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Symbiosis in the omics era

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In his ‘*Die Erscheinung der Symbiose*’ (1879), Heinrich Anton De Bary, professor of Botany and the founder of modern mycology, coined the word symbiosis (from the Greek ‘living together’) to describe species which live in close association for long periods. His work was mostly focused on associations from the plant kingdom, like those involving *Azolla* and lichens, and was also formulated in opposition to categories of parasitism and commensalism which were extensively used for the animal kingdom. However, over the years, the original concept of symbiosis has changed many times, to focus again on interactions based on food competition and predation. As one of the crucial concepts of symbiosis is that at least one member of the pair has to benefit from the relationship, other situations have been identified as symbiosis-related: parasitism, when the other member may be injured, commensalism, when it is relatively unaffected, or mutualism, when the second partner may also benefit. Indeed, part of the scientific community restricts the term symbiosis to only these mutually beneficial interactions, even though the borders among the typologies are not always so clearly defined.

In the past century, symbiosis was regarded above all as a descriptive catalogue of natural science events, rich in fascinating examples, some of which are very common (the ciliate *Paramecium bursaria* that engulfs unicellular green algae or the plant–fungal interactions known as mycorrhizae), while others are limited to highly specialized environments ([Douglas, 1994](#)). A good example of these extreme situations is given by a three-way symbiosis: a tropical panic grass growing in Yellowstone Park and surviving heat thanks to a symbiosis with an endophytic fungus which is infected by a virus ([Marquez *et al.*, 2007](#)).

A paradigm shift to the traditional naturalistic view was given by Lynn Margulis who underlined how the major point of symbiosis is not the benefit to the partners in itself but the possibility of acquiring new metabolic properties ([Margulis, 1981](#)). Symbiosis (syntrophogenesis in Margulis's terminology) is therefore regarded as an important evolutionary force which leads to biological novelties (new functions, new tissues, new organs and new organisms like lichens). According to this approach, the eukaryotic cell is also seen as the product of repeated symbiotic events. In the meantime, a specialized vocabulary has been developed to better describe the complexity of the symbiotic interphylum interactions taking into consideration the partner size as well as their topological relationships: the host is the larger partner (usually a eukaryote) while the symbiont is the smaller one (a prokaryote or another eukaryote); the symbiont may be located in an extracellular position or may occupy a niche inside the host cells. In this latter case, it is defined as an endosymbiont and is usually surrounded by a specialized membrane of host origin ([Douglas, 1994](#)). Furthermore, according to [Margulis and Chapman \(1998\)](#) symbiosis is defined as cyclic when the symbiont is acquired at each generation of the host, as happens in the symbiosis between *Hydra* and *Chlorella* and between legumes and rhizobia. The partners of the cyclic symbioses have an autonomous life style and may live as free-living organisms, at least for a part of their cycle. In

contrast, in permanent symbioses symbionts cannot live as free-living organisms and depend completely on their hosts. The symbiont life cycle thus depends upon that of its host, as it is passed from host mother to daughter in a vertical transmission mode that is opposite to the characteristic horizontal modality of cyclic symbioses.

The scenario envisaged by Margulis has received much confirmation and the concept that symbiosis is a source of evolutionary innovations is largely accepted and is now included in school text books. There are many reasons for this success: on one hand, the concept of symbiosis is a metaphor of a positive interaction and because of this the word is widely used not only in natural sciences, but in many other fields in a general context of sustainability (economics, management, psychology). Another interesting aspect is that unlike the Neo-Darwinism school, which did not consider symbiosis as an event fitting to Darwin's theory of evolution, today there is much interest in discussing symbiosis as a relevant aspect of evolution. It is in fact clear that Darwin had no conception of the gene and little knowledge of microbes, while, on the other hand, evolution of bacteria, including symbiotic ones, is also based on the generation of variation, which is winnowed by selection ([Hanage, 2010](#)). Last and even more important, the impressive data currently available in the field of microbiology, the development of high-throughput technological platforms, as well as the sequenced genomes of more than a thousand microbes, and hundreds among animals, plants, protists and fungi (<http://www.ncbi.nlm.nih.gov/sites/entrez?db=genome>) – i.e. the omics era – have led to new views on symbiosis.

