aggressive delinquents are found to be well qualified for their profession by being predominantly mesomorphic in body build and (presumably) somatotonic in personality. These constitutional traits also qualify them to be bank

presidents, executives or Harvard students. It is one thing to say that they are well adapted to an aggressive form of delinquency and quite another to imply that antisocial conduct (even in the limited terms of our own society) is more prevalent among individuals with this somatotype than among others.

SELTZER: A perusal of *Unraveling Juvenile Delinquency* will show that the selection of the delinquent group emphasized "persistent" offenders rather than "aggressive" offenders. Accordingly, the conclusion referred to in the monograph remains valid.

THE SOMATOTYPE, THE MORPHOPHENOTYPE AND THE MORPHOGENOTYPE

W. H. SHELDON

Department of Medicine, College of Physicians and Surgeons, Columbia University

During the ten years that have transpired since the first public perpetration of the concept of somatotyping, quite a number of those here today have shown interest in the difficult and fascinating problems associated therewith. The first task undertaken was that of recording certain aspects of human personality at an overt structural level in such manner as to offer an anchorage and a frame of reference for correlational inquiry at other levels of behavior. The main problem confronting us was that of defining norms, first for overt structural variation, and later for concomitant or independent variation at more complex levels called physiological, biochemical, immunological, and behavioral. It may be said that constitutional inquiry started with physical anthropology, although I think it has offered only an oblique contribution to the current academic conception of that subject. It will be only by finding a way to relate physical anthropology to physiology and biochemistry, to clinical medicine and to the social sciences, that the constitutional methodology may perhaps be able to bring in new life and new meaning at all of these levels.

If in the constitutional approach there is a contribution to the study of human genetics, I think it will be the same kind of contribution. The task we have set ourselves has been that of recording what is seen, or more technically, the task of applying an operational taxonomy to successive phenotypic presentations of human structure, and relating these phenotypic presentations to clinical and laboratory findings. Behind the successive phenotype presentations we assume that a genotype pattern is at work, but in constitutional work our concern has not been to try to describe the genotype as such, or to attempt to isolate specific genes. It has been our supposition that in the end it may prove very difficult to establish a sharp line between the structural presentation and the gene pattern determining it. If this is so, one way of getting at the gene structure may be by going about it the long way around, or by recording with infinite care and patience the changing presentations of the phenotype under the whole range of its conditions and environmental influences.

Perhaps a simpler way to put the matter would be to say merely that the aim of the constitution project has been to follow the human phenotype (systematically or classificationally) in both its biological and its social relationships. The watchword at the Constitution Laboratory is this: To re-establish the broken continuity between biological and social science.

That continuity is lost wherever the oneirophrenic proposition is entertained that bodily structure is to be considered one thing while personality, or mind, or even the genic pattern is considered as something else independent of it and out of the continuum with it.

In making the assumption that human behavior, whether physiological, hormonal or mental, is always structure in action, I suppose we follow Vaihinger's philosophy of *Als Ob*, although reversing the premise. You will recall that Vaihinger suggested we live and think *as if* Mr. G were running the show and therefore were carrying the responsibility for it. As a way of life that proposition offers many ameliorations. Vaihinger may have had an irreverent or possibly unchastened way of referring to Mr. G as God, thus calling the deity too familiarly by his first name, but he had no false notions of ultimate truth, and no illusion of immediate knowledge of Mr. G. He merely liked the idea of jettisoning the responsibility for human social control, and of thus avoiding the task of building a naturalistic foundation for social science. He preferred to live *as if* Mr. G had already established permanent criteria for human delinquency and for excellence of performance, thus abolishing any need for continuity between biological and social science, and also abolishing the virtue of genuine humility from human affairs.

Philosophically we reverse Vaihinger's premise and elect to proceed as if it were known, a thing given, that biological and moral matters on this planet lie in a continuum, and that human structure in action is human personality, whether conscious or unconscious. We assume then that the somatotype and personality are but differently measured and differently presented reflections of the same thing. That is, both are reflections of bodily structure at different levels of action, or more par-

ticularly, at different levels of measurability of the action. In a preliminary way I would define the somatotype, then, as the characteristic presentation of the individual at the level of overt morphology.

Such a point of view rests on a somewhat austere, monistic *Als Ob* assumption, but it is my dark presentiment that only through general acceptance of it will the great schismatic tragedy of this age be overcome, and will final human disaster for the time being be averted. The immediate tragedy lies in the schism between biological and social science, and I think the major cause of the schism inheres in a failure on the part of social scientists to face the implications of the structure-function continuum in human life. Constitutional research is essentially an inquiry into the various expressions of this continuum at different levels of manifestation. I think that this kind of research, if it could be given its head in human affairs, is perhaps now sufficiently operational and sufficiently oriented to organic structure to reach into the problem of social control. It might in time reach to some practical understanding of the patterning of our intricate mechanism of genetic determination of new structure, and might connect this up, in a single language system, both to the most overt manifestations of personality as revealed by the somatotype photograph, and to the practical function of relating these overt manifestations to more covert indications.

The unique contribution of constitutional research, if indeed any contribution can be claimed, has been that of contriving to reflect different levels of personality in a single language system and from a common frame of reference. In sanguine moments it has sometimes seemed possible that unity can thus be established between biological and social science, and that we may thereby emerge from the incessant terminological squabbles which have characterized the contemporary effort even to describe the social scene.

We are interested in the somatotype because it appears to be the most basic *general characteristic* of an individual, and some of us entertain the feeling that locked up in the enigma of the somatotype there is a clue to the crucial problem of bringing biological and social studies into a single focus. Until this can be done it will not even be respectable to mention the central problem of social science, which undoubtedly is that of controlled human breeding. Even today there are people among us who, on hearing the term breed or breeding, make a face like the face a nice New England grandmother I know used to make when the Grand Union Tea Wagon went by her house. Painted in big yellow letters on its red body were the letters G U T, which by no means made a nice word. You couldn't see the punctuation after the letters because the house was set too far back from the road. But that story had a happy ending, and the grandmother was pleased when the old yellow G U T was changed to a shiny black A & P.

Possibly we can effect a similar result by substituting the term applied genetics for controlled breeding, and of course there will not be "human stud farms" but bureaus of genetic research. It does make a difference how things are put, as a certain prominent politician found when he hired a biographer to write him up. He was worried about his brother who had been sent to the electric chair, and about his father who had been hanged. Brother Joe, the biographer wrote, occupied the chair of applied electricity in one of our largest institutions. Joe died in harness, and the father too died at the very height of his career.

The moral may apply to the term somatotype, which was used originally to refer descriptively or taxonomically to a *predicted trajectory* through which a particular human physique would pass under given conditions. This term has always carried a dynamic connotation. It refers in effect to an attempt to predict (from past and present indications) the structural future of the organism in question—always under given conditions. The somatotype attempts to supply an identification to the sum of genetic factors, which is to say, the sum of continuing influences relating to the structure of the organism. The somatotype is at worst a guess and at best a well proved formula intended to designate the fixed genetic influence, which in turn might be called the *morphogenotype*. Before it can be assumed that the somatotype does in fact reflect the morphogenotype with any accuracy, it is of course necessary to repeat the somatotype photography of the subject at as many points as possible throughout the course of the latter's life. Since two points are needed to determine a simple straight line it is understandable that more than two samplings of the phenotype will be needed in order to bracket the complex trajectory of the morphogenotype. Indeed there is no reason to suppose that by the method of somatotype photography it will ever be possible to know the morphogenotype *in toto*. What we do suppose, and assume for purposes of setting up an operational procedure, is that through highly standardized three-dimensional studies of the phenotype, repeated serially, we may be opening

one avenue of attack on the morphogenotype which would not be opened by other and more piecemeal attacks on the problem of genetic determination of structure.

Epigrammatically, the somatotype procedure is an attempt to identify the three-dimensional trajectory through which an organism is in the process of passing, from conception to dissolution. The morphogenotype might be defined as that ideal three-dimensional trajectory along which the organism has been predetermined by its genes to travel when environmental influences are held constant, or under certain conditions which I have elsewhere called basal. By basal conditions we mean environmental circumstances in which nutrition and exercise remain within certain expected limits and there is no serious pathological interference.

The *morphophenotype* is simply what you now see—literally, the form showing. It is the three-dimensional pattern of the organism at any given time and under the conditions prevailing. By such definition, the morphophenotype of course changes, from day to day and constantly from conception to death. The alleged controversy over whether or not the somatotype changes can arise only from a confusing of the somatotype with the morphophenotype. The latter changes with growth and aging, with nutritional variation, with pathology.

The *morphogenotype* is a name for the original hereditary and continuing genetic influence which cannot change, after conception has taken place, and the somatotype is the upshot of our best effort—even if only a crude and unsatisfactory effort—to gauge the morphogenotype. I think we can grant that this effort is still unsatisfactory without thereby laying claim to unseemly humility. It is not easy to master somatotyping. In the past it has not even been easy to get at the problem. Nature presents a sufficiently wide diversity of phenotype to baffle the taxonomic mind at almost every level of attack, and where nature has not left formidable obstacles man has constructed a few of his own. There are men living who do not seem particularly to *want* the problem of the somatotype to be mastered. If you doubt this, set yourself up a hobby of arranging and financing a long term project in this field.

Such a project needs to be planned for a greater span of time than that of one lifetime, and I am afraid there is grave doubt that much light can be shed on the vital underlying problems of human genetics until we have followed closely, for several generations, both the somatotype and its physiological and behavioral correlates as these reveal themselves in all the descendants of a group of contemporary subjects. Just how large a group this need be, and how selected, and how motivated to cooperate fully in such a research program, and how the job is to be financed and carried out—I will not this afternoon attempt to say. But there is our central problem, and all of these questions are important. However, they will remain secondary questions, or even *nonsequitor* until the primary decision to *do it* can be made.

The somatotype then is not to be confused with the morphogenotype but is only an attempt at the latter. Nor is it to be confused with the morphophenotype which—to use a nautical term—is but a single sounding contributive to the somatotype. The somatotype is the makeshift causeway by which we attempt to progress from phenotype to genotype; or better, it is a sort of trial pattern intermediate between phenotype and genotype by means of which we attempt to reconstruct the underlying genetic pattern from many presenting fragments. We can derive a guess at the somatotype from the pattern of a group of anthropometric measurements taken from the standardized photograph, or (with the height and weight history known, and the medical history, and with a certain background of experience) we can try to read the somatotype direct from such a photograph. In any case the somatotype, expressed as a series of numerals, is to be considered but a tentative representative of the morphogenotype—in statistical terms an assumed morphogenotype.

The question may be asked, *how many* somatotype observations, at what age periods, and under what varying conditions, ought to be made before one can feel tolerably sure that the somatotype is now indeed correctly bracketed and will not be likely to appear to change? The answer to this question of course depends in part upon the level of detail at which one has undertaken to express the somatotype. When the somatotype is represented only by the three numerals which are used to express the strength of each of the three primary morphological components, respectively, and when these numerals represent points on a 7-point scale, we have found that it is only the very exceptional individual who on a later occasion appears to present a somatotype different from that presented on an earlier occasion. In short, it is usually possible by standardized photography to determine the somatotype fairly accurately (at the level just defined) even from the first properly taken somatotype photograph. This is true at least in the case of adults. It

appears to be true also when the first photograph is that of a normally growing child. Each somatotype appears to follow its own trajectory faithfully from birth—and probably, we suppose, from conception—if environmental influences and pathology are held within the limits of reasonable expectation. The exceptional individuals who sometimes seem to depart from this rule usually present an excessive nutritional variation, either starvation of tissue or an unexpected laying down of fat. Such a deviation can usually be shown to be accompanied by at least one measurable disturbance of endocrine function, often by several disturbances.

It is a fair question to ask whether the endocrine dyscrasia itself is not usually an expression of, and endemic to, some underlying organic dysplasia carried in the *covert* morphogenotype although not revealed in the *manifest* morphophenotype—at any rate not revealed by the procedures we are employing now. Such a question need not imply an affirmative answer. It may be possible that the orchestra of the endocrines can sometimes go off the tune because of factors not related to its own genetic pattern, but it is at least likely that in those flagrant instances where the result is some gross alteration of the morphophenotype, the predisposing tendency will sometimes have been resident from the beginning in the endocrine pattern itself. In this connection it should be remembered that each individual stamps his own characteristic chemical structure on the building blocks which enter into his tissue, as truly as he molds the whole into a characteristic somatotype structure. The endocrine system makes up part of the total bodily structure and is quite as truly an expression of the reaction of the morphogenotype upon the available environment as is the skeletal or muscular system. If we could get at the endocrine system, and if we could somatotype it, we might be able to predict its behavioral tendencies as well as we can predict the trajectory of the somatotype.

The photographic somatotype reveals the general morphologic character of the organism as a whole, and expresses it in terms of an operational taxonomy which has been shown to be useful for correlational purposes. The endocrine system is contributive to the somatotype, is indeed an integral part of it, but the endocrines have not yet been described in terms of the continuous multidimensional distribution within which they almost certainly operate. Therefore we as yet have only fragmentary, eclectic knowledge of the endocrine-somatotype relationship. Similarly, we still lack a satisfactory key to an understanding of the relationship between the outward personality of an organism as seen in the somatotype photograph, and the inward personality which is expressed in the cellular structure.

One of the things we have learned recently is that the cells of which human bodies are built are not irreducibles, not shaped to a common mold like the bricks of houses, but cells are living things with personalities. Within the present century it may become possible to somatotype cells, and to see them in somewhat the same perspective as that in which we are now accustomed to see the human organism as a whole. Since every cell in the body carries the morphogenotype of the whole organism, in the sense that it carries what we call the "genes" of the organism, it seems a reasonable probability that the cell will be found to reflect a microscopic morphogenotype which will be as distinctive and characteristic as the macroscopic morphogenotype of the organism as a whole. Thus it may turn out that the personality of cells will throw light on the personality of organisms. It may then be possible to build up a body of psychological knowledge which will in fact bridge the gap between biological and social science. The problem of human delinquency—human failure—would then further merge with that of medical pathology, for it is likely that the delinquency that matters in our present human scene is not primarily "social" but cellular, and not merely cellular but deeper, within the genetic structure which is the vehicle of heredity.

The most important thing to know about a human organism, I should think, is the nature of its genetic influence, in-so-far as that can be read from what can be seen with our available equipment. Some of this genetic influence appears to be inferable from the somatotype, and there is reason to hope that more of it can be read when we are two or three decades further along in our acquaintanceship with the morphogenotype, both macroscopic and microscopic. Meanwhile the way seems to be open to expedite such an acquaintanceship remarkably by following the presenting organism with standardized three-dimensional photography and with correlation at all levels—chemical, physiological, clinical, behavioral. Photograph, observe and correlate, repeatedly and if possible at regular intervals.

DISCUSSION

ANGEL: Do you have evidence for any difference between delinquents and controls in onset

of puberty or bone age, which might help to account for the body build difference?

SHELDON: No, in my series of Boston delinquents we do not have data as to the onset of puberty or bone age.

BOYD: I am sure few of us would object to the idea that there are inherited constitutional traits in man. I would like to remark on one point, which I believe to be of fundamental importance. This is in regard to general methods of resolving a complex effect into its component elements. In the analysis of proteins by electrophoresis, separate proteins may be resolved into separate peaks in the photographs which are taken. But if they do not differ much in electrophoretic mobilities, the peaks representing them may be only partially separate. If partially separate, they may sometimes be resolved by reconstructing the individual curves from the combined picture. But if several proteins, only slightly different, are present, a sort of plateau may result, and a large number of hypothetical reconstructions may be possible. Artificial resolution into a number of hypothetical components may be attempted, but must be verified by actual physical or chemical separation later. If this cannot be done, the construction remains hypothetical, without real validity. I submit that this is the case with the constituents of the somatotype. How are we to know if only three components exist, and if the relative amounts have been correctly estimated? Unless these components, or features on which they are based, can be found to be segregating genetically, can one ever have any confidence in the objective reality of the components? The protein chemists long ago gave up such hypothetical reconstructions.

SHELDON: Dr. Boyd's provocative comment raises points which I suppose might bear further exploration, and I only wish that I were more competent to discuss with him the impingement of these upon his own field of biochemistry. The analogy between constitutional analysis and analysis by electrophoresis may be somewhat difficult to sustain but I suppose there does seem to be a point in common. By electrophoresis the complexity of serum proteins has been resolved, somewhat grossly, into albumin and at least three types of globulin. In a very general way somatotyping does for the classification of human structure-as-a-whole what electrophoresis does for the protein fraction of the serum. Somatotyping deals with a continuum of several interdependent variables, and electrophoresis also attempts to deal with a series of variables, but the two series of variables are quite different in kind, and the methods used are entirely different. Admittedly the mere separation of the serum proteins into four or five components, or the similar segregation of enzymes, hormones and so on, does not tell us the nitrogen content of these fractions or compounds, or the molecular weight, although it might be added parenthetically that an experienced individual in the field can and sometimes does hazard an educated guess with some confidence. However, this shortcoming does not preclude the wide application of electrophoresis to the study of certain types of cancer and to allied fields of medicine, for it is a helpful diagnostic aid. In a somewhat comparable way, I suppose, we cannot resolve the "somatotype pattern" of an individual by stating that he has *a* per cent of endomorphy, *b* per cent of mesomorphy and *c* per cent of ectomorphy, the respective compositions of each being *x* per cent of fat, *y* per cent of protein and *z* per cent of carbohydrate. Yet I would remind Dr. Boyd that the somatotyping procedures have proved to be of use in many fields of research, and that when used as a frame of reference they lead to valid correlation at a number of levels of human performance, including immunological and clinical performance. I would add too that since the writings of Tiselius in 1930, electrophoresis has made rapid strides and has undergone remarkable development in technique. It may be reasonable to suggest that the methods of somatotyping—now only ten years from their publicational beginnings—will in another decade undergo similar expansion both in adequacy and in general interest.

