9 May 1958, Volume 127, Number 3306 SCIENCE

Evolution at Work

The pressing problems today center on the mechanisms of evolution and the biological uniqueness of man.

Theodosius Dobzhansky

When hunger and other elemental needs are satisfied, people are apt to ask questions about human nature, about man's origins, and about his place in the scheme of things. Some people ask such questions even when hungry and suffering. It would be naive to claim that an evolutionary approach supplies all the answers, but it is relevant to these questions and may profitably be used as a guiding light in the quest for some of the answers. Accordingly, the two short papers by Darwin and by Wallace, read before the Linnean Society of London in 1858, mark a watershed in the intellectual history of mankind. These papers contained the essentials of the theory of biological evolution. They did not explicitly deal with man; but, in 1871, Darwin showed that man is a part of nature and a product of the evolutionary process.

The theory of evolution has not only become a focus of biology but has influenced human thought in much wider domains. Many people who are not biologists are at least dimly aware of this. By way of illustration, permit me to recount some reminiscences. A few years ago, as I stepped ashore from a small launch in a village on one of the tributaries of the Amazon River, I was met by a man who proved to be the local agronomist. His first question was, what influence might Lysenko's discoveries (of the spurious nature of which he was, of course, unaware) have on our ideas about evolution. In Egypt, a friend translated for me parts of a book recently written by a Coptic hermit who lived for many years in one of the desert monasteries. The book contained a very fair exposition of evolutionism, followed by a refutation on what, to the author, seemed sufficient theological grounds. Punta Arenas claims to be the southernmost city in the world; the region of the Straits of Magellan where it is located is sometimes described as the "Uttermost Part of the Earth." A Chilean friend and I were asked to give public lectures on evolution in the hall of the Punta Arenas City Library. We complied, and found that a part of the audience was not unfamiliar with the topic.

Historical Background

The idea of evolution in the broadest sense of universal and all-pervading change and development is with many of us a habit of thought. We take it for granted because in our lifetimes we have seen so many innovations—telephones and radios, automobiles and airplanes, plastics and antibiotics, atomic bombs and artificial satellites. Things were not always changing so fast. Lucretius, one of the most lucid thinkers of antiquity, was able to write that "all things remain the same even if you should outlast all the ages in living; and still more would you see them the same if you should never come to die."

Christianity is implicitly evolutionistic; it posits a historical process which moves from the Creation to the Fall, the Redemption, the City of God. However, it took some fourteen centuries to make it explicitly evolutionistic—from Saint Augustine in the 5th century to Vico in 1725, Condorcet in 1793, Darwin and Wallace in 1858, 1859, and 1871, and Marx in 1859 and 1867. Condorcet held that the history of mankind was a gradual but steady ascent from a primitive savagery to ever higher states: man is bound to reach perfection in a not too distant future. This cheerful view might sound almost too smug did we not know that it was written while its author awaited execution as a counter-revolutionary.

The idea of progressive evolution in human affairs reached the acme of popularity during the Victorian era. Civilization was supposed to bring ever more material and spiritual comforts, very quickly to some but, in the long run, to almost everybody. Those who were receiving the comforts readily believed that this admirable prospect would be realized most expeditiously through private enterprise and free competition. Marx recommended rather different methods, which he believed to be somehow deducible from Darwin's discoveries. He proposed to acknowledge his indebtedness by dedicating *Das Kapital* to Darwin—an honor which Darwin politely declined. Marxism is sometimes dubbed a Christian heresy; it promises a socialist City of God but is curiously vague about just what this blessed state will be like.

The favorable intellectual climate of the last century speeded up the acceptance of the discoveries of Darwin and Wallace. In turn, biological evolutionism exerted ever-widening influences on the natural and social sciences, as well as on philosophy and even on politics. Not all of these extrabiological repercussions were either sound or commendable. Suffice it to mention the so-called social Darwinism (*1*), which often sought to justify the inhumanity of man to man, and the biological racism which furnished a fraudulent scientific sanction for the atrocities committed in Hitler's Germany and elsewhere. But these are

---

Dr. Dobzhansky is professor of zoology at Columbia University. This article is adapted from a paper presented 27 Dec. 1957 during the Indianapolis meeting of the AAAS.

merely perversions of Darwinism. In the words of Paul Sears (*2*), "Charles Darwin did not kill the faith of mankind. He wrought mightily, and others with him, for a newer and greater faith—faith in universal order, whose secrets open themselves to men truly free to question, to communicate, and to arrive at agreement as to what they have seen."

One problem took precedence in biology during the latter part of the 19th and the early years of the current century. This was the validation of the evolutionary interpretations of the facts of zoology, botany, and anthropology. I have no wish to dogmatize, but this problem appears to have been definitively settled. The occurrence of the evolution of life in the history of the earth is established about as well as events not witnessed by human observers can be. The evidence has not satisfied quite everybody; a few people who are not ignorant of the pertinent facts are nevertheless antievolutionists. However, biological research directed towards producing more evidence that evolution has taken place is no longer urgent.

Guessing where new discoveries are likely to be made is a risky venture in science. And yet, a scientist is constantly forced to take this risk; the success of his work depends on the perspicuity of his guesses. With this reservation, it may be said that the most pressing problems of evolutionary biology seem at present to belong to two groups—those concerned with the mechanisms of evolution and those dealing with the biological uniqueness of man.

