Mapping the Geography of Symbiosis

James di Properzio

Wherever she looks—in the mud, the air, the cells of plants and animals, termite guts, or the tails of sperm—Lynn Margulis sees evidence of ancient microbial mergers or primary ongoing microbial activity sustaining life at all levels.

Nineteen-year-old Lynn Sagan saw amoebae for the first time through a high-quality microscope in a laboratory at the University of Wisconsin, Madison, where she was a graduate student in genetics. "I really liked amoebae," Lynn Margulis reminisces fondly. "I still do."

Working with the amoebae changed her life and helped define the focus of her subsequent scientific research. How does one take care of amoebae? "They tend to stick to the bottom of an open bowl, if they are healthy. They are fed ciliates [unicellular microbes covered with short, whiplike extensions], which are grown separately and added every day to their bowl. When a drop of food is added, they are activated; changing shape all the time, they flow toward the food, which they engulf. A struggle ensues; the actively swimming ciliate is subdued by digestive enzymes leaked into the food vacuole." This drama, which Sagan monitored in the lab every afternoon and early evening, had the precision and excitement of a lion hunt. "Well-fed amoebae," she says, "round up and proceed to reproduce by division in half an hour or forty-five minutes, and they reproduce on average once a day. Many more are produced than can possibly survive.

"If you don't clean them, they die," Margulis remembers. "Aspiration is crucial." She would use an aspirator to remove the top layer of dirty water and unhealthy or dead amoebae, reducing the volume of the bowl by about half. Then she would add a balanced salt solution made with double-distilled water. Margulis recalls this dirty work with great fondness: "I owe my passion for working on Saturday nights to the utter necessity of amoeba feeding and bowl cleaning every day," she insists.

Today, at age 64, Margulis is still focusing on and promoting microbes. To a science, taxonomy, that originated from naked-eye observations, she helped to bring a five-kingdom classification based on microscopic distinctions within the basic cell of each type of life. She has further shown that the symbiotic intertwining of life extends all the way from the microscopic level to the planetary level. Now, Margulis' latest theory offers the provocative claim that symbiosis, and not random mutation, is the wellspring of evolution.

The microcosm's spokesperson

Awake before the birds are singing, cycling to work before cars are on the road, and peering down a microscope at the open guts of termites before the doors to the building at her laboratory at the University of Massachusetts at Amherst are unlocked, Margulis has the energy of the swimming bacteria she so adores. Her ninth book, *Acquiring Genomes: A New Theory of Evolution*, was published in July, and she has authored or coauthored hundreds of scientific articles and dozens of popular essays. In addition, Margulis is a dedicated teacher and a keen scientific investigator of microorganisms. A geneticist by training and now distinguished university professor in the Department of Geosciences at the University of Massachusetts, she describes herself as a "spokesperson for the microcosm."

In championing the microbes, Margulis has made several significant contributions to our understanding of evolution. Her "endosymbiotic hypothesis," which states that the mitochondria in every animal cell and the plastids in algae and plants are actually different kinds of remnant bacteria that live symbiotically, is now included in every college biology textbook. She has spent a good portion of her career finding evidence for this idea—that components of plants and animals were once free-living bacteria that joined symbiotically with other free-living bacteria early in the evolution of life.

COURTESY OF JENNIFER MARGULIS

■ **Lynn Margulis, "spokesperson for the microcosm," traces her fascination with the microbial world to her experience with amoebae and bacteria in graduate school and the field (photo ca. 2002).**

Her latest research, which her new book will present to the intellectual public, explains the elusive source of evolutionary innovation by showing how organisms actually incorporate other organisms for new characteristics, which then may be inherited by future generations. *Acquiring Genomes* argues against the orthodox history of science today: Margulis contends that Lamarck, who claimed that organisms inherit acquired characteristics, was right. This proposition, far from opposing Darwin, puts Darwin's theory of evolution in a continuum with Lamarck that Margulis believes was already there.

Margulis further explains that Darwin himself was explicitly a staunch Lamarckian, not least because it was Lamarck who originally proposed a systematic theory of evolution. The "inheritance of acquired characteristics" was Lamarck's proposal for the source of innovation in evolution; that is, an organism might spontaneously change some physical characteristic in response to a threat or an opportunity, and that change would be inherited. Even Darwin had no proposal for the source of innovation (or "sports," as he termed variant organisms), and he recognized the need to explain how the marvelous profusion of innovations in the variety of life could arise in the first place. Only after the innovations appear does Darwin's contribution of natural selection begin to function—as the editor, not the source, of evolution.

