

## AD MEMORIAM

### Lynn Margulis (5.03.1938 – 22.11.2011)

Lynn Margulis, who died five days after suffering a hemorrhagic stroke on November 22, 2011 at her home in Amherst, Massachusetts, at age 73, was no stranger to controversy.

Margulis was born in 1938 in Chicago, Illinois. At the young age of 14, she enrolled in the University of Chicago, and graduated in 1957. She earned a master's in genetics and zoology at the University of Wisconsin in 1960 and a PhD in genetics from the University of California, Berkeley, in 1965.

Just a year later, in 1966, the young Boston University professor wrote a paper titled *The Origin of Mitosing Eukaryotic Cells*. That paper, which was a direct challenge to what she called the “ultra-Darwinian orthodoxy,” was rejected by no fewer than fifteen academic journals before being ultimately accepted into *The Journal of Theoretical Biology* in 1967.

Traditional Darwinian thought underlines the role of competition in pushing evolution forward. Indeed, competition is a critical component of modern evolutionary theory. However, the underlying theme of endosymbiotic theory (or endosymbiosis) holds that cooperation between organisms is perhaps a more important driver of evolutionary change. In the most extreme version of the process, also known as symbiogenesis, one organism consumes the other, but both survive and evolve over the course of time.

To understand just how controversial this was, it helps to start from a simpler process than symbiogenesis: symbiosis. Symbiosis is a system in which members of different species live in physical contact,



and in which each species ostensibly benefits from the arrangement (though Margulis would not have approved of my use of the word “benefit,” arguing that “cost” and “benefit” can not be quantified). Critically, that physical association must endure for “most of the life history of the organisms” (Margulis, 2009 talk).

It is trivial to point out that symbiosis is ubiquitous in the natural world. There are entire communities of bacterial microbes that make their homes on human skin or in the human gut. A casual walk through a garden gives more examples: weeds like clover have bacteria on their roots that helps them to survive in nitrogen-poor soil, and trees such as maple, oak, and hickory can have as many as three hundred species of fungi living among their roots. Margulis noted in her 1998 book *Symbiotic Planet*, “physical contact is a nonnegotiable requisite for many differing kinds of life.” (p. 5).

In symbiosis, however mutually dependent two species are on each other, they remain two distinct species, with their own unique characteristics and genetic profiles. Symbiosis describes an ecological relationship.

Things get more complicated when considering symbiogenesis, a process, which occurs when symbiosis results in new tissues, organs, or organisms. The first species can’t really be understood except in context of its relationship with a second species.

Margulis traced these ideas (if not the terminology) back to the American anatomist Ivan E. Wallin and to the Russian biologist Boris Mikhaylovich Kozo-Polyansky, who each argued that new species originate through symbiosis, rather than via random mutation and natural selection.

Wallin and Kozo-Polyansky were unfamiliar to each other, yet they arrived at the same set of ideas independently. Wallin, the son of Swedish immigrants, did not read Russian, though Kozo-Polyansky seemed familiar with the English- and German-language scientific literature.

It’s not that Darwin was wrong. Kozo-Polyansky did not reject natural selection outright, as his predecessors Merezhkovsky and Famintsyn had. Instead, he argued, it was symbiosis rather than mutation that was responsible for the novelty that natural selection, in turn, maintained and perpetuated. In a talk given at a 2009 conference on evolution in Russia, Margulis explained, the “maintenance of inherited changes in communities is [achieved] by natural selection but variation itself is not generated by Darwin-Wallace natural selection.”

And there certainly is evidence that the symbiogenesis can at least partially account for the early evolution of life on earth. The eukaryotic cells that combine to form plants and animals are descendants of earlier, simpler prokaryotic organisms. Later discoveries that organelles like plastids and mitochondria have their own DNA, and that their DNA was distinct from the DNA of the cell nuclei provided key evidence that ultimately convinced most evolutionary biologists of the veracity of endosymbiosis.

