EDITORIAL

INTERNATIONAL MICROBIOLOGY (2011) 14:183-186
DOI: 10.2436/20.1501.01.147 ISSN: 1139-6709 www.im.microbios.org

Lynn Margulis (1938–2011), in search of the truth

Ricardo Guerrero
President of the Spanish Society for Microbiology
rguerrero@microbios.org

It would have been impossible for INTERNATIONAL MICROBIOLOGY to comment on the microbiology-related events of the year 2011 without noting the death of Lynn Margulis, one of the most outstanding biologists of the 20th century and closely involved with this journal since its beginnings, in 1998, first as Associate Editor and, later, as Honorary Associated Editor. For me, the loss is both a professional and a personal one, as Lynn was an important scientific collaborator as well as a my partner for almost 30 years. Lynn Margulis (née Lynn Petra Alexander) died at her home in Amherst, Massachusetts, on November 22, 2011, after suffering a massive stroke. Her death was noted by the many newspapers and other media in the USA and, internationally, in prominent scientific journals and newspapers. The announcement was followed by tributes from her many colleagues, friends, and admirers and by those who, while intellectually at odds with her ideas on evolution, nonetheless recognized the value of her work. Rather than repeat what has already been written, this editorial will focus mainly on her relationship with Spain, the Spanish Society for Microbiology (SEM), and INTERNATIONAL MICROBIOLOGY.

But first let's consider the role of Lynn Margulis in the field of microbiology. Was she indeed a microbiologist? She was rarely seen in a lab coat, nor did she prepare microbial cultures or isolate strains for identification. However, her intellectual contributions were essential to many discoveries, reflecting her ability to see "the big picture" and thus to interpret both the research results obtained in her own lab and those of her colleagues in a broad range of related fields. She was an excellent observer of natural samples, usually in vivo,

Fig. 1. Lynn Margulis (1938-2011). Photo by I. Fernández, at the Institute for Catalan Studies, Barcelona, in April 2009.

under the photonic (as she liked to say) microscope. But she also had an extraordinary ability to interpret micrographs of any kind.

In addition, her intellectual curiosity motivated her to frequently browse through the older scientific literature, even in languages that she did not understand. It was on one such occasion that she came across the works of Russian biologists such as Andrei Sergeivich Famintsyn (1835–1918), Konstantin Sergeevich Merezhkovsky (1855–1921), and, especially, Boris Mikhaylovich Kozo-Polyansky (1890–1957), who throughout their careers had emphasized the role of symbiosis in evolution. Famintsyn had developed a theory of symbiogenesis but, despite claims to the contrary, did not succeed in isolating and growing chloroplasts from plant cells. Merezhkovsky later maintained that chloroplasts had originated from cyanobacteria and he coined the term *endosymbiosis* to describe the evolution of novel traits by symbiosis. But it was Kozo-Polyansky who suggested that symbiosis could explain the evolution of cell motility. Nowadays, the notion that both chloroplasts and mitochondria were once free-living bacteria that established a symbiosis with larger, different prokaryotes is fully accepted. Transmission electron microscopy clearly showed that the contents of both "eukaryotic" organelles closely resemble their respective bacterial ancestors, while molecular biology confirmed that chloroplasts and mitochondria not only had their own DNA but also were phylogenetically related to two groups of prokaryotes: cyanobacteria and proteobacteria, respectively.

During the late 20th century, Lynn Margulis and other microbiologists provided evidence that the most frequent and representative interactions among all the living beings on Earth are those of cooperation and symbiosis. The focus of Margulis' work was what are widely known as protozoa and unicellular algae but which she referred to as protists, or protoctista. As an outstanding protistologist, she studied these eukaryotic species not as single entities, but mostly with respect to their symbiotic relationships, which in many cases had evolved to become permanent ones; yet she also carefully analyzed independently existing microorganisms. Her near-intuition for the role of symbiosis in evolution led her to approach the field of microbiology from the viewpoint of ecology, i.e., the relationships among organisms and between them and their environment. A tenet of modern biology is that any kind of life establishes some kind of connection with other living beings. These connections include transient symbiosis; that is, partners meet, live together for a certain amount of time, and then, depending on environmental conditions, separate. But there are also examples of highly complex communities, such as those inhabiting the termite hindgut, that have remained unaltered for millions of years because the environment has not been disrupted by external changes. Over the few last decades, more and more symbiotic relationships involving the participation of bacterial species have been revealed, such as *Buchnera* and aphids, *Trychonympha* and its endosymbiotic bacteria, and *Wolbachia* and *Onchocerca volvulus*.

