CHAPTER 8

How to Understand Symbiosis?: The Conflict and Integration of Two Pictures of Life

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Cattle rely on anaerobic bacteria in the rumen to digest cellulose, and termites rely on bacteria and protozoa in the hindgut to digest lignin. It is estimated that the number of symbiotic microbial cells in the human body is ten times greater than that of human cells.[1] The symbiotic bacterial community living in the human gastrointestinal tract, which assists in digestion, has a total metabolic capacity comparable to that of the human liver.[2]

Biological symbiosis is a very common phenomenon in the living world, where mutualism and cooperation often exist between different plants and animals; at the same time, the survival of many plants and animals is also closely dependent on symbiotic microorganisms. The study

[1] Dwayne C. Savage, "Microbial Ecology of the Gastrointestinal Tract," *Annual Review of Microbiology* 31 (1977):107–133.

[2] Savage, 107–133.

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of "biological symbiosis" is almost as old as Darwin's theory of natural selection.

According to the historian of science Jan Sapp, the definition of "symbiosis" in modern biology was first given by the German botanist Anton de Bary in 1878. He first used the term "symbiosis" in his study of lichens to denote the phenomenon of "the living together of unlike named organisms."[3] According to Lynn Margulis, an American biologist, a Russian school of biology in the early 20th century emphasized the role of symbiosis in evolution: Andrei Sergeivich Famintsyn tried to isolate chloroplasts from plants and make them grow; Konstantin Sergeivich Merezhkovsky developed the theory of "two-plasm," which posited "intracellular cells," claiming that chloroplasts originated from cyanobacteria. He also coined the term "symbiogenesis," arguing that "evolutionary novelty has its origin in symbiosis." Boris Kozo-Polyansky, meanwhile, believed that cell motility has its origin in symbiosis.

However, these studies were almost "completely unknown" to early scientists in the English-speaking world. Until today, research related to microorganisms and biological symbiosis does not feature prominently in the mainstream science—and it has been especially slighted by English and American mainstream evolutionary biologists—for a long period of time. The relationship between symbiosis and evolution has yet to be seriously examined. The American anatomist Ivan Wallin emphasized the role of obligate microbial symbiosis in the origin of species, but was rejected and even ridiculed for his insights. The Frenchman Paul Portier, a contemporary of Wallin, also noted the importance of symbiosis to evolution and was similarly vilified.[4] So, what are the factors that have led to "biological symbiosis" becoming an issue historically avoided by mainstream evolutionary biology in Europe and the United States? Are there deeper influences from different generative contexts, such as cultural environments, social patterns, and local values?

[3] Jan Sapp, *Evolution by Association: a History of Symbiosis* (New York: Oxford University Press, 1994), 7.

[4] Lynn Margulis and Dorion Sagan, *Slanted Truths: Essays on Gaia, Symbiosis, and Evolution* (Göttingen: Copernicus, 1997), 298.

Two Pictures of Life

For quite a long period of time, there was, in fact, constant conflict between the competitive picture behind the classical natural selection paradigm and the cooperative picture presented by the biological symbiosis paradigm. We need not say more about the former owing to the popularity of Darwin's theory of evolution. As for the latter, however, we may divide biological symbiosis into three types of phenomena: first, symbiosis between microorganisms (including prokaryotes and lower eukaryotes); second, symbiosis between multicellular plants and animals, and microorganisms; and third, symbiosis between multicellular plants and animals. In the eyes of some scientists who support the idea of symbiotic evolution, the first two categories are the main sources of evolutionary novelty and constitute the basis for the origin and evolution of life on earth.

The inevitable barriers to communication between different views of nature and scientific traditions can be attributed to two reasons: on the one hand, the observed symbiosis occurs mostly between bacteria and multicellular plants or animals. These bacteria were once viewed by society and even by scientists as the enemy of plants and animals, a designation that seems at odds with the concept of symbiosis; on the other hand, Darwin's "survival of the fittest" competition model and symbiotic cooperation were in conflict. Because of these two reasons, mainstream scientists in Europe and America historically failed to seriously consider the relationship between symbiosis and evolution. This also, for a long time, caused the ostracization of those who researched symbiosis.