BUZZATI-TRAVERSO: It seems to me that, irrespective of its clinical value, any such classification of human types, as that presented by Dr. Sheldon, has little importance for the problem under discussion, the evolution of man, until it can be shown that such constitutional features are being inherited. There is of course no doubt that constitutional types are the product of both heredity and environment; for evolutionary considerations the problem boils down to the question: are physical and psychical traits, as revealed by the study of constitution, being inherited and how? The same question holds true in animals as well as in man, because any careful observer of animal species can distinguish, within the array of so-called normal phenotypes, different "types," different "constitutions." I am sure that it is very important at the present stage of development of studies on human and animal biology to try to clear up the question of the inheritance of

traits of this nature. But I do not think that this question can be solved only by means of more or less refined classifications of types. What is needed is a study of the inheritance of quantitative characters; this can be accomplished with a fair hope of success applying the modern statistical and genetical techniques of multivariate analysis and of polygenic characters, as I have already pointed out in my paper. It seems to me that we should start analyzing this problem on some animal that can be easily bred, in order to find out whether we can find out some "factor," in the multivariate analysis sense, which is transmitted from one generation to the next; then we should study how such factors are being inherited and how far can they be influenced by the environment; for this point the analysis of polygenic traits as developed by K. Mather can be very useful. Once cleared up the question experimentally, we can proceed to the study of constitutional types in man. But one can be sure that we shall not analyze, at this stage, the inheritance of constitutional types as such: such an investigation, if ever tried, would not be more meaningful than a study of the genetics of those morphological characters which are being used by taxonomists to classify species or subspecies in organisms other than man. The study of constitution, as it has been developed by the German and Italian schools and now by the studies of Dr. Sheldon is surely a very valuable contribution to the problem of the classification of mankind. But any effort along this line cannot bring any evidence as to the inheritance of body build and temperament in man.

SHELDON: Dr. Buzzati-Traverso has thoughtfully and considerately pointed out that to describe a "phenotypical" presentation of human organisms is not tantamount to explaining the differences. He implies that even after we have collected standard photographs of satisfactory samples of such populations as there are, and have described these as meaningfully and relevantly as may be possible, through a series of generations, we still will not have altogether explained how these different organic patternings came about. That is, we will not have differentiated perfectly between hereditary and environmental causation. Concerning this there can be no disagreement. But Dr. Buzzati-Traverso further suggests that *therefore* the plan of keeping standard photographic records of human beings, and of classifying them according to some standardizable frame of reference, would have little importance for the problem under discussion—the evolution of man. Here I think he is mistaken, although the mistake is in a good cause. He wants to deal only with specific, easily quantified traits, to isolate these and to study their inheritance. That is, he wants to purchase the advantage of perfect objectivity, perhaps at the price of relevancy. For my part, although I recognize the immense importance of the kind of research Dr. Buzzati-Traverso recommends, I believe he is on dangerous ground when he recommends *not* carrying out the converse, or the complement, of this kind of work. I believe it is as important to record the presentation of the human organism under the low power of the microscope as under the high power, and I fear that as a group we biological scientists have been slow to appreciate the possibilities in standardized life photography. We lose the plan of the woods in the study of the trees.

CAIN: The problem which Dr. Sheldon has set out to investigate seems to be purely taxonomic, namely, the description of a very polymorphic species. The method selected is to describe every individual in terms of three extreme types, chosen rather arbitrarily. If this is so, it is hard to understand the difficulties raised over the differences in the scatter diagrams for women and for men. If one sex in a particular fish is larger than the other, the ichthyologist cannot adopt different standards for his measuring to make the recorded data for both conformable. The real difficulty seems to be that whereas correlations are stated to be found between the scatter diagram for men, based on their physique, and the psychological tendencies of the same men, these correlations are not apparent in the diagrams for women. Apparently what has been demonstrated is a secondary sexual difference, but that gives no grounds for altering the taxonomic standards for women until correlations do exist.

SHELDON: In connection with Dr. Cain's comment it should be mentioned that in my talk I showed a slide presenting the distribution of somatotypes for 1,000 young women. This is from an incomplete and still unpublished study. The slide indicates that when women are somatotyped by the same criteria and standards that have been developed for men, they tend to mass quite dramatically toward the endomorphic pole, and away from the endopenic side of the distribution. Similarly, if men were to be somatotyped by criteria which yield a symmetrical three-coordinate distribution for women, the men would mass toward the mesomorphic pole, away from mesopenia. The problem is, shall we somatotype men and women against two different scales,

or shall we use a common scale for the two sexes? Dr. Cain favors the second alternative. I am at present inclined to agree.

DUNN: I should like to suggest that there is another approach to the relationship of the somatotype to heredity; namely, to begin not with the somatotype in which the genetic basis is unknown, but with persons of known genotype with respect to some important gene. The question would be: what is the somatotype variance of persons with one allele as compared with those with the other? There are marked differences in habitus, for example, between persons homozygous for phenylpyruvic oligophrenia and persons with the normal allele. I think it should not be difficult to extend such a study to genes without known morphological effects such as blood group genes on the general principle that most genes are pleiotropic and that those altering biochemical or metabolic processes may influence body build also. But the important thing is that one of the variables, namely, the hereditary one, should be controlled in the twin method, or known as in the method suggested above.

HUNT: A proposal of mine in print last year may be in order here. For genetic purposes, it may be worth while to determine accurate somatotypes on boys at the age of eight, and apply these to girls at the physiologically comparable age of seven years. If photographs from a longitudinal growth study were available, this method would result in somatotypes in the adult which would be outwardly quite different, but which shared rather similar processes of growth prior to the steroid hormonal growth phases. In my opinion, each somatotype so rated is the most likely to be genetically comparable for the two sexes.

SHELDON: This comment stresses the desirability of collecting a good series of standard constitutional photographs in connection with longitudinal growth studies. From such a collection it would be possible to make many corollary studies of the sort suggested by Dr. Hunt. The question of genetic comparability of the somatotype in the two sexes might be answered in the manner indicated, but it should be noted that with respect to some very important somatotype characteristics, such as mesomorphic development of the neck region, of the lower trunk, and of the thighs, the two sexes are already in many instances almost as divergent at age seven or eight as at any later age. That is to say, both sexes at age seven already show quite clearly what the adult morphophenotype is going to be.

NEEL: Dr. Sheldon has several times mentioned the desirability of studying the genetic aspects of the somatotype. It might not be amiss to remind ourselves of a rather spectacular piece of work along those lines, the attempts of the late Dr. Stockard to analyze the factors involved in the striking somatic differences between various breeds of dogs. The data well illustrate some of the complexities inherent in a broad attack upon the genetics of the somatotype.

MONTAGU: With respect to Dr. Neel's suggestion that we might profitably consult the work of Stockard for some light concerning the problems discussed by Dr. Sheldon, I should like to say that I believe that the sooner that work is forgotten the better! If there is anything to learn from Stockard's quaint attempts to cross poodles with Saint Bernards for such problems as we are here considering, it is precisely how not to approach the attempt to the solution of such problems. Stockard's extraordinary interpretations and extrapolations cannot be too strongly condemned. What he hoped to discover from the study of the hybrids of such complexly mixed breeds of dogs as he used we know, but that his was not the way to make such discovery we also know. There is, in fact, a strong resemblance between Stockard's and Sheldon's methods. I want to make it quite clear that I am making these remarks, in Dr. Sheldon's terms, as a "623," I am being "compassionately empathic." It seems to me that if we are ever to understand anything of the relation between constitution and behavior it will be necessary for us to study very limited parts of the phenotype. Our task should be to isolate unitary inherited somatic traits, instead of studying the organism as a phenotype made up of five arbitrary somatic components. Drs. Buzzati-Traverso, Dobzhansky and Washburn have already made essentially the same point, and it seems to me obvious that no progress can be made toward the solution of the relation between the genotype and the phenotype until we discover that relation by the only method which is capable of doing so, namely, that of genetics.

NEEL: (reply to Montagu): I assumed in my previous remarks that we were all familiar with certain deficiencies in Dr. Stockard's analysis of his problem. However, his data still stand. They illustrate very well some of the complexities inherent in certain types of attempts at a genetic analysis of somatotype differences. One can think of quite a number of scientific undertakings where although the original investigator's interpretation is no longer tenable, the data are valid

and useful. I am in full accord with the thesis that the most profitable approach to this problem lies in a detailed analysis of limited and readily definable aspects of the somatotype. But I am afraid I cannot agree with Dr. Montagu's suggestion that because of certain imperfections in Stockard's work we should ignore it entirely.

SHELDON: Dr. Montagu's point is, as he indicates, essentially the same one that has been stressed by Drs. Puzzati-Traverso, Washburn and others. He states flatly, "If we are ever to understand anything of the relation between constitution and behavior it will be necessary for us to study very limited parts of the phenotype." That is to say, in order to study the relationship between constitution and anything, we must omit studying the constitution—for the constitution is really the phenotype *as a whole*. This is an old problem in science, and even an old problem in psychology. Here we are dealing with an intolerance on the part of analytical protagonists for the problem and the task of maintaining the perspective of the whole. I have great empathy for Dr. Montagu's point of view (as he, being by his own claim a 6-2-3, indicates that he has for mine). Dr. Montagu is committed to a religion of environmental determinism in human affairs. This is a romantic and in some respects a courageous way of viewing the human scene. But it is dangerous, for it rests too much weight on one side of a complex balance. Because of this present fashion in some academic circles to overload the environmental basket with eggs, I think there is some need for a counter-emphasis. Moreover, I can afford this counter-emphasis now because it is well known that a quarter century ago, when it seemed to me that too much weight was resting against precisely the opposite side of the balance, and too little importance was given to environmental influences, I even more vigorously stressed the counter-influence that seemed then to be needed. That is, in psychology I taught a thoroughgoing behaviorism when psychology was a more or less complacent presentation of the operation of "the instincts." Dr. Montagu has indicated, in another place, that he thinks the constitutional emphasis is really a veiled form of racism, or fascism. My view is that the only adequate defense against this very danger lies in looking *at* (not away from) the presenting peculiarities and attributes of all sorts and breeds of human beings. The constitutional procedures amount essentially to an organizing and systematizing of the field of individual differences. To impute to the extension of this kind of knowledge the danger of its subversive misuse by future malevolent fanatics, is perhaps to question the wisdom of looking at reality at all. Dr. Montagu speaks with considerable emotion of Stockard's interesting although bizarre experiments on cross-breeding of certain widely divergent dog breeds. He says, "the sooner it is forgotten the better!" He adds, "There is a strong resemblance between Stockard's and Sheldon's methods." Does he mean, the sooner our knowledge of human constitutional differences is forgotten the better? Or does he suspect me of carrying out some human cross-breedings so bizarre and horrible as to frighten imagination? Whichever it is, I hope his fear is unfounded.

K. B. WARREN: Editorial note: Dr. Sheldon, in his discussion of the paper of Seltzer, which preceded his own, referred to observations on the "somatotype" of the American-born offspring of Italian immigrants, which differed from the "somatotype" of the European-born parents. It was not clear to the audience throughout the discussion of Dr. Seltzer's paper, or later throughout that of Dr. Sheldon, that the data referred to were those of Franz Boas on *stature* in Italian immigrant families. The following discussion of Dr. Dunn and part of that of Dr. Washburn, with Dr. Sheldon's reply, are therefore predicated upon a very general misunderstanding which was not cleared up until the discussion had ended.

DUNN: If the differences in somatotype between parents born in Italy and children born in the United States of America, which Dr. Sheldon referred to this morning, are statistically significant and drawn from the same population, then I do not see how we can avoid the conclusion that the changes in the children are due to differences between their environment and that of their parents.

A difference in gene distribution could hardly be brought about in one generation except by selection of material or sampling errors and I take it these have been guarded against.

This material should bear directly on the question of heritability of somatotype and I hope it will be studied further.

SHELDON: I did not mean to indicate that we know of any changing in the somatotypes of Italian children. I referred to the well known Boas report, which showed that the *stature* of first generation Italians in this country has tended to be greater than that of their parents. I added that in our own studies of college students several hundred of Italian extraction had shown a similar increase in stature over the reported stature of their parents. But we did not see the parents, and since the somatotype is independent of stature we had no

way of knowing what the parental somatotypes were. I did grant parenthetically, as a "generous gesture," that we had no proof that the somatotypes were *not* different from what they might have been in Italy.

Dr. Dunn's question is therefore *nonsequitor* to my intent, although I may very well have misstated myself. If now for the purpose of the argument, we assume it to be a fact that the somatotypes of first generation Italians in this country *are* different from what they would have been in Italy, even then I suppose that Dr. Dunn's conclusion would not follow. For then we would have to reckon with the possibility that different survival factors may be at work, favoring the survival of certain somatotypes that are not favored in Italy.

WASHBURN: Several comments have suggested twin studies and other methods of testing the genetical basis of the somatotype. This morning Dr. Sheldon mentioned that the somatotypes of the children of European immigrants were more variable and different from those of their parents. If this is true, it is clear that the somatotype is not inherited and the point does not need further investigation. It is to be hoped that these data will be published.

It is difficult for me to see how the inheritance of these somatotypes could be investigated directly. Since quantity of fat, only one of many items judged in typing, may be due to a variety of environmental or genetic causes, it is certain that a category of equally fat people are not uniform in any genetic sense. I think that past attempts at racial typing and classifications of pelvic form have shown that it is easy to set up classifications by selecting polar types and arranging the rest of the population as intermediates. However, time has shown that these classifications were useless as analytic tools. Cumbersome and, at best, of temporary descriptive utility, such classifications based on sorting individuals by superficial shape have been replaced by getting some understanding of the processes which cause the differences. If one wants to study the heredity of the somatotype, it will be necessary to analyze what is observed, determine what part is inherited, and then struggle with the genetics. Mere typing of individuals will not produce materials useful for genetic analysis.

SHELDON: I think I have answered the first paragraph of Dr. Washburn's comment in my answer to Dr. Dunn. The second paragraph might perhaps best be answered sentence by sentence, since the points are somewhat diverse. First, the question of fat. Dr. Washburn seems to have missed the point that the somatotype does not change with a change in nutritional state. A 4-4-4 may be fat or lean. As he grows fat he does not become a 6-4-2, but merely a fat 4-4-4. When a greyhound fattens he is not a St. Bernard but a fat greyhound. Second, the question of polar types and intermediate forms. True, it is easy to select types and to arrange populations in some superficial way as intermediate variants. This has been done many times, for many criteria, and one must agree with Dr. Washburn that such classifications provide no useful frame of reference as a rule. It is quite a different problem to determine what are the most fundamental or general components of variation in a population—the primary components—to ascertain where the poles of these lie, to quantify these components and scale them, and then to make use of them as a correlational frame of reference. Third, Dr. Washburn seems to suggest that we can now dispense with constitutional classification "by getting some understanding of the processes which cause the differences." Yes, we want to know the genesis of constitutional variation, but I doubt if we ever will until first we can describe it and objectify it in a systematic manner. It is the systematic effort at description that seems historically to have imposed too great a burden on the human mind. We have always wanted to name causes too quickly, but causes and events—genotypes and phenotypes—lie in a continuum, and I am afraid that there may be no way of cogently studying the genesis of the phenotype without at the same time systematically studying the phenotype.

K. B. WARREN: A lack of understanding between the workers in the field of human constitution and those in the field of genetics has long divided these two groups of investigators. Some of the criticisms made by geneticists have been given in this Discussion, and Dr. Sheldon has stated his case in answering them. One basic cause of the lack of understanding has, however, not been put into words, and that is the habit on the part of Dr. Sheldon and his coworkers of *assuming* that body build is genetically determined. The geneticists think that a genetic basis for constitution is possible, even probable, but in the face of a complete absence of evidence for the inheritance of the somatotype, it is most unfortunate for Dr. Sheldon to state, as he does in this paper, that "the somatotype attempts to

supply an identification to the sum of genetic factors," and to use the term "morphogenotype." This is begging the question, and can only alienate the geneticist, accustomed as he is to experimental evidence, from a fair consideration of Dr. Sheldon's descriptive data.

CONSTITUTION

CONCLUDING REMARKS OF THE CHAIRMAN

E. A. HOOTON

Harvard University, Cambridge, Massachusetts

INTRODUCTORY REMARKS

The study of the human constitution is the anthropology of the individual as contrasted with the anthropology of groups, with which physical anthropologists were mainly concerned up to the last decade.

It has become increasingly evident that the studies of "races" have tended to yield diminishing returns, partly because racial investigations are principally taxonomic, and partly because the relatively few hereditary structural characters that are used for racial classification seemingly have little to do with the physiology, the psychology, and the social behavior of the groups that possess them.

The study of constitution attempts to relate the anatomical structure of the individual to his physiology, his temperament, and other psychological qualities, and, ultimately, to his range of abilities and capacities in social behavior. It, therefore, has a very practical utility. The physical anthropologist approaches the problem by the study of the body build of the individual, not because it is assumed that his structure determines the other less tangible but possibly more important aspects of his personality, but rather because it has been found that a satisfactory classification of body build leads the investigator far more easily and quickly to an appraisal of the other aspects of his personality than can any study which begins with the less readily classifiable functional aspects of the individual.

SUMMARY

Dr. S. M. Garn's Paper

Dr. Garn summarized investigations of the relationship of body type to certain bio-chemical variables and to coronary disease in young adults, carried on by himself and by Dr. Menard Gertler at the Massachusetts General Hospital. The disease group consisted of 97 males who had suffered coronary occlusions before the age of 40 years. A control group was studied at a Cambridge soap factory.

Dr. Garn first pointed out a significant positive correlation between high endomorphy and high deposition of cholesterol, and a negative correlation between ectomorphy and amount of cholesterol.

He emphasized the fact that high cholesterol levels were characteristic of coronary patients, but that the cholesterol amount in coronary ectomorphs though high for their body type fell well below the cholesterol level of the other patients. This and similar findings in relating biochemical variables to body type, suggest the great importance of establishing medical "norms" on the basis of separate principal body type extremes rather than upon human subjects lumped together irrespective of body build.

Dr. Garn showed a high relationship between incidence of coronary disease at an early age and body types high in both the first (fatty) and the second (muscle-and-bone components).

He discussed the possible genetic basis of both bio-chemical variation and pathological susceptibility to body type.

Dr. C. C. Seltzer's Paper

Dr. Seltzer reported the relationship of body type to delinquency and to normal social behavior in an unique series of 500 pairs of boys, matched for age, ethnic origin, intelligence quotient, economic status and other variables which ordinarily obscure and complicate comparisons of delinquents and non-delinquents. This material was gathered by Sheldon and Eleanor Glueck and is the anthropological side of a much more extensive survey of the material. Dr. Seltzer had no access to the sociological, criminological, psychiatric, and medical findings on the material but was concerned exclusively with the body types of delinquents and non-delinquents and with their anthropometric features.

