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Ludwig von Bertalanffy

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On the Logical Status of the Theory of Evolution

I have accepted, with great pleasure, the invitation to take part in this symposium and wish to extend my thanks, in particular, to our excellent Chairman, Professor De Koninck, for his invitation, and for the efforts he has devoted to enable us to join in the present discussion. The present paper being the first in this series, it appears that it should be in the way of a general exposition of the problem — a most difficult task indeed for a brief lecture. Such presentation by necessity involves the danger of oversimplification, and is liable to be open to criticism from the scientific as well as from the philosophical side.

It seems appropriate first to make clear the logical status of the concept of evolution. As far as our direct observation and experimentation go, the world of the living, our present fauna and flora as well as that of earlier geological epochs, recorded as fossils, presents itself as a discontinuum. That is to say we find living organisms to belong to well-defined groups which are called species. To be sure, there are borderline cases, in particular, the so-called *rassenkreise* or rings of races, which, to use Dobzhansky's (1951) ¹ expression, have diverged almost too much to be considered as races, but not quite enough to be regarded good species, and which are generally, although not quite unanimously, considered to be just in the process of speciation. However, apart from a few cases of polyploidy in plants, no new species has arisen within our observation, let alone higher taxonomic units. Therefore, evolution is not a fact if we designate by this term something which is directly observable. Rather the concept of evolution is an extrapolation of certain facts the justification of which lies in the great amount of documentary evidence supporting it. I think the logical structure of the concept of evolution can hardly be better defined than it was by a German theorist, Tschulok (1923) ², some thirty years ago. Surveying the world of organisms, we find that it is not a chaos of different forms, but represents a gradually diversified manifoldness. That is to say, in the so-called natural system individuals arrange themselves into species, species into genera, genera into orders, and so forth up to classes, phyla, etc. We have, further, three basic facts of observation. First, so far as experience goes, organisms arise only by way of reproduction from

1. TH. DOBZHANSKY, *Genetics and the Origin of Species*, 3rd ed. New York, 1951.

2. S. TSCHULOK, *Deszendenzlehre*, Jena, 1923.

parental organisms. Secondly, only consanguinity produces organisms similar to their parents. Thirdly, notwithstanding this similarity of parents and offspring, occasionally and quite frequently, variations from the parental type appear. If now we assume that also in the past there was no other cause of similarity than consanguinity, and if we admit that many small variations may lead, over long periods of time, to large changes, then evolution gives a satisfactory explanation for the gradually diversified manifoldness in the world of the organisms. This concept allows to explain an extraordinary amount of data — all those facts which are usually called the proofs of evolution from palaeontology, comparative anatomy, embryology, biochemistry, biogeography, and so forth, and which may be found in any textbook. Furthermore, it allows to predict yet undiscovered facts, as when intermediates between presently separated groups are postulated and afterwards found in the geological record, such as *Archaeopteryx* as intermediate link between reptiles and birds, or the series of the *Therapsida*, leading from the reptiles to the mammals. Thus, evolution is a theoretically inferred reality, to use Tschulok's term. The theory of evolution is a general conceptual scheme from which many data, already known or still to be discovered, can be inferred.

Subordinate to the question whether evolution is to be assumed, are the two further questions how it has occurred and why. The second question is that of the course of evolution, the establishment of phylogenetic relationships or so-called genealogical trees in particular. This poses innumerable questions to the taxonomist, the anatomist, the palaeontologist, etc., but is hardly a subject for heated philosophical controversy. This is somewhat different with respect to the third issue, the question of the causes and factors of evolution.

It appears that it is not so much the general concept of evolution, but certain hypotheses on the causes of evolution which are at the basis of much resentment from the philosophical and theological sides. It may be well to remember that the doctrine of spontaneous generation, of a transition of inorganic material into living organisms, was disposed of only in comparatively recent times, although the idea of a transformation of inanimate stuff into organisms is certainly much more materialistic than the idea of evolution, the transformation of one species of organisms into another. The doctrine mentioned was maintained all through the Middle Ages, and even in the beginning of the 19th century, Goethe still believed that fleas may originate from wood shavings and urine. The theory of the origin of intestinal parasites by way of spontaneous generation was generally accepted until the German zoologist Leuckart discovered the life cycles of tape worms and other such organisms; and only Pasteur's work in the 1860s repudiated spontaneous generations for the bacteria. The idea of evolution is not a modern invention although, of course, empirical biology is. The Cannon Dorlodot, an authority in patristics,

even claims that, to the end of the 8th century, part of the Fathers of the Church have formally professed the theory of natural evolution of living beings, while no Christian author is known before the scholastic period who would have contradicted it (after Otis, 1950).¹

Thus, much philosophical argument stems from not distinguishing the principle of evolution from a certain hypothesis about its mechanism. This is the hypothesis known under the somewhat ambiguous name of Darwinism which is, in modern terms, rather generally accepted in the biology of to-day.

