

Doctora Honoris Causa

Lynn Margulis



UAB

Universitat Autònoma de Barcelona

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Discurs llegit
a la cerimònia d'investidura
celebrada a la sala d'actes del Rectorat
el dia 6 de juny
de 2007

UAB

Universitat Autònoma de Barcelona

Editat i imprès
pel Servei de Publicacions
de la Universitat Autònoma de Barcelona
08193 Bellaterra (Barcelona)

Imprès a Catalunya

PRESENTACIÓ
DE
LYNN MARGULIS
PER
ISABEL ESTEVE MARTÍNEZ

Excelentísimo y Magnífico Señor Rector,
Muy honorables autoridades,
Queridos colegas,

Es para a mí una gran satisfacción, tanto en el terreno académico como en el personal, presentar a la profesora Lynn Margulis al Claustro de la Universidad Autónoma de Barcelona para su investidura como doctora *honoris causa*. Ha sido muy difícil expresar en pocas palabras una trayectoria tan intensa, tanto a nivel científico como docente, y que deje a la vez traslucir su generosa personalidad.

La profesora Lynn Margulis se doctoró en el Departamento de Genética de la Universidad de California, Berkeley, en el año 1963, y tal vez esta fecha deba ser considerada el punto de partida de una brillante carrera científica. Durante los años sesenta demostró una extraordinaria capacidad de síntesis al reunir centenares de hipótesis y experimentos dispersos para formular de una manera coherente la teoría de la endosimbiosis para explicar el origen de la célula eucariota. En los años siguientes, viajó incansablemente para defender dicha teoría, actualmente aceptada y que constituye una de las bases más importantes de la moderna biología celular.

Su valiosa aportación a la ciencia puede descubrirse a través de los libros que ha escrito y pueden tomarse como referencia para descubrir esta faceta de su personalidad. La extraordinaria actividad científica que ha desarrollado hasta el momento presente la ha llevado a publicar más de cuarenta y cinco libros, ciento treinta capítulos de libros y un gran número de artículos con importantes contribuciones a la biología celular y a la evolución microbiana. Es imposible relatar, en tan corto espacio de tiempo, su importante labor científica, y es por ello que he intentado seleccionar algunos de sus libros más emblemáticos, escogidos entre los tres grandes temas que, a mi parecer, constituyen el mayor legado de la profesora Margulis: *La teoría de la endosimbiosis*, *La evolución de los primeros microorganismos* y su importante contribución a *La ecología global*.

La teoría de la endosimbiosis propone que la célula eucariota apareció de la evolución de asociaciones microbianas seriadas. Las llamadas «teorías de la simbiosis», expuestas por Portier (1918), Wallin (1927) y Schanderl (1948), habían ido apareciendo muchos años antes de que la profesora Lynn Margulis pudiera interesarse por el tema, sin que tuvieran ningún tipo de apoyo. En su libro *Symbiosis in cell evolution*, publicado en 1980, G. Evelyn Hutchinson mencionaba que, cincuenta años antes, las ideas publicadas en dicho libro habrían sido demasiado fantásticas para ser consideradas, pero la actitud de la comunidad científica sobre la importancia de la simbiosis para explicar el origen de la célula eucariota cambió radicalmente cuando se publicó su libro *The origin of eukaryotic cells* en 1970.

Hoy en día existen pruebas concluyentes a favor de la teoría de que la célula eucariota moderna (con orgánulos) evolucionó en etapas mediante la incorporación estable de las bacterias. Diferentes aportaciones justifican el origen de los cloroplastos y de las mitocondrias a partir de éstas, pero la profesora Lynn Margulis ha investigado, además, el posible origen de los flagelos de las células eucariotas (undulipodios) a partir de las espiroquetas.

Por otra parte, el interés que siempre ha mostrado para dar una visión global de la evolución de la vida en nuestro planeta la motivó para trabajar en uno de sus libros más reconocidos, *Early life*, traducido y publicado en lengua castellana por la editorial Reverté en 1986. Sobre este libro la autora escribiría: «Durante la mayor parte de la historia de la vida en nuestro planeta, el paisaje viviente semejó una desolada y remota playa en la que la mirada no pudiera descubrir ni rastro de animales o plantas. Solamente algunas manchas de color en los lodazales o las charcas costeras, algún bulto informe sobre las playas o los pantanos, darían algún indicio de los poco llamativos habitantes que pululaban por aquellos mares ancestrales».

El libro es una reconstrucción didáctica de la vida en sus comienzos, nada menos que en sus primeros tres mil millones de años, mucho antes de que hiciera aparición el más simple de todos los animales y de las plantas. Es un estudio de la historia ambiental de nuestro planeta desde los tiempos prebióticos hasta el presente, en el que la autora se pregunta por qué se tardó tres mil millones de años en evolucionar desde la célula más sencilla hasta el organismo multicelular más evolucionado. En definitiva, trata de la historia de este prolongado intervalo en la evolución que se produjo en el profanerozoico, un relato sobre las primeras células.

Quizás, uno de los aspectos más interesantes de este trabajo es que el escenario de la evolución es el ambiente de la Tierra, que puso en movimiento los procesos evolutivos y que fue después transformado por tales procesos a medida que las formas vivientes iban cambiando.

Siguiendo esta línea y considerando la idea de que la vida no podía seguir siendo tratada como un proceso separado del resto del cosmos, la profesora Lynn Margulis escribió el libro *Evolución ambiental*. En él se relatan las aportaciones de importantes científicos, como Michael McElroy, Antonio Lazcano y James E. Lovelock, entre otros, y las de la propia Lynn Margulis, que menciona las espiroquetas como posible origen del undulipodio (el flagelo de las células eucariotas).

Especialmente interesante ha sido la intensa colaboración que ha mantenido con el científico James Lovelock, autor de la hipótesis Gaia, que considera la Tierra un superorganismo capaz de autorregularse y que regula su superficie de modo muy diferente a como lo haría un planeta similar en tamaño y posición relativa respecto al sol, pero carente de vida.

El intenso trabajo documental y experimental realizado por la profesora Lynn Margulis ha quedado también reflejado en otros de sus libros, como *Symbiotic planet: A new look at evolution* (1998) y *Acquiring genomes: A theory of the origins of species* (2002), coescrito con Dorion Sagan. Además de éstos, son muy conocidos a nivel divulgativo: *What is sex?* (1997), *What is life?* (1995), *Mystery dance: On the evolution of human sexuality* (1991), *Microcosmos: Four billion years of evolution from our microbial ancestors* (1986) y *Origins of sex: Three billion years of genetic recombination* (1986).

Su trabajo con Karlene V. Schwartz nos ha proporcionado repetidas ediciones del libro *Five kingdoms: An illustrated guide to the phyla of life on Earth* (1998), en el que pretendía mostrar la diversidad de los microorganismos, no sólo bajo un punto de vista taxonómico, sino también evolutivo.

Además de bióloga, la profesora Lynn Margulis es también una excelente microbióloga. Su profundo conocimiento del mundo de los protistas motivó que fuese la editora del libro *Handbook of protoctista*, considerado de referencia para el estudio de estos microorganismos.

Paralelamente a su intensa labor científica, ha desarrollado también una importante actividad docente, no sólo en la Universidad de Boston y últimamente en la de Massachusetts, Amherst, sino también como profesora visitante de diferentes universidades de todo el mundo, entre ellas la Universidad Autónoma de Barcelona (1985-1986). El resultado es un importante legado audiovisual que ha preparado con diferentes colaboradores y que ha dado lugar a diferentes vídeos, CD-ROM y series de diapositivas. Algunos ejemplos son: *Five kingdoms of life* (1982), *The Gaia Hypothesis* (1985), *Plant-cyanobacterial symbioses* (2001) y *Eukaryosis: Origin of eukaryotic cells* (2003).

Como resultado de todo lo expuesto, la profesora Lynn Margulis ha sido requerida en distintas ocasiones para formar parte de diferentes comités internacionales y ha recibido numerosos premios y distinciones, como el grado de doctora *honoris causa* en trece universidades, tres de ellas españolas.

Finalmente, me gustaría hacer constar la vinculación de la profesora Lynn Margulis con la Universidad Autónoma de Barcelona y en especial con el Grupo de Microbiología Ambiental de la Unidad de Microbiología de la UAB. Esta relación se inició siendo el profesor Ricard Guerrero director del entonces Departamento de Microbiología y se ha mantenido hasta el momento actual. La profesora Margulis ha colaborado en las líneas de investigación desarrolladas por el mencionado grupo, analizando la diversidad de la laguna de Cisó (en el sistema cárstico de Banyoles, Girona) y la de los tapetes microbianos del delta del Ebro (Tarragona). En el primer periodo, cuando disfrutaba de un año sabático en la UAB, y posteriormente, realizando numerosas visitas tanto a la citada universidad como al delta del Ebro para estudiar los tapetes microbianos. Estos interesantes ecosistemas han sido considerados réplicas vivas de las rocas más antiguas de la tierra, los estromatolitos, rocas organo-sedimentarias que han permitido datar en 3.500 millones de años la aparición de la vida en nuestro planeta gracias a contener microorganismos fosilizados. Los microorganismos actuales, que viven en estas condiciones, deben soportar cambios muy bruscos en los parámetros ambientales, lo que ha motivado que el estudio de los tapetes microbianos sea, además, un hábitat de referencia para estudiar la vida en condiciones ambientales extremas.

Aunque la profesora Lynn Margulis ha realizado la mayor parte de estos estudios en la laguna Figueroa (Baja California, México), se ha interesado por los tapetes microbianos distribuidos por todo el mundo y, entre ellos, como he mencionado anteriormente, los del delta del Ebro. Como resultado de esta investigación, ha publicado conjuntamente con nuestro grupo diferentes artículos y también ha participado como profesora invitada en importantes congresos internacionales organizados por miembros de la UAB.

Son, por tanto, muchos sus méritos para que le sea concedido el doctorado *honoris causa*, pero me gustaría resaltar algunos de ellos. El primero es el esfuerzo extraordinario realizado a lo largo de toda su vida en favor de la ciencia y la divulgación científica. El segundo, y para mí tanto o más importante, es su capacidad para entusiasmarse y entusiasmar a sus colegas en cualquiera de los temas en los que ha trabajado en su dilatada carrera científica. Finalmente, quiero destacar su gran calidad humana y su generosidad, demostrada por su fácil disposición a colaborar e incluso a acoger en su laboratorio y en su propia casa a todos sus colegas, a los que considera amigos.

Por todo lo expuesto, Excelentísimo y Magnífico Rector, solicito que se otorgue el grado de doctora *honoris causa* a la profesora Lynn Margulis.

DISCURS
DE
LYNN MARGULIS

Evolution, from a Gaian perspective

What is «evolution»? What is the «evolutionary theory»? If evolutionary theory is a universal law, like the law of gravity or the periodic table of chemical elements, and it stems from accepted scientific knowledge, why is its teaching controversial? No rigorous and logical scientist appreciative of hard-earned data from nature disagrees about evolution's incontrovertible core. Then, why are so many who celebrate science as a most effective way of knowing about the world confused by lack of scientific unanimity? None doubts that gravity is the force that accelerates falling bodies, nor are statistics required to predict the explosive gas behavior when oxygen and hydrogen are sparked in a closed volume to form water! Then, why is not everyone convinced that «evolution is a *fact*, not just a theory»? When biologists will feel evolution of life from past life is as well established as gravity or the explosive chemical reaction of H₂ and O₂? Professionals in geology, biology and especially biochemistry concur: evolutionary phenomena proffer crucial organizing principles. So what is the problem? Evolutionary biologists act certain that they know *how* new life forms originate and complexify. And the answer is, as Charles Darwin cleverly pointed out, «natural selection».

Evolution is not a single fact; it depends on four observable processes. First, life requires the incessant flow of energy and matter to survive. Second, a species-specific biotic potential, a measurable quantity, is assignable: the number of offspring that, in principle, can be produced per generation. A human female has the potential to have 20 to 25 children. A single *Escherichia coli* cell that doubles in 20 minutes potentially reaches a population size the weight of the Earth in less than a week! Third, as Malthus indicated, all populations grow at rates more rapid than their immediate environment sustains. What Darwin called natural selection is simply this fact of elimination: Never do 100 percent of the offspring survive to reproduce 100 percent. Finally, offspring are not identical to their parent(s); observable inherited (genetic) change is easily measured.