The symbiotic origin of the eukaryotic cell has received crucial supports through the discovery of free-living prokaryotes with specific metabolic capacities, the sequencing of their 16S RNA, which has led to the construction of phylogenetic trees that shed light on bacterial taxonomic relationships, as well as through the genome sequencing of mitochondria and chloroplasts ([Martin, 2005](#); [Dagan and Martin, 2009](#)). The new information has made it possible to hypothesize the identity of the prokaryotic ancestors of organelles and to claim that most of the genes that were present in those ancient endosymbionts have been transferred to the nucleus during evolution ([Timmis et al., 2004](#)). Genes that relocated and became functional in the nucleus were deleted from the organelle genomes, reducing organelle genome size ([Timmis et al., 2004](#)). Much experimental evidence has demonstrated that a large fraction of the products of the nuclear genes so acquired are retargeted to their ancestral compartment; many others now function in new subcellular locations. Almost all present-day nuclear transfers of mitochondrial or plastid DNA give rise to non-coding sequences, dubbed nuclear mitochondrial DNAs and nuclear plastid DNAs. Intercompartmental DNA transfer therefore represents a significant driving force for gene and genome evolution, relocating and refashioning genes and contributing to genetic diversity ([Kleine et al., 2009](#)).

The new technical platforms have confirmed old hypotheses as well as have changed our views to a great extent, considering the symbioses which are widespread among the animal, plant, protists and fungal kingdoms, and which offer many exciting novelties. One of the most widespread symbioses in animals is given by obligate intracellular Gram-negative bacteria which live in special tissues of some insects such as aphids ([Douglas, 1994](#); [Moran et al., 2005](#)). Nowadays the genomes of some of these symbionts have been sequenced; their functional complementation with their host has been demonstrated through the finding that the bacterial genomes encode a number of enzymes needed to complete the synthesis of amino acids required by their host. In return, the aphid genome encodes enzymes that are needed by the bacteria to synthesize their lipopolysaccharide cell wall, and has lost genes that might otherwise repel infection by Gram-negative bacteria. Lastly, most ancestral genes of the bacteria are eliminated by deletion, resulting in some of the smallest known cellular genomes ([Moran et al., 2009](#)). Another intriguing example of symbiosis in insects involves co-speciating tripartite partners of host termites, cellulolytic flagellate protists in their gut and endosymbiotic bacteria of the protists ([Ohkuma, 2008](#)). The genome sequencing of the uncultivated endosymbionts

of far remote lineages of known bacterial species reveals their unexpected roles in nitrogen fixation and upgrading of nitrogen quality, which are crucial for their hosts to feed on sound wood ([Hongoh et al., 2008](#)).

Moving towards the plant kingdom, nitrogen-fixing symbioses have long been considered the paradigm for symbioses with relevance to society, as nitrogen is one of the most commonly supplied fertilizers. The genetics, and the cellular and molecular bases which regulate the development of both partners have been investigated in detail, and this has led to a dissection of the molecular dialogue between the symbionts and their host ([Den Herder and Parniske, 2009](#)). This symbiosis, however, still offers exciting experimental potentialities. [Marchetti and colleagues \(2010\)](#) have transferred a rhizobial symbiotic plasmid from a nitrogen-fixing bacterium into a phytopathogenic strain of *Ralstonia solanacearum* in order to understand what converts a pathogen into a symbiotic one. These researchers have been successful in detecting some crucial determinants (inactivation of *hrcV* structural gene of the type III secretion system and mutations in the *hrpG*-controlled virulence pathway virulence regulatory gene) which allow the transition from pathogenicity to symbiosis. Pointing to an evolution towards mutualism, the results demonstrate the potential of experimental evolution to decipher the mechanisms that lead to symbiosis, the relevance of the horizontal gene transfer, at least for the nodulating systems, and the possibility of correlating a phenotypic trait (symbiotic versus pathogenic) with specific molecular determinants.

