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SELF-ORGANIZATION AND THE THEORY OF EVOLUTION¹

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ABSTRACT

The author distinguishes three types of evolutionary theories: 1) ahistorical theories, constructed according to the methodological patterns of classical physics (mechanics), 2) supra-historical theories, in which the historical nature of the evolutionary process is reflected in a more complete (than only in the sense of the chronology of events) and richer, but its mechanism remains unchanged—"taken out of history," 3) fully historical theories, recognizing that the factors and mechanisms of evolution themselves are entangled in history: are subject to changes in the course of historical development. A prominent representative of the third type is the theory of Ivan I. Schmalhauzen. Some peculiarities of its methodological structure are analyzed. This analysis allowed to reveal the premises of the process of evolution understood as a process of self-organization and to determine the basis on which it can be concluded that the general theory of evolution is nothing else than a theory of biological organization.

Keywords: Synthetic theory of evolution, driving (and other) factors of evolution, theory of stabilizing selection, historical variability of factors and mechanisms of evolution.

EVOLUTION AND ORGANIZATION

In the methodological perspective, the problem of the relationship between evolution and organization is often presented as a postulate to supplement the historical approach with a structural and systemic approach. This standpoint seems unsatisfactory, as it suggests that these are two fundamentally independent approaches. It remains unclear whether the theory

¹ This paper is a translation of an article from the author's handwritten legacy; translated by Włodzimierz Ługowski.

of evolution or the theory of organization should be taken as the starting point. And in what relation will the central theses of both theories stand in each of these variants? The answer to this question is quite simple, albeit seemingly paradoxical: the fundamental biological theory is the general theory of evolution—which is nothing else than the theory of the development of biological organization.

With this understanding of the theory of evolution, the concept of "biological organization" becomes a category of this theory, i.e. a concept necessary to express its central theses. And vice versa: it is on the basis of these theses that the concept should acquire its definition.²

An in-depth analysis of the basic issues of biological organization within the theory of evolution—in its modern form—becomes absolutely possible, and this is because:

- while earlier in the theory of evolution the central place was occupied only by evolutionary processes and their mechanisms, today the issues of the stability of biological systems have also gained full civil rights;
- evolutionary processes were once considered only at one (organismal or population) level of biological organization; this one-sidedness has already been overcome—evolutionary processes are studied at various levels of the organization;
- the theoretical approach to the evolutionary process as a process of self-organization is deepened and consolidated [such an approach has recently gained support from cyberneticists and scientists studying the origin of life (Manfred Eigen, Hans Kuhn et al.)].

An example of such an approach can be the widely known theory of evolution, developed by academician Ivan I. Schmalhauzen (1884–1963). His work in cybernetics is prioritized to address the entire evolution of life on Earth as a self-organizing system.

The analysis of the basic content and methodological structure of the "pre-cybernetic" version of Schmalhauzen's theory, to which this article is devoted, will reveal the premises of the evolution process as a process of self-organization.³

² At one of the symposia gathering naturalists and philosophers, the author formulated this very idea—that the general theory of evolution is precisely the theory of the development of biological organization; he also analyzed a number of "organizational" concepts, viewing them as an integral part of the causal-explicative theory of evolution. This speech sparked a lively discussion. The speaker was accused of underestimating the role of the substrate in evolution and of taking the position of "organismocentrism." This article is intended to be an indirect response to those criticisms.

³ Scientific research is in our understanding a teleonomic system of actions and statements, aimed at causal explanation of empirical regularities (adequate to reality). An essential part of this system is the explicative theory. Theory is more than a set of sentences: it is a structured whole in which the empirical regularities of the examined processes (explanans) are derived from theoretical premises defining the factors of evolution and their mode of operation, i.e. the mechanism of the process (explanandum).

In the views of Schmalhauzen and Julian Huxley from the turn of the 1930s and 1940s, there are premises for such an approach to the evolution process, which treats it as a progressive increase in the level of morphophysiological organization. However, in the genetic theory of evolution, which is being developed at the same time, there are no such premises; even the very idea of evolutionary progress is frowned upon in it. It is enough to recall that in 1951 and 1955 Theodosius Dobzhansky claimed that one can talk about progress only in the sense of an increase in biomass on Earth; George G. Simpson's considerations are also known, who in his work *Meaning of Evolution* tried to subjectivize the concept of progress, making an exception for only one objective tendency "for life to expand."

The genetic theory of evolution was built on the foundation of population genetics in the sense that, firstly, its main concepts were taken from this arsenal (evolution is a change in the genetic makeup of a population; its mechanism is gene substitution, etc.), and secondly, that all theses of this theory can and should be directly tested in population-genetic experiments. Hence the tendency of this theory to an operationalist (in the Bridgman's sense) approach to concepts.

The first two editions (1937 and 1941) of Dobzhansky's *Genetics and the Origin of Species* provide a classic exposition of this theory. The author constructed his theory according to the methodological patterns of classical physics (mechanics). He spoke, in particular, of evolutionary "motion," "statics" or "dynamics;" as the causes of evolutionary changes, he pointed to additively acting factors, leading the population out of genetic equilibrium, etc. A theory of this type does not allow for the recognition of evolution as a process of self-organization. Despite the changes that the genetic theory of evolution underwent over the next few decades, its main features and methodological "ideals" remained intact. You can see this by reading the works of authors such as J. Maynard Smith, W. Ludwig, P. R. Ehrlich, R. W. Holm ands G. C. Williams.

THE THEORY OF EVOLUTION AND THE VARIETY OF EVOLUTIONARY PROCESSES

The theory of evolution—according to Schmalhauzen—is an independent branch of biology. Attempts to squeeze its issues into the framework of any of the other biological sciences end in failure. Efforts to situate it on a basis that is sufficient for other fields of life sciences are also fruitless. And so, the relationship between the theory of evolution and ecology is striking, because ecology, as the science of mutual relationships between organisms and their environment, has as its subject the "struggle for existence"—the process that is the basis of natural selection and evolution. However, outside the area of

interest of an ecologist, there are, for example, such important issues for the theoretician-evolutionist as the historical variability of forms—the subject of morphology and paleontology.