He found that the non-delinquent groups differed from the delinquents in presenting deviations in the direction of bodily disproportions (extreme values of the indicial relation of one dimension to another). That is to say the non-delinquent subjects showed far more numerous and extreme bodily disharmonies. The delinquents were, if

anything, larger and better-developed for their age than the socially "normal boys."

The delinquents presented far more cases of mesomorphic dominance (superiority in bone and muscle development) and the non-delinquents great excesses of the linear, fragile (ectomorphic types) and also of the extreme fat, round, (endomorphic types). But the general development of fat as well as that of muscle was greater in the delinquent groups.

Dr. Seltzer concluded that his delinquents were in general "normal" and even superior in physique.

He then essayed a speculative projection of temperamental and other personality traits of delinquents, not based upon the psychological and sociological findings in this particular study, but rather upon the correlation between body type and temperament established by Sheldon, and also by Seltzer himself and his colleagues in the Grant Study of "normal" Harvard undergraduates. From such correlative data Seltzer assumed that the delinquents would manifest the personality characteristics ordinarily found in extreme mesomorphs such as: boldness, love of adventure, "vital affect," fondness for contact sports, aggressiveness, callousness, pragmatism, leadership, etc.

The implication was that the delinquent mesomorphs would display in an extreme or marked fashion the somatotonia ordinarily associated with dominance of the second structural component.

Dr. Sheldon's Paper

Dr. Sheldon began by reconciling an apparent discrepancy between the findings of Dr. Seltzer that juvenile delinquents were "normal" and physically well developed, and his own conclusions in *Varieties of Delinquent Youth* to the effect that juvenile delinquents are "biologically inferior." He pointed out that Seltzer's material consisted exclusively of the hardened graduates of industrial and reform schools, whereas his own was drawn from a settlement center and consisted in the main of boys with behavior problems, mental defects, etc., not necessarily leading to professional criminality or habitual overt delinquency. He stated that the minority of his material, arising from the same background and of similar reform school status to that of Dr. Seltzer's larger group, displayed precisely the physical and personality characters ascribed to them by Seltzer.

Dr. Sheldon then embarked upon more general discussions of problems of constitution and of "somatotyping."

He first attempted a precise definition of the somatotype. The morphogenotype would be the assessment of the total genetic complex determining the "trajectory of the organism from conception to dissolution" in so far as hereditary factors do operate in such a determinative way. The morpho-phenotype is the visible, tangible body structure, taken "as is" at any point along the life trajectory. The somatotype is an attempt to approximate the general overall body type of the individual combining both the phenotypic and genotypic features, and relatively constant and unchanged throughout the life span.

Dr. Sheldon then discussed new material on the body type assessment of some 5,000 females. He pointed out that mesomorphy is constantly far below the male level and that females, when marked on male standards of component strength extend through the same ranges of endomorphy and ectomorphy, but are consistently down in the second component. Dr. Sheldon argued (and was supported in this contention by the summarizer) that an attempt to establish an entirely different gradation of the 7 point scale for females in the 3 components would result in utter chaos. (For example, if a 1-7-1 in females were equivalent in males only to 1-5-1, or 1-6-1.) It was pointed out by the summarizer that in all morphological observations quantitively graded some one standard of reference (for age, sex, and race) has to be adopted and all other groups assessed by that same scale. Otherwise, comparability is lost and innumerable new scales must be devised—all mutually unintelligible.

The concluding part of Dr. Sheldon's paper was the demonstration of the relationship of somatotypes to psychotic or psychiatric types in a number of distributions. He also showed some morphological and functional peculiarities associated with specific psychotic types.

After a prolonged discussion by geneticists and anthropologists of the possibility of determining the genetic basis of body type—some averring that such a task was possible and exigent, and others asserting that body type is principally phenotypical and as such of no importance to geneticists, the meeting adjourned.

CONCLUDING SESSION:
PERSPECTIVES OF FUTURE RESEARCH

HUMAN DIVERSITY AND ADAPTATION

THEODOSIUS DOBZHANSKY

Columbia University, New York

The principle that all men are created equal before the Law is the foundation of modern democracy. This principle was deduced, in the Age of Reason, from the Christian maxim that all men are equal before God. The simplicity of this idea of equality does not, however, satisfy everybody. Some overzealous partisans of democracy contend that men are not only equal but also biologically alike. Not a great deal of biological education is needed to see the fatuity of this contention, which is in addition mischievous because it opens the door to its own antithesis, namely the assertion that the incontestable evidence of biological diversity of men destroys the basis of democracy. For the purpose of democracy is precisely to enable diverse, although fundamentally kindred, persons to live together and to participate in common civilization. Democracy would be superfluous in a world of standardized mediocrity, and it becomes impossible when the basic kinship of men is forgotten.

The foremost purpose of science is to assist us to know ourselves, our fellow men, and our environment. Technology aims at progressively more and more complete control of the environment. The importance of understanding the causation and origin of differences among men should be clear both from scientific and from technological standpoints. The biological progress as well as the cultural development of mankind have sprung from this diversity. It must be understood and evaluated both as a biological and a cultural phenomenon.

Darwin proved that man is a part of Nature. But man lives in a cultural environment created by himself. This duality of man was, in fact, stated in Aristotle's famous dictum that man is a political animal. The history of ideas is replete with errors arising from disregard of this duality. Some reformers hoped to dispose of the biological man merely by wishing him away; others wanted to solve human problems as though the human species never evolved civilization and cultural inheritance. The history of the human species has been brought about by interactions of biological and cultural variables; it is just as futile to attempt to understand human biology if one disregards cultural influences as it is to understand the origin and rise of culture if one disregards human biological nature. Human biology and culture are parts of a single system, unique and unprecedented in the history of the living world. Realization of this fact should give to a biologist as well as a social scientist a feeling of humility. Neither of them alone can hope to understand man; only by a common effort can such an understanding be approached. Yet such a community of effort has been notoriously lacking up to now. Its development is perhaps the main condition for the successful advancement of a Science of Man.

Race as a Type and as a Population

Human diversity is, in its biological aspect, a part of the organic diversity. The extent of organic diversity is staggeringly great. In 1758, Linnaeus described 1,236 animal species; in 1946, Mayr estimated that close to one million species of animals have been described. Animal and plant species combined may eventually reach the two million mark. Now, understanding diversity and change requires greater effort than uniformity and stability. The acceptance by Linnaeus of the hypothesis of fixity of species was defensible from the standpoint of economy of thought, given the state of knowledge in his time. But habits of thought engendered by some hypotheses have a way of persisting even when their usefulness has long since disappeared. Thus, biology has substituted a theory of evolution in place of the notion of fixity of species some 90 years ago; and yet, to some taxonomists, a species is still not a changing population but a type established by its describer. A parallel situation has developed in anthropology.

The human species is highly varied, and we are more sensitive to differences between humans than to those between representatives of other species. The diversity of human races and individuals is too great to be easily apprehended. To make this diversity manageable, pioneer anthropologists assumed that at some time in the past there existed several homogeneous, or "pure," races, each with a certain complex of morphological,

and perhaps also psychological, traits. The modern diversity of humans is then ascribed to mixing of these basic racial types in various combinations and proportions. For example, Kant (1775) assumed four primary races: white, negro, Hunnic (Mongolian), and Hindu, and stated that it is "possible to derive from these four races all other hereditary ethnic characters, either as mixed or as incipient races..." (quoted from Count, 1950).

The assumption of a limited number of ideal racial types fitted well in the intellectual climate of the pre-Darwinian era. It harked back to the Platonic immutable Ideas which are only imperfectly manifested in the material world; it pleased the romantics who liked to interpret the present as an outcome of degradation or "denaturation" of a heroic past; and it sounded sufficiently like the Biblical story of the origin of the branches of mankind from the different sons of Noah to appease the theologians. But the ideal basic races soon became the hypothetical ancestors in human phylogeny. How seriously they were taken is evident from the fact that Virchow defined races as "acquired deviations from the original types." Topinard put it more subtly thus: "There are two ways of comprehending human races. According to the first, one considers only the general types common to widespread fragments of mankind, and one regards them, rightly or wrongly, as the expressions of more or less primitive races that have disappeared. According to the second way, one pictures races as the constituent elements of people; one seeks out the types, and multiplies them and supposes that they have been perpetuated without change throughout the upsets and the mix-ups of history and prehistory" (quoted from Count, 1950).

Hypothetical racial types can easily be constructed on basis of morphological data on recent populations, but such ideal types may only accidentally happen to correspond to historic reality. The variability of most human traits can be measured in terms of single linear scales. Men vary in height from tall to short, in head shape from brachycephalic to dolichocephalic, the hair varies from straight to woolly, from coarse to slender, from blond to black, the skin may have little pigment or much pigment, etc. It is an easy matter to devise two "primary" races with arbitrary combinations of extreme expressions of these variable traits. All existing human character combinations may then be imagined to have arisen through hybridization of these fictitious primary races. The chief reason why more than two primary races were usually assumed by creators of ideal racial types is that attempts were made to ascribe to them character combinations resembling some now living or fossil populations or specimens.

Fanciful pure races can be, and have been, created also on basis of genetic data. Persons with O, A, B, and AB blood groups occur in almost all countries, although with different frequencies. Three main alleles of a single gene, I^0, I^A, and I^B, are responsible for these blood groups. It can be imagined that at some time in the dim past mankind consisted of three races neatly homozygous for I^0, I^A, and I^B respectively, and that the present complex situation arose through miscegenation. Since I^0 is relatively commonest among American Indians, I^A in Western Europe, and I^B in Central Asia, the primary races could be supposed to have lived in or near these regions. Unfortunately for this theory, species of anthropoid apes are also polymorphic for alleles very similar to I^0, I^A, and I^B. Has racial purity been lost already in the common ancestors of man and the anthropoids?

Apparently rather more serious reasons led Haldane (1942) and Wiener (1943) to suppose that the presence of both Rhesus positive and Rhesus negative blood types in many modern populations is a fairly recent phenomenon. Since marriages of Rhesus positive fathers with negative mothers may be less fecund than other marriages, either the gene allele for Rhesus positive or that for Rhesus negative blood should be at a disadvantage in mixed populations. The disadvantageous alleles will tend to be eliminated, and populations will gravitate towards homozygosis and uniformity. According to Haldane, the mixture of Rhesus positive and negative alleles now found in European populations might have arisen some 10,000 years through miscegenation of uniformly positive and uniformly negative strains. The finding that Basques, which are on other grounds supposed to be remnants of early European populations, have uncommonly high frequencies of Rhesus negative alleles, while Asiatic people are almost uniformly Rhesus positive, seemed to favor Haldane's hypothesis.

Other, and no less plausible, explanations of the situation are however by no means excluded. Rhesus alleles may from time to time be converted into each other by mutation. No unreasonably high frequencies of mutation need be assumed to counterbalance the unfavorable effects of selection of the Rhesus negative allele. It is possible that individuals heterozygous for positive and negative alleles have, or had, selective

advantages in certain environments. If so, the Rhesus blood group situation is an instance of balanced polymorphism, similar to chromosomal polymorphism found in natural populations of some species of Drosophila and other animals. The relatively high frequencies of the Rhesus negative allele among the Basques may be due to genetic drift in small populations; the Haldane-Wiener hypothesis does not avoid the supposition that genetic drift was effective in the emergence of the "pure" Rhesus positive and negative races.

The notions of racial "types," of "primal" races, and the like, may perhaps be useful as mnemonic schemes for orientation in the observed diversity of human beings. These notions are, however, unrealistic, and they are misleading because they are intimately connected with the discredited blood theory of heredity, now replaced by the gene theory. The blood theory was universally accepted up to the nineteenth century, when the classical race concept was evolved. Since the importance of this fact has been ably discussed by other speakers in the present symposium, the following remarks will suffice.

According to the blood theory, your genotype is a blend of the heredities of your parents; the heredity of each of your four grandparents makes up a quarter of your endowment; that of each great-grandparent accounts for one eighth of your blend, etc. Mendel showed these views to be wrong. Although half of your genes came from your father and the other half from your mother, your parents carried just as many genes which they did not transmit to you at all as those which they did. Some of the genes which your parents had but which you have failed to inherit are present in the genotypes of your brothers or sisters (and if you have no brothers and sisters these individual genes are irretrievably lost). About one quarter of your genes are derived from each of your grandparents; but three quarters of the genes which were contained in the genotypes of your grandparents you have not inherited at all. In other words, your genotype does consist of genes handed down to you from your parents and other ancestors, without having been mixed or alloyed with the other genes which these ancestors carried but which they failed to transmit.

Every individual is a member of a population, of a biological community between members of which marriages are concluded. If the blood theory of heredity were valid, half of the hereditary variance present in a population would be lost in every generation, owing to the dilution of of heredity by crossing. In this case, the population would soon come to consist of genetically uniform individuals. It would become a "pure race." This "pure race" would possess characteristics approximately like the mean values of the traits in the original genetically variable population. The racial "type," defined as a system of mean values of all traits in a population, would then acquire some realistic significance, as a limiting state toward which a population would gravitate in time.

In actuality, the genes of individuals, members of a population, are drawn from the collection of genes which were present in the ancestors of that population. And, unless an individual dies childless, some, but almost never all, of his genes will live in his descendants. The hereditary variability present in a population does not decay from generation to generation, unless the population consists of very few individuals. No "pure races," in the above defined sense, can be formed, except in species that reproduce asexually or by long continued self-fertilization. Genetic polymorphism, not uniformity, is, and always has been, characteristic of human populations. Homogeneous "primary" races or constituent types are a myth.

Let us imagine that the human species becomes panmictic, i.e. that the probability of marriage of any two individuals of opposite sex is uniform regardless of the country of origin, of language, economic status, etc. Panmixia would not, as so often supposed by those unfamiliar with genetics, lead to all men becoming genetically uniform. Since gene differences are not levelled off by hybridization, panmictic mankind would include about as great a diversity of hereditary endowments as it does today. The same diversity of genotypes would, however, occur anywhere in the world.

The actual situation is remote from perfect panmixia. Of course, every human being is a member of a single species, mankind or *Homo sapiens*. But the species population is split up into a complex series of subordinate populations or isolates. These populations are the geographically isolated races, and socially isolated local or religious communities, linguistic groups, economic classes, etc. Even though these subpopulations may have indistinct boundaries and may not be easy to delimit, they are nevertheless the fundamental biological entities which the anthropologist must study. Since marriages are concluded more often within than between isolates, each isolate has its own gene pool, its hereditary endowment, which consists of genes carried by its members.

Not even the smallest in the hierarchy of human isolates consists of individuals with identical genotypes. It is improbable that any two humans, except for identical twins, may have similar genes. The only valid way to describe the genetic endowment of an isolate is to state the frequencies of various genes in the gene pool of this isolate. Isolates very often differ in frequencies of many genes. For example, the frequency of the blood group gene M^n is about 0.18 among some Australian Aborigenes and about 0.91 in some Eskimos. As mentioned above, the Rhesus negative allele is rare or absent in the Orient and in Oceania, but it has a frequency of about 0.15 in European and white American populations, and more than 0.5 among the Basques. It is, of course, possible that some genes may be wholly absent (frequency 0.0) in some populations but established to the exclusion of other alleles (frequency 1.0) in other populations. Thus, the genes that cause dark pigmentation of human skin are obviously much more frequent in populations of Central Africa than in those of Central Europe. Skin color is, however, a polygenic trait, and it is more probable that some characteristically "African" genes occur, and always occurred, in European populations, and vice versa (see below).

Relations of Intra- and Inter-populational Variability

It is easy to observe that individual members of every isolate have different heredities. This is intra-populational genetic variability or polymorphism. On the other hand, since many variable genes have different frequencies in different isolates, genetic differences may be said to exist also between populations. Genetic differences between populations are race differences. It is important to understand the relationships between the intra-populational polymorphism and the race differences. The fact of fundamental significance is that race differences are compounded of the same elementary gene differentials which occur between individuals within an isolate.

Intra- and interpopulational variability are manifestations of the same basic process: variability of the hereditary elements, genes. The evidence of this fundamental unity of human variation is unequivocal where genetically well understood traits are involved. For example, different alleles of the Rhesus series have different frequencies in different races. Thus, the gene Rh_0 is rare among whites but common among Negroes, while Rh_1 is relatively rare among Negroes and common among whites and especially among Mongoloids. Now, a member of the white population which carries Rh_0 is, in at least this one respect, more like many members of the Negro populations than like members of his own isolate. In any case, both Rh_0 and Rh_1 are not restricted to any one race.

Where the variable traits are genetically complex the situation appears, when superficially considered, quite different from the above. For example, nearly 100 percent of the population native in Central Africa have very darkly pigmented skins, while 100 percent of the native Europeans have relatively light skins. Two things must, however, be kept in mind in considering human skin color and similar traits. First of all, gene frequencies of 1.00 and 0 are merely the extremes of the spectrum of gene frequencies. Intermediate frequencies are often found in geographically intermediate populations. More important still, the skin color is determined not by a single gene but by a system of several, and possibly many, genes. The phenotypic effects of each of these genes taken singly are of the same order as, or smaller than, the amplitude of environmental modificability of the skin color. Such genes are called minor or multiple genes, modifiers, or polygenes.

Now, skin color varies not only between races but to a quite appreciable extent also among members of the "white" as well as the "black" populations. A part of this variability is, of course, due to modification by exposure, or lack of exposure, of the skin to sunlight. Hereditary variability of skin color is, however, also quite apparent within the races. It is quite possible and indeed probable, that this hereditary variability is due to scattered occurrence in individuals of a population of the same polygenes which when combined give rise to very different skin colors typical of other races of mankind. In other words, white populations probably contain the genetic building blocks from which very dark skin pigmentations may be constructed by natural or artificial selection. And conversely: Negro populations may harbor scattered lighter alleles of the polygenes which are characteristic of the white race. But the concentrations of any one of these alleles are so low that the darkest skins produced in white populations are still lighter than the lightest skins which occur in populations of Central Africa. Black babies are not born in white populations, and white ones in black isolates, for the same reason for which hitting a typewriter at random is unlikely to result in spelling out of unexpected discoveries.