Although widely criticized at the time, Margulis’s 1967 paper is now considered a landmark paper in evolutionary biology, and in particular, in endosymbiotic theory. Her predictions about mitochondria in animal cells and plastids in plant cells were confirmed. In 1995, evolutionary biologist Richard Dawkins said, “This is one of the great achievements of twentieth-century evolutionary biology, and I greatly admire her for it.”<sup>1</sup>

She took the ideas that she began formulating in her 1967 paper, and developed a book-length manuscript in 1969. After submitting it to one publisher, she did not hear back for five months when her manuscript was returned to her, without explanation. Eventually, she was informed that extremely negative peer-review prompted the publisher to hold the manuscript, though again, with no explanation. Over a year later, that book was published by a different

<sup>1</sup> Brockman J. The Third Culture. New York: Touchstone, 1995. 144 p.

publisher, but not without the aid and persistence of several of her colleagues. The theory that she described in her first book is now included in high-school and college biology textbooks.

But the more extreme reading of symbiogenesis is still a point of controversy. For example, in *Symbiotic Planet*, Margulis recounts a conversation she had with paleontologist Niles Eldridge. She asked him whether he knew of a case in which the formation of a new species had been documented:

He could muster only one good example: Theodosius Dobzhansky's experiments with *Drosophila*, the fruit fly. In this fascinating experiment, populations of fruit flies, bred at progressively hotter temperatures, became genetically separated. After two years or so the hot-bred ones could no longer produce fertile offspring with their cold-breeding brethren. "But, — Eldridge quickly added, — that turned out to have something to do with a parasite!" Indeed, it was later discovered that the hot-breeding flies lacked an intracellular symbiotic bacterium found in the cold breeders. Eldridge dismissed this case as an observation of speciation because it entailed a microbial symbiosis! He had been taught, as we all have, that microbes are germs, and when you have germs, you have a disease, not a new species. And he had been taught that evolution through natural selection occurs by the gradual accumulation, over eons, of single gene mutations (Margulis, 1998).

But for Margulis (as for Wallin and Kozo-Polyansky), this would have been a perfect example of speciation due to the symbiogenesis between the fruit flies and the bacterium. To that end, most of her professional career has been spent documenting cases of symbiogenesis in the natural world, and fighting against the prevailing view that random mutation and competition for resources are the central drivers of biological novelty and thus evolutionary change.

Margulis's work on symbiosis led her to support yet another controversial idea in the 1990s and 2000s, this one proposed in 1972 by British chemist James Lovelock. The basic idea of Lovelock's "Gaia theory" was that all of life on earth — that is, all organisms — is engaged in a symbiotic relationship with the environment in which life occurs, the inorganic material that sustains life. A strong reading of the Gaia theory holds that the atmosphere, the seas, and the entire geology of earth are regulated by the organisms that live on the earth such that their own survival can be fostered. While she has become almost as closely associated with the Gaia theory as Lovelock, she did not support some of the more metaphorical imagery he used to describe it. For example, he argued that Earth was a living organism, while she would have instead described the Earth less controversially as a big ecosystem comprised of many smaller ecosystems. Weaker versions of the theory are better accepted by scientific orthodoxy, as they simply state that life on earth and the environment in which it exists affect each other.

Margulis noted some similarities between symbiogenesis and Lovelock's Gaia theory. In fact, she dedicated the last eight chapters of her book *The Symbiotic Planet* to the idea. She was fairly measured in her support of the idea, writing that Gaia is "not an organism," but is "an emergent property of interaction among organisms," and that Gaia can be best understood as a "series of interacting ecosystems that compose a single huge ecosystem at the Earth's surface."

Her engagement with the Gaia theory did not, of course, mean that she stopped working to support symbiogenesis. Recently, she supported a controversial paper published by Donald Williamson in PNAS<sup>2</sup>, which claimed that caterpillars and butterflies evolved separately, and somehow fused into a single species later on. One biologist was even quoted<sup>3</sup> as saying that it would be better suited for the National Enquirer (a US tabloid magazine) than for the National Academy.