Throughout the 1970s, Lynn Margulis worked exclusively with eukaryotic microorganisms studying them from structural, physiological, genetic, evolutionary, and ecological perspectives. She was recognized as an expert in the field, as established by her role as coeditor, with John O. Corliss, Michael Melkonian, and David J. Chapman, of *Handbook of Protoctista*, which Lewis Thomas considered "a volume of similar scientific indispensability" as *Bergey's Manual of Systematic Bacteriology*.

It was in the early 1980s that Lynn Margulis began to consider prokaryotes. This late interest can be explained by the attitude that prevailed in microbiology during the years that she had worked towards her doctorate. At that time, bacteria were studied mostly in terms of pathogenesis and Margulis was not only uninterested in that viewpoint, she believed it was far too narrow. In 1983, she began the first of many collaborations with Spanish microbiologists—prokaryotologists indeed—first from the Autonomous University of Barcelona, and then, in 1988, from the University of Barcelona. In these pioneering studies in what was the still young science of bacterial ecology, she discovered the fascinating world of prokaryotic physiology and genetics. Her soon to be acquired detailed understanding of these microorganisms is reflected in the Introduction of the above-mentioned *Handbook of Protoctista*.

Her collaboration with Karlene V. Schwartz was a fruitful one, resulting in the publication of *Five Kingdoms: An Illustrated Guide to the Phyla of Life on Earth* (first edn., 1982), in the words of its authors "an illustrated guide to the diversity of life" and a book "about the biota, the living surface of the Planet Earth. A catalogue of life's diversity and virtuosity." Stephen Jay Gould, in the Foreword, called the book the "rarest of intellectual treasures" and drew upon its contents in pointing out that the greatest division among living beings was not "between plants and animals, but *within* the once-ignored microorganisms—the prokaryotic Bacteria and the eukaryotic Protoctista." Subsequent changes in our understanding of the relationships among living beings, brought about by the information obtained through DNA sequencing, have been incorporated in the more recent editions of this book.

Typically, great achievements are the result of many years of experience. But, in the case of Lynn Margulis, her unique way of thinking combined with fortuitous circumstances

Fig. 2. Lynn Margulis with friends from the Autonomous University of Barcelona and the University Barcelona during their official visit to the modern Library of Alexandria, Egypt on December 31, 2003.

resulted in discoveries already during her doctoral research that most scientists do not achieve in a lifetime and which quickly launched her career in biology. Thus, in the early 1960s, she developed the theory of serial endosymbiosis as an evolutionary mechanism explaining the origin of the eukaryotic cell. The theory followed from her appreciation of the fact that, in a world of nuclear inheritance, there were many cases of non-Mendelian heredity, for example, in photosynthetic mutants of plants and algae, in the cortical inheritance in *Paramecium*, and in the killer phenomenon of yeast. Lynn Margulis explored the scientific literature to find evidence for cytoplasmic heredity and predicted the existence of organellar DNA.

Her first paper (under her former name of Lynn Sagan) advanced her hypothesis but it was rejected by some fifteen editors before James Danielli, co-originator of the theory of the lipoprotein bilayer of membranes, dared to publish it in the *Journal of Theoretical Biology*, in 1967. Her hypothesis met with strong opposition from many colleagues, such as Roger Y. Stanier, who happened to meet Margulis in an elevator in at the University of California-Berkeley and told her that her strange theories on the origin of mitochondria and chloroplasts would never gain acceptance. Years later, after molecular biology and microscopy had proven Stanier wrong by providing overwhelming support for the hypothesis, he and Margulis, through mutual friends, were able to reconcile their intellectual differences with each other.

Mexico was the bridge that linked Lynn Margulis with the Spanish culture and language. At the age of 16, while doing anthropological field research in the country, Margulis learned to speak Spanish and was soon fluent. This ability was to later serve her well, as it allowed her to quickly feel at home in Spain—where, from 1983 on, she often traveled for research and teaching—and to lecture there in Spanish, thus gaining the further admiration of her Spanish students and colleagues. However, Margulis' academic activities were not confined to the lecture rooms of Spanish universities; rather, she was a popular speaker, often invited to give lectures and to participate in scientific meetings and workshops not only in university settings but also in museums, research centers, schools and high schools, cultural and commercial centers, and even ancient palaces and castles (in 2007 she inaugurated the new premises of Don Alvaro de Luna's castle, in Arenas de San Pedro, Ávila). She never failed to attract a large audience, with people often resigned to sitting on the floor of a packed auditorium. She received honorary doctorates from the Autonomous University of Madrid, the University of Valencia, the Autonomous University of Barcelona, and the University of Vigo. Many of her books have been translated into Spanish—several of them also into Catalan and Basque—and over the years they have remained very popular, particularly among high-school biology teachers and biology university students, as her "rebellious" writing and thinking continue to resonate among young people.

