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Bellagio Conference and Book
Symbiosis as Source of Evolutionary Innovation: Speciation and Morphogenesis

Conference — June 25–30, 1989, Bellagio Conference Center, Italy

This meeting, organized by Lynn Margulis, Kenneth H. Nealson and René Fester, funded by the Rockefeller Foundation, provided a unique opportunity for evolutionary theorists and symbiosis biologists to cross the boundaries of their respective disciplines and share ideas. A major task was to address the adequacy of the prevailing neodarwinian concept of evolution with respect to the relative importance of symbiosis in the origin of morphological and evolutionary novelty.

Twenty scientists from nine countries gathered to discuss these issues in an idyllic setting overlooking Lake Como amid the foothills of the Italian Alps. Everyone was accommodated on the shores of the lake; each morning we walked up through the fragrant gardens which terraced the hill to meet in the elegant Villa Serbelloni. To increase interaction among the scholars, short presentations by the individual participants were followed by lively round table discussions. Fascinating, amusing and convivial, the meeting was successful in fostering communication between academic disciplines: symbiosis biologists were made cognizant of the need for the publication of their work in the mainstream evolution literature, and evolutionary theorists were encouraged to more profoundly consider symbiosis in evolutionary models. Addressing a need for inclusion of mechanisms besides gradualism in the prevailing neodarwinian dogma, the participants, in publishing these abstracts, hope to enhance awareness among evolutionists from all disciplines of the significance of the persistent novelties generated by symbiosis. We believe these insights should be shared with readers of the *Symbiosis* journal.

Application materials for both international conferences such as this one and a residence program for individual scholars or artists are available from the Bellagio Center Office, Rockefeller Foundation, 1133 Avenue of the Americas, New York, NY 10036, USA. *René Fester*

Participants in the Bellagio meeting. Back row, from left to right: Mary Beth Saffo, Sorin Sonea, Peter Atsatt, David Lewis, Margaret J. McFall-Ngai, Silvano Scannerini, Jan Sapp, Russell Vetter, John Maynard Smith, Kris Pirozynski, Richard Law, Gregory Hinkle, Werner Schwemmler, Toomas Tiivel. Front row, from left to right: René Fester, Lynda J. Goff, Kenneth H. Nealson, Lynn Margulis, Kwang W. Jeon, Rosmarie Honegger, Paul Nardon. (Absent: Guerrero, Haynes, Kendrick, Price and Trench.)

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Book

Symbiosis as Source of Evolutionary Innovation: Speciation and Morphogenesis
Lynn Margulis and René Fester, Editors, The MIT Press, Cambridge, MA (USA)

Summaries of Chapters

Fungi and the Origin of Land Plants, *Peter R. Atsatt*
Although land plants have strong phylogenetic affinities with the charophycean green algae, they exhibit numerous fungus-like characteristics. The complex architecture of plants is achieved to a great extent by specialized degradative and absorptive processes akin to those utilized by fungi. Convergent evolution or the conservation of genes from an ancient mutual ancestor of fungi and algae provide convenient reasons for dismissing the possibility that land plants have both fungal and algal ancestors. As an alternative, I suggest the possibility that land plants may have evolved via the incorporation of a fungal genome into a green algal genome (Atsatt, 1988). here I consider the idea that plants are symbiotrophs and that this feature may have impelled the nutritional and developmental union of the two alternate generations, the haploid gametophyte and the diploid sporophyte. I explore a new paradigm that emphasizes digestive and absorptive feeding as key innovations that permitted the origin of the embryo, and later, pollen and seeds.

Symbiosis Inferred from the Fossil Record, *David Bermudes* and *Richard C. Back*
Since host and symbiont are seldom preserved together, there is little direct evidence of symbiosis in the fossil record. However, examination of the origin of certain eukaryotic organelles, *a posteriori* views of host phylogenies, and the various metabolic and ecological influences of symbionts on their hosts suggests that symbiosis has affected biological changes which may be represented in the fossil record. Symbioses have been correlated with the origin of new taxa, changes in size and shape and the relative ability to produce preservable hard-parts. Symbiotic effects on host physiology may be reflected in isotopic fractionation. The ecology and biogeography of many organisms is also effected by their symbioses. Studies of extant symbioses indicate that the establishment and ramifications of these interactions can occur rapidly. Permanent acquisition of a symbiont, which represents a large heritable change, thus provides a macro-evolutionary mechanism which may even account for some biological discontinuities observed in the fossil record. Examination of the fossil record suggests that evolutionary transmissions based on symbioses are detectable.

