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Words as Battle Cries: Symbiogenesis and the New Field of Endocytobiology

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Words as battle cries—symbiogenesis and the new field of endocytobiology

> . . . and there is the additional consideration, that each of the elements whose fusion goes to make up the impregnated ovum, is held by some to be itself composed of a fused mass of germs.
>
> —Samuel Butler 1898

Our minds are incarcerated by our words. The biological term *symbiosis* has been used in a way that obscures not only its literal meaning but also the phenomenon's instrumental role in evolution. Biology textbooks define *symbiosis* anthropocentrically—as mutually helpful relationships or animal benefits, implying social contract or cost-benefit analysis by the partners. This definition is silly—symbiosis is a widespread biological phenomenon that preceded by eons the human world and the invention of money.

Symbiosis was defined first by German mycologist H. A. DeBary (1879) as "unlike organisms living together." The phrase *unlike organisms* soon came to mean members of different species.

Lichens, complexes of fungi associated with photosynthesizers (either cyanobacteria or green algae), have served as examples of symbionts. The lichen fungus *Cladonia* on a petri plate grows as fuzz; the lichen alga *Trebouxia* in pure culture on the surface of agar as slime; but alga and fungus growing together as the British soldier is ground cover; superficially the lichen is a land plant (Figure 1).

Since the last century, scientists have recognized that symbiosis has the power to generate great biological novelty and discontinuity. I argue that symbiosis is far more innovative in the generation of biological novelty than is the accumulation of chance mutations, although the latter is more commonly credited as the basis of evolutionary change.

Students and teachers most often encounter the word *symbiosis* in its textbook definition. Authors of science texts typically describe symbiosis as follows:

- An internal partnership between two organisms in which the mutual advantages normally outweigh the disadvantages (Collocott 1972).
- An association that must always benefit at least one of the species, because otherwise it would soon dissolve (Minkoff 1983).

Even in current biological secondary literature, *symbiosis* is often taken to mean a "mutualistic biotrophic association" (Schiff and Lyman 1982) or a "mutually beneficial . . . relationship" (Avers 1989). However, the research scientists today studying symbioses embrace DeBary's original definition in modern guise: *symbiosis* refers to protracted physical associations among organisms of different species, without respect to outcome. These scientists reject the textbook and secondary analyses that gauge symbiosis on what might be considered customer satisfaction.

Symbiosis does not equal mutualism

If *symbiosis* is defined as a beneficial relationship between organisms of different species, it is difficult to distinguish it from *mutualism.* Recent biology texts use *mutualism* to refer to social relationships among organisms, of the same species or of different species, that need not be physically associated. Because symbiotic