Additionally, aside from its use by biologists, the concept of "symbiosis" has spilled over into other fields like history, economics, education, and art. This has led, to a certain extent, to the lack of a consistent general definition of the concept of "symbiosis," which has long been in a state of ambiguity. Margulis makes it clear that a direct cause of this situation is also related to Petr Alekseevič Kropotkin. This famous Russian theorist published a series of articles in the journal *The Nineteenth Century* starting in 1890, which were collected in the famous book *Mutual Aid*. The book describes critically the Darwinian picture of the "struggle for existence," particularly in response to Thomas Huxley's extension of the "struggle for existence" paradigm from the natural world to human society. Although Kropotkin did not mention the term "symbiosis" in *Mutual Aid*, this picture of mutualism, with its strong moral implications, has had a profound impact on later scholars—so much so that in the eyes of many scholars and the general public, symbiotic relationships are mutualism, which contradicts the idea of survival of the fittest.

As Margulis said, the work of Kropotkin and others "accentuated both the confounding of mutual aid with symbiosis and the imposition of human social analysis on descriptions of organismal interaction."[5] In her view, "human social concerns have inextricably permeated discussions regarding the participants in symbiosis."[6] Since most molecular, cellular, and evolutionary biologists saw "symbiosis" and "mutualism" as a political slogan, they avoided experiments and research related to symbiosis. This division between research fields exacerbated the biology community's inability to come to a consensus regarding symbiosis. According to Margulis, "The lack of consensus about first principles of symbiosis and evolution has serious consequences for both the teaching and the practice of evolutionary biology."[7]

Challenging the Classical Natural Selection Paradigm

Starting from the 1960s with the proposal and verification of the theory of the symbiotic origin of eukaryotic cells, people's understanding of symbiosis among microorganisms and organisms has increased, and symbiosis as a concept has grown in popularity. This led to a revolution in biology that has gone unnoticed for a long time, something that Jan Sapp has called the "quiet revolution."[8] In 1967, Lynn Margulis proposed Serial Endosymbiosis Theory (SET), which posits that eukaryotic cells evolved from a symbiosis between different types of primitive prokaryotic cells for the first time.[9]

[5] Margulis and Sagan, *Slanted Truths*, 300.

[6] Margulis and Sagan, *Slanted Truths*, 298.

[7] Lynn Margulis, "Symbiogenesis and Symbioticism," in *Symbiosis as a Source of Evolutionary Innovation: Speciation and Morphogenesis*, ed. Lynn Margulis and René Fester (Cambridge: The MIT Press, 1991), 3.

[8] Sapp, *Evolution by Association*, xiii.

[9] Lynn Sagan, "On the Origin of Mitosing Cells," *Journal of Theoretical Biology* 14, no. 3 (1967): 255–274.

In *The Origin of Eukaryotic Cells*, published in 1970, Margulis formally declared that after aerobic bacteria were devoured by amoebic prokaryotes, they evolved through long-term symbiosis into mitochondria. After cyanobacteria were devoured, they evolved through symbiosis into chloroplasts. And after spirochaetes were devoured, they evolved through symbiosis into primitive flagella.[10] At first, Margulis' theory was attacked. But the situation improved with the advancement of molecular biology and microbial genetics. After the DNA of mitochondria and chloroplasts was successfully extracted in the 1980s, it was revealed that their DNA was much different from the DNA of the nucleus but very similar to the DNA of bacteria and cyanobacteria. Not only could the rRNA of cyanobacteria be hybridized with the DNA of cyanobacteria itself, it could also be hybridized with the DNA of the chloroplast of *Euglena*. This indicates their homology, which verified Margulis' theory.

As the importance of biological symbiosis in the history of evolution was gradually being proved, biologists had to make a difficult decision. There was an unmitigable conflict between the competition paradigm of classical natural selection and the cooperation paradigm of biological symbiosis. Evolutionary biologists could choose to either continue as they had before and neglect the issue of biological symbiosis in their work, or they could use the concept of symbiosis to challenge the orthodoxy of Darwinian natural selection.

Margulis chose the latter path. Aided by ample research results in the fields of microbiology and symbiosis, she developed a theoretical framework with the aim of transforming the classical paradigm of the theory of natural selection. She believed that the prime source of evolutionary novelty was not random mutations and natural selection but symbiosis. Experimental evidence shows that mutations rarely produce heritable and favorable changes, nor does the accumulation of mutations cross species barrier to produce new species. Instead, organisms integrate foreign genomes through symbiosis, similar to corporate acquisitions and mergers that result in the acquisition of new skillful workers, allowing for the rapid acquisition of new, refined traits and the formation of novel evolutionary lineages.[11]

[10] Lynn Margulis, *The Origin of Eukaryotic Cells* (New Haven and London: Yale University Press, 1970).