<sup>2</sup> <http://www.pnas.org/content/106/47/19901>

<sup>3</sup> <http://www.scientificamerican.com/article.cfm?id=national-academy-as-national-enquirer>

While some criticized her for her at-times eccentric ideas, calling her a quack or even an embarrassment to science, some remember her in warmer ways. Indeed, it takes a great deal of courage to publicly espouse such controversial ideas. Leila Battison, a Ph.D. student at Oxford who learned from Margulis recalled<sup>4</sup> that she was “unfailingly kind and generous, warm, and welcoming.” Microbiologist Moselio Schaechter wrote<sup>5</sup> that his friend was “a most caring person and a devoted friend.”

Shortly after the publication of her 1967 paper, Margulis became the first female principle investigator to receive funding from NASA’s Exobiology/Astrobiology program, for her research on microbial evolution. But that did not end Margulis’s association with this particular NASA program. It was through the NASA exobiology/astrobiology programs that Margulis established a “Planetary Biology Internship” program, which allows graduate students to participate in research conducted at NASA facilities and in NASA-supported university laboratories. Even recently, Margulis spoke in 2010 at a NASA symposium that was organized to celebrate the fiftieth anniversary of NASA’s astrobiology program.

Outside of the laboratory, Margulis seems to have found tremendous value in communicating science to the general public. For example, she participated in teaching students from middle school through graduate school, served as a faculty mentor at Boston University, spent a great deal of time speaking in public, and wrote many books about science — both for academic as well as general audiences — some of which were co-authored with her son with Carl Sagan, Dorion.

Though born into a Jewish, Zionist family, and despite having had early experiences in the State of Israel, Margulis ultimately rejected organized religion, just as she rejected neo-Darwinism. In fact, she made a direct comparison<sup>6</sup> between her rejection of neo-Darwinism and religion: “I remember waking up one day with an epiphanous revelation: I am not a neo-Darwinist! It recalled an earlier experience, when I realized that I wasn’t a humanistic Jew.”

Throughout the course of her career, she was given numerous awards and honors. Among these are the 2009 Darwin-Wallace Medal, awarded every fifty years by the Linnean Society, the Nevada Medal, Sigma Xi’s William Proctor Prize, a NASA Public Service Award, the Miescher-Ishida Prize, the Commandeur de l’Ordre des Palmes Academiques in France. She was recipient of Guggenheim, Rockefeller Bellagio, and Sherman Fairchild fellowships, and too many honorary degrees to list. She was co-founder of two international societies: the International Society for Evolutionary Protistology and the International Society for Symbiosis, and served on committees for the National Academy of Sciences, NASA, AAAS, and the National Science Resource Center.

She is survived by her children Dorion and Jeremy Sagan (with her first husband, Carl Sagan), and Zachary Margulis-Ohnuma and Jennifer Margulis di Properzio (with her second husband, Thomas N. Margulis), daughters-in-law Robin Kolnicki and Mary Margulis-Ohnuma, son-in-law James di Properzio, and nine grandchildren: Tonio, Sarah, Hesperus, Athena, Etani, Leone, Miranda, Atticus and Madeline. She is also survived by her sisters Joan Glashow, Sharon Kleitman, and Diane Alexander, and by her dog Menina.