From these facts Darwin correctly inferred that life «descended with modification» from common ancestors. Overwhelming evidence for this fact (and none against) comes from, e.g., animal behavior, biochemistry, comparative anatomy, ecology, genetics, geochronology, microbiology, physiology, paleobotany, sedimentary geology, virology and zoology, amplifying Darwin's insight.

The living world's highest taxa: prokaryotes and eukarya

More than 30 million kinds of life, placed unambiguously into five huge groups (bacteria, prototists— including 50 phyla of ciliates, diatoms, red and brown seaweeds, slime molds, water molds—, fungi, animals and plants) evolved during the past 3500 million years from our small common ancestors: bacteria. Study of long-chain molecules such as chitin, DNA, lignin, protein, yields spectacular evidence for the shared ancestry of all living matter. Watery cell metabolism (chemical transformation by salt balance, synthesis of proteins and other metabolites always bounded by cell membranes) is incessant whether in aardvark or zoogloea.

Nature, with her prodigious diversity of life, reveals herself unlabeled. When generated (born, hatched, budded, laid, germinated or otherwise produced), a being like an infant lacks a name, bar code or other identifier. In the tropics, where life's maximal abundance is, the young offspring (seedling, hatchling, larva, zoospore, myxocyst, swarmer or germling) remains unrecognized and nameless unless scientifically described.

Estimates vary from 3 million to 100 million for the number of extant species, yet fewer than 2 million species of plants, fungi, animals, prototists and bacteria enjoy Latin binomial descriptions: Genus and species. We, *Homo sapiens*, have named the life around us: the garden pea, *Pisum sativum*; the black bread mold, *Rhizopus niger*; the mosquito-transmitted prototist of malaria, *Plasmodium vivax*, known to have a remnant chloroplast; the colon bacterium *Escherichia coli*. Carl von Linné (a convinced fixist: «Species totae sunt sicut Deus creavit») classified all his nearly 10,000 species in either of two kingdoms: Plantae and Animalia. Fewer than 250,000 fossils (most are «large microbes», gorgeous prototists: foraminifera, radiolaria, coccolithophores or diatoms) are named in the paleontological literature.

The Russian–American *Drosophila* geneticist Theodosius Dobzhansky titled one of his papers as «Nothing in biology makes sense except in the light of evolution». I paraphrase him by suggesting that today nothing in molecular biology makes sense except in the light of the evolutionary history of organisms in specific paleoenvironments. As Darwin noted, our classification systems should become genealogies. If our taxa classify, identify and name life accurately, our grouping will

reflect evolution; this is possible because strong inferences concerning the past are embodied in the living. The contribution to evolution of microbiology (*sensu lato*, the study of both bacteria and their protist descendants) has only recently begun to be appreciated. The cells of microbes are the units of life, hence the recognition of their importance in their own evolution; furthermore, the evolution of larger life forms is bound to the basic mechanisms of microbial evolution, metabolism and genetics.

The living world unambiguously is divided into two definitive never-overlapping categories: prokaryotes and eukaryotes. In spite of the immensely useful «three-domain» 16S rRNA classification scheme proposed by Carl Woese, only two fundamentally different kinds of life exist on Earth. No evidence from either the fossil record or the living world can be mustered for any «progenote» or other deviation from the prokaryote–eukaryote rule. This prokaryote–eukaryote divide remains the largest discontinuity in the living world. First recognized by Eduard Chatton and first analysed by the Delft School of microbiology (e.g., Albert J. Kluyver, Cornelis B. van Niel and Roger Y. Stanier) the list of differences between *Archaeobacteria*, *Eubacteria* and *Eukarya* unequivocally shows that the two prokaryote groups are far more closely related to each other than each of them is to any eukaryote. The cell, whether bacterial or mitotic (nucleated) is the unit of life.

The Serial Endosymbiotic Theory

No system of matter and energy flow less complex than a cell is alive. The presence of the nucleus is the only feature that uniquely defines the eukaryotes and distinguishes them from bacteria. The origin of the bacterial cell is the origin of life itself, whereas Serial Endosymbiotic Theory (SET) describes the subsequent origin of the nucleated cell by symbiogenesis. To proceed we need to explain how the ecological concept of «symbiosis» differs from the evolutionary term «symbiogenesis». Symbiosis refers to the living together of organisms of different species. Endosymbiosis, a topological condition, is a kind of symbiosis where one partner lives inside of another. Symbioses usually, if not always, have environmentally contingent outcomes. Symbiosis, not an evolutionary process *per se*, refers to physiological, temporal or topological associations with environmentally determined fates. Symbiogenesis, however, implies the appearance of new tissues, new organs, physiologies or other new features that result from protracted symbiotic association.

Two great classes of eukaryotic cell organelles, plastids and mitochondria, evolved symbiogenetically. Oxygen-respiring, heterotrophic α -proteobacteria were probably phagocytosed by anaerobic motile protists (like today's mastigamoebae). Genetic and metabolic redundancies were selected against as once free-living eubacteria evolved into the organelles we recognize as mitochondria. The descendants

of this merger include most heterotrophic protists such as most amoeba, cryptomonads, chilomonads and chytrids, oomycetes (like *Phytophthora infestans*, the potato blight organism). No doubt some motile protists ingested, but failed to digest, food — cyanobacterial cells— that eventually became symbionts. The retention of undigested cyanobacteria in well-lit waters led to permanent unions in which, once again, natural selection favored the reduction of genetic and metabolic redundancy. In this way algae, eukaryotic organisms that bear photosynthetic organelles in their cytoplasm, evolved and some became, eventually, the ancestors to the land plants. The *Apicomplexa* (a phylum which the malarial agent *Plasmodium* is assigned) apparently evolved from one lineage of such algae. The members of this phylum, including *Toxoplasma*, have retained a residuum plastid with its DNA, but they are no longer capable of photosynthesis. The principle of «use it or lose it» can be invoked. Natural selection does not plan ahead; the unused plastids that began as cyanobacteria were severely reduced as they evolved. The striking resemblance and genome's homology of some free-living bacteria (such as cyanobacteria) to certain intracellular organelles (such as green algal chloroplasts) bolsters the concept that certain bacteria have been trapped inside other cells for million of years.

With respect to the acquisition of mitochondria from free-living α -proteobacteria and that of plastids from free-living cyanobacteria, no one any longer doubts that the oxygen respiratory and photosynthesizing organelles evolved by symbiogenesis. Modern symbioses, both intra- and extracellular, that can be subjected to experimental analysis are of extraordinary importance for understanding evolution. How cells merge and how redundancy is reduced is especially relevant to the appearance of the first eukaryotes (which, by definition, were the first protists). Ironically, although most disease conditions are variations on the general theme of cyclical symbioses, few protistologists and microbiologists are familiar with the insightful, burgeoning literature that analyses these nearly ubiquitous associations. The study of genomics and proteomics will confirm or falsify this historical reconstruction that was made primarily based on observations of live organisms. Organismic biology coupled with direct knowledge of the fossil record are indispensable to evolutionary reconstruction. The techniques of molecular biology and sequence analysis by themselves are inadequate to the creation of testable evolutionary hypotheses.

Complex individuality and the evolution of the tethered nucleus

How did the distinctive nucleus evolve? What was the first eukaryote? In the past decade, since the publication of the second edition of my book *Symbiosis in Cell Evolution*, I have further developed the SET. New sets of data from three sources have permitted to make good progress toward understanding the crucial step of the origin of the nucleus. I reconstruct the transition from the earliest prokaryotic

(bacterial level of organization) during the Archean Eon (3500–2500 million years ago) to the complex individuality of the first eukaryotes. The Proterozoic Eon (2500–541 million years ago) was the backdrop for the appearance of cells at the protist level of organization. All eukaryotes, in the SET, are products of symbiogenesis whereas no prokaryote cell evolved by merger of whole-cell predecessors.

My hypothesis is that sulfur syntrophy united thermoplasmic archaeobacteria (such as *Thermoplasma acidophilum*) with motile *Spirochaeta*-like eubacteria in the evolution of the karyomastigont organellar system of swimming protists. The first eukaryotes were composed of at least two integrated bacterial genomes with a tethered nucleus (nuclear connector or rhizoplast, kinetosome-axoneme). This organellar system called the «karyomastigont» has been known to protozoologists since it was first described by C. Janicki in the 1930s. I interpret this organellar system (the karyomastigont of the so-called flagellates, which should be called mastigotes, zoospores of water molds and slime molds, many motile algal cells, etc.) as a legacy of that first genomic integration of these bacteria. The evolution of mitosis with its histone-coated, nucleosome-studded chromatin occurred under anoxic, acidic, organic-rich conditions prior to the symbiotic acquisition of oxygen-respiring α -proteobacteria that became the mitochondria. New biochemical data on the role of sulfur oxidation and reduction in nucleated cells and on free-living sulfur consortia, as well as geological information on the prevailing conditions of aquatic environments during the Proterozoic Eon make my evolutionary scenario plausible.

The karyomastigont concept of mastigont multiplicity was brilliantly developed by Harold Kirby, who was chair of the Zoology department of the University of California, Berkeley, when he died in 1952. It refers to the organellar system known to be present, although often inconspicuous in many kinds of nucleated cells. By definition, the karyomastigont has at least these three components: the nucleus, the nuclear connector and the kinetosome/centriole-axonemes. (In certain protists other components of the karyomastigont organellar system are routinely present, such as axostyles, peltas and Golgi apparatus, the latter known as the parabasal body.) We argue that the earliest nucleus was in the form of the minimal karyomastigont and that this organellar system was a response to selection pressure. The nucleus with the combined genomes of at least two different prokaryotes evolved to assure genetic continuity of the now integrated archae- and eubacterial symbionts. The nucleus itself began in the karyomastigont as the integrated symbionts, in an act homologous to conjugation between very different bacteria, fused to form the first eukaryote. The untethering of the nucleus in many lineages led to the free nuclei. Free nuclei seen today in animals, plants and fungi we interpret as the derived state. Tethered nuclei evolved simultaneously with the first protist. No missing links need to be hypothesized. Certain amitochondriate eukaryotes always were confined to anoxic environments and never had mitochondria. The nucleus, in this scenario preceded both the

mitochondria and the plastids. Indeed, in the bowels of xylophagous insects (wood-ingesting roaches and termites) and in anoxic mud all «intermediate stages» that we envision as steps in the origin of nucleated cells are still found today.

Evolution, 150 years after Darwin

Charles Darwin's landmark book *The Origin of Species*, which presented to scientists and the lay public alike overwhelming evidence for the theory of natural selection, ironically never explained where new species come from. He ultimately established a major idea entirely valid in our day. All species of life descended from related predecessors. All life, whether or not made by a deity in the very beginning, is connected back through time to preexisting, proximally similar life forms. Today, with our better understanding of cosmic evolution and the chemistry of life's origins, any requirement for a deity can be pushed back still further, to the mysterious origins of the cosmos in the Big Bang.

Darwin showed clearly how living things «beget» descendants that, inevitably, differ slightly from their parents. The survivors must have traits that are more conducive to survival in that particular environment than offspring that did not survive. Darwin gave this process of differential survival and reproduction the name «natural selection». Darwin conceded that the naturally selective process, by itself, did not seem to create novelty; rather, from the vast store variants, differing organisms in nature, it only eliminated offspring that already existed by their failure to reproduce.

The intrinsic limitation of Darwinian literature was analyzed in 1999 by Douglas Caldwell, who began with Darwin's 1859 book itself. The terms used by Darwin and the number of times those terms appear include: «beat(s)», 17; «death (dying)», 16; «destroy (destroyed, destruction)», 77; «exterminate (extermination)», 58; «individual», 298; «kill (killed, killing)», 21; «perfect (perfection)», 274; «race (races)», 132; «select (selects, selection)», 540; «species», 1803. By contrast, the following terms are absent from *The Origin of Species*: association, affiliation, cooperate, cooperation, collaborate, collaboration, community, intervention, symbiosis. One hundred fifty years later, the habit of ignoring metabolic and physical associations between organisms persists. Rather the important transmitted variation that leads to evolutionary novelty comes from the acquisition of genomes. Entire sets of genes, indeed whole organisms each with its own genome, are acquired and incorporated by others. The most common route of genome acquisition, furthermore, is by the process known as symbiogenesis. Symbiosis is simply the living together of organisms that are different from each other. When originally defined by Heinrich Anton de Bary (1831-1888), symbiosis was the living together of «differently named organisms». Symbiosis are long-term physical associations. Different types

of organisms may associate and fuse to make a third kind of organism. The fusion is not random. Symbiotic relationships occur under specific environmental conditions. Long-term stable symbiosis that leads to evolutionary change is called «symbiogenesis». These mergers, long-term biological fusions that begin as symbiosis, are the engine of species evolution. A very specific example of symbiogenesis in live organisms illustrate the point, the actual «plant-animal» hybrids. Slugs, the shell-less mollusks that eat your garden plants, have entirely green photosynthetic relatives.