The historical dynamics of forms also remains outside the field of view of experimental genetics. At the same time, genetics, which studies the foundations of hereditary variability, is far from analyzing the specific bonds between organisms and their sphere of being. Putting the regularity of the formation and dissemination of hereditary changes in the foreground, geneticists tend to overestimate them. Due to the limited tasks faced by ecology and genetics, these fields cannot provide the basis for the theory of evolution—but vice versa yes: as a fundamental biological theory.

"Darwinism," wrote Schmalhauzen, "investigates the regularities of the historical development of organisms and its driving forces." Taking into account the role of chance in particular phases of change, Schmalhauzen considers evolution to be a lawful and directed process. The task of the theoretician is not only to reveal its regularities, but also to explain them by analyzing the factors and mechanisms of evolution.

Such a causal and explicative character was given to the theory of evolution by Darwin, who tried to explain such regularities as the adaptive character of evolutionary changes, divergence of features, increase in organization complexity, irreversibility of the course of evolution.

Theorists do not have to complain about the lack of empirical regularities of evolution. What makes their task more difficult is rather the variety of directions and forms of evolutionary changes. In his theory, Schmalhauzen tries to take this diversity into account. His theory is clearly akin to Huxley's in this regard. Huxley, however, seems to overly succumb to the pressure of diversity, which makes it difficult for him to construct a logically coherent theory, while Schmalhauzen skillfully combines multiplicity with an indication of the basic feature of all manifestations of earthly life. This feature is the adaptive nature of the processes of biological evolution.

This thought runs like a guiding thread through the entire work of Schmalhauzen—the theoretical successor and creative continuator of the ideas of A. N. Severtsov. "According to Darwin," writes Schmalhauzen, "the purposefulness of the structure and functions of an organism is expressed in its adaptation to certain living conditions." Purposefulness understood in this way is "the basic feature of all life." Hence the logical conclusion: "Darwinism assumes that of all the problems of the theory of evolution, the question of the morphophysiological purpose of organisms should be resolved first."

⁴ И. И Шмальгаузен [I. I. Schmalhauzen], *Проблемы дарвинизма* [Problems of Darwinism], Moscow 1946, p. 6.

⁵ Ibidem, p. 132.

⁶ Ibidem.

By revealing the multitude of directions and forms of evolutionary processes, Schmalhauzen also establishes a hierarchy of problems in the theory of evolution. Central among them is the issue of adaptation. This must be borne in mind in order to be able to accurately recognize the foundations of Schmalhauzen's theoretical construction, which will be the subject of consideration in the next paragraph. In the meantime, let's stick to the very concept of adaptation.

The methodological clarity of the position taken by the author of *Factors of Evolution* is evidenced by the fact that he precisely separates the meaning of the theoretical concept of "adaptation" from recognizing organisms as "adapted" (objective reference of the concept). Since a certain degree of adaptation is an indispensable feature of life,7 the concept of adaptation is related to the very concept of life. Only a developed definition of life, difficult to formulate with the current state of knowledge, will allow us to define the concept of adaptation without falling into a vicious circle. Therefore, Schmalhauzen limits himself to only some aspects of adaptation, and the following seems important.

The adaptation of an organism (i.e. the purposefulness of its construction and functioning) depends on its interaction with the environment, its specific activity and way of life. When talking about the adaptation of an organism, one should bear in mind the correlations of its parts. The coadaptation of organs and their functions is, in a way, the internal side of adaptation to the environment. The adaptation of the body manifests itself not only in maintaining its own life activity but also in caring for offspring.⁸

It can be said—expressing Schmalhauzen's thought in a modern terminology—that an organism adapted to a given environment functions in it as a teleonomic system, focused on preserving its own life and that of its offspring. "It is necessary," wrote Schmalhauzen, "to study the structure and functioning of an organism in detail in order to be able to isolate features that are particularly important for its survival." "Maximizing survival can occur in many ways: by increasing the level of internal organization, protection from predators, increasing fertility, caring for offspring, and other ways." 10

So far, we have presented Schmalhauzen's views on the meaning of the term "adaptation" and on what characteristics of organisms may be responsible for a "high degree of adaptation." Turning to the question of the objective reference of this concept, however, Schmalhauzen asks what are the criteria for recognizing organisms as adapted to a given environment?

⁷ И.И. Шмальгаузен [I. I. Schmalhauzen], Пути и закономерности эволюционного процесса [Ways and Laws of Evolution Process], Moscow-Leningrad 1939, p. 232.

⁸ Íbidem, p. 69.

⁹ Ibidem, pp. 64-65.

¹⁰ Ibidem, p. 69.

"Apart from observing the fact of survival, in fact, we have no other criterion for adaptation."

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Separating the analysis of the theoretical meaning of the term "adaptation" from the issue of the criterion of adaptation (actual survival and leaving offspring) is the difference between the theories of Schmalhauzen and Huxley, on the one hand, and the genetic theory of evolution, on the other. In the latter, the pursuit of operational definition of concepts leads to the blurring of the difference between the driving factors of evolution (determining survival and reproduction) and the available observation and measurable experimentally differentiated reproduction (carriers of different genotypes). It is only on the basis of such a distinction between the two types of theories that it becomes understandable why the danger of a tautological definition of the term "natural selection," noted with some exaggeration in the framework of the genetic theory of evolution (C. H. Waddington, M. Lerner et al.),12 in fact, did not threaten this theory of evolution, which was moving towards the theory of self-organization.

FACTORS OF EVOLUTION

The theory of evolution is expected to explain the various aspects of life as it develops. This goal is served by determining the factors of evolution and the way they work—that is, the mechanism of evolutionary changes (explanans of the theory). The cognitive value of the explanans theses is confirmed not only empirically, by the fact that such factors occur in nature, but also by revealing the explanatory power of these theses, i.e. by showing that the regularities of evolution described in the explanandum can be derived from them.