Jason G. Goldman  
(University of Southern California; jason.goldman@usc.edu)

<sup>4</sup> <http://leilabattison.wordpress.com/2011/11/23/lynn-margulis-an-unforgettable-woman/>

<sup>5</sup> <http://schaechter.asmblog.org/schaechter/2011/12/lynn.html>

<sup>6</sup> <http://www.forward.com/articles/147959/>

## Selected Publications

### Books

- Margulis Lynn and Dorion Sagan.* (2007). *Dazzle Gradually: Reflections on the Nature of Nature.* Sciencewriters Books.
- Margulis Lynn and Eduardo Punset, eds.* (2007). *Mind, Life and Universe: Conversations with Great Scientists of Our Time.* Sciencewriters Books.
- Margulis Lynn.* (2007). *Luminous Fish: Tales of Science and Love.* Sciencewriters Books.
- Margulis Lynn and Dorion Sagan.* (2002). *Acquiring Genomes: A Theory of the Origins of Species.* Perseus Books Group.
- Margulis Lynn et al.* (2002). *The Ice Chronicles: The Quest to Understand Global Climate Change.* University of New Hampshire.
- Margulis Lynn.* (1998). *Symbiotic Planet: A New Look at Evolution.* Basic Books.
- Margulis Lynn and Karlene V. Schwartz.* (1997). *Five Kingdoms: An Illustrated Guide to the Phyla of Life on Earth.* W.H. Freeman & Company.
- Margulis Lynn and Dorion Sagan.* (1997). *What Is Sex?* Simon and Shuster.
- Margulis Lynn and Dorion Sagan.* (1997). *Slanted Truths: Essays on Gaia, Symbiosis, and Evolution.* Copernicus Books.
- Margulis Lynn.* (1992). *Symbiosis in Cell Evolution: Microbial Communities in the Archean and Proterozoic Eons.* W.H. Freeman.
- Margulis Lynn, ed.* (1991). *Symbiosis as a Source of Evolutionary Innovation: Speciation and Morphogenesis.* The MIT Press.
- Margulis Lynn and Dorion Sagan.* (1991). *Mystery Dance: On the Evolution of Human Sexuality.* Summit Books.
- Margulis Lynn and Dorion Sagan.* (1987). *Microcosmos: Four Billion Years of Evolution from Our Microbial Ancestors.* HarperCollins.
- Margulis Lynn and Dorion Sagan.* (1986). *Origins of Sex: Three Billion Years of Genetic Recombination.* Yale University Press.
- Margulis Lynn.* (1982). *Early Life.* Science Books International.
- Margulis Lynn.* (1970). *Origin of Eukaryotic Cells.* Yale University Press.

### Articles

- Sagan L.* On the origin of mitosing cells // *Journal of Theoretical Biology.* 1967. Vol. 14. P. 225–274.
- Margulis L.* Evolutionary criteria in Thallophytes: A radical alternative // *Science.* 1968. Vol. 161. P. 1020–1022.
- Banerjee S. and Margulis L.* Reversible inhibition of cilia regeneration in *Stentor coeruleus* by isopropyl-n-phenyl carbamate // *Nature.* 1969. Vol. 224. P. 180–181.
- Margulis L., Banerjee S. and White T.* Colchicine-inhibited cilia regeneration: Explanation for lack of effect in tris buffer medium // *Science.* 1969. Vol. 164. P. 1177–1178.
- Margulis L.* Recombination of non-chromosomal genes in *Chlamydomonas*: Assortment of mitochondria and chloroplasts? // *Journal of Theoretical Biology.* 1970. Vol. 26. P. 337–342.
- Margulis L.* Symbiosis and evolution // *Scientific American.* 1971. Vol. 224. P. 48–57.
- Lovelock J. E. and Margulis L.* Atmospheric homeostasis by and for the biosphere: The Gaia hypothesis // *Tellus.* 1974. Vol. 26. P. 2–10.
- Lovelock J. E. and Margulis L.* Homeostatic tendencies of the Earth's atmosphere // *Origins of Life.* 1974. Vol. 5. P. 93–103.
- Margulis L.* The microbes' contribution to evolution // *BioSystems.* 1975. Vol. 7. P. 266–292.
- Margulis L. and Chase D.* Microtubules in prokaryotes // *Science.* 1978. Vol. 200. P. 1118–1124.
- Mazur P., Barghoorn E. S., Halvorson H. O., Jukes T. H., Kaplan I. R. and Margulis L.* Biological implications of the Viking mission to Mars // *Space Science Reviews.* 1978. Vol. 22. P. 3–34.
- Margulis L., Chase D. and To L. P.* Possible evolutionary significance of spirochaetes // *Proceedings of the Royal Society of London, Series B.* 1979. Vol. 204. P. 189–198.