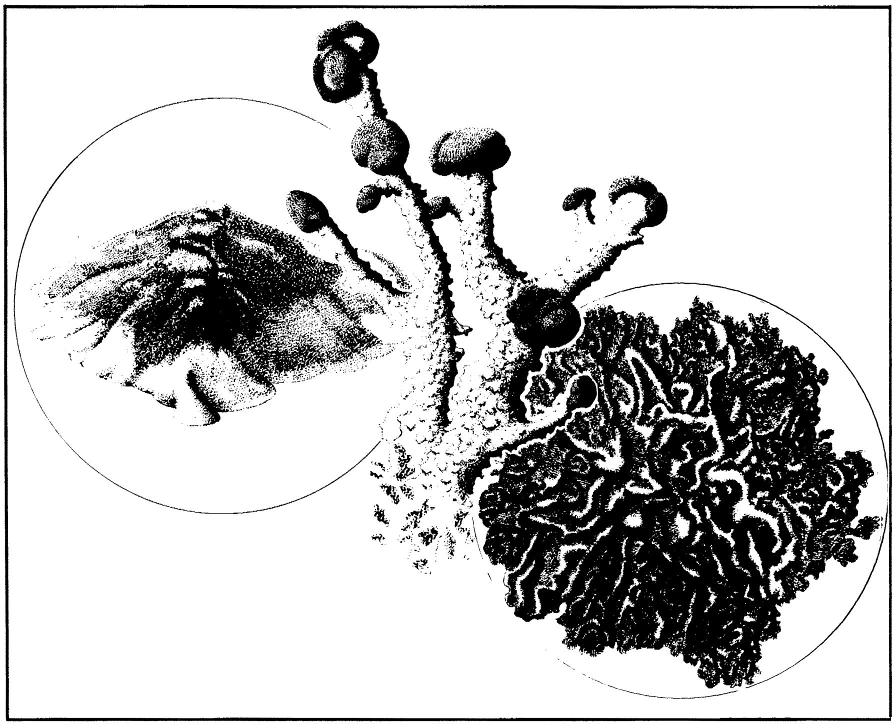

Figure 1. Two bionts and the holobiont *Cladonia cristatella.*

by Lynn Margulis

partners must be members of different species that are in physical contact with each other, according to textbook definitions, symbiotic relationships should be a subset of mutualistic relationships. Both symbiosis and mutualism are considered to be positive, or favorable, relationships, as opposed to negative relationships such as parasitism.

But complications abound. In practice, temporal and spatial aspects of symbiosis often are not described in texts. Symbiosis researchers examine whether or not the partners experience prolonged, permanent, cyclical, facultative, or casual relationships. Most writers focus instead on the impossible: proof that the association "benefits" the partners. Because the unassociated partners (e.g., the alga or fungus) cannot be grown under the same conditions as the lichen, a strict proof of "benefit" cannot be made.

Attempts to clarify meanings have compounded the problem, because measuring benefit (a unitless quantity), either in the field or laboratory, has not been not feasible. As the term *symbiosis* became nearly synonymous with *biotrophic mutualism*, new terms to indicate neutral relationships between physically associated organisms were invented (Lewis 1973b). *Commensalism* (from the Latin, meaning eating from the same table) describes two species of organisms physically associated with each other but deriving nutrients from a third (e.g., clownfish and sea anemones feeding on bacterial symbionts). *Phoresy* is used to describe the carrying of one organism by another (e.g., remoras by sharks).

A note about history

Almost entirely unknown to English-language scientists, a Russian school of biology science in the early 1900s emphasized the role of symbiosis in evolution. Andrei Sergeivich Famintzin (1835–1918) experimented with the isolation and growth of chloroplasts from plant cells. Konstantin Sergeivich Mereschkovsky (1855–1921) developed the "two-plasm" (cell-within-a-cell) theory, claiming that chloroplasts originated from cyanobacteria (blue-green algae). From this work, he invented the term *symbiogenesis,* the "origin of evolutionary novelty via symbiosis." Finally, Boris Michailovich Kozo-Polyanski (1890–1957) suggested that cell motility originated by symbiosis. Thus each of these three Russian scholars, all of whom held esteemed positions in Russian academia, contributed fundamentally to understanding of the concept of symbiogenesis (Khakhina 1979; Figure 2).

In the early 1900s in the United States, by contrast, there was little research on symbiosis. Anatomist I. E. Wallin (1883–1969) was prolific and enthusiastic in his early years when he stated his principle of symbionticism (1927), by which he stressed the importance of obligate microbial symbioses in the origin of species. But his ideas were rejected and ridiculed (Mehos 1990), and for the last 40 years of his life, while working at the University of Colorado Medical School, Wallin avoided symbiosis research.

Paul Portier, a French contemporary of Wallin, also emphasized the importance of symbioses in evolution (Margulis 1981, Portier 1918). Although Portier was supported by the king of Monaco, he too was aggressively attacked. The French scientific

Figure 2. The symbiogeneticists: Boris M. Kozo-Polyanski, Andre S. Famintzin, Konstantin S. Mereschkovsky, and Ivan E. Wallin.

community, led by microbiologist August Lumiére (1919), helped demolish Western enthusiasm for the role of symbiosis in evolution (Mehos in press).