Factors of Evolution

Darwin did not eschew making hypotheses concerning the forces which bring evolution about. Without a plausible explanation of how evolution might happen it would be hard to accept the idea that it did happen. The theory of natural selection was Darwin's answer, and from the vantage point of modern knowledge it can be seen that the answer was substantially correct. But Darwin was fully aware that, given the state of biology in his day, a causal analysis of the evolutionary process was unattainable. A number of discoveries in our time made possible at least a start in this direction. The chief one was the discovery and the rediscovery of Mendel's laws; then came the unraveling of the chromosome behavior in cell division, fertilization, and meiosis; the finding of mutations by de Vries and their study by Morgan and his school; the induction of mutations by x-rays and other agents, first revealed by Muller; and the foundation of population genetics by Hardy, Weinberg, and Chetverikov.

The dates of most of these discoveries fall between 1900 and 1930. Strange to say, it was during this period that some biologists professed much skepticism about the feasibility of explaining evolution in terms of the processes then being discovered. Bateson, one of the leaders of genetics in its formative years, was the foremost skeptic. This attitude is still lingering in some places, especially in continental Europe. New and unassimilated information has evidently acted like the proverbial trees which hid the forest.

A most creative phase of modern evolutionism opened around 1930. Perhaps for the first time in the history of biology, the leading roles in the development of a field passed to theoreticians using the tools of mathematical analysis, and their analysis far outdistanced the observational and experimental work. Fisher, Wright, and Haldane developed, almost simultaneously, a mathematical theory of Mendelian populations. The fundamental component of evolutionary changes was perceived to be the alteration of the frequencies of genic and chromosomal variants in living populations. Mutation, natural and artificial selection, random drift, and gene diffusion between populations are the agents known to bring about such alterations. These are, then, the causative factors of evolution.

The logical step towards a satisfactory theory of evolution should now be to study quantitatively the factors of evolution and their interactions in free-living, domesticated, and experimental populations. This is an exciting but difficult task; so great is the complexity of most evolutionary patterns that precise measurement is rarely attainable. Determination of the orders of magnitude of some of the forces may, however, be within the range of what is possible; even such rough approximations will shed needed light on the mechanisms of evolution.

Natural Selection and Balanced Polymorphism

It is not my purpose here to review the field of quantitative studies on the factors of evolution. I choose rather to consider some illustrative examples.

For many years natural selection was something which biologists frequently discussed but seldom did anything about. To Darwin, natural selection was an inference from a mass of indirect evidence; he argued that it should occur, but he did not claim to have directly observed natural selection acting to produce changes in free-living populations. This he could not do because the selective advantages and disadvantages which slowly change natural populations are mostly too small to be readily detectable. To be sure, one can observe elimination of victims of heritable malformations and diseases. Natural selection is, accordingly, often compared to a sieve, which lets some particles pass but sequesters others. Such a process can prevent the accumulation of hereditary diseases and consequent degeneration of a species. It is less easy to see how it may lead to adaptive improvements.

Studies on microorganisms have changed the situation considerably. In 1943, Luria and Delbruck (*3*) analyzed the origin of bacterial strains resistant to destruction by bacteriophages, and their type of analysis was rapidly extended to explain the origin of bacterial resistance to antibiotics and similar phenomena. Mutants which confer upon the bacteria their resistance to phages, or to antibiotics, arise from time to time in most or in all cultures. However, such mutants are too rare to be noticed unless a selective or screening agent is applied. When a suspension of phages is added to a bacterial culture, all the bacteria except for the few phage-resistant mutants are killed; when an antibiotic is added, only the resistant mutants survive. Ingenious methods have been devised for estimating how often the resistant mutants arise. For example, the frequency of the mutation for the phage resistance in the colon bacteria, *Escherichia coli,* is of the order of 10^{-7} to 10^{-8} per cell generation.

The selection of resistant mutants in bacteria is a process which resembles the sieve in the above analogy too closely to be a good model of the selective processes in higher, sexually reproducing, organisms, including man. Materials more suitable for the study of these processes have been found. Fisher (*4*) showed in 1930 that if the heterozygote for two genetic variants, A_1A_2, is superior in fitness to both corresponding homozygotes, A_1A_1 and A_2A_2, the natural selection will, in an outbreeding sexual population, act to maintain both A_1 and A_2 with frequencies that may readily be computed. Some twenty years ago, Ford (*5*) discovered this situation, known as balanced polymorphism, in nature in some butterflies. More recent studies show that balanced polymorphism is more frequent than was formerly suspected. Natural populations of the flies *Drosophila* have yielded some beautifully clear examples. Moreover, the selective pressures acting on some polymorphic natural populations are, as will be shown below, astonishingly great. This is a boon to the experimental evolutionist, for natural selection becomes at last observable and its magnitude measurable.

Here we may digress to consider the possibility that balanced polymorphism may occur in human populations. The problem is of more than academic interest, since balanced polymorphism has a property which is at first sight astonishing. Provided that the heterozygous carriers of hereditary defects or diseases are superior in fitness to the noncarriers, natural selection will maintain these defects in the populations. The work of Allison (*6*) on the sickle-cell anemia, and that of Ceppellini on the Mediterranean anemia, have yielded at least presumptive evidence of balanced polymorphism. The homozygotes for the respective mutant genes usually die of severe anemias, but the heterozygotes may not only be healthy but, at least under certain conditions, may be relatively immune to some malarial fevers as compared with the normal homozygotes. Carter, Penrose, and Wallace (*7*), among others, have considered the possibility that many genetic variants in man which are deleterious when homozygous may be beneficial when heterozygous. This possibility has often been studiously ignored or dismissed on insufficient grounds. It would greatly complicate several important issues, among them that of the genetic effects of atomic radiations on human and other populations. However, it is becoming evident that the oversimplified models of the genetic population structure are proving inadequate if not positively misleading. Since I recently had an opportunity to discuss this matter in *Science* (*8*), I leave it here with the remark that the need for a better understanding of the genetic processes taking place in living populations is now felt more keenly than ever.