It is a reasonable hypothesis that every major subdivision of mankind contains, in dispersed condition, the genic elements which are characteristic of, in the sense of being commonly met with in, other major population groups. This hypothesis should not be confused with the opinion rather current among anthropologists, that the now living mankind consists chiefly of so-called "secondary" races. These "secondary" races are supposed to have arisen through long-continued miscegenation of extinct or submerged "primary" ones. To a population geneticist the assumption of homogeneous "primary" races seems wholly superfluous. Intrapopulational variability found within human isolates is only what is expected in populations of a large and widespread sexually reproducing species. The essential similarity of the intrapopulational and the racial variability is a corollary of their common origin through processes of gene mutation.

One may safely reject the view that intrapopulational variability in man arose only through breakdown of uniform "primary" races. This rejection is, of course, wholly compatible with the admission that the predominant trend in the evolution of the human species has been, perhaps for several thousand years and certainly for several centuries, towards race fusion rather than towards race divergence. Much expansion and fusion of previously rather more distinct human populations is undoubtedly going on. This tends to increase the polymorphism within the isolates at the expense of the differentiation between isolates.

The intra- and interpopulational variabilities stand in a dynamic equilibrium. Race divergence occurs through differentiation of the gene contents of variable populations: individual differences are raw materials from which race differences are molded. But race divergence is not a one way street: race divergence may be arrested and race differences melted down again to increase the genetic variability within enlarged isolates. Race divergence becomes irreversible only when races become species. This occurs through development of reproductive isolating mechanisms of various kinds. For example, ecological isolation restricts populations to different habitats and hinders their members from encountering each other; sexual isolation makes males of one species less attractive to females of another species than their own males; hybrid inviability and sterility make the hybrids less viable or fertile than their parents. Any one of these mechanisms, or a combination of several, may make the exchange of genes between diverging populations impossible, or so infrequent that the differentiating force of selection outweighs the unifying effects of hybridization.

It does not take much discernment to see that human races have not diverged anywhere near the stage of complete reproductive isolation. They are kept distinct, as races generally are, by geographic separation in different countries. When this separation is removed, hybridization may be only temporarily restricted by social forces. Whether or not even rudiments of biological isolating mechanisms ever appeared between human races is uncertain. It is possible, though unproven, that sexual attraction is somewhat weaker between, than within, certain races. But this is more likely a sociological than a biological phenomenon. In any case, the specific unity of mankind is obviously intact.

Scientific Description of Human Diversity

Organic diversity, whether among humans or among other living beings, may be studied in two ways. The diversity may be observed, described, catalogued, and classified. But one may also study the mechanics of the origin of diversity, analyze causes which brought it about, examine the operation of these causes at present, and predict their probable effects in the future. The first way leads to description of the status of the diversity at our time level and of the historic development of this diversity. The second is concerned with the sequence of events that actually took place in the history of mankind only in so far as these events shed light on the causes which are still likely to be in operation and may determine future evolutionary changes. This second method seeks not so much description as causal analysis of human diversity. The first is connected with descriptive biology, while the second is related to experimental biology and particularly to genetics.

The first approach logically, and usually also chronologically, precedes the second. At least some description and classification are necessary to state correctly the problems of causation of human diversity. In zoology and botany the first approach was dominant until the beginning of the current century. Anthropology has ever since its inception as a science been devoted almost entirely to descriptive studies. And these studies have been on the whole very successful—in fact more so than they are often given credit for by insufficiently informed outsiders and often by anthropologists themselves.

It can not be gainsaid that no general agreement has been reached regarding the number and

the nomenclature of the racial subdivisions of our species. Thus, Coon, Garn, and Birdsell recognized 30 "racial stocks" (1950). This number is much larger than admitted by some, but much smaller than registered by other anthropologists. Such a lack of agreement has been stressed so often and so insistently as to obscure the important body of positive knowledge hidden behind this disconcertingly wavering facade. For despite all the difficulties of constructing a generally accepted classification of races, at least the external morphology of the inhabitants of different parts of the world is fairly well known. For example, there may be no consensus of opinion on just how to delimit the different branches of the white race which inhabit Europe, but there is little dispute about the morphological traits of the major populations which live on that continent.

Although many descriptive problems in anthropology still remain to be studied with the aid of classical methods of anthroposcopic measurement and observation, a fairly detailed inventory of human diversity is already available. This impressive body of information stands as a foundation on which, and on which alone, can further developments of anthropology be built.

As far as descriptive studies are concerned, important progress may result from observations on the incidence in populations of phenotypically discrete traits determined by single genes or by small groups of genes. The O-A-B-AB blood groups are the best studied example of such a trait.

The traits which have been used by classical anthropologists for racial studies are, with few exceptions, genetically complex. Skin color, nose shape, hair form, cephalic index, body height, are all determined by numerous interacting genes with individually small effects. Such genes are now called polygenes. It is difficult to estimate the numbers of polygenes involved in the formation of some traits. For example, it is not known just how many genes cause the difference in the shape of the nose, or in skin color, characteristic of negro and white races. This number must be fairly large, and it may not be practicable to identify these genes one by one.

It is no accident that anthropologists, and classical animal and plant systematists as well, chose to work mainly with highly polygenic traits. Discrete traits caused by single genes often vary in members of a population as much as they do between populations. Differences between populations in such traits can be stated only in terms of differences in the relative frequencies of the traits concerned, as we have seen for the human blood groups. But anthropologists liked to express the differences between the groups which they studied in terms of averages, rather than of frequencies. Polygenic traits vary continuously; members of a population seem to "gravitate" toward a certain average; in short, polygenic variability simulates transmission of heredity through miscible "bloods," rather than through genes.

The usefulness of polygenic traits is limited by their low phenotypic specificity. As stated above, the effects of polygenes are obscured by environmental modifications. More important still, two individuals of the same height, or with the same cephalic index, may owe their similarity to different polygene complexes. Two populations which agree in average height or in nose shape may, theoretically, not carry the same genes at all. A great variability in these traits may arise if such populations hybridize. In short, individuals and populations which are phenotypically similar in polygenic traits may or may not be similar genotypically. This is much less frequent with genetically well studied monogenic traits. Individuals with O, or with MM, bloods usually carry similar blood group genes regardless of what population these individuals belong to. The blood group distribution in the offspring of different marriages can usually be predicted with a fair degree of assurance. Genetically defined discrete traits can be understood more easily and fully than continuously varying polygenic traits. The apparent simplicity of the latter is deceptive.

One of the most urgent tasks in which anthropologists and geneticists may cooperate is the discovery and analysis of phenotypically clear-cut traits determined by single genes. Such traits will be more useful if they occur frequently in at least some populations than if they are rare. For this reason, the phenyl-thio-carbamide (PTC) taste blindness, or the blood groups, are more useful than albinism or polydactyly. Drs. Spuhler, Lasker, and Birdsell have reported several very hopeful new traits in their papers presented at this symposium.

It may appear at first sight that the best source of clear-cut genetic traits would be genetic analysis of the relatively less complex polygenic characters, such as eye or hair colors. Up to now this hope proved, however, little rewarding. As for even more complex polygenic characters, the prospect of their being resolved into simple genic differences is even more remote. Mather (1950),

the greatest authority on polygene inheritance, seems to hold such a resolution rather hopeless even in organisms genetically more favorable than man.

Genetically simple traits are nevertheless not rare in man. The writer is indebted to Drs. Boyd and Spuhler for the following list of such traits which may prove useful in raciological studies:

A. Mode of inheritance well established
1. A, B, O blood groups and subgroups
2. M, N, and S blood types and subtypes
3. Rhesus blood factors
4. Secretor factor and Lewis antigen
5. PTC taste reactions
6. Color perception
7. Lutheran antigen
8. Kell antigen
9. Duffy antigen

B. Mode of inheritance approximately established
1. Allergy
2. Ear slant
3. Ear lobe
4. Eye fold
5. Phlebograms of superficial vessels of antherior thorax
6. Fingerprint patterns (3 pairs of genes)
7. Middigital hair
8. Occipital hair whorl
9. Paramental cleft
10. Palmaris longus muscle
11. Peroneus tertius muscle
12. Pattern baldness
13. Handedness

C. Mode of inheritance poorly established or simply suggestive for further study
1. Curved little finger
2. Relative length of index and right fingers
3. Eye color
4. Hair color (brown series)
5. Red hair
6. Freckles
7. Hypotrophic lateral incisors
8. Carabelli's cusp
9. Shovel-shaped incisors
10. Mongolian spot
11. Naevus of Unna
12. Number of vallate papillae
13. Patterns of vallate papillae
14. Flexibility of first joint of thumb

It is important to have a clear idea about the significance of the studies on the distribution of single gene differences in human populations. The chief aim of such studies is not building of new racial classifications of mankind. The importance of single gene traits lies rather in their usefulness in understanding the nature of races—in causal rather than in descriptive studies. In principle, there is no reason why one could not classify mankind by any trait, polygenic or monogenic. A classification based on, for example, skin color need not be either better or worse than one built on hair form or on blood groups. To be sure, it is easier in practice to classify by skin color than by blood groups, because the color of one's neighbor is usually more evident than his blood group. It happens that certain Spanish and Portuguese populations resemble in the relative frequencies of the blood group genes I^0, I^A, and I^B some Australian Aborigine tribes. Few classifiers will, nevertheless unite the inhabitants of the Iberian Peninsula and the Australian natives in a single race. Such a classification would not be convenient for any purpose except, perhaps, for studies on blood transfusions.

It is a commonly held opinion that a superior racial classification must be based on many traits. This is however true only to the extent that different traits show a congruity in their geographic distribution. Such a congruity is indeed met with in some animal and plant species, chiefly in those in which the divergence of the constituent races has progressed almost to the point of transforming the latter into separate species. But human races are rather little differentiatied, in the sense that our species is remote from splitting up into derived species. The geographic distribution of human traits often shows quite striking independence. This can be seen quite clearly, for example, if one compares the geographic patterns of the variations in the pigmentation, cephalic index, height, and head size in populations of Europe and adjacent parts of Asia and Africa (see Coon, 1939). The difficulty of arriving at a wholly satisfactory classification of human races has not been obviated, but rather increased, by taking into consideration many independent traits (which, of course is not an argument against studying all possible traits).

The often met with geographic independence of human traits causes, however, most serious difficulties in attempts to discover the supposed racial "types." The difficulties disappear if human populations are described in terms of relative frequencies of variable genes or traits. For any population, large or small, can be uniquely characterized by stating the frequencies of the genes for genetically well analyzed traits in its gene pool. When the traits are not at present resolvable into genic differences, it is an important progress compared to the old-fashioned

approach to study the distribution of such traits one by one, as has been done, for example, by Neel, Laughlin, Mourant, Boyd, Birdsell, Lundman and others in their papers presented at this symposium.

Some Considerations Concerning Causal Study of Human Diversity

It has been stated above that the diversity of organisms which exist on earth is so enormous that pioneer biologists had, before all else, to make it manageable. To this end, a hierarchic classification was constructed. The problem of origin of the diversity had to be postponed until at least a tentative classification became available. The hypothesis of fixity of created species made the postponement intellectually acceptable for about a century. In 1859 Darwin showed, however, that this hypothesis is untenable. Since organisms are products of age-long development, biology had to study processes as well as states.

The development of anthropology took a course on the whole parallel to that of biology. People who live in different parts of the world seem to be so strikingly diversified that a racial classification had to be essayed before other tasks. But the problem of origin of human races did not appear quite so formidable as that of the origin of species, and there was no pressure from the theological side to regard races primordial entities. A valid solution of this problem was however out of the question before the mechanisms of biological evolution were discovered. A spurious solution appeared instead. This is the notion, expressed very clearly already in the eighteenth century, that the human (and other) species became differentiated through direct effects of climate, food, and other living conditions prevailing in different countries.

The hypothesis of direct modification by the environment proved sterile as a guide in research. However, because of the wide currency of this hypothesis, Darwin's evolutionism did not sound quite so novel to students of racial variation as it did to students of species. The advent of Darwinism opened up a new field of anthropological studies, dealing with the origin of mankind from pre-human ancestors. The great advances in this field are matter of common knowledge. But it is necessary to point out that surprisingly little thought, and still less actual research, has been done concerning the causes of human racial and intra-racial variation. It is nothing short of amazing that the hypothesis of direct modification by the environment can be found in modern treatises on anthropology, stated in almost the same way as it was expressed by Buffon about two centuries ago! Yet it is known for at least half a century that characters acquired through environmental modification are not inherited. Negroes have not become black because their ancestors were tanned by the tropical sun; the white race did not originate because its forbears were bleached under the cloudy skies of Europe.

According to the modern conception of the mechanics of evolution, the principal causative agent of evolutionary changes is adaptation to the environment through natural selection. Living populations change in the process of becoming better able to survive and reproduce in different environments. Organic diversity is, in the main, a response of living matter to the diversity of milieus found on our planet. In agreement with this general theory, it is reasonable to set up a working hypothesis, that racial differentiation of human populations is an outcome of different people having become biologically, as well as culturally, adapted to different environments which prevailed in the countries in which those people have lived. Similarly, the polymorphism found within human populations is, at least in part, a consequence of the diversity of modes of life pursued by different people.

It is an assumption made in many classical and modern anthropological writings, that most characters which differentiate human races are non-adaptive in nature. The hypothesis of adaptational origin of human diversity contradicts this assumption. It must be admitted at once that evidence bearing upon the validity of the hypothesis is at present altogether insufficient. Perhaps by far the most urgent of all tasks which face modern anthropology and human genetics is to obtain such evidence. Its present scarcity is due less to the difficulty of its acquisition than to a lack of awareness of its necessity. The action of natural selection on man has been, oddly enough, almost completely ignored. And yet, unless the diversification of our species has taken place largely through natural selection, modern biology is powerless to give a self-consistent account of human origins. Studies on the adaptive significance of human genetically variable traits should become the central problem of human biology.

It may be proper at this point to dispose of the strange notion which confuses the thinking about human evolution, namely that natural selection was important before the human level was reached, but that it became weakened with the advent of

culture, and largely abolished in modern industrial civilization. This notion springs from the idea that "natural" selection is a manifestation of the principles of "Nature red in tooth and claw," "Eat or be eaten," and that "life-or-death utility" of a trait is needed before natural selection can have much consequence in evolution. Now, all that selection actually means is that carriers of some genotypes leave, on the average, a greater surviving progeny than carriers of other genotypes, and "natural" is simply the converse of "artificial" selection, in which the perpetuation of different genotypes is influenced by conscious or unconscious choice exercised by an outside human agency.

Natural selection would be abolished only if every person born anywhere in the world were to have equal chance to attain reproductive age, and to produce equal number of offspring, except as directed by some human agency regulating survival and reproduction of populations. It stands to reason that nothing like this obtains in any population at present, just as nothing of this sort obtained in the past. What does happen in any species, and what did happen in mankind, is that the adaptive values of different genotypes undergo changes in the course of time. In Drosophila, traits which are adaptive in summer are not the same which are advantageous in winter or in spring, and some populations undergo evolutionary changes which make them genetically different at different seasons. In man, the adaptive values of certain traits, such as the ability to withstand exposure to cold without protective clothing, were doubtless higher in Acheulian Age Europe than they are now in New York City. The opposite is presumably the case for resistance to nervous breakdowns under the stress of modern "tempos" of living. Some traits, such as the ability to learn from experience and to become educated in the broadest sense of the latter word, have probably maintained their great usefulness from the dawn of humanity till now.

The adaptive values of many human traits doubtless change with time, in magnitude as well as in sign. To call the selective processes of the past "natural" and of the present "unnatural" is simply to becloud the issue by use of emotionally colored words. The fact of the matter is that the direction of the evolutionary process is at present different in some respects from what it was in the past. This evolutionary process has led to the emergence of a singular being who can evaluate the direction of his own evolution, and is potentially able to modify, and possibly even to control, the evolutionary process in accordance with his volition. Whether the past evolutionary trends are more or less desirable than the present ones is an issue which should be decided on the basis of rational considerations.

The changeability of the selective processes in human evolution is a source of difficulty in studies on human biology. The selective pressures which have brought about the racial differentiation in some traits may have become diminished, removed, or even reversed in sign. Let us assume, for the sake of argument, that the skin pigment has a protective function against overexposure to sunlight, and that the scarcity of pigment facilitates synthesis of vitamin D in the subcutaneous tissue. These functions were in all probability more important when people used little or no clothing and when concentrates of vitamin D were not available as at present. If a given trait is now adaptively neutral, this does not exclude the possibility that the same trait was important in the past and vice versa. A student of human evolution will, therefore, have to investigate the physiological as well as the psychological concomitants which different morphological traits may have. Furthermore, physiological and psychological traits must be studied in persons of different age and in as great a variety of environments as can be had. Lastly, inferences will have to be drawn regarding the adaptive significance of these traits at different stages of human phylogeny. Here is a very long neglected field for studies on the causative factors of human evolution.

Mutation and Individual Variability

The only known method of origin of hereditary variability is through changes in the genes or in the chromosomes. Such changes are termed mutations. Mutations are, thus, the primary source of all evolution. But mutations alone do not constitute evolution; the mutation process supplies merely the raw materials from which evolutionary changes may subsequently be constructed by other agencies, the most important of which is natural selection. Every gene has a certain probability of undergoing a mutational change in every generation. Though this probability may be very low for some genes, doubtless very large numbers of newly arisen mutants enter in every generation the gene pool of the human species. Since a mutated gene does not become swamped and lost in the sea of normal genes, mutant genes accumulate in the gene pool of every sizeable population.

The diversity of human genes has arisen ultimately through the mutation process. Evolution-

ary changes, adaptive or otherwise, take place only if raw materials from which they can be built are available among the store of mutant genes carried in a population. It is, however, important to keep in mind that most mutations that arise in any species are deleterious to their carriers. Mutation may be said to beget chiefly hereditary diseases of varying degrees of gravity. This fact may seem strange indeed—mutation appears to be a source of degeneration rather than a fountainhead of evolution. But a little reflection will show that, to be able to engender only useful mutants where and when needed, living matter must be endowed with a miraculous prescience of the future. Such a wondrous ability does not exist in our imperfect world.

The production of many ill-adapted mutants is the price which every species pays for the maintenance of its evolutionary plasticity. A minority of mutations are useful in some environments. The mutation process is itself under genetic control; in genetically well studied organisms inheritable variations in mutation rates have been discovered. Natural selection is, therefore, able to keep the frequency of mutations balanced between possible loss of plasticity at one extreme, and production of too many worthless variants on the other.