The collaboration between Lynn Margulis and the SEM started in 1985, when she participated in several SEM-sponsored conferences. In 1998, when INTERNATIONAL MICROBIOLOGY replaced *Microbiología SEM* as the official SEM journal, her help was invaluable during the transition period, when the journal also sought a new publisher. With the debut of INTERNATIONAL MICROBIOLOGY, published by the Spanish division of Springer-Verlag, Lynn Margulis, along with other outstanding microbiologists, was appointed Associate Editor. This was a responsibility that she took quite seriously and with the full force of her intellectual energies: encouraging researchers to submit articles to the journal, acting as peer reviewer, submitting research articles from her own laboratory, and contributing historical perspectives as well as book reviews. In 2004, she became Honorary Associate Editor but maintained an active involvement with the journal.

In an essay published in 1993, Lynn Margulis discussed what she called the "red shoe dilemma" that many women face when confronted with choosing between a professional career and family life. She remembered how—as a teenager—she was moved by the film *The Red Shoes*, in which a career conflict led a desperate ballerina to commit suicide. Lynn Margulis never even considered the need to choose. She recognized, however, that "children, husband, and excellence in original science are probably not simultaneously possible." About herself, she wrote: "Probably, I have contributed to science because I twice quit my job as a wife. I abandoned husbands but stayed with children. I've been poor, but I've never been sorry."

Many of the obituaries have referred to Lynn Margulis as an evolutionary biologist. It is true that most of her research focused on evolution, especially on the role of symbiosis as a major evolutionary mechanism. But she also studied symbiosis in and of itself, specifically, in the relationships formed by microorganisms with other microbial but also with non-microbial organisms. These diverse aspects of symbiosis sparked Margulis' passionate interest in the Gaia theory, postulated by British atmospheric chemist James E. Lovelock, to which she provided supporting (micro)biological evidence. She was indeed an advocate of microbes. She has left her footprint in the world of microbiology and will be remembered as one of the greatest innovative scientists of the 20th century. It would be difficult to summarize in only one sentence the main objective of Lynn Margulis' life and work; instead, I remember this quote from David Bohm (American physicist, 1917–1992), which lately she always cited at the end of her lectures: "Science is the search for truth... whether we like it or not."

Articles by Lynn Margulis published in the SEM journals *Microbiología SEM* (1985-1997) and *International Microbiology* (started in 1998)

Esteve I, Gaju N, Mas-Castellà J, Guerrero R, Margulis L (1995) Bacterial survival mechanisms in microbial mats. Microbiol SEM 11:397-399

Chapman MJ, Margulis L (1998) Morphogenesis by symbiogenesis (1998). Int Microbiol 1:319-326

Margulis L, Navarrete A, Solé M (1998) Cosmopolitan distribution of the large composite microbial mat spirochete, *Spirosymplokos deltaeiberi*. Int Microbiol 2:27-34

Wier A, Margulis L (2000) The wonderful lives of Joseph Leidy (1823-1891). Int Microbiol 3:55-58

Wier A, Ashen J, Margulis L (2000) *Canaleparolina darwiniensis*, gen. nov., sp. nov., and other pillotinaceae spirochetes from insects. Int Microbiol 3:213-223

Margulis L (2005) Hans Ris (1914-2004)–Genophore, chromosomes and the bacterial origin of chloroplasts. Int Microbiol 8:145-148

Book Reviews

Margulis L (1999) Darwin among the machines. The Evolution of Global Intelligence [by George B. Dyson]. Int Microbiol 2:57-58

Margulis L (1999) The Phototrophic Prokaryotes [by G.A. Peschek, W. Löffelhardt, G. Schmetterer, eds]. Int Microbiol 2:279-283

Margulis L (1999) J.D. Bernal. A Life in Science and Politics [by Brenda Swann, Francis Aprahamian, eds]. Int Microbiol 2:281-282

Margulis L, Chica C (2000) Orígenes. Del Big Bang al Tercer Milenio [by Alfred Giner-Sorolla, Mercè Piqueras]. Int Microbiol 3:263-264

Margulis L (2001) The biography of a germ [by Arno Karlen]. Int Microbiol 4:55-56

Margulis L (2002) What evolution is [by Ernst Mayr]. Int Microbiol 5:103-104

Margulis L (2002) Tuberculosis: the greatest story never told [by Frank Ryan]. Int Microbiol 5:151-152

Margulis L (2003) Lichens of North America [by Irwin M. Brodo, Sylvia Duran Sharnoff, Stephen Sharnoff] Int Microbiol 6:149-150

Margulis L (2004) Life on a Young Planet [byAndrew H. Knoll]. Int Microbiol 7:152