LECTURES IN BIOLOGICAL SCIENCES

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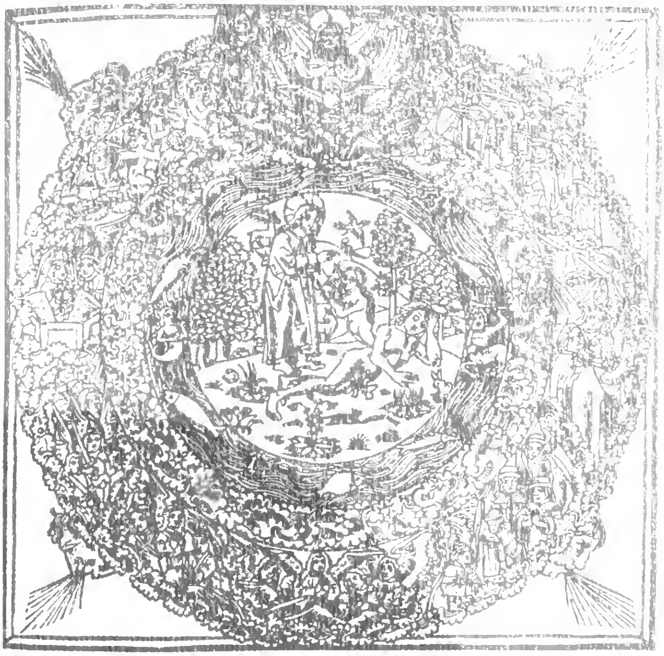

LECTURES IN BIOLOGICAL SCIENCES

presented by
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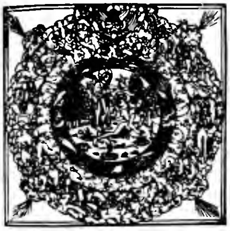

A symposium held December 3-5,
1959, sponsored jointly by
The University of Tennessee
Chapter of Sigma Xi and the
Biology Division, Oak Ridge
National Laboratory

edited by
J. IVES TOWNSEND

LIBRARY OF CONGRESS CATALOG CARD NUMBER: 63-14136

BOOK DESIGN BY HUGH BAILEY

SECOND PRINTING, 1966
THIRD PRINTING, 1967

FOREWORD

A symposium entitled *Lectures in Biological Sciences* was held on the Knoxville campus of The University of Tennessee, December 3-5, 1959, a week after the centennial date of the publication of Charles Darwin's *Origin of Species.* The five lectures were presented by scientists who have made important contributions to the study of evolution. The theme of the symposium was the nature and course of the evolutionary processes and their implications for man's physical and spiritual well-being.

It is perhaps particularly appropriate that what was probably the last of the celebrations of the Darwin Centennial was held in East Tennessee, near the town of Dayton where the last spectacular display of resistance to the acceptance of Darwin's theory of evolution once took place. The centennial celebrations, including that in Knoxville, were principally responsible for the vigorous efforts of many prominent Tennessee scientists and lay citizens to educate a large public to the knowledge that there is practically universal acceptance among scientists of the occurrence of evolution as an historical fact.

It is perhaps trite, but necessary, to note that our knowledge is incomplete; thus, details of the course of evolution and the mechanisms by which it operates are in the realm of theory. The lectures printed in this volume show us how ingenious are the experiments, observations, and insights that have been brought to bear on these theoretical problems and how much knowledge has been revealed as the result. They also remind us of how necessary it is to understand these problems if we are to understand ourselves and to achieve success in improving our destiny.

The philosophical implications of our knowledge of evolution were discussed to a greater or lesser extent by all of the speakers; for, as Professor Waddington said, and as Tennessee's experience has shown, "The theory of evolution is . . . inescapably connected with the other systems of thought by which man has attempted to understand and control his own nature, that is to say, the systems of religion, philosophy, and politics."

In his paper Dr. Norman G. Anderson discusses pertinent evidence from astronomy, geology, biochemistry, biophysics, and genetics that suggests the way in which life began on the earth, even how the earth itself came into existence. In this critical review Dr. Anderson proposes several specific lines of experimental study needed to fill gaps in our knowledge and to test the validity of several hypotheses that have been proposed. His speculations lead him eventually to consider a problem that especially excites the popular and scientific imagination in this space age, that is, the likelihood of the evolution of intelligent life elsewhere in the universe. Dr. Anderson also speculates about the probable reaction of some early Christian leaders, such as St. Thomas Aquinas, to suggestions that life arose spontaneously.

Professor C. H. Waddington reviews the development of population genetics and the implications of the three major concepts that the field has produced: the near universal and unexpectedly great abundance of genetic variation in natural populations; the generally increased fitness of heterozygotes; and the co-adaptation of genes in the gene pool. His consideration of the origin of genetic variability and the manner in which natural selection acts upon it leads to a discussion of the role of the environment. Professor Waddington tells of his remarkable discovery of how some environmental modifications that may be adaptive in *Drosophila* can be selected to produce consistently the adaptive types in subsequent generations in the absence of the environmental conditions that originally induced them. He then contrasts this kind of "acquired trait" with the modifications of an adaptive kind that the Lysenkoists, but not other scientists, suppose can be directly produced by the environment and then transmitted by the organism to its progeny.

Professor G. Ledyard Stebbins gives examples from a variety of literature to illustrate each of seven basic postulates that belong to the modern theory of causes of evolution. These summarize contemporary thinking about the ways in which, particularly, natural selection, mutation, genetic recombination, and isolation operate and interact in natural populations to produce genetic divergence, the splitting of species, or the origin of higher categories. He closes with a statement of his personal "evolutionary philosophy," in which he tells what he believes to be the implications and import of the modern theory of organic evolution.

Professor J. N. Spuhler pieces together the fossil evidence to show as complete a pedigree of modern man in his descent from lower primates as is at present possible. Along the way he traces the development of seven biological conditions that were necessary for the evolution of the social animal that modern man is. He shows how these conditions are mostly reflected in the structure of the cerebral cortex, and how some of them (for example, the ability to use speech) are believed to be both cause and effect of cortical expansion.

Professor Dobzhansky writes of the historical impact of insights into man's relation to and place in the universe. He then discusses how self-awareness and consciousness evolved concomitantly with the expansion of the cerebral cortex in our ancestors and made them truly human; how this led to the development of foresight and the experience of freedom, and left man filled with internal contradictions, but still so equipped that there is hope for him in the yet continuing, creative, evolutionary processes that produced him.

The symposium resulted directly from an informal meeting held by representatives of several science and research departments on the Knoxville campus in October, 1959, to consider a way to fill an acute need to emphasize and advance scholarship in the community. It was decided that this need could probably best be met by a continuing program of visits and lectures by eminent scholars in different sciences or humanities each year. D. A. Shirley, President of the Tennessee chapter of Sigma Xi, one of the sponsoring organizations, appointed to the Organizing Committee the following members of The University of Tennessee faculty: D. Frank Holtman, Arthur W. Jones, C. W. Keenan, Miss Madeline Kneberg, R. E. McLaughlin, Stanfield Rogers, A. J. Sharp, and J. Ives Townsend, Chairman. Alexander Hollaender, Director of the Biology Division, Oak Ridge National Laboratory, who has been especially prominent in efforts to modernize biological education in the institutions of the South, graciously accepted an invitation to serve as co-chairman of the committee and to have the Biology Division co-sponsor the symposium. He appointed Richard F. Kimball, also of the Biology Division, to serve on the committee. It would have been virtually impossible to organize the symposium without the close cooperation of all of the committee members. The symposium was financed through generous contributions from the Biology Division, Oak Ridge National Laboratory; the University's Departments of Bacteriology, Botany, Chemistry, Geology, and Zoology and Entomology; and a lectureship fund administered by the office of the President of the University.

Appreciation is due to Mr. Monroe K. Spears, editor of the *Sewanee Review*, through whose kind permission Professor Dobzhansky's article appears.

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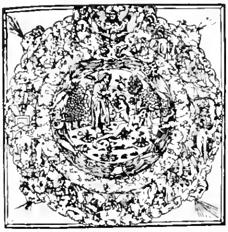

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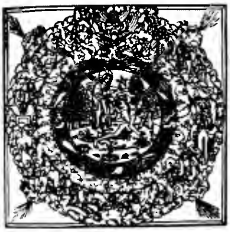

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†Operated by Union Carbide Corporation for the U.S. Atomic Energy Commission.

NORMAN G. ANDERSON is a Biologist in the Biology Division of the Oak Ridge National Laboratory and also a Lecturer in Zoology at the University of Tennessee. Dr. Anderson a cell physiologist by training, has published many papers on the isolation of nuclei and other cell components and the effects of ionizing radiation on biological systems.

THE ORIGIN OF LIFE HAS BEEN A SUBject for serious scientific consideration for only little more than a century. The popular view until comparatively recent times was that life continuously and spontaneously appeared. The damp earth presumably formed worms, bread brought forth molds, and decomposing matter spawned insects, rodents, and snakes. The conclusion that life inevitably and spontaneously appeared under proper conditions was not easily changed. Although Francisco Redi had proved in the seventeenth century that white maggots are simply the larvae of flies by showing that no maggots appeared on meat kept beneath a fine cloth and Spallanzani in 1765 had shown that heated and protected cultures did not grow molds, the matter was still not considered settled. Less than 100 years ago, in 1862, the French Academy of Sciences offered a prize to whoever, by means of convincing and accurate arguments, should illuminate the subject of the primary origin of living creatures. This prize was awarded to Louis Pasteur. Since his brilliant work, it has been almost universally accepted that all organisms now living descended from pre-existing organisms, and that no instance of spontaneous generation has occurred in modern times. The question we now ask is simply, can life ever arise spontaneously? Do the conclusions of Redi, Spallanzani, and Pasteur, which overthrew medieval notions based on poor and inaccurate observations, apply to all times and all places?

The first problem that confronts us in attempting to discuss the origin of life is the lack of an adequate definition of life. For the purposes of the present discussion we may adopt Bernal's suggestion (1951) that life is the embodiment of self-maintaining chemical processes within a certain volume. But no definition can hide the fact that living systems include a multiplicity of mechanisms that are only partly understood (Madison, 1953). We cannot expect to postulate in detail the origin of things we do not understand.

Rather we shall deal with degrees of probability and ask: Was the origin of life on earth such an improbable event that it might never occur again in the universe, or was the emergence of life inevitable on a planet such as ours?

The minimum conditions requisite for life to appear and survive are liquid water, the absence of extremes of acidity and alkalinity, the presence of certain salts, the absence of poisons and high radiation levels, and a long period of time at a relatively constant temperature. These factors, however, are not enough. Terrestrial cells are composed of certain alpha amino acids, nucleotides, and carbohydrates and gain their energy by decomposing sugars and organic or fatty acids. These compounds are only a few of the many thousand in their size range that can be synthesized in the laboratory. In nature we have known them only as products of living systems, as truly "organic" compounds. Where can we look for a supply of these substances before life appeared? And what are the chances of forming, from these compounds, molecules that duplicate themselves? Furthermore, if our early organisms were to nourish themselves on CO_2 and sunlight, how could a complex photosynthetic system, capable of the dozens of synthetic reactions seen in all plants, spring full-blown from barren primeval wastes? Could indeed such complete, organized complexity appear suddenly and synthesize from the very first its own amino acids, nucleotides, and carbohydrates, uniting these to form specific macromolecules that could coalesce in such a fashion as to form a perfect duplicate of the original cell?

In short, could such complex biochemical mechanisms appear and have the ability to metabolize, grow, and divide—to produce two living cells where only one existed before? Are not these things completely outside the realm of chance or random combination and therefore impossible for certain?

We do not know the answer. We can only examine such ideas and data as are available and make our own estimates. Let us consider especially two things: first, the building blocks from which the proteins of living cells are made; and second, the problem of growth and division on the simplest level—that of a molecule which can duplicate itself. For unless molecules can duplicate themselves directly or indirectly there is little chance that cells can.

THE BUILDING BLOCKS

1. Earth and Atmosphere

There is now overwhelming evidence that the entire visible universe is composed of the same set of 92 elements familiar to the student of terrestrial chemistry. However, the relative abundance of the elements here is very different from the average of the universe, because the universe is made principally of hydrogen. The interstellar medium, which is actually very rarified, is about 90% H, 9% He, with O, C, N, and Ne making up approximately 1%, and Fe, Si, Mg, S, etc., making up 0.2 to 0.3% (Sokolov, 1957). These exist not only as elements but also as compounds. In addition to CH, and CN found in space, enormous amounts of methane as well as ammonia are found in the atmospheres of Jupiter, Saturn, Uranus, and Neptune. Comet heads contain N_2 and C_2, C_3, CN, CH, OH, and CO as frozen unsaturated radicals. There is sufficient CO_2 in the atmosphere of Venus to form a 0.6-mile-thick layer at STP, while the atmosphere of Mars contains about twice the CO_2 found in our atmosphere. Of greater interest is the observation that certain meteorites, upon heating, give off carbon monoxide and methane as well as other gases. In addition, certain hydrocarbons have been observed. If we judge from the present make-up of the universe, therefore, we assume it is likely that many simple carbon compounds existed in space before the earth was formed.

It is now generally agreed that the earth and other planets condensed from a protoplanetary cloud surrounding the sun. Now, since the earth is not composed principally of H, it is evident that the condensation involved loss of the greater part of the mass of the original cloud. Two general views, with many variations, have been put forth concerning the details of this condensation.

Kuiper, Fesenkov, and others (reviewed by Fesenkov, 1957) suggest that the earth condensed as one large mass and that considerable heating occurred with two results. First, the original atmosphere was completely lost, and second, any carbon compounds formed in space were decomposed.

Urey, Levin, and others (Urey, 1952; Levin, 1959) have suggested a slightly different scheme in which many lesser condensations that resembled asteroids first formed. These had no atmosphere and were not hot. Gradually they collided to form large masses whose elliptical orbits swept out large volumes of space around the sun. Notice that here also the lighter gases would be largely lost as the new planet formed, but that no excessive heating occurred, at least on the planetary surface. The planets so molded retained some of the carbon compounds formed in space. In fact, it has been proposed that the organic compounds from the protoplanetary cloud played a decisive role in the origin of oil deposits on earth (Fesenkov, 1957). Thus, we are left with an earth devoid of atmosphere, with no surface water, but containing many carbon or "organic" compounds, and no life. Leakage of gases from the interior of the earth gave rise to the present atmosphere. In fact, this leakage still continues. The question of whether oil and associated gases are of vital or nonvital origin has been the subject of discussion extending over the last century. Some evidence now supports the conclusion that most deposits antedate the appearance of life and have been gradually seeping to the surface for millions of years. Water, which may also have been occluded in rocks and deep geological formations, rose to the surface faster, however, and gave rise to the early oceans. At a depth of 7 to 14 miles water may make up as much as 10% of the total weight of rock (Fesenkov, 1957). To release the amount of water now observed in the oceans, a granite layer must have been extruded that was 14 to 20 miles thick. The earth's crust is actually of this approximate thickness. Thus, we have a planet with liquid water condensed into primeval oceans, turning on its axis often enough to avoid extremes of temperature, and containing at the very outset some carbon compounds. The primeval atmosphere—still a matter of considerable discussion—was most probably composed of hydrogen, ammonia, methane, a small amount of CO_2, and water (Urey, 1952). The question arises, will any compound of interest to us be formed when such an atmosphere is irradiated by the intense solar ultraviolet irradiation? To examine this point, Miller, at Urey's suggestion, placed a mixture of H_2, NH_3, CH_4, and water in a closed vessel, sterilized it, and then generated ultraviolet light inside the vessel, using a high-frequency arc or a silent discharge. The results were surprising indeed (Miller, 1955).

Using partial pressures of 10 cm Hg for H_2, 20 cm Hg for CH_4, and 30 cm Hg for NH_3, Miller found that glycine, alanine, sarcosine, β-alanine, γ-aminobutyric acid, aspartic acid, and glutamic acid were formed. We have repeated Miller's experiments and found as many as 14 ninhydrin-positive compounds. In addition, a series of compounds that are almost universal metabolic intermediates, such as acetic, propionic, lactic, and succinic acids and urea, were identified. These are most unusual results. Fifteen per cent of the carbon placed in the apparatus was found in the compounds listed. The mechanism of building up amino acids seems to be via the Strecker synthesis.

2. THE GLOBAL REACTION SYSTEM

Consider, then, an atmosphere that for ages receives intense ultraviolet irradiation from the sun, producing in the atmosphere large quantities of organic compounds that fall with the rain into the sea. Now a solution covered by an atmosphere containing NH_3 will be somewhat alkaline. Organic acids, unlike amines, will not evaporate from alkaline solutions. The result is the accumulation of organic acids and the recycling of the short-chain amines into the atmosphere. In fact, they will be recycled until one of two things happens. Either they become converted into amino acids, which are not volatile under these conditions, or they will be converted into polyamines, which are only very slightly volatile. Therefore, the lower amines, which are almost universally toxic, would not have been stockpiled in the sea. The primeval earth was one gigantic reaction system beautifully adapted to produce vast quantities of both amino acids and other organic acids that animals, plants, and bacteria still utilize as metabolic intermediates. Ultraviolet radiation is not the only, or necessarily the chief, source of these compounds. Hasselstrom, Henry, and Murr (1957) have shown that glycine and aspartic acid were formed when ammonium acetate was exposed to β radiation, while Paschke (1957) demonstrated the formation of formate, glycine, and possibly alanine from ammonium carbonate irradiated by Co^{60} gamma rays. Present interest is no longer in whether amino acids could be, or indeed were, formed by natural processes, but rather in precisely by what mechanism and in what quantity.

Urey has suggested that the oceans at one time may have contained as much as 10% of organic material. Since the early sea is thought to have had a volume of 150 million cubic kilometers (Madison, 1953), this would mean approximately 15 million cubit kilometers of organic material would have been produced. This amounts to 3.6 million cubic miles of amino acids and other organic compounds. Assuming a sterile period of 1.5×10^9 years, only 153 pounds of compound per square mile of the earth's surface need be produced per year. This is not an unreasonable rate.

3. ACCUMULATION AND COMBINATION

No bacteria were present to decompose the amino acids and other substances formed, hence they could accumulate over vast periods of time. Abelson (1957) has recently shown by analyzing shells of the hard-shelled clam *Mercinaria mercinaria* that some amino acids are stable over such periods of time. This creature is abundant along the east coast of the United States today; in addition, fossil specimens as old as 25 million years have been found there. Abelson compared the amino acids from recent and ancient shells. Those amino acids, such as serine, that are not very heat stable were found only in the recent clams. Glutamic acid, glycine, alanine, valine, isoleucine, and leucine, however, were found in both ancient and recent shells. Calculations based on studies of the rate of thermal decomposition of alanine suggest that solutions of alanine might persist for a billion years at room temperature. Actually the age of the earth is about 3.26 billion years, and at least three-fourths of this time had passed before life began.

Given a plentiful supply of amino acids and nucleotides, would we expect proteins and nucleic acids to be synthesized? The answer that comes first and most easily is *no*. The probability of forming a decapeptide by chance combination, according to Blum (1951), is 10^{-20}. It requires energy to put amino acids together to form peptide chains—approximately 3000 cal/mole. One way of putting this much energy into a mixture of compounds is to use heat with very little water. Fox and co-workers (1957, 1958) have demonstrated the formation of many peptide chains by heating either single amino acids or mixtures, and suggest that similar processes may have been important in early protein synthesis. In contemporary organisms, energy-requiring syntheses are driven by coupled reactions in which energy-rich compounds such as adenosine triphosphate (ATP) are broken down to yield the required energy. Although it has been suggested that ATP was formed and accumulated in the primeval sea (Blum, 1951), such a suggestion does not appear plausible. Actually all the nucleotide triphosphates are extremely unstable when considered in terms of geological time.

The most important biochemical problem at present in any consideration of the origin of life is the synthesis of sufficient amounts of the purine and pyrimidine nucleotides, the building blocks of ribonucleic acid (RNA) and deoxyribonucleic acid (DNA). The first difficulty is that no "natural" mechanism for their synthesis has been proposed or demonstrated. In our repetition of Miller's classic experiment, for example, we found no evidence from ultraviolet-absorption measurements of material having the high 2600 Å absorption characteristic of nucleotides and of purine and pyrimidine bases. The fact that compounds of equal complexity, such as heme, can be made in the cell from glycine and acetate (as stressed by Gaffron, 1960) is not sufficient to demonstrate a "natural" mechanism, since those reactions still require participation of enzymes.