The minimal unit of life

The minimal unit of life is the cell. All microbes are composed of cells. All microbes are composed of cells. They can all be unambiguously classified either as bacteria (without nuclei) or protists or fungi (both of these groups are composed of cells with nuclei). The smallest and least complex free-living cells, those of some bacteria such as *Mycoplasma genitalium*, contain approximately 500 genes. Most bacterial cells contain between 2000 and 5000 genes. Some larger complex bacteria have nearly 10,000 genes. These bacteria therefore approach the numbers of genes typically found in the cells of nucleated organisms.

Life began probably more than 3800 million years ago. The detailed record of evolution, preserved in rocks both as fossils and as short- and long-chain extractable carbon compounds, overwhelms those who study it. Cellular life reflects its evolutionary history. Yet in spite of the diversity of clues by which the evolution of life is reconstructable, most self-described evolutionary biologists disregard cell biology, microbiology, and even the geological record. Many are so preoccupied with land-dwelling animals that they continue to believe that no record of evolution exists prior to that of that last 541 million years.

The formation and diversification of any new species is the outward manifestation of the action of subvisible forms of life: the smaller microbes, bacteria, their larger descendants, the larger microbes, protists and fungi, along with their intracellular legacies, organelles such as mitochondria and centrosomes. Evolution emerges from the fact that these small living organisms and their progeny tend to outgrow their bounds. The unseen beings that decimate our populations with virulent disease and provide soil nitrogen to our food plants play the major creative role in the genesis of the new species. The earliest life on Earth consisted of prokaryotic cells. Organisms made of eukaryotic cells did not appear on the scene until much later. Precisely when this evolutionary innovation took place has been the subject of much debate. Eukaryotic cells may be more than 2000 million years old, but they cannot be fewer than 600 million years old; by that time, marine animals and other large organisms dwelled along many seashores. The sequence of events that link

prokaryotic ancestors with their eukaryotic descendants is the subject of wide discussion, and different hypothesis, the subject of many laboratory investigations, have been put forward. The theory I favor is that at least three classes of organelles of eukaryotic cells originated by symbiosis.

Communication

Communication among the biota, the sum of life on Earth, in the entire biosphere, the place where life exists, is typified in millions of life forms. Communication at many levels has been widespread nearly since the origins of life itself. Enhancement of communication was made possible by the evolution of bacteria some of whom detect the Earth's magnetic field and its gravity. Bacterial population and community interactions greatly affected the oceans, lakes and rivers. Indeed bacteria were the first to change the regolith of planet Earth to soil. These denizens of the world in the Archean eon were followed by their consortial legacy: the eukaryotic microorganisms: protists. Some protist bodies (e.g., *Erythrodrinum*) are modified as eyes, others extend long tentacles (*Tokophrya* or modify them as fishing rods (*Acineta rara*). Other protists, single cells such as agglutinating foraminifera (an allogromid) capture, torture and feed on animals such a crustaceans. Communication between members of different taxa involves interactions at the population, community and other levels e.g., communities and ecosystems.

Even in the microcosm live-birth (viviparous) and desiccation-hardy propagules (spores, cysts, conidia) that evolved in ponds, lakes, soils insure communication through the hydrosphere and atmospheric. These microbial innovations insured communication at all levels at the Earth's surface from the beginning of the Archean Eon until the present. Chemical communication between trees and whale sonar systems and, more recently by people who talk, read and write electronically have augmented the non-stop tendency of life to reach out to communicate with other life forms. Communication modes that began in crowded bacterial communities have been in place and have expanded over the last 3500 million years.

Gaia and its humans

Derived simultaneously from the lively scientific imagination of James E. Lovelock and findings of international space exploration, the Gaia idea recognizes an ancient planet-wide physiological control system at the Earth's surface. Temperature, atmospheric gas composition, acidity-alkalinity, oceanic salt concentration, etc. are among factors that are regulated by the metabolism, growth, interaction, extinction and other machinations of life. Knowledge of the Gaia theory and its

implications has expanded. In an attempt to unite scientific research at all levels towards an understanding of our living planet, a new discipline, in essence, a Gaian program of research has emerged. To be acceptable to academics and grant-giving organizations this research program is usually called Earth System Sciences (ESS). The four-letter word «Gaia», however, is still often rejected by polite scientific society.

Although Gaia concepts are consistent with those of Darwinian (not necessarily neo-Darwinian) evolution, Gaian ideas recognize that evolution only occurs in an environmental context. For this reason we can recognize that machines and human technology are increasingly part of a global interliving system. The environment must fit the organisms as much as the organisms fit the environment, as Ian McHarg (1926-1996, author of *Design with Nature* and many other works) insisted. Indeed, in that book McHarg cited Soviet experiments with closed ecosystems that showed that the more kinds of living components a system included, the more effective it was at recycling its waste. Bacteria alone can recycle, for example, but if fungi are added to the closed ecosystem it functions more rapidly and efficiently. The addition of plants and animals further reinforces an ecosystem's purifying abilities. Because the larger components (e.g., plants and animals) were later to evolve, it stands to reason that human-fostered technology—the most recent form of «living organization» to evolve—may at some date in the future be integrated into still more adept ecosystems. The Gaian point with regard to machines is that, just because they are new, does not mean that they are «not natural». Whatever an ecosystem's make-up, energy, carbon and water must «creatively fit» the growth of its organisms and populations for it to persist as a whole and remains a going concern.

Human beings and technology are intrinsic to activities of the biosphere. The biosphere, the place where life resides extends ~20 km high at the Earth's surface, some 8 km to the tops of mountains and 12 km to the ocean's abyss. The biosphere encompasses uncounted numbers of life forms, including many not even documented by science. These all simultaneously indulge in various and usually unsupportable rapid rates of growth, necessarily matched by equally immense death rates; the masses of life forms trading materials and energy are experts in photosynthetic and chemosynthetic food production, and the intricacies of food sharing. For any one organism, independence from the biosphere, as Russian scientist Vladimir I. Vernadsky (1862-1945) noted, is precisely equivalent to death. Real life, therefore, more than our everyday abstractions care to reveal to us, is a matter of integrated wholes, not humanity as a lone cowboy roughing it out against the cosmic backdrop of divine space.

Lovelock's Gaia theory explains the tendency of the Earth's lower atmosphere to maintain its temperature, oxygen concentration, and alkalinity within rather narrow limits for million of years. The self maintaining properties of cells, organisms,

communities, and ecosystems are observable not only in the atmosphere but also in the surface sediments (soil, rocks) of planet Earth. Although the Gaian regulatory system was originally focused on the «gestalt» networking of members of more than 30 million extant species, increasingly the surmise arises that its operations extend to the inclusion not only of life forms but of machines.

Although not in of themselves alive, machines, like viruses, foraminiferan shells and beehives, can be seen to reproduce and evolve. We make and manufacture them, of course, yet increasingly machines become embedded in our systems of reproduction. Similar relationships have arisen before. Many flowering plants for example require animals to pollinate and disperse them—although they, like us and our machines, are technically biologically separate. The more we consider the role of communications and technological infrastructure in our survival at present numbers, the more apparent it becomes that we are no longer simply a mammal but more, as the 19th century painter and evolutionist Samuel Butler put it, a «machinate» life form.

A new look at life

The planetary worldview has been in part inspired by Lovelock's groundbreaking *Gaia. A New Look at Life on Earth*, as well as his biography, *Homage to Gaia* and its recent *The Revenge of Gaia*. An independent atmospheric chemist and biological theorist, Lovelock has been aided by chemical oceanographer M. Whitfield of the Marine Biological Association (Plymouth, UK). The original Gaia theory has been restated and extended: the composition of the reactive gases, the oxidation state, the acidity and the temperature of the lower atmosphere and surface sediments of the planet Earth are dynamically regulated by the activities of differentially reproducing interrelated organisms. The organisms in nature are always organized into communities: members of different species in communication with each other that live at the same time in the same place.

A whole Gaia style of thought is emerging in which perception is seen as a participatory phenomenon. Scientists and others who participate in the «Whole Earth approach» insist that humans become more aware that we are a factor in the sum of all organisms of the biosphere. Nonetheless, entrenched Judeo-Christian beliefs are still widely held by the rampant energy-consuming peoples of Western Europe and northern North America. The monotheistic concept that identifies the paternal family control with nationhood was an inculcating «meme» that began with modern written history. Those partaking of this meme or its variations often feel no responsibility for actions that were vindicated by a father-like power. This corporate or super-organismic lack of accountability occurred despite the fact that at certain junctures in history (e.g., during the Reformation) the same monotheistic deity was

invoked by opposed warring sides. As Stephen Jay Gould has suggested, perhaps it is the division of our brain into two hemispheres that makes us have such a grand, and ultimately insupportable, tendency toward dichotomization.

Even cosmopolitan thinkers who reject tribalism do not necessarily extend their view to a condemnation of anthropocentrism. Most still believe that we humans are the highest of all the animal species. Even more people think that we are not animals at all. Just as the Bible regards Jews as the chosen people the idea that people are superior to all other life forms is still taken as self-evident. Such traditional human ideas contrast with a Gaian perception of people inextricably, subordinately, linked to the supportive rest of the Earth's biota. Despite our self-focus on them, humans are objectively only a fractional and dispensable entity within an immensely complex system of plant, animal and microbial life. This Gaian system was here before we, courtesy of evolution, arrived; and it will be here after we (and our increasingly unrecognizable descendants) are gone.

The Gaian thought style represents in part a return to older ways of seeing and relating to nature. At the same time, its incorporation of modern science makes it more forward-thinking and accurate than many traditional views of humanity and our (central) place. (Much of the new scientific literature on Gaia can be found in a wonderful compendium called *Scientists Debate Gaia: A New Century*, MIT Press, 2004.)

Like life itself, these «old» and «new» thought styles are not dichotomous but arise from the same organically interconnected biosphere. Yet the prevailing thought styles have an undeniable advantage of momentum. All the weight of Western history and much reproductive success —so far!— attach to political groups that subscribe to the idea of man's domination of nature. Gaian, however, extends «horizontally» to other organisms and «vertically» beyond human history. In it, human beings and technology are intrinsic to activities of the biosphere. These all simultaneously indulge in various and often unsupportably rapid rates of growth, necessarily matched by equally immense death rates; the masses of life forms trading materials and energy are experts in photosynthetic and chemosynthetic food production, and the intricacies of food sharing. For any one organism, independence from the biosphere, as Russian scientist Vladimir I. Vernadsky (1862-1945) noted, is precisely equivalent to death. Real life is, therefore, more than our everyday abstractions care to reveal to us, a matter of integrated wholes, not humanity as a lone cowboy roughing it out against the cosmic backdrop of divine space.

What we humans reject as «spoiled food», for example, is healthy growth medium from the point of view of the dense populations of bacteria, yeast and other fungi that colonize our bread and meat. Though «waste» to us, the dung of cattle is both food

and shelter to the dancing *Pilabalus* mold and to dung beetle larvae. Uneaten cheesy crusts stuffed down a kitchen sink garbage disposal are not «wasted»; they become the source of nourishment for vast populations of bacteria, ciliates, mastigotes, germinating fungal spores, and other life forms ignored or systematically murdered by humans. These processes are not foreign; indeed an electric garbage disposal is but one of Gaia's many more recent forms of energy use and waste recycling.

The consortial quality of the individual also contradicts any notion of independence. What appears to be a single wood-eating termite consists, upon microscopic observation, of many millions of bacteria and protist microbes only a few kinds of which actually digest the cellulose of wood. The termite intestine by itself is devoid of ability to digest wood. Gaia is a consortial entity comparable to a single wood-ingesting termite, but of course she is far more complex. Consortia, associations, partnerships, symbioses, and competitive interactions between organisms extend to the global scale. Living and nonliving matter, self and environment are inextricably interconnected. The truth is that we are deeply conjoined to other organisms. No amount of political will alters this survival-friendly fact. Yet we tend to be barely conscious of our activities in their Gaian contexts. Wars, for example, accelerate at a specific time and place the inevitable natural selection of the recent primate *Homo sapiens*, preferentially destroying young males prior to their optimum reproductive period. Medical treatment tends to preserve many members of the population who, without it, would fail to reproduce.