Symbiosis, Nuclear Transfer and Species Evolution in the Parasitic Red Algae, *Lynda J. Goff*
Often the most unusual of biological phenomena teaches us the most biology. So it is in studies of symbiosis and cell-cell interactions. In our studies of one group of symbionts known as the parasitic red algae, we discovered that these parasites are able to inject nuclei into cells of their specific red algal hosts and "parasitize" the DNA replication machinery of the host to replicate the parasite nuclei within cells of the host. These nuclei are then transferred to other host cells, dispersing the parasite genome intracellularly throughout host tissue. Ultimately, the parasite nuclei are packaged into reproductive bodies and dispersed from the host. The entire process of parasite nuclei replication and dispersion is highly reminiscent of the cellular processes that follow fertilization in red algae and suggests that these parasites may have evolved as rogues of their host's life history stages. Molecular analysis via restriction fragment length polymorphisms (RLFPs) of the nuclear DNAs of the photoautotrophic red algae and their white-tissues parasites reveal that they are distinctly different as are host and parasite mitochondrial DNA. Molecular and cell biological studies reveal that the parasite lacks its own genetically distinctive plastid but maintains host plastid DNA within proplastids. Currently we are comparing ribosomal DNAs of hosts and parasites to determine if parasites originated from their host.

Predation as Prerequisite to Organelle Origin: *Daptobacter* **as Example,** *Ricardo Guerrero*
Eukaryotic organelles such as plastids and mitochondria contain DNA, ribosomes, and many other characteristics of free-living bacteria. Although most biologists agree that membrane-bounded organelles originated from free-living respiring and phototrophic bacteria, no adequate explanation of the method by which they originated is accepted. The relationships between prokaryotic phototrophs and their predators observed in several karstic, sulfur-rich lakes in eastern Spain, especially

Lake Cisó (Banyoles, Girona), provides a model of how the origins of organelles could first have occurred.

Daptobacter is a motile Gram-negative bacterium, capable of bacterial prey (host) recognition and penetration. Furthermore, once inside a heterologous bacterium (e.g., *Chromatium*), *Daptobacter* seals the plasma membrane and proceeds to divide by binary fission. This proliferation puts a severe selection pressure for survival on the host. Although subsequent steps of transition from lethality of the intracellular *Daptobacter* to host tolerance has not been traced in the *Chromatium* association, it probably followed a course comparable to that described by Jeon (this volume) for once-lethal bacterial symbionts in *Amoeba*. The development of permanent hereditary association of two heterologous microbial genomes from predation to co-existence offers a means of discontinuous evolution that is more rapid and more well-documented than the speciation by accumulation of favorable single-step mutations usually referred to in evolution textbooks.

Genetic Stability and Evolutionary Change: Mutation and Symbiosis, *Robert H. Haynes*
Intracellular symbiosis was an important source of evolutionary innovation early in the history of eukaryotic cells. Through such genomic alliances, bacterial cells were able to make megaevolutionary jumps in their biochemical versatility and in their ability to survive in increasingly noxious (e.g., aerobic or energy-depleted) environments. These inherited symbioses may be regarded as megamutations. Micromutations at the DNA sequence level and the macromutations associated with recombination, chromosomal rearrangements, transposons and other mobile genetic elements, together with megamutations, collectively provide the material basis of evolutionary innovations. Many mutations arise as a result of inefficiencies in homeostatic processes that normally repair DNA damage and maintain high fidelity DNA replication. Mutations also arise as a result of programmed responses of the genome to many diverse kinds of spontaneous or induced DNA damage as well as to other less specific types of cellular stress. The early development of mechanisms to increase the accuracy of nucleic acid replication and to repair or bypass DNA damage was essential for the evolution of the large genomes that must have been present even in primitive cells. The physicochemical origin of homeostasis is one of the major unsolved problems of precellular evolution.

