LYNN MARGULIS (1938-2011)

Pioneering American Biologist and Geoscientist

by Mark A.S. McMenamin

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Best known for what is now called endosymbiosis or endosymbiotic theory, American geoscientist and biologist Lynn Margulis played a critical role in convincing Western science that the chloroplasts of eukaryotic cells were descended from once free-living photosynthetic bacteria, and that mitochondria were descended from free-roaming parasitoid bacteria. Margulis was not the first to propose what would become her trademark theory, but from now on, the history of endosymbiosis theory will be divided into a pre-Margulis phase, a Margulis phase, and a post-Margulis phase.

Margulis served as midwife to a much broader concept, a concept that the Russian biologist Konstantin S. Merezhkovsky (1855-1921) called *symbiogenesis*. Symbiogenesis is defined as the origination of new organisms through the symbiotic association and unification of two or more species.

The Western reception of symbiogenesis had a long gestation and a difficult birth. It was Lynn Margulis who finally convinced us that endosymbiosis was required to understand the constitution of the eukaryotic cell. Margulis strived to uncover the full implications of symbiogenesis theory, doing so with an iconoclastic fervor.

Shortly after she arrived at the University of Massachusetts, Amherst in 1988, she and I began to work closely on subjects of shared interest, such as the Ediacaran fossil record and early Russian re-

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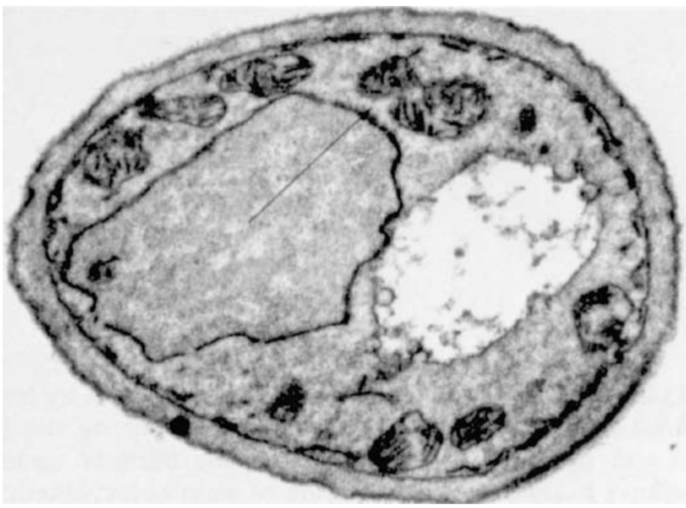
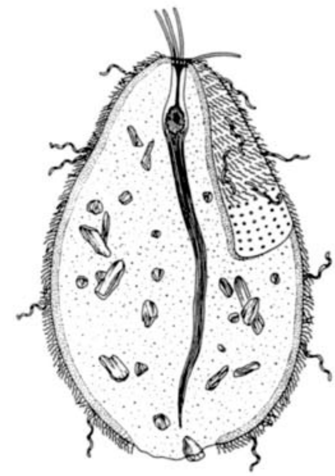


MITOCHONDRIA IN YEAST CELL

Margulis viewed mitochondria, which generate the energy for cell metabolism, as descended from free-roaming parasitoid bacteria. Here, an electron micrograph of a yeast cell, showing mitochondria (small black bodies). The arrow points to a mitochondrion that is apparently dividing.

Source: A.W. Linnane, Monash University, Australia, in Lynn Margulis, *Early Life* (Boston: Jones and Bartlett Publishers, Inc., 1984), p. 76



EXAMPLE OF A PROTOCTIST, WHICH EVOLVED FROM BACTERIAL SYMBIOSIS

The protoctist Mixotricha paradoxa. *Protoctists evolved from bacterial symbiosis, and are neither plant nor animal, Margulis said. This is an example of an individual composed of at least five kinds of organisms.*

Source: Lynn Margulis, *Symbiotic Planet: A New View of Evolution* (New York: Basic Books, 1998), p. 63.

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Margulis looking at Spirochaeta perfilievia*, a sulfide-requiring round body-forming spirochete bacteria, provided by her Russian colleague, Galina Dubinina, who studied the organism for 40 years.*

search. In one of our first discussion sessions at the university, we discovered a mutual interest in the work of the great Russian biogeochemist Vladimir I. Vernadsky (1863-1945).

Vernadsky was virtually unknown among our Western colleagues at the time. We developed this interest together for over 20 years, collaborating on the first full English translation of Vernadsky's great work *The Biosphere*.[1] The work continues to this day, and in my final project with Lynn, only a few months before her death, I uncovered in the Vernadsky archives at Columbia University, an exchange of letters between Vernadsky's son George Vernadsky and George Evelyn Hutchinson (1903-1991), discussing the preparation of Vladimir Vernadsky's research for a wider audience. Margulis expressed delight with this find in one of my last communications with her.