Not only do we lack evidence for an extra-vital synthetic system, but we also lack sufficient information concerning the stability of simple nucleotides. The purine deoxyribonucleotides, for example, can exist for only a few hours in acid solution at room temperature. If it should turn out that many nucleotides are not stable for long geological periods, we may need to revise considerably our concepts concerning the composition of the first cells. Since it is extremely difficult to conceive of a cell, however primitive, without nucleic acid, studies aimed at determining whether or not nucleic acid precursors could have accumulated are urgently needed. Such studies should include determination of the rate of breakdown of nucleotides as a function of time, temperature, pH, and ionic composition of the solution. They would not be difficult to perform with modern methods.

While the formation of even a small protein is a thermodynamically unlikely event, visualize an ocean containing, according to Urey (1952) and Madison (1953), 3.6 million cubic miles of organic compounds, existing over a period of 1.5 billion years. An event that is unlikely in a laboratory flask would occur many times in such a gigantic experiment.

GROWTH AND DIVISION

Large protein and/or nucleic acid molecules are not enough. Every grocery store is stocked with sterile cans of these substances that do not suddenly spring to life. What is required is a molecule that can duplicate itself and do something else besides—it must be both autocatalytic and heterocatalytic—at least eventually. How can a molecule duplicate itself? Fortunately, we now know a mechanism by which the two chains that make up the deoxyribonucleic acid (DNA) molecule can duplicate themselves.

This molecule is composed of two intertwining strands that are made of only four fundamental units. Each of these units contains a sugar (deoxyribose), phosphoric acid, and a purine or pyrimidine base, either adenine (A), thymine (T), guanine (G), or cytosine (C). The molecule's only uniqueness seems to lie in the order of these bases. The secret of the bonding of the two strands is in the pairing of the bases next to each other, A to T, G to C. This bonding seems to be very specific. Now if the two strands are separated, we find that, while they differ from each other, each contains sufficient information to duplicate its opposite. Using the triphosphorylated derivatives of the four nucleotides and a suitable enzyme, it is now possible to make double-stranded DNA from single-stranded DNA in a test tube. A working system for molecular duplication is therefore at hand. We do not know if the first proto-organism contained DNA. It is not impossible that the original ones did. The instability of deoxyribonucleotides in acid solutions is, in itself, a strong argument in favor of a slightly alkaline primeval ocean.

Given proteins and possibly nucleic acids in an ocean of organic compounds, what primitive organizations might occur? The physical problem is to get the necessary constituents in one place at one time. It has been proposed by Haldane (1957) that the cell constituents condensed on small oil droplets. Bernal (1951) has favored condensation on clay, adsorption and ion-exchange effects combining to achieve concentration.

However, cells originating at interfaces would be rather flat. A more appealing alternative based on the phenomenon of coacervation has been suggested by Oparin. In certain instances, when two colloids are mixed at a pH between their isoelectric points, the solution separates into two phases—one very poor in colloids, the other very rich. Colloidal mixtures of gelatin and nucleic acids will, in fact, form tiny droplets that superficially resemble cells (Evreinova, Korolev, and Agroskin, 1959). When lipids are present, a surface membrane may form; under some conditions, pulsating vacuoles have been observed. Now these droplets are not alive by any means. What has been demonstrated is that a mechanism exists for wrapping proteins and nucleic acids up as discrete blobs or cells.

If the surrounding sea contained all the compounds necessary for the molecules in a coacervate droplet to duplicate themselves, the droplet could grow. Its size might well be limited by the action of currents and waves—if it grew too large, it would be broken in two, only to grow again. This process could not go on indefinitely, because the store of organic compounds accumulated in the sea must someday have begun to give out. Now suppose these little cells used up almost all of one compound, which we shall call *A*. Now if perchance one photocell was able to make its own *A* from *B*, then it could continue to grow while all of its fellows starved. When *B* ran out, a lucky mutant possessing a new enzyme that could make *B* from *C* again would be able to thrive while others perished. And so, applying a clever suggestion of Horowitz (1945), we can conceive a scheme in which a very complicated set of enzymes was developed backwards. The process possibly ended with the metabolism of acetate and formate, two compounds probably present in great quantities. Only now do we really need to face the problem of the origin of photosynthesis in cells already well supplied with enzymes to use the products of photosynthesis.

Many suggestions as to when and how photosynthetic and autotrophic organisms evolved have been presented (Gaffron, 1960). The difficulty of oxidizing various organic compounds in a reducing environment has led to the proposal that some form of photosynthesis occurred at a very early stage.

It is not possible to begin to do justice here to the many proposals, based on comparative biochemical studies, that have been made.

DISCUSSION

Thus we pass almost imperceptibly from a gaseous cloud about the sun to cells whose survival depends on adaptation to changing conditions. Only those cells that *can* adapt, survive. The stage is now set for the gradual unfolding of the biochemical possibilities inherent in the elements—the results of which we now observe in the entire biosphere and reflect in ourselves. The evolution of cell division from simple mechanical breakage of droplets to the complex mitotic mechanism has been discussed in detail elsewhere (Anderson, 1956). The conclusion that life spontaneously appeared on earth would not, I think, have greatly surprised St. Thomas Aquinas or other early scholars who saw nothing unusual in the idea that living things could arise from inanimate substances.

How probable were these events, taken in their entirety? Certainly many of the individual steps are more probable than was once thought. The very first requirement, for example, is a planet with a suitable atmosphere and a stable temperature for long periods of time. When the near-collision hypothesis of the origin of the planetary system was in vogue, planetary systems were thought to be very rare—as rare as a special near-collision between two suns. With the emergence of the dust-cloud hypothesis, matters completely reversed. The rotation of a condensing cloud of cosmic dust may, in many instances, be sufficient to cause an excessive centrifugal strain on the condensing star if all the rotational energy ends up in the star. Present evidence, however, suggests that more than half the stars in our galaxy are double or multiple systems. The angular momentum may thus be absorbed by the rotation of double stars or of planets about the star. Actually, the larger stars appear to spin, whereas, the smaller stars show little or no measurable rotation. Although not demonstrated by direct observation, it is very probable that planets do indeed account for the slow spin of these small, sunlike stars. Since life requires that a planet have an even temperature over a long period of time, it is important to know which stars are most stable. Since luminosity, which is an index of the rate of stellar fuel consumption, increases as the 4th power of the star's mass, it is evident that the larger stars would have a shorter equilibrium state. It appears that only the stars belonging to the late F, G, and early K types offer a favorable environment for bioplanets; these smaller stars have both a longer stable state and a greater likelihood of extant planets to absorb excess rotational energy. About 10% of all stars fall in this favorable range. Let us make both an optimistic and a pessimistic estimate, following the original suggestion of Shapley (1957), and see what numbers appear (assuming approximately 10^{20} stars in the metagalaxy).

An optimistic estimate is that there are 5×10^{18} stars with planets of the proper temperature (assuming 10% of all stars have planets, and half of those with planets have one in the right orbit). If 1 in 100 of these suitable planets have evolved life, there are 5×10^{16} bioplanets, and if 1 in 100 bioplanets have evolved intelligent life, there are one-half million billion centers of intelligence.

Taking a more conservative view and assigning to each of the above probabilities a value of 1 in 1 million (1 in 1 million stars has a planet of the right temperature and size; 1 in a million such planets has life; 1 in a million such bioplanets has intelligent creatures), we still come out with 100 centers of intelligent life. It may be said, therefore, that it is extremely improbable that there is only one center. Indeed, it is likely that the subject of this paper has received a much more detailed treatment previously elsewhere, ". . . seeing," as noted by St. Paul (Heb. 12:1), "we also are compassed about with so great a cloud of witnesses."

Addendum added in proof: In the years since this lecture was presented a wealth of additional information has been gathered, and much supporting research done. Important projects incorporated in our space program are addressed to the question of the detection of extraterrestrial organic compounds and to determining the distribution of life in the solar system. What appeared, when this lecture was presented, as an almost purely academic consideration is now a central question in a large national program.

N.G.A.
April 16, 1963

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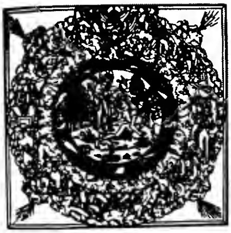

*A Russian translation of this paper has appeared in *Agrobiologia*.

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IN MAN'S NEVER-ENDING ENDEAVOUR to understand, and thus ultimately to control, the world in which he lives, the theories we associate with the name of Darwin have been among the most important advances in recorded history. It was Darwin's work that persuaded the human race to adopt a view of living creatures which at first sight seems complicated and unlikely, but which is really much more profound than the simpler ideas that had reigned previously. In earlier times mankind had in general been content to accept uncritically the picture of the living world he could see when he observed it during his short lifetime. The world appeared to be filled with many different kinds of animals and plants, which formed a number of species between which there were few intermediates. The horse and the ass were two different kinds, with little connection between them. There were, of course, some thinkers before Darwin who maintained that this lack of connection between species was illusory, and that over long periods of time species changed and were in reality connected by sequences of evolutionary alterations. It is, however, to Darwin that the credit must go for presenting the arguments for this conclusion so forcibly that the world as a whole was persuaded that it is correct. It is to him, more than to anyone else, that mankind today owes one of the most fundamental of its beliefs: namely, that the natures of the various living beings in the world are not elementary facts with which mankind is faced, but that the organisms inhabiting the earth's surface have been brought into being by causal processes which are in principle capable of being controlled and directed.

It followed from the theory of evolution that man himself, who can scarcely deny that he is an animal, must be subject to the laws of evolutionary change which affect all living things. The theory of evolution is therefore inescapably connected with the other systems of thought by which man has attempted to understand and control his own nature, that is to say, the systems of religion, philosophy, and politics. These are fields of human endeavour in which emotion is very powerfully at work. In tracing the history of Darwin's scientific theories from his day to our own, it is not surprising that we generally find that a worker who may make a valuable contribution in a certain area at the same time commits himself to statements which are less satisfactory in other parts of the enormously complex and emotionally charged field to which evolution is relevant. There are very few, if any, authors whose works we can accept in their entirety. Darwin himself escapes much criticism on this score, because he confined himself to establishing the fundamental main lines of his argument. He did not attempt—and indeed, owing to the backward state of the understanding of hereditary phenomena in his day, was not in a position—to discuss the precise way in which it affects human political and religious thought. The century since the publication of the *Origin of Species* has seen the rise and development of the science of genetics, and it has been only gradually, through the endeavours of many authors, each contributing something of value, but also something which should be rejected, that we have been working towards a true appreciation of how the theory of evolution should be formulated in terms of our new understanding of biological inheritance.

As is well known, the foundations of our understanding of heredity were laid when Mendel demonstrated that the characters of an organism are developed on the basis of certain hereditary potentialities which it receives from its parents, and further that these potentialities are carried in separable, discrete, hereditary factors—nowadays known as genes. It was not till about 1900 that this theory became widely known in the scientific world. Immediately many sets of experimental data were obtained which could be interpreted according to the Mendelian rules. There was for some time, however, a controversy as to whether Mendelian heredity is the most general or even the exclusive mode of biological inheritance, or whether it is a more special type of less importance. The older and alternative theory is that of blending inheritance. It supposes that the hereditary contributions from the two parents come together and fuse into an intermediate blend in the offspring. Darwin himself pointed out one of the difficulties that would arise for the theory of evolution if blending inheritance were the general rule. In each generation the hereditary differences between two parents would unite in a blend, so that variation would continually be disappearing from the population unless some other process created new variation as fast as it was lost. The only source from which such new variation could arise would appear to be the environment. Thus, if inheritance is of a blending nature, we are forced to conclude that the environment can engender new hereditary variation. This is the theory of Lamarck. Darwin appears to have felt himself driven in this direction, but was reluctant to embrace the theory wholeheartedly. He acknowledged that this question of the loss of variation under blending inheritance was the major weakness in his theory of evolution. Geneticists responsible for the first developments of Mendelian theory immediately recognized that the whole difficulty disappears if hereditary potentialities are carried by discrete unit genes which do not blend. The point was made very clearly by Bateson (1909) as early as 1908.

The early Mendelians, however, conducted their experimental work with hereditary characters that were clear-cut and easily recognizable variations from the normal. These, of course, present the easiest experimental material to handle. The situation led, however, in the hands of authors such as Bateson and De Vries, to the unfortunate suggestion that evolution has normally depended on sudden large-scale alterations. This view was quite different to that of Darwin, who had emphasized the imperceptible small steps with which evolutionary processes proceed. Biologists who, like Darwin, were impressed with the gradualness of evolution at first tended to reject the Mendelian theory as a general explanation of biological inheritance and as the underlying mechanism of evolutionary change. However, within a comparatively few years the Mendelians had demonstrated that even very slight, hardly perceptible, hereditary variations can be controlled by Mendelian unit genes, and that where we are confronted with a continuous range of variations the phenomena find their explanation, not in blending inheritance, but in the existence of numerous genes, each having a small effect. This was demonstrated in the first place by plant breeders such as Nilsson-Ehle (1909), working on wheat in Scandinavia, and East (1910) and others working on corn in the United States. Hereditary mechanisms dependent upon Mendelian genes may, therefore, produce gradual continuous evolution.

In characters that, within a population, vary continuously over a certain range, it has always been clear that the environment usually plays some part in determining the precise value which the character will have in a particular individual. The classical studies of Johannsen (1909) on pure lines of beans, and many other similar studies, have shown that these variations are, in general, not inherited. It became, therefore, a major preoccupation, both for the theory of evolution and for that of animal and plant breeding, to find methods of estimating the extent of the environmental variation, and to separate this from the hereditary variation which might be passed on to later generations.

It should be remarked, in the first place, that this problem has been historically very closely connected with political matters. It is clearly of profound sociological importance to determine whether the variations we see between men at the present day have been produced by environmental influences, which may be quite changed in the next generation, or whether they are the expression of relatively permanent hereditary qualities. Some of the early Mendelians unfortunately regarded this question in much too simple a manner, and attributed an overwhelming importance to hereditary factors. In the same manner, some of Darwin's early followers developed quite superficial social theories based on the simple transference to the human world of such phrases as "the survival of the fittest." It would be inappropriate here to attempt to summarize the whole confused history of the impact of Darwin on social theory. It is sufficient to point out that at the present day it has become rather widely recognized that man, with his development of methods of communicating information from one generation to the next through speech and writing, has produced what is, in effect, a second system of inheritance, which operates on top of, and in addition to, the biological mechanisms characteristic of the non-human biological world. It is only for those human variations which affect the bodily structure and composition—such things, for instance, as variation in blood group antigens, or shapes and colours of hair, skin, and other organs—that theories of biological inheritance are an adequate guide to human affairs. In all the other, and much more important, human variations, which affect mental qualities, we must never omit from our consideration man's alternative system of inheritance which arises from his existence as a social being who can, and indeed must, learn from his ancestors.

This human system of social inheritance clearly follows quite different laws from those of biological inheritance, and the evolution of man's mental and cultural abilities does not follow the laws of sub-human evolution. Cultural influences, that is to say, those that can be transmitted from one individual to another by processes of teaching and learning, can produce changes in man with incomparably greater speed than could be achieved by the biological mechanism of heredity.

An extremely striking case of this has ecently been described in detail by the American anthropologist Margaret Mead (1956). In 1928 she made a detailed study of the Manus tribe in New Guinea, a people who, at that time, were living in conditions comparable to those of the Stone Age. During the Second World War large numbers of American and Australian troops were based in this region, and the Manus people were brought into extensive contact with men in the twentieth-cenutry phase of cultural and political evolution. Mead made a renewed study of the Manus in 1953, and showed how they had acquired at least the rudiments of a democratic and technologically modern society. This stupendous evolutionary advance from the Stone Age to the present has taken place within the lifetime of single individuals; that is to say, it cannot have depended at all on changes in the genetic constitution of the population.

Man's endowment of biologically determined potentialities is, in fact, not so much the means by which the evolution is brought about, but rather the stabilizing factor that prevents retrogressive evolutionary changes going too rapidly. Even men who have lived for many generations under social and political conditions which prevent the development of the higher phases of human evolution fortunately retain intact the basic biologically determined hereditary potentialities, which can become fully realized as soon as the cultural conditions permit. It is only because biological heredity is relatively stable and is not easily changed by the environment that we can escape from the conclusion that the backward races of mankind are really inferior. By the recognition that man has two systems of transmitting information from one generation to the next—the biological system and a socio-cultural system as well—the study of continuous variation in man and the influence of the environment on it becomes liberated from considerations of a political nature.

The formulation of the theory that continuous variation depends on the joint action of many genes, each with small effect, allowed an extremely rapid development of our understanding of the genetical situation within sub-human populations which are involved in evolutionary change. As a first step, the processes of natural selection were expressed in mathematical terms by authors such as Sewall Wright (1931), Haldane (1932), and Fisher (1930). The fundamental advance in understanding which was involved in these developments was the change from the consideration of evolution in terms of the genetics of individuals to a consideration in terms of populations. The basic unit considered by the mathematician was not the individual organism but a population of interbreeding organisms. Within such a population there will be different alleles of very many genes, and the mathematical formulae express the ways in which the frequency of the different alleles change as natural selection or other processes operate on the population. The development of this point of view began about 1930, and by now the theory of population genetics has become a large and elaborate subject. It is only possible to mention one or two of the major advances.

Perhaps the most interesting question that has arisen from the theoretical investigations is the possibility that populations may sometimes be reduced to such small numbers that purely stochastic fluctuations in the frequency of alleles may result in evolutionary changes, which will then not be strictly controlled by natural selection. The importance of this phenomenon, which is often known as genetic drift, has been particularly stressed by Sewall Wright (1931). On the other hand, others of the theoreticians, such as Fisher (1930), have argued that it is not likely to be of much practical importance in nature. Only detailed investigation of actual natural populations can settle this, and the matter is still under debate.

The theory of population genetics was soon reinforced by experimental studies of actual populations as they exist in nature. The first major advances in this field were made by a group of Russian geneticists. Tschetverikov (1926) seems to have been the first to draw any practical conclusions from the consideration that the phenomenon of dominance implies that wild populations may contain very many more recessive genes than a casual inspection would suggest. Following his lead, several of his pupils in Russia, such as Dubinin (1934), and others who later worked outside the Soviet Union, such as the Timofeeff-Ressovskys (1940), and Dobzhansky (1951), as well as geneticists from many other countries, have profoundly increased our knowledge of the genetic endowment of populations evolving in the field.

From these studies three major new points have emerged. In the first place, the wealth of genetic variation within a natural population has turned out to be much greater even than the early students expected. In the early days of population genetics, it was thought that a population consists of individuals most of whose genes are of the same set of standard wild-type alleles, with occasional rare recessive alleles at some few loci. It has been found, however, that, although this picture is true enough if we consider only allelic differences which produce very marked effects, the idea that there are standard wild-type genes is not adequate if we examine the matter in detail. On the contrary, at almost every locus a population is found to contain a number of slightly different alleles, all of which produce relatively normal individuals, but individuals with slight differences between them. Nearly all individuals taken from a wild population are, in fact, heterozygous for very many more genetic factors than anyone had suspected.

From this basic fact, two further consequences seem to be emerging. On the one hand there is much evidence, particularly emphasized, for instance, by Lerner (1954), that the heterozygotes for these minor allelic differences are usually fitter than either of the two homozygous types. In so far as this is so, natural selection will not lead to a state of genetic purity in a population, but will preserve a heterozygous condition, that is to say, one which contains much genetic variability. Further, the studies, particularly those of Dobzhansky (1955), have shown that each local population of a species contains a collection of allelic differences which are such that they interact with one another to give favourable heterozygotes or gene combinations, whereas genes taken from one population often give rather bad results when combined in hybrids with genes from a different population. It is usual to speak of the whole collection of genes which are found in a population as the "gene pool." Dobzhansky's work, just mentioned, leads to the conclusion that within the gene pool of a single population the genes are co-adapted to one another.

These developments in the field of population genetics are making possible a much more profound understanding of the processes of natural selection. Before the complexity of the genetic structure of wild populations was fully understood, work had already been carried out on the natural selection of characters controlled by single genes with marked effects. There are comparatively few cases in which evolutionary changes in such characters have been observed to proceed at rates fast enough for detailed scientific study. One of these is the appearance of melanic forms in *Lepidoptera* in industrial areas. The existence of natural selection, favouring the dark forms in areas contaminated by industrial smoke and the light forms in uncontaminated areas, was demonstrated by Heslop-Harrison (1920), and is still being studied in detail, for instance, by Kettlewell (1955). In quite recent years the appearance of populations of insects resistant to insecticides, such as DDT, has posed both an important practical problem and a wonderful opportunity for the study of evolution (Crow, 1957; Oshima, 1958). In many cases, however, these resistant forms have turned out to depend on the cooperative action of many genes, rather than on a single one with large effect.

