LYNN MARGULIS, CHAMPION OF THE ENDOSYMBIOTIC THEORY AND SYMBIOGENESIS (1938–2011)

I first met Lynn Margulis at a workshop and summer school I organised in Ballyvaughan, Co. Clare, in the summer of 2000. This meeting was part of a European Science Foundation-funded programme called CYANOFIX, and was focussed on Cyanobacterial Symbioses. We were delighted in getting Lynn to participate, largely through the efforts of Birgitta Bergman, a colleague at the University of Stockholm, who was also involved in running the meeting, as well as getting her to contribute to a Special Issue of *Biology and Environment*, 'Commentaries on Cyanobacterial Symbioses'. I also recall subsequent interactions with her at Meetings of the International Symbiosis Society, and we served together on the editorial board of the journal Symbiosis. As a student I remember discussions of what was then called the 'endosymbiotic theory' and had a copy of her book *The Symbiotic Planet* (Margulis 1998), but had never met her in person. Already a Member of the National Academy of Sciences, since 1983, and a recipient of the National Medal of Science (presented by President Bill Clinton the previous year), she was a globally recognised scientist and, by recommendation, a star performer in front of an audience. She did not let us down, giving a bravado and thought-provoking performance of endosymbiosis and symbiogenesis with a variety of visual aids, including a cine camera that taxed our somewhat limited visual aids systems.

Our current acceptance of the endosymbiosis 'theory'—that the nuclear and chloroplast organelles and perhaps other cellular structures had an ancient free-living prokaryotic ancestry and were, in fact, long-lived symbionts in eukaryotic cells—belies the controversy and ridicule associated with it and its proponent(s) in the 1960s. In truth the idea had been first suggested by the infamous Russian botanist Constantin Mereschkowsky in a paper published in 1905, in which he recognised a key fact—plastids have the ability to divide independently of the rest of the cell and do not arise de novo—indicating the potential at least for a free-living existence. Even a link between the chloroplast and its potential free-living ancestor, a cyanobacterium, was intimated by Mereschkowsky, if never fully explored (Martin and Kowallik 1999). Mereschkowsky also coined the term 'symbiogenesis', which was subsequently used in an evolutionary context to refer to the perceived, partner-associated, origin of new traits. Rather surprisingly, perhaps, given the more recent controversy, these ideas were initially popular, only falling out of favour after the First World War. Lone proponents of the idea in the 1920s, such as Ivan Wallin (Wallin 1927), apparently received little attention (Martin *et al*. 2001). However, all of this changed in the late 1960s when two papers appeared that essentially supported an endosymbiotic origin for both the chloroplast and mitochondrion by, as she was then, Lynn Sagan (Lynn Margulis) and the Norwegian, Jostein Goksøyr (Goksøyr 1967; Sagan 1967). While both proponents deserve recognition for this proposal it was Lynn Margulis who advanced and at the same time, re-invigorated the concept, with her paper published in the *Journal of Theoretical Biology*. This paper provided a wider assessment of the role of endosymbiosis in the evolution of eukaryotic cells; this paper, reputedly, was rejected by 15 previous journals. Soon after, these ideas were further elaborated on in her book Origin of Eukaryotic Cells in 1970 (Margulis 1970), and she became the focus, as well as the champion, of endosymbiosis.

Today, we know that the evidence, based largely on a wealth of molecular information, supports an endosymbiotic origin for chloroplasts and mitochondria. The origin of other

structures is still hotly debated as is the evolutionary significance of symbiosis (symbiogenesis). To what extent are new tissues, new organs or new physiologies a consequence of partner-associated interactions and how do they contribute to fitness? I have previously suggested, for instance, that symbiosis can be viewed as a way of utilising the tried and tested technology of ancient prokaryotes to address deficiencies in the ability of organisms to respond to altered environmental conditions or to acquire new or limiting resources (Osborne 2007). Contrary to popular belief these partnerships may not be mutually beneficial. In many respects addressing this and other aspects of the evolutionary significance of symbiosis is part of the legacy that Lynn Margulis has left for the scientific community to answer.

Variously described as 'tough', 'combative', 'courageous' and, yes, 'controversial'—in the sense that she often challenged orthodox views, most recently with her proposal of a link between syphilis and AIDS—she was also called a 'maverick' scientist. She was, to various degrees, almost certainly all of these things. For many years she almost single-handedly shouldered the 'responsibility' for the endosymbiotic theory, which must have proved a daunting challenge in itself. At the meeting in Ballyvaughan we talked about a number of things, including the birth of my son Joshua a few days earlier—someone at the meeting had mentioned this to her—and how difficult it must have been to leave the family at this particular time. She was also very supportive of our work on the Gunnera–Nostoc symbiosis. Perhaps, more importantly, she was good fun! And who else can say that they 'danced', if dancing is the right word for it, with Lynn Margulis?

Lynn Margulis, champion of the endosymbiotic theory, RIP.

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