The specificity of Schmalhauzen's approach to the factors and mechanisms of evolution consists in distinguishing "necessary premises" from "factors" of evolution, and among the latter—in distinguishing "driving" factors from "others."

In Schmalhauzen's theoretical construction, driving factors play a major role. These include the struggle for existence and natural selection.

Both the struggle for existence and natural selection are invariants¹³ of evolution: throughout the history of the living world, organisms have been drawn into the struggle for existence and thus subjected to the action of se-

¹¹ Ibidem, p. 68.

¹² C. H. Waddington, *The Strategy of the Gene*, London 1957; M. Lerner, *The Concept of Natural Selection*, Proceedings of the American Philosophical Society, 1959, 101 (2).

¹³ On the concept of invariant see: A. Lubomirski, *Rozwój i niezmienniki* [Development and Invariants], in: *Ewolucja biologiczna. Problemy informacji i rozwoju. Szkice teoretyczne i metodologiczne* [Biological Evolution. Problems of Information and Development. Theoretical and Methodological Studies], Cz. Nowiński (ed.), Ossolineum, Wrocław 1976, pp. 155–163.

lection. The driving factors of evolution are causal in this case—in the "strong" sense of the word: they not only cause evolutionary changes, giving them an adaptive character, but also produce new organic forms. Creating new forms, of course, does not mean creating them "out of nothing," but transforming the "raw material" which is a necessary premise for evolution. This material is genetic variability related to heredity. Heredity and variability—as immanent features of organisms—should also be considered as invariants of evolution ("convariant reduplication" by Timofeeff-Ressovsky's et al.).¹⁴

However, heredity and variability—which in Schmalhauzen's conception are the premises of evolution—are not among the driving factors. Evolution would be impossible without heredity and variation; when they occur, the struggle for existence and natural selection act as causes of evolution. If by "cause" we mean simply the totality of necessary and sufficient conditions for evolutionary change (and this understanding has become widespread under the influence of positivist thought), it would make no sense to distinguish necessary premises from driving factors.

Heredity, variability, the struggle for existence and natural selection—together they form a complex of conditions necessary for the course of evolution. However, the term "driving factor" expresses something more: it points to its guiding role in the creation of new organic forms from the "raw material" offered by genetic variation.¹⁵

There is another meaning behind the distinction between "driving" and "non-driving" factors. We will return to this, however, after considering the central concepts of Schmalhauzen's theory—"struggle for existence" and "natural selection"—and their relationship to each other.

In the scientific literature, the concept of driving factors of evolution has been discussed quite extensively. Here, therefore, it is enough to dwell only on those of Schmalhauzen's theses that are related to the topic of our article.

The "struggle for existence" expresses the "complicated relations between the organism and its biotic and abiotic environment." Darwin's concept of "struggle for existence" reflects an important feature of organisms, namely, their activity in relation to the environment.¹6 This activity is expressed in the "acquiring" of the necessary substances and energy by an organism from the environment, in defence against attackers and in reproduction. This activity of is opposed by resistance from the environment, which results in the annihilation of a certain number of individuals from a given population or preventing them from reproducing.

¹⁴ Н. В. Тимофеев-Ресовский, Н. Н. Воронцов, А. В. Яблоков, *Краткий очерк теории* эволюции, Moscow 1969 [Kurzer Grundriß der Evolutionstheorie, Jena 1975].

¹⁵ This idea refers in a way to the Aristotelian understanding of matter and form, as well as to the concept of formal cause. The most important thing here, however, is that the causal relationship means something more than just a constant succession of phenomena—it also includes the idea of natural (biological) necessity.

¹⁶ И. И. Шмальгаузен [I. I. Schmalhauzen], *Факторы эволюции* [Factors of Evolution], Moscow 1946, p. 127; Edition in English: Philadelphia—Toronto 1949.

The struggle for existence is always connected with elimination understood in this way. All other things being equal, individuals that are less well adapted (in some respects) perish or do not leave offspring, while those that are better adapted survive; elimination is selective. This is related to another aspect of the struggle for existence—the competition between individuals. If a certain number of individuals of a population or species face the same danger, or if they are subject to the same constraints on survival and reproduction, then natural selection becomes possible for some of them, namely, those that have been able to avoid threats or overcome barriers. "Natural selection," Schmalhauzen writes, "is closely related to the struggle for existence: it fully depends on its occurrence. It is a process diametrically opposed to elimination and directly defined by competition.¹⁷

The nature of the struggle for existence is always determined by the specific mutual relations of the organism and the environment—created in a given place, time and conditions. Different forms of elimination are associated with different forms of natural selection and mark different directions in the process of evolution. As a necessary and sufficient premise of natural selection, the struggle for existence, figuratively speaking, plays the role of "commanding," and selection "executing her commands."

Although there are various forms of elimination and competition, the explanans of Schmalhauzen's theory emphasizes that "only individual natural selection, based on the competition of individuals within a group, has a creative character." ¹⁹

Both the struggle for existence and natural selection are population phenomena, since competition takes place between individuals within a population, and the elimination of some individuals automatically entails the selection of others. At the same time, however, selection, as the reverse side of the elimination of some individuals, is precisely the selection of individuals—and its population dimension should not obscure this fact. When analyzing Schmalhauzen's theory, one should not avoid recognizing this fact, even under the threat of being accused of "organismocentrism."²⁰

¹⁷ И. И. Шмальгаузен [I. I. Schmalhauzen], *Проблемы дарвинизма* [Problems of Darwinism], op. cit., p. 261.

¹⁸ И. И. Шмальгаузен [I. I. Schmalhauzen], *Факторы эволюции* Factors of evolution], op. cit., p. 131.

¹⁹ Ibidem, p. 137.