[11] Lynn Margulis and Dorion Sagan, *Acquiring Genomes: A Theory of the Origins of Species* (New York: Basic Books, 2003) 72.

Describing the course of evolution, Margulis said, "Family trees usually are grown from the ground up: a single trunk branches off into many separate lineages, each branch diverging from common ancestors. But symbiosis shows us that such trees are idealized representations of the past… The tree of life is a twisted, tangled, pulsing entity with roots and branches meeting underground and in midair to form eccentric new fruits and hybrids."[12] Margulis got the idea that symbiosis is the primary source of evolutionary novelty from Ivan Wallin. Wallin had earlier pointed out in his 1927 book *Symbioticism and the Origin of Species* that biological evolution consists of three features: the origin of new species, the retention or destruction of formed species, and the direction or progress of evolution, while natural selection can only explain the second feature and the other two aspects need to be explained by "other unknown factors," of which symbiosis is the most important one.[13]

Margulis referred to the symbiotic whole of all life on Earth, together with its environment, as "Gaia," an integrated living system.[14] In *A New Bacteriology*, Sorin Sonea et al. conveyed a similar view, saying that all bacteria combined to form a global superorganism. In this model, different strains of bacteria act as differentiated cells of this superorganism, sharing the same gene pool via lateral gene transfer while at the same time possessing metabolic diversity. This research team likened the complicated functions of the bacterial superorganism servicing the ecosphere to a supercomputer, possessing massive data storage capacity and a well-developed internal communication network.[15] The difference between Margulis' Gaia and the bacterial superorganism of Sonea and his team is that the latter only includes bacteria, while Gaia includes all life forms. The holism expressed by both models, however, is the same. Margulis views multicellular plants and animals as the products of symbiotic evolution among prokaryotes; they can essentially still be viewed as the symbiotic community of a group of single-celled organisms. In this way, the relationship between cells in the bodies of plants and animals,

[12] Lynn Margulis, *Symbiotic Planet: A New Look at Evolution* (New York: Basic Books, 1999), 52.

[13] Ivan Wallin, *Symbioticism and The Origin of Species* (Baltimore: Waverly Press, The Williams and Wilkins Company, 1927), 3–7.

[14] Margulis and Sagan, *Acquiring Genomes*, 70.

[15] Sorin Sonea, Maurice Panisset, *A New Bacteriology* (Boston: Jones & Bartlett, 1983), 85, 112–123.

between plants and animals and their symbiotic bacteria communities, between different prokaryotes, can all be considered symbiotic relationships. As a result, the boundaries between different biological individuals becomes blurred.

The Battle for Gaia: Dawkins vs. Margulis

The views of those like Margulis are difficult to accept for scientists who adhere to the classical model of natural selection. Richard Dawkins is one of the sternest critics of the Gaia Hypothesis.

The main reason Dawkins and others oppose the Gaia Hypothesis is that Gaia is posited as being a single entity that cannot reproduce to form a population; it thus fails to meet the criterion for being a life—the ability to reproduce.[16] In their view, reproduction and natural selection are the most important properties of life. The Neo-Darwinist John Maynard Smith said, "the picture suffers from the drawback that is fatal to all holistic models of evolution, from the Gaia Hypothesis downwards, of losing all sight of the units of selection, and hence of lacking any model of the dynamics of evolutionary change."[17] This criticism has its validity because Margulis always stressed the symbiosis of different organisms but ignored the phenomenon of reproduction among the same species and, thus, the process of natural selection caused by reproduction and variation. In *The Selfish Gene*, Dawkins noted that biological symbiosis is always mutually beneficial behavior and that it can always be explained with the "selfish gene" strategy: individuals of different species carrying different genes cooperate through symbiotic behavior, thus making the whole system more adaptive; as a result, individuals that engage in altruistic behavior are in turn rewarded—their genes are preserved.[18]

In his writings, Margulis has made severe criticisms of the Neo-Darwinists represented by Dawkins. Margulis and Dawkins stand at the "opposite ends" of contemporary biological thought, with very different views on the object of biology, the unit of life, the nature of life, the

[16] Lawrence E. Joseph, *Gaia: The Growth of an Idea* (New York: St. Martin's Press, 1990), 56.

