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Review article

Evolutionary Significance of Symbiosis; Development of the Symbiogenesis Concept

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Abstract

The theoretical and historical significance of symbiosis as a mechanism of evolution (symbiogenesis) are considered. The evolutionary role of symbiosis lies in the complexity of individual organization and emergence of new complicated organisms based on unification of two or more symbionts. Ever-increasing relationships between the components of a symbiotic association can lead to a new complex integrated morphophysiological entity. Symbiogenesis is based on comparative analysis of the changes in the organization of a number of symbioses.

The main stages in the development of the symbiogenesis concept are characterized. The contribution of Russian scientists in the investigation of evolutionary significance of the symbiosis is evaluated.

Keywords: symbiosis, evolution, symbiogenesis, history of the concept

There are two main approaches towards the understanding of the evolutionary significance of symbiosis.

One approach is that the organisms united in symbiosis are subject to evolutionary transformations under the influence of their joint life. These transformations arise from the interests of their coadaptation and are directed to satisfying the needs of a partner. As a result of their coadaptation, the symbionts move farther away from free-living forms. Symbiosis leaves a mark upon the symbionts' organization, functions and life cycle.

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With this approach to the understanding of the evolutionary role of symbiosis, it is the analysis of co-evolutionary relations of the organisms in ecological systems that is of crucial importance while the problem itself is a part of ecological evolutionary investigation.

Another approach consists of recognizing the fact that, in some cases, symbiotic associations in the process of selection directed to strengthening the beneficial connection between the partners and integrity of the whole system, can lead to formation of a new complex individual or organ. In such an interpretation a "constructive" role of symbiosis is emphasized. This makes it possible to single out the question of the evolutionary significance of symbiosis in understanding the causes of evolutionary change.

In the evolutionary theory, the idea that the increasing complexity of organization occurs by gradual accumulation of subtle mutations has become very well established. The long, cumulative process of such step-by-step changes leads to the differentiation or dissolution of a previously integrated system, the parts of which gradually become more and more independent of one another.

However, evolutionary theory would benefit if it were proven that a more effective path to increasing complexity of organization existed, i.e., the phenomenon of the ever-increasing integration of the symbionts.

The term "symbiogenesis" is applied to the evolutionary process proceeding in the direction of ever more profound connection between symbionts which results in so intimate a relationship between them that a new complex individual arises. The uniqueness of symbiogenesis as a mechanism of evolution was precisely (Khakhina, 1972, 1979) described by academician A.L. Takhtadzhyan. He called it a process of the "assembly" of a complex system from largely "prefabricated parts" (Takhtadzhyan, 1973, 1991).

The progressive integration of bionts in a symbiotic association does not always result in unification or the origin of new individuals. In most cases, the hurdles to overcome are so great that, despite being protracted coexistence, in the historical sense, movement in the origin of a new complex organism does not occur.

Comparing forms of association by the extent of the relationship between the partners reveals a series of basic stages in the union of the organisms. At the beginning of this series stand those associations characterized by a small degree of unity between the partners, for example, the community relations between ants and aphids.

The next stage of the unification includes association with more extensive relationships between components. The symbiosis between the hermit crab and the sea anemone, or among several species of epiphytes, are good examples.

In these symbioses physiological and morphological unity are missing. An association in which one of the members is transformed in such a way as to become a link in the metabolic process of the other partner is a significantly more advanced form of symbiosis. An example is the symbiosis between the mastigotes of the order Hypermastigida and the termites, in whose intestines these wood-digesting protists inhabit.

In certain cases, one of the organisms becomes a structural part of the organization of its partner (for example, zoochlorellae, zooxanthellae, kappa-particles, etc.).

Finally, the ultimate stage of the synthesis of organisms includes associations which are bound so completely that it is possible to relate them to the various stages of the formation of a new complex organism whose life is regulated by a single physiology and which has newly arising organs (for example, lichens).

The revelation of a series of successive stages of transition from loose associations, the components of which are bound by community relations, to increasingly closely connected associations and, later, to a union of biological systems into an organism with physiological bonds between the symbionts is the basis for proposing evolution by means of symbiosis (symbiogenesis).