Mutual-aid biology

Human social concerns have inextricably permeated discussions regarding the participants in symbiosis. These concerns have contributed to the misconstruing of the term. Belgian biologist-politician P. J. Van Beneden (1873) first used the term *mutual aid* in describing "repayment" for services among "lower animals." Wholesale extrapolation from "the society of men" to "the community of animals" became especially evident in Peter Kropotkin's *Mutual Aid* (1902). A Russian prince exiled to London, Kropotkin sought answers to questions of human relations in nature:

> Mutual aid is met with even amidst the lowest animals, and we must be prepared to learn some day, from the students of microscopical pond-life, facts of unconscious mutual support, even from the life of micro-organisms. (Kropotkin 1902, p. 10)

Kropotkin's analyses of animals, "savages," "barbarians," medieval city-dwellers, and modern society all extend his theories that

> . . . mutual aid is as much a law of animal life as mutual struggle, but that, as a factor of evolution, it most probably has a far greater importance, inasmuch as it favours the development of such habits and characters as insure the maintenance and further development of the species, together with the greatest amount of welfare and enjoyment of life for the individual, with the least waste of energy. (Kropotkin 1902, p. 6)

To Kropotkin and many subsequent scholars, the idea of symbiosis and mutual aid—cooperative forces in evolution—was to be contrasted with the idea of competition—a negative force leading to the struggle for existence. Kropotkin's work accentuated both the confounding of mutual aid with symbiosis and the imposition of human social analysis on descriptions of organismal interaction.

Most Western scientists have regarded symbiosis and mutualism as political slogans, therefore choosing not to focus experiments on these biological phenomena. For most of this century, then, symbiosis research was divorced from cellular, molecular, and evolutionary biology.

Evolutionists and most other biologists—both experimental and theoretical—still consider symbiosis analyses to be remote to evolutionary analyses (Keller and Lloyd in press). Symbiosis is ignored, or only defined, in the major textbooks of evolution (e.g., Avers 1989, Ayala and Valentine 1979, Ehrlich and Holm 1963, Futuyma 1986, Kimura 1983, Minkoff 1983).

Only two English-language biology textbooks use symbiosis as their organizing principle. One, designed for undergraduates, is an excellent introduction to symbiosis (Ahmadjian and Paracer 1986); it describes dozens of associations by taxa. The second, an erudite and useful graduate text, is dedicated to the experimental analysis of symbiosis (Smith and Douglas 1987). But neither book evaluates symbiosis as a major mechanism of generating heritable variation in evolution.

Obscurity and funding

Symbiosis remains an obscure, primarily botanical subfield of biology and, at least in the United States and United Kingdom, is still not funded per se. In contrast to mainstream zoological pursuits (e.g., parasitism and infestation [which are associated with disease and thought to require urgent scientific investigation and high levels of funding], cladistics, or systematics), the healthy, positive, perhaps even feminine connotations of symbiosis and mutualism have suggested that research on these topics is relatively unimportant. Indeed, this term-contentiousness has impeded research. Most of my colleagues[1] would agree that mention of symbiosis in a grant application tends to deny funding.

This prejudice leads to limited support for symbiosis research. There have been studies, assisted by the Office of Naval Research, of bacteria harbored in the light organs of luminous fish. Agricultural research funds have fostered analyses of leguminous plant associations with nitrogen-fixing bacteria. And zoologists have been encouraged by oceanography and marine science programs to study algae of coral reefs. However, in these investigations, symbiosis is seldom considered to be a means of generating inherited variation in evolution.

Evolutionary novelty

Whereas all biologists agree that mutation (base-pair changes, deletions, duplications, and transpositions) is a major source of evolutionary novelty, few emphasize the importance of other mechanisms. These alternative mechanisms include karyotypical alterations (polyploidy, increase in number of chromosome sets; polyteny, increase in amount of DNA per chromosome; and Robertsonian fusions, chromosomal translocations). Raikov, a Soviet cytologist, has stressed polyenergy (the increase in number of homologous genomes in a nucleus) as a mechanism of evolution in ciliates and other protoctists (Raikov 1982).

Karyotypic fissioning refers to the phenomenon, in mammals, in which an extra centromeric synthesis in a fertile member of the population leads to a doubling of the number of chromosomes, because each single metacentric is converted to two telocentrics. Because no total change in the amount of DNA per karyotype occurs, fissioning tends to be benign with respect to viability and fertility. In spite of a great deal of evidence in its favor, the importance of karyotypic fissioning in mammalian evolution has been almost exclusively argued by Neil Todd, publisher of the *Carnivore Genetics Newsletter* and adjunct professor at Boston University (Margulis 1981, Todd 1970).