Current Status of the Theory of the Symbiotic Origin of Undulipodia (Cilia), *Gregory Hinkle*
Undulipodia (cilia), kinetosomes and their related organelles (e.g., centrioles), remain an enigma to those interested in cell evolution and the origin of the eukaryotic state (Wheatley, 1982). Two mutually exclusive theories have been proposed to explain the origin of undulipodia: the direct filiation theory and the symbiotic theory. This paper reviews the status of the symbiotic theory, including information on our continuing search for tubulin-like proteins in prokaryotes (spirochetes) and the implications of the recent discovery of extensive amounts of DNA in the kinetosomes of the unicellular alga *Chlamydomonas reinhardtii*.

Fungal Evolution: Symbiosis and Morphogenesis, *Rosmarie Honegger*
Not in all symbioses between fungi and photo-autotrophic hosts has the symbiotic way of life triggered evolutionary innovation at the morphological level in the fungal partner. The two extremes include: the small, phylogenetically ancient group of vesicular-arbuscular mycorrhizal fungi which have remained morphologically simple while their morphologically complex hosts have diversified ecologically and taxonomically; and the polyphyletic group of lichen-forming fungi, many of which have developed morphologically complex vegetative structures and become taxonomically diverse while their inhabitants, unicellular green algal or cyanobacterial photobionts, have remained simple. Both competition for space in which aposymbiotic photobionts occur and the scarcity of some of these photobionts in many terrestrial ecosystems probably imposed a strong evolutionary pressure on the lichen symbiosis, leading to the formation of three-dimensional thalli in which the photobiont population is harbored and controlled by the mycobiont. Asexual production of symbiotic propagules (isidia, soredia, phyllidia and others collectively called dispores) in a large number of lichen species allows the exploitation of ecological niches in which compatible photobionts are either rare or absent.

Amoeba **and X-Bacteria: Symbiont Acquisition and Possible Species Change,** *Kwang W. Jeon*
A progress report has been presented on the study of symbiosis between amoebae and X-bacteria, in which virulent infective bacteria lost their virulence and became integrated in their hosts, bringing about changes in the host phenotype. While the reasons for the mutual dependence between the amoebae and the Gram-negative rod-shaped intracellular bacteria are not fully known, syntheses of new cell proteins are involved in the host-symbiont interactions. These may be comparable to nuclear-mitochondria and nuclear-chloroplast metabolic interactions. The amoeba-bacteria symbiosis serves as a good model to study the role of symbiosis as a mechanism for cellular changes and speciation.

Fungal Symbioses: Evolutionary Innovations, *Bryce Kendrick*
Fungi having two life forms cyclically differentiate resistant propagules (spores) and trophic forms (cells and mycelia): (1) Spores — microscopic, sealed dispersal units produced and released in enormous numbers are therefore virtually omnipresent; and (2) mycelia — branching, filamentous, exploratory, indefinite, feeding thalli which collectively are virtually omnivorous. These life forms render fungi successful opportunistic colonizers of an enormous range of substrates. They can grow saprobically on substances exuded, secreted or excreted by other contiguous or adjacent organisms. Considering this longstanding intimacy, it is not surprising that such relationships have led to permanent and cyclical trophic symbioses of fungi with plants and animals.

The Symbiotic Phenotype: Origins and Evolution, *Richard Law*
Symbiosis gives a new angle on the old and much debated issue of evolutionary innovation. Symbiotic phenotypes, which come about from the joint expression of genes in associating individuals, have been documented in a wide range of symbioses. The importance of symbiosis as a source of novel phenotypes depends on the following three processes, at least. (1) Chance associations of individuals which have some effect on one another. We may expect such events to be most frequent in abundant species of strongly interactive communities. The prevalence of such communities is a matter of current debate among ecologists. (2) Retention of the incipient symbiotic phenotype during reproduction of the partners. For multicellular organisms this creates a serious hurdle. The hurdle is evidently not insuperable, but the diversity of mechanisms that retain continuity observed in extant symbioses points to a lack of a general solution to the problem of inheritance. (3) Subsequent evolution of the symbiotic phenotype. This depends on evolutionary changes which take place separately in the interacting populations. Although fixation of the symbiotic phenotype can occur, this is by no means guaranteed. These features suggest that symbiosis is less common as a source of evolutionary innovation than change generated within species, although symbiotic phenotypes, when they do occur, can be of great biological importance.