Natural Selection in Experimental Populations of Drosophila

The trait which proved to be highly favorable for experimental studies on evolution is a cryptic one. Many natural populations of most species of *Drosophila* are polymorphic for variations in the structure of certain chromosomes, due to so-called inversions of blocks of genes. These variants of the chromosome structure are inherited as simply as are the genes that determine the blood groups for which human populations are polymorphic. A further similarity is that the flies which carry different chromosomal types are externally as indistinguishable as are people with different blood groups. The chromosomal types may, however, be diagnosed easily and precisely in stained preparations of the salivary glands of the fly larvae. Every race or population of a given species of *Drosophila* may be characterized in terms of the relative frequencies of the different chromosomal types which it contains (*9*), just as human populations can be described in terms of the relative frequencies of the different blood group genes.

But here the analogy ends, since the chromosomal types which a *Drosophila* carries may easily be shown to influence its fitness, while the problem of the functional significance of the blood groups in man is still full of uncertainties. The experiments with *Drosophila* are arranged as follows. We collect a sample of the population in some natural locality where the flies occur; place the females singly in laboratory culture bottles and allow them to produce progenies; examine the chromosomes in these progenies and pick out the strains which carry the desired chromosome types; and make up a mixture of flies carrying certain chromosome types in known proportions. This mixture is placed in specially constructed population cages in which the flies will breed freely for as many generations as the experimenter may allow. These populations are kept under controlled conditions which can be varied at will, and at desired time intervals we take samples of eggs which the flies in the cages deposit and investigate the chromosomes in the larvae which grow from these eggs.

Such experiments show that the fly which is fittest in most environments usually turns out to be a heterozygote. A fly in which the two chromosomes of a pair differ in structure, say A_1A_2, enjoys hybrid vigor, heterosis, as compared with the homozygotes, A_1A_1 and A_2A_2. There is every reason to think that this heterosis occurs in the environments in which the flies live in nature as well as in the laboratory. The chromosomal polymorphism is balanced polymorphism. Furthermore, at least some of the chromosomal heterozygotes are favored by amazingly powerful selective forces. The magnitude of the selection can be estimated from the speed with which the frequencies of the different chromosomal types undergo changes in the experimental populations, and from the equilibrium proportions that are eventually reached. Thus, in a certain experiment with *Drosophila pseudoobscura*, the following situation was observed: Taking the fitness of a heterozygote, A_1A_2, to be unity, the fitnesses of the homozygotes, A_1A_1 and A_2A_2, proved to be 0.90 and 0.41, respectively (*9*).

Consider the meaning of these figures. The adaptive value of the homozygote A_2A_2 is less than one-half of that of the heterotic type, A_1A_2. Taking the heterozygote as the standard of fitness, the homozygote, A_2A_2, having less than 50 percent of the standard fitness, must technically be classed as a semilethal. Or one may say that the homozygote A_2A_2 is afflicted with a hereditary disease, or a constitutional weakness. Now, this would not greatly surprise us if A_2 were a mutant obtained in the laboratory, under the influence of, say, x-ray treatments. But A_2 is a permanent component of many flourishing populations of *Drosophila* in nature. The A_2A_2 homozygotes are not laboratory artifacts: they occur abundantly in nature.

Seasonal Genetic Changes in the Make-up of Drosophila Populations

Not enough is known about the adaptive functions which the chromosomal polymorphism performs in nature. Quite possibly these functions are different in different species of *Drosophila*. Observations on populations of *Drosophila pseudoobscura* in some parts of California furnish a clue for this species. In these populations, the relative frequencies of different chromosomal types change with the seasons; some chromosomes are more common in spring than in summer or in fall, while other chromosomes show the reverse seasonal trends (Fig. 1). *Drosophila* produces in nature several generations per year—we do not know just how many. At any rate, natural selection is so intense that the populations undergo genetic reconstructions which fit them to seasonal changes in their environments. Here, then, are evolutionary changes, microevolutionary ones to be sure, which are observable directly in nature in a free-living animal species.

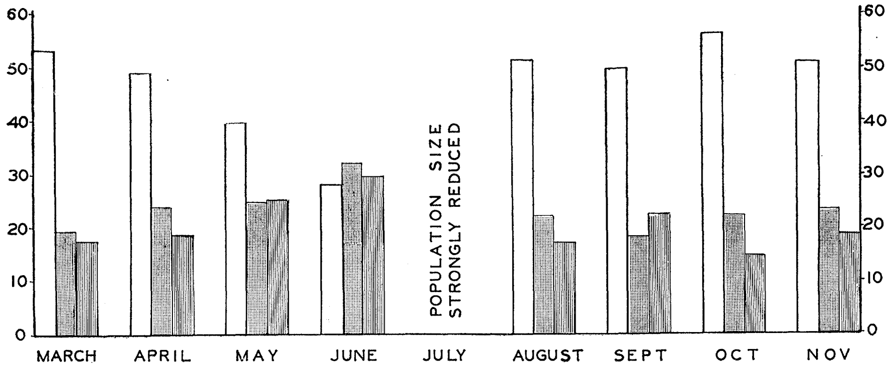

Fig. 1. Seasonal genetic changes in a population of *Drosophila pseudoobscura* inhabiting a certain locality in California (Piñon Flats on Mount San Jacinto). The heights of the columns indicate the average percentages of three different chromosomal types in different months in samples taken from 1939 to 1954. (Data of Dobzhansky, Epling, *et al.*)