In every species we find hereditary variations, called mutations in modern terminology. For example, in the pet of the geneticist, the fruit fly *Drosophila*, some 500 mutations are known which range from trifling minutiae, like shades of eye color or the variation of some bristles, up to deep-reaching alterations, if, for example, a certain mutation has four wings instead of the two characteristic of flies. Mutations are undirected, that is, they show no direct relationship to function, adaptiveness, or environmental conditions. The majority of mutations are disfavorable, and only a comparatively small number may present, generally or under certain environmental conditions, an advantage as to the original form. Furthermore, spontaneous mutations, as well as those that can be induced by outside factors, such as radiation, temperature, or chemical influences, are accidental with respect to external conditions. If, for example, mutations are produced by a raise of temperature, they are in no way adaptive to temperature; only the rate of mutations, occurring also otherwise, will be increased.

Secondly, there is selection. In any species we find an enormous overproduction of offspring which, however, does not lead to an unrestricted increase of the number of individuals. Mutations may be indifferent, advantageous or disadvantageous. If a mutation is unfavorable, it will soon be eliminated by selection. Favorable ones are preserved, and the individuals possessing them will be more likely to reproduce. Through incessant repetition of this process over long periods of time, it will lead to the evolution of new species and to their progressive adaptation to environment. It can be proved mathematically that a mutation which appears at a very small rate, and even if it presents only a small selective advantage, will become established and will supplant the original form in the course of a comparatively limited number of generations. Mathematical analysis also shows that selection pressure is greatly superior to mutation pressure. That is, even a small selective advantage in a positive or negative way is much more effective than mutation in a certain direction would be without selection. The consequence is that

1. L. OTIS, *La doctrine de l'évolution*, T.I, *Un exposé des faits et des hypothèses*, Montréal, 1950.

directiveness of evolution in the sense that it works against selection is all but impossible ; in the sense that it works without selection, it would be effective only over exceedingly long periods of time.

To the factors mentioned, a third is to be added, the so-called drift principle of Sewall Wright. If a species is subdivided into small populations which are isolated from each other, the mere accident of gene-combination can lead to the result that different mutations are established in these populations and regions, irrespective of their selective value. This may lead to the splitting-up of an originally uniform species into different subspecies and finally different species.

Thus, according to current theory, evolution is essentially based upon random mutation, selection, and chance action within small isolated populations. It is this accidental or chance-like character of evolution that has aroused passionate criticism. On the other hand, it is propounded in a dogmatic way which seems unwarranted. Genetical research has been carried through in the last fifty years on some dozens of animal and plant species. It is a basic principle in science to admit only theories that can be proved experimentally. However, it is a rather bold extrapolation to contend that, in two billions or so of the existence of life on our planet, nothing else has happened as what we have seen in two and a half score of years in some dozens of laboratories in America and Europe.

From the standpoint of general biology, the fundamental issue of evolution is not the origin of species, and not even the origin of classes or phyla — it is the origin of organization. A living organism is not a sum total of morphological elements or adaptive characters, but a complex organization whose function depends on the interplay of innumerable parts and partial processes, and where even a slight disturbance may lead to fatal results — witness the fact that the number of lethal mutations much surpasses that of indifferent and advantageous ones. Consequently, the origin of new species, not to speak of higher taxonomic units, means a re-adjustment of organization at almost all levels. Compare two species like mouse and rat which an experimenter has a daily opportunity to observe, and which are rather closely related. Their difference is not merely a matter of those characteristics which are enumerated in a taxonomical key. There are profound differences in the pattern of development and growth, in cellular metabolism, as when, for example, a certain carcinogen may produce tumors in one but not in the other species, in the instinctive and behavioral patterns which presuppose corresponding differences in nerve paths, centers, and hereditary co-ordinations, and so forth *ad infinitum*. Thus it appears that we have to look for evidence with regard to organizational principles and rules characterizing their changes. Admittedly, our knowledge of these organismic laws is in the first beginnings. But it seems that this viewpoint

