likely to be one of immense importance as the Academy moves into its second century of high scientific endeavor.

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THE EVOLUTION OF LIVING SYSTEMS

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The number, kind, and diversity of living systems is overwhelmingly great, and each system, in its particular way, is unique. In the short time available to me, it would be quite futile to try to describe the evolution of viruses and fungi, whales and sequoias, or elephants and hummingbirds. Perhaps we can arrive at valid generalizations by approaching the process in a rather unorthodox way. Living systems evolve in order to meet the challenge of the environment. We can ask, therefore, what *are* the particular demands that organisms have to meet? The speakers preceding me have already focused attention on some of these demands.

The first challenge is to cope with a continuously changing and immensely diversified environment, the resources of which, however, are not inexhaustible. Mutation, the production of genetic variation, is the recognized means of coping with the diversity of the environment in space and time. Let us go back to the beginning of life. A primeval organism in need of a particular complex molecule in the primordial "soup" in which he lived, gained a special advantage by mutating in such a way that, after having exhausted this resource in his environment, he was able to synthesize the needed molecule from simpler molecules that were abundantly available. Simple organisms such as bacteria or viruses, with a new generation every 10 or 20 minutes and with enormous populations consisting of millions and billions of individuals, may well be able to adjust to the diversity and to the changes of the environment by mutation alone. In addition, they have numerous mechanisms of phenotypic adaptation. A capacity for mutation is perhaps the most important evolutionary characteristic of the simplest organisms.

More complex organisms, those with much longer generation times, much smaller population size, and particularly with a delicately balanced coadapted genotype, would find it hazardous to rely on mutation to cope with changes in the environment. The chances that the appropriate mutation would occur at the right time so that mutation alone could supply appropriate genetic variability for sudden changes in the environment of such organisms are virtually nil. What, then, is the prerequisite for the development of more complex living systems? It is the ability of different organisms to exchange "genetic information" with each other, the process the geneticist calls recombination, more popularly known as *sex*. The selective advantage of sex is so direct and so great that we can assume it arose at a very early stage in the history of life. Let us illustrate this advantage by a single example. A primitive organism able to synthesize amino acid A, but dependent on the primordial soup for amino acid B, and another organism able to synthesize amino acid B, but dependent on the primordial soup for amino acid A, by genetic recombination would be able to produce offspring with the ability to synthesize both amino acids and thus able to live in an environment deficient in both of them. Genetic recombination can speed up evolutionary change enormously and assist in emancipation from the environment.

Numerous mechanisms evolved in due time to make recombination increasingly precise in every respect. The result was the evolution of elaborately constructed chromosomes; of diploidy through two homologous chromosome sets, one derived from the father, the other from the mother; of an elaborate process of meiosis during which homologous chromosomes exchange pieces so that the chromosomes of father and mother are transmitted to the grandchildren not intact, but as newly reconstituted chromosomes with a novel assortment of genes. These mechanisms regulate genetic recombination among individuals, by far the major source of genotypic variability in higher organisms.

The amount of genetic diversity within a single interbreeding population is regulated by a balance of mechanisms that favor inbreeding and such that favor outbreeding. The extremes, in this respect, are much greater among plants and lower animals than among higher animals. Extreme inbreeding (self-fertilization) and extreme outbreeding (regular hybridization with other species) are rare in higher animals. Outbreeders and inbreeders are drastically different living systems in which numerous adaptations are correlated in a harmonious manner.

The result of sexuality is that ever-new combinations of genes can be tested by the environment in every generation. The enormous power of the process of genetic recombination by sexual reproduction becomes evident if we remember that in sexually reproducing species no two individuals are genetically identical. We must admit, sex is wonderful!