Such a process is possible because each stage of the unification of heterogeneous organisms is a form of adaptation to the environment and is selected in the struggle for existence. The driving force of such a process is group selection which leads to the increase in the extent of integration of the symbiotic partners.

Finally, in the process of evolution, the extent of relationship between organisms in a symbiosis varies. In the evolution of the majority of ecosystems, these changes always take place at the community level. In some cases, however, the evolutionary transformations of the symbiotic relationships proceed so far – and the integration of the components becomes so profound – that the community relations develop into physiological ones, and the components become parts (tissues, organs) of a new, complex individual. The evolutionary change of community relations, resulting in the formation of a new complex organism, or symbioorgan, from the components of a symbiosis, can be labeled symbiogenesis (Khakhina, 1979, 1983).

The idea of participation of symbiosis as a mechanism of evolution is closely associated with Russian evolutionary thought. The concept of symbiogenesis has passed through four stages.

The first stage (the late 1860 to 1907) was characterized by experimental investigations of symbiosis, and the evolutionary-theoretical works of A.S. Famintsyn (1835–1918), and K.C. Merezhkovsky (1855–1921).

The second stage (1907 to the beginning of the 1920s) is marked by the development of up-to-date and logical arguments in favor of the concept of symbiogenesis and formulation of the idea of a cell as a "symbiotic complex." The most important feature of the first two stages is the fact that symbiosis was viewed as an evolutionary mechanism in addition to those discovered by Charles Darwin.

The characteristic feature of the third stage (from the beginning of the 1920s to the end of the 1930s) consisted in reviewing the concept from the positions of Darwinism. Due to the efforts of B.M. Kozo-Polyansky (1890–1957), the principle of natural selection was taken as a basis of evolution through symbiosis.

The subsequent two decades, especially the 1950s, were marked with a pause in its development, whereas the fourth, current stage, began in the 1960s with revival of interest in the symbiosis concept.

Famintsyn first formed his ideas about the significance of symbiosis as a mechanism of evolution at the beginning of this century in 1907, when he presented his work "On the Role of Symbiosis in the Evolution of Organisms." He asserted that the increasing complexity of the organization and functions of organisms during the process of evolution may occur not only through the differentiation of simpler, early forms, but also on the basis "of the symbiotic unification of independent organisms into a living unit of a higher order" (Famintsyn, 1907b, p. 143).

Results of investigations on lichens and the discovery of their zoospores in 1867 were the major bases of Famintsyn's ideas on the significance of symbiosis in evolution. The general conclusions resulting from this research were: green cells of lichens can exist outside the body of the lichens; like algae and fungi, green cells can develop zoospores; lichen "gonidia" are similar to single-celled algae in structure and reproduction (Famintsyn and Baranetsky, 1867).

The symbiotic nature of lichens indicated to Famintsyn the clearest role of symbiosis in evolution. Lichens, Famintsyn wrote, are of particular interest in that they are "the first directly observed case of the origin of a more complex plant form through the unification and interaction of simpler forms" (Famintsyn, 1907a, p. 11); that is, they are "an incontestable case of the participation of symbiosis in the evolution of organisms" (1918, p. 281).

Famintsyn's experimental works (including research on the formation of zoospores in different species of lichens, the study of symbiosis in several species of invertebrates and algae, observations of the behavior of chloroplasts in the seeds and shoots of sunflowers, and the extraction of chloroplasts from plant cells and their attempted artificial cultivation) were directed toward a single goal: to explain and model the process of formation of the complex organism from simpler forms.

The concept of the plant cell as "a symbiotic complex" was formulated by Famintsyn in 1907, although the idea of the origin of the cell by symbiosis had arisen already in 1868.

According to his interpretation, a plant cell is the result of evolutionary symbiosis of two simple organisms: "a green with chloroplasts and an amoeba-like formed by plasma and nucleus (Famintsyn, 1907a, p. 4). S. Schwendener, guided by this discovery as well as his own observations, reached his conclusion about the complex character of lichens (Schwendener, 1869). The main organelles (chloroplasts, centrosomes, nuclei) arise not by differentiation of plasma but were independent structures of symbiotic origin in the cell.

He experimented with the isolation of chloroplasts, hoping to obtain direct proof of the symbiotic origin of the plant cell. This work did not yield the expected results.