The acquisition of additional genomes as a mechanism of evolution of prokaryotes has been widely discussed, and it was evaluated as an extremely important force by Sonea and Panisset (1983). The special case of homologous genome acquisition known as meiotic (or eukaryotic) sex

[1]Personal communication from J. W. Hastings, Harvard University, Cambridge, MA; B. Kendrick, University of Waterloo, Canada; L. Muscatine, University of California, Los Angeles; K. H. Nealson, Center for Great Lakes Study, University of Wisconsin, Milwaukee; J. Sapp, University of Melbourne, Australia; D. C. Smith, Edinburgh University, Edinburgh, Scotland; and R. Trench, University of California, Santa Barbara.

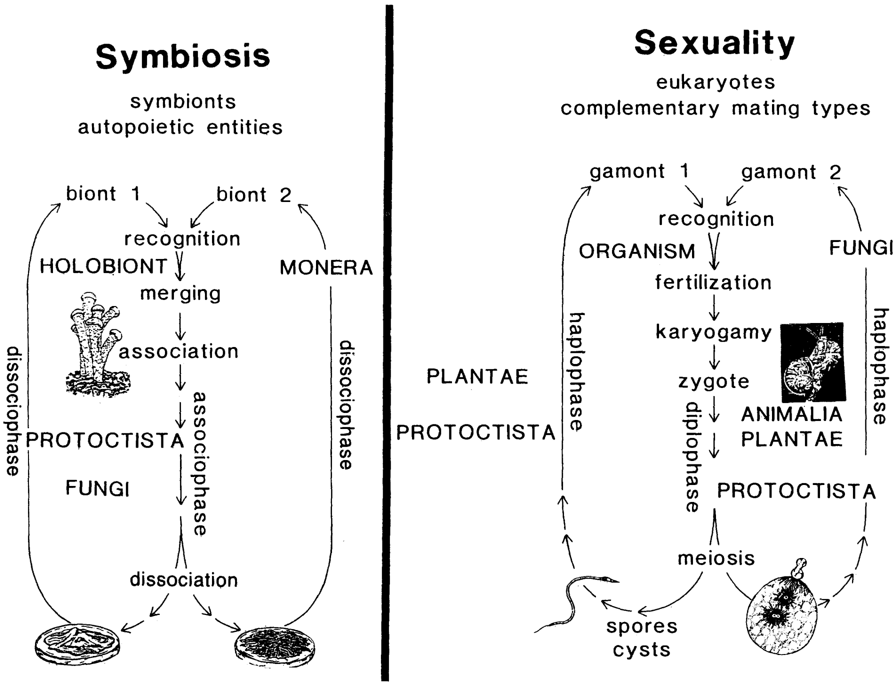

Figure 3. Cyclical symbiosis and meiotic sexuality are analogous. Both symbiotic and sexual partners must sense and recognize each other; their bodies (bionts and gamonts) or representative cells (biont cells and gametes) must merge (fusion, conjugation, or fertilization); integrating mechanisms (association and karyogamy) must establish and maintain the integrity of the new individual (holobiont and zygote), and, at a subsequent time in the life cycle, dissociation or reduction by meiosis ensues to form bionts or haploid gametes. Although meiotic sexuality is a more ritualized process than cyclical symbiosis, both are likely to be maintained by selective pressure on the unassociated symbiont or the haploid under certain recurring environmental conditions.

is, of course, described in most English-language textbooks on evolution. Yet the intimate relationship between sex and symbiosis and their analogous components (Figure 3) is overlooked.

The analogies between the processes of recognition, fusion, and emergence of new individuals in both sex and symbiosis are obscured by differences in the terminology for the two processes, as can be seen in Figure 3. Few scientists are aware of the acquisition and migration of foreign nuclei in the establishment of the dikaryon (in red algae rendered heterokaryotic) and the occurence of nuclear parasitism as an evolutionary phenomenon. Research on acquisition of foreign nuclei has been done almost exclusively by phycologists Lynda Goff of the University of California at Santa Cruz and Annette Coleman of Brown University (Goff and Coleman 1987).