However, even sex has its drawbacks. To make this clear, let me set up for you the model of a universe consisting entirely of genetically different individuals that are *not* organized into species. Any individual may engage in genetic recombination with any other individual in this model. New gene complexes will be built up occasionally, as a result of chance, that have unique adaptive advantages. Yet, because in this particular evolutionary system there is no guarantee that such an exceptional individual will engage in genetic recombination *only* with individuals having a similarly adaptive genotype, it is inevitable that this exceptionally favorable genotype will eventually be destroyed by recombination during reproduction.

How can such a calamity be avoided? There are two possible means, and nature has adopted both. One method is to abandon sexual reproduction. Indeed we find all through the animal kingdom, and even more often among plants, a tendency to give up sexuality temporarily or permanently in order to give a successful genotype the opportunity to replicate itself unchanged, generation after generation, taking advantage of its unique superiority. The history of the organic world makes it clear, however, that such an evolutionary opportunist reaches the end of his rope sooner or later. Any sudden change of the environment will convert his genetic advantage into a handicap and, not having the ability to generate new genetic variability through recombination, he will inevitably become extinct.

The other solution is the "invention," if I may be pardoned for using this anthropomorphic term, of the biological species. The species is a protective system guaranteeing that only such individuals interbreed and exchange genes as have largely the same genotypes. In this system there is no danger that breakdown of genotypes will result from genetic recombination, because all the genes present in the gene pool of a species have been previously tested, through many generations, for their ability to recombine harmoniously. This does not preclude considerable variability within a species. Indeed, all our studies make us realize increasingly how vast is the genetic variability within even comparatively uniform species. Nevertheless, the basic developmental and homeostatic systems are the same, in principle, in all members of a species.

By simply explaining the biological meaning of species, I have deliberately avoided the tedious question of how to define a species. Let me add that the species can fulfill its function of protecting well-integrated, harmonious genotypes only by having some mechanisms (called "isolating mechanisms") by which interbreeding with individuals of other species is prevented.

In our design of a perfect living system, we have now arrived at a system that can cope with the diversity of its environment and that has the means to protect its coadapted, harmonious genotype. As described, this well-balanced system seems so conservative as to offer no opportunity for the origin of additional new systems. This conclusion, if true, would bring us into a real conflict with the evolutionary history of the world. The paleontologists tell us that the number of species has increased steadily during geological time and that the multiplication of species, in order to compensate for the extinction of species, must occur at a prodigious rate. If the species is as well-balanced, well-protected, and as delicate as we have described it, how can one species be divided into two? This serious problem stumped Darwin completely, and evolutionists have argued about it for more than one hundred years.

Eventually it was shown that there are two possible solutions, or perhaps I should say two normally occurring solutions. The first mode occurs very frequently in plants, but is rare in the animal kingdom. It consists in the doubling of the chromosome set so that the new individual is no longer a diploid with two sets of homologous chromosomes, but, let us say, a tetraploid with four sets of chromosomes, or if the process continues, a higher polyploid with an even higher chromosome number. The production of a polyploid constitutes instantaneous speciation; it produces in a single step an incompatibility between the parental and the daughter species.

The other mode of speciation is simplicity itself. Up to now, we have spoken of the species as something rigid, uniform, and monolithic. Actually, natural species, particularly those that are widespread, consist like the human species of numerous local populations and races, all of them differing more or less from each other in their genetic composition. Some of these populations, particularly those at the periphery of the species range, are completely isolated from each other and from the main body of the species. Let us assume that one of these populations is prevented for a long time from exchanging genes with the rest of the species, because the isolating barrier—be it a mountain range, a desert, or a waterway—is impassable. Through the normal processes of mutation, recombination, and selection, the gene pool of the isolated population becomes more and more different from that of the rest of the species, finally reaching a level of distinctness that normally characterizes a different species. This process, called "geographic speciation," is by far the most widespread mode of speciation in the animal kingdom and quite likely the major pathway of speciation also in plants.

