Lynn Margulis *

The Champion of Symbiogenesis

The origin of the eukaryotic cell has puzzled scientists for over a century. Although several theories were proposed to explain the origin of eukaryotic cells, it was the carefully crafted tale of the evolution of organelles by Lynn Margulis in 1967 that provided the most logical and comprehensive series of events leading to the presence of mitochondria and chloroplast in the extant eukaryotic cell. I came across her work as an undergraduate in science in the 1990s. For me, symbiosis is as synonymous with Lynn Margulis as evolution is with Charles Darwin.

Symbiogenesis

Lynn Margulis was a Master's student at the University of Wisconsin in 1960. She was influenced by the work of Hans Ris and Walter Plaut on the presence of genetic material in the chloroplast of *Chlamydomonas*, a unicellular green alga. Her interest in the origins of life was shaped by a course in theoretical biology, natural history, and by association with a PhD student in physics, Carl Sagan, famous for his contribution to space science and search for extra-terrestrial intelligence, better known as SETI. Lynn had the uncanny ability to assimilate and put together evidence from diverse disciplines, including natural history, microbiology, paleontology, and geochemistry. She put together a 48-page classic paper at the age of 29 years, just two years after receiving a PhD from the University of California, Berkeley. This paper, 'On the Origin of Mitosing Cells', was perhaps the most credible treatise on the origin of organelles in the present-day eukaryotic cells. Lynn was able to put this together without having performed experiments but by poring over evidence, the majority of it in literature not in English, from the work of Schimper, Mereschkowski, Wallin, and Kozo-Polyansky, among others. Although the idea of symbiogenesis of chloroplasts was raised by several scientists before Lynn, she provided the most lucid, chronological sequence leading to the evolution of organelles in eukaryotic cells. She credited her predecessors and drew extensively from naturalists, microbiologists, microfossil evidence, and geochemistry to support her ideas. She expanded on her ideas further in subsequent books. The idea of an endosymbiotic origin of mitochondria and chloroplast has withstood the test of time. Indeed, genomics provided the most convincing evidence that the mitochondria and chloroplast DNA are closed and circular like the DNA of extant prokaryotes. These organelles also divide by binary fission like bacteria

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and contain their own protein-synthesizing machinery similar to extant prokaryotes.

Origin of Mitosis

Lynn spent a great deal of her scientific career trying to prove that the 9+2 homologue (a structure composed of polymerized tubulin) present in flagella/cilia and centrosome in the eukaryotic cells were endosymbiotic in origin. She proposed that these came about by the engulfment of a spirochete-like ancestor by the host cell. Unlike mitochondria and chloroplast, which carry their own circular DNA and protein-synthesizing machinery, the 9+2 homologue has no DNA and limited resemblance to the spirochete. Lynn argued that these cilia or centrosomes have limited metabolic function, and their genome must be too small to detect. The endosymbiotic origin of cilia and centrosome does not have wide support thus far, despite her efforts throughout her life to gather evidence for this.

Five Kingdom Classification of Living Organisms

Lynn Margulis was a supporter of the five-kingdom classification proposed by Robert Whittaker in 1969. The kingdoms included Animalia, Plantae, Fungi, Protista, and Prokaryota, or Monera. Lynn suggested Protoctista, in place of Protista, including unicellular eukaryotes and some multicellular eukaryotes such as red alga and slime molds. The protoctists are not monophyletic, i.e., they do not naturally form a clade because they do not have a common eukaryotic ancestor. Nevertheless, the five-kingdom classification is in use. Analysis of ribosomal RNA sequences from different kingdoms by Woese and Fox in 1977 indicated that archaea are as far from eubacteria as they are from eukaryotes (plant, animal, and yeast). This led to the splitting of Monera into eubacteria and archaea and a six-kingdom classification.

GAIA Hypothesis

Proposed by James Lovelock, a chemist from the UK, this hypothesis considers Earth to be a self-regulated system of interaction between living organisms and the inorganic component of the Earth to sustain life on this planet. Lynn Margulis was a co-developer and champion of the hypothesis and helped accumulate evidence for this. GAIA paradigm remains a controversial topic for many scientists in the field.

Legacy of Lynn Margulis

Lynn Margulis not only had intellectual commitment to her hypotheses but also had boundless energy to pursue them relentlessly. She displayed this in her support for symbiogenesis and the GAIA hypothesis. She did not allow criticism and prejudice of her contemporaries to cause her to retreat or give up on her beliefs. Scores of scientists after her confirmed the validity of the endosymbiotic origin of mitochondria and chloroplast. Like other influential scientists, all her theories did not turn out to be true. She spent a good part of her career trying to prove the endosymbiotic origin of cilia and centrosomes. Although she did not succeed, her persistence is an example for all scientists who pursue an idea contrary to mainstream beliefs. She called herself a Darwinist but rejected neo-Darwinism. She rejected the reductionist approach of scaling down life to genes and molecules alone. In her mind, the fastest way to gain an advantage in the competition for resources is not by the slow process of mutations in the nuclear genes but by networking between organisms in nature. She believed that symbiosis and endosymbiosis result in traits acted upon by natural selection. Lichen (fungi and algae) and Lokibacteria with methanogenic bacteria are two simple examples of symbioses in the present-day. Lynn described eukaryotic cells as multi genome systems over 50 years ago. Today, experts studying the microbiome in humans (and other animals) describe animals and their microbiome as holobiont, a scaled-up version of Lynn's multi genome system. In the past decade and a half, the microbiome (of humans and other animals) has emerged as one of the most important drivers of health and fitness in animals. This is possibly the fittest tribute to Lynn's persistence that symbiosis promotes evolution in biological systems.

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