Ironically money is thrown at environmental problems in isolated attempts to buy easy solutions. Yet Gaia «her»self has not been seen as an entity worthy of scientific study. Research on the detection of biospheric regulatory phenomena is not directly funded. Because Gaia research does not fit neatly into single academic fields or budget categories such as meteorology, biology, geochemistry, or wildlife management, biogeological research at a planetary level remains understaffed and underfunded.

An argument can be made that Gaian science is neither properly a subfield of biology nor of ecology. Study of Gaia, the evolution of the environment replete with its interactive life forms and their changes over four billion years, is far broader than any academic discipline. Many specialties, minimally paleontology, geochemistry, microbiology, atmospheric chemistry, and botany are needed for Gaian science. As the scientific investigation of the system which supports us and any civilization we are lucky enough to leave behind, Gaian studies are really more vital and relevant than many other funded sciences; they should be widely encouraged. If our country is often not on speaking terms awareness of our absolute dependence upon non-human life, it is extremely valuable in battling prevailing, unexamined, and ultimately selfishly self-destructive ideologies such as: «nature is pristine and should be preserved», or «nature is a bunch of resources to be plundered».

Responses of the press and the reading public to Gaian processes have been arbitrary and oriented toward crisis. The distorted biased «hot topics» include an increase in atmospheric carbon dioxide, water pollution, acid rain, and the ozone hole. By waiting to respond until the social crises are upon us, we run the risk of violent positive feedback processes, increased natural catastrophes and cultural disintegration. Lovelock, for example, suggests that increased storms can be expected in the wake of anthropogenic activities. Of course, and not to be too dichotomous, increased Gaian consciousness can have the opposite effect.

Gaia continuity

How does Gaia function? By sensing the galactic, solar system and planetary cycles and responding to them. All life forms react to changes in the environment. As alterations of the properties of the biosphere occur, usually via celestial and terrestrial cycles, life responds. Many, but certainly not most of the responses are conscious. Since the first anaerobic fermenters succumbed to or avoided oxygen and the first spirochetes wriggled toward the sugars in an organic ooze, sensory systems of the living have greatly expanded and complexified. Even cognition, the reorganization of sensory input toward the emergence of meaning-coupled-to-action (e.g., swimming away from insult) is a bacterial virtuosity present on the Earth for millions of years.

Bacteria were the earliest life form to evolve: their unprecedented activities in photosynthetic and chemical production, cell reproduction, genetic recombination of sex, networking, skyscraper architecture, air pollution and other environmental changes altered the Earth's surface long before the evolution even of a single marine animal.

Environmental modulation of temperature, chemical composition of the atmosphere and soils, acidity/alkalinity as well as salt oceanic concentration has depended on the physiological wisdom of the small and larger microbes. Our knowledge is gained by comparison of the details in the fossil record with observations of the behavior and metabolism, genetics and physiology of members of the five great taxa of life today (bacteria, protists, fungi, animals and plants). By inference, from the prodigious sensitive and communicative extant life forms on planet Earth we can look at Gaia's ancient history and conclude that what we call «the environment» is really «the body». The Earth, so far, is the only living planet we know. Gaia is the name of her protracted exquisite physiological system that evolved in response. In the Archean eon the means to break down the solar gradient were discovered. Since photosynthesis was invented by bacteria over 3000 million years ago the Earth has been a dazzling living rock whirling in space.

We have much to learn from bacteria, to prepare soil for plant growth, to recycle the inert nitrogen gas in the air and of course to conserve and recycle water. Most importantly, bacteria are the only organisms that can photosynthesize and, photosynthesis the process of food production by use of light-energy. Arguably photosynthesis has been the most important invention that has maintained the living world throughout its more than 3500 million years history. Cell swimming is a bacterial invention that evolved prior to any animal muscle or any swimming plant sperm. Some bacteria generate energy in the dark from fool's gold (pyrite). Others make rocks. Some bacteria with tiny magnets in their bodies orient and swim north more accurately than fish. Some bacterial cells promptly begin to reproduce when, after 48 hours of roiling in boiling water without pause, the water cools. Still other bacteria can eat out the intractable four percent protein between carbonate crystals of a clean clam shell. More bacteria inhabit your mouth right now than the number of people who lived on Earth in the last million years. Your body contains a greater number of bacterial than human cells.

Those who hate and want to kill all kind of bacteria indulge in self-hatred. Our ultimate ancestors, yours and mine, descended from this group of life forms. Not only are bacteria our ancestors, but also, if I am correct, as the evolutionary antecedent of the nervous system, they invented consciousness. The affects we recognize as sensitivity to light, sense of touch, hearing, smell of feces and food, indeed, our senses in general, evolved from a property properly called «bacterial consciousness». A dictionary definition of «consciousness» is «awareness of the world around one». Evidence for bacterial awareness abounds in the scientific literature. Many bacteria glide toward oxygen gas and away from sulfide, or swim to edible sugars and away from strong acids or dangerous salt solutions. Others eschew oxygen or cold water but make a beeline for the seaside mud hole where sulfide bubbles out. Many kinds of bacteria respond to light by basking in it. When light intensity is too high, some synthesize «sunglasses», brown pigment that prevents sunburn. Others sense desiccation. They dry out entirely even while bathed in water! Such strategies lead them to overwinter, hibernate or estivate, in dry mud.

In the merger process among bacteria community members, relationships change: aggression give way to truce, accommodation follows cannibalism and predation, and co-habitation succeeds in some with great perseverance through the ages. Our nucleated-cell ancestral prodigies (which could swim, metabolize sugar, regulate salts, breathe oxygen, produce sulfide gas and take in live bacterial food) evolved because of their exquisite sensitivity: attraction to sugars and each other, struggle, fusion, eventual incorporation and integration by compromise. Our sensibilities come directly from the world of bacteria. The vast numbers of incessantly moving but mute bacterial denizens ignore us as they eat, grow and reproduce, as we ignore them. Very few, only the «freaks»

CURRICULUM VITAE
LYNN MARGULIS

PRESENT POSITION

Distinguished University Professor
Department of Geosciences
University of Massachusetts
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HONORS

National Academy of Sciences
Russian Academy of Natural Sciences (1997)
National Medal of Science, President William Clinton (1999)
Alexander von Humboldt Prize, Berlin (2002-2005)

EDUCATION

The College, University of Chicago (1954-1957); 12th grade certificate (1955);
AB, Liberal Arts (1957)

University of Colorado, Department of Biology (summer, 1957)

University of Wisconsin (1957-1960)
Master of Science (1960) **Aspects of RNA Stability in *Amoeba proteus***
Joint Degree in the Departments of Zoology and Genetics

University of California, Berkeley (1960-1963)
Doctor of Philosophy (January 1965) **An Unusual Pattern of Thymidine
Incorporation in *Euglena***
Department of Genetics

FELLOWSHIPS AND SCHOLARSHIPS

- 1955-1957** University of Chicago Scholarship
1957-1958 Teaching Assistant, General Zoology, General Biology, University of Wisconsin
1958-1959 Research Assistant, University of Wisconsin, Department of Botany
1961-1963 NIH Traineeship, Department of Genetics, Berkeley
1976-1977 Sherman Fairchild Distinguished Scholar, California Institute of Technology
1979 Guggenheim Foundation Fellow (research on early life on Earth)
1991 Rockefeller Foundation (Bellagio Conference and Study Center, Bellagio, Italy)
1992 Faculty Fellowship Award, University of Massachusetts, Amherst
1997 Montgomery Fellow, Dartmouth College, Hanover, New Hampshire
2000 Collegium Helveticum Fellow, Switzerland
2002 Hanse-Wissenschaftskolleg Fellow, Delmenhorst, Germany

FIELD EXPERIENCE

- 1952** Work on a communal agricultural settlement, Moshav Moldeth, Israel.
1956 Anthropological field research on medical practices (the modern doctor and the *curandero*) in Tepoztlan, Morelos, Mexico. (With Dr. Oscar Lewis, registered as student in the University of Illinois for this research.).
1965 Bogotá, Medellín, Cali, Tunja (Colombia, South America). Director, Biology, Peace Corps Colombia Project (Brandeis University). Assessment of Peace Corps Program in Action.
1966 Bogotá, Medellín, Cali, Tunja (Colombia, South America). Director, Biology, Peace Corps Colombia Project (Brandeis University). Assessment of Peace Corps Program in Action.
1966 Mexico, DF, Mérida, Yucatán, Mexico. Dissemination of elementary science materials.
1967 Akosombo, Ghana, West Africa. Education Development Center. African Primary Science Project Workshop (now SEPA: Science Education Project for Africa).
1970 Brazil, IBCEC (Instituto Brasileiro de Educação, Ciência e Cultura) Consultant, Science Education.
1976 Short course on cell evolution, Barcelona, Spain.
1977 Laguna Figueroa, Baja California Norte, Mexico.

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- 1979** Laguna Figueroa, Baja California Norte, Mexico (Guggenheim fellowship supported).
- 1980** Laguna Figueroa, Baja California Norte, Mexico.
- 1981** Laguna Figueroa, Baja California Norte, Mexico.
- 1982** International geological field trip, Caborca, Sonora, Mexico. Field work, Laguna Figueroa, Baja California Norte, Mexico.
- 1983** May-June. Earthwatch fieldwork, Laguna Figueroa, Baja California Norte, Mexico.
October. Fieldwork, Laguna Figueroa, Baja California Norte, Mexico.
Oct.-Nov. NACIC/NACSEX (North-American-Cuban Scientific Exchange): Field work, Salina Bido, Matanzas; Short course at the Pedagógico (Enrique José Varona) and Cuban Academy of Sciences, Havana.
- 1984** Field work, Laguna Figueroa, Baja California Norte, Mexico.
- 1985** Lakes Banyoles and Cisó, Girona, Spain.
- 1986** Laguna Figueroa, Baja California Norte, Mexico.
- 1988** Laguna Figueroa, Baja California Norte, Mexico.
- 1989** Laguna Figueroa, Baja California Norte, Mexico.
- 1990** Laguna Figueroa, Baja California Norte, Mexico.
- 1991** Laguna Figueroa, Baja California Norte, Mexico; Guerrero Negro, Baja California Sur, Mexico; Delta del Ebro, Spain.
- 1992** Laguna Figueroa, Baja California Norte, Mexico; Guerrero Negro, Baja California Sur, Mexico; Delta del Ebro, Spain.
- 1993** Delta del Ebro, Spain; Sippewissett Marsh, Cape Cod, Massachusetts.
- 1995** Teaching. El Albúfero, Valencia, Spain.
- 1997** Estero «el Pozo», Estero «la Tovar»: Nayarit, Mexico; Delta del Ebro, Spain.
- 1998** Banyoles, Lake Cisó, Girona, Spain.
- 1999** Santa Pola, Alicante, Spain; Es Tremp, Mallorca, Spain.
- 2001** Tiputini Biodiversity Station Amazonas and Quito area Ecuador.
- 2002** Mayaguez, Ponce, Puerto Rico.
- 2003** Crete Coast near Heraklion.

LANGUAGES

Spanish, French (speaking and reading), Italian (speaking, reading, translation of scientific materials into English at a slow rate), Portuguese (translation of scientific materials into English at a slow rate).

EMPLOYMENT HISTORY

- 1963-1964** Research Associate, Department of Biology, Brandeis University, Waltham, MA.
- 1963-1965** Lecturer, Department of Biology, Brandeis University, Waltham, MA.
- 1963-1967** Consultant, staff member. The Elementary Science Study (ESS), Educational Services Incorporated (ESI).
- 1965-1966** Biology Coordinator, Peace Corps Colombia Project (Brandeis University). Teacher training and retraining in mathematics and science (summer).
- 1966-1967** Adjunct Assistant Professor, Department of Biology, Boston University.
- 1967-1971** Assistant Professor, Department of Biology, Boston University.
- 1971-1977** Associate Professor, Department of Biology, Boston University (tenure, 1973).
- 1977-1986** Professor of Biology, Boston University.
- 1978** Instructor, Chatauqua short course, Hartford, CT. NSF program (with Cyril Ponnampereuma).
- 1980** January-March. Visiting Professor, Department of Marine Biology, Scripps Institute of Oceanography, La Jolla, CA. University of California, San Diego.
March-June. Visiting Professor of Paleobiology, California Institute of Technology, Pasadena, CA. Division of Geology and Planetary Science.
July-August. NASA-Ames, Planetary Biology Microbial Ecology, summer research course (faculty), University of Santa Clara, Santa Clara, CA.
- 1981-** present Co-administrator of Planetary Biology Internship (PBI), with John Stolz (1981-1984), David Bermudes (1984-1985) and Michael Enzien (1985-1989), Gregory Hinkle (1990-1991), Lorraine Olendzenski (1992-1994), Michael Dolan (1995).
- 1982** July-August. NASA-Ames, Planetary Biology Microbial Ecology, summer research course (co-director), University of Santa Clara, Santa Clara, CA.
- 1983** Instructor, Chatauqua short course, Amherst, Mass., NSF Program (with Betsey Dyer).
- 1984** July-August. NASA-Ames, Planetary Biology Microbial Ecology, summer research course (co-director), San José State University, San José, CA.
- 1985, 1986** June-September, January-April. Visiting Professor, Departament de Microbiologia, Universitat Autònoma de Barcelona (Bellaterra), Spain.