[17] John Maynard Smith and Eörs Szathmary, *The Major Transitions in Evolution* (New York: Oxford University Press, 1995), 189.

[18] Richard Dawkins, *The Selfish Gene* (Oxford: Oxford University Press, 2006), 181–186.

origin of life, and research methods for life sciences. See Table 8.1 for a breakdown of their differences.

The difference in their ideology can be summed up as a difference in the understanding of biological individuality. In Margulis' view, the fundamental property of the biological individual is metabolic associations and cooperation. Cells are the most basic units of life. From cells to organisms, and then to the ecological system and even the whole Gaia, are all different levels of biological individuals with autonomy. In Dawkins' view, the fundamental property of the biological individual is self-replication and natural selection. Genes are the most basic units of life, while plant and animal organisms are merely survival machines for genes without autonomy. The views of Margulis and Dawkins represent

Table 8.1 Comparison of Margulis' and Dawkins' biological thought

	Margulis' views	*Dawkins' views*
The concept of the "self"	Autopoietic organisms at different levels may all become "self". The boundary of the self is variable.	Only the selfish gene has "selfness". The boundary of the self is rigid.
The role of cells and organisms	Cells are the most basic units of life. Autopoietic organisms at different levels, from bacteria to plants and animals and Gaia, all have autonomy.	They act as survival machines for genes. They derive from genes and serve genes. They lack autonomy.
The essence of life	Metabolism	Reproduction and natural selection
The origin of life	Life began from something like the cell membrane structure.	Life began from self-replicating macromolecules.
Scientific research methodology	Emphasizes experimental observations	Emphasizes mathematical and computational modeling
The relationship between symbiosis and natural selection	Symbiosis creates evolutionary novelty. Natural selection does not create novelty, but filters extant species.	Evolution is driven by selfish genes for the purpose of self-replication and self-preservation. Symbiosis is only a strategy on the level of the phenotype.

the two different understandings of the nature of life and the biological individual in contemporary biology.

Viewed in a larger context, the opposition of these two pictures reflects the contradiction between two scientific traditions (the mathematical-scientific tradition and the natural history tradition) and two views of nature (the mechanistic view of nature and the organismic view of nature) in the contemporary life sciences. Margulis points out that the Neo-Darwinists' ideas embody the mechanistic view currently prevalent in biology: they are all extremely envious of the mathematical-physical approach, "Computer jocks (former physicists, mathematicians, electrical engineers, and so forth), with no experience in field biology, have a large influence on the funds for research and training in 'evolutionary biology.'"[19]

In my view, the population reproduction model and the dynamics of natural selection are the theoretical basis for Neo-Darwinists' mathematical and computer modeling. This is perhaps why they insist on reproduction and natural selection as the most important criteria for judging life. On the other hand, Margulis strongly advocated a view of life based on the theory of Autopoiesis proposed by Humberto Maturana and others.[20] The nature of autopoietic entities is physiological in character, metabolic and diverse, relying on actual observation rather than mathematical and computational modeling for its research. This can be seen as a modern version of the organismic view of nature.

The Collaborative Framework: A New Paradigm for Life

In recent years, John Dupré and others have proposed using the concept of collaboration to integrate different understandings of life—the picture of cooperation and the picture of competition.[21]

In the competitive picture proposed by scientists like Dawkins, genes are the most basic selfish individuals competing with each other. The

[19] Margulis and Sagan, *Slanted Truths*, 266.

[20] Margulis and Sagan, *Slanted Truths*, 267.

[21] John Dupré and Maureen A. O'Malley, "Varieties of Living Things: Life at the Intersection of Lineage and Metabolism," in *Processes of Life: Essays in the Philosophy of Biology*, ed. John Dupré (New York: Oxford University Press, 2012), 206–209.

"selfish gene" becomes the most basic explanatory model, and even the apparently cooperative behavior of biological symbiosis is interpreted as serving the respective interests of the "selfish gene." Looking for compromise among disparate views, Dupré and others disagree with the idea that cooperative behaviors should be reduced into deeper-level of selfish behaviors. They instead suggest that selfishness and cooperation might better be understood within a framework of collaboration. They explain the concept of collaboration as "interaction between components of a system that lead to different degree of stability, maintenance, or transformation of that system." Collaboration from this point of view covers a range of interactive processes that may include both cooperative and competitive activities. At one end of this continuum, the goal of participants may be completely aligned, while at the other end, relationships may be largely or wholly hostile.[22]