Both experimental and other sources of information formed the basis of Famintsyn's theory regarding the role of symbiosis in evolution, related to his understanding of the teaching of Charles Darwin. While recognizing the enormous significance of Darwin's works, Famintsyn found distinct shortcomings in his concept. Darwin's doctrine of natural selection provided a satisfactory explanation of causes of adaptations; but the causes of the origin of evolutionary complexification remained unresolved (Famintsyn, 1894).

Famintsyn tried to find an evolutionary factor which would fill this gap in Darwin's doctrine and explain the causes of development from the simple to the complex. Even in his works from the 1890s Famintsyn allowed: complex organisms might arise "through the unification of elementary organisms... and the transformation of the aggregate of them into an entity of a higher order." This thesis became his basic doctrine.

Famintsyn must be acknowledged as the founder of the scientific approach to symbiogenesis.

In the first years of the twentieth century, K.S. Merezhkovsky began to develop ideas similar to those of A.S. Famintsyn about the evolutionary significance of symbiosis. Nevertheless, their approaches to these ideas differed.

Merezhkovsky suggested the term "symbiogenesis" in 1909 and later gave a detailed definition: "I called this process symbiogenesis, which means: the origin of organisms through combination and unification of two or many beings, entering into symbiosis" (Merezhkovsky, 1920, p. 65).

He suggested two relatively independent hypotheses for the general concept of symbiogenesis. The first assumed a symbiotic nature of the plant cell of chromatophores (chloroplasts). The second hypothesis is known as "the theory of two plasms".

Merezhkovsky's idea on the symbiotic origin of chromatophores began from his assertion that their continuity was an established fact. Chromatophores are not "organs of the cell and never were," he wrote, they should be viewed as "independent organisms that 'never established associations in colorless animal cells, having entered into a close symbiotic relationship' with them" (Merezhkovsky, 1905, p. 596). He considered their high order of self-sufficiency and functional independence from the nucleus as an argument for their symbiotic nature. He also compared chromatophores (chloroplasts) to typical endosymbionts (zoochlorellae and zooxanthellae). Their resemblance seemed so compelling as to suggest the existence of a "complete analogy" between them. Of all arguments raised by Merezhkovsky in favor of the symbiotic origin of chloroplasts, this argument met the most criticism (Famintsyn, 1907a; Kozo-Polyansky, 1924; Gollerbach and Sedova, 1974). He attributed the great similarity of chloroplasts and cyanobacteria to the role of symbiosis in their origin. The most probable ancestors of the chloroplasts were like *Aphanocapsa* or *Microcystis*.

Thus, as early as 1905 Merezhkovsky rigorously formulated the hypothesis on the symbiotic nature of the photosynthetic apparatus of the plant cell. It was based on the acknowledgement of the direct phylogenetic tie between blue-greens and chloroplasts and the assumption of hereditary consolidation, i.e., intracellular symbiosis as a mechanism of their origin.

In the "theory of two plasms" Merezhkovsky assumed a dual nature of the organic world; all life consists of two essentially different plasms.

The first "mycoplasm" gives rise to all bacteria and fungi, blue-greens, and cell organelles: plastids and nuclei. "Amoeboplasm" lies at the foundation of all animals and plants. However, mycoplasm is also present in the cells of animals and plants: in the cells of animals it is in the nucleus, whereas in plant cells it is in the nucleus and plastids. The first bearers of mycoplasm and amoeboplasm, emerged in various epochs in the Earth's history. The first organisms, consisting of mycoplasm, were bacteria. Amoeboplasm emerged later. This plasm appeared in the form of small "monera without nuclei," which move like amoebae and feed on bacteria. The bacteria, were eaten but not always digested by amoeboid monera. Remaining inside the body of the monera, these bacteria sometimes entered into symbiosis. Amoeboid monera and bacteria, having united in a physiological relationship, then formed a single independent organism and gave rise to flagellates and amoebae – the initial forms of the animal kingdom. However, in the process of evolution, still a second stage of symbiosis came into being: an establishment of new representatives of mycoides inside amoebae and flagellates occurred as blue-greens themselves, evolved from primary bacteria. This second symbiosis gave rise to the several separate branches of the plant kingdom, which had evolved independently of each other.