From what has been said above about the genetic structure of populations, it seems probable that most evolutionary changes by which species become adapted to the subtle variations of their environment will involve many allelic differences rather than few. The growing points of our present investigation of natural selection are, therefore, the study of the changes which can be brought about in co-adapted gene pools, rather than the study of one or two genes of strong effect. Similarly, in the study of artificial selection as it is involved in animal or plant breeding, we again find that it is necessary to think in terms of the statistical alterations in the frequencies of many genes.

Population genetics deals with what may be called the technology of evolution—such matters as the range of genetic variability that will be present in a population, the rate of change under natural selection or under the influence of statistical fluctuations, and so on. The most fundamental problems concerning evolution are, however, of a different kind. They are the two related questions of the manner in which new genetic variation comes into being, and the nature of the influences which the environment exerts over the direction in which evolution will proceed. In pre-Darwinian evolutionary speculations, such as those of Lamarck, these two questions were thought to be intimately connected. With the rise of modern genetics and its application to evolutionary theory, the two problems were for some time thought to be quite unconnected with one another. It is only in the last few years that we are realizing that, in fact, they are closely connected, although the connections are of a more complex nature than earlier biologists had supposed.

We have by now a very large, but still very unsatisfactory, body of information concerning the processes by which new hereditary variation arises. The unit hereditary determinants, or genes, are found to undergo occasional alteration, a process known as mutation. Mutations may occur spontaneously, that is to say, in circumstances in which no particular causal antecedents can be assigned to them. At one time it seemed adequate simply to suppose that, since the gene must have a highly complex molecular structure, mere thermal agitation or similar chance processes might bring about mutational changes. It was easy to comprehend in these terms the fact that physical influences which produce ionization throughout the cell increase the frequency with which mutations occur. It has gradually become apparent, however, that the frequency of mutation, both spontaneous and radiation induced, varies from one type of cell to another, and from stage to stage in the development of rapidly altering cells such as the gametes. It is clear then that mutation is, either primarily or at least secondarily, dependent on the metabolic condition of the cell. The interpretation of this is still very uncertain. Further, we now know a considerable range of chemical substances which can increase the frequency of mutations. But again their exact mode of operation is still not fully understood. In some cases, particularly in bacteria, there is evidence that certain genes are more sensitive to the action of particular mutagens than others. This, perhaps, suggests that in these cases the mutations are brought about by direct chemical interaction between the mutagen and the gene itself, but in most cases it seems more probable that a number of stages intervene between the action of the added chemical and the final gene mutation.

In evolutionary theory, the point of first importance is that in all these cases of induced mutation the mutagenic stimulus merely increases the frequency with which a wide range of mutations occurs. It does not direct mutations into any particular channels. These phenomena do indeed involve the production of new hereditary variation under the influence of environmental factors; but in the first place these factors are of very special kinds, such as ionizing radiations or certain potent chemicals, and in the second place the type of hereditary variation produced has no precise relationship to the type of environmental influence which is operating. At the stage in the history of genetics reached by the middle 1940's, there appeared to be very little connection between the origin of new hereditary variation and the directive action of the environment on the course of evolutionary change. The situation was conventionally summed up by saying that mutation was a "random" process.

In more recent years the situation has already developed to a certain extent. A few types of phenomena have been discovered in which hereditary changes are produced which are not random, but are rather precisely directed by the agent employed

(McElroy and Glass, 1957). One such type of process is transformation or transduction in bacteria. This is, however, not a very close model of the origin of new hereditary variation. In transformation or transduction, part of the hereditary material of one strain of bacterium is carried into another strain, into whose genetic endowment it becomes incorporated. Thus, if we take into account the donor strain as well as the recipient, nothing new arises; the process is comparable rather to hybridization than to mutation.

A phenomenon which may ultimately prove more enlightening in relation to mutation is that of induced enzyme synthesis. Bacteria, and to a certain extent other cells also, when placed in contact with chemical substances which could be the substrates of a group of enzymes, often develop the capacity to produce the appropriate enzyme in considerable quantities; this property may persist in the progeny for a considerable number of generations. The process is certainly not as yet fully understood. It seems rather probable that we are dealing here more with the activation of already present hereditary potentialities than with the origin of quite new potentialities. However, it may be that this is too pessimistic an interpretation, and that we are sometimes confronted with cases of the directed modification of the hereditary materials by the other constituents of the cell with which they are in metabolic relations.

Even if it is as yet not certain that such metabolically directed mutations are involved in enzyme induction, our understanding of the chemical nature of the hereditary substance has certainly reached a point where we can begin to think seriously about the metabolic activities of the gene as a constituent of the dynamic system of the cell. There can now be little doubt that genes are essentially composed of deoxyribonucleic acid (DNA) and protein. Most of the evidence, particularly that from bacterial transformation, suggests that it is the DNA which carries the specific character of the gene. This compound is built out of four nucleotides which are joined together in long sequences; two such linear threads are then twisted round one another to form the complete DNA molecule. The DNA is certainly in close chemical relation with protein, and it must also be responsible for the synthesis of new DNA which is an exact replica of the old; it may very well be involved in other chemical changes also. The nature of its chemical activity is, indeed, still very little understood. There seems, however, no reason why one should not hope eventually to understand, and finally to influence, its chemical activities, and thus to obtain some control over the order in which the nucleotides are built into sequences, and in this way eventually over the proteins which the DNA specifies. Already it has been possible to alter the nucleotide sequences in a very crude way; for instance, they have been altered by supplying the cell with chemical analogues of the purine and pyrimidine bases. Such substitution of an abnormal for the normal chemical grouping has so far resulted only in a general increase of undirected mutation, but along these lines a more precise, and more directed, control may eventually be attained.

In recent years several other phenomena have been studied whose relation to gene mutation is not so clear, but which may ultimately prove very illuminating. On the one hand, there are several immunological phenomena in which changes are induced which persist through several generations of cells, though not usually through several generations of individuals (Medawar, 1956). The induction of immunological tolerance by the administration of an antigen to an early embryo is a particularly striking case. Perhaps of a different type is the phenomenon of graft hybridization, investigated particularly by Glouschenko (1957), and the induction of changes which, it has been claimed, follow the injection of certain tissues into animals, as in the experiments of Kushner (1958) and Benoit *et al.* (1957). These phenomena, if they can be substantiated and shown to occur in a wide range of materials, are of the greatest possible interest. However, it cannot be claimed that their mechanism is as yet at all understood. It is not clear whether we are dealing with something comparable to bacterial transformation, or with something comparable to the alterations which virus or virus-like proteins may undergo when transferred from one species to another, or with something allied to the mechanisms of immunological processes, or even conceivably with true metabolically induced mutations.

However such problems may eventually be resolved, it appears most improbable that any of these recently discovered mutation-like processes can provide models for the kind of directed origin of variation which would be relevant for the theory of evolution. In all the processes described above, the agents to which one might be tempted to attribute the capacity to direct mutation are highly complex products of biological activities. They are such things as DNA from one strain of bacteria which may be introduced into another, or the tissues of one plant or animal which are brought in contact with those from a different species. These are not events of the kind which can form the basis of the general processes of evolution. If we wish to seek for any influence which can direct the appearance of variation of evolving populations in general, we shall have to find it in the environment, that is to say, in the inorganic surroundings in which the animal lives and in such interactions with other species as it is likely to undergo in its normal course of existence.

During the earlier phase of the development of the genetical theory of evolution, the role of the environment was reduced to that of being a mere filter through which new hereditary variants had to pass; it became merely the agent of natural selection and little else. It was, of course, realized that the environment plays a part in producing the characters which organisms exhibit. Indeed, the whole development of the genetics of continously varying characters depended on methods for separating and distinguishing the hereditary contribution and the environmental contribution to the range of variation which is found. For instance, it was shown that one can distinguish the extent to which variations are hereditarily determined by comparing near relatives, such as parents and offspring, or by measuring the response to selection of given intensity. From such data estimates can be made of the heritability of a given character, that is to say, the portion of the variance actually found which can be attributed to hereditary factors which will pass on to the next generation. The remaining variability can be attributed in the main to the environment. In the early developments of this theory it appeared sufficient to regard the environmentally produced variability merely as a complication which tends to obscure the underlying genetic situation. Having been detected and distinguished, it was omitted from further consideration. This implies that the environment plays no part in bringing about, or controlling, the direction of the variability on which evolution depends.

The most extreme alternative view of the role of the environment in evolution is to suppose that it can directly produce new hereditary variation of a kind appropriate to the influences which are operating. This view, of course, has a long ancestry reaching back to the theories of Lamarck. In recent years it has been defended by a group of Soviet biologists working under the influence of Michurin and Lysenko. Their work has, however, not won general acceptance in the non-Soviet world. This is partly on practical and partly on theoretical grounds. There are, of course, very many cases, both in controlled experiments and in general agricultural practice, in which animals and plants have been submitted to abnormal environments and have not undergone any hereditary changes, either of an appropriate or an inappropriate kind. The difficulties which have been encountered in trying to produce strains of European dairy cattle for use in the tropics is one example (Mahadevan, 1954, 1955). Thus, the phenomena of induced hereditary change which Lysenko and his followers have described must demand some rather special conditions and certainly do not occur whenever the environment is altered. However, if there are special conditions in which such changes are produced, biologists outside the sphere of the Soviet influence have been unsuccessful in finding them.

In addition to this negative practical evidence, most biologists find it difficult to envisage any mechanism by which such effects would be expected to occur. Even if we suppose that there is, in addition to the well-understood chromosomal system of hereditary determinants, a much more elaborate cytoplasmic system than at present seems probable, it is still rather difficult to imagine any way in which such factors as light intensity, temperature, etc., would eventually become transformed into *appropriate* alterations in the hereditary system. Perhaps it is just conceivable that something similar to, but much more far-reaching than, induced enzyme synthesis could bring about such results. At present, however, most geneticists concerned with evolution regard such claims as at best not proven and do not feel justified in granting them an important place in the general theory of evolution.

It remains true, however, that evolution has produced many phenomena which suggest quite strongly that the environment is not wholly without influence on the nature of the variations which occur. For instance, we often find that local races of plants which live under peculiar environmental conditions exhibit, as hereditary properties, characters exactly similar to those which we would expect to be produced as developmental modifications by the environment (Clausen and Hiesey, 1958). For instance, alpine races often have short stems and long root systems. These are hereditary qualities of the alpine race, as can be proved by growing its seed in a lowland situation. On the other hand, if seeds from a lowland race are grown in the mountains, the resulting plants will be modified by the environment in the direction of the alpine type. There is a considerable variety of data of this kind, and it appears to be quite unreasonable to suggest that the developmental modifications which the environment can produce are quite irrelevant to the evolutionary process.

It is not necessary, however, to suppose that the environment acts by the direct induction of appropriate variation, in the way suggested by Lamarck and Lysenko. It was pointed out some twenty years ago, by both Soviet geneticists and others (Schmalhausen, 1949; Waddington, 1940, 1942), that an alternative mechanism is possible, and recently experiments have been carried out which show that the process suggested can be realized in practice (Waddington, 1957).

If a heterogeneous population of animals is subjected to some new environmental stress, this will produce in them a variety of developmental modifications. Some of these modifications may be of adaptive value. There will then be natural selection favouring hereditary potentialities for reacting in an adaptive manner to the environmental stress. As generations pass, and selection proceeds, the population will eventually come to consist of individuals all of whom will in the new environment develop the corresponding adaptive phenotype. Now it is a general observation that developmental processes exhibit not only some flexibility, which allows for the production of adaptive modifications, but also some tendencies towards inflexibility, which insure that development frequently attains the normal end result even if the circumstances in which the individual develops are somewhat unusual. If a population is subjected for many generations to natural selection for its capacity to undergo a certain developmental modification in an unusual environment, it may acquire such a strong tendency in this direction that, if it is transferred back into the original environment from which it came, the developmental modification is still produced, even though the precipitating environmental stress is now absent. The character which was originally acquired may in this way, after many generations of selection, become independent of the environmental cause. It becomes "assimilated by the genotype."

It is important to distinguish this mechanism, by which acquired characters may be forced by selection to become inherited, from the earlier theories which supposed that acquired characters may be inherited without selection having played any part in the process. The distinction can be seen very clearly in some of the experiments which have been performed to demonstrate genetic assimilation. For instance, if *Drosophila* pupae are submitted to an environmental stress in the form of a high temperature for a few hours, many of them exhibit developmental modifications which take the form of changes in the venation of the wings. One modification which has been studied in detail is the partial or complete disappearance of the posterior cross-vein. This acquired character is not inherited. Even if the environmental stress is applied to a population for many generations, there is no change in the frequency with which the response occurs, unless selection is also operating. This can be demonstrated most clearly if one makes the experiment with an inbred strain. In such a strain there is no genetic variability available, and even if selection occurs it cannot be effective. On the other hand, if selection is applied to a heterogenous population, which is submitted to the environmental stress in every generation, the frequency of the response can be rapidly increased. It can also be decreased, in spite of the repetition of the environmental stress, if selection is exerted against the capacity to respond in this manner. We are, therefore, certainly not dealing with the inheritance of an acquired character, but with the results of selection for, or against, a certain capacity for developmental modification.

Although this mechanism is quite different from the Lamarckian one, or that supported by Lysenko, its evolutionary consequences will be very similar. In considering evolution we may always think in terms of many generations. There is plenty of time available in which natural selection can act. In the experiments with the missing cross-vein in *Drosophila*, strong artificial selection was applied. In each generation the population was propagated only by individuals which acquired the character of the missing cross-vein. After only about twelve generations of intense selection, the character had become genetically assimilated; that is to say, it appeared in individuals which had been reared under normal temperatures and to which no environmental stress had been applied. Under natural conditions selection would usually be less stringent, but one must expect that similar results would be achieved over a longer period. We have then a mechanism by which, on the evolutionary time scale, acquired characters could be converted into inherited ones.

It is interesting to remember that at the period when Darwin, and still more Lamarck, discussed the inheritance of acquired characters, the basic problems of evolutionary theory were not clearly distinguished from one another, and no such science as population genetics had been contemplated. In that period the concept of inheritance was capable of two quite different interpretations. We usually discuss Lamarck's views as though he were using the word "inheritance" with its present sense, to mean the transmission of a character from one pair of parents to their immediate offspring. This is the elementary phenomenon studied by genetics. It is only fairly recently, however, that it has been clearly distinguished from a completely different phenomenon. The word "inheritance" might also be used to mean that, if the individuals in a population acquire a character from their environment, the frequency with which this character occurs will be greater in some evolutionary-derived population many generations later. This is the type of phenomenon with which population genetics is concerned. The argument of the last few paragraphs shows that, even if we reject Lamarck's theory when it is interpreted in terms of simple genetics, there are good grounds for accepting it when it is interpreted in terms of evolutionary-population genetics.

The view that has been put forward above gives no grounds for suggesting that the environment directly stimulates the appearance of new hereditary variation. The individual differences in the capacity to respond to stress, on which selection operates, may well have been present in the population before the stress was applied. However, there is one important conclusion concerning natural variability which must be drawn. Selection for capacity to respond to stress will produce individuals whose developmental systems are easily modifiable in certain appropriate directions and are resistant to modifications which would produce harmful alterations. The types of stability and instability which are thus built into the developmental systems of the organisms must influence the manner in which new hereditary variability is expressed. A random change in the molecular configuration of the hereditary material will affect a system of developmental reactions which are easily modified in certain directions and more stable in other respects. Random mutations of the genes will therefore tend to produce phenotypic effects which are not completely random, but which are to some extent determined by the earlier selection which has determined the modificability of the developmental system.

In this short summary of modern ideas about evolution, we see that Darwin's theory of natural selection has provided the basis for the great advances in our understanding which have followed the development of modern genetics. The theoretical and experimental studies of population genetics, both in the laboratory and in nature, have given us a much deeper insight into the mechanisms by which natural selection operates. They culminate at the present time in the notion of a co-adapted gene pool, but we can still see many vistas for future development opening in front of us. When one regards the twin problems of the manner in which the environment influences evolution and of the origin of new variation, again the theory of natural selection provides the essential clue. It remains very uncertain that the environment has any direct effect in producing new variation. On the other hand, it seems quite certain that selection for response to environmental stresses is a process of the greatest importance. On the one hand, it can, over an evolutionary time scale, lead to characters which were originally acquired, becoming later inherited. On the other hand, it produces organisms whose developmental systems have certain characteristics of stability and instability, which must profoundly influence the expression of random changes occurring in hereditary materials. The ideas of Darwin, allied to those arising from embryology and Mendelian genetics, can take over whatever was of value in the earlier speculations of Lamarck.

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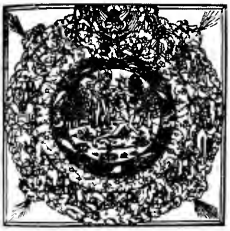

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SINCE THE TIME OF CHARLES DARWIN, the concept of evolutionary change has permeated the entire field of biology. It is accepted without question by all working biologists, because of the immense body of facts which now demonstrates its existence. Furthermore, change through time is now recognized as one of the guiding principles of the universe, from stellar galaxies to human societies. Biologists of modern times are relatively little concerned with showing that change has taken place. Even the directions which evolutionary changes have taken in particular groups of plants and animals have proven to be a less rewarding field of study than the mechanism of evolutionary change. The challenging question which most modern evolutionists are trying to answer is: "What forces or processes can bring about the evolution of a population of organisms into a new type, with a different appearance and a changed way of life?"

This was, of course, the main question which Darwin himself was trying to answer. To do this, he developed the theory of natural selection, for which he was able to gather together a body of factual evidence, much of it experimental, which in his day appeared impressive enough to convince most biologists that his views were correct.

But in the period after Darwin's death, and particularly in the early part of the twentieth century, experimental biology made great strides, both in the facts about living things which it uncovered and the techniques of investigation which it developed. The biologists of this time, moreover, were concerned chiefly with the mechanism of life. This mechanism can be understood best by intensive studies of individual organisms, while evolution is best understood by means of the comparative study of populations. Consequently, biological techniques and standards of experimentation far outstripped those which were used by Darwin and which were adequate in his day, without contributing much to our understanding of evolution.

This fact explains in part the low opinion which many biologists of a generation ago held in regard to Darwin's theory of natural selection. In addition, the rediscovery of Mendel's laws of inheritance focused attention upon unit characters, or conspicuous differences between organisms which are inherited as single units. When the origin of such unit characters by genetic mutation was demonstrated in the evening primrose *(Oenothera)* by De Vries and in the fly *Drosophila* by Morgan, this seemed to many biologists to spell the doom of the natural selection theory, based as it was on the accumulation through selection of small differences between individuals.

The past thirty years have seen a great revival of interest in Darwinism, and an added confidence not only in the correctness of the evolutionary theory itself, but also in Darwin's explanation of natural selection. This revival has been brought about by scientists who have applied modern quantitative and experimental methods to the sphere of action in which the evolutionary processes are actually at work. This is the genetics of natural populations. Population genetics has erected three great pillars which can support the edifice of evolutionary theory. First, it has shown that multiple factor or polygenic inheritance is the way in which most differences between natural populations are inherited. This leads to the corollary that, as Fisher (1930) and many others have maintained, mutations with relatively small effects, which contribute to the almost imperceptible differences between individuals upon which Darwin relied, play a larger role in evolution than the conspicuous mutations observed by De Vries and Morgan. Second, population genetics has accumulated a great body of evidence showing that the selective value of any single gene depends partly upon the other genes with which it is associated in any individual. This fact disposes simultaneously of any theories which would make either the individual organism or the gene the basic unit of evolutionary change. Mendelian segregation tells us that the individual is merely the temporary home of a collection of genes which is partly scattered and assembled anew with each successive generation of individuals. The rarity of mutations makes each gene a relatively permanent entity, but as an evolutionary unit its significance is reduced by its changing adaptive values. Because of this fact, Dobzhansky (1955) and others have correctly recognized the "Mendelian population" in sexually reproducing organisms as the basic unit of evolutionary change. The third pillar erected by population genetics is the quantitative, experimental approach to the study of selection itself. In the last century, evolutionists tried to establish the validity of natural selection chiefly by showing how a particular characteristic, such as body color, could have a selective advantage in a given environment. They failed to realize that the interactions between an organism and its environment are extremely complex, so that the way in which a characteristic is advantageous is often indirect and very hard to demonstrate conclusively. Population genetics has taught us that the best way to show the action of natural selection is to demonstrate statistically that a given gene, or gene combination, has an adaptive advantage in a known, controlled environment. This demonstration is relatively easy in organisms which are well known genetically, and can sometimes lead to a further study of how selection acts.