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- 1986** May. Visiting Scholar, Marine Science Research Center, State University of New York, Stony Brook, Long Island, NY.
- 1986-1988** University Professor, Department of Biology, Boston University, Boston, MA.
- 1988** January. Visiting Professor, Departament de Microbiologia, Universitat Autònoma de Barcelona (Bellaterra), Spain.
September. Visiting Professor, Boston University Marine Program. Woods Hole, MA. Symbiosis course.
- 1988-1993** Distinguished University Professor, Department of Botany, University of Massachusetts, Amherst, MA.
- 1993-1997** Distinguished University Professor, Department of Biology, University of Massachusetts, Amherst, MA.
- 1994** September. Visiting Professor, Boston University Marine Program. Woods Hole, MA. Symbiosis course.
- 1995** September-December. Visiting Professor, George Mason University, Fairfax, VA. Protist Evolution course.
- 1997** November-December. Visiting Professor, Boston University Marine Program. Woods Hole, MA. Symbiosis course.
- 1997** present Distinguished University Professor, Department of Geosciences, University of Massachusetts, Amherst, MA.
- 1999** November-December. Visiting Professor, Boston University Marine Program. Woods Hole, MA. Symbiosis course.
- 2004** Adjunct Professor, Department of Microbiology, University of Massachusetts-Amherst, MA.

SABBATICALS

- 1973** Autumn, University of Washington, Seattle, Departments of Microbiology and Zoology.
- 1983** Autumn, Boston University; Havana, Cuba (Cuban National Academy of Sciences).
- 1986** Spring, Boston University; Barcelona (invited by Spanish government).
- 1997** Autumn, University of Massachusetts.

COMMITTEES AND EDITORIAL ASSIGNMENTS

National Academy of Sciences ad hoc Committee on Exobiology (1974-1976).
AAAS Electoral Nominating Committee (1974).

Space Science Board, National Academy of Sciences-Committee on Lunar and Planetary Studies (1975-1977).
Chairman, *ad hoc* Committee on Outer Planet and Satellite Contamination (Uranus, Titan, Neptune) (1976-1977).
Space Science Board Member (1977-1980).
Chairman, Space Science Board Committee on Planetary Biology and Chemical Evolution (PBCE) (1977-1981).
Associate Editor, **Precambrian Research** (Elsevier) (1979-1996).
Editorial Boards: **Endocytobiosis and Cell Research** (1984-1993), **J. Molecular Evolution** (1980-1984), **J. Theoretical Biology** (1979-1984), **Origins of Life** (1981-1987), **Symbiosis** (1985), **BioSystems** (1979-1993), **International Microbiology** (1998).
American Association for the Advancement of Science, Section G, Member-at-large (elected) (1981-1984).
NASA Workshop on Global Habitability (June 1982).
NASA Advisory Council Member (1982-1986).
Commonwealth Fund Book Committee (Lewis Thomas, Chairman) (1982-1993).
Mission of NASA Committee (1983).
MacArthur Foundation Fellowship Nominating Committee (1982-1983; 1997).
Associate Managing Editor, **BioSystems** (1983-1993).
National Academy of Sciences, Advisory Board of the National Science Resources Center (NSRC) (1987-1994); Executive Committee (1994-1999).
American Association for the Advancement of Science, Section G, President-elect, president, past-president (1989, 1990, 1991).
Executive Council, International Society for the Study of the Origins of Life (ISSOL) (1989-1992).
Earthwatch, Advisory Council Member (1991-1998).
Mellon Foundation, Massachusetts Institute of Technology (MIT), Science, Technology and Society - History of Life Sciences Program, Advisory Committee (1991-1994).
Smithsonian Air & Space Museum film, «Cosmic Voyage», Advisory Committee (1991-1995).
National Academy of Science video, «Space Age», Advisory Committee (1991).
Harvard University, Dept. of Organismic and Evolutionary Biology, Visiting Committee (1991-1992; 1994-1997).
Microcosmos Project, Boston University School of Education, International Board of Directors (1989-1997).
The International Society for the Study of the Origin of Life, Councilor (1989-1993).
Canadian Biodiversity Institute, Board of Directors (1997-1998).
International Symbiosis Society, Councilor (1997-1999).
National Center for Science Education, Inc., Supporter (1999).

NASA Institute for Advanced Concepts (1999-2001).
NAS Walcott Award Committee (2002).

INTERNATIONAL INVITED LECTURES
(title of presentation)

- 1970** Pont-à-Mousson, France: The Origin of Life, 3rd International Conference (Origins of cells).
London, United Kingdom: Museum of Natural History (Origins of cells).
- 1972** Montreal, Canada: 24th International Geological Congress (Microbial mats).
- 1973** Barcelona, Spain: 1st ISSOL Meeting, International Society for the Study of the Origin of Life (Origins).
- 1974** Bristol, United Kingdom: Society for Experimental Biology, Symposium 29 (Symbiotic theory of the origin of eukaryotic organelles: Criteria for proof).
- 1975** Beerse, Belgium: International Symposium on Microtubules and Microtubule Inhibitors (*Stentor*; Evolution of mitosis).
Leningrad, USSR: International Botanical Congress (Origins of cells).
- 1977** Mainz, Germany: Influence of the biosphere on the atmosphere (Gaia).
Banyuls-sur-Mer, Villefranche-sur-Mer, Gif-sur-Yvette, Paris and Orsay, France (Microtubules and spirochetes) (in French).
- 1978** London, United Kingdom: Royal Society (Symbiotic spirochetes).
- 1979** Mexico City, Mexico (Evolución Celular) (in Spanish).
- 1980** Paris, France: Télévision Nationale Française (in French).
Grasse, France: Biologie et la Terre, summer school (Formation des systèmes planétaires).
Berlin, Germany: Dahlem Conference on Mineral Deposits and Evolution of the Biosphere.
- 1981** Sassari, Italy: Congress, European Molecular Biology Organization (Microtubules in microorganisms).
- 1982** Mexico City, Mexico: International Geological Correlation Program, Projects 157 and 160, The Precambrian (Microbial mats).
Renesse, Netherlands: International Symposium on Biomineralization (Protist minerals).
Barcelona, Spain: Universitat de Barcelona, inauguration of new biology building.

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- 1983** Havana, Cuba: Academia Nacional de Cuba, 3 lectures (in Spanish).
Banyuls-sur-Mer, France: International Society for Evolutionary Protistology (*Paratetramitus*).
Mainz, Germany: Fourth Meeting, International Society for the Study of the Origin of Life (ISSOL).
Lund, Sweden: International Congress on Coevolution of Animals and Plants (Origins of cells).
Havana, Cuba: Cuban Academy of Sciences, two weeks of courses and ten lectures.
Plymouth, United Kingdom: Marine Biological Association (Gaia and microbial mats).
- 1984** University of Puerto Rico, Mayagüez, La Parguera: 5 invited lectures on cell evolution.
Ensenada, Baja California, Mexico: Centro de Investigaciones Científicas y Educación Superior de Ensenada (Tapetes microbianos).
Mexico City, Mexico: Universidad Nacional Autónoma de México, Departamento de Divulgación de Ciencia.
- 1985** Ottawa, Ontario, Canada: International Society for Evolutionary Protistology (ISEP).
Bristol, United Kingdom: Society for Experimental Biology, International Conference.
Villefranche-sur-Mer, France: Cell Motility Symposium (Evolution of motility).
Salamanca, Spain: Universidad de Salamanca, Microbiology Department (Cell evolution).
Barcelona, Spain: Universitat de Barcelona (Cell evolution).
Madrid, Spain: Fundación Areces (Archaeobacteria and microbial evolution).
Valencia, Spain: (Tapetes microbianos; La célula eucariótica).
Venice, Italy: Global Environmental Research Organization (Man's role in changing the global environment).
- 1986** Cambridge, United Kingdom: Darwin College (Origins of life).
Orsay, France: (Origine de motilité cellulaire).
Oldenburg, West Germany: (Microbial mats and Gaia).
Zurich, Switzerland: University of Zurich biology faculties (Symbiosis as a mechanism of evolution).
Venice, Italy: Global Environmental Research Organization (Microbial communities: From cells to planetary surfaces).
Brussels, Belgium: Inst. voor Hygiene en Epidemieologie (Spirochetal origin of undulipodia).

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- 1987
- Berkeley, Calif., USA: 5th ISSOL Meeting (International Society for the Study of the Origin of Life) (Symbiosis in evolution).
Eilat, Israel: (Symbiosis and the origin of neosemes).
Rehovot, Tel Aviv, Israel: Weizmann Institute (Spirochetal origin of undulipodia).
London, United Kingdom: Royal Society, Systematics Association (Secession of protoctista from the plant and animal kingdoms).
Bellaterra, Barcelona, Spain: Council of Europe, Intensive Course (Early evolution of cells).
London, United Kingdom: International Society for Evolutionary Protistology (ISEP) (Spirochetal origin of undulipodia).
Cornwall, United Kingdom: Worthyvale Manor (Microbial mechanisms of Gaian control).
Turin, Italy: NATO workshop (Cell-to-cell signals in plant, animal and microbial symbiosis).
Paris, France: First French Congress of Sedimentology (Sedimentation et la vie commune ancienne microbienne).
Barcelona, Spain: Museu de la Ciència (Influencia de la vida sobre el planeta terra).
Barcelona, Spain: Universitat de Barcelona, Departamento de Geologia, dedication of new geology building (Early life on Earth).
- 1988
- Perugia, Italy: International center for epistemological studies (Gaia and microbial mats, spirochetes and brain).
Perpignan, France: Les journées Edouard Chatton (Des procaryotes aux protistes eucaryotes).
Groningen, The Netherlands: Groningen University (Gaia and the early evolution of life).
Barcelona, Spain: University of Barcelona (Morphology of large symbiotic spirochetes).
- 1989
- Cambridge, United Kingdom: 113th Meeting of the Society for General Microbiology, Cambridge University (Evolution of earliest eukaryotes).
Moscow, USSR: Moscow University (Evolution and symbiosis).
Leningrad, USSR: Leningrad State University (Symbiosis in cell evolution).
Leningrad, USSR: Institute of Cytology (Origin of undulipodia from symbiotic spirochetes).
Madrid, Spain: Universidad Autónoma de Madrid (Influencia de la hipótesis de Gaia en los conceptos de evolución).
Milan, Italy: Università Degli Studi di Milano (Symbiosis as a mechanism of generating evolutionary novelty) (in Italian).
Turin, Italy: Experimenta '89 Pianeta Vita (Gaia and biospheres).