which I have emphasized for a long time (cf. Bertalanffy, 1952),¹ is gaining ground and the actual evidence concerning it is increasing. In particular, the work of the German zoologist, Rensch (1947),² is to be quoted which is closely related to this topic. According to Rensch, neither the organization of the animal body, nor the environmental conditions allow for evolution completely at random, but there are limiting conditions which in many cases act as a direct evolutionary constraint. In this discussion, only a few remarks can be offered as to where such principles may be found.

One possible way is to look for parallelisms in evolutionary changes. Such parallelisms can be observed at three subsequent levels. The first level is that of the genes. It is a well-known fact that many genes and, correspondingly, the mutations they undergo, are homologous in related species, and that there are homologous genes and mutations even in species which are taxonomically rather distant. For example, large regions of the chromosomes are homologous in different drosophila species, such as *Dr. melanogaster* and *virilis*. The same applies to higher taxonomic units. There is a certain gene, called a^+ , that causes pigmentation in the flour moth (*Ephestia kuehniella*) by way of a hormone-like substance, known to be a rare amino-acid, kyurenine. In drosophila, there is a gene, v^+ , which makes vermilion eyes of a certain mutation to take on the dark red of the wild form, the chemical intermediate being the same. Thus the genes a , albino, in the moth, and v , vermilion eyes in the fruit fly, are homologous, and so are the genes a^+ and v^+ , wild type in both species. In this way, species which are widely different taxonomically, such as the flour moth and drosophila, rabbit and man, have certain genes in common, and consequently show parallel mutations. Parallel mutations within smaller or larger groups are a common phenomenon. For example, there are bearded and non-bearded varieties, brittled and firm ears, summer and winter forms to be found within different species of wheat. Again, the genus Rye repeats the series of species found in the genus Wheat. This is the so-called law of homologous series (Vaviloff), expressing that parallel series of mutations may appear in different taxonomical units. As was mentioned earlier, mutations are, in general, undirected. The phenomenon of parallel mutations indicates, however, that genes can undergo mutations in many ways, but not in an infinite number of ways.

A second class of parallelisms is found in variations which are similar phenotypically, but are due to mutations of non-homologous genes. For example, there are albino forms in widely different species,

1. L. VON BERTALANFFY, *Problems of Life. An Evaluation of Modern Biological Thought*, New York and London, 1952.

2. B. RENSCH, *Neuere Probleme der Abstammungslehre*, Stuttgart, 1947.

such as rabbits, mice, cats, humans, and so on. Some of these mutations may be due to mutations of homologous genes ; others to mutations of genes which are different and non-homologous. Parallelisms of this kind are found abundantly in botany, zoology, anthropology, palaeontology, zoogeography, and animal husbandry. Genes interfere in the complicated process that leads from a fertilized ovum to the completed organism. Such interference will be possible in many, but not in an infinite number of ways. For this reason, variations which are identical phenotypically, *i.e.* in their appearance, may arise from mutations of different genes, or may even occur as so-called phenocopies, that is, non-inherited parallel variations due to environmental factors. Developmental conditions seem to impose certain restrictions upon hereditary changes, in particular if the result is to be viable. In other words, possible evolutionary changes will not be completely at random.

Thirdly, there are parallelisms where the genetic as well as the developmental basis is different. There seem to be principles which allow only certain trends in evolution. An often-quoted example is the evolution of the eye. Lens eyes constructed according to the principle of a camera are found in a very similar form in the scallop, the cuttle fish, and the vertebrates. Phylogenetically, these animals are widely different, and so they are embryologically. In invertebrates, the eye is developed from the epidermis, in vertebrates from the brain. Nevertheless, once the way towards a complicated eye is taken, there seems to be no other course than the successive stages of a flat eye, a socket eye, and a lens eye, and thus we find them in the most divergent classes of animals. Simpson (1951)¹ has criticized the argument, pointing out that the parallelisms between the eyes of the octopus and man are only picked-out examples of a great array of photoreceptors that includes almost any conceivable construction. This, of course, is agreed but it does not seem to invalidate the argument ; *viz.*, that the formation of a complex organ like an eye, although tried in different ways, has only one or a few solutions that are technically satisfactory. We may compare this with industrial progress. The early automobiles, as built in 1900 or so by American and German inventors, present the most different forms of awkward carriages. The inherent necessities of construction, however, have led to parallel developments and eventually to a common standard, so that, as far as the essential parts and not the trimming is concerned, there is not much difference between modern cars of different brands, although their « ancestral lines » were different. Something similar seems to apply to basic principles of organization. The evolution of a secondary body cavity, of metamerism, of a circulatory system, etc., is found both in annelids and in chordates ; classes that are antithetic

