

HOW IMPORTANT IS LIVING TOGETHER? THREE FACETS OF SYMBIOSIS CONCEPT

JOSEF LHOTSKY

*Department of Philosophy and History of Sciences, Faculty of Science, Charles University, Viničná 7, Prague 2, 128 43, Czech republic
email:lhotsky1@natur.cuni.cz*

This text is one of the outcomes of my Ph.D. research in the programme "Theoretical and evolutionary biology" on Charles University, Faculty of Science.

Abstract: The conception of symbiosis as biological interactions between different species is well established in contemporary biology since its introducing in late 19th century by A. de Bary. However, to date, symbiosis is primarily understood to be an ecological concept despite of its "Janus" face in form of the evolutionary importance of the phenomenon. In 1909, K. Merezkovsky coined the term symbiogenesis for expression the fact that new species can arise throughout symbiosis, and much more later, in the second half of the twentieth century, L. Margulis has shown that symbiosis is a crucial aspect of process of evolution. I argue here that there is yet another facet of the term, which results from the previous, but yet it is autonomous: symbiosis as a universal model for theoretical biology.

Keywords: science of life, theoretical biology, symbiosis, symbiogenesis

1 The Birth of Symbiosis: Transparent Relationships on higher Levels of Organization

The term *symbiosis* (from Greek, meaning "living together") was introduced into biology by German botanist Heinrich Anton de Bary (1831-1888) in 1879. However, de Bary previously used the word in a speech at the Congress of German Naturalists and Doctors at Kassel in 1878. Even one year before another German botanist Albert Bernhard Frank (1839-1900) coined the term *symbiotism*, which was semantically *de facto* identical. De Bary defined symbiosis as "the living together of unlike named organisms" (Sapp 2003; 1994) and up to present days, the definition still holds more or less, since symbiosis is described as close relationship of two or more phylogenetically (that is what "unlike names organisms" means in practice) distinct organisms.

In fact, these converging efforts were a natural result of an attempt to grasp intellectually the recent discovery of Swiss botanist Simon Schwendener (1829-1919) who showed that lichens are dual organisms composed of the fungus (typically a member of the Ascomycota group) associated with green algae (commonly *Trebouxia* or *Nostoc* genus). At the same time, the terms as parasitism, comensalism, as well as mutualism were defined by Belgian zoologist Pierre-Joseph van Beneden (1809-1894), who derived them from *per analogiam* projection of human society (Sapp 1994). As a consequence, the symbiosis concept of de Bary firstly included all possible complex associations on a parasitic-mutualistic scale, and secondly became a new paradigm of biological sciences how to look at the nature of interactions between living beings (more precisely the living objects, in terms of modern scientific language) as counterbalance to the Darwinian "struggle" (Darwin 1985) (note that struggle is more specific than "fight", the semantic realm is wider and closer to "efforts to").

During the last decades of the nineteenth century, many botanists (because they were botanist, who payed attention to one-cell organisms) used the scheme outlined by van Beneden for the classification of the various functional relationships involving microorganisms. The main attention was focused primarily on organisms at the interface of plant and animal kingdom, i.e. on chlorophyll-containing protists, and some procaryotes – although the term procaryotes as well as eukaryotes still did not exist and bacteria as so-called Schizomycetes belonged to kingdom of plants. Moreover, some kinds of facts like the association of bacteria with legumes or corals with photosynthetic algae did not escape this new perspective. It was crucial in this regard the gradual appreciation of the phenomenon of mycorrhizal symbiosis, which was noticed and described by above-mentioned A. B. Frank in 1885; Frank is also the author of the generally known term mycorrhiza, symbiosis of fungal mycelium and roots of higher plants. It should be mentioned that

this kind of discovery is not trivial matter and it alone would be a great success. Frank's benefit, however, went even further: he said that fungi in this strange association in some way favor the plant, so their function is *positive*. This belief, however, encountered stiff resistance of his contemporaries, which is understandable, because there was no precedent for cooperative behavior on such level (or in general: life was seen as competition, the struggle for existence) and fungi were generally considered as typically parasitic organisms.