- Rambler M. B. and Margulis L.* Bacterial resistance to ultraviolet irradiation under anaerobiosis: Implications for pre-Phanerozoic evolution // *Science*. 1980. Vol. 210. P. 638–640.
- Sagan D. and Margulis L.* The Gaian perspective of ecology // *Ecologist*. 1984. Vol. 13. P. 160–167.
- Margulis L. and Sagan D.* Evolutionary origins of sex // *Oxford Surveys in Evolutionary Biology*. 1984. Vol. 1. P. 16–47.
- Margulis L. and Bermudes D.* Symbiosis as a mechanism of evolution: Status of cell symbiosis theory // *Symbiosis*. 1985. Vol. 1. P. 101–123.
- Guerrero R., Pedrós-Alio C., Esteve I., Mas J., Chase D. and Margulis L.* Predatory prokaryotes: Predation and primary consumption evolved in bacteria // *Proceedings of the National Academy of Sciences, USA*. 1986. Vol. 83. P. 2138–2142.
- Sagan D. and Margulis L.* Bacterial bedfellows // *Natural History*. 1987. Vol. 3. P. 26–33.
- Lazcano A., Guerrero R., Margulis L. and Oró J.* The evolutionary transition from RNA to DNA in early cells // *Journal of Molecular Evolution*. 1988. Vol. 27. P. 283–290.
- Margulis L.* Serial endosymbiotic theory (SET): Undulipodia, mitosis and their microtubule systems preceded mitochondria // *Endocytobiosis and Cell Research*. 1988. Vol. 5. P. 133–162.
- Margulis L.* Words as battlecries — Symbiogenesis and the new field of endocytobiology // *BioScience*. 1990. Vol. 40. P. 673–677.
- Margulis L.* Introduction to “Symbiontism in the light of recent cytological investigations”, by Ivan E. Wallin // *BioSystems*. 1993. Vol. 31. P. 181–183.
- Margulis L.* Archaeal-eubacterial mergers in the origin of Eukarya: Phylogenetic classification of life // *Proceedings of the National Academy of Sciences*. 1996. Vol. 93. P. 1071–1076.
- Margulis L., Jorgensen J. Z., Dolan S., Kolchinsky R., Rainey F. A. and Lo S-C.* The *Arthromitus* stage of *Bacillus cereus*: Intestinal symbionts of animals // *Proceedings of the National Academy of Sciences*. 1998. Vol. 95. P. 1236–1241.
- Margulis L. and Chapman M. J.* Endosymbioses: Cyclical and permanent in evolution // *Trends in Microbiology*. 1998. Vol. 6. P. 342–346.
- Guerrero R., Haselton A., Solé M., Wier A. M. and Margulis L.* *Titanospirillum velox*: A huge, speedy, sulfur-storing spirillum from Ebro Delta microbial mats // *Proceedings of the National Academy of Sciences*. 1999. Vol. 96. P. 11584–11588.
- Margulis L., Dolan M. F. and Guerrero R.* The chimeric eukaryote: Origin of the nucleus from the karyomastigont in amitochondriate protists. In *Colloquium on Variation and Evolution in Plants and Microorganisms: Towards a New Synthesis: 50 Years after Stebbins* // *Proceedings of the National Academy of Sciences*. 2000. Vol. 97. P. 6954–6959.
- Wier A., Dolan M. F., Grimaldi D., Guerrero R., Wagensberg J., and Margulis L.* Spirochete and protist symbionts of a termite (*Mastotermes electrodominicus*) in Miocene amber // *Proceedings of the National Academy of Sciences*. 2002. Vol. 99. P. 1410–1413.