This special volume of *Symbiosis* is dedicated to Professor Margalith Galun, Founding Editor and Editor-in-Chief of *Symbiosis* from 1985 to 2006, and organizer of the 1st International Symbiosis Congress in Jerusalem, in 1991.

From the President of the International Symbiosis Society

The 5th International Symbiosis Society Congress was held at the Zoology Institute of the University of Vienna from the 4th to the 10th August, 2006. More than 200 symbiosis researchers gathered and came from some thirty-five countries. The level of participation, the quality of the presentations, and the presence of numerous students reinforced the fact that symbiosis has emerged as a fully integrated discipline encompassing both the Life and the Earth Sciences.

The results of the numerous studies have key implications for many scientific fields. These include ecology, medicine, physiology and systematics; all of which are related to evolution. Furthermore, recognition of the importance of symbiosis in evolution is emerging through the discoveries of a wide diversity of life in the deep sea biome and through paleontological and geological investigations. For example, by the time of the next Congress in 2009, it is possible that the "punctuated equilibria" patterns of Phanerozoic fossil life, observed by Niles Eldredge and Stephen J. Gould, will be explained by acquisition and integration of symbionts. Symbiogenesis most likely permitted new morphologies or enabled the newly merged organisms to colonize habitats unavailable to the isolated ancestral partners.

I had the pleasure of co-organizing the ISS Congress with the accomplished marine biologist, Monika Bright, and her wonderful colleagues, and support staff, at the University of Vienna. The International Symbiosis Society is very grateful for this leadership and camaraderie. To some degree, a science society is only as successful in promoting the discipline as the major international meeting it hosts. The outstanding 5-ISS event in Vienna bodes well for the future of the International Symbiosis Society over the next three years until members gather again, for the next congress in the summer of 2009 under the leadership of the Symbiosis Research Group (Heidi Goodrich-Blair, Margaret McFall-Ngai, Cameron Currie, et al.) at the University of Wisconsin at Madison, USA.

This splendid volume of *Symbiosis* includes a selection of the field, laboratory, and review papers which were presented at the 5-ISS Congress in Vienna. These contributions underline the healthy status of symbiosis as a discipline, and of our growing Society.

Douglas Zook, President

Our Discipline Comes of Age – Foreword to *Symbiosis* Volume 44

In his preface, Douglas Zook, President of the International Symbiosis Society (ISS), describes the spectacular success of the 2006 Vienna Congress that attracted over 200 scientists from thirty-five countries. The Congress covered 20 parent fields. The papers and discussion provided an impetus for the new and coherent view of symbiosis as a discipline that is presented in this volume of the journal.

In any symbiosis, at least two differently named organisms (the "bionts") live together in physical proximity for most of the life history of at least one of them. Regardless of the structure and arrangement of the bionts, whether attached or inside one another (e.g., epibiotic or intracellular), the two or more bionts comprise the "holobiont". All symbioses begin with unassociated, free-living organisms that merge to varying degrees. Their temporal relations may be either permanent or cyclical; indeed symbioses constitute ubiquitous ecological phenomena.

Cyclical symbioses are comparable to meiotic sexuality. In any meiosis-fertilization cycle, the mating partners are close relatives whereas in symbioses the associates may be members of different phyla, classes or even kingdoms. For all symbioses, the free-living relatives of the bionts provide clues as to the reasons why the partners merged. The relationships of the bionts grade from casual and occasional for one of the partners to permanent genetic intimacy. In cyclical symbioses, each partner lives unassociated during particular times: from hours in the day to seasons of the year or even longer. Re-association re-forms the holobiont with temporal periodicity. Sometimes, as in the case of chloroplasts of plant cells, the relationships become intimate, permanent and irreversible.

Biont integration usually begins with behavioral association. Thus, hungry translucent slugs or marine worms are attracted to the nourishment that leaks from all photosynthesizers and chemoautotrophs, for none are 100% efficient at retention of photo- or chemosynthate. Wriggling spirochetes slurp exudates from carbohydrate fermenters in anoxic habitats. They gain footholds on the slippery outer membranes of parabasalids or intestinal epithelia. Metabolic, gene product or even genetic fusion, may follow repeated behavioral interaction. Attempted mergers and loose fusions may disintegrate if conditions permit independent growth of one or the other partner. Environments change, some partners die. The stability of the holobiont relative to its constituent bionts is relentlessly honed by natural selection.