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- Lyon, France: Endocytobiology IV, the IVth International Colloquium on Endocytobiology and Symbiosis (Serial endosymbiosis theory: Origins of intracellular motility systems).
 Ottawa, Ontario, Canada: Science '89-Canada's Future Science Teachers of Ontario (Science is not reading from a textbook).
 Barcelona, Spain: Societat Catalana de Biologia (Simbiogénesis: Generación de novedades biológicas por simbiosis).
 Worthyvale Manor, Cornwall, United Kingdom: The Third Annual Symposium on the Gaia thesis and its Implications, Wadebridge Ecological Centre (Symbiogenesis and Gaia).
- 1990**
 Canary Islands, Spain: Santa Cruz de Tenerife, Universidad International Menéndez Pelayo (Arqueobacterias y el origen del nucleocitoplasma).
 Salamanca, Spain: 25 Años de Biología en la Universidad de Salamanca (Arqueobacteria y los cinco reinos; Gaia y evolución).
 Spoleto, Italy: Science and culture. Festivale di Spoleto (Nascita della vitta) (in Italian).
 Seville, Spain: Universidad International Menéndez Pelayo (El hombre como comunidad microbiana).
- 1991**
 Frankfurt, Germany: Johan Wolfgang Goethe-Universität (Symbiosis, sex and the evolution of cells; Gaia as living Earth from space: Importance of microbial communities).
 Barcelona, Spain: Societat Catalana de Biologia (Simbiogénesis y biología molecular; Las comunidades bacterianas y los Protoctista; Los grandes grupos de organismos: monarquía o república?).
 Lake Como, Italy: Bellagio Rockefeller Foundation Study Center (Gaia; Nature walks).
- 1992**
 Valencia, Spain: Universitat de Valencia (Simbiogénesis y simbioticismo como mecanismos evolutivos).
 Amsterdam, The Netherlands: University of Amsterdam (Biodiversity: Molecular biological domains, symbiosis and origins of higher taxa).
 Alfred Nobel's Björkborn, Karlskoga, Sweden: Nobel Symposium 84. Early Life on Earth (Combinatorial generation of taxonomic diversity).
 Taormina, Sicily, Italy: University of Messina, European Science Foundation (Microbes, minerals and early Earth: Co-evolution of the organic and inorganic world).
 Barcelona, Spain: ISME-6 (International Society for Microbial Ecology) (Individuals as microbial communities); Consell Superior, Centre d'Investigació: Desenvolupament (Simbiogénesis: Mecanismo de la evolución).

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- Copenhagen, Denmark: Royal Danish Academy of Sciences and Letters, 250 Anniversary Symposium: Biodiversity in a Changing World (Biodiversity and symbiogenesis: From species to kingdoms).
- Edinburgh, Scotland: University of Edinburgh (Symbiosis and speciation).
- Cambridge, United Kingdom: King's College, Science for the Earth (A pox called man).
- Leiden, The Netherlands: University of Leiden (Symbiogenesis and the origin of species).
- Nijmegen, The Netherlands: Vakgroep Microbiologie en Evolutiebiologie, University of Nijmegen (Origins of species: Importance of symbiogenesis).
- Lancaster, United Kingdom: British Ecological Society (Symbiogenesis: Origins of species and higher taxa).
- London, United Kingdom: Royal Entomological Society (Origins of species via symbiogenesis).
- 1993**
- Edinburgh, Scotland: University of Edinburgh. International Science Festival.
- Santa Maria di Imbaro, Italy: 7th Conference and General Assembly of International Federation of Science Editors (What to do about standards for 30,000,000 nonhuman species of organisms?).
- Barcelona, Spain: 7th International Society for the Study of the Origin of Life (ISSOL) 10th International Conference of the Origin of Life (Symbiogenesis and species origin).
- Oslo, Norway: Society of Parasitology. XIV Symposium Lecture (Parasitism and parasitology: Anachronistic flags).
- Barcelona, Spain: Museum of Science (Los microorganismos: evolución, domesticación y origen de especies). University of Barcelona, Dept. of Microbiology (*De Spirosymplokos a undulipodia*). Universitat Pompeu Fabra, School of Journalism (Gaia y la evolución de la vida: papel de los microorganismos en la biosfera).
- Madrid, Spain: Autonomous University of Madrid (Origen de las especies: simbiosis y microcosmos).
- Uppsala, Sweden: Uppsala University (Origins of species: Evolution by symbiosis).
- Stockholm, Sweden: Stockholm University (Symbiogenesis: Evolution of cells).
- 1994**
- Oxfordshire, United Kingdom: Green College, Oxford University (A Century Without Symbiogenesis is Enough).
- Uppsala, Sweden: Uppsala University (Origins of Species: Evolution by Symbiosis).

Stockholm, Sweden: Stockholm University (Symbiogenesis: Evolution of cells).

London, United Kingdom: The Linnean Society (Hogg's Protoctista).

Edinburgh, Scotland: Edinburgh International Science Festival (Science and Environment).

Oxfordshire, United Kingdom: Green College, Oxford University (The self-regulating Earth).

Tokyo, Japan: NTT DATA, «New Paradigm Session» (From Microbe to Gaia: Symbiosis and Humanity).

Valencia, Spain: University of Valencia (Are there irresoluble enigmas in the origin of life problem?; Symbiogenesis: The Basis of Individuality and Speciation).

San Sebastián, Spain: University of the Basque Country (Evolucion celular).

Halifax, Nova Scotia, Canada: (ISEP) International Society for Evolutionary Protistology (Symbiogenesis); Canadian Institute for Advanced Research (Cleveland was correct; cell mergers, symbiont strife as conciliation became sex).

Vancouver, British Columbia, Canada: University of British Columbia (Symbiogenesis and Species Origins; Gaia: The Living Earth from Space; Power to the Protoctists, Our Ancestors); Simon Frazer University (Power to the Protoctists, Our Ancestors).

Barcelona, Spain: Universitat Autònoma de Barcelona (El origen de la vida y de la célula).

1995 Madrid, Spain: 1st Bioscience Symposium (Molecular and organismal biodiversity: The new frontier).

Bahamian Field Station, San Salvador Island, Bahamas (Biodiversity and its five kinds of beings: It's time to put life back into biology).

Valencia, Spain: UIMP Summer Course (Procarionts: eucarionts. Les cèl·lules eucariòtiques com a comunitats microbianes).

Barcelona, Spain: International Federation of Science Editors, IFSE-8 plenary lecture (Science for the year 2010).

Bergen, Norway: University of Bergen (Symbiogenesis and the origins of eukaryotic cells: 30 years later; Bacterial ancestry of motility organelles).

Laxenberg, Austria: Institute for Applied Systems Analysis, Tjalling Koopmans Distinguished Lecture Series (What Is Life?).

The Hague, Netherlands: Beijerinck Centennial (Evolution of cell organelles).

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- 1996
- Barcelona, Spain: Societat Catalana de Biologia. Universitat de Barcelona (Comunidades microbianas: El origen del individuo).
Oxford, United Kingdom: Gaia in Oxford II (Symbiogenesis: Organism/superorganism to ecosystem/Gaia).
Devon, United Kingdom: Schumacher College summer course (Gaia theory & living systems: From macrocosm to microcosm).
Belfast, Ireland: Linnean Society (The meaning of microbes: How do we preserve knowledge?).
Paris, France: Collège de France (Evolution by symbiosis).
Montreal, Canada: Kefir Symposium (Kefir and symbiosis) (Symbiosis and the living Earth from space).
Hamilton, Ontario, Canada: McMaster University (Archeal-eubacterial merger in eukarya origin).
- 1997
- Barcelona, Spain: Museum of Science (What is life?).
Montreal, Canada: University of Montreal (Symbiogenesis).
Gothenburg, Sweden: NFR Forum of the Origins of Life (Eukaryosis as symbiogenesis: Cells from bacterial communities).
Nuevo León, Mexico: Autonomous University of Nuevo León (Simbiogénesis en el origen de la célula eucariótica).
Valencia, Spain: University of Valencia (¿Qué es la vida?); Symposium of Cryptogramic Botany (La vida fotosintética: Simbiogénesis y los orígenes de las algas).
Guelph, Ontario, Canada: University of Guelph (Symbiogenesis: Bacterial consortia in the origins of eukaryotes).
Madrid, Spain: Centro de Investigaciones Biológicas (Simbiogénesis en el origen de la célula).
Valencia, Spain: Bancaja Foundation (Gaia y evolución ambiental).
- 1998
- Barcelona, Spain: Instituto de Investigaciones Pesqueras, La Barceloneta (Simbiosis y evolución).
Girona, Spain: Institut d'Ecologia Aquàtica, Universitat de Girona (Papel de las bacterias en la simbiogénesis y la evolución).
Madrid, Spain: Autonomous University of Madrid (Discurso: Una revolución en la evolución).
Madrid, Spain: Autonomous University of Madrid. Origins of species and evolutionary changes (symbiogenesis and molecular evolution: future).
Málaga, Spain: Vicerrectorado de Investigación. Universidad de Málaga (Simbiogénesis y evolución).
Montpellier, France: 16th World Congress of Soil Science (Invited commentator on aims of soil science).
Cortona, Italy: Cortona Week XI: Future and future vision (From Gaia to microcosm).

1999

London, United Kingdom: Linnean Society: Gaia perspectives 1998 (Gaia: The Earth as seen from space).

Barcelona, Spain: Museum of Science (What Is Sex? Spanish edition).

Banyuls-sur-mer, France: Université Pierre et Marie Curie, Observatoire Oceanologique de Banyuls. Laboratoire Arago (Evolution of sexuality).

Alicante, Spain: (Gaia: La tierra viva desde el espacio).

Tübingen, Germany: University of Tübingen Crafoord Lecture (Gaia: Ancient symbiosis as seen from space).

Oldenburg, Germany: University of Oldenburg, Honoris Causa (Science of our living Earth: From Archean ecology to Proterozoic prototists).

Oban, Scotland: Scottish Association for Marine Biology (Speciation via Symbiosis; Symbiosis and living sands).

Zaragoza, Spain: Cajal and Consciousness (The conscious cell).

Barcelona, Spain: Museum of Science (Roundtable «On complexity»).

Stellenbosch, South Africa: University of Stellenbosch (Symbiotic planet: A new look at evolution; Evolution by symbiosis).

Edinburgh, Scotland: International Science Festival (Evolution of cells and the need for religion).

London, United Kingdom: Imperial College (Symbiosis and natural selection).

Alcobendas, Spain: CosmoCaixa, Vísperas de Ciencia (Biosfera: Influencia del origen y la evolución de la vida en el medio ambiente).

Valencia, Spain: Gaia 2000 Conference (Gaia becomes respectable: Modes of confirmation of Gaia theory).

Barcelona, Spain: University of Barcelona (What physicists need to learn from biologists: Movement and deep time).

Ballyvaughan, Galway, Ireland: ESF-CYANOFIX (Endosymbiosis and the evolution of organelles).

La Paz, Mexico: Center for Biological Research of the Northwest (Gaia y el microcosmos: Evolución de la célula).

Barcelona, Spain: Societat Catalana de Biologia (Origen de las especies por simbiogénesis).

Universitat de Barcelona, Microbiology class (Espiroquetas: Diversidades y complejidades).

Guadalajara, Mexico (Symbiosis and evolution).

Madrid, Spain: Origins of Species Conference (El origen de las especies).

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- Quito, Ecuador: Universidad San Francisco de Quito, Commencement Address (Simbiogénesis y el origen de las especies).
- Valencia, Spain: University of Valencia (Origen de las especies y adquisición de genomas).
- Zurich, Switzerland: Collegium Helveticum, ETHZ, Scientist in Residence, Chair: Toward a Theory of Life Symposium (Evolutionary innovation and the origin of species); Seminar (Social context of science); Teacher-training workshop (The carbon cycle: What happens to trash and garbage?); Raths Steiger Lecture (Symbiogenesis in the Evolution of Life).
- 2001** Barcelona, Spain: Parc Científic de Barcelona. International Symposium: New Frontiers in microbial ecology and international activities of ASM (Symbiogenesis and Evolution).
- 2002** Delmenhorst, Germany: Hanse Institute of Advanced Study (Before species: Environmental evolution on early Earth).
- Bamburg, Germany: 30th Symposium for AvH Research Awardees (Symbiogenesis and symbiointicism, not random mutation, as source of Darwin's inherited variation).
- Oldenburg, Germany: University of Oldenburg, ICBM-Kolloquium (Eukaryosis).
- Amsterdam, The Netherlands: Royal Netherlands Academy of Arts and Sciences Biogeology Symposium (Gaia and biochemistry).
- Madrid, Spain: Universidad Complutense Madrid (El flujo de energía y la vida).
- Barcelona, Spain: Museum of Science (Learning about genetics. Dialogue with Dr. María Arca).
- Bremen, Germany: Wurtzburg Lecture (Amber, termites and the origins of cells).
- Wurtzburg, Germany: Biozentrum Lecture (Evolution of cells).
- Bamberg, Germany: 30th Symposium for A.V. Humboldt Research Awardees (Symbiogenesis and symbiointicism, not random mutation, as source of Darwin's inherited variation).
- Dusseldorf, Germany: University of Oldenburg ICBM-Kolloquium (Origin of the nucleus).
- Tarragona, Spain: La Caixa Cultural Center (Gaia y el origen de las especies).
- Lérida, Spain: La Caixa Cultural Center (Adquisicion de genomes: Una teoria de l'origen de les espècies).
- Berlin, Germany: Frei Universitat Berlin (Termite symbionts).
- Bremen, Germany: Bremen University (Science education).