Before such an incipient species qualifies as a genuine new species, it must have acquired two properties during its genetic rebuilding. First, it must have acquired isolating mechanisms that prevent it from interbreeding with the parental species when the two again come into contact. Secondly, it must also have changed sufficiently in its demands on the environment, in its niche utilization (as the ecologist would say), so that it can live side by side with mother and sister species without succumbing to competition.

Kinds of Living Systems.—In our discussion of the evolution of living systems, I have concentrated, up to now, on major unit processes or phenomena, such as the role of mutation, of genetic recombination and sex, of the biological species, and of the process of speciation. These processes give us the mechanisms that make diversification of the living world possible, but they do not explain why there should be such an enormous variety of life on earth. There are surely more than three million species of animals and plants living on this earth, perhaps more than five million. What principle permits the coexistence of such a wealth of different kinds? This question troubled Darwin, and he found an answer for it that has stood the test of time. Two species, in order to coexist, must differ in their utilization of the resources of the environment in a way that reduces competition. During speciation there is a strong selective premium on becoming different from pre-existing species by trying out new ecological niches. This experimentation in new adaptations and new specializations is the principal evolutionary significance of the process of speciation. Once in a long while one of these new species finds the door to a whole new adaptive kingdom. Such a species, for instance, was the original ancestor of the most successful of all groups of organisms, the insects, now counting more than a million species. The birds, the bony fishes, the flowering plants, and all other kinds of animals and plants, all originated ultimately from a single ancestral species.

Once a species discovers an empty adaptive zone, it can speciate and radiate until this zone is filled by its descendants.

To avoid competition, organisms can diverge in numerous ways. Dr. Hutchinson has already mentioned size. Not only has there been a trend toward large size in evolution, but also other species and genera, often in the same lines, have evolved toward decreased size. Small size is by no means always a primitive trait.

Specialization for a very narrow niche is perhaps the most common evolutionary trend. This is the characteristic approach of the parasites. Literally thousands of parasites are restricted to a single host, indeed restricted to a small part of the body of the host. There are, for instance, three species of mites that live on different parts of the honey bee. Such extreme specialization is rare if not absent in the higher plants, but is characteristic for insects and explains their prodigious rate of speciation. The deep sea, lightless caves, and the interstices between sand grains along the seashore are habitats leading to specialization.

The counterpart of the specialist is the generalist. Individuals of such species have a broad tolerance to all sorts of variations of climate, habitat, and food. It seems difficult to become a successful generalist, but the very few species that can be thus classified are widespread and abundant. Man is the generalist par excellence with his ability to live in all latitudes and altitudes, in deserts and in forest, and to subsist on the pure meat diet of the Eskimos or on an almost pure vegetable diet. There are indications that generalists have unusually diversified gene pools add, as a result, produce rather high numbers of inferior genotypes by genetic recombination. Widespread and successful species of Drosophila seem to have more lethals than rare or restricted species. It is not certain that this observation can be applied to man, but this much is certain, that populations of man display much genetic variation. In man we do not have the sharply contrasting types ("morphs") that occur in many polymorphic populations of animals and plants. Instead we find rather complete intergradation of mental, artistic, manual, and physical capacities (and their absence). Yet, whether continuous or discontinuous, genetic variation has long been recognized as a useful device by which a species can broaden its tolerance and enlarge its niche. That the same is true for man is frequently forgotten. Our educators, for instance, have tended far too long to ignore man's genetic diversity and have tried to force identical educational schedules on highly diverse talents. Only within recent years have we begun to realize that equal opportunity calls for differences in education. Genetically different individuals do not have equal opportunities unless the environment is diversified.

Every increase in the diversity of the environment during the history of the world has resulted in a veritable burst of speciation. This is particularly easily demonstrated for changes in the biotic environment. The rise of the vertebrates was followed by a spectacular development of trematodes, cestodes, and other vertebrate parasites. The insects, whose history goes back to the Paleozoic nearly 400 million years ago, did not really become a great success until the flowering plants (angiosperms) evolved some 150 million years ago. These plants provided such an abundance of new adaptive zones and niches that the insects entered a truly explosive stage in their evolution. By now three quarters of the known species of animals are insects, and their total number (including undiscovered species) is estimated to be as high as two or three million.