The papers that comprise this volume of *Symbiosis* illustrate the fact that symbiosis research has come in from the esoteric periphery to the center ring in the circus of life. Symbioses are the rule, not the exception in the ancestry of eukaryotes. Former symbionts are now permanent organelles; examples include the α-proteobacterial ancestors of mitochondria and the cyanobacterial ancestors of plastids in all algal and plant cells. Alternatively, as in associations between chloroplasts and the green slugs, *Elysia*, or *Placobranchus*, holobiont cyclicity is modulated by seasonal change. In bacteroid-forming rhizobia of leguminous plants, holobiont formation is very sensitive to shortage of fixed nitrogen in soil. The lives of nucleated organisms involve some form of past (and often current) symbiotic association. With delight, we note that from its former outlying tributary, the discipline of symbiosis has entered main stream biology.

"Medical symbiotics", a term coined by Professor Jessica Hope Whiteside of Brown University (in preparation), can be viewed as a highly specialized field within symbiosis. The study of cyclical relations, between microbes (primarily bacteria) and vertebrates (especially hominid mammals), is called by medical practitioners the "basic science of infectious disease". Because symbiosis is a subfield of ecology, symbiosis researchers naturally recognize the relevance of the holobiont's environment to its physiology and reproductive mode. Local habitat conditions invariably affect the course and rates of development and reproduction in both unassociated bionts and of the holobionts derived from them.

Symbiotic partnerships are ecological phenomena sensitive to environmental change. As soon as they become habitual or intimate and novelty arises from them, symbiosis leads to symbiogenesis. Organellar systems may emerge such as the karyomastigont (Margulis et al., 2006) or new organelles develop as in the sulfide-oxidizing trophosome bacteria of *Riftia pachytila*, the deep sea tube-worms. Thus, new kinds of cells, tissues, organs or organ systems can come into being. Once "symbiogenesis" has occurred, new varieties or even new species appear. The powerful role of symbiogenesis was first recognized by Konstantin S. Merezhkovsky (1855–1921). He recognized the importance of symbiogenesis for innovation relative to change by accumulation of chance hereditary variation. The awareness that branches on phylogenetic trees do not only bifurcate, but that lineages anastomose is revived after a century of dormancy. The article by Merezhkovsky (1905) "La plante considérée comme un complex symbiotique" (Sapp, 1994, 2005; Sapp et al., 2002; Emelyanov, 2007) was the pioneering contribution that demonstrated just how prevalent is the phenomenon of symbiogenesis in nature.

The understanding that symbiogenesis is a major source of evolutionary complexity, a process that gives rise to innovation in evolution, was provided in a small book by

Boris Kozo-Polyansky (1924) which reviewed the current biological literature of the period. Unlike his Russian predecessors, A. Faminstyn (1907) and K.S. Merezhkovsky (as discussed in Khakhina, 1992), Kozo-Polyansky did not reject Darwin. He viewed Darwinism as more than a mere process of elimination of unfit organisms by natural selection. He was the first to explicitly couple evolutionary innovation by symbiogenesis with Darwin's natural selection and so generate a coherent "new principle of biology". He recognized that Darwin's natural selection acts on holobionts to preserve them (Khakhina, 1992).

Western science will be able to judge for itself the prescience of Kozo-Polyansky's "new principle of biology" when, in 2008, Professor Victor Fet from Marshall University, Huntington, West Virginia (a specialist in scorpions and their mitochondria) publishes his translation and commentary. Members of our International Symbiosis Society and others are likely to be astonished when they read Kozo-Polyansky's clearly stated "new principle of biology" that details evolution by symbiont integration. It is remarkable that Kozo-Polyansky collected works on *Ardisia*-bacteria, *Gunnera-Nostoc*, *Azolla-Anabaena*, cycads-cyanobacteria, Blochmann bodies in many insects, mycorrhizae of many plants, and aphid-bacteria. It is astounding that this Russian biologist from Voronezh, and not Edouard Chatton (director of Laboratoire Arago, Banyuls-sur-Mer, France), made explicit the evolutionary implications of his principle. Kozo-Polyansky recognized the great gap between eukaryotes ("true cells", those with nuclei) and omni-present and omni-capable "elementary units of life" (the "blue green algae", "cytodes", "bioblasts" or "nepheloids"). While Chatton tabulated examples and named "la vie procariotique" and "la vie eucariotique", it was Kozo-Polyansky who discussed the evolutionary passage from one to the other. He posited that fusion of cytodes and bioblasts formed the nucleated "true cells"; he applied the principle of symbiogenesis to explain this largest gap in the living world. Furthermore, he wrote "Even the possibility that the blepharoplasts [a relatively large microtubule-organizing center precursor to many kinetosomes of plant sperm such as those of ferns and cycads] evolved by symbiosis should not be ignored". Kozo-Polyansky's ideas resembled those of anatomist Ivan Emmanuel Wallin (1927) who spent his final 40 years at the University of Colorado Medical School in Denver. Wallin introduced the terms "*prototaxis*" (the innate tendency of one kind of organism to respond to another kind) and "*symbionticism*" (microsymbiotic complexes, mostly bacteria and nucleated cells) to describe some of the phenomena that Kozo-Polyansky analyzed (Mehos, 1992).