²⁰ This concept was introduced by K. M. Zawadski. However, some authors use it in discussions as "long-range weapons." Scientific literature has recently been enriched by Zawadski's valuable book *Развитие эволюционной теории после Дарвина* [The Development of Theory of Evolution after Darwin], Leningrad 1973. It includes a huge amount of factual material and proposes a new approach to the history of evolutionary theory in the post-Darwinian period. Unfortunately, it is difficult to agree with some of Professor Zawadski's conclusions, in particular with his belief in the unity of the synthetic theory of evolution. Professor Zawadski, rightly emphasizing the need to confront theses of theory with empirical material, pays too little attention to the organizing role of theory and the importance of theoretical constructions in the development of scientific thought.

In the light of this theory, we cannot talk about the selection of genes, genotypes, reaction norms, phenotypic features, etc. Changes in the genetic composition of the population, reaction norms, etc. are derivatives of the natural selection of individuals, and the direction of these changes is determined by the relations of the struggle for existence. The mechanism of evolution, according to Schmalhauzen, consists of several interrelated links, which include:

- struggle for existence;
- natural selection of individuals within a population as a result of the struggle for existence;
- selection-related change in the genetic make-up of a population, exacerbated in successive generations by recombination of genes.

Any attempt to replace the selection of individuals within the population by the selection of genes, genotypes and their transmission, or any attempt to reduce the struggle for existence to natural selection—is, in our opinion, a significant departure from Schmalhauzen's theory.²¹

Natural selection always has to do with the morphophysiological structure of the organism, realized in given conditions, i.e. with the specific phenotype of particular individuals. Schmalhauzen's theory, developed in the 1930s, differs because of this thesis from the genetic theory, according to which the evolutionary dialogue takes place between the environment (represented by selection) and genes (and their mutations).

For Dobzhansky, this involved a "genetic reduction" of phenotypic traits to "underlying genes."²² In the 1940s and 1950s, the views of the proponents of the genetic theory on this issue gradually changed: the belief, that natural selection "favors (or eliminates) phenotypes rather than genotypes, began to prevail.²³ Thus, the genetic theory assimilated the thesis that had been advocated for a long time by representatives of the second current of the synthetic theory of evolution. However, with a different construction of the explanans, even an identically sounding thesis takes on different meanings in both streams.

In the "self-organization theory," the statement that selection has to do with the phenotype realized in given conditions means that the organism in the entire course of its individual development (ontogeny) is subject to "environmental control," i.e. the pressure of the struggle for existence. Natural selection, on the other hand, summarizes the comparative assessment of

²¹ The tendency to blur the difference between the theoretical concepts of both currents of synthetic theory seems wrong. It is very surprising that W. Berg, a close relative of Schmalhauzen, in presenting (in two prefaces) his position on the factors of evolution, makes no mention of the struggle for existence and actually reduces his concept of natural selection to that of the representatives of the genetic theory of evolution.

²² Cz. Nowiński, *Kryzys struktury teorii ewolucji* [A Crisis of the Structure of Evolution Theory], Studia Filozoficzne, 1969 (2), pp. 47–67.

²³ R. Mayr, Animal Species and Evolution, Cambridge 1963.

organisms of a given population as teleonomic systems from the point of view of their functioning in a given environment.

Within the framework of the genetic theory, however, this thesis cannot be given a similar meaning, because it would have to be admitted at the same time that evolution is based not on transgenerational mechanisms (studied by population genetics) but on the mechanisms of the struggle for existence within one generation. Emphasizing the role of the phenotype here is tantamount to valuing ontogenesis and its regularities, however, not in the relationship "ontogenesis—struggle for existence" but in the relationship "genotype—its realization in ontogenesis."

Abandoning the primitive, unambiguous correlation of "features" of phenotype and genes (or genotype and phenotype) allows advocates of the genetic theory to recognize the importance of epigenesis and buffering of developmental processes. Buffered ontogeny shields certain mutations from selection based on phenotype traits, and these may turn out to be the same across genotypes.

The peculiarities of ontogeny processes may therefore affect the rate of evolutionary change; they also increase the proportion of chance, because, as Adam Urbanek notes, "natural selection is like a gambler pulling cards from a deck, seeing only their identical shirts, unable to assess their real value."²⁴ This is the case from the perspective of genetic theory, which focuses on genetic and population processes, making them a model of evolutionary changes.

From a different point of view—oriented towards the concept of selforganization—the "snag" created by the ambiguous correlation of phenotype and genotype is also noticed, but interpreted differently: the buffering of ontogenesis, its autonomization and regulatory nature accelerate the pace of evolution.

Let us now turn to the "non-propelling" factors of evolution. When analyzing the struggle for existence and natural selection, we referred to a variety of processes: ecological, organism-population (such as dynamic relations "organism-environment," elimination of individuals and their selection within the population), etc. It is obvious, however, that the operation of the "driving" factors of evolution leads also to changes at the genetic level, namely to changes in the genetic composition of the population; by their very nature they transcend the boundaries of a single generation.

However, the mere ascertainment of the genetic consequences of natural selection, or the recognition of heredity and variability as the necessary prerequisites for evolution, does not yet provide an answer to the question of the essence of the action of the factors of evolution—their role that should be taken into account in the explanans of the theory.

 $^{^{24}}$ A. Urbanek, $Rewolucja\ naukowa\ w\ biologii$ [A Scientific Revolution in Biology], Warszawa 1973.

Consider the example of the genetic reserve of variation to which Schmalhauzen paid special attention. Well, this "mobilization reserve" does not determine the direction of evolutionary changes—even in conditions conducive to its activation. Instead, it increases the rate of transformation by increasing the efficiency of selection, providing it with material in the form of an additional pool of diversity.

Schmalhauzen is far from considering population-genetic models as models of evolution, but this does not prevent him from using the findings of Fischer, Wright or Haldane to consider the role of "non-drivers." Thus, the evolutionary potential of natural selection is determined, in his opinion, by the genetic diversity of individuals in a population according to Fischer's so-called fundamental law of selection. In turn, according to Wright, the possibility of an increase in the rate of evolution appears with the splitting of a species into a series of relatively isolated populations. In a word, population and genetic factors play an important role in determining the pace of evolutionary changes—they can decrease or increase them.