Nevertheless, a clear definition (*clare et distincte* along to Descartes) of symbiosis has never existed and the problem of ambiguity persists to present. Since its introducing, the term was associated with two basic approaches to definition: either as a synonym for mutualism in narrower sense (with an apparent Achilles heel in the form of essentially anthropocentric evaluation of benefit-cost on information basis known *ad hoc*), or in the original intention of de Bary as any close cohabitation of different organisms, regardless of the specificity of interactions, especially the trophic ones – i.e. including all forms of interrelation that somehow affect, either positively or negatively, the survival of the particular partners. The thing is, however, that the phrase "any close cohabitation" is virtually beyond the possibilities of any precise definition. Nonetheless, regardless of choosing any of these two basic ways of symbiosis understanding, it started becoming obvious for supporters of both approaches that it were bacteria what played a significant role in symbiosis – if only because, due to their size, they always meet the requirement of "close" living with partner organism. Moreover, just emerging science of cell biology could not fail to notice some similarities between bacteria and some of the inner structures of eukaryotic cells; and this was very important observation.

After its discovery, symbiosis soon became considered to be a form of interaction between different organisms in which joint existence is beneficial for the individuals and secures for the partners an essential selective advantage. Thus, the value of symbiosis was defined by the fact that, upon entering into an association, an organism became better adapted to the environment because of the use it makes by the peculiarities already possessed by its partner (Khakhina 1992). Despite this apparent evolutionary dimension, symbiosis has been (and still is) in the first place an ecological concept (even though ecology as separate discipline was only forming at that time): it comprise knowledge about "true" organisms before our very eyes, studied by botanist or zoologist. So the **ecological aspect** is the first and most common facet of symbiosis concept, which legacy we can find up to present in ways of how to teach this topic: as a part of ecology, with respect to specific examples in nature, scattered throughout many otherwise unrelated fields of research.

Nevertheless, the second facet of symbiosis concept – one can even say its Janus face – is, as has already been written (Sapp 1994), the **evolutionary aspect** of that phenomenon.

2 The Evaluation of Symbiosis: Relationships hidden in Time

Under the weight of a new arising knowledge, it has become suddenly clear to some researchers that the interactions with symbiotic bacteria play an important role in living world and are probably not an obscure and/or marginal phenomenon (bacteria are due to their volume and their cellular properties practically ubiquitous; you can find them in deep ocean as well as in the Earth's crust to a depth of several kilometers), but apparently the fundamental basis of life-processes. The dual nature of lichens, nitrogen fixing bacteria, mycorrhizal fungi or photosynthetic algae living in the bodies of various protist suggested time and space-depending continuum of both organisms from the partially to complete interdependence.

In this regard, symbiotic interactions can be divided into a continuous range of mutual dependence of both partners, where on the one side are endosymbionts long established within the cell like mitochondria or chloroplasts (and, in fact, eukaryotic cells themselves), or endosymbionts living inside the bodies of other organisms. On the other side are external interactions. Given that bacteria are everywhere around us, in all habitats and all environments, microbial symbioses are ubiquitous, and their importance is in no case marginal (eg. Hoffmeister & Martin 2003): bacteria can perform many of activities impossible for their hosts, such as photosynthesis, sulfur metabolism, nitrogen fixation, digestion of cellulose, the synthesis of amino acids, vitamins, growth factors, sugars, or enzymes, etc.

The ingenious combination of these findings with cytology, which showed the presence of self-reproducing bodies inside the cells of plants and animals, has led some biologists to believe that this cellular organelles, and possibly even eukaryotic cells themselves, are possibly symbiotic structures, it means organisms/organelles of symbiotic *origin*. One of the first important researchers on this field was Russian botanist Andrey Sergeevich Famintsyn (1835-1918).