Supported by these three pillars, evolutionists have erected a theory of how evolution works which has often been called the "synthetic theory," and sometimes the "Neo-Darwinian theory." Natural selection still serves as its cornerstone, but the mutation theory, Mendelian genetics, and the statistics of population dynamics are almost equally important components of its foundations. The symposia which were held in various parts of the world during the year of the Darwinian centennial, 1959, impressed most of their participants with the degree to which biologists actively working in the field of evolution are agreed on the soundness of this theory. A generation ago, many leading biologists felt that none of the processes which had been invoked to explain evolution was satisfactory and that the true explanation would come with the discovery of some hidden "cause" not then known. Now most biologists agree in believing that the major causes of evolution are known, but that no one of these causes is sufficient in itself. Mutation, genetic recombination, and natural selection are complementary to each other. The task of the future lies chiefly in showing how these processes act in relation to each other and to the changing environments through which the earth has passed and is passing.

SEVEN BASIC POSTULATES

At the Cold Spring Harbor Symposium of 1959, the present writer became so strongly impressed by the solidity and implications of this widespread agreement about the major processes of evolution that he undertook to formulate a series of seven basic postulates which seem to express the extent of the agreement and may serve as solid foundations for future working hypotheses about how the processes of evolution operate. The discussion presented there (Stebbins, 1959b) served as a summary of the symposium, which it concluded, and was therefore illustrated solely with examples taken from that symposium. In the present article, the same postulates will be discussed in a broader fashion, with examples selected from all of the evolutionary literature as most clearly illustrative of the postulate being discussed. One must remember, however, that, in a discussion as brief as the present one must be, only a tiny fraction of the available evidence can be reviewed.

The first basic postulate can serve as a summary of the present introduction, or of the entire discussion. Its validity depends upon that of the other six, so that no particular evidence needs to be cited in its favor. It is stated as follows:

At least in higher animals and plants, evolution proceeds principally as the result of the interaction between four indispensable processes: mutation, gene recombination, natural selection, and isolation.

THE ROLE OF MUTATION AND GENE RECOMBINATION

The next two postulates are stated as follows:

Second, mutation neither directs evolution, as the early evolutionists believed, nor even serves as the immediate source of variability upon which selection may act. It is, rather, a reserve or potential source of variability which serves to replenish the gene pool as it becomes depleted through the action of selection.

Third, the mutations which are most likely to be accepted by selection and so to form the basis of new types of organisms are those which individually have relatively slight effects on the phenotype, and collectively form the basis of polygenic or multiple-factor inheritance.

These two postulates are complementary to each other. Together, they express the conclusion that in sexually reproducing organisms both mutation and genetic recombination are essential contributors to the gene pool. This can be defined as the supply of hereditary variation in a population on which natural selection can act. The existence of a great store of variability in the gene pool is best shown by two types of experimental evidence: first, from experiments with artificial selection and second, from experiments which have uncovered concealed genetic variability by obtaining certain chromosomes or chromosome segments in the homozygous condition.

To understand the meaning of recent experiments with artificial selection, we should first make predictions as to what the limits of selection would be on the basis of two contrasting hypotheses. One hypothesis assumes that the gene pool is very small, so that selection changes populations by increasing the frequency of favorable mutations just as soon as they occur, and cannot be effective unless favorable mutations are constantly occurring at a reasonably high rate. We may call this the hypothesis of *direct selection* of favorable mutations. Either by direct statement or by implication, we can recognize this hypothesis as basic to the thinking of De Vries, Johannsen, Bateson, Morgan, and most geneticists of a generation ago.

The second hypothesis assumes that the gene pool is very large, so that, if a population is placed into a new environment and subjected to selection in a new direction, new gene combinations are sorted out from the supply of genes already present in the gene pool, and selection can be effective for many generations even if no new mutations occur. We can call this the hypothesis of *indirect action,* since it assumes an indirect rather than a direct connection between mutation and selection.

If evolution usually proceeds by direct selection of new mutations, then the limits of selection would be set by the rate of favorable mutations, which is always very low. Selection would change the population for only a very few generations. This assumption was made by De Vries, Bateson, and particularly Johannsen, and was apparently borne out by Johannsen's well-known experiments with the garden bean. On the other hand, if the gene pool of most populations is large and diverse, then selection can be expected to change a population in the same direction for many generations, even if no new mutations occur at all.

Recent selection experiments with corn, *Drosophila,* mice, chickens, and other cross-fertilizing populations of higher plants have consistently shown that such populations are capable of responding to selection for many generations on the basis of the genetic variability stored in them. Two good examples are the Illinois corn experiment and the selection experiments by Mather and his associates for the number of abdominal bristles in *Drosophila.*

The Illinois experiment, described by Woodworth and Jugenheimer (1948), was as follows: In 1895 the agronomists at the University of Illinois decided to find out the number of generations in which they could produce a change in a characteristic by continuous artificial selection, using a cross-fertilizing population of field corn. They selected for four different characteristics—high protein of the kernels, low protein, high oil content of the kernels, and low oil. This experiment was continued for fifty generations; the most recently published results were obtained in 1959 (the experiment was briefly interrupted during the last war). In all four lines the population responded to selection for at least thirty-five generations. In the case of high oil and low protein, a significant change took place in the populations even between the forty-fifth and fiftieth generations. During the experiment, the protein content was more than doubled in the high-protein line and reduced to less than half of the original concentration in the low-protein line. Even greater results were obtained by selecting for high and low oil content. The kernels of the original population contained 4.7 per cent of oil. After fifty generations of selection, the mean oil content in the high line was raised to 15.4 per cent, and in the low line it was lowered to 1.0 per cent.

The facts which we know about mutation rates in corn tell us definitely that the Illinois agronomists must have been sorting out genetic differences which existed in their original population. Since in each line of corn being selected the number of plants raised per generation was between 200 and 300, the total number of plants raised during fifty generations in each line was between 10,000 and 15,000. We do not know the actual rates of mutation for changes in oil or protein content. But the data of Stadler (see Dobzhansky, 1951) on rates of mutation for other characteristics in corn tell us that for a particular characteristic the occurrence of one mutation in 50,000 plants is a relatively rapid rate. Hence the occurrence of even one mutation in the desired direction during the course of the experiment is rather unlikely. The slow, steady way in which the populations responded to selection shows that many genetic differences were being sorted out. Since these differences could not have arisen by mutation during the course of the experiment, they must have existed in the gene pool of the original, unselected, but cross-fertilizing population.

The experiments of Mather and his associates (Mather and Harrison, 1949; Mather, 1955; Breese and Mather, 1957) on selection for high and low number of abdominal bristles in *Drosophila* gave similar results. In these experiments the response to selection was less regular than in corn, and the undesirable secondary effects, particularly the appearance of a high degree of sterility, were more marked. The actual response was in a series of short bursts, lasting five to twenty generations, and separated by intervals of several generations during which no response to selection occurred. Nevertheless, selection was effective even after one hundred generations, and the calculations of Mather and Harrison, like those given above for the corn experiment, show that the response to selection was based upon genetic differences already present in the gene pool of the initial population, rather than mutations occurring during the course of the experiment. Furthermore, Breese and Mather (1957) tested six different marked regions of one chromosome for genes affecting the difference between the line selected for high and that for low bristle number. They found such genes in every region, which suggested that the gene pool contained a very large supply of genes affecting bristle number, at many different loci. Indirect evidence leading to the same conclusion was obtained by Clayton and Robertson (1955), who found that an inbred line of *Drosophila*, which would be expected to contain a smaller gene pool than the crossbred population used by Mather and Harrison, responded very slowly to selection for increased bristle number.

The experiments of Goodale (1937, 1942) and MacArthur (1944) on selection for body size in mice, and those of Lerner (1958) on shank length in chickens have yielded similar results, indicating that large gene pools for various characteristics are normally present in populations of cross-fertilizing higher organisms. The experiments of King (1955) on selection of *Drosophila* for resistance to DDT showed that the gene pool of this fly contains so many genes which affect DDT resistance that, if two lines derived from the same original wild population are kept apart and subjected to simultaneous but independent selection for resistance, they will each acquire a different combination of genes for DDT resistance.

A second type of experiment which has explored the nature of the gene pool is the analysis of hidden variability by artificial inbreeding, usually accompanied by special ways of manipulating the chromosomes so that their role in determining this variability can be understood. Most of these experiments have been conducted on various species of *Drosophila* by Dobzhansky and his associates. They have shown us that natural populations of this fly not only possess a great store of hidden genetic variability, but also that this variability is highly organized. Genetic linkage serves to bind together adaptive combinations of genes on particular chromosome segments. Often the adaptiveness of a particular linked combination depends not entirely upon its own properties but on its interaction with another combination in a different, but homologous, chromosome. Such chromosome segments are said to be co-adapted (Dobzhansky, 1951). A fly containing such pairs of interacting homologous chromosomes has heterosis or hybrid vigor. In many species, the integrity of such combinations is preserved by means of chromosomal rearrangements, particularly inversions of chromosomal segments. The fact that natural selection can increase the frequency of chromosomal rearrangements because of their value in promoting hybrid vigor has been demonstrated experimentally by Dobzhansky and Pavlovsky (1955) and Levine (1955). Furthermore, Levene, Pavlovsky, and Dobzhansky (1958) have shown that this complexity of the gene pool strongly affects the adaptive value of genes. The adaptive value of a gene can increase or decrease not only through changes in the external environment, including the other living organisms with which the population is associated. Even if these factors remain constant, a gene can change markedly in adaptiveness as it becomes associated with different genes during the continuous process of segregation and recombination which goes on in any cross-fertilizing population.

These facts have led Dobzhansky (1955) to the "balance hypothesis" of population structure. According to this hypothesis, adaptiveness is normally maintained through a combination of genes and chromosomal segments kept in the heterozygous condition. Individual genes do not usually respond directly to selection as separate units, but rather their adaptive value depends upon the way in which they contribute to the gene pool. Large numbers of genes are thus kept in the germ plasm because their effects are neutral or actually beneficial in heterozygous combinations with other alleles, when these same genes would be strongly disadvantageous or actually lethal if they were present in the homozygous, or "pure," condition.

The experiments of modern population genetics, therefore, tell us that natural selection acts indirectly upon a spectrum of variability generated largely by genetic recombination which takes place in a very complex fashion. Mutation serves to replenish the store of variability as it becomes depleted through selection. Most of the genes which enable a population to change in response to a new environment are not newcomers which have recently appeared through mutation; they are "old-timers" which presumably originated by mutation many generations ago and have been preserved either as hidden recessives or as contributors to some past adaptive complex.

This principle does not mean that genes with large effects on the appearance of the individual never play an important role in evolution. On the contrary, some of the most striking demonstrations of the action of natural selection which have been made in recent years have involved such genes. The most striking example is industrial melanism. In the industrial areas of Europe, populations of moths have become completely transformed in a few years from light- to dark-colored types through selection of dominant mutations for dark color. The experiments of Kettlewell (1955) have shown conclusively that these changes were the result of natural selection and have told us much about how selection has acted. In other examples, resistance of insects to insecticides has been shown to result largely from the selection of single mutations with large effects (Dobzhansky, 1951).

In plants, genetic information recently obtained about the columbine, *Aquilegia* (Prazmo, 1960), suggests that the distinctive features of its flower were originally acquired through the cccurrence and establishment of a single gene with large effects. The columbine differs from all of its relatives in that its petals bear long spurs containing nectar. This serves to attract animal pollinators, which may be bumblebees, hawk moths, or hummingbirds, depending upon the species of columbine. The related genera all have white flowers without spurs and are pollinated by various kinds of insects. A single species of *Aquilegia* closely related to the columbine, but without spurs on its petals, is found in eastern Asia. When this species was crossed with the common European columbine, the spur of the latter was found to be determined by a single dominant gene, although many different genes affected its length. We can suppose, therefore, that the new direction of evolution, which started long ago in the columbine genus and evolved species having flowers with a variety of shapes, sizes, colors, and spur lengths, was originally triggered off by the establishment in a population of a single mutation with a conspicuous and highly adaptive effect.

THE POSITIVE EFFECT OF NATURAL SELECTION

The fourth basic postulate is stated as follows:

The role of natural selection is much more than the purely negative one of eliminating unfit types. By greatly increasing the frequency of gene combinations which otherwise have a very low chance of appearing, selection has an esssentially creative and progressive effect.

The experiments on the genetic structure of populations which have already been reviewed can themselves be regarded as strong evidence in favor of this postulate. Even more striking evidence has recently been obtained from experimental studies of mimicry in butterflies. The phenomenon of mimicry, or resemblance in outward appearance between a distasteful or harmful species and an unrelated, harmless species, was used even in Darwin's day as evidence for the power of natural selection. Although some biologists in more recent times have been skeptical of the existence of this phenomenon, the recent experiments of Brower (1958a, b, c) have established its validity beyond reasonable doubt. She offered specimens of the distasteful monarch butterfly to jays under carefully controlled conditions and showed that birds "trained" to avoid the monarch butterflies would also refuse to eat its mimic, the viceroy, although this butterfly was shown to be completely palatable to birds.

Sheppard (1959) has recently studied the genetic basis of mimicry in African butterflies of the swallowtail genus *(Papilio)* by extensive hybridization between the different mimicking forms which occur in a single species *(P. dardanus)*, as well as crosses between mimetic and non-mimetic forms. These studies have shown clearly that mimetic forms will become more common and their mimicry will become more perfect in regions where the distasteful models are the most frequent. Where models are rare, mimicry is imperfect and variable within the same population, while in regions where the distasteful species is absent, the species consists entirely of non-mimetic forms. Crosses between mimetic and non-mimetic forms show that the general features of the mimetic pattern are determined by a single gene with a large effect, but that perfection of the mimicry is brought about by the action of many modifying genes, each with a small effect. In *Papilio dardanus* of central Africa there exist half a dozen or more different mimetic forms, each of which mimics a different species or subspecies of distasteful butterfly, with three different genera represented among the models. The different mimetic races are all determined by different allelomorphic genes at a single locus, with each of these major or "switch" genes giving the butterfly a superficial resemblance to a particular model. In regions where the model is abundant, the "switch" gene responsible for mimicry of that model has gathered around itself a collection of modifiers at many different loci, which have perfected the resemblance between mimic and model to a remarkable degree. The evolution of mimicry in these butterflies has, therefore, been brought about by natural selection of many different genetic changes, some with large and others with small effects. These have all been brought together into a harmonious combination which adapts the population to a special situation (i.e., the presence of a particular distasteful model). There is good reason to believe that this type of progressive action of natural selection on a number of highly specific genetic changes has been responsible for all of the extraordinary adaptations found in nature, such as the remarkable shapes and color patterns of such flowers as orchids and milkweeds, the unbelievably complex instincts of such animals as spiders and solitary wasps, and the social behavior of bees, ants, and primitive men.

The Origin of Species

The fifth and sixth basic postulates of the modern synthetic theory of the causes of evolution concern the problem of the origin of species:

Fifth, the continued separation of new adaptive lines of evolution from related lines with different adaptations requires the origin of barriers of reproductive isolation, preventing or greatly restricting gene flow between them. This separation is essential for maintaining the diversity of adaptations which exists in any one habitat, and so should be regarded as the basis of species formation.

Sixth, the origin of reproductive isolation, like that of new adaptive types, requires the establishment of many new genetic changes, including structural alterations of the chromosomes and cytoplasmic changes as well as gene mutations.

These two postulates place the origin of species on a different level from the origin of different adaptations or races of a single species. Both processes are based upon natural selection of genetic differences, but for the origin of species natural selection must sort out differences of a very special kind. These affect the behavior of a population toward certain specific related populations rather than its adaptation to the environment as a whole.

A recent symposium on the species problem (Mayr, 1957) has shown us that the problem of the nature and origin of species is by no means solved and that divergent opinions exist both as to what species are and how they came into being. Nevertheless, a large array of facts obtained from a great variety of experiments tells us that species are distinct from each other chiefly because they are separated by barriers which restrict or prevent gene exchange between populations.

The basic importance of reproductive isolation in maintaining adaptive diversity within a community of organisms is evident from the widespread occurrence of two phenomena which have been much studied in recent years, hybridization and character displacement. If two related populations which have been isolated from each other in different habitats are permitted by environmental changes to come together, then their subsequent evolution will depend upon the degree of reproductive isolation which has developed between them. If they are still able to cross and produce fertile hybrids, the result of their contact will be the production of an intermediate, hybrid swarm, in which the identity of the original populations will become lost to a greater or lesser degree. Numerous examples of this can be cited, particularly in higher plants (Stebbins, 1950, 1959a). On the other hand, if their ability to intercross and produce fertile hybrids is so much reduced that each population can maintain intact its own adaptive properties, then the populations will tend to compete with each other. Since direct competition tends to destroy reproductive capacity, natural selection will favor genotypes of each population which are as differently adapted as possible from the norm of the competing population and so will cause the two populations to diverge from each other. Lack (1947) has shown that in the finches of the Galapagos Islands, a race of a particular species, if it is the sole occupant of a particular island, will have a rather wide and generalized range of variation. Another race of the same species, which on a different island is sharing its habitat with a distinct but related species, will have a narrower and more specialized range of variation. This phenomenon, known as character displacement, is also described in ants by Brown and Wilson (1956), who review additional examples in birds.

The diversity and genetic complexity of reproductive isolating barriers are evident from a great wealth of observational and experimental evidence, which is summarized in part by Stebbins (1950), Dobzhansky (1951), and Mayr (1957). If all of the barriers separating two related species are studied, they are found to be of various sorts, and any two species are usually isolated by many different kinds of barriers. Sometimes the species can be easily hybridized artificially, and fertile offspring can be raised under human supervision, but they nevertheless fail to hybridize in nature because of differences in their breeding seasons, mating instincts, or similar factors. The distinctness of various species of pines in California is of this nature (Stebbins, 1950), as is also the separation of the mallard from the pintail duck. In other instances, as in the wild rye *(Elymus)* genus of grasses and its relatives (Stebbins, 1959a), natural hybrids are common, but they are so sterile that they rarely, or never, reproduce. More common, however, are examples in which two related species are separated from each other by a variety of barriers. A classic example is *Drosophila pseudoobscura* and *D. persimilis,* which are separated by different temperature requirements for maximum sexual activity, an instinctive tendency for females to mate with males of their own species, sterility of F_1 hybrids (which is complete in the male sex), and weakness or sterility of backcross progeny from the partly fertile F_1 females (Dobzhansky, 1951).

We can also see how diverse and complex the reproductive isolating barriers between two species can be by crossing two related species many different times, using as parents different races of the same pair of species. Such experiments have been performed in *Drosophila* (Dobzhansky, 1951) and various groups of higher plants, such as the tarweeds, *Madiae* (Clausen, 1951); the phlox family, *Polemoniaceae* (Grant, 1957); and the grasses (Stebbins and Vaarama, 1954). In each example, the same kind of result has been obtained. Both the ease of crossing and the fertility of the F_1 hybrid differ greatly depending upon the particular parental strains used. Any widespread species contains a great store of genetic variability, including not only genes which affect the adaptation of the population to its environment, but also those which help or hinder the ability of a species to cross and exchange genes with individuals of another species.

The genetic complexity of reproductive isolating mechanisms is shown by studies of segregation for fertility in later generations of hybrids between partly interfertile species. Two good examples are the hybrid between *Galeopsis getrahit* and *G. bifida,* of the mint family, analyzed by Müntzing (Stebbins, 1950, p. 231), and that between *Drosophila pseudoobscura* and *D. persimilis* (Dobzhansky, 1951). In both examples segregation was very complex, and indicated that many different gene pairs were contributing to the sterility barrier. Less complete data from many other crosses point in the same direction. The inability of two species to cross and form fertile hybrids is not acquired through the appearance of one or two mutations with profound effects. Like other differences between races and species, it is built up gradually through the accumulation of many genetic differences, each one with a small effect.