"Neo-Darwinist claims that mutation is the source of innovation," says Margulis, "have been proven wrong in the genetics lab." Instead, she describes how organisms can incorporate whole bacteria into themselves, using the whole bacterial genome to actually change their DNA. "Bacteria make friends easily and develop enemies and other intimacies. They enter the lives of larger organisms and form part-

COURTESY OF JENNIFER MARGULIS

Twice married, Margulis has identified wife, mother, and first-class scientist as mutually exclusive jobs. She quit her role as a wife twice to concentrate on those of mother and scientist. Here she shows one of her five grandchildren a rock that may be the fossil remains of a freshwater microbial mat—from what is now the Sahara desert (photo ca. 2002).

nerships," she explains. "Real innovation toward the complex results when natural selection leads to the perpetuation of mergers."

Questioning the status quo is what Margulis does best. Her scientific theories, like her colorful life and flamboyant personality, are not without controversy. Married and divorced twice (first to astronomer Carl Sagan, whom she met when she was 16), the mother of four children and grandmother of five, she continues to challenge the scientific establishment. Some contend that her ideas go too far.

Editor's Note:

In his foreword to *Acquiring Genomes,* evolutionary biologist Ernst Mayr gives high appreciation to most of its teachings, including Margulis' and Sagan's theory that new living forms can be established through symbiotic relationships involving the incorporation of new genomes. At the same time, he disputes their suggestion that this theory restores the validity of Lamarckian inheritance, that is, the principle that acquired characteristics can be inherited.

Childhood's end

"My parents could not do my sixth-grade homework," Margulis, née Lynn Alexander, explains. "I didn't know there was such a thing as a scientist."

In the apartment where she lived on the south side of Chicago, Lynn read voraciously to escape from the bickering and chaos of her family. Her parents, Morris Alexander, a civil rights lawyer, and Leone Wise, a housewife, were socialites. They had frequent guests, drank copious quantities of alcohol, and went to parties. "They did all the things I can't stand," Margulis recalls. "I was bad, too. I was bossy, rude, hyperactive, and self-centered until I realized I could control my own destiny. Then I got happy." The eldest of four, Lynn cared for her younger sisters and daydreamed about becoming a writer and explorer. During her childhood, she had only one "scientific" moment, which she remembers as the only evening when she was not scheming to get away from her family obligations.

When she was 12, her

Margulis locates her initial impetus to read scientific literature precisely: Nat. Sci. 2, second year, the College, University of Chicago.

younger sister Sharon had a classmate named John Urey, the son of the Nobel Prize–winning scientist, Harold C. Urey. One night her parents invited the Ureys for dinner. "My mother was nervous for a whole week before," Margulis remembers. "She had never seen or talked to a scientist in her life, let alone a Nobel Prize winner." Harold Urey, who discovered deuterium (heavy hydrogen), had also supervised the first early-life experiments, which produced amino acids out of what were surmised to be the hydrogen-rich gases of the earliest atmosphere. But Lynn's mother was much less interested in questions of science than questions of social niceties: "My mother was afraid her table linens and scantily polished silver service would be questionable," laughs Margulis.

At 14, Lynn was accepted by the College at the University of Chicago, a Great Books liberal arts program with a fixed curriculum of science, philosophy, literature, and mathematics. "I took the placement exam, and I got into college," she explains. At 16, she left home for good.

COURTESY OF LYNN MARGULIS

Lynn Alexander (left), age 16 and already in her second year of college, with her three younger sisters and her mother, Leone Alexander, in the middle (photo ca. 1955).

Something else happened in her sixteenth year that would change the course of her life. Going up the stairs of Eckhart Hall, to a women's lounge where she liked to study, Lynn met Carl Sagan, who was on his way down. Even then, 19 years old and a graduate student in physics, he was a celebrity. "Everyone knew who he was," Margulis recalls. In her 1998 book, *Symbiotic Planet,* she describes Sagan: "Tall, handsome, with a shock of brown-black hair, and exceedingly articulate, even then he was full of ideas." Although her father found him arrogant and her mother was suspicious of his intentions, Lynn was drawn to his enthusiasm and his interest in science. She writes further that "his love for science was contagious." After they started dating, her family teased her. "My father would chant: 'She used to go with Zionists, now she goes with scientists' . . . I hated that."

They married on June 6, 1957, when Lynn was 19 years old, and had two sons: Dorion, born in 1959, and Jeremy, born in 1961. With two small children and a jealous husband, Lynn found life with Carl contentious. Their marriage ended in 1964. Although Sagan only reluctantly participated in the upbringing of their children and paid inadequate child support, they remained friends until he died of cancer in 1996.

En route to five kingdoms

Margulis locates her initial impetus to read scientific literature precisely in time and place: Nat.