Thus, what happened was the redirecting of prevalent way of thinking about symbiosis; in other words, the transition from ecological relations to relations physiological, and later also cellular. That was a crucial point, because there were found structures similar to free-living prokaryotic organism in eukaryotic cells. Was it mere coincidence? How did these structures originate? What can we say (if it is possible at all) about their evolution?

During the end of nineteenth century, the possibility of evolution by the sudden, radical steps, in contrast to gradualistic processes, has been abundantly discussed. And here comes again the symbiosis on the scene: because one of the ways how to break statistic improbability of such non-gradualistic evolution is increasing of complexity through the union of previously prepared blocks, i.e. through fusion of previously symbiotically living systems. So, the possibly role of symbiosis in evolution gave birth to a new term, *symbiogenesis* (i.e. “born from symbiosis”), introduced by Russian botanist Konstantin Sergeevich Merezhkovsky (1855-1921) in 1909 and explained as “the origins of organisms through combination and unification of two or many beings, entering into symbiosis” (Khakhina 1992).

Between years 1905-1918, Merezhkovsky wrote a serie of articles where he argued that chloroplasts, then called chromatophores, are actually symbiotic micro-organisms inside cells, and that nucleus and cytoplasm also emerged through a blend of two distinct phylogenetic lines. On the opposite side of the Atlantic ocean, in the United States, argued during the thirties an American Ivan Emanuel Wallin (1883-1969) in favor of the symbiotic origin of mitochondria from the originally independent microbial partners of individual cells. Wallin was a great promotor of the idea of symbiogenesis and particularly its role in the evolution of species (Wallin 1927). Similar ideas about the importance of symbiosis were circulating marginally throughout Europe – fundamental is the work of Russian scientists (Kozo-Polyansky 2010; Khakhina 1992) (besides experimental researchers like Famintsyn and Merezhkovsky also researchers-theoretician like Boris Mikhaylovich Kozo-Polyansky, 1890-1957); in France is known a work of Paul Jules Portier (1866-1962) (Sapp 1994); and also several others (Khakhina 1992). But with the exception of those few, no more scientists was interested in this topic until the sixties.

At that time, American microbiologist Lynn Margulis (1938-) has completely independently of her predecessors “rediscovered” the forgotten concept of symbiosis as a possible major factor in evolution and its participation on important evolutionary events - in this case on a process of origin of some cellular organelles. Increasing evidence led Margulis in the sixties to formulating and publishing the so-called theory of serial endosymbiosis (Margulis & Sagan 2002; Margulis 2000), under which the

eukaryotic cell is a conglomeration of various bacterial partners. The answer of academicians was of course very inconsistent. Leading figures of biological research were quick in claim that the whole concept is unscientific because it is quite possible to test it.

Soon, however, it has begun to show that Margulis was probably right: it has been found that mitochondria and chloroplasts contain their own DNA and the electron microscope also confirmed their structural similarity with bacteria. Consequently, in the eighties, molecular biology proved without any doubt similarity of DNA sequences in chloroplasts with those from DNA of cyanobacteria, and sequences in mitochondrial DNA with those from DNA of alpha proteo-bacteria group – and *de facto* confirmed in this way their common origin from once free-living microbial ancestors. Thus, despite the early self-conscious receiving over the scientific community, theory of influence of symbiosis in process of evolution has been soon accepted and has become one of the fundamental concepts in modern biology (Douglas 2010, 1994; Khakhina 1992; Margulis 2000; Margulis & Sagan 2002, Margulis & Fester 1991; Overmann 2006; Paracer & Ahmadjian 2000; Sapp 2003, 1994; Smith & Douglas 1987).

