From modern symbioses… to the origin of the eukaryotic cell

Mauro Mandrioli
Department of Life Sciences, University of Modena and Reggio Emilia, via Campi 213/d, 41125 Modena

The origin of eukaryotes is still one of the most enigmatic and challenging questions in evolution. Since the recognition of the prokaryotic–eukaryotic transition as 'the greatest single evolutionary discontinuity' of life about half a century ago [1], prokaryotes with some typical "eukaryotic features" have been found [2], but true intermediate forms representing transitional structures between prokaryotes and eukaryotes were never found.
In the last years, several papers clearly showed that symbiosis is an adaptive process that can act as a precious source of phenotypic complexity [3] suggesting that, accordingly to an old suggestion of Francois Jabob [4], at each level of a structured system, units may associate to form a unit of higher level. Indeed, as stated by Nowak some years ago [5], natural cooperation may be the third fundamental principle of evolution in addition to mutation and natural selection since "evolution is constructive because of cooperation. New levels of organization evolve when the competing units on the lower level begin to cooperate".
A large set of data suggested that the evolution of eukaryotes could be the result of the symbiosis between two (or more!) prokaryotes, but the means by which the endosymbiont got access into its host poses a mechanistic challenge to this scenario. At present we have an unprecedented chance to study "modern" symbiosis in different species (and in particular in insects), where the interactions between hosts and symbionts may be studied at a genomic level revealing an unexpected exchange of genes and interactions between them. In particular, the study of intracellular symbiont bacteria (such as "*Candidatus* M. mitochondrii" and *Wolbachia*) could greatly help to understand how symbionts can enter cells or, as reported for "*Candidatus* M. mitochondrii", access to specific organelle starting a cross talk with the host genome.
Even if a large amount of work is still requested, the origin of the eukaryotic cell could be the most successful example of symbiosis, where the interaction between two prokaryotes (which begun as a predatory or a parasitic relation) evolved into a symbiotic mutualistic interaction.
Some years ago, Grosberg and Strathmann [6] suggested that, on the basis of the low complexity of the molecular mechanisms involved, the evolution of multicellularity could be described as a minor major transition. In a similar manner, eukaryotes could have "easily" evolved by symbiosis without any intermediate forms with prokaryotes.

[1] Stanier RY et al., 1963, The microbial world, 2nd ed. Englewood Cliffs, NJ, Prentice-Hall, 1963
[2] Furest JA, 2005, Annual Review of Microbiology 59, 299–328
[3] Moran NA et al., 2007, Proceedings of the National Academy of Sciences USA, 104, 8627
[4] Jacob F, 1977, Science, 196, 1161–1166
[5] Nowak MA, 2006, Science, 314, 1560–1563
[6] Grosberg RK, 2007, Annual Review of Ecology, Evolution, and Systematics, 38, 621-654