Roughly three types of changes may be distinguished among mutations. The first and most numerous class are variations deleterious in different degrees—from complete lethality to near neutrality. Second, the alterations that are adaptively approximately neutral. And thirdly, the variants which are adaptively valuable in some environments. Of course, these three classes are not clear-cut; there exist mutants of all degrees of harmfulness and usefulness. The same mutant is often deleterious in some environments, neutral in others, and useful in still others.

Deleterious mutants, the hereditary diseases of various grades, accumulate in populations until an equilibrium is reached between the rate of their origin by mutation and their elimination by natural selection. The elimination of deleterious dominant mutants is an efficient process, because any carrier of such a mutant is subject to the adverse action of selection. Deleterious recessives reach relatively high frequencies in the gene pool, because they are sheltered from natural selection while carried in heterozygotes and subject to elimination only in the relatively rare homozygotes. Let u be the mutation rate, i.e., the fraction of normal genes which change in every generation to become mutants of a given kind. Let the average numbers of surviving progeny of a normal individual be unity, and that of a mutant $(1-s)$. The fraction s is known as the selection coefficient, and $(1-s)$ as the adaptive value or fitness (the adaptive value is sometimes also written as w). Now, deleterious dominant mutants will accumulate in the population up to the frequency u/s, while recessive hereditary diseases up to a much higher level $\sqrt{u/s}$.

The number of "genetic deaths" caused in every generation by hereditary diseases can, theoretically, be decreased by eugenic measures, but ultimately it depends upon the occurrence of mutations. Unfortunately, no means to suppress their occurrence are yet known; their frequency can, however, be very considerably enhanced by exposure of the gonads to X or Gamma rays. As Muller has insistently pointed out, indiscriminate use of atomic energy will increase the mutation frequencies and, hence, the "genetic deaths."

Deleterious mutants are obviously important from the standpoint of public health, and medical geneticists will devote their efforts to the study, alleviation and where possible control of hereditary diseases. From the standpoint of human phylogeny, mutants deleterious in all existing environments are evolutionary chaff. Haldane (1949) has, however, pointed out that hereditary diseases which afflict and kill individuals of postreproductive age may under some circumstances have been favored by natural selection, because of the advantage accruing to the tribe from removal of useless members. Inheritable maladies of old age are not deleterious mutants in technical genetic sense, because they do not interfere with the perpetuation of the genotype. Hence, the paradoxical results that some of the worst scourges that flesh is heir to, such as cancer, might actually have arisen as an adaptive evolutionary change.

Intra-Populational Polymorphism

With the possible exception of old age diseases, the contamination of populations by deleterious genes is maintained by the mutation pressure. Natural selection is always behindhand in its control of deleterious mutants. A deleterious mutant may be said to have a certain average expectation of life in a population before it is finally extinguished by selection. But apart from this morbid variability, human populations quite regularly contain genetic diversity of a different kind. For example, most populations include some genetically taller and genetically shorter people; some lean, stocky, and fat persons; some individuals of O, A, B, and AB blood groups, etc.

Regular presence in populations of several genotypes is known as polymorphism (intra-populational polymorphism).

The environment in which members of a population live is constant neither in space nor in time. This is true for physical, biological, and especially for cultural environments. Each of the different genotypes present in a population may make its carriers adaptively superior to others in different environments. Such a polymorphism is termed adaptive. Adaptive polymorphism is maintained and controlled by natural selection; its biological role is to increase the fitness of the population as a whole, by making it able to exploit most efficiently a wide variety of environments. A polymorphic population is better able to withstand irregular and sudden changes of the environment than a uniform one; the polymorphism acts as a buffer against environmental shocks.

Some traits which show polymorphism in human populations appear to be neutral, i.e., are not known to affect the fitness of their carriers in any environment. An example of such an apparently neutral trait are the classical blood groups. Since the adaptive significance of human traits is altogether insufficiently studied, caution is needed in classifying any trait as neutral. A seemingly neutral trait may be merely an outward expression of a genetically determined physiological property which has important effects on fitness. Thus, it is conceivable, although by no means proven, that possession of O, A, B, and AB blood groups is correlated with relative immunity or susceptibility to some disease or diseases. Haldane (1949) has correctly pointed out that the failure to detect such correlations may be due to nobody having so far approached the problem with proper methods. Haldane has made some suggestions in this respect which are certainly worth following.

On the other hand, it seems to tne writer excessively dogmatic to deny outright the possibility of existence of polymorphism in human populations in traits which are really neutral, i.e., do not affect the fitness of their carriers to any appreciable extent. As we shall see presently, there may exist agencies that would maintain such adaptively neutral polymorphisms. We come again to the conclusion that classification of the adaptive nature of human traits is the most urgent problem of anthropology.

There is ample evidence that, in organisms other than man, a genetic trait may be deleterious in some but favorable in other environments. Such a trait is, of course, discriminated against by natural selection in some situations but favored in others. The net result will be that the polymorphism will tend to persist, the frequency of the trait in the populations being a function of the relative abundance of the situations of the two kinds. It is quite likely that some human traits owe their maintenance to mechanisms of this type. Muller (1950) has speculated that myopia may be one of them. Nearsightedness was probably dangerous to primitive man in many situations, but it might have been advantageous to a few individuals who specialized in making arrowheads or in other fine work. Under conditions of industrial civilization, the disadvantages and advantages of myopia have largely disappeared, except probably in mate selection.

Recent work on populations of some insects, especially of Drosophila flies, has disclosed the wide occurrence and importance in adaptation of so-called balanced polymorphism. Balanced polymorphism arises if a heterozygote for a pair of alleles or of gene complexes is superior in fitness to both corresponding homozygotes (i.e., adaptive values arranged in the order $Aa > AA \geq aa$). Natural selection will, then, preserve both alleles, A and a, in the population indefinitely; the frequencies of these alleles will reach an equilibrium which can be predicted if one knows the fitness of the competing genotypes. What seems at first sight paradoxical, is that an equilibrium between A and a will be established even if one or both homozygotes, AA and aa, are adaptively very inferior types, provided only that the heterozygotes, Aa, possess a superior fitness. The solution of this paradox is that the mechanism of natural selection enhances the adaptive level of interbreeding populations, even at the expense of producing some inferior individuals. It can be shown that the average adaptive level of a population as a whole under balanced polymorphism is reached when the superior heterozygotes and the ill-adapted homozygotes attain their equilibrium frequencies.

How widespread is balanced polymorphism in human populations is entirely conjectural at present. Mankind shows intra-populational polymorphism for many traits, such as blood antigens, PTC taste blindness, etc., which seem adaptively quite neutral, and which nevertheless show considerable variations in their incidence in different races. The possibility is not excluded that balanced polymorphism is involved in at least some of these cases. Indeed, suppose that the heterozygous carriers of the MN blood group possess, or possessed in the past, some adaptive

advantages over the homozygotes *MM* and *NN*. This would account for the maintenance of the polymorphism in these blood groups. Furthermore, if the advantages of the heterozygotes vary in different climates, or with different diets, or with respect to susceptibility to different diseases, the racial variations in the frequencies of the antigens M and N could be accounted for.

Balanced polymorphism should be considered a possible explanation also in cases when a harmful trait shows fairly high incidence and persistence in some populations. This is true, for example, for the gene for Mediterranean anemia (thalassemia), which is lethal when homozygous and yet is fairly common in some populations of the Mediterranean region. As pointed out by Neel and Valentine (1947), such a situation could arise if the heterozygous carriers of this gene possessed some selective advantage under conditions of Mediterranean countries. In reality, these heterozygotes show a mild form of anemia. This seems to contradict the hypothesis, but it is still possible that the heterozygotes may have a positive adaptive value because of resistance to some infection. The question thus remains open.

A similar hypothesis may be made concerning the maintenance of Rhesus negative blood group genes in human populations. Since a certain proportion of Rhesus negative/Rhesus positive heterozygotes are eliminated during the intrauterine existence in Rhesus negative mothers, the Rhesus negative allele is at a selective disadvantage in populations in which its frequency is between 0 and 50 per cent. As we have seen above, this even led to the conjecture that the intra-populational polymorphism for Rhesus alleles is a result of relatively recent race mixture. The possibility that the heterozygotes have some advantage in survival or reproduction overbalancing their early disadvantage may be regarded an alternative hypothesis which deserves to be tested. One should never lose sight of the fact that the adaptive value of a genotype which determines its fate in populations is a net result of interaction of numerous variables; carriers of some genotypes may be at a disadvantage in some respects but may possess a superior overall fitness because of other properties.

Perhaps biologically the most important of all forms of intra-populational polymorphism in man are the variants of human organization referred to as constitutional types, somatotypes, morphophenotypes, etc. The early fumbling attempts to establish a division of human populations into "types" seemed to a geneticist all too obviously invalid. Thus, to have three types, like those of Kretschmer's, coexist in interbreeding populations, these types would have to be determined by two or three gene alleles. But if so, what is the origin of the numerous intermediates and "dysplastics"? If, on the other hand, the pyknic, athletic, and asthenic types differ in many genes, the types will be engulfed in a sea of gene recombinations within few generations. The fallacy of the early typologists lay in their failure to realize that the human genotype is compounded of discrete units, genes, which segregate and become recombined in inheritance. The fundamental error here involved is similar to that in raciological speculations which assumed two or several races coexisting in the same populations.

In this respect, Sheldon's (1940, 1942) conception of three variable constitutional components represents a distinct step forward. The extreme ectomorphs, mesomorphs, and endomorphs should in no sense be treated as prototypes from which the far more common intermediate, or balanced, somatotypes are derived. For it is reasonably clear that these intermediate somatotypes are the adaptive norms of our species which have been molded by natural selection in the evolutionary process. The extreme somatotypes, Sheldon's 711, 171, 117 and the neighboring ones, most likely represent the poorly adapted genotypes which the process of gene recombination must yield from time to time. If, as is possible, balanced polymorphism is involved in production of the variety of somatotypes, the extreme somatotypes may correspond to adaptively inferior homozygotes, which this genetic mechanism must unavoidably produce to maintain optimal frequency of superior heterozygotes.

As the writer sees it, the crucial problem of constitutional research is clarification of the genetic basis of the empirically arrived at morphophenotypic classes. Needless to say, the first task is to find out how great a variety of morphophenotypes can arise on the basis of a given morphogenotype. But the fundamental issue concerns the nature of the genetic mechanisms which engender the variety of constitutional types found in the human species. The most remarkable fact indicated by constitutional studies, especially by the pioneer work of Sheldon, is the existence of a network of correlations between morphology of the body frame (somatotype), and physiological, pathological, psychological, and psychiatric traits. Such correlations may be developmental, i.e., they may arise because the

genes involved are pleiotropic. Pleiotropic genes have manifold effects, often on apparently unrelated traits. Correlations may also be purely genetic, due to a lack of panmixia in a population which consists of several partially isolated racial types. The correlations betweem different traits characteristic of the negro, or of the white race, observed among the inhabitants of New York City are chiefly of the latter type. The same, or similar, somatotypes seem however to occur in different human races, albeit with different frequencies. This strongly suggests that the correlations revealed by constitutional studies are developmental rather than genetic.

Although, to the best of the writer's knowledge, no study of the inheritance of somatotypes has ever been undertaken, it might be not premature to look for serviceable working hypotheses for such studies. The polymorphism which the students of human constitutions have begun to describe and classify may be produced by a relatively small number, perhaps as few as half a dozen, of genes or integrated combinations of linked genes, with far-reaching pleiotropic effects which extend into every aspect of human morphological as well as physiological and psychic organization. The traits influenced by these major pleiotropic genes are, of course, further varied by minor genetic modifiers of the polygene type. Whether or not the major pleiotropic genes form systems of balanced polymorphism is a matter of pure conjecture at present. Ilowever that may be, one is led to suspect that these genes may be the most important hereditary determinants which genetics and anthropology could study.

Neutral Traits and Genetic Drift

The danger of assuming that any given human trait is adaptively neutral has been pointed out above. The biological meaning of human variability is pretty much *terra incognita*; even the major selective influences which operate in human evolution are largely unknown. It is, nevertheless, doctrinaire to assert, as has been done by Fisher and his followers, that the evolutionary fate of all genetic variability is governed by natural selection. For example, there is no assurance that the O-A-B-AB blood groups do not in any way affect the fitness of their carriers; such effects may be discovered any day. And yet, it is unwarranted to affirm that such influences must be present. The adaptive significance of human traits should be studied; the problem can not be settled on *a priori* grounds.

Suppose that the blood group allele I^0 mutates to I^A or I^B at a rate u per generation. Since gene mutation is a reversible process, the alleles I^A and I^B may mutate back to I^0. Assume that the rate of this reverse mutation is a fraction v per generation. Regardless of what the initial frequencies of the genes may be in a population, the alleles will eventually reach equilibrium concentrations determined by the relative magnitudes of the mutation rates. It is possible to show that the equilibrium level for the allele I^0 will be $v/(u + v)$, and for the alleles I^A and I^B combined $u/(u + v)$. Most human populations, and those of the anthropoid apes as well, are polymorphic for the genes I^0, I^A, and I^B. To explain the origin and maintenance of this polymorphism, one needs to assume neither miscegenation of hypothetical "pure" race, nor pressure of natural selection. All that is needed is that the genes undergo mutation with finite frequencies.

The mutation hypothesis alone admittedly does not fully account for the available facts. It is well known that the incidence of I^0, I^A, and I^B varies in different populations. Theoretically, this may be a result of variations in the mutation rates, u and v, in different races. An alternative explanation is that the racial differences in the blood group frequencies are caused by genetic drift.

This is not an appropriate place to describe the mechanisms of genetic drift, which have been studied in detail by Sewall Wright. The essence of the story is that the frequency of a gene in a population, if not affected by mutation and selection pressures, will tend to remain constant from generation to generation. Perfect constancy will however obtain only in ideal infinitely large populations. In finite populations the gene frequencies will oscillate, and the oscillations will be the larger the smaller are the populations. During most of its existence, man was a relatively rare species, broken up into numerous tribes, many or most of them endogamous by custom or by necessity. Furthermore, epidemics, wars, and starvation from time to time reduced many of these tribes to small numbers of individuals. Supposing that all the tribes had originally the same frequencies of the alleles I^0, I^A, and I^B, these frequencies would drift apart in the course of time.

The validity of the above genetic drift hypothesis depends upon how often appreciable segments of the now living mankind are derived from endogamous tribes with small genetically effective

populations. The problem here involved is far from simple, and cooperation of cultural anthropologists, archeologists, historians, and even sociologists is essential for its solution. For the genetically effective size of a population is not identical with, but may be very much smaller than, the number of individuals in it. The effective size is influenced by many variables, such as marriage customs and taboos, average numbers of children per family, state of public health, and economic security. Some information relevant to the genetic drift hypothesis in application to man is doubtless available in anthropological, sociological, and historical studies. The literature has never been examined from this point of view by biologically trained students. A very interesting beginning of a synthesis of biological and sociological data is presented in the paper of Professor Birdsell read at this Symposium.

Just how small must be the genetically effective populations to make the genetic drift an important differentiating agent depends upon several conditions. If a gene is subject to frequent mutation, or if the populations are not perfectly endogamous, genetic drift may not be important in a population which would change by drift in the absence of mutation and of exogamy. Long continued selection pressures, except for very weak ones, overpower the effects of drift. Racial differentiation may be produced by genetic drift in some traits and by natural selection in other traits in the same species. Regardless of whether genetic drift has caused racial differences in traits such as the blood groups, it is reasonably clear that race formation as a whole can not be accounted for by drift alone.

Role of Selection in Race Differentiation in the Human Species

Most human populations are polymorphic with respect to the blood groups, since they contain individuals with O, A, B, and AB blood types. When populations are compared, they are often found to differ in relative frequencies of the same blood types. Since the blood groups are not known to affect the fitness of their possessors, it is possible to entertain the hypothesis that the blood group polymorphism is originated and maintained by opposed mutation rates to and from the various blood group alleles; and that the different incidence of the blood groups in different populations is due to genetic drift in small endogamous tribes. A similar hypothesis can not be applied to racial traits which involve integrated polygene complexes instead of single genes.

Consider, for example, the difference in skin color between the populations of Central Africa on one hand and those of Europe or of America on the other. This difference is controlled by an unknown, but doubtless fairly large, number of genes. Much variation in skin color occurs also within populations, and it is quite probable that these individual variations are caused by scattered occurrence of the same gene alleles from which the race differences are compounded. Nevertheless, every individual native in Central Africa carries enough pigment genes to make his skin dark, and every native of Europe has enough alleles for light pigmentation to make his skin light.

Genetic drift is an evolutionary accident. Although a succession of such accidents may in the course of time add up to important evolutionary events, it is quite unlikely that it could produce organized systems of genes, such as are involved in skin pigmentation of different human races. It is vastly more probable that dark skin color enhances the fitness of its possessors in climates in which dark races have developed, and that light skin is adaptive in climates similar to those of Europe and northern Asia. If so, the differentiation of the human species into dark-skinned and light-skinned races would be controlled largely by natural selection, the genetic drift taking, at most, a subordinate role. It has been pointed out that classical anthropologists have, for reasons of their own, chosen to classify mankind chiefly by genetically complex traits. What has been said about the racial differences in skin color applies generally to traits controlled by polygene systems. Although genetic drift could easily produce variations in the incidence of the component genes in different populations, natural selection is the only known agency which could be held responsible for racial differentiation in polygenic traits. This inference stands however untested by direct evidence, since next to nothing has been done to reveal the adaptive significance of human genetic traits.

Bolk's (1929) well known fetalization hypothesis tried to visualize complexes of traits in which human races are known to differ as outward expressions of a phylogenetic trend towards retention in the adult organization of certain embryonic characteristics. Keith (1928) and Marett (1938) put forward the no less audacious hypothesis that racial traits are external manifestations of different levels of endocrine functions. The interest of both hypotheses lies in that they were among the first attempts to envisage the structural

distinctions between humans as resultants of underlying physiological variables. In this way, groups of morphological traits seemingly meaningless from the standpoint of adaptation and fitness may conceivably be translated into the language of selective advantages and disadvantages. Neither Bolk nor Keith have however essayed this last but essential step. No attempt has been made to explain just why it is advantageous for some populations to be more and for others to be less fetalized, or why some people profit by higher and others by lower, functioning of certain endocrine glands. The physiological evidence in favor of Bolk's and Keith's hypotheses is also none too secure. It is dubious physiology to say that lack of pigmentation in a white baby makes him resemble a negro fetus.