The abundance, diversity and beauty of the symbioses, described in the pages of this new volume of *Symbiosis*, are notable. It is clear that individual unassociated bionts, many of which are ancestral to higher taxa, have become transformed by merger to produce new organisms. Nowhere is this more impressively documented than in the superb review by Frank Ryan, *"Viruses as Symbionts"*. His exhortation that symbiologists should no longer dismiss the importance of viruses, and his admonition to cease and desist perpetuating current misunderstandings, must be appreciated by all. Ryan deserves deep respect for his claim that the term "horizontal gene transfer" obfuscates our understanding. The central role of the viruses in maintaining various specific holobionts, for example *Elysia*, cold-tolerant grasses, *Mesorhizobium* in plants and parasitic wasps, becomes obvious after you read his review. We feel strongly that a title like *"Viruses as Non-Autopoietic Symbionts"*[(1)] would have been more apt. Viruses by themselves are not symbionts, in principle. They lack the self-defining 'bounded by a membrane' cellular identity of life that must be maintained by active metabolism. Yet, what became strikingly clear to us, is that viruses rapidly and unerringly transfer relevant, crucial, small replicon-genomes that are essential to holobiont function. This poorly known fact begs to be studied further by a more direct search of virus particles in cyclical symbioses. Another issue raised by Ryan is even more significant. He points out that the environment of the biont partners, the holobiont and the go-between viruses must be studied together as co-ordinated aspects of regulated phenomena. Population size and health depend on viral activity and the integration of viral genomes into animals, plants, and probably protoctists and fungi as well. Viral integration commonly uses the reverse transcriptase mode (RNA-to-DNA transcription) with long terminal repeats. Viruses replicate, evolve and critically affect their carriers, in this way. Is it then a coincidence that Mark Alliegro and Michael Chapman's cover article, in this volume, shows that one product, of the at least five new centrosomal RNAs, is a reverse transcriptase?

We invite you to feast on this symbiotic smorgasbord, as the importance of the discipline becomes ever more recognized. Challenge your friends and colleagues to learn more about symbiosis and the real history of life on Earth: chemical conversation, merger, fusion, and increasing complexity. All visible forms of life are chimeras, from the tiny viral sequences that cause syncitial (=plasmodial or coenocytic) fusion of the cells of the mammalian placentas, to the herds of placental wildebeest on the Serengeti plain. Life has evolved for 3000 million years by attraction, fusion, ancient alliance and emergence of new levels of complex individuality. Natural history revives with the increasing pursuit of modern structural, molecular, and field symbiosis-related research. We, our food, our pets and this "whole experiment in green"[(2)] and blue planet are a living testimony to evidence of Kozo-Polyansky's "new principle". Symbiosis is the rule and, to us, the major force of evolutionary innovation (Sapp, 1994).

The awareness of the importance of symbiogenesis will soon spread beyond the International Symbiosis Society and readership of our *Symbiosis* journal to the wider scientific community. Understanding of the role of symbiosis in the biosphere, and the impact of our own activities, destruction or nurture, are clues to the survival of our species. Indeed, the sustainability of agriculture, aquaculture and forestry, as well as our quality of life, requires our awareness of the continuing importance of symbiosis and symbiogenesis, and how it has changed the world.

(1) Or even more appropriately: *The Role of Viruses in Symbiont Integration.*

(2) *"A little madness in the Spring*
Is wholesome even for the King,
But God be with the Clown
Who ponders this tremendous scene
This whole experiment in green
As if it were his own"
Emily Dickinson, 1830–1886

Lynn Margulis
John Hall
Margaret McFall-Ngai

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