Parental Care.—Let me discuss just one additional aspect of the diversity of living systems, care of the offspring. At one extreme we have the oysters that do nothing whatsoever for their offspring. They cast literally millions of eggs and male gametes into the sea, providing the opportunity for the eggs to be fertilized. Some of the fertilized eggs will settle in a favorable place and produce new oysters. The statistical probability that this will happen is small, owing to the adversity of the environment, and although a single full-grown oyster may produce more than 100 million eggs per breeding season, it will have on the average only one descendant. That numerous species of marine organisms practice this type of reproduction, many of them enormously abundant and many of them with an evolutionary history going back several hundred million years, indicates that this shotgun method of thrusting offspring into the world is surprisingly successful.

How different is reproduction in species with parental care! This always requires a drastic reduction in the number of offspring, and it usually means greatly enlarged yolk-rich eggs, it means the development of brood pouches, nests, or even internal placentae, and it often means the formation of a pair-bond to secure the participation of the male in the raising of the young. The ultimate development along this line of specialization is unquestionably man, with his enormous prolongation of childhood.

Behavioral characteristics are an important component of parental care, and our treatment of the evolution of living systems would be incomplete if we were to omit reference to behavior and to the central nervous system. The germ plasm of a fertilized egg contains in its DNA a coded genetic program that guides the development of the young organism and its reactions to the environment. However, there are drastic differences among species concerning the precision of the inherited information and the extent to which the individual can benefit from experience. The young in some species appear to be born with a genetic program containing an almost complete set of ready-made, predictable responses to the stimuli of the environment. We say of such an organism that his behavior is unlearned, innate, instinctive, that his behavior program is closed. The other extreme is provided by organisms that have a great capacity to benefit from experience, to learn how to react to the environment, to continue adding "information" to their behavior program, which consequently is an open program.

Let us look a little more closely at open and closed programs and their evolutionary potential. We are all familiar with the famous story of imprinting explored by Konrad Lorenz. Young geese or ducklings just hatched from the egg will adopt as parent any moving object (but preferably one making appropriate noises). If hatched in an incubator, they will follow their human caretaker and not only consider him their parent but consider themselves as belonging to the human species. For instance, upon reaching sexual maturity they may tend to display to and count a human individual rather than another goose. The reason for this seemingly absurd behavior is that the hatching gosling does not have an inborn knowledge of the Gestalt of its parent; all it has is readiness to fill in this Gestalt into its program. Its genetically coded program is open; it provides for a readiness to adopt as parent the first moving object seen after hatching. In nature, of course, this is invariably the parent.

Let us contrast this open program with the completely closed one of another bird, the parasitic cowbird. The mother cowbird, like the European cuckoo, lays her eggs in the nests of various kinds of songbirds such as yellow warblers, vireos, or song sparrows, then to abandon them completely. The young cowbird is raised by its foster parents, and yet, as soon as he is fledged, he seeks other young cowbirds and gathers into large flocks with them. For the rest of his life, he associates with members of his own species. The Gestalt of his own species is firmly imbedded in the genetic program with which the cowbird is endowed from the very beginning. It is—at least in respect to species recognition—a completely closed program. In other respects, much of the behavioral program of the cowbird is open, that is, ready to incorporate experiences by learning. Indeed, there is probably no species of animals, not even among the protozoans, that does not, at least to some extent, derive benefit from learning processes. On the whole, and certainly among the higher vertebrates, there has been a tendency to replace rigidly closed programs by open ones or, as the student of animal behavior would say, to replace rigidly instinctive behavior by learned behavior. This change is not a change in an isolated character. It is part of a whole chain reaction of biological changes. Since man is the culmination of this particular evolutionary trend, we naturally have a special interest in this trend. Capacity for learning can best be utilized if the young is associated with someone from whom to learn, most conveniently his parents. Consequently there is strong selection pressure in favor of extending the period of childhood. And since parents can take care of only a limited number of young, there is selection in favor of reducing the number of offspring. We have here the paradoxical situation that parents with a smaller number of young may nevertheless have a greater number of grandchildren, because mortality among well cared for and well-prepared young may be reduced even more drastically than the birth rate.