A new era in biological understanding of human races may have been inaugurated with the publication of the remarkable essay of Coon, Garn, and Birdsell (1950). Begging forgiveness of the authors, the contents of this essay may be described as a series of conjectures about the possible adaptive significance of racial traits. Thus, the short stature of peoples living on the eastern fringe of Asia is correlated with the often scanty rice diets prevalent in these lands. On the contrary, the large and powerful body frame of certain Indian and Cro-Magnon hunters is related to their need for strength and endurance and to their meat diets. The tall, lean, and shallow bodies of desert dwellers may be viewed as adaptations to the extreme dry heat. Conversely, the short and chunky bodies of most arctic peoples are more efficient in heat conservation. The Mongoloid facial structure is characterized as a product of "climatic engineering" adaptive to resist extreme cold. Finally, it is pointed out that infectious and deficiency diseases in urban and semi-urban conditions were up to recently, and still are in the congested cities outside the area of modern industrial civilization, very powerful selecting agents. It is quite possible that the apparently fortuitous bodily structures of various human races are actually responses to the action of these selective forces.

Coon, Garn, and Birdsell are fully aware that most of their inferences are as yet not supported by sufficient direct evidence. But hypotheses such as theirs are very timely, and indeed overdue, to stimulate interest in causal analysis of human variability. After all, the primary function of a working hypothesis is to arrange facts into suggestive patterns capable of guiding observations and experiments into meaningful channels. An anthropologist working alone can do little more than to provide such hypotheses. Testing them requires cooperation of anthropologists, physiologists, medical men, and geneticists. Our medical colleagues should observe and record the anthropological characteristics of their patients. Morphological and physiological traits of people are not fortuitous; they are outward signs of biological constitutions that are important in health as well as in disease. Medical genetics should not be conceived only as compilation of a catalogue of rare hereditary disorders, but also as a study of the reaction norms of different human genotypes in different environments.

The Biological Uniqueness of Man

Some of Darwin's contemporaries fought his conclusion that man is descended from animal ancestors as downright blasphemy. Since people seldom retain a balanced view of things while fighting, Darwinists countered by asserting that man was and still is nothing but an animal species. This view was eagerly taken up by those who needed a plausible excuse to justify man's inhumanity to man. Exploitation and subjugation of the weak were declared in accord with inexorable laws of nature. Naive biologism served also as a propaganda weapon in the hands of those who wanted to free mankind from ancient superstitions and who finally robbed it of sense of purpose of life.

Now, more than ninety years after the publication of the *Origin of Species*, only some uninformed and misguided souls still fight Darwin's thesis that man is a part of nature. Oddly enough, the anti-evolutionists have recently found allies among the self-styled "progressive" Lysenkoists in Russia. These "advanced" materialists, together with religious fanatics and cranks, now find that treating man as a living organism "degrades him to the level of beasts." Man, it appears, should be exclusively a product of social and economic forces. This retreat from common sense puts the clock back more than a century.

Mankind is a biological species. But this species has evolved an adaptive mechanism of unprecedented effectiveness—the human brain. The appearance of this mechanism constituted a turning point in human evolution, and perhaps in the evolution of the Cosmos. The human species has begun to acquire a complex of adaptive traits which overshadow all previous adaptations. These adaptive traits make up a large part of what is known as culture. Man responds to challenges of his environments, both physical and

cultural ones, chiefly through discovery and invention; all other biological species respond through alteration of their biological heredity. Cultural evolution is vastly more rapid and more efficient than biological evolution, because cultural attainments can be passed in the human species independently of biological descent on which the transmission of biological heredity necessarily depends.

Although the transmission of culture short-circuits biological heredity, the capacity to evolve, acquire, and transmit cultural traits can exist solely in possessors of human genotypes. The human species contains a variety of genotypes almost as great as the number of living individuals, and yet the carriers of a vast majority of these genotypes are potentially able to acquire any one of the existing cultural patterns. But it can not be too strongly emphasized that this remarkable plasticity of human intellectual development, this susceptibility to cultural influences of all kinds, is by far the most important trait determined by the human genotype. The genotypes of apes and monkeys make them incapable of using symbols, and hence to assimilate anything resembling human culture. Inaccessibility to culture also results from substitution of a mutant gene for idiocy or similar disorders in otherwise normal human genotypes. Human cultural evolution has become possible only because a species has evolved a genetic constitution which permits cultural receptivity and transmission. But once that genetic structure has appeared, the evolutionary potentialities of the human species began to unfold. This is because the cultural development and the genetic evolution became mutually stimulating influences. Human culture is not possible without human genetic makeup; human genotype is an adaptive failure outside cultural milieu.

Dobzhansky and Montagu (1947) have put forward the hypothesis that the most important evolutionary trend in the human species is towards genetically determined educability, i.e., ability to learn from experience and to modify one's behavior accordingly. From the dawn of humanity to our own time, educability increased the fitness of its possessors. Natural selection has, consequently, favored ever higher development of educability. This trend is the specifically human feature of evolution of *Homo sapiens*.

Selection for educability has occurred, and is still continuing to take place, in all races of the human species and in all cultures, from most primitive to the most highly advanced. The biological structure of man has resulted from this selective process. The point which is easily overlooked is that the genetically conditioned educability favor diversity, and not uniformity, of human individuals as well as of human cultures. Plasticity of developmental patterns would result in uniformity of phenotypic outcomes of individual developments only in homogeneous environments. In heterogeneous environments plasticity results in diversity. Students of personality are in substantial agreement that the most important influences which guide the development of human personality are found among the interpersonal relationships. These relationships are highly variable, the more so the more advanced a culture becomes. The result is the endless diversity of human personalities. Herein lies the biological meaning of the unique evolutionary pattern of the human species. For the polymorphism which a biological species evolves is an adaptive response of the living matter to the diversity of environments which this species encounters.

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POPULATION GENETICS AND SOCIAL ANTHROPOLOGY

CLYDE KLUCKHOHN AND CHARLES GRIFFITH

Harvard University, Cambridge, Massachusetts

One of the cherished axioms of American anthropology is the unity of the science of man or, at very least, the indispensable importance of the close collaboration of workers whose central interests and specializations may be tagged as biological, cultural, psychological, or sociological. Most anthropologists agree that the human biologist needs to know at least as much about human behavior as he does about such strictly biological subjects as, say, ichthyology and plant pathology. Conversely, the social anthropologist must familiarize himself with genetics and other aspects of human biology. If his reading and research do not take him beyond sociology, economics, government, and the other so-called social sciences, he ceases to be, in the strict sense, an anthropologist.

Since this audience is composed of geneticists and physical anthropologists, we shall confine ourselves to pointing out some of the ways in which social anthropology can assist in the solution of some problems of human biology. To a group of sociologists we should reverse our emphasis, for our position is that most questions in the human sciences have both a biological and a cultural dimension and that any unilateral approach can provide only answers that are within a highly abstract frame of reference as opposed to that of concrete reality.

The first and obvious area of collaboration is in doing field work. This is simple in principle but important in practice. The social anthropologist has or can do the surveys to construct reliable charts of the relevant societies, cultures, or sub-cultures. For the human biologist to attempt field work without these is like entering a vast and bewildering territory without a map. Each culture has its own distinctive motivational patterns, and the cooperation of subjects will often fail to be obtained if the investigator uses the incentives that may work well enough in his own class, region, or culture. The meaning of many responses to items on questionnaires will be unclear or actually wrong unless there is cross-cultural translation.

As much experience has demonstrated, it is not even possible to take a census correctly if social structure and culture are imperfectly known. In some groups, for example, the same individual has as many as six or seven equally legitimate names, and cases have occurred where he has been solemnly counted under at least several of his aliases. In other groups, the restriction upon the direct naming of the dead is so strong that moderately reliable fertility and morbidity rates cannot be obtained unless the culturally sanctioned way around this dilemma is discovered—and there usually is one. When working through interpreters of non-European languages, it is absolutely essential to check on the translations of kin terms, and this is possible only if the kinship structure is known. In matrilineal cultures, for example, parallel cousins will ordinarily come through as "brothers" and "sisters." Sometimes a somewhat acculturated interpreter, half realizing the distinction from our point of view or at least discriminating between biological kin and classificatory kin, will give the rendering "half-brother" (for parallel cousin) —to the utter confusion of all save the most carefully and completely worked out genealogies. In polygynous societies which have had contact with Christian missionaries there is more often than not a propensity to deny the very existence of subsidiary wives and their children. In some cultures the dates of births are given with remarkable accuracy. In others relative dates are trustworthy but absolute dates and ages hopelessly confused. In still others a mother may give the age order of her own children incorrectly. It can be demonstrated that the 1940 United States Census is notably inaccurate on certain data for ethnic and minority groups because the enumerators were ignorant of sub-cultural differences. In short, the human biologist will do well to work with the cultural anthropologist if he wishes to get the maximum amount of reliable information.

So far as research problems and the analysis of data are concerned, there are many inviting possibilities for collaboration, many of which have already been alluded to by other speakers at this symposium. Dr. Coon's excellent paper, in particular, enables me to be mercifully brief. It seems nevertheless worthwhile to reiterate some points made by him and others and to make a few new ones.

The splendid work done by blood group investigators throughout the world would be of yet greater scientific value if the populations compared were strictly comparable as socio-cultural entities. In some instances, the groups examined are of merely geographical character, in others such unity as they have is linguistic, class, subcultural, etc. Comparison of such entities is, of course, entirely legitimate for certain purposes, but the units used in any given analysis must be of the same order or misleading conclusions on the biological side may be drawn. It would also be valuable if certain populations, such as the European Basques, which have been so intensively studied by Mourant, Race, and others were to be investigated in comparable detail by cultural anthropologists. A supplementary research task where biologists and anthropologists could well cooperate would be the study of Basque groups in the New World because here socio-cultural forces are operative in altering the incidence of blood group genes.

In general, it should be emphasized that all sub-groups within a people or nation provide inviting research opportunities. The cultural beliefs of such relatively endogamous minorities as the Mormons interfere with random mating and set interesting problems for the geneticist. The careful genealogies encouraged by the Mormon Church would facilitate the investigation. Does social class in the United States, which certain American anthropologists and sociologists have written so much about of late, have an identifiable biological basis? The studies of Professor Robert Lamb of Massachusetts Institute of Technology among some of the "first families" of the Revolutionary period and their subsequent economic and political fortunes would provide a nice lead for the geneticist. The unrivalled possibilities from this point of view in India have already been drawn to our attention: as many as 5,000 endogamous groups, some of which have been endogamous for perhaps 100 generations, ranging in size from a few hundreds to 4,000,000 individuals. Conversely, certain cultural practices making for exchange of genes between different breeding isolates merit investigation. From the "primitive" field one may instance the corroborees in Australia and ceremonials among the Navaho Indians—both occasions on which people from different groups and areas are thrown together under circumstances of relative sexual freedom.

The connections between genetic, dietary, and cultural factors in fertility and morbidity rates urgently need systematic exploration. Dr. Montagu has pioneered in this general area in his studies of adolescent sterility in primitive societies. The work of the Yap expedition of the Peabody Museum of Harvard University is another example. But many aspects of this research territory have not even been reconnoitered.

The closely related fields of psychosomatic medicine, constitutional anthropology, and culture and personality all require research designs which take full account of both the biological and the cultural side. At the population level new methods and theories in human genetics are needed before a description of what Dr. Strandskov has called the allelotype will be meaningful in terms of the above categories. Nevertheless current research can ask many of its questions in ways which do not implicitly negate one factor or the other. Investigations in criminal anthropology have sometimes taken account, though not always adequately, of certain sociological factors but hardly of the cultural. The study of somatotypes has included psychological variables but has lacked both a genetic and a cultural underpinning. It is greatly to be regretted that much current writing in culture and personality appears to be based on the premise that the genetic factor can be ignored because the techniques are not yet available for demonstrating directly its causative role in certain matters of crucial importance. However, some of us have been at pains to point out that the slogan "culture and personality," if taken literally, is as indefensibly one-sided a determinism as "biology and personality."

If one were to take literally some of the more extravagant pronouncements of a few of my colleagues in cultural anthropology, one would think that swaddling alone or some single discipline of child training were responsible for the distinctive features of personality. The diaper or Scott Tissue school of culture and personality won't wash—to mix my metaphors. If cultural child training practices and other institutions of the culture were the only things of importance, we should find a much less diversity in personality than we do find in fact. No, the situational and biological factors (Kluckhohn, 1948a) are also of great significance and sometimes of crucial significance. Except for the co-twin method and for a few abnormalities of personality like juvenile amaurotic idiocy it is difficult at present to deal rigorously with the biological dimension. We are making a modest attempt in the case of the personality formation of a group of Navaho children whom my associates and I have been following since birth (Kluckhohn, 1947). We now have rather

good biological data of certain sorts but the analysis of this against psychological and projective tests, behavioral data, and life history records has not begun. There should be many independent efforts to compare, for example, the Rohrschachs, TATs, and the like of parents and children and of siblings. We have a number of complete family records and also longitudinal testing. It would also be particularly useful to examine the protocols for separated monozygotic twins and even for ordinary siblings brought up in different households. Only by subjecting the measures used in culture and personality studies to such analysis can we hope to isolate—at least in part—the effects in personality formation due to cultural practices and to genes.

Certainly we think the presumptive evidence strong that the distinctive qualities of each culture and the personality type or types modally associated with that culture will be fully understood only when the genetic predispositions and limitations of that population are described as completely as possible. We venture even to mention one large-scale hypothesis of an admittedly speculative sort. If the data permit any general contrast between "primitive" and "modern" cultures, it is perhaps the generalization that "primitive" cultures tend strongly to be involuted. That is, it is not that "intricacy" and "complexity" are lacking at the "primitive" level. Rather, the fact is that the number and variety of patterns are limited. Variation is variation on a restricted number of themes, but this variation is often extraordinarily involved. As Goldenweiser has remarked, von den Steinen's characterization of primitive art as "eine gebundene Kunst" can properly be extended to say of "primitive culture" —"eine gebundene Kultur." Now is there any possible connection between this thesis and the circumstance that "primitive" groups are ordinarily rather small and rather inbred?

To avoid too many empty or thin generalizations, we shall confine ourselves in the remainder of this paper to more concrete material. Let us begin with brief reference to selection and migration. Various forms of cultural selection from the killing of twins and widows to Nazi practices are familiar. Dr. Coon has given some particularly good examples as regards fertility. One might add the possible effects of ceremonial continence in such highly ritualized cultures as that of the Zuni Indians. The investigation would have to include the problem of unconscious biological selectivity for the priesthood in such societies. Among the Navaho there is evidence that a propensity on the part of both men and women to become diagnostician-shamans turns up in certain family lines with greater frequency than seems explainable on the basis of intra-family social influence (Kluckhohn, 1939).

Linton (1933) gives an excellent example of cultural selection which is perhaps not well known to geneticists. Among the Tanala of Madagascar, the largest kinship unit is the gens, made up of various lineages tracing descent from a common ancestor. The people of a gens are scattered among as many as fifty villages. Marriage within the village is ordinarily endogamous, though marriage within the same lineage is forbidden. Marriage within the gens is preferred.

The Zafiakotry and Maromena gentes represent the extremes of skin color within the Tanala tribe. Individuals within the former exhibit a skin color comparable to that of American Negroes who would be called "full blood." The members of the latter gens are described as "extremely light brown." In the Zafiakotry gens all unusually light children are said to be killed, and the reverse is true for the Maromena. In both cases, incidentally, the rationalizations are the same: children deviant in skin color would grow up to be sorcerers, thieves, lepers, or given to incest. It would be interesting to discover to what extent this practice has diminished the percentage of undesired genes in each sub-population. Both gentes follow the same mating system, with enjoined cross-cousin marriage. The whole problem could be set up in terms of Davenport's hypothesis for skin color with corrections for the mating system.

Migration is, of course, one of the major factors that may alter the frequency of genes in a population. Dr. Snyder in his classic chapter "Blood Groups of the Jamaicans" in Davenport and Steggerda's *Race Crossing in Jamaica* pioneered in this as in so many other fields. In this case the migration, though not the precise sources in Africa of the Negro elements of the mixture, was definitely established. Archaeologists, ethnologists, and linguists postulate specific movements of people in prehistoric or protohistoric times. In the favorable instance the work of geneticists might weaken or support such hypotheses. A good many attempts of this sort have been carried out; far more await collaborative effort. I shall mention only two examples. The linguist, Whorf, has asserted that the language of the Hopi Indians of Arizona shows phonetic and morphological resemblances to certain cognate languages in Mexico which are closer than those of Hopi to such related tongues as Paiute, Ute, and Shos-

honean spoken in nearby regions. If the ancestors of the present Hopi did move northward from Mexico, this would be of tremendous importance to the whole reconstruction of the history of Pueblo culture. Presumably if the ancestral Hopi were from Mexico there ought to be demonstrable biological affinities with one or more of the native populations still in Mexico. Another inviting study would be a biological comparison of the two Comanche bands which have been separated for some hundreds of years and which became culturally very divergent.

The remainder of this paper will be devoted to an examination of a few implications of one aspect of social anthropology, kinship systems and marriage practices, for population genetics. In 1921, Sewall Wright published papers providing a mathematical basis for the determination of the genetic composition of a population and applying this method to various types of mating such as brother-sister and first cousin. For each type he traced the decrease of the heterozygotes in the population for 15 generations and then showed the proportion that would exist after an infinite number of generations.

We shall first use Wright's thinking in considering several empirical kinship systems. It should be noted at the outset, however, that these are still ideal cases in the sense that it is assumed that the system works perfectly. As will be shown later with respect to the Ramah Navaho, this assumption has its flaws. No prescribed patterns of marriage are followed without deviation through many generations. The norm for symmetrical cross-cousin marriage, for example, to function perfectly demands a constant sex ratio, equal fecundity in all marriage groups, no disruption due to deaths caused by plagues or war. These conditions are never fulfilled in practice. Moreover, as Wallis (1950) has recently pointed out, even these conditions are not sufficient because of unequal distribution of sibships. There are also always marriages that cross generational lines, thus disturbing, incidentally, the mechanical operation of the Hardy-Weinberg law. Finally, there is the joker that all relatives designated by the same kinship term are not necessarily biologically equivalent. If cross-cousin marriage is culturally prescribed without differentiation between maternal and paternal lines, it still makes a difference if a disproportionate number of men marry their mother's brother's daughters as opposed to father's sister's daughter. More important still is the case where marriage with a true biological relative is called for but where a classificatory relative is easily accepted. Ego may not only marry his father's or mother's cross-cousin rather than his own: he may in fact marry a terminological cross-cousin to whom actual relationship is exceedingly remote. The true drift toward homozygosity is more often than not much slower than expressed by the ideal case.