Further light on these evolutionary changes comes from laboratory experiments. The seasonal genetic changes indicate that the adaptive values of the chromosomal types vary in different environments. The carriers of some of the chromosomes are relatively fitter in spring and those of others are superior in summer or in fall. Experiments bear this out; the adaptive values of the chromosomal types are exquisitely sensitive to environmental modification. The series of adaptive values of three chromosomal types cited above (1:0.90:0.41) was observed in experimental populations kept at 25°C. Lowering the temperature by 9°, to 16°C, makes the adaptive values uniform, or so nearly so that no differences can be detected in our experiments within the limits of resolution. The genotype which causes a hereditary infirmity at 25° is completely "cured" at 16°C. This emphasizes how meaningless may be the distinctions between "superior" and "inferior" hereditary endowments if the environment is not specified.

The seasonal genetic changes in *Drosophila pseudoobscura*, observed in nature in the population of Piñon Flats, Mount San Jacinto, California, have been reproduced rather fully in experiments (*9*). In nature, a certain chromosome type increases in frequency at the expense of another type between March and June, the changes are reversed between June and September, and the frequencies remain static from September to March. The kind of genetic changes which occur in nature during the summer months have been easily imitated in experimental population cages kept at 25°C. The winter stability is reproduced if the same population cages are kept at 16°C. All attempts to duplicate the spring situation in population cages were unsuccessful. The experiments of Birch (*10*) showed why this should be so; the changes which occur in nature during spring can be copied experimentally only if the fly larvae do not live in crowded conditions (as they always do in population cages).

Alteration of Drosophila Populations in California (1940–1957)

The seasonal genetic changes observed in nature in *Drosophila pseudoobscura* are evolutionary changes by definition. However, because of their cyclic character, the alterations induced at one season are reversed at the next season. The biological significance of the chromosomal polymorphism lies evidenty in that it confers a marvelous adaptive plasticity upon the populations. The populations are able to respond by adaptive genetic changes to temporary, and even to seasonal, shifts in their environments. This is, of course, a kind of evolutionary luxury which only a rapidly breeding animal, like *Drosophila*, is able to afford.

The genetic plasticity also permits, however, rapid modifications in response to more lasting alterations in the environment. This creates an opportunity for the direct observation of these evolutionary changes in nature. Changes in the relative frequencies of chromosomal types lasting for several years have been recorded in some populations of *Drosophila pseudoobscura*. Some of these changes may have been caused by succession of droughty and wet years, but this is not established securely. Recently it was discovered that still another, and apparently more enduring, change is going on in certain populations of the same species.

Reference has been made above to the fact that populations or races of a *Drosophila* species may be described in terms of relative frequencies of different types of chromosomes in their chromosome pools. Such a description was made in 1944 for *Drosophila pseudoobscura*, on the basis of samples of the populations of this species collected in western United States and in Mexico, chiefly during the period 1938 to 1940. This study showed that a chromosome type, denoted as PP, is the dominant form (occurring in more than 50 percent of the chromosomes) in Texas and also along the eastern face of the Rocky Mountains. The PP chromosomes wane in frequency as one proceeds westward. Among the approximately 20,000 chromosomes scored from populations of California, only four PP chromosomes were found, in three different localities. This is a very low frequency, 0.02 percent (Fig. 2).

The first intimation that the populations were changing came in 1946 and 1947, when the population of Mather, in the Sierra Nevada of California, was found to contain about 0.5 percent of PP chromosomes. None were found there in 1945. However, in 1950 the frequency of PP stood at 2.8 percent, in 1951 at 4.5 percent, in 1954 at 11.1 percent, and in 1957 at 10.0 percent. Similar changes took place on Mount San Jacinto, where C. Epling found the first PP chromosome in 1951. By 1955 the frequency had risen to 7.7 percent.

In an attempt to elucidate the nature of these changes, in the summer of 1957 I sampled the populations of ten localities in California and of ten in Arizona and Utah (*11*). More or less adequate population samples had been taken in or near all these localities in 1940, 1941, or earlier. The striking fact which this study has revealed is that, between 1940 and 1957, the PP chromosomes have become fairly common in every one of the California populations sampled. Their frequencies now range between 5.0 and 12.0 percent (Fig. 3). Furthermore, the waxing of PP chromosomes has taken place chiefly at the expense of another chromosome type, denoted CH, the frequencies of which have markedly waned in most California populations.

In contrast to the genetic upheaval in the California populations, no spectacular changes were found in Arizona and Utah. In 1940 as well as in 1957, some PP chromosomes (fewer than were found in California in 1957 but more than in 1940) and some CH chromosomes (fewer than in California) occurred in the populations of Arizona and Utah. This is important, since a conjecture which had to be excluded was that the sharp rise of PP in California might have been due to a westward migration of the eastern (Texan) populations, in which PP chromosomes are predominant.

The rise of PP chromosomes in California represents a more impressive evolutionary change than appears at first sight. The average frequency of PP in California populations was close to 0.02 percent in 1940 and 8 percent in 1957. This is a 400-fold increase. The estimated mean number of fly generations in natural habitats over a period of 17 years is probably of the order of 100 (more than twice this number could be obtained in the laboratory). A 400-fold increase in the frequency of a genetic variant in 100 generations bespeaks a quite considerable magnitude of the adaptive advantage, and hence of natural selection.

