NATIONAL ACADEMY OF SCIENCES

RALPH EMERSON

1912—1979

A Biographical Memoir by

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Biographical Memoir

Photograph by Dr. Marion Cave; courtesy, M. Fuller

Ralph Emerson

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April 19, 1912–March 12, 1979

BY MELVIN S. FULLER

RALPH EMERSON, who became one of the giants in American mycology, was born in New York City on April 19, 1912. He was the great-grandson of Ralph Waldo Emerson's brother and the youngest of five children born to Haven and Grace Emerson. Haven Emerson, a physician and pioneer in the profession of public health, was a dedicated, strong-willed, and hard-working man. His unflinching adherence to basic values and principles had a profound effect upon the lives of his children. Ralph and Robert never escaped his influence. Both became distinguished biologists and were members of the National Academy of Sciences. Another son, Jack, while not an academician, founded and successfully ran the J. H. Emerson Instrument Company in Cambridge, Massachusetts. One daughter (Ethel) was an M.D., the other (Ruth), a successful teacher.

Although Haven Emerson worked hard at his chosen profession, he had an intense interest in gardening and forestry. These hobbies, and very likely the pressures of five

NOTE: I have presented a biographical sketch of Ralph Emerson elsewhere (*Mycologia*, 72:857–67) and cited herein as Fuller (1980). Another important biographical sketch, cited herein as Cantino (1979) appeared in *Experimental Mycology*, 3:107–20. The present sketch emphasizes the research contributions of Ralph Emerson.

children in New York City during the summer, resulted in the acquisition of a farm at Southold on Long Island. It was the family place at Southold that Ralph regarded as home, and although he was to spend most of his adult life as a Californian, he never missed a chance to return there with friends and family to renew memories of those carefree summers when he was growing up. All of his pre-college education was received at the Ethical Culture Schools of New York City. In 1929 he entered Harvard University, where he was awarded the bachelor's (cum laude) and master's degrees (1933, 1934) and the Ph.D. (1937). It was during those early years at Harvard that he came under the influence of William H. Weston, who introduced him to the water molds and to *Allomyces*; the latter fungus would receive a major portion of Emerson's research attentions. From 1937 through 1939, Ralph was in the laboratory of Professor F. T. Brooks at Cambridge University in England as a Rockefeller Foundation National Research Council Fellow. While in Cambridge he continued to study *Allomyces* and to isolate water molds. His thesis work with *Allomyces* had convinced him that in order to understand the aquatic fungi, one must isolate and grow them in pure culture. In 1939 he returned to Harvard University as a research fellow, where he continued his work with *Allomyces* and put the finishing touches on his now classical (Emerson, 1941) monograph of the genus.

In 1940 Ralph Emerson joined the faculty of the Department of Botany of the University of California at Berkeley. There, except for a short period during World War II and the usual sabbatical leaves, he would spend his entire career. Emerson was hired to replace the distinguished marine algologist, William Albert Setchell, and, in preparation for teaching a course on the algae, he spent the summer of 1941 at the Hopkins Marine station in Pacific Grove, where he took Gilbert M. Smith's course on the algae. Those early years at Berkeley, however, were devoted to teaching general botany and, as other faculty became involved in the war effort, Ralph found himself teaching introductory physics as well.

On July 17, 1942 he married Enid Merle Budelman, a music major who found herself taking introductory botany with Ralph. Ralph and Merle had two children, Peter, born on September 20, 1944, and Grace, born on February 13, 1947.