Considering the role of genetic factors in evolution in a slightly different aspect, it is usually stated that genomes, shaped in the course of the historical process of evolution, in fact limit the paths and possibilities of further changes, setting in particular the limits of acceptable mutations.

However, a closer analysis also reveals the other side of this issue. Schmalhauzen is known to have opposed the widespread view that the emergence of new organic forms was the result of the accumulation (preserved by selection) of "lucky" (beneficial) mutations. Individual mutations, as he emphasized, are usually harmful: they violate the structures and functions formed in the course of long-term evolution, in the course of which organisms adapted to the environment, and their organs adapted to each other. The formation of new, harmonic forms can in no way be the result of a combination of a series of harmful mutations. Even if a mutation is (under the given conditions) useful in some respect, it is highly unlikely, due to the pleiotropic effect of genes, that its other manifestations will turn out to be just as "lucky."

From this, Szmalhauzen draws the conclusion that one of the factors of evolution is not individual mutations, but gene recombinations. With sexual reproduction and diploidy, the number of possible combinations is enormous; therefore, there may be those whose beneficial effects are preserved and the negative ones are neutralized. In the next steps of natural selection, mutations are "processed" in such a way that their harmful manifestations are neutralized and their beneficial manifestations are amplified. The result is a new form, different from the previous ones, adapted to the environment and functioning in a harmonious way.²⁵

 $^{^{25}}$ Schmalhauzen considers these problems in detail in his book *Пути и закономерности эволюционного процесса* [Ways and Laws of the Process of Evolution], 1939, and in a number of articles from this period. It is interesting that here too there is an analogy between his views and

According to Schmalhauzen, evolution entered the path of forming new, progressive forms of life, and natural selection became creative in the full sense of the word, only when an orderly mechanism of gene recombination was formed.

Comparison of the situation in the early phase of evolution, when genetic recombination does not yet occur, and the material is provided by single mutations, with the situation where we are already dealing with a wealth of recombinant variability, allows us to conclude that genetic recombination opens up new possibilities for the operation of natural selection. Previously, selection could only accept or reject a mutation, but could not influence its phenotypic expression. The emergence of the mechanism of genetic recombination allowed to remove this limitation. From then on, a gradual "processing" of the mutation could begin, improving its phenotypic expression and neutralizing the harmful, while strengthening the beneficial "novelties."

The genetic factor created a new possibility by removing a pre-existing constraint. However, this possibility could materialize only because an invariant of the evolution process is the struggle for existence and its result, i.e. natural selection. By realizing these new possibilities, selection becomes more flexible and efficient in creating new life forms.

The example of recombination shows that genetic factors, while not themselves among the driving factors (i.e. causes) of evolution, co-determine its direction and effects—allowing for a new way of natural selection.

This brief review of the ways in which the non-driving factors of evolution work has shown us that they either limit or expand the field of selection, increase or decrease the rate of change. Let us return now to the question of the drivers of evolution for a moment's consideration of the well-known theory of stabilizing selection. This will create an opportunity to show another side of the interrelationships driving and other factors of evolution.

In a situation of achieved balance between the organism and the environment, stabilizing selection maintains and consolidates the developed adaptive norm. Of course, the elimination of deviations from the norm also leads to the reduction of variability, to the "normalization" of the population and thus to the narrowing of evolutionary possibilities. However, the elimination of deviations from the norm entails other, much more distant consequences, which are also very important for the course of evolution.

Well, organisms sometimes react to random, short-term changes in the action of external factors. These reactions are undesirable, as the conditions soon return to normal, and the selective advantage remains with individuals with a lower reaction standard, those that have not reacted to a temporary change in environmental conditions or internal factors (mutations).

As a result, selection favors the survival and procreation of more stable individuals. The means of this stabilization may be different: at least some genetic apparatus, such as diploidy, the dominance of the norm, co-adaptation of genes or intracellular regulatory systems. It also includes mechanisms of ontogenetic development, such as a complex system of morphogenetic correlations, shifting the upper and lower thresholds of normal tissue reactivity, development of regulatory mechanisms of ontogenesis or development autonomization.

Stabilizing selection cooperates in the formation of these mechanisms, thus favoring the reconstruction of the genetic apparatus and ontogenesis with its mechanism. This, in turn, affects how natural selection works in a feedback loop. Let's take a closer look at this on the example of morphogenetic correlations. As a rule, they have a hindering effect on evolutionary changes, as it is not only individual organs and their reactions that are at stake here, but also the relationships between them. The situation changes when, under the action of stabilizing selection, a regulatory system of ontogenetic processes is created and reaches the degree of complexity and precision that characterizes higher vertebrates.

Under these conditions, evolutionary changes in one section of the morpho-physiological organization entail changes in other sections. The correlative regulatory system thus becomes a factor accelerating the evolution of the population by ensuring the possibility of a comprehensive, harmonious reconstruction of organisms. At the same time, selection will be more effective and less dependent on random factors, such as single mutations.

Two types of conclusions can be drawn from the above analyses.

• According to Schmalhauzen's theory, the hereditary stability of the morpho-physiological structure and reaction of organisms can be expressed to varying degrees. This stability and the balance of organisms of a given population in relation to the environment is the result of evolution. The theory discussed here seeks to explain not only evolutionary changes, but also the resulting states of equilibrium and stability.

The principles of genetic construction of the theory of evolution are fundamentally different from Schmalhauzen's theory. According to her, the factors of evolution (mutations, selection, etc.) upset the genetic equilibrium of a population. Within this theory, the causal explanation of genetic balance, described by the Hardy–Weinberg law, is redundant: the balance is given in advance, only deviations from it need to be explained.