In fact, the only comparable evolutionary change ever observed in free-living animals is the development of the so-called industrial melanism in England and in some localities on the continent of Europe. Dark variants, due to single dominant mutant genes, appeared in several species of moths approximately one century ago. Now these variants have become frequent in populations of localities in which the vegetation is polluted by industrial fumes. This has been brought about by the action of natural selection, since the dark variants appear to be protectively colored on polluted, and the light ones on unpolluted, vegetation (*11*). The spread of the melanic variants in moths is thus caused by human interference (industrial pollution) with the habitats of certain free-living species. The cause which has brought about the rise of PP chromosomes in the California *Drosophila pseudoobscura* is, unfortunately, unknown. There is, however, some circumstantial evidence that this cause is not man-made. If this is so, the genetic alterations in these *Drosophila* populations represent the greatest observed effect of natural selection in an animal species not appreciably influenced by man.

Microevolution, Mesoevolution, and Macroevolution

It is needless to labor the point that the evolutionary changes described above are small compared to those which led from the eohippus to the modern horse, or from an australopithecine-like animal to man. The former are microevolutionary and the latter macroevolutionary changes. Nevertheless, microevolution and macroevolution are parts of a single continuum, and studies on the former help to elucidate the latter. After all, the knowledge of the atomic fission and fusion reactions gained in laboratories helps in understanding the evolution of stellar systems, although even the biggest hydrogen bombs generate amounts of energy which are puny compared to those produced in the sun or in stars. This argument is not meant to imply that studies on macroevolution may be dispensed with. The evidence of paleontology, while not completely clear and consistent, is in favor of the view that macroevolution is compounded of mi-

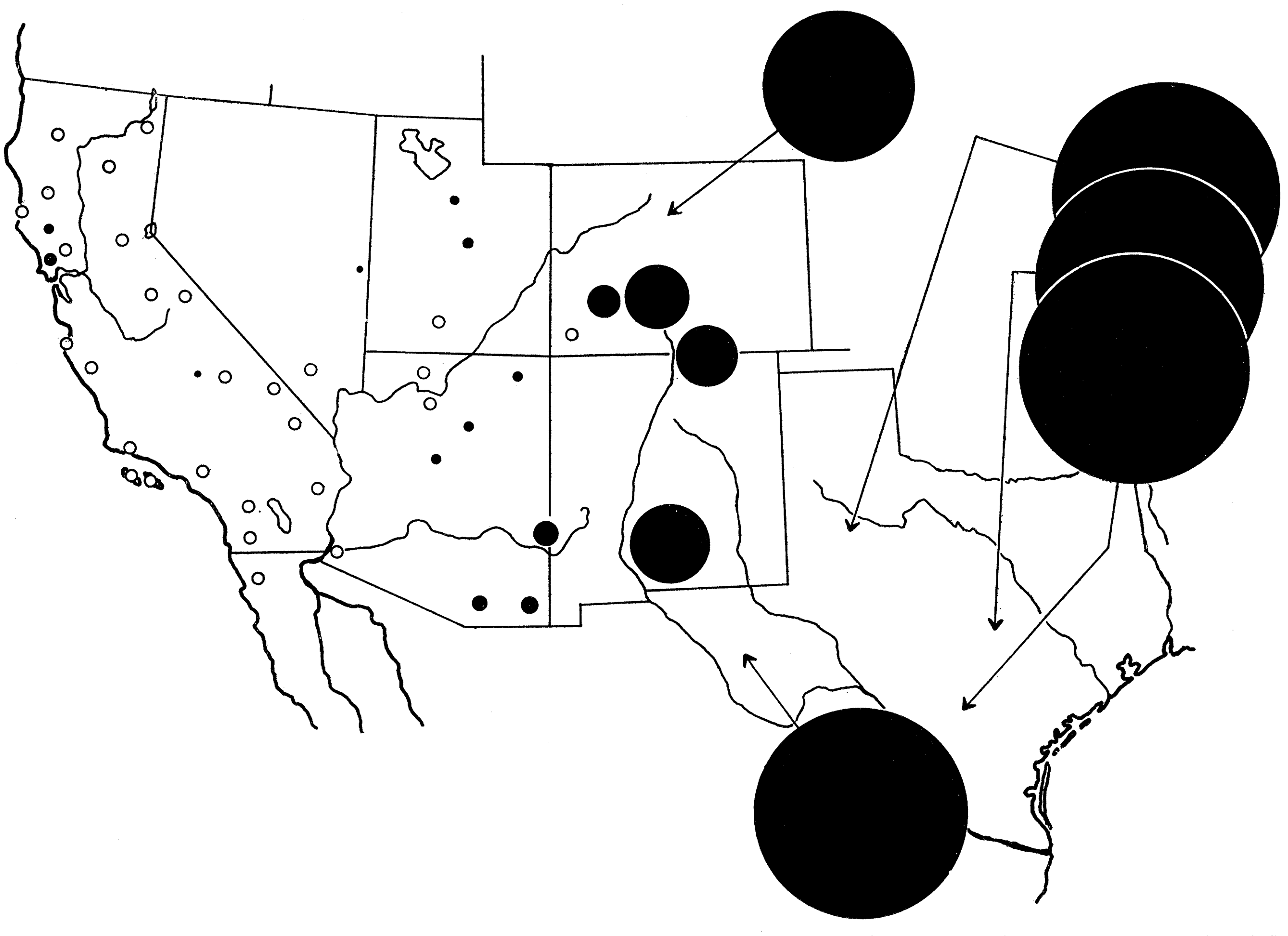

Fig. 2. The status of populations of *Drosophila pseudoobscura* in the southwestern United States according to samplings made chiefly in 1940 and earlier. The diameters of the black circles are proportional to the frequencies of a certain type of chromosome (PP) in the populations of different localities. Open circles indicate populations in which this type of chromosome was not encountered.

croevolutionary events. The problem of macroevolution is, then, essentially that of the patterns of microevolutionary events which yield macroevolutionary changes of different kinds.