Symbiogenesis and Symbionticism, *Lynn Margulis*
Does the acquisition and integration of symbionts lead to speciation? As a population of animals or plants becomes permanently infected with specific microorganisms, with time, are these animals and plants assignable to new species? Does symbiosis, as a prolonged association of organisms of different species, lead to the origin of higher taxa beyond the species level? Do heritable and cyclical symbiotic associations lead to obvious evolutionary novelty? These are the questions each participant of the Bellagio meeting was asked to address. Each paper makes a contribution to the fundamental problem of the role of symbiosis in the generation of evolutionary innovation. In short, our query, as we enter the last decade of this century, is: What is the status of the concept of "symbiogenesis?", an idea developed in the last decade of the past century.

A Darwinian View of Symbiosis, *John Maynard Smith*
A number of stages in evolution, characterized by the way in which the genetic material is arranged and transmitted, can be recognized: replicating molecules, populations of molecules within compartments, prokaryotic cells, eukaryotic cells, sexual populations, plant and animal organisms, animal societies. The transition between these stages is discussed. Two problems are common to these

transitions. First, how is it that selection among entities at a lower level (e.g., genes within cells, cells within organisms, individuals within societies) does not disrupt integration at the higher level? Second, did the transition come about by the coming together of a set of genetically similar entities which later diverged or by a symbiotic association of genetically dissimilar entities? Possible answers to these questions are discussed.

Luminous Bacterial Symbioses and Adaptive Radiation in Fishes, *Margaret Jean McFall*
Bacterial light organs in vertebrates are restricted to the more recently evolved groups of bony fishes. Further, when such associations do occur, they characterize all of the members of a particular family or genus. These correlations support the idea that within that group the evolution of a symbiosis may represent a key innovation or at least have been one of a suite of characters driving radiation of that group. The present paper examines these ideas, with particular emphasis on the radiation of leiognathid fishes and the role that morphology of the light organ system plays in defining the symbioses of these fishes with their luminous bacterial partners.

Symbiosis in Weevil Evolution, *Paul Nardon* and *Anne-Marie Grenier*
Based on our knowledge of weevils (especially *Sitophilus oryzae* and *S. zeamais*), we are firmly convinced that the principles of neodarwinism should be reassessed. It is impossible to explain adaptation, innovation and complexification by a single mechanism; at the same time, we cannot reject mutagenesis as a source of variation or the concepts of population genetics, particularly the role of selection. It is inconceivable that an endosymbiotic relationship between a bacterium and an insect, such as we observe in *Sitophilus*, could be established in one step. In the case of these weevils the innovations due to symbiosis are considerable, particularly at the metabolic level. We also observe some morphological (color) and behavioral (flight) modifications. The divergence between two sibling species (*Sitophilus oryzae* and *S. zeamais*) could be the consequence of the presence of different symbionts in each species, resulting in nucleocytoplasmic incompatibility and sexual isolation (sterile F1). The *Sitophilus* model has proven particularly interesting for the study of the effects of symbiosis at the cellular, genetic and organismic levels.

Luminous Bacterial Symbiosis with Nematodes, *Kenneth H. Nealson*
Xenorhabdus luminescens are bacteria symbiotic in nematodes of the group *Heterorhabditis bacteriophora*, where they are carried in a non-growing state as gut symbionts of the third-instar infective juvenile (foraging, or non-feeding) stage. The bacterial-nematode symbiosis is actively pathogenic against a large number of different insect hosts. The acquisition of symbiotic bacteria adds several new properties to the nematode pathogenic state, including luminescence, pigmentation, antibiotic production, increased toxicity towards insects and an enhanced ability to complete the worm's life cycle inside the infected insect. The nematode has also undergone some extensive structural and functional alterations, presumably as a result of its involvement with the symbiotic bacteria. The innovations provided to the nematode via symbiosis and the postulated adaptations made in response to the symbiotic acquisition are the topics of this report.