Symbiosis (as relationship), and especially its possible effect, symbiogenesis as a process by which a new organisms, i.e. species (sic!) may arise, has been rehabilitated from the phenomenon of marginal importance to the essential element of many biological fields of research and became the next vanishing point of evolutionary biology, parallel to the newly developing post-neodarwinism in form of selfish-gene theory (Dawkins 2006). Accordingly, besides the classical neodarwinism, where the driving force for natural selection are only mutation, an alternative evolutionary model for arising of new entities in evolution has developed since the seventies: symbiogenesis, evolution by merging into symbiotic complex and their follow-up fusion (on evolutionary time scale). It has never achieved greater public acclaim, though current knowledge of the evolution of both prokaryotes and eukaryotes clearly show that it should be definitely not underestimated. Surprisingly, although the symbiosis as one of the major sources of evolutionary innovations have been proposed since its inception in the nineteenth century, we do not find this idea in any standard histories and treatises on evolutionary biology (Sapp 2003).

This is partly caused because “classical” evolutionary biology was primarily formed and focused on evolution of higher groups of eukaryotes, i.e. on evolution after so-called Cambrian explosion; in other words, on last 600 million years (and, additionally, it was rather zoocentric). But this is not even 80% of the history of life on Earth, if we realize that its origin is traditionally dated to around 3.5 billion years in the past. If we want to consider the evolution as a whole, it is necessary to expand beyond its zoocentric part (in fact just a component). It is clear now that the evolution of prokaryotes, including the origin of eukaryotic cell itself, is an important part of the whole theory of evolution. Symbiotic interactions leading to symbiogenesis have acquired in evolutionary biology its irreplaceable status, for it is apparent that they have played a central, major role in the emergence of novelties in phylogeny within the “tree of life” (or rather “web of life”? – see in Sapp 2009).

Current biology simply cannot disregard no longer the matter of fact that any individual eukaryotic organism is, and has evolved, as a result of an extremely complex consortium of many species, which (metaphorically) must “strive” (as opposite of “struggle”) for coexistence through joint cooperation on the functional integrity of the whole. It is a sophisticated ecosystem of cross-linked connections of linkages, where the resulting character always depends on the context of other relationships in which it is located.

Finally, this bring us to the third facet of symbiosis concept, that is indirectly (but fundamentally) resulting from previous two: the

aspect of universality of a principle. It is *interactions*, no matter on level, what is the best model for description of *specificity of biology* as science (see below), hence symbioses as *biological interactions* are the most appropriate model for field of theoretical biology, because it can enable, I suppose, re-establishing of foundations of biology as a coherent system of inter-linked knowledge. Moreover, there could be a possibility in future to put science of biology together with humanities on the same theoretical basis and thus overcome ancient nature vs. nurture debate.

3 The Meaning of Symbiosis: Relationships as true “Missing Links”

Biology as so-named separate science is relative new invention of Late Modern Age. Examination of living and knowledge of life sciences was always, quite naturally, an integral, implicate part of medicine, which, however, and not pejorative, was not any *-logy* (from greek word *logos*), but rather traditional teachings based on exchange of experiences. However, *post factum* of that specific transition of knowledge of life into *biology* as a separate science, all knowledge yet collected was needed to fit now within a defined core which are to be living beings. But it is really not easy to find something unquestionably specific on life, a kind of standard in biology. Be alive seems to be appropriate term for all (hylozoisms), or, conversely, for nothing (modern mechanism). Modern period requires an object, a fungible item, but new science of biology hardly offers something like it – rather it seems as a great collection of pragmatism and teleology in nature. The undeniable autonomy of life whispers stilly what Immanuel Kant expressed by words that no further Newton for field of biology will be ever exist. *In medias res*, in other words, how to make a living things objectively knowable, contributed at the late nineteenth century cellular physiology, and, finally, several decades later came the definitive answer through the molecular biology.