This problem is beyond the confines of the present discussion: macroevolution cannot be observed at work; only the end-products of its action on our time level can be studied. However, we have recently succeeded in producing in experiments some genetic changes which seem to transcend the limits of microevolution, and for which I have suggested a tentative label of "mesoevolution" (*13*).

Reference has already been made to natural selection in experimental populations of *Drosophila*. A mixture of flies with chromosomes of different types, but derived from a natural population of the same geographic locality, is introduced into a population cage; the proportions of these chromosomal types may change from generation to generation, until equilibrium frequencies are attained. The position of the equilibrium depends upon the environment in which the population is kept. The changes observed are microevolutionary ones; the experiments have been repeated many times, and, if reasonable precautions are taken, the results of the selectional changes are predictable and repeatable.

Evolution as a Creative Process

Now, something else is observed if what may appear to be a minor variation is introduced into the experimental procedure. An experimental population is made up in which the different types of chromosomes are derived from natural populations of different geographic regions; for example, one kind of chromosome may come from California and the other from Texas or from Mexico. In many populations of such geographically mixed origins, natural selection produces alterations in the proportions of the different chromosome types. However, the course which the selection takes in geographically mixed populations is remarkably erratic. Replicate experiments, with the same genetic materials and conducted in similar environments, often give significantly divergent results. In some populations the changes may be rapid and in others sluggish; in some, balanced equilibria may be established and in others, one of the chromosomal types may be lost (*13*).

This may seem to be a strange and even disconcerting situation. Is it not the criterion of validity of a scientific experiment that its results should be reproducible? Yet in these experiments we face a real biological indeterminacy, and this fact is fraught with implications. Evolutionists, particularly those who work with fossils, long ago pointed out that the evolutionary transformations which occur in a group of organisms are unrepeatable and irreversible. The macroevolutionary changes represent unique and nonrecurrent evolutionary histories. Notwithstanding many instances of parallel or convergent evolution, we have no reason to think that any form of life has arisen two or more times independently.

The experiments on *Drosophila* populations of geographically mixed origin throw some light on this situation. The key to the problem lies in the prodigious, and indeed prodigal, efficiency of sexual reproduction in the creation of novel genetic endowments. It is easy to show that with n genes each represented by m variants (alleles), the number of potentially possible gene combinations is m^n. An estimate of 1000 for the number of genes (n) and of 10 for the number of alleles per gene (m) would be very conservative, at least for higher organisms. But the number 10^{1000} is so great that only a negligible fraction of the potentially possible gene combinations can ever be realized.

These apparently fanciful calculations bear directly on the experimental findings. Although we do not know just how many genes segregate and recombine in the populations of geographically mixed origins, the numbers must be fairly large. Some of the many possible different gene patterns that confer high fitness upon their bearers in the experimental environments arise in different populations; whichever of these patterns happens to arise first is picked out by natural selection and serves as the starting point of subsequent evolutionary changes. The replicate populations, though originally alike genetically and exposed to like environments, follow different evolutionary paths. Perhaps no two experimental populations of this sort will have identical histories, any more than two evolutionary lineages in nature will have.

Evolution is not striving to achieve some foreordained goal; it is not the unfolding of predetermined episodes and situations. Macroevolutionary, and to some extent also mesoevolutionary, changes are unique, nonrecurrent, and creative. It is necessary to make quite clear what is meant by creativity of biological evolution. This is a creative phenomenon because evolution brings about novel and harmonious genetic equipments which enable their carriers to survive in some environments. These genetic equipments are mostly new combinations of genes. But the process of formation of new gene combinations is not of the kind to which one can apply the French saying that "the more it changes the more it remains the same thing." Organic development is not gradual accretion of traits produced by the genes independently of each other; the adaptive value of a genetic equipment is a function of all the genes which in the organism are acting in concert.

Man as a Product of Evolution

Man was not programmed in biological evolution, because evolution has no program. In one sense, man, *Drosophila,* and all other forms of life are evolutionary accidents. If slightly different environmental opportunities had been offered to their far and near ancestors, quite different creatures might have arisen as a result of evolutionary transformations. Even with similar opportunities, the formation at critical times of gene combinations different from those which actually were formed also could have turned the evolutionary changes to different paths.

But, in another sense, man is not a product of a chance concatenation of lucky throws of the genetic dice. The old analogies purporting to describe the fortuitous nature of evolution are wrong. The genetic equipment of the human species is not like a watch which arose by the accidental coming together of disjointed parts of the mechanism, nor is it like a poem accidentally typed out by a monkey pounding the keys of a typewriter. Such analogies overlook the fact that natural selection introduces an antichance quality in evolution. The bodies of our animal ancestors were going concerns and not merely human bodies under construction; these animals were as fit to live in their environments as we are in ours.

Evolution is a response of living matter to the challenges of environmental opportunity through the process of natural selection. The response of the human species, or rather of the species ancestral to man, was a unique one—it developed the genetic basis for the accumulation of, and for the extragenic transmission of, a body of learned tradition called culture. The relations between culture and its genetic basis are all too often misunderstood. This topic is too complex and important to be dealt with lightly, but the basic facts are simple enough. Genes determine the possibility of culture but not its content, just as they determine the possibility of human speech but not what is spoken. The cultural evolution of mankind is superimposed on its biological evolution; the causes of the former are nonbiological without being contrary to biology, just as biological phenomena differ from those of inanimate nature but are not isolated from them (*14*).