Some small populations in Australia and limited areas of Melanesia have bi-lineal descent and practice double first cousin marriage between cross cousins (Murdock, 1949). With such marriage, practised ideally and consistently, heterozygosity decreases to 13.7 per cent at the end of 15 generations.

Societies based on unilineal descent with cross-cousin marriage are rather numerous. In Australia, matings of this type are found among the Kariera in the West, the Urabunna, Wolgal, and Ngariago near the Fortescue and DeGrey rivers, the Kabi and Wakka in Queensland. It occurs among the Dravidian peoples of South India, in Ceylone, the Vedda Buin of Bougainville, the Tanna of the New Hebrides. In North America unilineal cross-cousin marriage occurs among the Miwok in California, the Haida on the Northwest Coast, and many tribes having the Crow and Omaha types of kinship systems. In Africa the Ashanti provide an excellent example, the genetic effects of which have been studied by Buxton (1927). Examination of the standard deviations and coefficients of variations of a series of anthropometric measurements indicates a highly homogeneous population. There are also some indications of the appearance of rare recessives in the homozygous state. This case appears to be an empirical demonstration of the decrease of heterozygosity after long-continued cross-cousin marriage. The series is smaller than could be wished, but this is at least a partial model for collaboration, for the describer of the kinship system (Rattray) enlisted the cooperation of a human biologist (Buxton). It might be especially rewarding to compare two groups which were presumptively random samples from the same population 20 or 30 generations ago but which since that time had practiced different forms of mating—e.g. own cross-cousin mating versus random mating outside the immediate family or even mating with paternal parallel cousins as in many Islamic groups.

Various kinship systems, both patrilineal and matrilineal, prescribe second cousin mating. However as Wright has shown this has comparatively little effect in changing the genetic composition of a population. From an assumed population equilibrium of 25 per cent *AA*, 50 per cent

Aa, and 25 per cent *aa*, the proportion of heterozygotes would decrease only to 49.1 per cent in 15 generations. Comparison of the anthropometric data from Arnhem land in Australia published by Howells and Warner (1937) with the Ashanti data shows the standard deviations of the former to be greater in thirteen out of fourteen comparable measurements, even though the Australian population is considerably smaller. Although various qualifications on this interpretation need to be made, it seems probable that this difference in variability represents at least in part the effects of cross cousin as opposed to second cousin marriage.

It should be very rewarding to test various hypotheses about genetic drift on the aboriginal peoples of a total continental area. For South America, the data, serological, morphological, and anthropometric are available only in part, but specifically pointed field work could fill in the gaps rather quickly. The cultural facts supply some of the requisites for a nice research design. The native peoples of South America can be conveniently divided into three main groups: the Andean, the Tropical Forest, and the Marginal. Each group tends to be somewhat distinct as regards general cultural orientations. The Andean and Tropical Forest exhibit quite similar population densities, but differ in the major emphases of the kinship systems. The Marginal area presents very small breeding populations.

The density of the native population is heaviest in the coast regions of the Andean area. Here the density averages above 75 persons per 100 square kilometres reaching 390 per 100 square kilometres in some areas. The eastern part of the Andean region and the bulk of the Tropical Forest region has a population density of from 12 to 30 persons per 100 square kilometres, reaching to 75 along the Amazon. The size of native communities is generally consistent with the density of population. The communities in the Andean region vary from 500 to over 3,000 inhabitants. Community size in eastern Brazil and along the Amazon is nearly comparable, ranging from 150 to 3,000. The most characteristic part of the Marginal area presents 50 to 150 inhabitants per community. In almost all of these non-urban regions the degree of European admixture is small, and most populations and cultures have been relatively stable for at least a few centuries.

In spite of many small and large variations, the kinship systems within the Andean and Tropical Forest areas have a degree of consistency in major emphasis. Throughout the Andean region there was a marked tendency toward endogamy both in clans and moieties. In the Tropical Forest region, the major themes are exogamy and unilineal descent. This tends to be true for the Marginal peoples, too, but there geographic and ethnic isolation makes for rather intense inbreeding, exogamic rules notwithstanding.

There is thus the possibility of various paired comparisons on heterogeneity, gene loss, and the like. Inbreeding within segments of sizable populations in the Andean area can be set off against outbreeding in populations of similar size or against inbreeding of a different sort involving the totality of small communities. The effects of various types of exogamy in the Tropical Forest area could be studied—for instance, between tribes which forbid cousin marriage and those which allow or prefer it. The investigation of interbreeding at the borders where peoples from two main areas meet might also be fruitful.

Finally, we wish to present some portions of the natural history of one small breeding population, the Ramah Navaho, to whom you have already been introduced by Dr. Spuhler. Since our biological data are not yet fully gathered and since those available are incompletely analyzed, it would be premature to venture any general interpretations of a genetic order at this time. These are, however, facts which must be carefully considered in the eventual formulation of conclusions. Perhaps the presentation of these facts, mainly cultural, now will serve to remind us all of the hazards inherent in any too hasty marriage of one beautiful abstraction—mathematical genetics—to another beautiful abstraction —an anthropological kinship system.

The Ramah Navaho as of September 1, 1948 included 296 males and 318 females, a total population of 614, though this figure could be increased by about 20 were one to include certain individuals who reside there part of each year or who have resided there from time to time over the past 20 years. The Ramah Navaho are geographically isolated from other Navahos by the Zuni Reservation and by Anglo and Spanish-American settlements and ranches. The nearest Ramah Navaho family is some thirty miles from the closest Navaho family in another locality. The Ramah Navaho are comparable to a Navaho "band" in the structure of that tribe in at least the two centuries preceding the Navaho captivity which began in 1864. And there is evidence that the degree of outbreeding of the Ramah Navaho, including that with non-Navaho groups, has abundant parallels among the bands of the proto-

historic period. It is our conviction that indeed this was the case in pre-European times, certainly with the Navaho and almost certainly with most Indian tribes of at least the American Southwest. The archaeological record shows more and more clearly that we have tended to underestimate the amount of trade, communication, and, inferentially, personal contact that occurred in North America before the advent of the horse.

After the Navaho captivity at Fort Sumner ended in 1868, a number of Navaho families drifted into the Ramah area where some of them had hunted and farmed prior to 1864. Most of the original group were related in one way or another. The leader was married to two sisters. His own sister and a brother of his wives and their mates also settled at Ramah. So did the leader's younger brother, his maternal uncle, two more distant kinsmen and their wives. The leader also brought a Walapai Indian as his slave. This Walapai married a Navaho woman from another group, but they and their children settled at Ramah. Gradually a few other Navaho families with some, though not very close biological ties to the original group, came to the Ramah area. About 1880 four Chiricahua Apache women, three of them full sisters, the fourth a maternal first cousin of the other three, married Ramah Navahos. One of them brought her son by a marriage to a Navaho man from another area. About 1895 a Laguna Indian man married a Ramah Navaho woman and settled there. About 1900 a Yaqui Indian from Mexico married a Ramah woman. All of the above marriages resulted in many descendants from the outsiders. Only one child from a Spanish-American is known or rumored. According to gossip and supported by skin color and other features several children have been sired by a local Anglo in recent years. However, in one family line there are phenotypical indications of admixture which must have occurred 50 or 60 years ago. In sum, the "founders" of this population were already heterogeneous in the genetic lines represented. During the seventeenth, eighteenth, and early nineteenth centuries the Navaho tribe in general absorbed large numbers of Indians from other Southwestern and Mexican groups, captured Spaniards, and half-breed Navaho slaves who escaped from Spanish or Mexican masters. In spite of all this, Boyd and Boyd (1950) conclude from their blood group data that the Ramah Navaho represent an "unusually pure" Indian group.

A picture of the present population would include the fact that a large number of the youngest generation have Chiricahua Apache ancestry, an appreciable number Walapai, Laguna, and Yaqui, a few Spanish-American or Anglo. Of course, two or more of these lines are united in the ancestry of many individuals. Probably Ute at least should be added, for this is one of the clans in the Ramah area, and the clan is known to have had at least one Ute ancestress in the not too distant past. Of living members of the population born in Ramah 70 had one parent who came from a different Navaho group, five had a Walapai parent, eight an Apache parent, two a Yaqui, two a Laguna, two a Zuni (an earlier Zuni marriage left no surviving children), and one a Mexican. In addition, 22 men and eight women moved into the community on marriage. All are Navaho except one Zuni. As recently as ten years ago, there was only one "foreign" woman at Ramah, but matri-local residence is breaking down.

The official mating system is comparatively simple. Nineteen exogamous clans are represented in the Ramah population. However, four of these are represented by single in-marrying males, and only six of the twenty have memberships comprising more than 16 individuals. The two largest clans include about 40 per cent of the total population. The individual may not marry into the clan of either his father or his mother. In other words, first cousin marriage of any kind is forbidden. In the whole history of this group there have been only four cases of matings between members of the same clan. One involved a double cross-cousin mating, two others simple cross-cousin mating. Each of these instances was that of actual biological cousins. The fourth case violated the cultural taboo, but there was no traceable relationship between the individuals concerned. There have been five cases of marriage into the father's clan, but only two of these involved a traceable relationship, namely that of second cousins. It should be noted that intra-clan marriages among the Navaho population at large would more often than not be between quite remote relatives, but at Ramah, with a few exceptions, there is demonstrable biological connection between all clan members.

In addition, certain clans are linked together exogamously. At Ramah none of the clans with large membership are linked to each other so that this supplementary cultural restriction upon possible matings is comparatively slight. Let us look at some specific data. Because of clan and clan group exogamy, the males of the two largest clans are allowed to mate with only about 60 of the females of reproductive age out of about 120 females of reproductive age in the present popu-

lation. If we take the next to smallest of the clans that may be considered "native Ramah," the situation is quite different. This clan has a total membership of 47. Women of reproductive age number 12, men, 10. These 10 men have culturally denied to them as mates only the 12 women of their own clan plus 8 women of reproductive age of other small clans which are considered linked. Exogamy as regards the linked clans is less and less seriously enforced by cultural sanctions. Even the older Navahos do not agree completely as to which are "partner clans." There is evidence that this kind of prohibition was not taken as rigorously as that against members of one's own and one's father's clan even a hundred years ago. In general, it may be said that the effect of clan and clan group exogamy is toward panmixia within the breeding population and toward the procurement of mates from outside communities. It tends toward forcing genes from other Navaho groups, other Indian tribes, Spanish-Americans, and Anglos to be spread widely in the population rather rapidly. To some extent, also, as usual, the culture interferences with and on mating tend to cancel each other out.

Polygynous marriage is permitted but tends to vary with economic situation. In only three cases in this community has one man been married to three women simultaneously; all other polygynous marriages involve only two wives. At present, there are seven polygynous matings, all except two with full biological sisters. Until recently it was extremely rare for a man to marry two women who were not closely related: sisters, half-sisters, parallel cousins ("sisters" according to Navaho kinship terminology), a woman and her sororal niece, a woman and her daughter by a previous mating. There are no stepdaughter marriages at the moment, but there have been five in the history of this population.

Thus far we have been dealing mainly with mating systems in the strict sense—i.e., the normative patterns of the culture as they would be given by informants to an enquirer. However, there are mating practices, dependent upon explicit and implicit cultural attitudes, which are of vital significance to the population geneticist but which will never emerge from the most correct chart of the kinship system. For example, the attitudes toward sex, marriage, and divorce are extremely important. The Navahos put few impediments in the way of the exchange of genes, apart from the exogamic regulations. Sex is a good thing (Kluckhohn, 1948b) and a natural thing. Divorce is extraordinarily simple. Of some 300 men who have sired offspring in this group, only seven have restricted themselves to a single mate, and of these, all save two died young. The modal number of regularized marriages per male approaches three, and the genealogies record six or more marriages for a considerable number of men who have completed their part in the reproductive cycle. Of course the fact that many women have produced children by different men and the same men by different women is very convenient for the geneticist.

Another cultural practice of genetic interest is that of crossing generational lines. Nor is this simply a matter of old men taking young wives. The Navaho think it very sound for an experienced woman who is widowed or divorced and has a nice herd of sheep to take a lad as her second mate. This is thought advantageous to both parties. Of all matings recorded nearly 15 per cent involve individuals separated by 20 years or more. This practice makes calculations based on the Hardy Weinberg law difficult.

Marriage, to the Navaho, is not nearly so much a compact between a man and a woman as an arrangement between two family groups. Hence there is constantly recurring exchange between two family lines. Sometimes as many as five siblings from one family will be mated to five siblings from another. If a sibling is not available to carry out the reciprocity, a half-sibling or a first cousin from the same clan will be produced. The levirate and the sororate are also practiced, though not with complete regularity. We have not yet calculated the exact frequency of this repeated exchange of genes between two family lines, but it can be said that marriages which do not involve this principle are decidedly in the minority. It is clear that such a practice may effect the genetic composition of a population. Take, for example, three such matings, each of which has one member heterozygous for a gene pair. If each marriage has four children, there are 16 chances out of 18 that one child will turn out with the double recessive.

This practice also tends to slow down somewhat the dispersal of genes by random mating between clans where mating is not closed by the rules of exogamy. It might also be mentioned in this connection that there is some disposition to marry into the clan of the mother's father or father's father.

Doubtless some of these factors, such as stepdaughter marriage, occur so infrequently that they can properly be neglected in dealing with the genetic composition of this population.

Nevertheless it seems to me that a mathematic either more complicated or possibly far more simple than any yet devised is required to handle the concrete problems in all their empirical detail. We need your help.

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CONCLUDING REMARKS OF THE CHAIRMAN

CURT STERN

Department of Zoology, University of California, Berkeley, California

The trend toward specialization in science is met by successful, wide reaching trends toward unification of separate disciplines. This conference is witness of the growing together of anthropology and genetics which has taken place during the last decade. Our meetings were not so much a mutual education than a mutual consideration of problems of common concern. The anthropologists spoke the geneticists' language, and the geneticists had already gone beyond their Drosophilae or mice to some knowledge of the anthropological problems. Moreover, the speed in the spread of knowledge from one field to the next, and the bearing of very contemporary studies in basic general genetics on the problems in the special field of anthropological genetics, as well as the stimulus from the latter field to thinking in the former, was an experience which gave us all happy satisfaction.

"The origin and evolution of man" was dealt with on two main levels, the origin of the human stock including the evidence on fossil men, and the problems of human racial differentiation. At the end, the topic of constitutional polymorphism within racial groups, a polymorphism which transcends racial delineations, was presented to us.

The analysis of man's origin, carried on from the points of view of the taxonomist, comparative anatomist, and paleontologist, included Simpson's basic considerations on time and sequence, on lineages, parallelisms, divergence and convergence, on trends, orthogenesis, and reversibility in evolution; Schultz's presentation of facts on the variability of numerous traits in catarrhine primates including man with an interpretation of differences in terms of fetalization in regard to some features, acceleration in regard to others, conservatism for still others; Washburn's experimentally underlined, pheno-genetically oriented discussion of the succession in the evolutionary sequence of specifically human traits pointing to the primary event of changes in the pelvis and the gluteus maximus, which were then followed secondarily by the growth of the brain. The different evolutionary rates of such parts as jaws, teeth, and brain are now apparent from the paleontological record and are not unexpected even though they caused consternation to some earlier investigators.

Within the framework of these basic facts and concepts, McCown and Stewart then reviewed critically the fossil evidence on hominids and tried to evaluate the relation of the Neanderthal group of man to the sapiens type. On the one hand the number of fossil individuals available is now considerable, and a new method of age determination, the fluorene test, gives significant clues as to the chronology of finds; on the other hand, the fossil record is still very incomplete and the discovery of the "progressive Neanderthals" as well as of the Fontéchevade skulls has increased the complexity of the problem. It seems, however, that such a complexity relates more to the details than to the large outline. As puzzling as the details are, one is impressed by the abundance of links to be fitted together rather than by the missing of links. Mayr, from the point of view of the neo-systematist surveyed the array of fossil human remains. He suggested that all hominids, living and extinct, should be included in the single genus *Homo*, and that the species sapiens should be subdivided into such subspecies as *H. sapiens sapiens*, and *H. sapiens neanderthalensis*. This taxonomic tendency to "lumping" has the advantage of not separating too widely the members of continuous lineages but the nomenclatural problem cannot escape the difficulty of all evolutionary taxonomy, namely, the attempt to "freeze" a continuous flow at arbitrary or accidentally determined moments.

In all these presentations of the fossil origin of man, genetic concepts were used in the attempts to interpret and clarify: mutation, selection, gene drift, migration, population size, isolate, and systems of mating found their appropriate places. The tune had been set by Strandskov's introductory discussion with its definition of the useful term "allelotype" and by Buzzatti-Traverso's survey, based on analyses of experimental populations of flies, of a great variety of genetically important factors which determine the survival and the changes in allelotypes of populations.

Thieme's presentation of an unusually thorough survey of Puerto Rican populations served both as a demonstration of the many interweaving components of environment, as for instance, geography, climate, parasites, mode of occupation, culture, and nutrition, and as a warning not to accept too easily samples of populations as overall representative. Some of the studies reported later could have profited from a fuller realization of this difficulty.

The second large topic of the conference, the genetic analysis of racial traits, began with speakers who had taken comprehensive censuses of the frequency of heredity diseases in two populations. Böök dealt with the inherited neuropsychological disturbances in a small isolate in Northern Sweden, and Kemp laid before us a remarkably complete picture of the genetic morbidity load of an isolate of four million people, the Danish. Neel restricted himself to a discussion of two blood diseases in man whose peculiarities provided the opportunity for some fundamental questioning. Thalassemia and sickle disease occur mostly in specific, though large, populations and are strongly subjected to negative selection. How is the selective elimination of the disease-causing alleles counteracted? Is it a high mutation rate from normal to abnormal which replenishes the store, or do the heterozygotes make up in reproductivity what is lost in the lethal homozygotes? If mutation, why is it restricted to specific populations which, particularly in the case of the Mediterranean anemia, are by no means sharply differentiated from neighboring populations? Does the mutable allele mutate only in a genetic background found primarily in Mediterranean peoples, a multifactorial background which does not accompany *in toto* the diffusion of the allele into adjacent people? If positive selection for the heterozygotes is instrumental, will present indications for the existence of such a phenomenon account for what must have taken place for thousands of years?