The simplest collaborative phenomena are combinations of physical and chemical interactions, such as the chemical process in which atoms combine to produce molecules, which have properties that are not found in any of the atoms of which they are composed. But the combination of molecules and atoms alone is not enough to produce life; reproduction and metabolism are also required. Reproduction is emphasized in the competitive picture of life, while metabolism is emphasized in the cooperative picture of life. Dupré et al. emphasized a broader perspective of life as a collaborative enterprise and believed that reproduction and metabolism both should be seen as fundamental properties of life. They provided two kinds of symbiotic phenomena as examples of collaboration. One is intracellular symbiosis, such as that of aphids and the symbiotic bacteria *Buchnera* in their cells. Another is extracellular symbiosis, such as the massive reduction of the genomes of symbiotic bacteria during evolution.[23] Obviously, these two classes are far from encompassing all symbiotic relationships, but they show us the close connection between the collaborative framework and the concept of symbiosis.

[22] Dupré and O'Malley, *Processes of Life*, 207–208.

[23] Dupré and O'Malley, *Processes of Life*, 216–220.

The Unit of Collaboration: The Holobiont

In summary, it is clear that there is no single definition of biological symbiosis. Therefore, I will try to further clarify the concept of symbiosis in the framework of "collaboration", and one of the core tasks is to redefine the concept of holobiont and prove that a holobiont is a unit of collaboration.

What is a holobiont? For a long time, this term was mostly used by biologists studying coral reefs. According to the U.S. National Oceanic and Atmospheric Administration (NOAA), holobiont is a collective term referring to the totality of a coral animal, its endosymbiotic zooxanthellae, and the associated community of microorganisms. Later, the meaning of this term was further extended. In describing hologenome theory, Ilana Zilber-Rosenberg et al. defined the holobiont as "the animal or plant with all of its associated microorganisms."[24] In my opinion, this definition is still ambiguous. "All of its associated microorganisms" can refer to a wide-ranging plethora of microorganisms, from tightly bound endosymbionts, such as the intracellular symbiotic bacteria of aphids, to those microorganisms living on the skin of animals, and even to those living close to it in the surrounding environment. Would the latter still be considered part of the holobiont? A clearer spatial-temporal boundary is needed for further definition. Multicellular plant and animal organisms as hosts generally have a clear spatial-temporal boundary. Thus, a clearer definition of holobiont can be given by using this existing boundary. At the 2011 conference of the International Society for the History, Philosophy, and Social Studies of Biology (ISHPSSB), I proposed this definition: "The holobiont is the symbiotic complex formed by a multicellular animal/plant organism and the microbial community living inside its body."

Additionally, we may look at the concept of immunological continuity, a new criterion for defining the organism proposed by Thomas Pradeu: "An organism is a functionally integrated whole, made up of heterogeneous constituents that are locally interconnected by strong biochemical interactions and controlled by systemic immune interactions that repeat

[24] Ilana Zilber-Rosenberg and Eugene Rosenberg, "Role of Microorganisms in the Evolution of Animals and Plants: The Hologenome Theory of Evolution," *FEMS Microbiology Reviews* 32, no. 5 (2008): 723–735.

constantly at the same medium intensity."[25] Applying this criterion to the complex formed by a mammal and the symbiotic microbes that live within it, Pradeu believed it can be considered an organism formed of heterogeneous constituents: "These bacteria have permanent and constitutive biochemical interactions with other parts of the host. There is no fundamental difference between interactions of the host's immune receptors with these symbiotic bacteria, and interactions of the host's immune receptors with endogenous constituents." Then, he extended this conclusion to other complexes composed of plants and animals and their endosymbiotic microorganisms.[26]

Using the holobiont concept, I propose the following revision to Pradeu's above formulation: "A holobiont meets the criteria of immunological continuity between its components, thus satisfying the criteria for being judged as an organism."

In the holobiont, since the two sides of the symbiosis are closely related for most of the life cycle, forming an integrated organism, it becomes obvious that this unit can be regarded as a unit of natural selection, i.e., a unit of "collaboration." Thus, "cooperation" and "competition" actually constitute two different perspectives from which to examine and analyze the living world. They are not antithetical but complementary and interconnected.

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[25] Thomas Pradeu, "What is an Organism? An Immunological Answer," *History and Philosophy of the Life Sciences* 32, no. 2/3 (2010): 258.

[26] Pradeu, 'What Is an Organism?' 247–268.

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