Nevertheless: any way the biology is ultimately convertible to physico-chemical principles expressible through mathematical notation, there is still something beyond (in words of M. A. Simon (1971): “Biology differs from physical science because its objects are different.”). Something, we do not treat with in these disciplines (and therefore we cannot it yet), whereas for biology it is crucial and specific: **the meaning** (in sense of context-dependent information, no teleology there). The first indications of this fact began to appear in the first half of the twentieth century through the forming systems theory, based on newly emerging science - cybernetics. The subsequent formulation of information theory and the obvious analogy with some of the most essential features of living organisms, such as with the text-like nature of DNA primary structure or the genetic code, which have been discovered during the fifties and the sixties due to molecular biology, has led to the introduction of the concept of information into the biological sciences. Despite the widespread enthusiasm in adoption of information into the arms of biologists, yet there has been the general underestimating of the complementary phenomenon of the true meaning. Actually, any information is information **only** in connection with something (nothing super-natural: let say “an adjusted system”) *what recognize it as such*, and must therefore bear some meaning for a recipient (it means for this system) (Markoš *et al.* 2009).

Biology, in contrast to other sciences, is enriched by the critical dimension of information. Physics or chemistry only need the description of the alphabet and simple grammar which is quite sufficient for them, but *does not deal with meaning*: do not try (because do not need) to understand the dimension of, for instance, natural (as opposite to formal) language, which can be seen just up in the phraseme or in the Shakespearean verse (Markoš & Faltýnek 2010). Living organisms are complex areas of mutual ties with historically established background, among which exist significant flows of information. A comprehensive study of such systems is very difficult task, so the (molecular) biology is logically limited to the study of isolated subsystems –

specific information pathways and their importance in the next proximal system above. A more complete evaluation of the meaning as quantity is hampered by the very fact that the meaning as a scientific concept is not yet properly defined – because the exact and empirical sciences have never needed it.

The point is, that this principle of such spatio-temporal coherence of living systems based on these ties, interrelations, relationships of things, is what is all about. Organisms have a time dimension, ontological, but above all historical: phylogenetic, evolutionary. Additionally, there is the dimension of relationships not only in time (hereditary material and how to use it), but as well in space (spatial conformation of DNA, interrelations as e.g. DNA-RNA, RNA-protein, protein-protein, etc.). Living world has a character of a network, it is a web of interactions, and it is always exactly their **setting**, what tell us about “core” properties of such biological entities – *far enough from just knowing the structure* of elements. Again, what counts, and maybe first of all, is the setting, i.e. *relationships* between particular elements of such network. Hence, biology can be defined as a science about specific interactions on all possible levels of organization of “living matter”. Symbiosis concept, as a formal description of such relationships, is then the most appropriate basis for how to explain them and how to put them in a coherent system of knowledge.

As a conclusion, the phenomenon of symbiosis is absolutely crucial for the current theoretical biology, areas of its interest should be the explaining the realm of living world from unifying perspective outlined from all the data available in numerous biological disciplines, which are otherwise *a priori* separated by interdisciplinary barriers; that all for trying to come up with unexpected relationships, quantify them using all the possible tools, and makes specific predictions for further research with feedbacks back to the basic research.

Symbolically, the symbiosis concept seems to show the trinity of facets, each of which results from the previous, each from which is autonomous in its own way, but only together are in fact in their wholeness. And it is this wholeness of one universal principle, which we can model due to our long-standing biological experiences with phenomenon of interactions in realm of science of life, i.e. with concept of symbiosis. I suppose that this new approach has the explanatory power for advances in such biological tasks such as more accurate definition of life (the exhaustive one is still missing in biology, after centuries) or re-definition of biological “individual” (see in text above) as well as re-definition of biological species, *inter alia*. Moreover, and this is worth attention, it is possible to put biology as well as humanities on *this* theoretical basis, because no matter what kind of elements we have (amino acids, proteins, tissues, individuals, herds, ecosystems, ideas, languages...), but rather what kind of inter-linking we have, i.e. what kind of context, what kind of meaning – “patterns that connect” in words of Gregory Bateson (Bateson 2002; Goodwin 2010). In this sense, the phenomenon of symbiosis is the true missing link in biology.

At least, this topic deserves further research.