It has often been pointed out that most of the precise knowledge of the genetics of morphological human traits comes from the study of anomalies, while we know little about the genetics of normal traits. There is a general interpretation available which points to the analogy of the difference between two different well functioning models of an automobile on the one hand, and the difference between a functioning and non-functioning vehicle on the other hand. The difference between the former two is complex, dependent on numerous minor "polygenes," that between the latter is usually simple, depending on some major defect. Spuhler has brought to us facts which, if confirmed on a wider basis, will make this analogy less valid than one may have thought. That normal morphological variations concerning the patterns of certain superficial veins of the peroneus tertius muscle and of the vallate papillae of the tongue seem controlled by single or few loci gives some hope that other normal traits too may yield to relatively simple genetic analysis. Of course, there is great *a priori* likelihood that many normal trait variations are the result of individually inconsequential and only jointly decisive differences in a large number of genes. However, side by side with such truly polygenic differences, there may well exist others in which the effect is due to some major locus, perhaps supported by additional loci with minor action. Data bearing on this question are all too few, but the apparently relatively frequent, more or less pure segregation of racially distinguishing features as early as in the grandchildren of racial intermarriages suggests a relatively simple genetic basis. New studies on negro-white crosses, perhaps in Brazil, or of Mongoloid-Caucasoid crosses appear highly desirable, particularly if the observed traits are not treated as wholes but separated into genetically independent components. Lasker's discussion of racial traits in teeth, dealing separately with crown pattern, root pattern, occlusion, and other attributes may serve as a prolegomenon for such a task. Boyd gave us a general survey of the problems encountered in the genetic analysis of various racial traits.

The blood groups, of course, are the pride of the human geneticist. Race's comprehensive and lucid discourse gave a survey of the many now known facts, together with a weighing of the role of selection in the establishment or maintenance of the polymorphism so typical for the blood groups. The evidence for selective forces on Rh and Kell alleles is undisputable and demands the kind of hypotheses for maintenance of equilibria, if there are such, as discussed for thalassemia. With respect to the A-B-O and the M-N properties the story is less clear and one will await new data with great interest.

Specific application of blood group genetics to populations in the Mediterranean area, to Eskimos, and to Australian aborigines were reported by Mourant, Laughlin, and Birdsell. Mourant traced the gradients of various alleles of several loci along geographical lines and tried to reconstruct the origin of the present Mediterranean populations

from the mixture of various elements (not genetically pure themselves, of course), still found separate in relatively unchanged state in Sardinia, and in the Basques, plus a minor African contribution. Laughlin's study on the Eskimos took account of the blood group frequencies as well as of morphological traits. The various data agree in showing that the Eskimos in spite of their spread over a range of 8,000 miles are a single unit, in which divergent small isolates should not be regarded as the archetypes but rather as deviants most subject to drift. Birdsell also studied simultaneously blood properties and morphological traits. By setting up models of gene flow and assuming different numbers of tribal barriers to gene diffusion from immigrating populations into aboriginal, earlier present, populations, he arrived at a new hypothesis regarding the region of entry of the Carpentarian people into Australia. In detail, some features of the present gene distribution point to drift as a cause, others to the action of selection. Birdsell's emphasis on "genetic space" as a primary variable in race serves as a marker for the concepts employed. Suggestions of microevolution of skull measurements in Greece covering about 4,500 years, and their relation to estimated population sizes were offered by Angel.

It was obvious that these studies on racial traits should not stand without a more general consideration of the concept of race as such. Montagu took upon him this task, stressing the statistical nature of the concept, that is, emphasis on the existence of only relative differences in allele frequencies rather than of complete differences. He advocated the replacement of the emotionally weighted, popularly misunderstood and therefore misleading term "race" by "ethnic group." In the discussion of this proposal some supported this stand. Others felt that the present *clarification* of a concept which terminologically is probably not eradicable should be made public; that race formation was an inevitable stage in evolution; and that the concept of race needs to be wrangled with anew in each generation, just as such concepts as atom, and gene—or freedom, or democracy.

In parentheses it may be asked whether some allele frequencies do not perhaps reach practically unity in one of the major racial groups and zero in others, whether, in other words, some racial differences are absolute rather than statistical. It would certainly remain true that the great majority of human genes is held in common by all men, but we should not assume dogmatically that fixation of different alleles of some loci may not have occurred in alternate groups.

The cultural anthropologist, Coon, reminded us of very important general aspects of racial origin, persistence, and decline. The manifold cultural elements in the selection of mates, the ability to produce offspring, the reproductive longevity of individuals, and the ability of certain individuals to influence group survival are not items which can at present be evaluated quantitatively. Nevertheless, their existence and far-reaching significance can hardly be doubted. This type of interrelation between culture and biological events has and still does play an immense role in the racial composition of humanity as a whole and within more limited groups.

The papers on constitution placed before us a different type of variation than those discussed by the speakers on individual or racial genetic differences. The variability presented by constitutional types is not only unknown in its genetic foundation but has perhaps an unusually large environmental component. Certainly no analysis of the genetics of constitutional types is yet available and Sheldon's promise of such an analysis after three generations of observations from birth to death is hardly encouraging. However, the prospects are not as dim, and one may expect some important, if preliminary, information in a nearer future. To one geneticist at least it would not be a surprise if heritability of constitutional types would be demonstrated. The problem is basically the same as with other complex traits where it is not the alternative of heredity versus environment which is being elucidated but the question of the relative contributions of these agents to the observed variance. For such an analysis modern statistical methods are available. Devices such as the study of foster children in relation to genetic and adopted parent types, and of children in orphanages should also be employed. Special attention might have to be paid to the existence of non-genetic prenatal influences although it remains to be shown whether the important recent data on such influences in the causation of congenital anomalies have perhaps only limited significance.

At the moment, the practical importance of the correlations discovered by Garn between constitution and biochemical or morphological traits, may be considerable, and the correlation found by Seltzer between constitution and juvenile delinquency, may be food for thought, but their implication for the origin and evolution of man, past and future, are unknowns. Sheldon's bold

attempt to bridge the schism between the biological and sociological sciences is too breathtaking to be easily followed by more pedestrian souls. The existence of important interrelations between human constitution and sociological phenomena is by no means denied or doubted by such a waiting attitude.

The final papers in this Symposium, by Dobzhansky and Kluckhohn, dealt with perspectives of future research. These are summarizing papers themselves, full of suggestive comments and thoughts. Even more than for all other contributions touched upon in this utterly inadequately brief review it should be said: Study for yourself!

A few concluding remarks may be permissible. The political implications of statements or conclusions regarding the origin and evolution of man have been in our minds again and again. The emotional weighting of such terms as species, race, delinquency, breed, purity, eugenics, selection, and others is heavy. Knowing the terrible harm which has grown out of misconceptions, or for which these misconceptions were used as attempted justification, there is a tendency to shy away from conceptual regions, or from terms, which might be exploited by ill-will or stupidity. I believe, that science should not yield to such derived impulses. We should look for the truth wherever it can be found. We should not assume that facts do not exist because their uncritical postulation has been detrimental. On the other hand, we should, of course, be most careful not to draw conclusions which go beyond the facts and, on the contrary, emphasize the limitations of our knowledge. Finally, we should scrupulously avoid subjective value judgments. All this admittedly is very difficult!

These thoughts apply particularly to the problems of eugenics. Whether we like it or not, selective forces cannot be excluded from acting in our societies and nations. A thorough study which will enable us gradually to control selection is in the tradition of human cultural evolution. That the control of the future human evolution is a most delicate problem which calls for scientific understanding not yet available, for human understanding and gentle handling, does not, in my opinion, subtract from a long range need for such control.

I fear that this sketchy panorama of the conference and my having taken advantage of being the last speaker to voice some personal opinions would make for but feeble applause at the end. I shall therefore shift to a final task which will find unanimous approval. This conference of anthropologists, students of constitution, and of medical and general geneticists has brought together individuals of different backgrounds and different attitudes. It has given us American investigators the benefit and the pleasure to meet with our colleagues from England and India, Italy and Sweden, Denmark and Japan, Brazil and Germany. It has been held in the unusually congenial and informal atmosphere which has always distinguished the symposia of the Long Island Biological Laboratory. The arrangement of such a meeting is a great task which the visitor easily underestimates. To its director, Dr. Demerec, whose labors and thoughts are responsible for these meetings, to the organizers of the program, Drs. Dobzhansky and Washburn, and to the efficient helpers in the office, in the kitchen, and at the registration desk, we all express our most sincere gratitude.

DISCUSSION

COUNT: The Symposium has chosen for its final consideration that of problems for further research. With all due and high regard for the presentations from the various speakers, it remains true that large areas pertaining to the origin and evolution of man have hardly been touched upon at all (at least during the six days of my attendance, and as far as I could ascertain by inquiry). May I comment on the following three areas:

1. Ontogenetic growth in relation to evolution;
2. Constitution, in its more general meaning than that of somatotyping and its concomitants;
3. Culture as an artificial ecology having a selective value.

1. Let us ask first, When a phenotype is a mutant in any character, just when did the mutation occur in its life? For instance, did the mutation occur within the spermatozoon, the egg, or was it induced perhaps by the contact of the two alleles on zygosis? At all events, the mutation probably occurs before the ontogenetic cycle has progressed very far, and at some point of great biological plasticity. Some mutations alter morphological and physiological dimensions. Theoretically, these lend themselves to differential measurement in comparison with the parent. For very many of them, at least, this means also alterations in growth gradients.

The measurements which anthropometrists take, and which conventionally are compared by the device of indices etc., admittedly are a substitution of a geometric framework for the subject

under scrutiny. Chest circumference, for instance, can hardly have a one-to-one correspondence with some activity of one or several genes peculiar to it. At the same time, there exists no other way of tracing ontogenetic alterations of morphology than by some metric scheme, except in so far as we leave the phenomenon on the purely descriptive level. In any metric scheme, as fitted to the individual subject, there can be no absolute frame of reference, no morphocentric point of origin from which the individual should develop ontogenetically by differential expansion in all directions; at least, none that is practicable.

Now, whether or not the morphological, physiological, and biochemical changes which amount to the evolution of man out of a protohominid stock, be gradual or saltatory, at least the changes must be expressed during the ontogenetic development of individuals as gradually unfolding traits of a phenotype. The usual paleontological comparison, however, is between adult individuals—the end-products of the processes. Comparison is done as though the adult of an earlier stage had given rise to an adult of a later stage. The paleontologist is aware, of course, that in making such comparisons he is indulging in a kind of shorthand; nevertheless, it does not correspond to the actual events. The real evolution for which mutation was responsible has been first of all a germ-plasm evolution—a genetic change of which the phenotype is but an outward expression. The phenotype, one might say, is the genotype's device for meeting the external, physical environment.

Perhaps a mathematical diagram may be useful at this juncture. Let O_1 O_2 $O_3 \ldots O_n$ be the germ-plasms, or, if preferred, certain genes, in a series of evolving generations 1 2 3 ... n. Then let generation O_1 pass through the ontogenetic stages a_1 b_1 $c_1 \ldots Z_1$, in which Z_1 is the definitive adult; and so on for the other digits. Paleanthropology compares the forms Z_1 Z_2 $Z_3 \ldots Z_n$ (letting Z_n represent neanthropic man), as though the chain of evolution ran through them. But it does not: the continuity runs through O_1 O_2 $O_3 \ldots O_n$, while the continuities a_1 b_1 $c_1 \ldots Z_1$ etc. take off at right angles to them. In the evolutionary series, the continuity is that of the O's; in the ontogenetic series, the continuity runs through the subscript numbers, severally, of any series abc ... Z. Genetic mutation actually occurs within members of the series of O's. A mutation in, say, eye-color of a fruit-fly can be a matter involving but a one-generation change. In the diminution of the jaws of man, on the other hand, we have a change operative over a very long time and involving an indefinite number of generations. Is this a *series* of mutations, or is it to be thought of as one durative mutation (or polygenic mutation, duratively expressed)?

To date, we have this great gap between genetics and the phylogenetic aspects of ontogeny: There exist, on the one hand, the mechanisms established more or less definitively by the geneticists; on the other, the obvious alterations in the shape, size, and behavior of the growing human organism over a period long enough to allow genetic alterations to occur. Of prehominid immature forms, we are beginning to recover a few fragments; it is not inconceivable that some day, with a careful use of interpolations, we may be able to fit growth-curves and their mathematical formulations to these forms and, by comparing them with those from extant man, recover something of the quantitative picture of the *evolution in growth-rates* which eventuate in those adults on which at present we base all our comparisons.

It must be obvious that there will then be a different genetic approach to the problem than that obtaining today in, say, the treatment of the blood-types in anthropology. (I say this in full awareness that the blood-typing of a neonatus is a different matter from blood-typing an adult.) The point is, that problems of sheer presence or absence of a gene in a *population* lie in a different dimension from those where a process sets in that progressively changes *individuals* over a long series of generations.

2. Whether Sheldonian methods of somatotyping are useful to the problems of human origin and evolution, was not brought out in this Symposium. Perhaps it is too early to tell. One thing, I believe, is certain: constitution is a real biological phenomenon, morphological, physiological, biochemical, psychological, whatever be the devices for identifying and measuring it; hence it cannot but be relevant to man's origin and evolution.

The range of body build in protanthropic and paleanthropic men is still unknown, and undoubtedly will remain so for a long time to come. Even if there were sufficient fossil material available (there is no reason at present for believing that it ever will be), there exists as yet no proven technique for determining constitutional type from skeletal remains. Moreover, even if we did know the constitutional typology of *Sinanthropus, Homo neanderthalensis, et al.*, we are far from knowing that they represent anything more than collateral lines which are not actually ancestral to man. Thirdly, we do not know the

genetics of constitutional type in extant man. Fourthly, the bearing of constitutional type upon race is almost totally *terra incognita.*

Yet every student who has attacked the problem of constitution with regard to race, is aware that there is relationship between them. It cannot be said that a people which presumably is fairly homogeneous racially when compared with some other that is manifestly heterogeneous racially, shows a smaller range of constitutional type than its comparate; at least, we have no ascertained law to that effect. On the other hand, it is quite obvious that Balts as a whole differ constitutionally as well as racially from the Ceylonese. The problem has two aspects: Do *any* examples of exactly the same constitutional type exist among both Balts and Ceylonese? And, in populations admittedly possessing the same constitutional types, are the proportionate incidences the same in both? But if constitution is more than morphology—if it has its physiological and psychical components—then a given people must have its pattern of living determined in important part by its genetic constitution. This is the capital of a people; its cultural life is the story of its investment of this capital.

3. This last remark furnishes a convenient transition to the third and final comment.

Perhaps there are more European than American anthropologists who realize the problems lying in this area: the area of social biology.[1] The importance of genetics in this area is enormous; it is an area which will determine the evolution of man in the foreseeable future. The features of this area might well have been handled at the juncture where Dr. Kluckhohn delivered his paper. Since they were not, at least they should be mentioned for the sake of the record.

That genetic laws are as fully operative upon man as upon any other animal, can hardly be disputed. His origin, evolution, and differentiation consequently are as fully dependent upon them as in the case of any other animal. But at the same time, he is uniquely panecumenical, and he is not so by virtue of some fantastic range in biological adaptability; it is by virtue of a peculiar, self-induced ecology—the artificiality called culture which operates within the strictures of physical nature. This means that, as compared with other organisms, the proportionate factors of hybridization, isolation, taxonomic differentiation, present a peculiarly human pattern. Natural selection and drift seldom operate solely and immediately within a natural environment, but immersed, so to speak, within the medium of the artificial environment termed culture.

Thus, for instance, only man possesses social class. Suppose we assume, for the sake of a first exposition, that all classes have equal biotic potentials and express them equally: social class nevertheless is assortative in that it tends to concentrate levels of intelligence and varieties of native endowment into classes; and to varying degrees classes are endogamous. This in itself should gradually make for genetic differences between classes that presumably are statistically significant. This phenomenon has no parallel among other animals. Suppose, next, that the classes are not equally reproductive. This may be due to a difference in biotic potential, or it may be merely a difference in its effective expression; in either case, the difference is one engendered by class, which is socio-economic, and not biologically determined. Over a number of generations, the relative as well as absolute expression of biotic potential of each class fluctuates. The fluctuation will be in either a plus or a minus direction, per class. It is not necessarily true that the middle class, for instance, will continue indefinitely to reproduce at a lower rate than a lower class, or that its reproductive rate will always tend to lower itself. In terms of centuries, the configuration of all these graphs is not necessarily, and probably is not, that which characterizes the last hundred years or so.

Man's panecumenical character means, of course, that he is peculiarly high in his mobility—again a cultural phenomenon. This means that during his evolution he has hybridized at all levels of racial diacritic.

The breedings of man are furthered, channeled, or inhibited by many other cultural factors; perhaps, in the last analysis, by all of them; but, unless I am mistaken, they have not been as much investigated in this country as they have in Europe; in any case, they have not been very much investigated anywhere. Modern highly "civilized" societies are sessile; they never migrate as totals; yet transportation encourages the meeting of males and females from far more widely separated locales than in the case of non-literate societies. None the less, more often than not the socially sanctioned matings occur between members of one and the same cultural unit known

[1] A new book by Dr. Ilse Schwidetzky, *Grundzüge der Völkerbiologie*, has inspired and encouraged me to write the ensuing remarks. I am much her debtor. But the questions of ethnic or social biology are not new.

as a nation. Matings, that is, are determined not by biological factors alone. This is the fact which induced Sir Arthur Keith, I believe, to judge that nations are incipient, new race formations. Whether his judgment is valid or not, at least the raciologist includes in his categories "harmonized" races whose genetic antecedents are those of hybridization between two or more originally "pure" races.

In brief, a Symposium on the origin and evolution of man would do well to consider the ecological factors that are peculiar to man which affect his breeding-habits and the types of selectivity that operate upon them.

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