Galls, Flowers, Fruits and Fungi, *Kris A. Pirozynski*
The origin of flowers and fleshy fruits of angiosperms is viewed as successive transformations by gall-making arthropods of preangiospermous reproductive sporophylls and components of angiospermous flowers, respectively, via incorporation of microbial DNA into the plant genome. Flowers, as modified reproductive shoots, incorporate many characteristics of the organoid galls of mites and homopteran insects. Fleshy fruits often resemble the histologically complex galls induced by Diptera and Hymenoptera. Circumstantial evidence indicates that gall-makers can generate novel morphogenetic responses in plants; that the earliest "faithful" pollinating insects were related to gall-makers or ecologically linked with gall symbionts or products; that the radiation of fleshy fruits coincided more closely with that of certain gall insects than with that of flower types; and that frugivorous birds were initially insectivorous and ecologically linked with gall symbionts before they adapted to a — still incomplete — diet of fruit. Considerations of this hypothesis suggests that plants assumed

genetic control of gall morphogenesis and that a gall modification was selectively favored if it improved function of the affected organ or conferred new advantages. Although horizontal gene transfer from galls to plants is hypothesized, the mechanism of such transfer and the source of any exogenous plant DNA remains to be determined. I speculate that gall genetic determinants are derived, by simplification, from microbial gut symbionts, which possibly include tumorigenic fungi.

The Web of Life: Over 3.8 Billion Years of Trophic Relations, *Peter W. Price*
Large organisms such as plants and many animals should be more realistically regarded as microcosms of permanently associated symbionts. In many cases such symbionts evolved from necrotrophic associations, and, therefore, much of the evolution of biotic complexity has resulted from the once-deleterious interactions. Microorganisms inhabited the earth 3 billion years before the metazoa and plants and solved many problems in biosynthesis and biotic interaction. Their capabilities were subsequently utilized by larger organisms simply by close association with microorganisms. The necrotroph-to-symbiotroph transition can be very rapid, as illustrated by the *Amoeba*-bacterium evolutionary pathway. Necrotrophs can facilitate adaptive pathways for hosts either by evolution directly into symbiotrophs or by providing an agent through which a new antagonist can exploit the host. Thus the evolution of life on earth has depended extensively on former pathogens which add biotic complexity to the host's lifestyle. The life of larger organisms is nested inextricably within the opportunities provided by microorganisms, many of which originated as once life-threatening necrotrophs of the larger species. Such associations have resulted in rapid and repeated major adaptive radiations accounting for the majority of species on the earth today.

Symbiogenesis and Evolution: Nephromyces-Bacterial Endosymbiosis in Mogulid Tunicates, *Mary Beth Saffo*
Most models of the evolution of mutualism have been based on consideration of "external" interoorganismic associations such as plant-insect interactions. This focus has led to misleadingly restricted views of the nature and significance of mutualism, which are tested provocatively by considerations of persistent endosymbioses. A tripartite endosymbiosis among molgulid ascidian tunicates, a heterotrophic protist *Nephromyces* and intracellular, Gram-negative bacteria are used as an example to discuss: (1) the impact of endosymbiosis on evolutionary innovation, and (2) the usefulness of cyclically reestablished endosymbioses in suggesting fresh perspectives on the biology of mutualism. Studies of the molgulid-*Nephromyces*-bacterial symbiosis and of other endosymbioses suggest that permanent endosymbioses have significant ecological impact. They further suggest that mutualism is a balanced, complex interaction which can be shifted to a necrotrophic association or to non-interaction in physiological time by changing environmental circumstances. Cyclically reestablished endosymbioses provide experimentally tractable systems for testing theoretical models of mutualism.