The ways in which natural selection can build up reproductive-isolating barriers are by no means fully understood, but evidence concerning them is accumulating. For instance, in both frogs (Moore, 1957) and fishes (Minamori, 1957), races of the same species which are adapted to growth under different optimal temperature conditions may produce abnormal embryos when crossed with each other. This is apparently the result of disharmony in interaction between genes controlling different rates and temperature optima of embryonic growth.

In plants, the sterility of interspecific hybrids is often due largely to differences between the parental species in chromosomal structure (Stebbins, 1950, 1958). Within certain species, such as *Trillium kamschaticum* (Kurabayashi, 1958), special cytological techniques have revealed many differences between both individuals and races in respect to small details of chromosome structure. These differences are partly correlated with both the climatic features of the present environment in northern Japan, where the species is common, and with the geological history of that region. Since chromosomal diversity in this species runs parallel with diversity in morphological characteristics, we can suspect that natural selection has operated in similar ways to bring about both kinds of differences. Although the chromosomal differences between the races of this particular species of *Trillium* are not great enough to cause hybrids between races to be sterile, the related species of *Trillium* differ from *T. kamschaticum* in respect to more numerous chromosomal differences of the same kind. Furthermore, although hybrids between diploid species of *Trillium* are not known, a wealth of evidence from hybrids between species in other plant genera (Stebbins, 1950, 1958, 1959a) shows that chromosomal differences such as those which exist between the diploid species of *Trillium* can be responsible for hybrid sterility. Furthermore, this sterility can be overcome by doubling the chromosome number. This places together in the same hybrid nucleus duplicate sets of chromosomes, which are consequently able to pair normally and produce viable gametes.

Once reproductive isolating barriers have arisen, they can be strengthened and reinforced by natural selection which favors those individuals of a species having an instinctive tendency to mate with others of their own species. This process has been fully discussed by Dobzhansky (1951, 1958).

A final way in which species-separating barriers can be formed is as a secondary result of hybridization between preexisting species. The process of amphiploidy, or the production of fertile, true-breeding species by doubling the chromosome number of sterile hybrids, is now well known to geneticists, and numerous examples have been described, both in the garden and in nature (Stebbins, 1950, 1959a). In addition, more recent experiments have shown that highly sterile, though slightly fertile interspecific hybrids can produce more fertile offspring in later generations without change in chromosome number. Furthermore, some of the fully fertile strains which can be bred from such offspring may form partly sterile hybrids when crossed with either of the original parental species (Stebbins, 1959a). This is apparently brought about by the effects of genetic recombination, which in rare instances may build up a new harmonious recombination of those genetic differences which were responsible for the original sterility barrier.

Half a century ago, many evolutionists believed that the critical experiment which would demonstrate our understanding of evolutionary processes would be the production under controlled conditions of a new species. This they defined as a population which would breed true and would be reproductively isolated by hybrid inviability or sterility from all other pre-existing populations. Amphiploids, or doubled hybrids, fulfill this qualification in every respect, and the partially isolated segregates with unchanged chromosome number which have been produced in *Elymus, Nicotiana*, and *Delphinium* come close to it. While the former constitute a special type, rare or lacking in the animal kingdom, segregates of the latter type might be expected in all types of organisms. Furthermore, since partial sterility is found in many hybrids between different races of the same animal species, the origin of new species from such hybrids would require the addition of only a few mutations to the extreme segregants which gene recombination can produce in the progeny of such hybrids. The origin of species, one of the most crucial steps in evolution, is well on the way to becoming understood.

The Major Trends of Evolution

The seventh and final basic postulate about evolutionary processes is as follows: The origin of genera and other higher categories, as well as the longtime trends which have given rise to increasingly complex and highly organized forms of life, results from the continuation into geologic spans of time of the processes responsible for evolution on the racial and species level. The only new element which must be considered is the increasingly evident extinction of populations intermediate between the successful lines.

The first type of evidence in favor of this postulate is the fact that some of the same kinds of differences which in one group of organisms may form the distinction between genera, or even families, can in a related group exist as differences between species of the same genus or even between races of the same species. This has been illustrated elsewhere for the grass family (Stebbins, 1956).

Even more convincing evidence has been obtained from careful studies of fossil lineages, particularly in mammals. This evidence is carefully reviewed by Simpson (1953, 1960). He has shown that the earliest representatives of lines which led eventually to very different kinds of animals were so much alike that they would unquestionably be placed in the same group if their descendants were not known. For instance, ancestral lineages of the modern horse, rhinoceros, and the Biblical cony *(Hyrax)* can all be traced back through a succession of fossil forms to the Eocene period, fifty to sixty million years ago. At this period, these lineages have converged to such an extent that the forms representing them are much alike in size, shape, head form, and tooth structure. Furthermore, the different representatives of the same lineage which followed immediately after each other in time were usually so much alike that they could easily be visualized as having evolved through the accumulation of many relatively small genetic differences.

To be sure, many examples are known in which a new type of animal or plant appears suddenly and seems to be completely separate in respect to many large differences from any earlier fossil form. To explain these apparent saltations Simpson assumes that the fossil record contains many highly significant gaps. Furthermore, both his evidence and logical arguments suggest strongly that those conditions which would be most likely to bring about the origin of a new major adaptive complex and hence a new higher category would also be most likely to produce gaps in the fossil record. Organisms which exist as large populations in a stable environment have the greatest chance of being preserved as fossils, but are the least likely to give rise to new adaptive types. New departures in evolution are most likely to occur when a system of relatively small populations, partly isolated from each other, is evolving in a rapidly changing environment. This combination of conditions is perhaps more unfavorable than any other for preserving such forms as fossils.

If, as Simpson believes, apparent saltations are produced by a combination of rapid evolution plus unfavorable conditions for fossilization, then those groups with the poorest fossil record should have the largest number of apparent saltations, and the improvement of our knowledge of the fossil record should progressively fill in the gaps. Recent progress in fossil discovery has shown this to be true in a striking fashion. In particular, the fossil history of man, which a generation ago had to be interpreted on the basis of fragments which could almost have been counted on the fingers of one's hands, now is illustrated by a variety of prehuman types, many of which are represented by a considerable number of individual fossils. As Le Gros Clark (1959) has emphasized, these new finds have definitely filled in some of the gaps. They have made it highly probable that the fossil primates which are waiting to be unearthed will eventually give us a continuous sequence extending from the ape- or monkey-like common ancestor which existed thirty or forty million years ago up to modern man.

SOME THOUGHTS ON AN EVOLUTIONARY PHILOSOPHY

This discussion will close with some thoughts on how our present knowledge of evolution could affect our philosophy of life. The point of view adopted here is entirely personal, and I make no apologies for it. The facts upon which it is based are derived from a variety of sources, and most of the ideas have already been expressed by a number of other writers.

When we apply the concepts of evolution to our own past, we quickly realize that man is the product of two different kinds of evolution. Our bodies have evolved in the same way as those of other mammals, particularly primates. As mentioned above, the fossil record of man's ancestors is gradually being laid bare. We now can reconstruct with some assurance the way in which our ancestors first started to walk erect, to use tools and fire, and to hunt game in groups or primitive societies. We are sure that the size of the human brain increased gradually, as did also man's ability to make better tools. If, therefore, we consider only our bodies, we must conclude that we are no more than large apes that walk erect and have unusually large brains.

But our present way of life does not depend only upon our bodies and our brain power. Our minds and our social organization contribute far more to human nature than our bodies. Furthermore, our minds and social behavior, although based upon the foundation of our biological, genetic heredity, must nevertheless be reconstructed in each generation by learning. From our parents, our teachers, and from the leaders of our society we acquire a vast store of cultural heredity, which has been built up slowly and carefully by the thousands of generations of men who have preceded us. It is upon this heritage that our present way of life depends. When men first began to make tools, wear clothes, build shelters, and talk to each other, they set in motion a new kind of evolution, which we call socio-cultural evolution. Although built upon the foundations of organic evolution, socio-cultural evolution follows new directions and is governed by new principles. The familiar biological processes of mutation and genetic recombination are replaced by invention, learning, and cultural spread, or diffusion. Selection exists in socio-cultural evolution, but it makes progress through differential survival of customs and inventions rather than of men. It is thus radically different from the natural selection which guides organic evolution.

Finally, cultural evolution produces its effects in an entirely new way. Through organic evolution, organisms became modified to suit their environment; socio-cultural evolution enables man to modify the environment to suit his own needs. Animals became adapted to cold climates by developing fur; man, by building furnaces or by borrowing fur from animals. Birds became able to fly by growing wings and profoundly modifying their bodies; we fly infinitely higher and faster by elaborately designed machines, which even transport a bit of low-level, warm, temperate climate many miles above the earth.

Most important, organic evolution is opportunistic in direction. It is governed by the chance combination of environmental factors and the types of organisms which happen to exist at any one time. Socio-cultural evolution, on the other hand, is determined at least in part by man's own foresight and his ability to conceive of a better way of life for himself and his descendants.

We cannot overemphasize the fact that socio-cultural evolution is totally new in quality and has made man qualitatively different from all animals. This is true in spite of the fact that its beginning depended largely upon quantitative increases in brain power, and that in particular mental characteristics, like the ability to learn, memorize, and communicate with each other, we differ only in degree from the more intelligent kinds of apes. One of the most important facts about all of evolution is that from time to time new qualities emerge through more complex organization of simpler substances and systems. On the chemical level, we see this in many compounds which have properties very different from the chemical elements and simpler compounds of which they are built. The properties of salt and the elasticity of rubber are examples. Life itself differs from non-living matter only in having a special type of very complex organization. Since the dominant theme of cultural evolution has also been increasing complexity of organization, one need not be surprised that it has generated entirely new qualities. Our minds, our foresight, and our social structure, although they are the products of evolution, are nevertheless completely real and new. They set us apart from animals just as truly as if they had been specially created.

Another important fact about socio-cultural evolution is that it progressed for a very long time through traditions and learning which were passed down to each successive generation by word of mouth, without benefit of writing. Men have been able to speak to each other for at least five hundred thousand years; they have had brains as highly developed as ours for at least seventy-five thousand years; they have had such spiritual beliefs as that in an afterlife for at least fifty thousand years, as witnessed by ancient graves which include implements for use in the world to come. But writing as a means of perpetuating tradition is barely six thousand years old. Now everything we know about modern peoples who are not, or were not, able to write leads us to believe that among them reason dominates only the immediate events of their lives. Their social structure and their plans for the future are bound up in their emotions and are passed on from generation to generation by spoken rules, stories, chants, poems, and incantations, surrounded with the symbols of religious worship. We do not know how religion began, but we can be sure that it has guided man's evolution for at least a hundred thousand years. Before the advent of writing, the stability of society depended upon the ability of children to learn from their elders the spoken word, and this was developed largely through the force which the symbols of religion gave to certain essential moral precepts. The ability to receive these words and to accept these precepts must, therefore, have had as high a selective value in primitive society as any other characteristic. Spiritual qualities must have been essential to the earliest rational men. Consequently, we must think of man as basically spiritual, regardless of whether we believe that religion was given to him by a supernatural supreme being, or whether, as I believe, we consider that it evolved through the socio-cultural process. The ability of men to put their ideas into writing, thus rendering them much more precise and constant, has enabled us to substitute rational thinking for many of the superstitions of the older religions, and we have not reached the end of this process. Nevertheless, the ties which bind us to our traditional heritage, which enable us to work together, and which stimulate our dreams for the future are still made up largely of emotional and spiritual attachments, and the experience of those nations which have attempted to sever them and substitute purportedly rationalistic philosophies like Marxism have emphasized sharply for us the dangers of such a course.

Hence to the questions, "Why am I here?" and "What is the meaning of life?" I give these answers: Whatever mind or spirit that I possess, as well as the comforts of the civilization in which I live, has been given to me by the work, care, and ideals of my own parents and teachers, their parents and teachers, and so on back through the ages. I owe to them an immense debt, which I can repay only through following their examples, and, like them, learning how to work with my fellow men and to develop ideals and dreams which I can pass on to future generations. And because I believe that human progress has been shaped in the past not by the unalterable will of an inscrutable supreme being, but by the hopes, ideals, and working together of men and women like ourselves, I can hope that whatever I do that is of worth will make the world better for future generations than it would have been if I had not made the effort. This is the greatest satisfaction for which I can hope in either the present life or any conceivable future existence.

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IN THIS PAPER ON HUMAN EVOLUTION I want to stress the biological history of those qualities which are really most distinctive of man as an animal. The most important thing about man is the way he behaves. Every man knows that man is an intelligent animal. Man's ability to make and use tools and his ability to make and use symbols for communication are historically the most important accomplishments leading to his present level of intelligent behavior. These abilities have a biological basis. Also, they go beyond that basis. The fact that man does communicate with symbols makes man different from everything else on earth.

This uniqueness has to do with symbols and their modes of reproduction and inheritance. Symbolic reproduction and symbolic inheritance depend on events that occur in the central nervous systems of two or more individuals and not on events that occur in gonads. We say communication takes place when a signal produced by the sender alters the behavior of the receiver. But communication is called symboling when the signal has very special properties. As Langer (1942, p. 49) said, "Symbols are not proxy for their objects, but are *vehicles for the conception of objects.* To conceive a thing or a situation is not the same thing as to 'react toward it' overtly, or to be aware of its presence. In talking *about* things we have conceptions of them, not the things themselves; and *it is the conceptions, not the things,* that symbols directly 'mean.' Behavior towards conceptions is what words normally evoke; this is the typical process of thinking."

Symbols are inherited in a different way than genes. It is an unalterable biological law that new individuals (zygotes) must inherit their genes—specific pieces of deoxyribonucleic acid molecules—from other individuals that existed in the past. The inheritance of symbols differs in kind. A grandfather may take over and use, or misuse, symbols from his grandson. A son gets his genes from his parents and from no one else, but he may get his symbols from any source he contacts, whether older or younger, related or unrelated genetically. A descendant is stuck with the genes he gets from his ancestors. A symboling animal, in the following sense, is time free. A grandfather cannot inherit genes from his grandson; he can learn (culturally inherit) symbols from his grandson.

Man's ability to symbol and to make and to use tools after a fixed and set style has a basis in his body. Students of human evolution used to think man acquired his present biological shape before he got his ability to use tools and to symbol. We now have direct evidence that the presumable Pleistocene ancestors of man made and used tools in the daily economy of life before they developed a shape that most of us would recognize as near kin. The hard facts of the fossil record may be interpreted to say that near-man gained one of his human-like attributes, tool use, before he had his contemporary physiognomy.

The historical record of tool use is much clearer than the record of the ability to symbol. We know we have it now; we must infer how far back we can push it in the past. It is quite possible that the history of tool use may tell us something about the history of symboling. Kroeber, Pumphrey, and Haldane (see Haldane, 1955) independently suggested the origin of symboling probably was coincidental with the technological revolution of the Upper Paleolithic. During the Lower Paleolithic, the patterns of tool manufacture were remarkably stable over some 400,000 years. Starting with the Upper Paleolithic, say 35,000 B.C., there was great diversity in the patterns of tool manufacture, along with regional styles of tool types, over relatively short periods of time. This we know from archeology. And from linguistics and ethnology, we know the natural history of symboling is characterized by comparatively rapid rates of change. So it is plausible to assume that the symboling revolution took place at the same time as the tool-making revolution of the Upper Paleolithic.

Now, in order for us to make a jump between a communicating animal and a symboling animal, I have to describe some of the fossil skulls in a time sequence illustrating the phylogeny from Miocene ape to modern man. I will also list some seven biological changes which illustrate some of the evolutionary paths leading from our ancestors who neither used tools nor symboled to our ancestors who did both.

I will describe illustrations of some morphological features of four primate genera which are passable candidates for being on the main line of human evolution. I am not going to discuss the bony bumps and ridges over which the specialists love to quibble, but rather, I want to stress the general evolutionary changes on which most anthropologists agree. And I will emphasize changes which correlate with differences in behavior (see also Washburn and Avis, 1958).

Before discussing the fossils, I should mention that I will use the term "hominid" to refer to the taxonomic family which includes modern man and his ancestors as far back as they were separate from the pongid family. I will use the term "hominoid" to refer to the superfamily which includes the pongids and the hominids, that is, the superfamily which includes both man and the apes, living or fossil. I will try to restrict the term "man" to members of the genus *Homo,* but I, as others, may be inconsistent and use "man" to refer to any member of the hominid line.

Now let us look at the representatives of the four known genera (see Le Gros Clark, 1955, 1959; and Howells, 1959, for more extended accounts).

REPRESENTATIVES OF THE KNOWN GENERA

1. PROCONSUL

Proconsul was one of the Early Miocene apes who lived along the shores of Lake Victoria in East Africa about twenty-five million years ago. This is the earliest ape whose skull is well known from the fossil record. The work of Le Gros Clark and Leakey (1951) and others tells us something about the rest of the *Proconsul* body. The members of the species we are considering, *Proconsul africanus,* were animals about the size of a big baboon or a rather large dog. They ran on four feet, but they were also skillful in climbing trees and perhaps occasionally stood semierect on their hind feet.

I am going to assume that *Proconsul* was an ape, that is, a member of the pongid family along with the living great apes—the gibbon, chimpanzee, orangutan, and gorilla—and the fossil apes like *Dryopithecus.* The apes are sufficiently diverse in morphology to warrant their placement in three subfamilies: *(a)* the hylobatine for the gibbons with a history back to the Oligocene; *(b)* the proconsuline; and *(c)* the pongine for the living great apes and their ancestors, like *Sivapithecus* and *Dryopithecus,* back to the Miocene.

The proconsulines lack certain specialized features of the pongines. Their teeth are more primitive, they have no simian shelf uniting on the inside of the two halves of the lower jaw, they lack the large brow ridges of the living great apes, and their trunk and limbs retain features of a generalized quadrupedal primate rather than the specialized features of the arboreal pongines. *Proconsul* offers the best evidence now available as to what our Miocene ancestors may have looked like. It is almost certain—as certain as a negative can be—that they did not manufacture tools and that they did not symbol.

2. Middle Miocene to Pliocene Hominoids

Lack of recovered fossils forces us to leave a blank, or several blanks, for genera representing a period of some twenty-four million years in the hominid branch of hominoid phylogeny. Young students who wish to make paleontological history might well look for representatives of these genera. If hominoid genera evolved at the same rate as equine genera in the Miocene and Pliocene, we may hope to find at least three now unknown genera in the hominid phyletic line. Unfortunately fossiliferous Pliocene deposits are rare in Africa, which is the most promising place to look.

Hürzeler (1958) and some other investigators insist that *Oreopithecus* fills one of the Pliocene blanks. Thanks to Hürzeler, we now have a much flattened but almost complete skeleton of *Oreopithecus* from the Pliocene lignite deposits of Tuscany in central Italy. When this 1958 find is fully described, we will have a better idea of its phylogenetic placement than was possible on the basis of the fragmentary upper and lower jaws recovered in the last century. In the meantime, I must report that the phylogenetic placement of this most interesting hominoid is uncertain.

3. AUSTRALOPITHECUS

These hominids of the Lower Pleistocene are especially noteworthy for our purposes because they *(a)* had upright, or at least, nearly upright, posture and moved on their two hind feet; and *(b)* because they exhibit the earliest evidence of tool manufacture by primates. These now fully authenticated locomotor and manipulatory activities are all the more interesting because the australopithecines had brains only one-third the volume of that of modern man.

These South African near-men are known from hundreds of excellent fossil specimens from four sites in the Transvaal and one site in Bechuanaland. There is no reasonable doubt that the australopithecines are hominids and not pongids. They do not look exactly like modern man, but there is no reason to expect that they should.

The geographical distribution of *Australopithecus* includes East as well as South Africa and perhaps extends to southeastern Asia. A jaw fragment from near Lake Eyasi in northern Tanganyika is of *Australopithecus* type, and the mandibular fragments called *Meganthropus* from the Lower Pleistocene of Java are placed in the australopithecine group by some authorities.

The newest member of this group was discovered on July 17, 1959, by Mary and Louis Leakey They recovered a skull and shinbone of a young adult male in the Lower Pleistocene beds of Olduvai Gorge in Tanganyika. These fossils, called *Zinjanthropus* by Dr. Leakey (1959) are of the general australopithecine sort.

4. PITHECANTHROPUS

From the neck down, the members of the genus *Pithecanthropus* were very like ourselves, and like us, they were tool makers, fire users, and meat eaters. From the neck up, they differed from us in having smaller brains and larger jaws. These hominids were sufficiently like modern man in their skeletal morphology that some students assign them to an extinct species within the genus *Homo*.