The sequence of events I have just outlined describes one of the dominating evolutionary trends in the primates, a trend that reaches its extreme in man. A broad capacity for learning is an indispensable prerequisite for the development of culture, of ethics, of religion. But the oyster proves that there are avenues to biological success other than parental care and the ability to learn.

One final point: how can we explain the harmony of living systems? Attributes of an organism are not independent variables but interdependent components of a single system. Large brain size, the ability to learn, long childhood, and many other attributes of man, all belong together; they are parts of a single harmoniously functioning system. And so it is with all animals and plants. The modern population geneticist stresses the same point. The genes of a gene pool have been brought together for harmonious cooperation, they are coadapted. This harmony and perfection of nature (to which the Greeks referred in the word *Cosmos*) has impressed philosophers from the very beginning. Yet there seems to be an unresolved conflict between this harmony of nature and the apparent randomness of evolutionary processes, beginning with mutation and comprising also much of reproduction and mortality. Opponents of the Darwinian theory of evolution have claimed that the conflict between the harmony of nature and the apparent haphazardness of evolutionary processes could *not* be resolved.

The evolutionist, however, points out that this objection is valid only if evolution is a one-step process. In reality, every evolutionary change involves two steps.

The first is the production of new genetic diversity through mutation, recombination, and related processes. On this level randomness is indeed predominant. The second step, however—selection of those individuals that are to make up the breeding population of the next generation—is largely determined by genetically controlled adaptive properties. This is what natural selection means; only that which maintains or increases the harmony of the system will be selected for.

The concept of natural selection, the heart of the evolutionary theory, is still widely misunderstood. Natural selection says no more and no less than that certain genotypes have a greater than average statistical chance to survive and reproduce under given conditions. Two aspects of this concept need emphasis. The first is that selection is not a theory but a straightforward fact. Thousands of experiments have proved that the probability that an individual will survive and reproduce is not a matter of accident, but a consequence of its genetic endowment. The second point is that selective superiority gives only a statistical advantage. It increases the probability of survival and reproduction, other things being equal.

Natural selection is measured in terms of the contribution a genotype makes to the genetic composition of the next generation. Reproductive success of a wild organism is controlled by the sum of the adaptive properties possessed by the individual, including his resistance to weather, his ability to escape enemies, and to find food. General superiority in these and other properties permits an individual to reach the age of reproduction.

In civilized man these two components of selective value, adaptive superiority and reproductive success, no longer coincide. The individuals with above average genetic endowment do not necessarily make an above average contribution to the gene pool of the next generation. Indeed the shiftless, improvident individual who has a child every year is sure to add more genes to the gene pool of the next generation than those who carefully plan the size of their families. Natural selection has no answer to this predicament. The separation in the modern human society of mere reproductive success from genuine adaptedness poses an extremely serious problem for man's future.

In this brief discussion of the evolution of living systems, I have been unable to do more than outline basic problems. We are beginning to understand the role of mutation, of genetic recombination, and of natural selection. The comparative study of the overwhelming multitude of diverse living systems has only begun. Because much of our environment consists of living systems, their study is of great importance. Indeed it is a prerequisite for understanding ourselves, since man also is a living system.

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*PHYSIOLOGICAL AND CULTURAL DETERMINANTS OF BEHAVIOR**

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The preceding lectures have presented an exhilarating panorama of man's scientific discoveries ranging from the creation of the elements during cataclysmically violent explosions in the ancient vast galaxies of space to the more recent evolution