Living Together: Symbiosis and Cytoplasmic Inheritance, *Jan Sapp*
Symbiosis as a source of evolutionary innovation has been suggested by various biologists since the first decade of the twentieth century. However, until recently, such views ran counter to the major research programs and doctrines pertaining to heredity and evolution. The lack of attention to symbiosis in heredity and evolution was the result of several issues, including focus on the destructive attributes of bacteria, on competition as a major driving force in evolution, on gene mutation as the principal source of evolutionary novelty and on the chromosomes of the cell. It was not until cytoplasmic DNAs associated with chloroplasts and mitochondria were detected that symbiosis began to be recognized as having evolutionary potential. However, the larger implications of symbiosis for evolutionary change and the mechanisms underlying this process remain largely unaddressed.

Glomaceae, Endocytobiosis and Fungal Evolution: A Lost Opportunity?, *S. Scannerini* and *P. Bonfante-Fasolo*
The Glomaceae, one of the most ancient families of the fungal kingdom, are obligate symbionts and

responsible for vesicular arbuscular mycorrhizae, the most widespread symbiotic associations between fungi and plants. Electron microscopic observations demonstrate that these fungi occasionally harbor both bacteria living in vacuoles and bacteria-like organelles or organisms, the so-called BLOs, which are free in the cytoplasm. This paper provides: (1) a list of VAM fungi and of the host plants in which these two types of endocytobionts have been found; (2) a description of the endocytobionts' cytological features; and (3) speculations on their functional significance. The experimental data are discussed in order to evaluate the role of endocytobiosis in the evolution of the fungal taxon. Moreover, some experimental approaches are suggested with the aim of answering the question of whether symbiosis has been the main innovative factor in evolution in these fungi.

Insect Symbiogenesis as a Model for Speciation, Morphogenesis and Cell Differentiation, *Werner Schwemmler*

Bacteria, animals and plants can be classified into three distinct physicochemical composition groups according to pH, osmotic values and the ratios of inorganic ion concentrations and organic molecule concentrations in their intracellular or extracellular sap. The widespread existence of these types enables a direct comparison between the physieochemical composition of consumers and their food producers. Examples of such relationships are found in the order Hemiptera. Intracellular bacterial symbioses tend to be absent when the insect consumer and feed producer belong to the same physicochemical type. If the insect and its food organism differ in type, extra- or intracellular microbial symbioses usually exist. The conclusion is drawn that endosymbiosis compensates for this difference. The leafhopper species (Cicadina, Homoptera, Hemiptera) proliferate within their ecological niches only through the aid of their endocytobionts (intracellular bacteria-like symbionts). The symbionts are passed on to the next generation via the egg. They move into insect organs (bacteriomes) where they multiply. If the infection of the egg by the endocytobionts is experimentally prevented, normal development ceases; only head-thorax embryos without abdomens develop. Thus, endocytobionts are indispensable in leafhoppers for speciation, morphogenesis and oogenesis (cell differentiation).

The new interdisciplinary research field of endocytobiology is concerned with, among other things, mechanisms of hereditary intracellular symbiosis. The process of evolution was and is driven and controlled by the various mechanisms of biological micro-, meso- and macroevolution. During the emergence of a species, transitions are smooth only in the case of microevolutionary processes (gradualism). The transition from one basic biological type to another — for example, from procytes to eucytes (prokaryotic and eukaryotic cells) — is not a continuous process but occurs in jumps (punctuated equilibrium). Therefore, symbiogenesis must be considered as the generally applicable mechanism for speciation, morphogenesis and cell differentiation in cellular and multicellular evolution. The process of symbiogenesis is ongoing, as can be seen with the example of leafhopper endocytobiosis. Analyses of cases of extant symbiogenesis are a basis for any reconstruction of biological evolution.

Bacterial Evolution without Speciation, *Sorin Sonea*

In nature bacteria and their virus-like plasmids and prophages function only as interchangeable and disposable elements of successful temporary symbioses, all being constituents of the single global bacterial organism. There may be hundreds of plasmids and prophages that can successively visit a bacterial strain. This results in a large variety of endosymbioses. Moreover, most bacteria live in mixed communities of metabolically complementary strains, thereby forming ectosymbioses. As a consequence of such temporary symbioses, which are easily improvised or modified, the bacterial world evolved as an increasingly unified global organism. Its basic elements: cells, plasmids and prophages became extremely diversified and also standardized for easy associations. They function today as specialized construction blocks and not as distinct organisms; they do not form species. Temporary bacterial symbioses also paved the way for the origin of eukaryotes and for many of their major evolutionary steps. By accepting in permanent successive endosymbioses several already easily associable basic bacterial elements (cells, prophages and plasmids) already conditioned for temporary endosymbioses, the eukaryotes'ancestor and its offspring rapidly underwent a radical evolution which resulted in the formation of organisms and of species.