Neo-Darwinism Is Dead

One day while walking together across the Amherst College campus, Margulis turned to me and announced that Neo-Darwinism was dead and that, as a result, we needed an entirely new evolutionary paradigm. At the time, I was unaware of any credible challenge to the prevailing evolutionary model. Lynn proceeded to explain how the stepwise natural selection required by the Neo-Darwinian Modern Synthesis had never actually been demonstrated in the vast majority of cases.

The concept that most major evolutionary changes occurred by slow accumulation of mutations, lacked decisive scientific support. Rather, all known cases of what might be called speciation in the laboratory involved sudden reproductive isolation via genital infections, rendering the infected individuals able to interbreed only with conspecifics that had already contracted the same venereal disease.

For Margulis, this was compelling evidence that symbiogenesis was not only responsible for the makeup of the eukaryotic cell, but that it was also responsible for virtually all speciation events in animals, plants, fungi, and protists. In other words, symbiosis equates to evolutionary transformation at both the macroevolutionary (new major cell types) and microevolutionary (new species) levels.

The great Russian symbiogeneticist Andrey S. Famintsyn (1835-1918) had arrived at a similar conclusion a century before, noting that the major steps in evolution are not in the least elucidated by Darwin, and remain, as before, an unresolved question. Margulis framed this as an astonishing scientific insight, and I have since come to realize that once again she was on the trail of something important, a major advance in science that would be fully revealed only after much argument and debate, finally leading to acceptance by the scientific community.

By 1989, Margulis was in full swing with this aspect of her research, spearheading conferences and sponsoring book projects with the aim of showing that virtually all evolutionary innovation was the result of symbiogenesis. We might even say that it was Lynn Margulis, not Charles Darwin, who actually explained the mechanics of the origin of species.

A Contagious Enthusiasm

Margulis's enthusiasm for moving science forward was contagious, and inspired by endosymbiosis theory, groundbreaking Russian research, and the Lovelock-Margulis articulation of the Gaia hypothesis, my wife, Dianna, and I proceeded to consider the biosphere as a whole from a symbiogenesis perspective. Our primary goal was to enhance Mount Holyoke College's introductory geology course, *History of Life* (Geology 102).

I wanted, at long last, to provide my students with an adequate explanation for how and why vascular land plants transformed dry land surface into undulating forest. Our solution, the idea that cooperation among fungi, vascular plants, and other organisms in a vast symbiotic network—a geophysiological entity we called Hypersea, with the ability to induce upward nutrient flow (hypermarine upwelling)—was published by Columbia University Press in 1994 as *Hypersea: Life on Land*.

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Margulis answers questions from students on a field trip to Harvard Forest, in Petersham, Mass., during a course on Environmental Evolution.

1. *The Biosphere*, Vladimir Vernadsky (New York: Copernicus, 1998) English translation ed. Mark A.S. McMenamin.

In her foreword to the book (she also took the splendid cover photomicrograph), Margulis announced that *Hypersea* blended Vernadskian biospheric thinking and Lovelockian Gaian spatial "connectedness" to allow us to "look wide-eyed upon a land surface whose history we thought we understood. Returning to where we stood before, enlightened by a century of biological and paleontological insight, we now see this place for the first time."

Her foreword encapsulates the classic Lynn Margulis approach to appreciating the full symbiogenetic glory of the natural world.

Due at least in part to her difficulties with the Neo-Darwinian synthesis, Margulis astonished many of her colleagues by changing her departmental affiliation from biology to geosciences. This made good sense, for Margulis had come to admire how the geosciences superintend a rich temporal data set that biologists tend to neglect.

For example, the great American geologist Preston Cloud determined that the Cambrian Explosion must represent a truly massive case of punctuated evolution. Cloud argued that the filter feeding apparatus (*lophophore*) of a brachiopod couldn't function properly as a brachiopod filtering loop without a completely bivalve shell.

The first brachiopods in the fossil record are fully formed bivalve filter feeders. This does not mean that there were no intermediate stages. However, there is no evidence that early brachiopods developed by the countless generations of gradual, incremental change demanded by conventional Neo-Darwinian theory.

Margulis took Cloud's insight a step further, urging me to consider the possibility that the relatively sudden appearance at the Cambrian boundary of numerous different types of skeletons, composed of different types of biominerals, might very well represent yet another case of symbiogenesis. I was initially skeptical, but sure enough, the shell structure of an Early Cambrian stem group (mickwitziid brachiopods) proved to be packed with spherules of hydroxyapatite. These tiny spherules might best be interpreted as the permineralized fossil remains of coccoid symbiotic microbes.