Lecturing to advanced grad students at the University of Massachusetts, Margulis explains a video showing a composite, single-celled organism, *Mixotricha paradoxa*, which has five distinct genomes (photo ca. 2002).

Sci. 2, second year, the College, University of Chicago. She read Gregor Mendel's experiments with the breeding of garden peas and Vance Tartar's experiments grafting 14 stentors (giant horn-shaped ciliates with huge waving mouthparts) to each other. Tartar noted that the grafts survived, and the monster stentors reorganized back to normal even if it took weeks.

This sophomore-year curriculum fascinated her. She wondered why, when a yellow pea plant is crossed with a green pea, all the offspring in the first generation are green but the next generation is yellow; how a monster stentor "knew" to correct its misshapen body. These questions drove her to read as much as she could about heredity and genetics.

After graduating from the University of Chicago in 1957, Lynn undertook graduate study in genetics at the University of Wisconsin, while Carl earned his Ph.D. at the University of Chicago's astronomy department in Williams Bay, Wisconsin. In the University of Wisconsin's genetics program—where she fell in love with amoebae—the scientists from various departments worked together. Her committee was an eclectic group. Walter S. Plaut was a botanist, Hans Ris a zoologist, and James F. Crow a geneticist, but all three were extremely interested in heredity at the level of the plant or animal cell. Under Plaut's tutelage, she obtained a master's degree in genetics in 1960. "I got a master's degree the year Jeremy was born," she recalls. "I thought I would not be able to go on . . . or I would have gotten a Ph.D. at Wisconsin."

Carl was awarded a postdoctoral Miller Fellowship for $7,200 a year, so they moved to Oakland. After being in California caring for her two young sons while reading cell biology and genetics, Lynn was told by Plaut that his good friend Daniel Mazia might be willing to take her as a graduate student. Mazia became her informal adviser, but the genial professor had so many students that she had to find someone else to study with.

Her thesis adviser was Max Alfert, a Jewish refugee from Nazi Germany. "He graduated almost no one," Margulis remembers. She left Berkeley in 1963, with the research and writing of her dissertation almost completed, obtaining her degree in 1965, after she had published her thesis, "Unusual Pattern of Thymidine Incorporation in *Euglena*," *The implication became clear. Bacterial cells are the units of life, and all organisms with nucleated cells are composite multiples.*

in a peer-reviewed journal. "The committee couldn't be bothered to meet and review the paper, so I just published it," says Margulis.

The Sagan family moved to Boston in 1963 when Carl was hired by the astronomy department at Harvard University. Lynn landed an instructorship at Boston University, where she would remain for 22 years. She began her career by teaching introductory biology. Through the subsequent years as a teacher and reasearcher, she recognized that the most fundamental gap between types of life forms was not that between plants and animals but that between bacteria and everything else. The implication became clear. Bacterial cells, which lack a nucleus, are the units of life, and all organisms with nucleated cells are composite multiples. "The folk taxonomy is animals, plants, germs, and people," Margulis explains. "Having to teach stuff that was half truth or untruth, based on a false dichotomy between animals and plants, led me to want to document the problem."

With zoologist Karlene Schwartz, Margulis wrote a major contribution to taxonomy, *Five Kingdoms*, which was published in 1982. In it, they fleshed out and illustrated a concept originated by ecologist Robert Whittaker. The five kingdoms system identifies five categories of organisms as rational kingdom divisions: bacteria (the prokaryotic or nucleus-lacking microbes), protoctists (algae, slime molds, and other nucleated eukaryotic organisms formed by symbiosis from bacteria), fungi (mushrooms, molds, and yeasts, all of which reproduce by spores), plants (organisms that develop from spores and embryos retained by the mother's tissue), and animals (organisms that develop from eggs fertilized by sperm). This system also provided an evolutionary perspective on the taxonomic groups, much lacking and needed since Lamarck. But the path of evolution it suggested was one of prokaryotes combining into cooperative unions of more complicated cells, in which symbiotic teams became eventually a single new organism.

While she was at Boston

COURTESY OF LYNN MARGULIS

Margulis (right) worked with zoologist Karlene V. Schwartz to produce *Five Kingdoms*, the only complete and consistent taxonomic system that covers all published materials (photo ca. 1982).

COURTESY OF LYNN MARGULIS

Margulis includes rocks and even dry-land terrain in her territory of investigation because microbes play such a prominent role in processes affecting Earth's geology. Here, with paleontologist Stephen M. Rowland from the University of Nevada, she examines sedimentary rocks (photo ca. 1988).