In the context of environmental ecology, mycorrhizae play a major role, due to their widespread presence and their importance in the nutrient cycle. The genome sequencing of two ectomycorrhizal fungi, their transcriptomic analysis ([Martin and Nehls, 2009](#); [Martin et al., 2010](#)) as well as a certain knowledge of the network of interactions which exist between plants, fungi and bacteria ([Bonfante and Anca, 2009](#)) have pushed mycorrhizae into the mainstream of biology. In the meantime, metagenomics approaches, which allow researchers to 'surf' on massive data streams to unravel genomes of unknown species, and to catalogue a multitude of sequences from soil ([Martin and Martin, 2010](#)), are opening new scenarios in the symbiotic world: biomes, or whole communities, may be sequenced. Such projects have already led to the discovery of a new symbiotic world thanks to a programme whose goal was to sequence and understand the microbes that live in the human body and their contribution to human health and disease. Through such metagenomic approaches, [Gill and colleagues \(2006\)](#) completed the first comprehensive survey of the human gastrointestinal tract, providing a new vision of this symbiotic niche. Coming back to the original definition of symbiosis, this represents a giant leap: symbiosis can also be considered the result of a multitude of organisms (super organisms) linked in a network of interactions, where microbial, plant, fungal and animal attributes are amalgamated.

Given the growing importance of these findings for environmental microbiology, it is not surprising that both *Environmental Microbiology* and *Environmental Microbiology Reports* have collected a consistent group of contributions which offer a taste of the different topics that have been labelled as symbiotic interactions. In this special issue, readers can first surf on symbioses thriving in marine environments: [Petersen and colleagues \(2010\)](#) illustrate the dual symbioses present in hydrothermal vent fields, while [Guerrero-Ferreira and Nishiguchi \(2010\)](#) investigate the differential gene expression in bacterial symbionts living in squids, and [Webster and colleagues \(2010\)](#) uses deep sequencing to describe the diversity of bacterial sponge symbionts. Plant–fungal interactions are the dominating symbioses in soil environments: it may be for this reason that they are very well represented in our special issue. [Lumini and colleagues \(2010\)](#) used a 454 platform to reveal the biodiversity of arbuscular mycorrhizal fungi along a land-use gradient in a Mediterranean environment, while [Krzanic and colleagues \(2010\)](#) demonstrate how ectomycorrhizal fungi may play a role in heavy metal tolerance when associated to their host plants, *Pinus sylvestris*; in addition, because mycorrhizae are often considered a three-way symbiosis, [Deveau and colleagues](#)

(2010) probed deeper into the nutritional interactions existing between *Laccaria bicolor* and the helper bacterium *Pseudomonas*. The syntrophic network created during the establishment of symbiosis was also well illustrated by Müller and colleagues (2010) who dissected the complex mechanisms underlying this event, starting from genomics information, while Ikeda-Ohtsubo and colleagues (2010) demonstrated the evolutionary origin of an endosymbiont of flagellate protists in termite guts and claimed that endosymbionts have been acquired among free-living members in this complex microbial community.

The ‘omics’ era (genomics, transcriptomics, metagenomics, metabolomics, proteomics, etc.) in conjunction with more traditional approaches (microbiology, ecology, theoretical biology, etc.) has provided the tools for great advances in our understanding of prokaryotes, protists, animal, plant and fungal symbioses, such as are highlighted in this special issue. These advances are of course not possible without the dedication and contributions of scientists who form and test hypotheses. Thus, it is with great sadness that we acknowledge the passing of mycorrhizal symbiosis researcher Dr Gopi Podila. His studies on the genomics and transcriptomics of ectomycorrhizal fungi have made a significant contribution to our understanding of a symbiosis which is crucial for tree life. He will be missed.

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