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- Berlin, Germany: A.V. Humboldt Research Fellowship residency (Gaia view of the Earth).
- Oaxaca, Mexico: ISSOL Conference (Cell motility and of the origin of Centrioles; From Microcosmos to Gaia).
- Monterrey, Mexico: Universidad Autónoma de Nuevo León, Monterrey, México (Simbiogénesis y evolución).
- Ponce, Puerto Rico: Universidad Católica de Puerto Rico (Simbiogénesis y el origen de las especies).
- Montreal, Canada: Quebec University of Montreal (Thiodendron-like consortia to chimeric archaeotists).
- Barcelona, Spain: University of Barcelona (Cell structure and spirochete communities: *Thiodendron* and *Mixotricha*).
- Valencia, Spain: Universitat de València (Una revolución en la evolución).
- Barcelona, Spain: Museu de la Ciència de la Fundació “la Caixa” (Peces luminosos: historias de ciencia y amor).
- 2003** Barcelona, Spain: Palau de la Virreina (Comida y la complejidad del individuo); Palau Macaya (Sculpture of the tree of life); Palau de la Música (Science as a Culture, Science as a way of knowing).
- Valencia, Spain: University of Valencia, Bujassot Campus of Science (Honoris Causa series).
- Oslo, Norway: The 16th Kongsberg Seminar, Norwegian Geoscience Centre, The Rosenqvist Lecture (Gaia: The living Earth from space); Sackler Lecture (Cell evolution in the Proterozoic Eon).
- Madrid, Spain: Fundación Ramón Areces ASM (El universo microbiano: de millas a micras; The microbial universe: from miles to microns).
- Halifax, Canada: Fourth International Symbiosis Congress, St. Mary’s College (Bacterial integration and evolutionary innovation).
- La Coruña, Spain. XV Bienal de la Real Sociedad Española de Historia Natural (Simbiosis en evolución).
- Madrid, Spain: Las culturas de la ciencia y la tecnología. Conferencia inaugural del seminario. Eulalia Lecture (Gaia y la evolución de las máquinas); Banquete Lecture (Hunger and ecosystems).
- Barcelona, Spain: Catalan Foundation for Research (Talks with Lynn Margulis, a dialogue with Prof. R. Guerrero); Aula European School (Symbiogenesis and photosynthetic animals: Development of an idea that has changed biology).
- 2004** Barcelona, Spain: Institut de Ciència del Mar, Secció de Microbiologia SCB (Ecologia microbiana proterozoica: simbiosi i origen del nucli).

Bellagio, Italy: Rockefeller Foundation Bellagio Study and Conference Center (Cell evolution: Mitotic motility and sensory cells).

Devon, United Kingdom: Schumacher College summer course (Earliest ecosystems and the microbe's contribution).

Barcelona, Spain: Word Women's Forum (A new culture of living and living together; To rethink the world).

Seville, Spain: Huelva, la Rábida Course (Contribución de los microbios a la evolución).

Leiden, The Netherlands: Institute of Biology, Leiden University; Acquired Genomes Symposium (Evolutionary Consequences of Endosymbiosis: Origin of the nucleus).

Vienna, Austria: Third International PhD Symposium, Institute of Molecular Pathology (Composite Individuality: Transition from bacterial to eukaryote genomes).

Genoa, Italy: Festival of Science (Life on Earth: A bacterial view).

Madrid, Spain: Centro de Investigaciones Biológicas (CIB) (Integración de genomas y formación de nuevos individuos; Simbiogénesis e Innovación).

Barcelona, Spain: Department of Microbiology, Barcelona University (Origen de la célula eucariótica).

2005 Madrid, Spain: Banquete: metabolismo y comunicación (Bacterial Communication).

Tokyo, Japan: The NISTEP International Conference «Seamless culture through science communication» (Doing science as a way of knowing: Living sands and the epic of evolution).

AWARDS

Boston University Faculty Publication Merit Award for 1967 (Shell) (February 28, 1969)

George Lamb Award, Outstanding US Botanist, University of Nebraska, Lincoln (1971)

Diamond Award: Travel to Leningrad, for International Botanical Congress (Summer 1975)

Fellow of the Association, AAAS («To Lynn Margulis, for her contributions to cell biology, in particular for her studies on the origin of eukaryotic cells») (1975)

NASA Public Service Award (October 1981)

United Methodist Church Award for Teacher Scholar, Boston University (1982)

Elected member, National Academy of Sciences (Section 27 Ecological and evolutionary biology) (1983)
University of Chicago Citation for Professional Achievement (1985)
Boston University MacDonald Award for Excellence in Research (1986)
Boston University Nominee, Nationwide Salute: American Association of Higher Education and the Carnegie Foundation for the Advancement of Teaching, for extraordinary educational leadership to the campus and beyond (1986)
Miescher-Ishida Award, International Society for Endocytobiology (first winner) (1986)
Distinguished Service Award, National Association of Biology Teachers (1988)
Commandeur de l'Ordre des Palmes Académiques de France (1989)
Honoris Causa Doctor of Science, Southeastern Massachusetts University, North Dartmouth, MA (1989)
Honoris Causa Doctor of Science, Westfield State College, Westfield, MA (1989)
Honorary Member Plaque, International Society for Evolutionary Protistology (ISEP), Orsay, France (1990)
Honoris Causa Doctor of Science, Plymouth State College, Plymouth, NH (1991)
Distinguished Faculty Lecturer, University of Massachusetts, Amherst, MA (1992)
Chancellor's Medal for Distinguished Faculty, University of Massachusetts, Amherst, MA (1992)
Distinguished Lecturer in the Life Sciences, Boyce Thompson Institute of Plant Research, Cornell University, Ithaca, NY (1994)
Honoris Causa Doctor of Science, Washington College, Chestertown, MD (1995)
Annual Lecturer, 95th Opening Session, ASM General Meeting, Washington, DC (1995)
Elected Fellow of the World Academy of Art and Science (1995)
Honoris Causa Doctor of Science, Tulane University, New Orleans, LA (1996)
Honoris Causa Doctor of Science, University of Montreal. Montreal, Quebec (1997)
Nevada Award, Desert Research Institute, Las Vegas, NV (1998)
Elected Fellow of the American Academy of Arts and Sciences (1998)
Honoris Causa Doctor of Science, Autonomous University of Madrid, Canto Blanco, Spain (1998)
Distinguished Service Award, American Institute of Biological Sciences, Baltimore MD (1998)
Dr. rer. nat. Honoris Causa, University of Oldenburg, Oldenburg, Germany (1999)

Sigma Xi William Proctor Prize for Scientific Achievement, Minneapolis, MN (1999)

Honoris Causa Doctor of Science, Union College, Schenectady, NY (2001)

Distinguished Academic Outreach 2000-2001, University of Massachusetts Commonwealth Award, Interpretive Scientist. Massachusetts Cultural Council (2001)

Honoris Causa Doctor of Science, San Francisco University, Quito, Ecuador (2001)

Honoris Causa Doctor, University of Valencia, Spain (2001)

Faculty Grant Award (course design grant) for video of the «Cosmos to Humanity» course (2003)

Honoris Causa Doctor of Science, Rutgers University, NJ (2004)

Nomination to the NASA Honor Group Achievement Award NIAC Science Council Member (2003)

Rockefeller Foundation (2004)

Honoris Causa Doctor of Science, Bates College, ME (2005)

Alexander von Humboldt Prize, Berlin (2002-2005)

President of Sigma Xi, The Scientific Research Society (2005-2006)

Faculty Grant Award (course design grant) for video of the «Cosmos to Humanity» course (2003)

Honoris Causa Doctor of Science, Rutgers University, NJ (2004)

Nomination to the NASA Honor Group Achievement Award NIAC Science Council Member (2003)

Rockefeller Foundation (2004)

Honoris Causa Doctor of Science, Bates College, ME (2005)

Honoris Causa Doctor University of Vigo (2007)

PROFESSIONAL SOCIETIES

Catalan Society for Biology (Member of Honor, 1986)

International Society for Evolutionary Protistology (ISEP, Co-founder; Honorary Life Member)

International Society for the Study of the Origin of Life (ISSOL, Councilor 2002-2005)

Marine Biological Laboratory, Woods Hole, MA (Corporation Member)

Sigma Xi (University of Massachusetts Chapter)

Phi Beta Kappa (University of Massachusetts)

Phi Kappa Phi (University of Massachusetts)

The Linnean Society (London)

International Symbiosis Society (Councilor)

Gaia: The Society for Research and Education in Earth System Science.
University of East London (Honorary President)
Boston University Graduate School (1966-1969; 1972-1973; 1987-1988)
National Science Foundation (1968-1972; 1978-1979)
SGER-NSF Grant (1990-1992)
NASA Life Sciences (1970-1995)
Richard Lounsbery Foundation Research Trust Funds (1985-88; 1997-98;
1999-2003)
UMASS College of Natural Sciences and Mathematics (1988)
NASA Space Sciences (1995-2001)
Tauber Fund (2004)

ARTICLES

- 1958** Plaut, W. and L. A. Sagan. Incorporation of thymidine in the cytoplasm of *Amoeba proteus*. **Journal of Biophysical and Biochemical Cytology** 4: 843-846.
- 1965** Sagan, L. An unusual pattern of tritiated thymidine incorporation in *Euglena*. **Journal of Protozoology** 12:105-109.
Sagan, L., Y. Ben-Shaul, H. T. Epstein and J. A. Schiff. Studies of chloroplast development in *Euglena*. XI. Radioautographic localization of chloroplast DNA. **Plant Physiology** 40: 1257-1260.
- 1967** Sagan, L. On the origin of mitosing cells. **Journal of Theoretical Biology** 14: 225-274.
- 1968** Margulis, L. Evolutionary criteria in Thallophytes: A radical alternative. **Science** 161: 1020-1022.
Margulis, L. and T. N. Margulis. A note on the equivalence of characters: Pheneticist vs. phylogeneticist. **Systematic Zoology** 17: 477-479.
- 1969** Banerjee, S. and L. Margulis. Reversible inhibition of cilia regeneration in *Stentor coeruleus* by isopropyl-n-phenyl carbamate. **Nature** 224: 180-181.
Margulis, L. New phylogenies of the lower organisms: Possible relation to organic deposits in Precambrian sediment. **Journal of Geology** 77: 606-617.
Margulis, L., S. Banerjee and T. White. Colchicine-inhibited cilia regeneration: Explanation for lack of effect in tris buffer medium. **Science** 164: 1177-1178.
Margulis, L., J. A. Neviackas and S. Banerjee. Cilia regeneration in

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- Stentor*: Inhibition, delay and abnormalities induced by griseofulvin. **Journal of Protozoology** 16: 660-667.
- Neviackas, J. A. and L. Margulis. The effect of colchicine on regenerating membranellar cilia in *Stentor coeruleus*. **Journal of Protozoology** 16: 165-171.
- 1970 Makrides, E. B., S. Banerjee, L. Handler and L. Margulis. Podophyllotoxin, Colcemid and cold temperature interfere with cilia regeneration in *Stentor*. **Journal of Protozoology** 17: 548-551.
- Margulis, L. Recombination of non-chromosomal genes in *Chlamydomonas*: Assortment of mitochondria and chloroplasts? **Journal of Theoretical Biology** 26: 337-342.
- 1971 Banerjee, S. and L. Margulis. Inhibition of cilia regeneration by antineoplastic agents. **Cancer Chemotherapy Reports Part 1** 55: 531-537.
- Margulis, L. Cytoplasmic genes: Our Precambrian legacy. **Stadler Genetics Symposia** 1 & 2: 79-88.
- Margulis, L. Symbiosis and evolution. **Scientific American** 224: 48-57.
- Margulis, L. Whittaker's five kingdoms of organisms: Minor revisions suggested by consideration of the origin of mitosis. **Evolution** 25: 242-245.
- 1972 Banerjee, S., V. Kerr, M. Winston, J. K. Kelleher and L. Margulis. Melatonin: Inhibition of microtubule-based oral morphogenesis in *Stentor coeruleus*. **Journal of Protozoology** 19: 108-113.
- Margulis, L. Symbiose en evolutie. **Natuur en Techniek** 40: 394-407.
- Younger, K. B., S. Banerjee, J. K. Kelleher, M. Winston and L. Margulis. Evidence that the synchronized production of new basal bodies is not associated with DNA synthesis in *Stentor coeruleus*. **Journal of Cell Science** 11: 621-637.
- 1973 Banerjee, S. and L. Margulis. Mitotic arrest by melatonin. **Experimental Cell Research** 78: 314-318.
- Blumberg, S., S. Propst, S. Honjo, T. Otaka, J. Antanavage, S. Banerjee and L. Margulis. Induced reversible pigment alteration in *Stentor coeruleus*. **Transactions of the American Microscopical Society** 92: 557-569.
- Margulis, L. Colchicine-sensitive microtubules. **International Review of Cytology** 34: 333-361.
- 1974 Deshpande, K. L., S. Banerjee, J. K. Kelleher and L. Margulis. Cilia membrane abnormalities induced by streptomycin and other aminoglycoside antibiotics in *Stentor coeruleus*. **Cytobios** 11: 185-199.