University, Margulis met her second husband, Thomas N. Margulis, then an assistant professor of chemistry at Brandeis University. Their marriage ended after 13 years and two more children: Zachary, born in 1967, and Jennifer, born in 1969. "I quit my job as a wife, twice," Margulis explains of her second marriage. "It's not humanly possible to be a good wife, a good mother, and a first-class scientist; no one can do it. Something has to go."

Gaia

Since 1975 Margulis has come most prominently into the public eye through her support for the Gaia hypothesis, which was proposed originally by James Lovelock, a British atmospheric scientist. The Gaia hypothesis considers Earth, including water, air, and all forms of life, as a single, complex system. Lovelock initially contacted Margulis after noticing that certain aspects of the atmosphere cannot be adequately explained by atmospheric chemistry and physics; in fact, the atmosphere is *dramatically* not as it should be if only physical and chemical forces were governing it. For one thing, Lovelock could conceive of no possible process whereby physical and chemical forces alone could produce or maintain the high level of oxygen in the atmosphere. Lovelock concluded that biological factors must have an enormous influence in determining its composition.

In 1975, Lovelock and Margulis coauthored an essay, "The Atmosphere as Circulatory System of the Biosphere—The Gaia Hypothesis." In this now-classic article, the authors explained that certain aspects of the atmosphere (temperature, composition of gases, oxidation reduction state, and acidity) form a self-balancing system, and that these system components are products of evolution.

Gaia is a big idea. The massive complexity of the system encompassed by the Gaia hypothesis means that it cannot be tested or demonstrated by a single experiment. Nonetheless, Lovelock and Margulis have convincingly argued that the long-term continuity of the atmosphere's temperature and composition demonstrates a primary role played by microorganisms in governing the atmosphere's characteristics. The water system of the planet, the rocks of its crust, and the atmosphere have all been influenced as much by the evolving system of life as the surface of the island of Manhattan has been influenced by the intentional actions of humans.

Margulis draws lessons from the Gaia hypothesis that reach beyond explanations of atmospheric properties. "*Homo sapiens sapiens* are filled with arrogance. We think we are at the center of the universe and the center of life on Earth," she grumbles. "But Gaia teaches us that

People are just beginning to realize that "all life that we can see with our eyes comes from symbiosis," Margulis repeats.

humans are not at the center; in fact, they aren't even central to life on Earth. Bacteria have survived devastating impacts. Bacteria thrive on what we see as pollution; they will survive a nuclear winter. We think we have the power to wipe out life, but we only have the power to wipe out ourselves, our pets, our corn, and other visible totems of our lifestyle. All the life you see with the naked eye is just the tip of the iceberg."

COURTESY OF LYNN MARGULIS

■ **Margulis' scientific recognition includes election to the National Academy of Sciences in 1983 and receipt (shown here) of the National Medal of Science from President Bill Clinton in 1999.**

Playing in the mud

Margulis left Boston University to join the faculty at the University of Massachusetts at Amherst in 1989. She has found the hometown of poet Emily Dickinson to her liking.

"Laminated, brightly striped sediment underlain by gelatinous mud especially moves me," Margulis wrote in a 1990 article, "Confessions of a Nature Lover." "In other words," she says now, "I like to play in the mud . . . especially the stinky, sulfurous kind—mud that is teeming with microscopic life." She also enjoys hiking the Metacomet and Monadnock trail, taking her students to study the rocks and life in the Harvard Forest, and listening to classical music.

Margulis' lecture schedule is booked almost three years in advance, typical for a celebrity but unusual for a scientist. Her office phone rings constantly, and she has given lectures and received awards—including election to the National Academy of Sciences in 1983 and the National Medal of Science in 1999—in more than 20 countries.

On Main Street in Amherst is a plaque decorated with a microbial mat community, featuring cyanobacteria (the bacteria that produce our oxygen). The quote, by Margulis, says that life makes its own environment.

People are just beginning to realize that "all life that we can see with our eyes comes from symbiosis," Margulis repeats. "But I don't think I'm successful. I don't measure success by popularity, people, or my bank account. I can't stand the attention. I care about science—reconstructing the history of the microcosm. I am still working on the four-part theory that I started as a genetics graduate student. Three of the four postulates have been shown to be correct."

Her next task? To show definitively that sperm tails and cilia in other nucleated cells are the fruit of symbiosis, of ancient liaisons between nucleated cells and bacteria with biomotorized tails. "This fourth, and last, part has not been verified at all," she acknowledges. "But I think we can prove it."■

James di Properzio is a science writer and editor. He has published scholarly and reference articles on science and philosophical topics and is editing Lynn Margulis' forthcoming Luminous Fish.