In Schmalhauzen's theory, however, the stability and balance of the "organism-environment" system is not something "given from above"—but shaped historically. This allows us to pose the question of what role the degree of stability obtained in its previous phases plays in the further stages of evolution.

• The driving factors of evolution (the struggle for existence and natural selection), producing new adaptations, new organic forms, new relations in the apparatus of heredity, and finally new, more stable forms of ontogenesis, thus modify the character of the previously existing non-driving factors (genetic and ontogenetic). The feedback from the modified non-propelling factors towards the driving ones leads in turn to a change in the mechanism of evolution. Evolution, "guided" by a certain mechanism, therefore changes (reorganizes) this mechanism itself. Moreover, on the basis of the above analyses, it can be assumed that in the course of evolutionary changes—and under their influence—their mechanism is improved: in the sense that it becomes more and more independent of accidental influences and more and more effective. These assumptions are confirmed by Schmalhauzen's concept of evolutionary progress, which we will now analyze.²⁶

THE THEORY OF EVOLUTION AS A THEORY OF SELF-ORGANIZATION

Schmalhauzen considers the evolution of life on Earth from two points of view. On the one hand, evolution is a multiplicity of diverse processes, running in different phyla and in different geological epochs. Investigating these processes allows us to establish certain empirical regularities. On the other hand, evolution is treated by Schmalhauzen as something more than a collection of individual processes: namely, as a uniform historical whole, directed in its development. Schmalhauzen's concept of progress fits precisely into the context of the process of evolution as a coherent whole. The genetic theory of evolution offers no basis for such a holistic view. It is not surprising, therefore, that the issue of evolutionary progress has not found an appropriate place in her field and only recently has begun to pave its way. Let us briefly recall Schmalhauzen's characterization of evolutionary progress. Namely, it include:

- an increase in the morpho-physiological complexity of the organization associated with the accumulation of adaptations of the widest possible understanding;
- increase of individual adaptive capacity in its various forms;
- increasing complexity of correlation mechanisms, which are becoming more and more regulatory;
- autonomization of ontogenesis;

²⁶ Beginning in 1938, Schmalhauzen considered in his works elements of the theory of progress, taking into account the proposals formulated in this respect by academician A. N. Severtsov, but also making a significant own contribution. A detailed exposition of this concept is contained in the last part of his monograph Факторы эволюции Factors of Evolution].

- increase in the importance of the hidden reserve of mobilization variability in the population;
- activating various forms of the struggle for existence, increasing the intensity of metabolic processes and the pace of life;
- the increasing selectivity of elimination and selection, as well as the increasing efficiency of selection and the increase in the rate of evolution.

Progress understood in this way can, generally speaking, be presented as an increase in morpho-physiological complexity—as well as an increase in the ordering of the mechanism of evolution, which works more and more effectively.

With the increase in morpho-physiological organization goes hand in hand the expanding scale of control of the environment. The selective nature of selection, in the face of the ongoing competition of teleonomic systems (organisms) as to the effectiveness of their functioning in a given environment, gives evolutionary changes an adaptive direction. The historical timescales of the evolution of terrestrial life, as well as the accumulation of broad-profile progressive changes, make it likely that species with a high degree of organization will emerge.

The evolution of life on Earth, taken as a historical whole, thus gives a picture of the emergence of organic forms with an increasing degree of organization. Along with the increase in the selectivity of elimination, the very mechanism of evolution is also perfected, its orderliness and independence from accidental influences increase.

Schmalhauzen's theory in the 1930s and 40s did not yet include the statement that perfecting the mechanism of evolution over time is a biological necessity. Explicitly, this phrase appeared in the author's cybernetic works in the 1950s and 1960s. However, already in the first phase of developing his theory, Schmalhauzen clearly sees that the process of evolution, accompanied by an increase in the level of morpho-physiological organization, is a process of self-development. He writes about it in the last chapter of the book *Roads and Regularities of the Evolutionary Process*, entitled "Evolution as the historical self-movement of the organism-environment system." This historical self-movement, associated with an increase in the degree of organization, in the modern sense is a self-organizing system. So here we are dealing with the theory of self-organization.

AN HISTORICAL APPROACH

Schmalhauzen often emphasized the importance of the historical method in his works. The "historical approach" is usually understood to refer to the history of life in explaining biological processes and regularities. At the same time, however, in the biological literature "historical explanation" is often understood simply as genetic explanation (in the methodological sense). Well, this identification does not seem correct to us. The difference between the analysis of the origin of a given system, state or event and the explanation of the empirical regularities of a certain process within the framework of historical theory is fundamental. Let us look at Schmalhauzen's theory from this angle: first, at its explanandum (defining the features of evolution as a historical process) and then at its explanandum (revealing the specificity of explanation on the basis of a theory of the historical type).

Its explanandum can be characterized as follows.

- In the process of evolution, taking place in the geological time scale, new (compared to earlier) species forms are created.
- These forms are adapted to their surroundings. If by adaptation we mean a state of dynamic equilibrium between the population (species) and the environment, then the evolutionary process can be defined as a series of successive transitions from one such state to another.
- In the course of evolution, there is no return from new species to preexisting ones. In this sense, the process of evolution is irreversible.
- The process of evolution is directed: its course increases the complexity, integration and activity of organisms—and the scale of environmental factors they control expands. This is the direction of morpho-physiological progress.

The emergence of new species forms in the process of evolution, its orientation and irreversibility characterize it as a historical process. It follows that the historical character of the process in Schmalhauzen's theory cannot be reduced to a mere chronological sequence of events according to the "arrow of time."

A diametrically opposed point of view was taken by the genetic theory of evolution in its early phase. Dobzhansky²⁷ strongly opposed causal explanation to historical one. He believed that for the analysis of always and everywhere equally acting factors of evolution (mutation, migration, drift and selection), the parameter of geological time is of no importance. In his theo-

²⁷ Th. Dobzhansky, Genetics and the Origin of Species, New York 1937.

ry from this period, the causes of the evolutionary process are considered, the "historical" nature of which can only be said to be in the sense that they are ordered "according to the arrow of time."