By 1944 few students remained at Berkeley, and Ralph was asked to join the U.S. Department of Agriculture's Emergency Rubber Project at Salinas, California, as a microbiologist. Rubber was being made from the guayule shrub but, during the retting of the guayule, undesirable thermogenesis was caused by microorganisms and temperatures often reached 60°C. With his colleague, Paul J. Allen, Ralph isolated numerous thermophilic fungi and bacteria from the retting guayule. Although the war ended in 1945, and his association with the Emergency Rubber Project was terminated, Ralph took many of these cultures back to the Berkeley campus in 1946, and they formed the basis of future research. Ralph would never teach a course on the algae, because phycologist George F. Papenfuss had been hired and was on the campus when he returned. Instead, he developed an outstanding course on "phycomycetes" and "ascomycetes." This course became famous in Berkeley (Fuller, 1980; Cantino, 1979), and through his own writings (Emerson, 1958) and those of his students, the Emerson methods of preparing living fungi for class study became an important contribution to mycology. In 1948, with his first Guggenheim Fellowship in hand, Ralph returned to Harvard to spend a year with W. H. Weston. New water molds would be isolated and cultured (see Cantino, 1979), including relatives of *Allomyces* and representatives of fermentative forms that produced lactic acid. These latter fungi could not be kept in culture prior to the discovery by Emerson and his first graduate student, E. C. Cantino (1948), that daily neutralization with sterile base allowed them to grow, and sometimes reproduce. Emerson was already involved in unraveling the puzzle of fungi growing at lowered oxygen levels and in the complete absence of oxygen. His subsequent sabbaticals (1956-1957 and 1972-1973) would be spent in Costa Rica stalking those water molds adapted to life in pools and streams where oxygen was limiting.

Cantino (1979) and I (Fuller, 1980) have chronicled Emerson's contributions as a teacher, member of the university community in Berkeley, and as a member of the scientific community at large. He always gave generously of himself, and at times his own research suffered; yet, as I hope to document here, the research was extremely important and the contribution great. Emerson always spoke with pride of his Berkeley colleagues who were members of the National Academy of Sciences. Yet he, as his own harshest critic, never expected to be elected to membership in the Academy—his students and other activities had kept him from amassing the bibliography he felt was essential to membership. How gratifying it was to him, and to those of us who benefited from his generosity, when Ralph Emerson was elected to membership in the National Academy of Sciences in 1970 and recognized for, in addition to his research, his abilities in teaching and in dealing with the problems of the societies that he served as an officer.

In 1977, following the Second International Mycological Congress, Ralph and his former student Howard Whisler set off on another quest for tropical aquatic fungi. A major goal for Ralph was to rediscover *Blastocladiella variabilis*, an organism described by Harder and Sörgel in 1939 from soil collected in the Dominican Republic. He returned from this trip to the West Indies with many soils from which he would attempt to isolate aquatic fungi. During the year of 1977–1978, he isolated numerous fungi from these soils and was looking forward with enthusiasm to retirement and the opportunity to spend all of his time with these and other aquatic fungi. His students had planned to honor him and his impending retirement with a celebration and workshop in Athens, Georgia, during August of 1978. But something was amiss. He became ill during the spring of 1978 and, following numerous periods in and out of hospitals, learned that he was a victim of cancer. He fought hard and vowed that he would be at the workshop, but by mid-July he sadly indicated that he would be unable to attend. On March 12 of 1979 the courageous year-long struggle ended.

As one reviews the research contributions of Ralph Emerson, it is clear that he practiced what he preached—that one should study the biology of an organism or group of organisms and not just the taxonomy, ecology, physiology, or what have you. Had Emerson been content with less than the whole of biology, he could not have made the significant contributions reviewed below. For my convenience, I am dividing his research into the following categories: the biology of *Allomyces*, thermophily in fungi, fermentative water molds, and teaching-performing fungi. Many, although not all, of the twenty-two Ph.D. students he had are mentioned here, because Emerson generously turned over his exciting research problems to students.

THE BIOLOGY OF *ALLOMYCES*

One doesn't know when Ralph Emerson first settled upon *Allomyces* as a subject for study. It is clear, however, that by the time Ralph received his bachelor's degree in 1933, he had come under the influence of that great teacher of mycology, William H. Weston, and had decided upon the study of *Allomyces.* Ralph spent the summer of 1933 working with C. B. van Niel at the Hopkins Marine Station of Stanford University. He knew that, in studying the genus *Allomyces,* he wanted to be able to grow the fungus in pure culture. With the aid of van Niel, he initiated nutritional studies and developed a yeast starch medium (YpSs) that is still the medium of choice for *Allomyces,* as well as many other aquatic fungi. When Emerson began his studies on *Allomyces,* the life histories of some isolates had been worked out, but there was considerable confusion as to nomenclature and species descriptions. For his Ph.D. studies, Emerson gathered together fifty-one isolates of the genus *Allomyces.* By the time (1939) he finished putting together his now classical monograph (Emerson, 1941) of the genus *Allomyces,* he had worked out the life cycles of the different species and experimentally determined those characteristics that were least variable and, hence, usable for distinguishing species, as well as for grouping them in clear-cut subgenera. This monograph is exemplary and a starting point for modern biosystematic work with water molds. Emerson spent the two years in Cambridge writing up this monograph of *Allomyces* and doing additional crosses between strains. With Dennis Fox he identified the orange pigment in the male gametangia of *Allomyces* as γ-carotene. This was the first positive determination of the chemical nature of a pigment in the cytoplasm of an aquatic fungus.