Pithecanthropus had a wide distribution in the Old World. Two forms, Djetis and Trinil, are from Java, and one form, Choukoutien or Peiping, is from northeastern China. Peiping man is known from the skeletal parts of more than thirty individuals and Java man from those of several individuals. Many students assign the three lower jaws and the parietal bone of Ternifine man, from a site southeast of Oran in Algeria, to *Pithecanthropus*. All the specimens of *Pithecanthropus* are of Middle Pleistocene age.

5. HOMO

By the second half of the Middle Pleistocene, we have the earliest known members of the genus *Homo* represented by such forms as Steinheim and Fontéchevade. During the Upper Pleistocene, representatives of *Homo* were widespread in Europe, Africa, and Asia. The Neanderthals, Solo, Boskop, and Cro-Magnon peoples may be mentioned as examples. These populations were rather similar to our own in general morphology, and, judging from their implements for hunting and domestic use, their way of life was rather similar to that of some of the hunting and gathering peoples who survived into historic times. Everyone agrees that some, if not all, members of the genus *Homo* have culture.

SEVEN BIOLOGICAL CONDITIONS

This sequence of four known genera gives us an outline for discussion of seven biological topics which indicate some of the general preconditions for the beginning of culture (Spuhler, 1959). They are:

1. Accommodative vision
2. Bipedal locomotion
3. Manipulation

4. Carnivorous-omnivorous diet
5. Cortical control of sexual behavior
6. Systematic symbolic vocal communication
7. Expansion of the cerebral cortex

I do not mean to imply that these seven conditions alone changed a population of apes something like *Proconsul* into a population of men something like *Homo*. Compared to the average effect of single gene substitutions, the biological changes exemplified by these conditions are probably to be measured on a larger scale. The conditions do not represent unit mutations, although mutation is the ultimate source of the genetic variation in each condition. Some of the conditions involve change in function and arrangement of pre-existing parts. The order of listing is not strictly chronological nor is it strictly phylogenetic. Evolutionary changes in some of the seven conditions were interdependent and roughly synchronous.

We will now consider the seven conditions in the order listed above. At several points, our consideration will be helped by the introduction of comparative material based on observation on the living, higher primates.

1. ACCOMMODATIVE VISION

By early Miocene time, twenty-five million years ago, vision had long been established as the primary discriminative sense in the higher primates. Of course, vision has been an important sense in vertebrates as far back as we know them. It provides data on the position, size, shape, texture, color, and velocity of objects at a distance. Vision makes possible the great goal-oriented mobility of vertebrates in pursuit of food and in protection from enemies. The most complex vertebrates, birds and mammals, interact with their external environment predominantly by information which enters via the eyes, goes to visual centers in the brain, and then triggers the action of the motor organs.

Of course the sense of smell is also an important way of knowing about the external environment. The ability to receive and act upon information about the type and intensity of smell from an external object is part of the explanation for the early success of the mammals. Proper reception of information about the smell of a dangerous or attractive object does not require that the head be turned in a proper direction. Mammals can smell in any direction where molecules are diffused through the air. Even when asleep we can smell smoke before seeing the flame. The amount of trade-goods all peoples spend on odorants and deodorants testifies to the continued importance of the sense of smell in our mammalian heritage. But vision is relatively much more important; contrast the handicap of not being able to smell with that of not being able to see.

Some of you may wonder why, if in fact the olfactory sense is of diminished importance in hominids, man has such a large external nose. Man, indeed, does have a large external nose. It is one of the ways you can tell your human friends from your simian friends.

Historically it is correct to call our nose a "nose." Functionally it would be more correct to call it a "respirator." Our nose is the only peripheral organ of smell we have, but only a small part of it is directly concerned with the sense of smell. Its business part is really the inside surface area, which is a little larger than a dollar bill. Most of this area functions primarily for respiratory purposes. The total area of the olfactory end organ is about that of a dime.

Man has retained a large nasal area for respiratory and olfactory use. The external nose was left sticking out in front of the face for rather complex reasons having to do with the expansion of the cranial part of the skull along with the contraction of the muzzle or the smelling, feeding, and breathing part of the skull. And as we will see, the position of the face and jaws with reference to the cranium changed when man's ancestors acquired upright, bipedal posture and locomotion.

There is not time to go into a full comparative inventory of the primate senses. The sense of hearing is of obvious importance in human behavior. For example, it is more difficult to socialize and enculturate a deaf child than a blind child. But aside from some differences in auditory range, the acoustic sense of higher primates and many other mammals is much the same, whereas the visual sense of the higher primates has undergone considerable evolutionary change.

Under selective influence of the arboreal habitat, primate vision became predominant and was perfected into a leading sense. If we compare Eocene primates and other early mammals with contemporary primates, we see that the position of the eyes in the head has changed. They have moved from a side position to a front position. The arrangement with both eyes on the front aspect permits an overlap in the fields of vision. Both eyes inspect a common section of the external world, and thus binocular vision and depth perception is possible. The loss in ability to see out of the sides of the head was more than compensated for by the ability to see in depth from the front of a head mounted on a movable neck. It was further compensated for by having several individuals look—as a social group.

We can understand the real significance of these anatomical shiftings by comparing the optic chiasma of side-looking and forward-looking mammals. In man, about 40 per cent of the nerve fibers from the retina do not cross over at the optic chiasma. In most non-primate mammals, nearly all of the optic fibers cross over. This means that the functional representations of the retinas of both eyes are transmitted to the same cortical hemisphere in man, whereas in many mammals the right visual cortex does not know what the right retina is "seeing," and the left visual cortex does not know what the left retina is "seeing." Seemingly there is an integrative advantage in having the visual representations of both eyes projected to the same area of the brain, or, in fact, to duplicate areas of the brain.

Visual behavior is one of the key differences between the nocturnal prosimians (lemurs, etc.), who are mostly solitary or go about in pairs, and the diurnal, more social monkeys and apes. This difference between the prosimians and the *Anthropoidea* is perhaps the largest gap in non-human primate social behavior. With arboreal, sitting-up, or upright posture, vision in the monkeys and apes gained a fine association with manipulation. In a moment we will see it become *super-vision*—a guide and control of expert manipulation.

The relationship between the evolution of binocular vision with good depth perception and fine manipulation goes both ways. As Polyak (1957) wrote: ". . . vision itself [in the monkeys and apes] became more refined and the intellectual absorption and mental utilization more complete and lasting, as the skilled movements became more complex and more efficient." This system of two-or-more-way causation is of general importance. Upright, bipedal locomotion freed the hands for manipulation and helped to establish full eye-hand coordination.

2. Bipedal Locomotion

We do not know for certain whether man's ancestors were brachiators before they became bipedal. The question is still open. We lack the needed fossil evidence from the Miocene and Pliocene periods. The presumptive evidence from comparison of living forms can never be conclusive on this problem, as the evidence is without time depth.

I agree with Gregory, Washburn, and others that brachiation was most probably a feature of man's biological history. Those who oppose this view tend to put too much stress on the often misunderstood "rule" that evolution is irreversible. This rule is properly applied when a paleontologist asserts he can tell a fossil whale, or a fossil marine reptile, from a fossil fish, although all of them are streamlined for marine life; it is misapplied when a comparative anatomist asserts man could not be descended from a brachiator because, for example, the long flexor tendon of the thumb is present in man but absent in certain brachiating pongids.

On the most elementary level, all morphological variation is explainable (the environments being specified) in terms of gene mutations. The presence and absence of certain muscles and their tendons have been shown to be under fairly simple gene control in human populations (Spuhler, 1951). The phenomenon of reverse mutation is well established in experimental organisms. I see no theoretical difficulty in the assumption that a population of Miocene or Pliocene apes under a set of selective pressures where 99 per cent lacked a long flexor tendon of the thumb could be ancestral to a later population of hominoids under a different set of selective pressures where 99 per cent possessed a long flexor tendon of the thumb. The same holds for other relatively minor variations in the skeletons, musculature, or dentition of primates.

From general principles and the evidence of comparative anatomy alone, it is very hard to derive a man-like shoulder from a quadrupedal monkey. It is easier to derive it from the shoulder of a brachiating pongid. Since man shows a whole complex of traits which, considered together, go with brachiation, there is presumptive evidence of a brachiation stage in human phylogenetic history. The quadrupedal monkeys have a small acromial process of the scapula, a short clavicle, a high attachment of a small deltoid to the humerus, and no costo-clavicular ligament. Man and the pongid brachiators have a large acromial process, a long clavicle, a low attachment of a large deltoid, and a strong costo-clavicular ligament.

The most economical historical explanation of man's arms, shoulder, and thorax is that his ancestors were brachiators in the sense of use of the forelimbs as a means of grasping handholds above the head and of swinging the body forward in arboreal progression. There is no reason to suppose that they were specialized brachiators, such as the contemporary gibbons with long arms and hook-like hands.

This assumption allows an explanation of the broad, relatively shallow thorax of man and the complex anatomy of his shoulder. It happens that use of the arms for manipulation of tools would favor selectively a broad thorax with widely spaced shoulders. But since the earliest evidence of tool use is late in hominoid history, I would prefer to explain the anatomy of the thorax and shoulder as a heritage from brachiation rather than a convergent resultant of tool use.

But let us return to what we know more directly about the mode of locomotion in fossil hominoids. The fore-limb of *Proconsul* is beautifully preserved in the fossil record (Napier and Davis, 1959). The "arm" and shoulder of this Miocene primate show both quadrupedal and brachiating features. It was not a specialized brachiator like the modern gibbon, but it was structurally capable of arboreal travel using overhead, grasping arm movements. It was also capable of ground locomotion in a quadrupedal manner.

It would be an extraordinary bit of good luck should the only Miocene hominoid whose skull and fore-limb has been recovered be a member of the phylum directly ancestral to man.

The skull of *Proconsul* is sufficiently different from the skull of living pongids that several investigators assign it to a separate subfamily. It is enough for our purposes to assume *Proconsul* represents one of several sorts of hominoids living in the Miocene and that one of these phyla was, in fact, ancestral to modern man.

The pelvis of *Proconsul* is unknown and the hind-limb is represented only by fragments. The rich fauna and flora associated with *Proconsul* suggests this Miocene hominoid occupied a region containing both open savannah with grass and low shrubs and scattered forests with large trees and an abundance of vines. The ecological setting gives additional evidence that *Proconsul* was an able climber of trees as well as an adept ground runner.

Australopithecus is the first known primate with upright, bipedal locomotion. This conclusion is supported by the anatomical evidence from pelvic remains of five different individuals, plus fragments of leg and foot bones. The general morphology of the australopithecine pelvis and leg resembles modern man in those features which make his upright, bipedal posture possible. The way the australopithecine head was mounted atop the spinal column gives further indirect evidence of a man-like, bipedal locomotor habit.

There are some detailed features of full human bipedalism not found in *Australopithecus*. It may be that these South African near-men did not possess the anatomical equipment to sustain a ten-mile run in pursuit of an eland after the fashion of a modern Bushman. These locomotor parts are fully developed in *Pithecanthropus* from Java and Peiping, whose leg bones are within the range of variation of *Homo*.

By the opening of the Pleistocene a million years ago, man's ancestors were fully bipedal with free hands which could be, and were, used to handle tools. We will see that this was a master adaptation demanding other adaptations leading to man's capacity to be like the primates who read this. If I were more poetic, I would say something here about near-men standing with their soft underbellies exposed to the saber-like canines and claws of vicious carnivores or to the saber-like canines and nails of vicious baboons, defending themselves, after a group decision, with the jawbone of a wildebeest. I'll let the matter go by saying that, as soon as we find upright, bipedal primates, we also find evidence that they were using tools. The australopithecines achieved the visual and postural apparatus which allowed free and controlled use of the hands.

3. MANIPULATION

We now know that small-brained, bipedal hominids of the australopithecine family manufactured tools, following a standardized pattern. The best evidence is from the living site occupied by *Zinjanthropus* in Lower Pleistocene times in the Olduvai Gorge in Tanganyika. This ancient living site, once occupied by near-men, was discovered and excavated by Mary and Louis Leakey in the summer of 1959. A nearly complete skull and tibia of a near-man were found in association with nine pebble tools of Oldowan culture and 176 waste flakes which had resulted from the making of the tools on the spot. The raw material for these tools was not available nearby and had to be transported from a distance.

Proconsul may have made occasional use of stones and sticks as temporary tools, after the fashion of the living monkeys and apes. There is no evidence that *Proconsul* manufactured tools. By Pleistocene times, as we have just seen, the australopithecines engaged in tool manufacture. If Dart is right, these near-men also made extensive use of tools improvised from the bones, horns, and teeth of the mammals they killed for food. Thousands of artificially broken pieces of stone and some recognizable stone implements were found in association with *Pithecanthropus* in the cave deposits of Choukoutien. Both flakes and cores were used, and some of the flakes were trimmed into points or scrapers. Rough choppers were made by removing flakes from lumps of quartzite. Although the *Pithecanthropus* were regular and systematic tool makers, they seemingly made little attempt to standardize the tools. With the arrival of the genus *Homo,* tools of standardized variety and specialized purpose were extensively manufactured.

A good start toward precise manipulation was achieved by quadrupedal apes like *Proconsul.* When they sat up, their hands were temporarily free and no doubt were used to bring objects close to the peripheral organs of vision, taste, and smell. But something like a quantum jump is made when the hands are continually free for such activity in a bipedal animal like *Australopithecus*. Then the arms and hands, chiefly under the guidance of vision, become principal organs for interaction with the immediate external environment. Catching food, eating, grooming, fighting, toolmaking, and tool use become special activities of the hands.

These manipulations, accompanied by a rich flow of sense data, including those from the more developed proprioceptive arm-and-hand muscle sense, enlarge the flow of information to the brain which, in turn, fosters development of association areas for storage of past experience with the hands, and guides and initiates new hand movements. The motor and sensory projection areas are significantly expanded in the cerebral cortex of primates with accomplished manipulation.

The neural delay required when some extra-organic tool is interposed between stimulus and response probably had much to do with the further development of cognitive behavior in the hominids and perhaps with the first ability to symbol and the start of human language. We know that australopithecines carried stones several miles to a living site, where these stones were later made into designed tools. We infer that *Australopithecus* carried these tools on trips away from the living site for use in hunting. This sort of behavior implies thinking about things that are remote in space and/or time. The australopithecines, thus, furnish the earliest historical instance of displacement in hominid behavior. The coadaptation of the hands, senses, and projection and association areas in precise manipulations seems a first basis for the subsequent development of human intelligence.

4. CARNIVOROUS-OMNIVOROUS DIET

Food-getting behavior is, of course, a fundamental activity of all animals. There is little doubt that modern man eats a greater variety of food than most other living primates. The chimpanzee and gorilla take mostly vegetable food. The chacma baboons of South Africa feed principally upon fruits, roots, tubers, and bulbs, although they eat insects, scorpions, lizards, bird eggs, and such small or young mammals as they are able to capture. It would seem, from the ecology of its habitat, that *Proconsul* probably was a vegetarian-omnivore like the living baboons (Chesters, 1957).

Fortunately we have good historical evidence on the diet of the extinct hominids. The fossilized bones of small or young animals were found at Olduvai in association with the tools, skull, and tibia of *Zinjanthropus*. Since these animal bones (from rats, mice, frogs, lizards, birds, fish, snakes, tortoises, young pigs, antelopes, and ostriches) were in all cases broken apart, whereas the hominid skull and tibia were intact, Leakey infers the animals were part of the local australopithecine food supply. The flora and fauna associated with the South African near-men connote that they lived in open grassland or parkland much like the landscape of the Transvaal today (Brain, 1958). Dart has assembled a large amount of evidence that the australopithecines were hunters of baboons, antelope, and other mammals of fair size (Dart and Craig, 1959).

By Middle Pleistocene times, the *Pithecanthropus* of China was a hunter of large mammals as well as a gatherer of plant food. The excavations at Choukoutien tell us much about the food habits of Peiping man (Chaney, 1935). He, or she, is the first known hominid cook. Abundant fragments of charred bones in the Choukoutien deposits reveal Peiping man roasted cuts of horse, bison, rhinoceros, and other game animals which no longer live in northeastern China. Thousands of shell fragments of the hackberry are associated in the Choukoutien breccia with quartz tools and bone fragments. The modern hackberry *(Celtis)* occurs as a small tree or bush in the semiarid regions of Asia and North America. Its fruit was used extensively by the Indians of the American Southwest. We may suppose Peiping woman gathered the berries from bushes in the Western Hills and stream borders near Choukoutien, took them home, and mashed the shells in preparation for her family meals.

The change to a partially carnivorous diet supplied by large animals had extremely important implications for the social organization of the early hominids. We must assume the early hominids hunted in groups. And, like the carnivorous, band-hunting gray wolves—aside from man, the most sociable of the beasts of prey (Murie, 1944)—it is likely these hunting bands employed signals to coordinate their hunt. (I will return to this matter of "wolf calls" a little later.)

Here, of course, I am speculating. Modern wolves are not Pleistocene australopithecines. We will never have a motion picture of australopithecine hunting methods. We do have motion pictures showing the coordinated activity of two baboons pursuing and killing a young antelope. And we do have motion pictures showing the coordinated activity of two or more members of primitive human hunters engaged in similar activity. It is certain that the early hominids killed large animals for food. Also it is clear that carnivores that take large animals get a large supply of calories at each kill. This concentrated food is more easily transported to a central, continually used shelter or campsite than is low-calorie and bulky plant food, especially before extra-somatic containers were available.

We know *Australopithecus* and *Pithecanthropus* made tools; we know they killed animals for food. We infer the members of the latter genus, and perhaps the former, must have been tool carriers as well as tool users. Food-getting behavior is the clue to their carrying of tools. As I suggested earlier, tool carrying implies a type of cognitive behavior not required in the occasional use of natural "tools" (White, 1942; Bartholomew and Birdsell, 1953). It implies behavior with insight and purpose. It implies a mental event which occurs prior to the starting on the hunt, a mental association of the tool with an activity (the getting of food by killing an animal) which is to occur in the future. This type of minding has not been observed in captive monkeys nor chimpanzees. The archaeological record demonstrates it was a consistent part of hominid behavior by Middle Pleistocene times.

The availability of compact animal protein high in calories is a good basis for food sharing. Of non-human living mammals, it is only the carnivores that share gathered food (in the sense that a dominant animal supplies food for a subordinate animal). Human children, long after weaning, are dependent on food supplied by an older male or female. It is unlikely that the extended dependency characteristic of human children could develop in a society without food sharing. The amount of information which needs to be transduced in a communication system for plant eaters, a group in which each mammal gets his own food, is small compared to that needed in a group which cooperates in the hunting of large animals and bringing the resultant food to a central place for distribution among subordinate members of the group. The food-getting behavior of Pleistocene hominids puts a premium on social behavior. This brings us to a biological factor important in the social organization of primate groups.

5. Cortical Control of Sexual Behavior

On a fundamental biological level sex, obviously, has the same function in the human species as in other mammals: it is the way new members are recruited into the species, and it provides the genetical advantages of gene recombination. On the social level sexual behavior offers one of the strongest contrasts between non-human primate and human behavior. Here, however, as in many other biological characters, the behavior of man is less distinct from that of the apes than the behavior of the apes is from that of other mammals. In the majority of mammals, sexual behavior is seasonal, and the mating periods correspond to times when the female has a high probability of ovulation and conception, since the reproductive physiology is timed so that births occur during a period when the maximum amount of food is available for the newborn. In such mammals, including the lower primates, copulation is invoked by the release of gonadal hormones in the body fluids. In animals with sexual seasons we can induce copulation out of season by hormonal injections or prevent copulation in season by gonadectomy. The living primates fall into a graded series according to the degree of hormonal control of sexual behavior. In man and the chimpanzee, and probably also in the other pongids, copulation is strongly under cortical control and is not prevented by gonadectomy (Ford and Beach, 1951).

An important primate adaptation for culture is the change from wired-in reflex pathways to neural connections over association areas where learning and symboling are involved in the physiological control of activities like sleep, play, and sex. Man is qualitatively different from other primates in that a large part of sexual behavior is under symbolic, that is, cortical, rather than under glandular control. The cortical control of sex makes possible the cultural regulation of sexual behavior, and the symbolic regulation of sexual behavior is one of the bases of kinship systems and the incest taboos. The symbolic recognition of social kinship (which in many human societies may depart from the facts of biological kinship) makes possible the regulating of mating, in terms both of exogamy and endogamy, and these regulations make possible cooperative relationships in social groups larger than the biological family. Human societies are the only primate societies which organize sexual behavior in the interest of the economic activity of the group as well as in the interest of reproduction (White, 1959; Sahlins, 1959).