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- Lovelock, J. E. and L. Margulis. Atmospheric homeostasis by and for the biosphere: The Gaia hypothesis. **Tellus** 26: 2-10. Reprinted 1999 in **Global Aspects of the Environment** 1: 57-64.
- Lovelock, J. E. and L. Margulis. Homeostatic tendencies of the Earth's atmosphere. **Origins of Life** 5: 93-103.
- Margulis, L. On the evolutionary origin and possible mechanism of colchicine-sensitive mitotic movements. **BioSystems** 6: 16-36.
- Margulis, L. Origin and evolution of the eukaryotic cell: Introduction. [In Proceedings of the First International Congress of Systematic and Evolutionary Biology]. **Taxon** 23: 225-226 [entire symposium, pp. 225-270].
- Margulis, L. and J. E. Lovelock. Biological modulation of the Earth's atmosphere. **Icarus** 21: 471-489.
- Winston, M., E. Johnson, J. K. Kelleher, S. Banerjee and L. Margulis. Melatonin: Cellular effects on live stentors correlated with the inhibition of colchicine-binding to microtubule protein. **Cytobios** 9: 237-243.
- 1975 Banerjee, S., J. K. Kelleher and L. Margulis. The herbicide trifluralin is active against microtubule-based oral morphogenesis in *Stentor coeruleus*. **Cytobios** 12: 171-178.
- Margulis, L. The microbes' contribution to evolution. **BioSystems** 7: 266-292.
- 1976 Margulis, L. A Review: Genetic and evolutionary consequences of symbiosis. **Experimental Parasitology** 39: 277-349.
- Margulis, L. The theme (mitotic cell division) and the variations (protists): Implications for higher taxa. **Taxon** 25: 391-403.
- Margulis, L., J. C. G. Walker and M. Rambler. Reassessment of roles of oxygen and ultraviolet light in Precambrian evolution. **Nature** 264: 620-624.
- Ormerod, W., S. Francis and L. Margulis. Delay in the appearance of clamp connections in *Schizophyllum commune* by inhibitors of microtubule protein assembly. **Microbios** 17: 189-205.
- 1977 Cooper, G. and L. Margulis. Delay in migration of symbiotic algae in *Hydra viridis* by inhibitors of microtubule protein polymerization. **Cytobios** 19: 7-19.
- Margulis, L., H. O. Halvorson, J. Lewis and A. G. W. Cameron. Limitations to growth of microorganisms on Uranus, Neptune and Titan. **Icarus** 30: 793-808.
- Margulis, L., H. O. Halvorson, J. Lewis and A. G. W. Cameron. Some general principles of planetary quarantine leading to an assessment of the limitations to growth of microorganisms on Uranus and Neptune. **Life Sciences and Space Research** 15: 101-106.

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- Margulis, L. Biology begins. A review of **Origin and Early Evolution of Life**. T. Fenchel. **The Quarterly Review of Biology**. 79: 206-207.

STUDENT THESES¹

- 1969 Van Wie, C. C. An electron microscopic investigation of the intact and shed membranellar bands of *Stentor coeruleus*. Master of Arts. Boston University.
- 1976 Harwood, C. S. Isolation and characterization of *Maremonas rubrum*, gen. et sp. nov.; a red marine bacterium. Master of Arts. Boston University.

¹ First reader and major professor unless noted otherwise.

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- Kelleher, J. K. Interaction of anti-microtubule agents with tubulin *in vitro* and in *Stentor coeruleus*. Doctor of Philosophy. Boston University.
- 1977 Cooper, G. J. Microtubule protein polymerization inhibitors and uptake and migration of symbiotic algae in *Hydra viridis*. Master of Arts. Boston University.
- 1978 Dyer, B. D. *Reticulitermes flavipes* hind gut ecosystem: Flagellate niches analyzed by selective defaunation. Master of Arts. Boston University.
- Giusto, J. P. Chromosomal mechanisms in catarrhine evolution. Master of Arts. Boston University.
- To, L. P. Ultrastructural and biochemical characterization of the hindgut microbiota of dry wood termites. Doctor of Philosophy. Boston University.
- 1979 Fracek, S. P., Jr. Colchicine, nocodazole and trifluralin: Different effects of microtubule polymerization inhibitors on the uptake and migration of endosymbiotic algae in *Hydra viridis*. Master of Science. Boston University.
- Giovannoni, S. J. A strain of red *Beneckea* from cyanobacterial mats of Laguna Mormona, Baja California. Master of Arts. Boston University.
- 1980 Rambler, M. B. Ultraviolet irradiation of bacteria under anaerobic conditions: Implications for Prephanerozoic evolution. Doctor of Philosophy. Boston University.
- Thorington, G. U. The algal and bacterial symbionts of *Hydra viridis*: Metabolic relations and transmission through the host sexual cycle. Doctor of Philosophy. Boston University.
- 1982 Gong-Collins, E. J. Isolation and characterization of a new strain of *Bacillus megaterium* and a new species of *Pseudomonas* from the microbial mats at Laguna Figueroa, Baja California del Norte Mexico. Master of Arts. Boston University. (Published: Gong-Collins, E. and D. L. Read, 1985, A new strain of *Arthrobacter* isolated from a laminated microbial mat, **Microbios** 42: 45-57; Gong-Collins, E., 1986, A euryhalic, manganese- and iron-oxidizing *Bacillus megaterium* from a microbial mat at Laguna Figueroa, Baja California, Mexico, **Microbios** 48: 109-126.)²
- 1983 Sharifi, E. Was the legume-*Rhizobium* symbiosis originally parasitic? A review. Master of Arts. Boston University. (Published: Sharifi, E., 1984, Parasitic origins of nitrogen-fixing *Rhizobium*-legume symbioses: A review of the evidence. **BioSystems** 16: 269-289.)

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- 1984 Brown, S. W. Organisms which persist in desiccated microbial mat from the Laguna Figueroa, Baja California, Mexico. Master of Arts. Boston University. (Published: Brown, S., L. Margulis, S. Ibarra and D. Siqueiros, 1985, Desiccation resistance and contamination as mechanisms of Gaia, **BioSystems** 17: 337-360.)
- Dyer, B. D. Protoctists from the microbial communities of Baja California, Mexico. Doctor of Philosophy. Boston University.
- Fracek, S. P., Jr. Tubulin-like proteins of *Spirochaeta bajacaliforniensis*, a new species from a microbial mat community at Laguna Figueroa, Baja California del Norte, Mexico. Doctor of Philosophy. Boston University. (Published: Fracek, S. P., Jr. and J. F. Stolz, 1985, *Spirochaeta bajacaliforniensis* sp. n. from a microbial mat community at Laguna Figueroa, Baja California Norte, Mexico, **Archives of Microbiology** 142: 317-325.)
- Mehos, D. C. Symbioticism as a biological principle: Ivan Wallin's theory of organic evolution. Master of Arts (History Department). Boston University. (second reader)
- Stolz, J. F. The effects of catastrophic inundation, (1977-1983), on the composition and ultrastructure of a stratified microbial mat community, Laguna Figueroa, Baja California, Mexico. Doctor of Philosophy. Boston University.
- 1985 Obar, R. Purification of tubulin-like proteins from a spirochete. Doctor of Philosophy (Chemistry). Boston University. (second reader) (Published: Obar, R. and J. Green, 1985, Molecular archaeology of the mitochondrial genome, **Journal of Molecular Evolution** 22: 243-251.)
- 1986 Moynihan, B. E. *Chlorella desiccata* sp. n.; a new *Chlorella* forming desiccation-resistant cysts. Master of Arts. Boston University.
- 1987 Bermudes, D. G. Distribution and immunocytochemical localization of tubulin-like proteins in spirochetes. Doctor of Philosophy. Boston University.
- 1988 Fleischaker, G. R. Autopoiesis: System logic and origins of life. Doctor of Philosophy (University Professors Program, philosophy of biology). Boston University.
- 1989 Stricker, J. A. Evidence for centrin- and tektin-like proteins in *Spirochaeta halophila*. Master of Arts. Boston University.
- Tzertzinis, G. Immunochemical characterization and partial amino acid sequence of tubulin-like protein from *Spirochaeta bajacaliforniensis*. Doctor of Philosophy. Boston University. (second reader)

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- 1990** Enzien, M. V. Microbial mats: Early diagenesis and studies of live and fossil organisms. Doctor of Philosophy. Boston University.
Kang, J. K. Cyanobacteria, algae and fungi of the Black Zone at Bailey Island, Maine: Composition, ecology and comments on cyanobacterial systematics. Master of Science. University of Massachusetts, Amherst. (Reader, committee member)
- 1991** Mas-Castellà, J. Acumulación de poli-b-hidroxialcanoatos por bacterias: Distribución en la naturaleza y biotecnología. Doctor of Philosophy. Universidad de Barcelona. (Reader and member of tribunal)
- 1992** Ashen, J. B. Ultrastructure of new microbial mat and termite spirochetes and the symbiotic origin of undulipodia. Master of Science. University of Massachusetts, Amherst.
Hinkle, G. J. Symbiosis and organelle origins: Undulipodia and the origin of eukaryotes. Doctor of Philosophy. Boston University.
- 1993** Olendzenski, L. The cyst-forming ciliate *Pseudocohnilembus pusillus*: Growth and encystment in response to salinity, pH, desiccation and food depletion. Master of Science. University of Massachusetts, Amherst.
- 1995** Antequera, V. P. Análisis comparativo de la organización genómica de la familia Chromatiaceae. Revisión de la actual clasificación. Doctor of Philosophy. Autonomous University of Barcelona. (Reader, member of tribunal).
- 1996** Teal, T. H. Spirochetes and a new bicosoecid, *Acronema sippewissettensis*, from anoxic salt marsh habitats: Morphological studies. Master of Science. University of Massachusetts, Amherst.
- 1997** Kolnicki, R. Karyotypic fissioning and lemur evolution. Master of Science. University of Massachusetts, Amherst. (Second reader, member of committee)
- 1998** D'Ambrosio i Palau, U. Evolutionary and structural study of *Cadudeia versatilis* sp. nov. ("Rubberneckia") and *Snyderella tabogae*: Parabasalids (amitochondriate protists) in the dry wood-eating termite *Cryptotermes cavifrons*. Master of Science. University of Massachusetts, Amherst.
- 1999** Dolan, M. Amitochondriate protists: Symbiotic trichomonads of dry-wood-eating termites. Doctor of Science. University of Massachusetts, Amherst.
Jorgensen, J. Z. Isolation and cultivation of spore-forming filamentous bacteria from *Porcellio scaber*. Master of Science. University of Massachusetts, Amherst.
- 2000** Navarrete, Antoni. Caracterización ecofisiológica y bioquímica de los tapetes microbianos del delta del Ebro. Doctor of Biological Sciences. University of Barcelona, Spain. (Reader, member of tribunal).

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- 2002** Melnitsky, Hannah. Termite hindgut symbionts: Clues to early eukaryotic evolution. Honors thesis, Bachelor of Science. University of Massachusetts, Amherst.
- 2003** Bateman, Kenneth. (in progress). Master of Science. University of Massachusetts, Amherst. (Second reader, member of committee).
- 2004** Werle, Sean F. The biology, ecology and cytogenetics of the genus *Axarus* (Diptera: Chironomidae) in the Connecticut River. Doctor of Science. University of Massachusetts, Amherst. (Reader and member of committee). Student Theses in progress
- Dunthorn, Micah. Bromeliad ciliates. Doctor of Sciences. University of Massachusetts, Amherst.
- Scofield, Bruce. Biological cycles and geocosmic sciences: Astrology as natural history maligned. Doctor of Sciences. University of Massachusetts, Amherst.
- Stephens, Elizabeth. Symbiotic bacteria on termite protists and *Spirochaeta-Thermoplasma* co-cultures. Doctor of Sciences. University of Massachusetts, Amherst.