Human Evolution at Work

The genetic equipment of our species was molded by natural selection; it conferred upon our ancestors the capacity to develop language and culture. This capacity was decisive in the biological success of man as a species; it enabled man to acquire unprecedented powers to change and control his environment at will. The very success of culture as a nonbiological adaptive instrument means, however, that man has crossed the Rubicon—he has become specialized to live in man-made environments.

Some strange conclusions are sometimes drawn from the above facts. One is that human biological evolution has ended and has been replaced by evolution of culture. Another is that all men are uniform in their genetic equipment, at least insofar as the latter conditions the capacity to undergo socialization and acculturation. Another is that man's "intrinsic" intelligence (whatever that may mean) has not changed since the times of the Cro-Magnon, or even of the Java man. Still another is that natural selection no longer operates in modern mankind, since men live in such hopelessly unnatural environments.

All these notions overlook the simple fact that it is precisely because the capacity to create, absorb, and transmit culture is so decisive in the success of man as a species that natural selection works not only to preserve but also to augment this capacity. Human biological and cultural evolutions are not separated in watertight compartments. They are interacting processes. All men are equal in rights, but they are most certainly not biologically uniform. Our genetic diversity does influence our tastes and aptitudes for different occupations and professions. But this does not make some of us superior and others inferior; no human being should ever be used as a means to an end.

All human societies, the civilized even

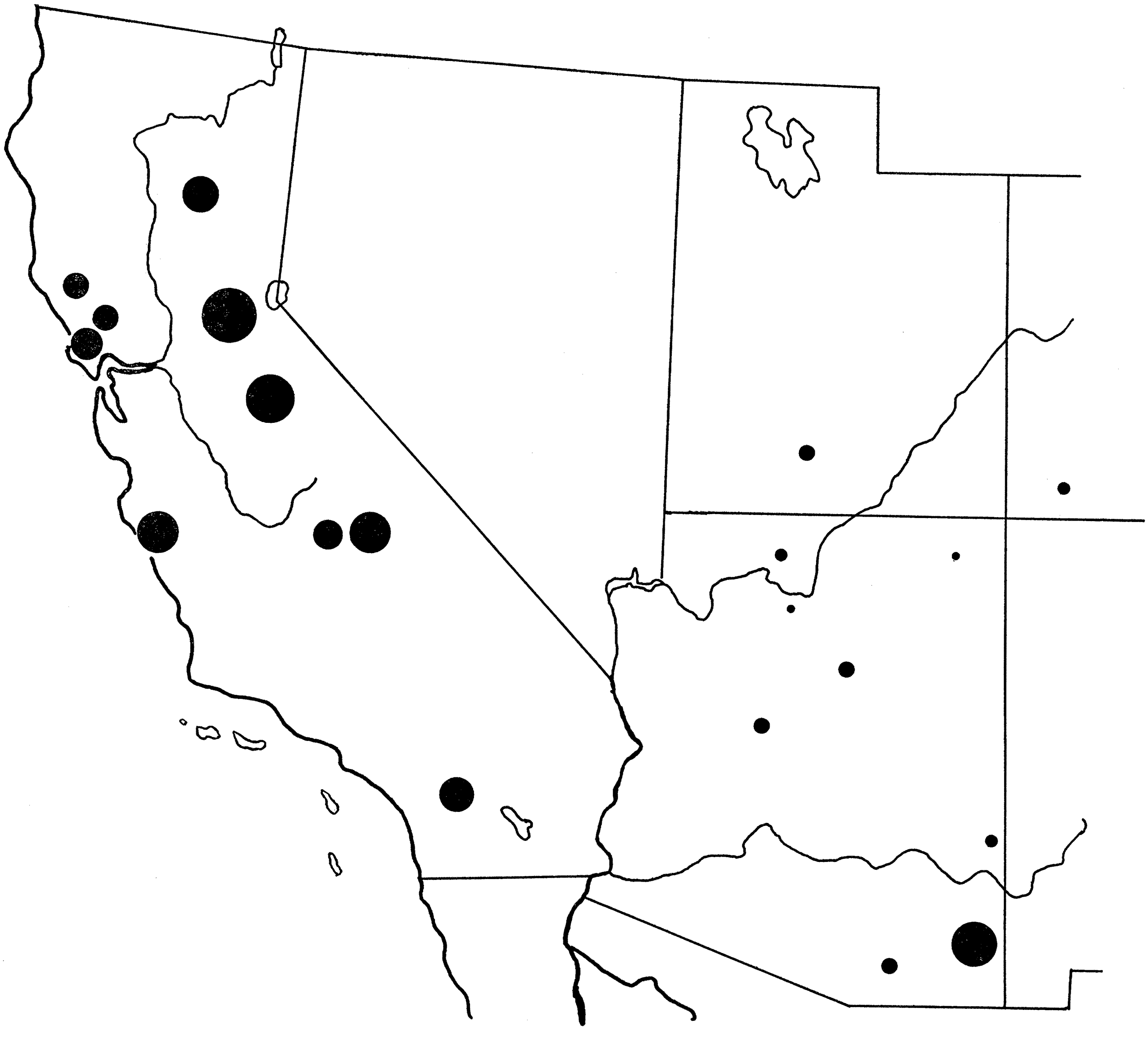

Fig. 3. The status of populations of *Drosophila pseudoobscura* in the southwestern United States in 1957. The diameters of the black circles are proportional to the frequencies of a certain type of chromosome (PP). Although the scale of the map is larger than that of the map in Fig. 2, the scale of the black circles is the same in both figures.

more than the primitive ones, have numerous vocations to be filled. Natural selection has made all healthy human beings trainable for the performance of diverse duties. This is, then, a biological adaptation which makes people multiform, not uniform as is sometimes supposed. Educability, the ability to be trained, is consistently fostered in man by natural selection. And yet, the carriers of certain specialized genetic equipments, such as musicians or poets, may excel in the performance of some specialized functions.