As the above analysis of Schmalhauzen's theory shows, factors and mechanisms are not "supra-historical"—they are entangled in historical processes and in their course they themselves undergo changes.

This analysis also shows that the role of chance decreases over the course of the evolutionary process. Adaptive changes are becoming more and more orderly, drowning out accidental disturbances of internal and external provenance.

The evolutionary variability of the mechanism of evolution significantly enriches its historical character. Schmalhauzen's theory, taking into account the direction and irreversibility of evolutionary changes—as well as the variability (directed) of the mechanism of evolution itself—represents the "historical approach" highly consistently. It is a historical theory—in the full sense of the word.

It is worth noting that such a view of evolution is an extremely rare phenomenon. Much more often the historical nature of the evolutionary process is understood in the sense of:

- a chronological sequence of events,
- the irreversibility of the evolutionary process, or else
- emergence of new genre forms in its course.

At the same time, the same mechanism of evolution is assumed to remain unchanged. The mechanism understood in this way does not depend on its historical course, it remains as if "taken out of history," has a suprahistorical character.

From the point of view we are interested in here, therefore, three types of the theory of evolution can be distinguished.

- Ahistorical theories. This understanding of evolution was approached by Dobzhansky in the early stages of the development of the genetic theory. Assuming the "historical" (in the sense of "chronological") character of the evolution process, he abstracted from the historical process in the theory of evolution, trying to approach the methodological model of classical physics. This is also the nature of some theories formulated on the basis of molecular biology, aiming at explaining all biological processes, including evolution, by referring to the laws of physics and chemistry. The idea of such an ahistorical theory became the guiding thread of J. Monod's book *Chance and Necessity*.
- Transhistorical theories, in which the historical nature of the evolution process is reflected in a fuller and richer way, but its mechanism remains unchanged—"taken out of history" (Simpson's theory is an example).

• Fully historical theories, recognizing the entanglement in history of the very factors and mechanisms of evolution—assuming that these factors and mechanisms are subject to change in the course of historical development.

TOWARDS A GENERAL THEORY OF EVOLUTION

In our opinion, Schmalhauzen's theoretical considerations suggest in what direction it is worth looking for a solution to one of the most difficult methodological issues of contemporary evolutionism: is it possible to construct a general theory of evolution, and if so, on what foundations? This problem was posed already in 1942 by Julian Huxley, but he failed to solve it.

The theory of evolution, according to Huxley, is essentially "comparative evolutionism;" it consists of a number of partial theories describing evolutionary regularities specific to various parts of the living world. The "comparative evolutionism" understood in this way is crowned with a certain superstructure of a series of quite general statements such as: the direction of selection is adaptive, selection directs mutational variability, "improves" living matter (according to Huxley, these are Darwin's poorly justified claims, based "on three facts and two deductions").28

Such a position is, of course, unsatisfactory, so it is not surprising that Huxley returned to this issue in the 1950s, recognizing the unity of the historical process of the evolution of life on Earth (and therefore also the unity of theory) and linking it to the problem of progress. The latter, in his opinion, refers to such biological "improvements" that make further ones possible. This series of unlimited refinements leads to the emergence of ever higher types of organization, which in turn entails a succession of dominant types that change from era to era. Significantly, in the early stages of evolution there were many possible ways to increase the degree of organization, but from the Pliocene onwards only one thread of further progress remains open, i.e., that leading to man. In short, for Huxley, the unity of evolution and its holistic character is expressed in the fact that it is possible to distinguish in it the main path of biological progress, which is carried out at the expense of "failures" of many types of plants and animals—the advantage of extinction over further development.

However, this solution by Huxley also seems to us to be insufficient. Firstly, it is difficult to consider development running along a certain "highway" as a "natural necessity." It is also difficult to exclude the element of chance, which undoubtedly plays a role in the evolution of specific lineages.

²⁸ Cz. Nowiński, *Syntetyczna teoria ewolucji: Julian Huxley* [A Synthetic Evolution Theory], Kwartalnik Historii Nauki i Techniki, 1972 (4), pp. 708–715.

Secondly, the focus here was only on limiting opportunities in the course of evolution, and the emergence of new development opportunities remained on the sidelines.

In Schmalhauzen's theory, the issue discussed here is clear. The direction of evolution is determined in it by the relations of the struggle for existence that have developed at a given time, in a given place and under given conditions. From these specific relations (determined, on the one hand, by the historically shaped properties of organisms, and on the other hand—by a given system of environmental factors), it is impossible to eliminate the moment of chance.

So how can we talk about the natural direction of evolution here? In various, sometimes even contradictory lines of development, we find different regularities. It seems, however, that Schmalhauzen's theory, which strongly emphasized the evolutionary role of specific conditions of the struggle for existence—and thus seemingly hindered the path to a general concept of evolution—also indicated a possible way out of this difficulty.

Schmalhauzen, analyzing the variability of organisms, divides them into stable and labile. Labile organisms in their individual ontogenesis depend on various accidental influences from the environment, while stable organisms are independent of random events in their development. Thus, they differ in the degree of autonomy of morphogenesis.

Taking into account the action of natural selection, Schmalhauzen distinguishes organisms:

- stable in a homogeneous, constantly changing environment;
- labile in such an environment;
- stable in a diverse, constantly changing environment;
- labile in such an environment.

These analyzes lead the author to some conclusions regarding the operation of selection. It is worth paying attention to the way concepts are created, the level of abstraction at which they are formulated. There is no question here of one or another type of food, its lack or abundance, the presence of these or other enemies (predators or parasites), that is, what is important for the formation of given, specific relations of the struggle for existence. Abstraction tends to free itself from specific factors (internal and external). Schmalhauzen, on the other hand, speaks of dependence (or lack of it) on random environmental factors; about its oneness or diversity; about its regular (or not) changes; about changes in the relationship between a homogeneous environment undergoing transformation in a specific direction and an organism whose morphogenesis is autonomous (or not).