We must now examine hominid symbolic use in some detail.

6. Systematic Symbolic Vocal Communication

Human language, that is, systematic symbolic vocal communication, is an overlaid or secondary physiological function. The organs of speech used in language are of quite diverse primary action. The mouth, tongue, teeth, and lips had an alimentary function, and the lungs and diaphragm a respiratory function, long before they took a part in articulate speech. Articulate speech requires the coordinated movement of about one hundred muscles, most of them paired. The coordination of movement in most muscles involves corrections and adjustments via proprioceptors, the senses which tell us the position of parts of our body. But the muscles working the voice box lack proprioceptive sense, and feedback control of speech comes by way of the ear and the 8th cranial nerve. When we talk, the diaphragm, voice box, tongue, lips, and jaw work smoothly and precisely if we are to be understood. The 10th nerve controls the adjustments of the vocal cords, and the 5th nerve controls the position of the lips. Both of these use branchial muscle, while the 12th nerve moves the tongue with somatomotor muscle.

Although the voice box is homologous in all primates, its position in the throat differs in man from that in other primates. The voice box of non-human primates is in slight, to close, contact with the soft palate and the base of the tongue. This difference in position, together with differences in the inner structure of the voice box itself, is the reason why chimpanzees, for example, cannot make long, resonant sounds. As one consequence of man's upright posture and the bending of the craniofacial axis, the voice box in man is moved down the throat away from contact with the soft palate, thus forming an oral chamber which makes possible the human sort of vocal performance (Kelemen, 1949).

The neural mechanism of speech in the higher brain centers is not fully understood. The wide variation in localization of a primary lesion leading to aphasia—the inability to use spoken or written language with normal symbolic control—indicates the brain mechanism of speech is highly complex. We may classify aphasia into two types, each with three divisions, according to the location of a lesion in the (1) motor, or expressive, and (2) sensory, or perceptive, brain systems, and its location in the (a) cortical, (b) subcortical, or (c) intercortical areas (Rehberger, 1946):

(1) Motor aphasia—failure of symbolic expression. The symbolic output in articulation, writing, or gesture is deranged.
    (a) Cortical—loss of articulation or (often) writing with loss of word memory but no loss of understanding of spoken or written language.
    (b) Subcortical—loss of articulate speech but retention of word memory.
    (c) Intercortical—inability to repeat words heard or seen but ability to understand their meaning.

(2) Sensory aphasia—failure to comprehend vocal or visual symbols.
    (a) Cortical—loss of memory of the meaning of words heard and/or seen.
    (b) Subcortical—word memory is intact but is cut off from the usual mental connections which may, however, be recalled by a roundabout path.

(c) Intercortical—cannot associate its name with an object seen nor associate its appearance with an object named.

These results from the neurological study of aphasia show the sensory, steering, and motor apparatus for articulate speech are wired together in the cerebral cortex and cephalocentric systems.

Visual communication by body movements or gestures is poorly developed in the prosimians but highly developed in monkeys and apes (Yerkes and Yerkes, 1929; Zuckerman, 1933). Seemingly, a major part of all social communication in monkey and ape bands is visual; vocalization is used mainly to attract attention of animals not looking at the sender. Haldane (1955) has remarked that imitation of visual signals is rare in animals for the obvious reason that animals do not have mirrors. A baboon cannot see itself snarl, and its postures look different to itself than to others. But primates do hear themselves vocalize. A call made by X produces sensations in X like a call made by Y. There is feedback of vocalization via the ear.

If we assume with Haldane (1955) that when X imitates Y's call this tends to alter X's internal state in a way which leads to performance of the action predicted by Y's signal, it is clear that the ability to imitate vocal signals is of assistance in the coordination of social action. We know that near-men hunted and took large animals. It seems safe to assume that, once the chase was on, vocal signals allowed members of the hunting band to coordinate their activities while keeping the prey in sight. The source of sound waves, with a wave length which differs from the distance between the two ears of the hearer, may be localized directionally. In this connection it is of interest to remember that gray wolves use three calls in group hunting: The rallying call is a howl which signals "game too strong to manage alone." The hunting call, a higher pitched howl vibrating on two notes, keeps the pack oriented to the prey. The closing-in call, a combination of short bark and howl, is a signal to attack the victim (Seton, 1953).

It is easy to imagine that the roar of a lion, followed by a few bites, could become (by classical conditioning) the sign of a lion. Imitation of the roar, in the absence of the lion, would be a step in the direction whereby signing becomes symboling.

Children at play often exemplify symboling. Having never seen a real tiger or a real elephant, a child may say: "Play like this block of wood is a tiger and that rock is an elephant." The block and the rock are symbolic surrogates for the imaginary tiger and elephant. There is nothing in the nature of rocks and blocks which gives them the temporary meanings stated. The meaning of symbols is not intrinsic in stuff. The children bestow the meanings by agreement or convention.

How was this feat accomplished in the history of man, and how is it accomplished in the history of a child? Greenberg (1959) finds the key in the idea that in every speech community some utterances are partly alike both in sound and in meaning: "For example, the utterances 'Take the apple!' and 'Take the banana!' are partly alike in sound and meaning. What is different phonetically between the utterances refers to what is different about the two situations and what is the same refers to what is constant. If we now take the sentence 'Drop the apple!' the contrast between this situation and the one correlated with 'Take the apple!' confirms our analysis of 'take.' All this has doubtless been facilitated by experience during the period in which the child learns such words as 'apple' and 'banana' as isolates, not yet as parts of symbols, i.e., sentences. The evidence that analysis has taken place is the ability, having learned the three sentences, 'Take the apple!', 'Take the banana!', and 'Drop the apple!,' now to understand or reproduce the new sentence 'Drop the banana!' without previous experience of it. It is this power that language possesses of analyzing experience and then combining the parts isolated by analysis into new syntheses that enables us to talk of past and future experience. . . ."

Hockett (1959) distinguishes the following four design features always present in human language but absent in the signal "language" of gibbons and chimpanzees:

(1) Displacement—ability to talk about things remote in space or time; the ability to insert a time gap between the stimulus to communicate and the act of communication. (Note this linguistic meaning of "displacement" differs from the meaning assigned by students of animal behavior.)

(2) Productivity—the ability to produce an understandable utterance that is new to the speaker and hearer and to the species.

(3) Traditional transmission—the ability to transmit a communication system by learning. (This ability is a part of other chimpanzee behavior but seemingly is not extended to their call system.)

(4) Duality of patterning—the ability to combine a relatively small number of meaningless but differentiating vocal elements (phonemes) into an unlimited number of meaningful elements (morphemes).

We do not know the neurological basis for these four abilities. We have strong reason to believe that the expansion of the temporal and parietal lobes of the cerebral cortex may be both a cause and an effect of these four abilities. This brings me to the last biological condition preadaptive to human behavior which I will discuss here.

7. EXPANSION OF THE CEREBRAL CORTEX

The opening sentence in a definition of *Homo sapiens* by Le Gros Clark (1955) is "A species of *Homo* characterized by a mean cranial capacity of about 1,350 cc. . . ." A brain large in both relative and absolute terms is one of the diagnostic features of modern man. Among living animals, for example, a 150-pound sheep has a one-quarter pound brain, a 1500-pound cow has a one-pound brain, while a 150-pound man has a three-pound brain (Brody, 1945). Living primates in general have large brains relative to body weight. Big brains were not typical of the earliest primates, but an evolutionary trend toward increase in brain size is characteristic of most primate phyla (Simpson, 1949; Clark, 1959).

When the log of brain weight among mammals in general is plotted against the log of body weight, we find that brain weight increases by the 0.66th power of body weight. The slope of the regression line is steeper in primates in general where brain weight increases as the 0.79th power of body weight (von Bonin, 1955). If we use this general primate equation and man's body weight to predict his brain weight, we obtain a figure only

80 per cent of the actual value. Thus modern man has a larger brain than is typical of primates in general by about one-fifth.

We also have physiological evidence that man has a remarkably spacious brain. Crile (1941) discovered a close relationship for animals in general between metabolism and brain weight. He found 1 gram of brain is required to produce by oxidation 12.12 calories of heat in 24 hours. This relationship holds for a wide range of animals from grasshoppers to elephants; of the hundreds of animals examined by Crile, only man and the chimpanzee were way off the curve. In terms of Crile's physiological criterion, man's brain is indeed huge. A man of 150 pounds has a basal metabolism of about 1650 calories a day. He would require only 135 grams of brain to execute his basal metabolism. Since the average brain weight for modern man is 1345 grams, he has a brain mass nearly ten times larger than would be required for basal metabolism alone. An 84-pound chimpanzee had a basal metabolism of 1090 calories and an estimated brain weight of 430 grams. Thus the chimpanzee brain is about five times larger than required for a day's production of basal energy by oxidation. In the sheep, an animal not noted for intelligence, the brain weight-metabolism factor is only 1.11. (The raw data for chimpanzee and sheep are from Brody, 1945.)

We should neither overemphasize nor underemphasize the importance of relative brain size for intelligent behavior. Overall brain size is a poor predictor of intellectual ability within our own species (excluding, of course, the lower, or microcephalic, limits). We know of extreme cases where men of demonstrated high intellectual ability differ in brain volume by a factor of two. Still, when we consider differences between species of living animals, relative brain size is the best available single predictor of capacity for intelligent behavior. It is the internal organization of the brain that counts. The volume of the neocortex in *Homo* is about 58 per cent of total brain volume compared to 46 per cent in the lower primates (Harman, 1957). The ratio of the volume of nerve cells to the total volume of the gray matter in the visual cortex is 50 per cent higher in man than in the chimpanzee (Haug, 1958).

Brains of living primates differ in their surface characteristics. The brain surface in man is highly convoluted. A large sheet of cerebral cortex in man is packed into a cerebral box, the human cranium. If spread out flat the human cerebral cortex would be a square of tissue about 2 feet at the edge. Mechanically it is the problem of putting a napkin 24 x 24 inches into an 8-inch bowl. It has to be folded up to get in. But the cortex grows up within the skull. As it increases in volume, it takes on folds to fit within the endocranium. Some of the folds are mechanical, to go around bends in the base or other parts of the growing container and brain. Other folds reflect internal differences in the cellular make-up of the cortex itself. Before we take up certain evolutionary changes in hominid brains, let me remind you of the general surface anatomy of that organ.

The cortical surface of the brain is folded into convolutions separated from each other by depressions. The longer and deeper depressions are called fissures or sulci. The longest and deepest fissure (the lateral fissure of Sylvius) begins on the part of the brain lying behind the eye and beneath the temple and passes backwards and upwards to and above the position of the top of the ear. The frontal and parietal lobes of the brain are situated above, and the temporal lobe below the lateral fissure. A second large fissure (the central fissure of Rolando) crosses the surface of the cerebral hemisphere from above downwards and separates the frontal from the parietal lobe. The central fissure runs from a position at the top, close to the vertex of the head, obliquely forward in the direction of a point lying beneath the cheek arch.

This brings us to the question of how much we can learn about the brains of ancient primates from skull parts preserved as fossils. We know about over-all size and general shape with considerable accuracy. The patterns of the meningeal blood vessels are often beautifully reflected on the endocranial walls, but we have yet to learn the significance for behavior, if any, of variation in these patterns. Since the brain makes a partial record of its convolutional complexity on the skull which contains it, we can have a rough idea of the surface anatomy of the brain from the skull alone. A check on the reliability of this procedure is available by taking endocranial casts of modern primates whose brains are available for study. Unfortunately we cannot tell as much from the surface of the endocranial cast as from the brain itself. The exact details of the fissures cannot be predicted from the endocranial cast alone. Fortunately, we can tell a little about the general degree and pattern of fissuration and the relative size of the various lobes. As the brain is an exceedingly important part of man, it is a happy circumstance for human paleontology that the general features of its surface anatomy may be reconstructed from fossil evidence.

We may illustrate this general line of argument by considering the brain of *Proconsul*, which is known from a partial endocranial cast. In the simplicity and arrangement of the cortical fissures, *Proconsul* resembles the Old World monkeys rather than the pongids or hominids. Also the petrous bone (which houses the inner ear) of *Proconsul* has a large subarcuate fossa. This fossa, or depression, found in monkeys generally but not in the great apes or hominids, holds the floccular lobe of the cerebellum. The available evidence suggests the brain of this early Miocene ape was primitive and monkey-like compared to the brain of the living apes, of *Australopithecus,* and of the later hominids (Le Gros Clark and Leakey, 1951). Not enough of the skull of *Proconsul* is preserved to make a good estimate of its cranial capacity—a rough estimate based on the published drawings would be of the order of 175 to 225 cc.

The brain of the australopithecines reaches a volume of from 450 to 550 cc. This is within the range of brain size in the living great apes, but you must remember that the australopithecines were relatively small hominids, with a body weight for adults as low as 70 to 90 pounds, so that relative brain mass would be larger in the near-men than in a living gorilla. Several available endocranial casts indicate that the surface features of the cerebrum in *Australopithecus* is of hominid, and not pongid, design (Schepers, 1946). In *Pithecanthropus,* hominids of about the same body size as modern man, the endocranial volume overlaps the lower normal size limit in *Homo*, with a mean of 860 cc. for the Javanese, and of 1075 cc. for the Chinese, specimens. And as might be expected from the archaeological record of their behavior, the brains of *Pithecanthropus* show the beginnings of the expansion of the temporal and parietal lobes characteristic of modern man.

Recent studies on functional localization in the somatic sensory and motor centers of the cerebral cortex give us very interesting and suggestive information on the evolution of the brain in primates. I want to close by calling your attention to some of this neurophysiological work—especially that by Clinton Woolsey of Wisconsin on monkeys and that of Wilder Penfield on man.

"The electrophysiological technique of determining the afferent projection areas has provided a new method for study of localization of function in the cortex and, because it yields a very detailed story of the relations of specific parts of peripheral sensory mechanisms to specific parts of the central receiving areas, it provides not only the means of determining the extent of cortex concerned with a given sensory mechanism but, from the detailed pattern of organization of the system, it permits clear identification of homologous parts in different species." (Woolsey, 1958). By tactically stimulating a peripheral part, say in a toe or finger, an electrical potential is evoked in the cortical receiving area, for example, in the postcentral sensory area. By electrically stimulating a central part, say in the precentral motor projection area, a muscular response is evoked in a peripheral part, for instance, in the finger or toe. The current passes from the stimulated place in the precentral convolution down the corticospinal tract to the anterior horns of the spinal cord on the opposite side and thus to the motor nerves going to the hand or foot.

In order to picture the basic organization of the pre- and postcentral projection areas, it will help if you keep in mind an outline drawing of a rabbit or a monkey as seen from the side. The projection centers for the ends of the legs are nearest to a line corresponding to the bottom of the central sulcus. The centers for the head end of the animal are in the lower parts, and those for the tail end are in the upper parts of the central sulcus.

Now, in our outline drawing, we make the area of each anatomical part proportionate to the relative area in the cortex which receives sensory connections from, or sends motor connections to, that particular region of the body. For example, if the cortical projection area for the thumb is larger than that for the big toe, we will make the thumb larger and the toe smaller in our outline drawing, or cortical map.

(I am oversimplifying the actual situation in order to show some comparative differences in homologous areas in the cortical maps of different species. In addition to the pre- and postcentral projection areas, there are well-organized supplementary motor areas in the anterior cortex and second somatic sensory, visual, and auditory areas in the posterior cortex. Further, the sensory areas are not completely sensory, and the motor areas are not entirely motor.)

Maps showing the localization in the four somatotopically organized areas of the Rolandic region are available, in roughly comparable detail, for the rat, rabbit, cat, marmoset, macaque, chimpanzee, and man (Woolsey, 1958). The size of the motor area which controls various muscles relates to the skill in using the muscle and not to the size of the muscle. In the rat, rabbit, and cat the cortical centers for the various body parts are arranged (in orientation, proportion, and relation of part to part) much as they exist in the actual somatic animal. As one might expect from a knowledge of the history and habits of the primates, the hand achieves a high degree of corticalization. In the chimpanzee and man the cortical representation of the hand in both pre- and postcentral fields has increased to such an extent that the cortical centers for the face lose continuity with the center for the back of the head and neck. In the cortical map, the great expansion of the hand in the hominoids has severed the face from the occiput. The cortical topography of the macaque shows an intermediate situation in that the separation of face from occiput occurs in the postcentral area but not in the precentral. And, to add to the nicety of this graded series, the New World marmoset shows a transitional status in the postcentral area and a basic mammalian, or rat-rabbit-cat-like status, in the precentral gyrus.

Each of the first six of our seven biological conditions which are preadaptive for man's capacity to symbol and to have culture is reflected in the structure of the cerebral cortex. Especially in the motor projection areas we see evidence that man's long history of tool use and shorter history of language are both a cause and an effect of cortical expansion. The cortical motor areas which are most involved in tool use and in speech are much expanded in man's brain. These morphological changes, along with others we have mentioned, illustrate some features of the biological preadaptation of hominids for culture. Culture is a biological adaptation with a non-genetic mode of inheritance, and it is culture which accounts for the pre-eminence of man as the human animal.

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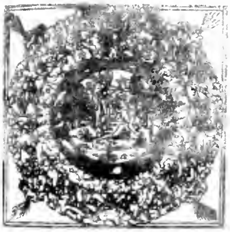

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IN FEBRUARY, 1616, GALILEO GALILEI was haled before the Holy Inquisition in Rome to answer charges of having nurtured and bolstered the heresy invented by an obscure Pole, Nicolaus Copernicus, whom death had made unavailable for questioning. The Roman authorities were committing a blunder; heretical or not, the teachings of Copernicus and Galileo were demonstrably true. We may nevertheless admit that Cardinal Bellarmin, Galileo's prosecutor and judge, had valid reasons to feel perturbed. Copernicus and Galileo so altered man's image of himself that they started the process of his alienation from his world. Instead of living at the center of a compact universe created specifically for him to live in, man found himself a resident of a second-rate planet revolving around a second-rate sun, lost in cosmic spaces. This increased manyfold the mystery which made the Psalmist exclaim: "What is man, that Thou art mindful of him, and the son of man, that Thou visitest him?"

Dingle rightly said that "the undying glory of Galileo's contribution to thought is that, though only half-consciously, he discarded the everyday common-sense world as a philosophical necessity."[1] But man has to come to terms with what he knows about himself and his relation to his surroundings. Descartes responded to the schism between man and the universe by his philosophy of radical dualism of mind and matter. Man could still be the center of a spiritual world, even though he had to surrender the physical universe as something wholly outside himself and independent of himself. Newton's grand synthesis showed the universe to be a wondrously orderly mechanism, running smoothly according to fixed and inexorable laws. These laws are neither friendly nor inimical to man; man could not alter them, but he could discover them and control them by obeying them. Nature's orderliness may make nature eventually

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[1] Quoted in P. Frank, *Philosophy of Science* (Englewood Cliffs, N.J., 1957), p. 1.

predictable. This was a comforting thought; and yet, it did not wholly remove the sting from Pascal's anguished cry: "The eternal silence of these infinite spaces frightens me."

The Cartesian dualism was soon abrogated in favor of a new monism, but this time a materialistic monism. Laplace boasted to Napoleon that in his studies on celestial mechanics he found God an unnecessary hypothesis. Helmholtz, the discoverer of the law of conservation of energy, wrote in 1847 that "The task of physical science is finally to reduce all phenomena of nature to forces of attraction and repulsion. . . . Only if this problem is solved are we sure that nature is conceivable."[2] But if this be true of physics, why not also of biology and psychology? Descartes believed animals to be mere machines, but regarded man as a possessor of an un-mechanical soul. John Locke concluded, however, that the human mind contains nothing which did not enter in via the senses. The sense organs operate by means of physical forces, albeit very complex and subtle ones. Descartes proved to be the loser and Locke the gainer. Man's arrogant illusion of spirituality, and even of rationality, was steadily eroded during the nineteenth century, and finally dissolved by Freud early in the current one.