Literature:

1. Bateson, G.: *Mind and nature: a necessary unity*. Cresskill: Hampton Press, 2002. 220 s. ISBN 1-57273-434-5
2. Darwin, CH.: *The Origin of species: by means of natural selection or the preservation of favoured races in the struggle for life*. London: Penguin Books, 1985. 476 s. ISBN 0-14-043205-1.
3. Dawkins, R.: *The selfish gene*. Oxford: Oxford University Press, 2006. 360 s. ISBN 978-0-19-929115-1.
4. Douglas, A. E.: *The symbiotic habit*. New Jersey: Princeton University Press, 2010. 202 s. ISBN 978-0-691-11341-8.
5. Douglas, A. E.: *Symbiotic interactions*. New York: Oxford University Press, 1994. 148 s. ISBN 0-19-854286-0.

6. Goodwin, B.: *Bateson: Biology with Meaning*. In: Hoffmeyer, J. (ed.): *A Legacy for Living Systems*. Berlin: Springer, 2010. 288 s. ISBN 9781402067051.
7. Hoffmeister, M., Martin, W.: Interspecific evolution: microbial symbiosis, endosymbiosis and gene transfer. *Environmental Microbiology*, 2003. 5(8):641-649.
8. Khakhina, L. N.: *Concepts of Symbiogenesis. A Historical and Critical study of the Research of Russian Botanists*. New Haven and London: Yale University Press, 1992. 176 s. ISBN 0-300-04816-5.
9. Koyo-Polyansky, B. M.: *Symbiosis: a new principle of evolution*. Cambridge, Massachusetts and London: Harvard University Press, 2010. 198 s. ISBN 978-0-674-05045-7.
10. Margulis, L.: *Symbiotic Planet: A New Look at Evolution*. New York: Basic Books, 2000. 160 s. ISBN 0465072720.
11. Margulis, L., Sagan, D.: *Acquiring Genomes. A Theory of the Origins of Species*. New York: Basic Books, 2002. 240 s. ISBN 0-465-04391-7.
12. Margulis, L., Fester, R. (eds.): *Symbiosis as a Source of Evolutionary Innovation. Speciation and Morphogenesis*. Cambridge, Massachusetts and London: MIT Press, 1991. 454 s. ISBN 0-262-13269-9.
13. Markoš, A., Faltýnek, D.: Language Metaphors of Life, *Biosemiotics*, 2010. DOI 10.1007/s12304-010-9097-6.
14. Markoš, A., Grygar, F., Hajnal, L., Kratochvíl, Z., Neubauer, Z.: *Life as its own designer: Darwin's Origin and Western thought*. Berlin: Springer, 2009. 214s. ISBN 9781402099694.
15. Overmann, J. (ed.): *Molecular Basis of Symbiosis*. Berlin: Springer, 2006. 310 s. ISBN 3-540-28210-6.
16. Paracer, S., Ahmadjian, V.: *Symbiosis. An Introduction to Biological Associations*. New York: Oxford University Press, 2000. 291 s. ISBN 0-19-511806-5.
17. Sapp, J.: *The New Foundations of Evolution. On the Tree of Life*. New York: Oxford University press, 2009. 425 s. ISBN 978-0-19-538849-7.
18. Sapp, J.: *Genesis. The Evolution of Biology*. New York: Oxford University Press, 2003. 364 s. ISBN 0195156196.
19. Sapp, J.: *Evolution by Association. A History of Symbiosis*. New York: Oxford University Press, 1994. 255 s. ISBN 0195088212.
20. Simon, M. A.: *The Mater of Life. Philosophical Problems of Biology*. New Haven and London: Yale University Press, 1971. 258 s.
21. Smith, D. C., Douglas, A. E.: *The Biology of Symbiosis*. London: Edward Arnold, 1987. 302 s. ISBN 0-7131-2939-5.
22. Wallin, I. E.: *Symbiogenesis and the Origin of Species*. Baltimore: The Williams & Wilkins company, 1927. 171 s.

Primary Paper Section: E

Secondary Paper Section: H