The best-understood examples of morphogenetic innovation and speciation come from studies of symbioses, including lichens (Honegger in press). Well-documented cases of new species emerging include fish with luminous bacteria (McFall-Ngai in press), weevils that lose bacteria (Nardon and Grenier in press), and the amebas that survive bacterial infection (Jeon 1990). The amebas incorporate former food bacteria, which form new intracellular organelles. As a result, more complex new species of free-living amebas emerge (Sagan and Margulis 1987).

Future symbiosis research

Before the founding in 1983 of the International Society for Endocytobiology (ISE) by the two German scientists, Werner Schwemmler (an insect-bacteria symbiogeneticist) and H. E. A. Schenck (who studies the chemistry of *Cyanophora* and other algae), the fields of intracellular symbiosis and evolutionary studies had separate histories. Virtually all of recent Western evolutionary biology had emerged as "neo-darwinism" from population genetics.

Endocytobiology is defined by the ISE as the study of "intracellular space as oligogenetic ecosystem." The ISE regards all intracellular symbionts as objects of its study (Schenck and Schwemmler 1983, Schwemmler and Schenck 1980). This newly defined field is rooted in descriptions of bacterial symbionts and their correlation with studies of eukaryotic cell organelles (Lee and Fredrik 1987). The history of the field is recorded in the original scientific literature collected by Dyer and Obar (1985).

The ISE, by publishing three international colloquia (two held in Germany and one in New York; Lee and Fredrick 1987, Schenk and Schwemmler 1983, Schwemmler and Schenck 1980) and articles in their journal *Endocytobiosis and Cell Research*, has begun to unite biologists from disparate traditions in common pursuit of cell origins. A new journal, *Symbiosis* (founded in 1985), published by Miriam Balaban and edited chiefly by lichenologist Margolith Galun in Rehovot, Israel, offers an outlet for scientists who experimentally investigate the molecular and cellular bases of symbioses.

Now a symbiosis of journals is under discussion: *Symbiosis* and *Endocytobiosis and Cell Research* are planning a protracted physical association. The new name is currently under discussion: it will probably be called *Endocytobiology and Symbiosis*. This journal would, for the first time, unite those scientists studying all kinds of symbioses with those studying intracellular organelles and cytoplasmic heredity.

The appearance of this new journal will offer neo-darwinist evolutionists and experimental endocytobiologists a regular forum for professional interaction. Most of the scientists who consider themselves endocytobiologists do not attend meetings in general evolutionary biology. Thus, as is usual in the sociology of science, potential conflict, as well as integration, is limited by lack of communication (Fleck 1979).

The history of endocytobiology has been described in *Mosaic* (Fisher 1989), a magazine published by the National Science Foundation. The issue, which was dedicated to new research results in cell biology, launched endosymbiosis into the biological mainstream as an important mechanism of organelle origin and cell evolution. This article has aided communication among biologists and prompted the process of reintegration of their subfields. Considering the historical contributions of eastern European scientists, translation of Fisher's article into the Russian language is in order.

Conclusions

"Words become battle cries," wrote Ludwig Fleck (1936), describing the penchant of the scientist to fret about labels. Indeed, both endocytobiology and symbiogenesis are simultaneously neo-lamarckian and darwinian evolutionary ideas. Mitochondria, plastids, and other organelles began as bacteria; thus acquired characteristics—including their genomes—are inherited.

The Russian school recognized symbiogenesis as an evolutionary mechanism. Even British novelist and philosopher Samuel Butler described cells-inside-cells in eloquent literary terms at the turn of the century (Butler 1923). Furthermore, Darwin himself was a lamarckian. He even anticipated symbiogenesis when he wrote, "We cannot fathom the marvelous complexity of an organic being; but on the hypothesis here advanced this complexity is much increased. Each living creature must be looked at as a microcosm—a little universe, formed of a host of self-propagating organisms, inconceivably minute and as numerous as the stars in heaven" (Darwin 1868, p. 453).

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