Merezhkovsky's entire concept of "two plasms" is undoubtedly highly speculative, yet it contains opinions which deepen and expand biological knowledge. The "theory of two plasms" necessarily carried with it recognition of symbiosis as the cause of the origin and evolution of organisms. A new general system of the organic world required reexamination of traditional phylogenetic schemes. Acknowledging the reality of plant and animal kingdoms, Merezhkovsky believed that such a division was insufficient. In his opinion, more fundamental differences exist among extant organisms - more fundamental than those by which plants and animals are distinguished from one another, which are concerned mainly with the inner structure of the organisms's cells.

Merezhkovsky clearly posed the question of the existence of two large, independent groups: prokaryotes and eukaryotes.

The concept of the natural division of organisms into prokaryotes and eukaryotes is now fundamental in constructing higher taxa of living beings.

Merezhkovsky attempted to explain the emergence of intracellular structures. The cell's nucleus and chromatophores differed from cytoplasm in a variety of ways. The assertion that, in the course of evolution, the amoeboplasm gave rise directly to mycoplasmic organelles was improbable. The only possible mechanism by which the inner cell structure arose was symbiosis. Merezhkovsky's idea could be expressed in modern terms: endosymbiosis was the leading factor, under whose influence the eukaryotic cell emerged from the primary prokaryotic cell.

The work of B.M. Kozo-Polyansky was of major significance for the concept of symbiogenesis during the 1920s and 1930s. His works have been regarded essentially as a new stage in the development of the symbiogenesis hypothesis — the stage of the investigation of the evolutionary role of symbiosis based on Darwinism. Kozo-Polyansky saw a particular form of the evolutionary process occurring by selection in which the natural synthesis of organisms into a single symbiotic system within a system of interacting factors acquired fundamental significance.

The acknowledgement of natural selection as the driving force of the development of the organic world and the understanding of symbiosis as one of the factors of evolution also formed, according to Kozo-Polyansky, the essence of the symbiogenesis theory as one of a variety of evolutionary concepts within Darwinism. "The theory of symbiogenesis is a theory of selection relying on the phenomenon of symbiosis" (Kozo-Polyansky, 1932, p. 25). The connection between symbiogenesis and the Darwinian principle of natural selection seemed to him so close that, in the event of the demise of the selection doctrine, the theory of symbiogenesis would fall as well.

Kozo-Polyansky objected decisively to symbiosis as a driving force of evolution. He persistently emphasized that symbiogenesis must not be interpreted as a universal mechanism of evolution, equal to the influence of natural selection.

Thus, Kozo-Polyansky's main accomplishment in tackling this question was to unite the symbiogenesis hypothesis with Darwin's teachings.

Kozo-Polyansky devoted much attention to describing the basic concepts of symbiogenesis. There were three: symbiosis, consortium, and symbiogenesis. Symbiosis is a special form of adaptation, ensuring the biological progress of its participants. Concept of consortium corresponds in content to "formative symbiosis" by Famintsyn. The emergence of consortium (symbiotic organisms) is a historical process and can be called "symbiogenesis." However, he also devoted great efforts to substantiating the concept with fact. His work entitled "A new Principle of Biology. An Essay on the Theory of Symbiogenesis" (1924) was devoted to this problem.

Kozo-Polyansky concentrated on several categories of facts; the first relating to symbiotic processes among the most primitive organisms. To this group, which he called "cytodes," he relegated bacteria and blue-green algae (Cyanophyceae). The capacity of cytodes to form consortia is of special interest: zoogloea-consortia can serve as good models of eukaryotic cells. "The study of cytodes in their symbiotic life leads to the recognition of their participation in the formation of the cell in general, as well as their part in the role of its organelles," wrote Kozo-Polyansky (1924, p. 25).

The second group of facts relates to cell organelles. The physiological independence of cell organelles from the nucleus on the one hand, and their similarity to "cytodes" on the other, caught the attention of scholars. Plastids "could not fail to be autonomous beings, residing in cells not unlike chlorella and xanthella" (Kozo-Polyansky, 1924, p. 38).

Kozo-Polyansky supported the idea of the origin of the cell nucleus from symbiotic bacteria. He concludes that in mitochondria as well "one must see symbiotic cytodes or entire systems of such organisms" (ibid., p. 54).