This way of creating concepts allows us to free ourselves from the concrete-empirical image of the struggle for existence, and introduces it into the game of abstract relations of homogeneity, diversity, repetition, dependence, independence, etc. When we talk, for example, about changing the

relationship between a homogeneous, constantly changing environment and an organism with a morphogenesis independent of external factors—this is what we have in mind the relation of relations, so quite a high-order abstraction is involved here. Thus, we break away from empirically available evidence, such as the presence of oxygen in the environment, the availability of certain proteins, the proximity of this or that parasite, etc.

We therefore abstract here, in short, from the specific conditions of the struggle for existence, which include, among other things, case element. It may be assumed that this abstraction holds the secret that makes it possible to deduce "evolutionary progress" from the premises of the explanans. The formulation of a general theory of evolution is possible only at such a high level of abstraction.

The biological necessity of abstractly conceived directions of evolutionary progress can be demonstrated by deriving it from the explanans of the theory. Specific theories of evolution, on the other hand, are concretizations of theses of the general theory, obtained by reducing abstractions—taking into account the specific conditions of the struggle for existence and selection that occurred in various geological epochs for some "regions" of the living world. The analysis of factors and mechanisms within these specific theories of evolution will, in turn, allow for the explanation of individual phylogenetic lines.

In conclusion, it may be worth emphasizing that for the general theory of evolution understood in this way, an appropriate source of mathematical apparatus seems to be the currently developed cybernetic theory of self-organization. This is a much better perspective than trying to mathematicize the theory of evolution on the basis of population genetics.

FINAL REMARKS

We have outlined the main ideas of Schmalhauzen's theory above. Some of the peculiarities of its "methodological structure" have been analysed. This analysis allowed

- to reveal the premises of the process of evolution understood as a process of self-organization, as well as
- to determine on what grounds it can be said that the general theory of evolution is nothing more than a theory of biological organization.

Concluding remarks will deal with these two issues.

²⁹ The role of higher-order abstractions (predicates of a higher logical type) in the construction of the general theory of evolution, starting with Darwin, is discussed in the paper: Cz. Nowiński, *Biologie, théories du développement et dialectique*, in: J. Piaget (ed.), *Logique et connaissance scientifique*, Gallimard, Paris 1969, pp. 862–892.

• The premise for understanding a specific process of self-development is the discovery of the underlying dialectical contradiction, the unity and struggle of opposites, or in other words, opposing and at the same time mutually conditioned tendencies. Schmalhauzen took this dialectical approach as the basis of his theory. This is generally known, so there is no reason to dwell on it any longer. It is worth noting, however, the difference between the two types of theories belonging to the general trend of the synthetic theory of evolution. Some representatives of the genetic theory of evolution are also ready to recognize that two opposing tendencies lie at the basis of the evolutionary process. However, in their view, these are a tendency to disorder-due to mutation-and a tendency to order-due to natural selection. Schmalhauzen, in our opinion, goes deeper: he writes about "opposite" relations between organisms (of a given population) and their environment. The latter is a necessary condition for the existence of organisms, because it is from it that they derive the substances and energy necessary for life—but at the same time their relations with the environment lead to elimination in the struggle for existence, which results in selection.

As can be seen from the above, according to Schmalhauzen, the mechanism of evolution consists of several interrelated links (struggle for existence, natural selection and change in the genetic composition of the population). The tendency of representatives of the genetic theory to "dissolve" the struggle for existence in natural selection is an obstacle to a deeper understanding of the process of evolution as a process of self-organization.

• In the process of historical self-development of the living world, the complexity and ordering of organisms (the morpho-physiological process), as well as the ordering of the very mechanism of evolution, increase; it is in this sense that we are talking about a process of self-organization here.³⁰ The mechanism of evolution adopted by Schmalhauzen leads to the "growth of order," due to the fact that the organisms of a given population, competing with each other for food, protection against enemies and the ability to leave offspring, are subject to systematic control throughout their lives in the struggle for existence. and comparative assessment in terms of the effectiveness of their functioning as teleonomic systems, aimed at sustaining life and passing it on to offspring.

In Schmalhauzen's theory, two different processes were separated: (a) control according to the criterion of functional efficiency and (b) regulation of the composition of the population. Control is carried out in the course of the struggle for existence in a given biocenosis; on its basis, regulation takes place through natural selection within the population. Control is

³⁰ The concept of organization refers only to such an ordered whole in which the order of elements is governed by the principle of teleonomy. In a living organism, such a principle is to maintain one's own life and pass it on to offspring.

thus exercised in a system hierarchically superior to the population as an evolving unit. The conditions for optimizing the functioning of the organisms are also met, as the control criterion is the appropriate parameter.

The genetic theory of evolution, built on the foundation of population genetics, treats the concept of the struggle for existence as a metaphor and disregards the activity of organisms as teleonomic systems—so, of course, it does not create premises for the theory of self-organization.³¹

- The formulation of a general theory of evolution, justifying the natural necessity of the main directions of the evolutionary process, is possible only at a high level of abstraction, using predicates of a higher logical type. At this level of abstraction, the moment of chance, present in individual phylogenetic lineages, remains aside. The condition for the methodological correctness of such a theory is the separation of two planes:
 - the construction plane of the theory, in which statements concerning its regularity (explanandum) are derived from theses relating to the factors and mechanisms of evolution (explanans), and
 - a theory-testing platform that requires reference to specific facts and processes, established by observation or experiment.

The general theory of evolution, formulated on these principles, is capable of explaining the regularities of the development of biological organization—and contains no other content.

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The most important of his publications concern the philosophical foundations of the synthetic theory of evolution, the concept of species, natural selection and biological progress.

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³¹ I take this opportunity to express my gratitude to Professor W. G. Pushkin, the discussion with whom on the issues of the theory of self-organization was interesting and useful for me.

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