The Darwin-Wallace theory of evolution arrived in 1858 and 1859, in the midst of a period of uninterrupted successes of physical sciences and their technological applications. This theory completed the picture of the universe as one vast machine, called "Nature," of which man is but a tiny part. Neither the boundless cosmos, nor even the creatures which live around us, were made for our benefit or were designed with us in view. Nor have the animals and plants appeared suddenly; the relative perfection of their bodily structures and functions and their marvelous adaptions to their environments have all arisen slowly and laboriously in the process of evolution, which extends for at least two billion years back into the history of our planet. Furthermore, this process involves only "natural" causes, and at that, of a seemingly rather unedifying sort, called "struggle for existence" and "survival of the fittest."

Finally came the heaviest blow, or what seemed such to some

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[2] *Ibid.*

of Darwin's contemporaries and still seems to a few of ours. A theory of the evolutionary origin of man was implicit in Darwin's *On the Origin of Species* published in 1859, and it was made explicit in 1871, in *The Descent of Man*. Far from being the center of the cosmos, man is merely one of more than a million biological species which inhabit the earth. What seemed to some people especially hard to put up with was, curiously enough, that man's nearest relatives in the animal kingdom turned out to be apes and monkeys, beasts held in so low an esteem in the folklore that they seemed unworthy of a place next to man even in the zoological system.

This feeling, that the possession of relatives apparently so disreputable as monkeys constitutes a derogation of human dignity, a biologist finds hard to understand. An hypothesis regarded as likely by many evolutionists is that all life is monophyletic, descended ultimately from a common ancestor who bridged the gap between the animate and the inanimate nature. Anything that lives is therefore our kin, and it deserves that reverence for life which Albert Schweitzer expresses: "The fundamental idea of our conscience, to which we come back each time we want to reach comprehension of ourselves and of our situation in the world, is: I am life wanting to live, surrounded by life wanting to live. Meditating upon life, I feel the obligation to respect any will-to-live around me as equal to mine and as having a mysterious value. A fundamental idea of good then consists in preserving life, in favoring it, in wanting to raise it to its highest value, and evil consists in annihilating life, injuring it, and impeding its growth."[3]

1. Progress in Evolution

The history of life is a long succession of cycles of births, reproductions, and deaths. But this is not simply an endless recurrence of the same eternal forms. Darwin showed that the history of life consisted of more than futile repetitions. In the perspective of time, individual life cycles are seen to cohere in spirals; evolution has involved changes, and these changes were on the whole progressive. The immense complexity and the

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[3] A. Schweitzer, *An Anthology* (Boston, 1947).

marvelous designs of living bodies have not arisen all at once; they reached their present state of near-perfection only gradually.

The doctrine of progress is certainly older than Darwin. In fact, it was the congruence of Darwin's theories with the spirit of his time, to which a belief in progress was fundamental, which accounts for their enthusiastic reception. Belief in progress is a part of our heritage from the Age of Enlightenment, the eighteenth century. During the eighteenth and the nineteenth centuries most people were getting materially better off, at least in the parts of the world swayed by the industrial revolution. It was a gratifying and even a thrilling thought that this improvement is not only a natural but also an inevitable process, that people are becoming better as well as better off, and that this progress will eventually result in something like heavenly bliss, formerly promised only to an elect few and only beyond the grave.

This doctrine was stated with a most refreshing directness by Condorcet in 1793. Condorcet saw in human history a succession of ten stages, rising from primitive barbarism to ever greater perfection, and he dreamed that the tenth and last stage was drawing near while he wrote about it. The positive philosophy of Comte, published between 1830 and 1842, saw the progress in three stages, from a primitive theological, through a metaphysical, to a scientific one. This progress will "transform artificially the species into a single individual, immense and eternal, endowed with a constantly progressive action on exterior nature." Spencer, who managed to be both a predecessor and a successor of Darwin, wrote in 1850 that progress ". . . is not an accident, but a necessity. Instead of civilization being artificial, it is a part of nature; all of a piece with the development of the embryo or the unfolding of a flower. The modifications mankind have undergone, and are still undergoing, result from the law underlying the whole organic creation; and provided the human race continues, and the constitution of things remains the same, these modifications must end in completeness."[4]

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[4] For a discussion of Comte's and Spencer's philosophies of progress, see J. C. Greene, "Biology and Social Theory in the Nineteenth Century: Auguste Comte and Herbert Spencer," in M. Clagett's *Critical Problems in the History of Science* (Madison, 1959).

Two world wars and the blighted hopes of the Russian revolution left only doctrinaire Marxists still convinced that progress is "scientifically" inevitable, that it will have its ultimate fulfillment in a communist paradise, and that this kind of paradise will be a desirable place to find oneself in. To everybody else recent history is proof that progress is not at all inevitable and not a necessary part of nature. It occurs only as an outcome of effort and ordeal, of creative inspiration, favorable circumstances, and plain luck.

2. Utilitarian Character of Evolution

Our planet offers a great variety of opportunities for different modes of living. To adopt new ways of life, organisms must undergo evolutionary changes. Aquatic animals have in several lineages given rise to descendants living on land, as in the case of higher vertebrates evolving from fish-like ancestors. Some terrestial animals turned aquatic again, as with the whales, whose ancestors were land-dwelling mammals. Living on land is obviously not inherently better or more desirable than living in water, or vice versa. Fishes are still well off in water; so were the whales until men started to hunt for them, and so are many land animals. Each form of life is at least tolerably competent in its own sphere. However, by changing and becoming adapted to a variety of modes of living, organisms become able to exploit many more opportunities for life than any single organism could be competent to utilize. Thus life expands and masters the earth.

About a million years ago, at the beginning of the Ice Age or perhaps at the close of the Tertiary, there appeared a biological species in which biological evolution has transcended itself. This species, man, differs from others by its possession of a body of learned tradition called culture. All organisms inherit the structure and functions of their bodies by way of biological heredity. So does man; but he acquires also a store of knowledge, belief, and ways of behavior by learning and education. Biological heredity is transmitted through the sex cells; culture is passed by way of language; the genes only in the direct line of descent; culture between members of a society who may or may not be biological relatives.

Biological heredity and culture are interrelated; the possibility of culture is conditioned by heredity. Culture can originate, endure, and grow only in the possessors of human genes. This simple fact is important, and its consequences must be appreciated. The fountainhead of the ability to gain and transmit knowledge lies in human genes; but human genes are a product of biological evolution, and biological evolution is fundamentally utilitarian. The genetic equipment of the human species is what it is because it proved to be useful. Indeed, biologically considered, man is by far the most successful species. He has spread all over the world, learned to control and utilize some of the forces of nature, and forced other species to serve his needs. This biological success became possible not because of any particular strength or aptitude of the human body but because of the might of the human intellect. Man's ascendancy is the fruit of his genetically conditioned powers of knowledge and understanding.[5]

3. MAN'S ABILITY TO KNOW AS A PRODUCT OF EVOLUTION

It is remarkable that evolution, though lacking design or foresight, nevertheless results so often in furtherance of the harmony between the organism and its environment. One could not expect it to do so always, however. Evolutionary changes sometimes result in failure. Failure of life is death, extinction.

The biological success of a species is often due to the excellence of its organization in only one or in a few respects. In the bird of prey, this is its keen eyesight and powerful flight; in the prey it is concealment and escape; in many parasites it is tremendous fecundity; in man it is the ability to learn and to know. The evolutionary origin of man's ability to learn and to know tends, however, to limit and circumscribe this ability. To oversimplify the issue, man can know chiefly what is useful for him to know.

It must be admitted that the problem of the origin of human understanding has thus far eluded solution in evolutionary terms. Everyone will agree that in man empirical knowledge is useful for survival. But it is not quite clear what is the bio-

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[5] See G. G. Simpson, *Meaning of Evolution* (New Haven, 1949), and A. Roe and G. G. Simpson, ed., *Behavior and Evolution* (New Haven, 1958).

logical utility of abstract and theoretical knowledge. The solution may be that in human affairs "utility" has a deeper meaning than appears on the surface. Man is not a solitary animal; he is a social and, in Aristotle's words, a political animal. Man's survival depends not alone on his having enough to eat and on successful avoidance of physical hazards of the environment. It depends also on man's ability to arrive at a mutual accommodation with his neighbors.

Interpersonal relations are facilitated by the use of language. So are the processes of instruction and learning. The biological adaptive function of communication by means of language is beyond question. Now, the establishment of language depends upon the ability to form and to deal with generalizations, symbols, and abstractions. The word "stone" or "water" does not refer to just one particular object, but to classes of objects having in common the property of stoniness or of wateriness. The so-called languages of animals do not involve the use of such generalizing or abstract thought, or at most involve the barest rudiments of it. The human kind of language is a phenomenon which has little precedent on the subhuman level.

4. Symbolic Thought, Language, and Self-Awareness

Without doubt, natural selection has favored the development and strengthening of the ability of symbolic and abstract thought. This ability, almost totally foreign to the animal world at large, has set man apart as a biologically unique species, equipped to pursue a quite novel way of life. There is no need to stress the importance of this ability to social man; its loss owing to injury or to inherited defects makes a human being an idiot, helpless in a human community.

However, the ability to form symbols, generalizations and abstract ideas is not subservient to linguistic needs alone. A basic ability of this sort opens up avenues of cognition quite foreign to the animal world and inaugurates a variety of new possibilities of further evolutionary developments. Natural selection is opportunistic; it favors properties which are useful at the time and in the place of their establishment, regardless of whether these properties will be useful or harmful in the future.

Extinction of biological species is the price which life often pays for this opportunism. The extinct forms are those which were driven by natural selection into blind alleys of adaption to environments which subsequently ceased to exist. But there is another side to the opportunism of selection. Once in a while it endows an organism with novel abilities. The house mouse, the rat, the house fly, the cockroach were probably only moderately successful species before the advent of man and his civilization. Yet they happened to fit snugly into certain adaptive avenues inadvertently created by man. The same was probably true of the ancestors of most animals and plants which man has domesticated.

Such accidental emergence of qualities which become useful only in environments which the species encounters in the future is referred to as preadaption. Preadaption does not mean that the evolutionary process somehow has a foreknowledge of the future. It means simply that evolution is a creative process which may lead to appearance of completely new qualities, some of them potentially useful and others devoid of utility or even injurious to their possessors. Human evolution doubtless involved occurrences of this sort. Natural selection has endowed man with a genetic equipment which opened up the possibilities of symbolic, abstract and generalizing thought. This novel ability has been highly adaptive because it resulted in the emergence of language. But the same ability brought with it also other developments which proved equally crucial for man. The capacity for abstract thought had as a corollary or a by-product the inception of self-awareness. Man tasted the forbidden fruit; he became conscious of himself and of his environment; he attained the status of a person in the existential sense. This was, as we see it in retrospect, the close of the prehuman and the opening of human evolution.

Perhaps it is this crucial event of the evolutionary development which the biblical symbolism describes as the Fall. The passing of the happy state of a simple child of nature brought heavy penalties. Man became, and he still remains, a creature rent by internal contradictions. He is a paradoxical being, capable of unspeakable egotism and cruelty, but also of love, abnegation, and self-sacrifice. The subconscious life of man is replete with queer sexual urges and traumas, and his conscious activity is often guided by desires of economic gain or by an appetite to dominate others. But man is also ashamed of his defects and suffers from his depravity. He is able to construct in his imagination worlds different from the actual one, and can visualize himself in these imaginary worlds. His imagination tells him that he is not what he ought to be. Biologists have been afraid to probe the terrifying depths of human nature. These depths have been explored by thinkers like Plato, Dostoevsky, Kierkegaard, Nietzsche, and more recently, and in what I feel is fair to describe as quasi-biological and quasi-scientific terms, by Freud. But the riddle of man is in part a biological riddle. It is evident that Man, the whole man and not merely his bodily frame, has biological components. The settings of man's spiritual evolution have taken shape in his biological evolution.

Now, whether man's self-awareness is, as such, adaptive in the biological meaning of the term may well be questioned. It does not necessarily help man to harmonize his existence with his environment. It may even be disadvantageous under many conditions. Among the consequences of self-awareness are the thirst for freedom and aspirations of self-transcendence. Is this biologically useful to man? It rather seems that complacent mediocrities and willing slaves are favored in most human societies. In a sense, human self-awareness and consciousness can hardly be regarded as legitimate products of adaptive evolution. They came, as it were, through a back door of the evolutionary process.

The hypothesis that they are products of biological evolution, at all, may easily be challenged. But if not, where did they come from? It is incumbent upon us to consider whether this hypothesis can be sustained. I believe that it can; it is not an ad hoc hypothesis. It is an application to man of a reasonably well-known biological principle.

5. SUCCESS AND IMPERFECTION IN EVOLUTION

Establishment in organic evolution of adaptively useless and even harmful traits is not an infrequent occurrence. This does not contradict the principle of utilitarianism of natural selection.

The proviso necessary for such an occurrence is that useless traits must be by-products of the same genetic constitution which yields also traits of overriding usefulness. Examples are not hard to find either in human or in animal or plant evolution. In man, the erect body posture has become established in human evolution because it freed the hands from walking duties, and thus permitted their employment for delicate manual operations. The adaptive value for the human species of the possession of well-developed hands is sufficiently obvious. But the erect body posture in man entails disharmonies in several bodily functions. The difficulty of childbirth is perhaps the most evident of these disharmonies, and it is clearly disadvantageous from the standpoint of natural selection.

Why, then, has the erect posture become a fixed trait in the human species? In a sense, this is just another manifestation of the opportunism of natural selection. We often speak of natural selection as favoring this and discriminating against that trait. In reality, the selection perpetuates some and fails to perpetuate other genetic constitutions, and not traits. It is the organism as a whole that survives and reproduces, or remains childless and dies. Therefore, possession of a very useful quality may compensate for some concomitant weaknesses.[6] Our species is a biological success because of its intellectual capacity. Man is biologically specialized to control his environment by the force of his powerful brain, not by that of his relatively weak body. The self-awareness is, biologically, an adjunct of this powerful brain. Man's biological success became a reality despite the tragic discords within him.

It may seem odd that the genetic equipments of so many living organisms, both lower and higher ones, show obvious, and even glaring, imperfections. This is not what romantics generally expect to find in nature's products. But this is what might be anticipated among the products of a natural creative process. Organic evolution is such a process. It lacks foresight and the ability to construct things according to a predetermined plan. I like to illustrate the principle that the organization of living beings is not free from shortcomings by the example of the man-

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[6] T. Dobzhansky, *American Naturalist* 90, 1956.

o'-war bird. This is a superb flier commonly observed along tropical seacoasts. It is evidently a highly successful form of life, judging by how common and widespread it is. And yet, although it gets its food from or near water, its plumage is not water-repellent and easily becomes waterlogged. The legs of the man-o'-war bird are so weak that the bird is unable to rise into the air except from an elevated perch.

Man's genetic equipment is responsible for the biological success of our species, and yet it is not the acme of perfection. Like the man-o'-war bird, man has his strength in his spiritual flight and his weakness in his spiritual legs. Man is able to form mental images of things and of situations which do not yet exist but which may be found, brought about, or constructed by his efforts. Man is endowed with foresight. His powers of cognition enable him to plan for the future. He can build objects and devise acts which he has not observed or committed previously. The adaptive potency of foresight and of creative imagery in the biological success of man is too obvious to need emphasis. Although his genes failed to provide him with wings, he has become a flier far more powerful than the man-o'-war bird.

6. FREEDOM

Foresight is an adaptive trait of commanding significance. However, the possession of this trait has as its adjunct another property of man's nature, the adaptive value of which is even more questionable. This is the basic existential experience of freedom. Man cannot only contrive new objects and actions; he also feels free to execute some of his plans and leave others in abeyance. Human freedom is adaptively double-edged. The experience of freedom gives man the supreme joy of being the master, rather than a slave, of his own nature and of the external world. But it also burdens him with a sense of responsibility. Man knows that he is accountable for his acts; he is able to foresee the consequences of his plans, and accordingly either pursue or avoid a given course of action. This is a dreadfully heavy load to carry.

Man's genes fail to tell him which things are good and which are bad, or which acts are right and which are wrong. The knowledge of good and evil is gained only through the experience of freedom. A cat, a mouse, a bird, or an insect meets with no such problems. Their actions are forced upon them by their genes and by their environments, including their previous experiences. All this is much more difficult and complicated in man. Freedom is an awesome gift. Man's reactions to freedom are contradictory and conflicting. He strives for freedom, and may even be ready to pay for it with his life. And yet, he may not only sacrifice his freedom for apparently trivial gains, but often enjoys the absence of freedom. The most extreme slavery is one that makes the slave unaware of his bondage.

7. THE EVOLVING UNIVERSE

Darwin did, in a sense, carry to completion the work of Copernicus, Galileo, and Newton. After Darwin, the image of the universe as an immense clockwork includes not only the inanimate nature but the world of life and of man as well. But a ray of hope has become visible in the frightening depths of Pascal's infinite spaces. Darwin and his successors altered the Newtonian image of the universe in quite an important respect. They showed that the universe was not always as it is today; that it has changed greatly with time, albeit gradually and slowly; that it has had a history. Moreover, and this is most important of all, the universe is a going concern capable of further change; it is evolving.

The sublimely lawful and rational universe of Newton was created once and for all, beautifully finished, in fact too perfect to admit change, either advancement or deterioration. Newton could not suppose the universe to be very old, since he did not refute Bishop Usher's calculation, which placed the Creation in the year 4004 B.C. Neither could Newton, who was a diligent student and commentator of the Book of Revelation, believe that the universe would have much of a chance to evolve in the future. The universe of the evolutionists is quite different from Newton's; it is not necessarily eternal, but in any case very old, some five billion years according to recent estimates. There is no compelling reason known why it could not endure infinitely into the future.

Evolutionism did not restore man to the place at the center of the universe from which he was dismissed so abruptly by Copernicus. Nor have we been given reasons to fancy that either cosmic or biological evolution was enacted in order to produce man. However, there is nothing to prevent—and much to encourage—us to think that man is the crowning achievement of the evolutionary process to date here on earth, and possibly in the cosmos. Although not central in Creation, man may still be central in importance; the emergence of man may have been the most significant event of the evolution of the universe. Moreover, and this is where our view of the universe differs most radically from Newton's, evolution marches on. The inorganic, the organic, and human natures are all in the process of change.

In our modern world changes are so numerous and so rapid that it is hard for us to realize that the idea of universal evolution is really a very novel one. Within the living memories of some of us, there appeared telephones and radios, automobiles and airplanes, atomic bombs and sputniks, two world wars were fought, mighty empires went into dissolution, the "Unchanging East" showed itself capable of intense dynamism, etc. Ancient wisdom was on the whole inclined to regard changes as illusory. Buddhist and Hindu sages were especially insistent that the world of the senses is both evil and unimportant, and that man should strive to transcend it to attain a vision of what is eternal and unchanging. A wise man, thought the philosopher-emperor, Marcus Aurelius, "considers the periodic destructions and rebirths of the universe, and reflects that our posterity will see nothing new, and that our ancestors saw nothing greater than we have seen."

The fierce resistance to evolutionism on the part of fundamentalist Christian sects has obscured the fact that Christianity has an inherent and indispensable evolutionary idea at the core of its world view. To be sure, the Judeo-Christian tradition has taken over from oriental religions the myths of the Garden of Eden and of the Fall at the beginning of the world's history. Therefore, it views the historical process as having suffered a catastrophic deterioration at its inception. However, the fall of man was followed by a new ascent. Progressive revelation of God to man through the patriarchs and the prophets was followed by the appearance of Christ. This is taken to be the ineffably pivotal event and the watershed of the history of the cosmos. Starting from this watershed, the historical process is going on towards its consummation in the Kingdom of God.

I do not wish to be understood as meaning that the theologians were or are evolutionists in the modern sense of the word. Excepting the Fall, the events of the history of the cosmos have almost always been pictured as due to direct interventions of God. Even Reinhold Niebuhr, in whose views the idea of the world-historical process seems to be central, regards human nature as too corrupt to aspire towards the role of an important agent of the evolutionary process.[7] Any such aspiration is, to Niebuhr, a form of hubris—overweening pride. The consummation of history can occur only through an act of God's grace.

I am not competent to argue with Niebuhr, nor is this necessary. For what is important is that a century after Darwin, the idea of evolution has become the core of civilized man's image of mankind and of the world in which men live. This is not a static and finished world, and mankind is on the march. Creation is not an event which has taken place some six thousand years ago; it is a process and not an act; it is not completed and it is going on before our eyes; there is hope for man, and not only in afterlife but on this earth as well.

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[7] R. Niebuhr, *The Nature and Destiny of Man* (New York, 1941).

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