Cell Symbiosis, Adaptation and Evolution: Insect-Bacterial Examples, *Toomas Tiivel*
The membrane system of eukaryotic cells plays a key role in making associations possible between nucleocytoplasm and endocytobionts. Bacterial invaders are surrounded by host-derived membranes as soon as they enter host cells. Endocytobiotic vacuoles form between the casing and the microorganisms, making it possible for both partners to preserve their individualities, control transfer of metabolites in both directions and regulate the multiplication of endocytobionts by selective removal. Adaptation to endocytobiosis is often connected to the acquisition of new genetic material involving specialization and change in both the structure and functions of partners.

Cyanophora paradoxa **Korschikoff and the Origins of Chloroplasts,** *Robert K. Trench*
The Serial Endosymbiosis Theory (SET) on the origins of chloroplasts (Margulis, 1970; 1981) and the various modifications thereof (Taylor, 1974; Gray and Doolittle, 1982) proposes that some chloroplasts originated through polyphyletic associations among various cyanobacteria and the precursors of eukaryotic cells (Raven, 1970). Since chloroplasts are genetically semi-autonomous, relying on nuclear encoded genes, cytoplasmic translation and transport of gene products for their biosynthesis (Ellis, 1982; Bottomly and Bohnery, 1982), a central component of the SET involves the transfer of genes from the incorporated cyanobacteria to the nuclei of their hosts. This gene-transfer process has been documented in *cyanophora* organelles and their kterotrophic nucleocytoplasm.

Symbiosis and the Evolution of Novel Trophic Strategies: Thiotrophic Organisms at Hydrothermal Vents, *Russell D. Vetter*
What is the significance of symbiosis in modern evolutionary theory? Symbiosis is a way of bridging lineages with different metabolic capabilities. It is perhaps the only way to acquire a complex metabolic pathway such as chemoautotrophy once an organism has passed an evolutionary branch point. Prior to 1979 no one expected or predicted the occurrence of thiotrophic animals, i.e., clams, vestiminifera and other animals gaining energy by sulfide oxidation. Today, however, we see that by incorporating a bacterial genome, this mode of nutrition became possible. Aside from the physiological adaptations required by both partners, the evolutionary significance of thiotrophic symbioses is that the organisms now have a new symbiotic phenotype. They are freed from the competitive interactions of their ancestral forms (e.g., competition for food particles) and now compete for entirely different limiting resources (e.g., hydrogen sulfide). Competition among thiotrophic organisms for the sulfide in hydrothermal vent-water and the relative resistance of different species to heat, pressure, sulfide toxicity and hypoxia has driven the evolution of thiotrophic hydrothermal vent organisms in entirely new directions from the ancestral phenotypes. Thus, the acquisition of novel metabolic pathways through symbiosis can even lead to evolutionary innovation at the community and ecosystem level.)

TEL AVIV UNIVERSITY אוניברסיטת תל-אביב
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הפקולטה למדעי החיים
ע"ש ג'ורג' ס. וייס
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The Department of Botany, Tel-Aviv University, receives and evaluates on a continuous basis applications from candidates for Postdoctoral Associate positions available to persons with a doctorate degree and applicable research training and experience. The temporary (1-3 year) research positions emphasize different aspects of plant cell and organismic biology depending on funding sources. Positions may be available in, for example: Plant cell biology, regulation of gene expression during different stages of development and in transformed plants; gene structure and function; introduction of foreign genes in plants; pathogenic and symbiotic plant-microbe interactions; mitochondria and plastid biogenesis; photosynthesis; nitrogen fixation; tissue culture selection; phytopathology; fungal physiology; taxonomy and ecology of higher fungi; pollination ecology; allelopathy; ethnobotany; root biology; ecophysiology; marine botany; function; structure and differentiation of vascular systems.

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