1. G. G. SIMPSON, *The Meaning of Evolution*, New Haven, 1951.

in their type, their phylogeny and ontogeny. It appears that there are general laws of organization which allow evolutionary progress only in certain directions.

Thus, a living organism appears not an aggregate of characters accumulated at random, but as being governed by definite laws of the system as a whole. In certain cases, we are able to state these laws in a mathematical way. This is shown most clearly in the consequences of changes in body size which are a common phenomenon in evolution. Usually, although in no way without exception, evolution follows the rule of a progressive increase in body size which can be found in many groups of animals. Increase in body size may, by way of different relative growth of organs, entail far reaching changes in proportion and consequently changes of form. For example, in the human newborn the length of the head is about $\frac{1}{4}$ of the total length of the body ; in the adult, it is only $\frac{1}{8}$. This is a consequence of the fact that the relative growth of the head is less than that of the rest of the body. The reverse is true for the legs which grow relatively faster, and for this reason the adult has relatively longer legs than the newborn. In many cases, relative growth is governed by a simple mathematical expression known as the law of allometric growth (Huxley, 1932).¹ The allometric law applies as well to developmental as to evolutionary changes, as may be seen in two classical examples. In the titanotheres, a family of extinct ungulates of the tertiary period, the earliest forms which were the smallest, did not have any horns. In the species appearing later, horns are developed the size of which progressively increases with increasing body size till they reach monstrous proportions. Thus, the phylogenetic increase of body size is correlated with the increase of the relative size of the horn, this process following a mathematical law. Another classical example is the evolution of the horses, characterized by progressive increase in body size, progressive elongation of the skull, and progressive reduction of the number of toes. The elongation of the skull in the evolution of the horses in relation to body size again follows a simple mathematical law so that it has been said that hundred millions of years of evolution appear to be governed by a simple arithmetic formula.

Such examples illustrate that, in certain cases, it is possible to establish quantitative laws of evolution. The second example shows even something more: The elongation of the horse's skull is connected with important functional and adaptive changes. The relative increase of the preorbital region allows an animal of considerable body size easier to reach the ground for grazing ; it gives space for the large molars, important for a big herbivorous animal. These adaptive changes are intimately connected with the change of pro-

1. J. HUXLEY, *Problems of Relative Growth*, London, 1932.

portion in the skull and, consequently, with the increase in body size. Thus, changes like those in body size do not affect one character only, but may have complex and partly functional and adaptive consequences. There are a number of factors known which may lead to harmonic transformations : the so-called pleiotropism of the genes, that is the fact that mutations in one gene often influence not a single character, but may lead to correlated transformations in different systems of organs ; regulations in development, where changes in one character may entail adjustments in other systems ; hormones which, controlled by genes, in their turn control the structure and function of the organism as a whole ; the so-called phenomenon of compensation, and so forth. Investigation on these lines is only in the beginning, but it appears obvious that the organism must not be considered as an aggregate of parts accumulated at random, but as a system whose parts are in intimate interaction, and which is governed by definite laws.

Thus it appears that evolution can be considered to be not a series of accidents the course of which is determined only by the change of environments during the history of the earth and the resulting struggle for existence which leads to selection within a chaotic material of mutations. Rather it appears a process essentially co-determined by organismic laws, some of which can be indicated at present, and about which we may hope to learn more in the future.

This, I think, is as far as the scientist can go. His ultimate goal is the establishment of laws which mirror certain relations in the world of phenomena. About the inner essence of things, the ultimate reasons, he is silent. The biologist will be able to penetrate, by way of experiments, into ever deeper and more remote levels of nature ; to establish progressively more refined models to put in order his observations, and to establish laws which characterize certain aspects of the phenomena. He will not unveil, however, the mystery of what is called Life.

LUDWIG VON BERTALANFFY.