Natural selection is active in all human societies, including the most advanced ones (*15*). It must be understood that there is nothing esoteric about the "naturalness" of natural selection. All that "selection" means is that the carriers of different genetic equipments contribute unequally to the gene pool of the succeeding generations. If the relative contributions are decided by human choice, the selection is artificial. If not, it is natural. Natural selection usually maintains or enhances the Darwinian "fitness" or "adaptedness." But "the fittest" is nothing more spectacular than the parent or grandparent of the greatest number of surviving descendants.

It is erroneous to equate Darwinian fitness with excellence in human estimation. Reproductive success may favor genetic equipments which we may hold to be undesirable on other grounds. Selection does not even guarantee that the species will endure; most biological species of the past have become extinct, without issue, and yet their evolution was controlled by natural selection. This is because selection promotes what is immediately useful, even if the change may be fatal in the long run.

The biological evolution of our species continues to be at work. Perhaps no other problem of science is more challenging than the understanding of the biological and cultural evolutions of mankind in their interactions. As pointed out above, evolution in general has no program, and the evolution of man is no exception. No biological law can be relied upon to insure that our species will continue to prosper, or indeed that it will continue to exist. However, man is the sole product of evolution who knows that he has evolved and who has continued to evolve. It is up to man to supply the program for his evolutionary developments which nature has failed to provide. He has gained some knowledge which is a basis of hope that the problem is not impossible of solution.

This is an inspiring task but also a crushing responsibility. Albert Schweitzer once wrote that "our age has discovered how to divorce knowledge from thought, with the result that we have, indeed, a science which is free, but hardly any science left which reflects" (*16*). I hope that these angry words do not accurately describe the situation. We need and we have at least some science which is free and which reflects. It is our primary responsibility as scientists to see to it that such science prospers and bears fruit. Moreover, such science ought not to be a monopoly of some kind of technological elite. People at large, and particularly men of action who make the decisions which control so much in our lives, need not be as woefully ignorant of even the simplest principles of science as they are. At least some of the ideas which guide our work as scientists are not beyond the understanding of people of average intelligence who are not scientists professionally. The idea of evolution is one of them. As expounded by Darwin, it is one hundred years old, but we have barely begun to understand its full consequences (*17*).

References and Notes

1. R. Hofstadter, *Social Darwinism in American Thought* (Beacon, Boston, 1955).
2. P. Sears, *Charles Darwin. The Naturalist as a Cultural Force* (New York, 1950).
3. S. E. Luria and M. Delbruck, *Genetics* 28 (1943).
4. R. A. Fisher, *The Genetical Theory of Natural Selection* (Oxford Univ. Press, Oxford, 1930).
5. E. B. Ford, *Biol. Revs. Cambridge Phil.* Soc. 12 (1937).
6. A. C. Allison, *Ann. Human Genet.* 19 (1954).
7. *Effect of Radiation on Human Heredity* (World Health Organization, Geneva, 1957).
8. T. Dobzhansky, *Science* 126, 191 (1957).
9. ——, *Evolution* 1 (1947); *Proc. Intern. Congr. Genet. 8th Congr. Stockholm* (1949).
10. L. C. Birch, Evolution 9 (1955).
11. Unpublished data.
12. H. B. D. Kettlewell, *Heredity* 10 (1956).
13. T. Dobzhansky, *Atti congr. intern. genet. 9th Congr.* 1 (1954).
14. ——, *The Biological Basis of Human Freedom* (Columbia Univ. Press, New York, 1956).
15. T. Dobzhansky and G. Allen, *Am. Anthropologist* 58 (1956).
16. A. Schweitzer, *An Anthology* (Beacon, Boston, 1947).
17. I wish to thank my colleagues Drs. J. A. Beardmore, L. C. Dunn, and J. A. Moore for critical readings of the manuscript of this article.

University of Michigan Radiocarbon Dates II

H. R. Crane and James B. Griffin

A list of 109 radiocarbon dates obtained since the time of the last report (*1*) is presented in this paper (*2*). The technical method by which the dates were measured has not been changed in any essential way. Two complete counter systems are in continuous operation. The counters are Geiger counters, filled with carbon dioxide and carbon disulfide at approximately atmospheric pressure. At present the background counting rate is 6.5 counts per minute, and eight additional counts per minute are obtained from carbon of zero age. The duration of the count on each sample is at least 48 hours, and in many cases it is 72 hours. Approximately every fourth sample placed in each counter is of known C^{14} content: CO_2 derived either from 200-year-old wood (by ring count) or from petroleum. There is no detectable secular change in the results of the calibration runs.

The calibration figures used in calculating dates are "moving averages" based upon the last several calibration runs. For this reason, in the calculation of the standard deviation, the calibration figures are treated as if they contained four times as many counts as would be obtained in a 48-hour run. Therefore the major part of the contribution to the standard deviation comes from the run

---

Dr. Crane is professor of physics at the University of Michigan, Ann Arbor. Dr. Griffin is director of the Museum of Anthropology at the University of Michigan.