BU Photography

Margulis at Boston University in 1982.

The importance of symbiosis in the acquisition of early animal shells remains an unsettled question, but here again, Lynn Margulis may be on the right track.

The Oxygen Revolution

Preston Cloud is also known for his discovery of the Oxygen Revolution, announcing the discovery at the same time that Margulis was about to publish her endosymbiosis research. The Oxygen Revolution occurred approximately 2 billion years ago, when diatomic oxygen gas released by photosynthesis (Photosystem II) overwhelmed Earth's reservoirs of native and ferrous iron, thereby allowing oxygen to accumulate in the oceans and atmosphere and thus completely altering the geochemistry of the planet.

Russian scientists are chagrined at the fact that Cloud, apparently unfamiliar with Vernadsky's work, was able to link the Proterozoic banded iron formations to the concept of an anoxic early Earth atmosphere.

Discovery of the Oxygen Revolution by all rights should have gone to the

Courtesy of Mark McMenamin

A 1975 photo of visiting and resident scientists at the Clean Lab (now Cloud Lab), at the University of California at Santa Barbara. Lynn Margulis is third from right in the front row. Preston Cloud is first from left; Stanley Awramik is first from right; and, in the rear row, Elso Barghoorn is third from right.

Russians, but in this particular case, the honors went to an American. This discovery, along with the plate tectonic revolution and symbiogenesis theory, constituted one of the great American geoscience contributions of the 20th Century. Margulis was very much front and center among the giants in this amazingly fruitful episode of American geoscience achievement.

In a 1975 photograph from the Clean Lab (now Cloud Lab), at the University of California, Santa Barbara, Lynn Margulis appears in the middle, beaming like a school girl, with Preston Cloud to her far right and Stanley Awramik (my graduate advisor) to her far left. Behind Margulis in the photograph stands Elso Barghoorn, the Amherst College/Harvard University professor of whom Margulis always spoke with great admiration.

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Margulis exporing microbialites at the Moroccan field site studied by one of her graduate students.

Barghoorn was graduate advisor and mentor to many of the scientists (and their students) who conducted most of the best and most original research on early life on Earth, in what we may now refer to as the Golden Age of American Geoscience (ca. 1965-2000).

In this golden era of field and laboratory research, Americans collected lunar rock samples (the Clean/Cloud Lab was originally designed to receive the Apollo mission Moon rocks), confirmed plate tectonic theory, discovered the oldest fossils known, named the supercontinent Rodinia (using the Russian language root word for *homeland* to honor the Russian geoscience contributions), linked the decline of stromatolites to the emergence of animals, discovered the oldest fossils of complex life, confirmed endosymbiotic theory, and identified the Oxygen Revolution, among many other groundbreaking scientific advances.

It may be some time before the world witnesses a comparable series of discoveries in the Earth sciences. The heady excitement of discovery after discovery was a wonder to behold. I will never forget the excitement, in pre-digital graduate school as Stan Awramik's research assistant, of developing the first photographic images of what may very well be the world's oldest microfossils, watching their images slowly emerge (*de profundus*) on the glossy print photo paper in the faint red safe light of the darkroom.

Nor will I ever forget the excitement of flipping over a slab of siltstone on a mountainside slope in Sonora, Mexico, and discovering the earliest evidence for complex life on the Earth.

Champion of the Unorthodox

Probably due to the long list of rejections she accumulated while trying to promote endosymbiosis theory early in her career, Lynn Margulis was always ready to champion an intriguing new concept or a potentially fruitful (if unorthodox) new approach. This inevitably led her to advocate ideas that many of her less adventuresome colleagues would consider fringe science or worse, such as her endorsement of AIDS "denialism" (Margulis held a microbial-consortial view of the etiology of AIDS).

Such aberrations must be seen in the context of the classic Lynn Margulis approach to research, an approach always ready to challenge the scientific establishment, always ready to consider a new direction, and always ready to advance the science.

I attribute this tendency to her acute sense that science is an eternally unfinished project, with the next big advance just around the corner. She combined this with an intense desire to communicate a sense of possibility and discovery to her students.

As part of scrutiny of yet another unorthodox idea, Margulis set up a transatlantic Skype interview with the great German paleontologist Adolf "Dolf" Seilacher, asking him to discuss with students his ideas about the non-animal nature of the Ediacaran fossils. This interview, delivered in Seilacher's rich Teutonic baritone, was only one of a marvelous series of recorded interviews that Margulis collected from her vast network of colleagues.

Seilacher's Skype interview has become a mainstay of my popular first year seminar course *Geology 115: Emergence of Animals*. Margulis was a favorite guest lecturer in my classes, and she will be greatly missed.