Upon examining the origin of centrioles and the blepharoplasts (the basal apparatus of mastigotes), Kozo-Polyansky emphasized the possibility that they were homologous structures. He saw, both in centrioles and in the blepharoplast, a good model of the undulipodium-bearing cytodes.

Kozo-Polyansky concluded that "the cell is a collection of heterogeneous, autonomous, live units, leading a symbiotic type of life" (ibid., p. 63).

The third group of data relates to the existence in nature of complex, "whole-entity" organisms and the presence in plants and animals of tissues and organs, which are, by their origin, bound in the mutual existence and live activity of organism-symbionts (mycorrihizae, glands of aquatic ferns and liverworts, the coralloid organs in all species of cycads).

Modern study of symbiogenesis, the evolutionary significance of symbiosis, began in the 1960s. Data considered proof of symbiogenesis were gathered from lichenology, algology, protistology, cytology, molecular biology, virology, and other fields of contemporary biology.

Data detailing evolution of gelatinous (=Gallertflechten) lichens: *Leptogium issatschenkoi, Collema ramenskii* Elenk., *Saccomorpha arenicola, Pseudoperitheca murmanica* (A. Elenkin and his school) serves as irrefutable proof of symbiogenesis as the mechanism of origin of these organisms.

The group of gelatinous lichens is especially interesting in that it includes forms which have advanced to various stages of the relationship between partners. Comparative morphological studies were made of the transformation of the external appearance of the thallus and the character of the interrelations of the components within this group as successive stages of the integration of the cyanobacterium of the genus *Nostoc* with the hyphae of the fungus, beginning extracellularly in the sheaths of these forms. The study of symbioses among gelatinous lichens has shown that the origin of lichens is a complex evolutionary process, in which the strengthening and complexification of the symbiotic relationship between the constituent components plays a leading role (Gollerbach and Sedova, 1974).

Research on several of the most advanced forms of endocyanelles (*Geosiphon pyriforme, Glaucocystis nostochinearum, Cyanophora paradoxa*) serves as another irrefutable proof of symbiogenesis (for details, see Khakhina, 1979).

Comparison of these endocyanoses showed that the development of symbiotic unions is accompanied by morphological and functional specialization and subjugation of the individuality of symbionts, expressed as the alteration of a series of features of the symbionts compared to the organization of corresponding free-living algae.

Research on symbiotic cytoplasmic particles (Kappa-particles, i.e., bacteria of the genus *Caedobacter*) of several strains of *Paramecium aurelia* directly support symbiogenesis (Preer et al., 1974).

For arguments in favor of symbiogenesis, data from the most important organelles of the cell, chloroplasts and mitochondria, is of exceptional interest: chloroplasts and mitochondria represent intracellular systems possessing a high degree of autonomy. Cytological continuity through a series of cell generations and the presence of their own genetic apparatus and protein synthetic system are the most important features showing the high degree of individuality and autonomy of chroloplasts and mitochondria (Gibor and Granick, 1964; Sisakyan, 1964; Nasyrov, 1975, Dubinin, 1976).

Other evidence accumulating in support of the symbiogenetic origin of plastids compares traits of chloroplasts with representative cyanobacteria. Similar traits of structural organization, genetic and biochemical attributes exist which have provided bases for the confirmation of their common origin. Various data regarding a high degree of autonomy and similarity to bacteria have been attained with regard to the other important organelle, i.e., mitochondria (Leninger, 1974; Roodyn and Wilkie, 1970; Margulis, 1970). Data comparing the characteristics of mitochondria and bacteria are extremely important for demonstration of their symbiotic origins. The latest data, showing the metabolic abilities of plastids and mitochondria, lead to the modern interpretation of their origin and evolution of eukaryotic cell organization.

The hypothesis of the origin of the eukaryotic cell by symbiosis has been newly revived by Lynn Margulis (1970, 1975, 1985) and strongly supported by some others. Thus, analysis shows symbiosis to be a real but limited mechanism of evolution. As for its significance for such fundamental transformations as the origin of the eukaryotic cell, it still remains debatable, though there is evidence in its favor, which now raises it to the higher level. The idea of symbiosis as part of the mechanism of evolution is a rather fruitful addition to the explanation of the means for increasing the complexity of organization of an individual presented by Charles Darwin.

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