Early in 1948 Ralph convinced his second Ph.D. student, John L. Ingraham, to take up the nutritional study of *Allomyces* that had been started fifteen years earlier with C. B. van Niel. They succeeded in developing a minimal medium for *Allomyces.* Leonard Machlis, a colleague on the Berkeley faculty who had been working on the mineral nutrition of green plants, aided Ingraham and Emerson in their studies and was, in the process, converted to the study of *Allomyces,* a fungus that occupied most of Machlis' research time for the remainder of his career.

When Ralph returned to Harvard for a sabbatical in 1948-1949, he found Weston with a student, Charles M. Wilson, who was a most able chromosome cytologist. Wilson might have done his thesis on *Sordaria* had he not come under the influence of Ralph Emerson. Instead, he would do his thesis on meiosis in *Allomyces*. This study, which yielded the first published findings in 1949 (Wilson and Emerson), would constitute the first critical step-by-step study of meiosis in an aquatic fungus. These cytological observations helped Emerson to better understand the crosses he had made earlier at Harvard and in Brook's laboratory at Cambridge. In the fall of 1950, Wilson went to Berkeley to spend a postdoctoral year with Emerson. The results of that collaboration, along with seventeen years of data from crosses Emerson had made with *Allomyces*, would yield another landmark paper on *Allomyces* and fungi in general. For the first time, a microorganism that could be grown in culture under controlled conditions was used for a combined study of taxonomy, natural and artificial hybridization, polyploidy, and chromosome behavior. Emerson thought the stage was set to make *Allomyces* as important to genetics as *Neurospora* and *Drosophila* had become. In spite of genetic studies by later students, Jean Foley Grieder and Sharon K. De Long, however, the unraveling of inheritance mechanisms in *Allomyces* eluded Emerson, and the potential of *Allomyces* as an organism for genetic study is yet to be realized. Had this work by Emerson and Wilson not been done, however, the first chemical characterization of a plant sex hormone would not have been possible. Machlis and his colleagues, who discovered and characterized sirenin, were able to accomplish their work on the sex hormone because they used strong male and female strains resulting from the crosses of

Emerson and Wilson. After the fifties and early sixties, Emerson became more involved with other fungi, but *Allomyces* was always there on the back burner for interested students to work on. Gina Purelis Skucas would work with the formation, composition, and ultrastructure of resistant sporangia. Phyllis Morrison worked on the control and ultrastructure of gametangial development in *Allomyces*. With Jack Robertson, Emerson described *Allomyces reticulatus*, the discovery of which resulted from Emerson's growing interest in what others would call the ecology of fungi. Although Emerson had not succeeded in bestowing genetic fame on *Allomyces*, he had, through his exemplary work, made *Allomyces* world famous. By the 1960s laboratories all over the world were studying *Allomyces*; the number of laboratories studying *Allomyces* continues to grow.

THERMOPHILY IN FUNGI

In an earlier characterization of Ralph Emerson, I (Fuller 1980) said that he lived by the motto that: "if a job is worth doing, it is worth doing well." Thus, in 1944, when he was called upon by the U. S. Government to serve as a microbiologist with the Emergency Rubber Project in Salinas, California, he was not satisfied to just isolate those fungi and bacteria responsible for thermogenesis in the retting guayule shrub. When his relationship to the project was terminated, he did not leave what he had done in Salinas behind and return to the water molds. There were too many questions to be answered about what fungi grew at temperatures of 40°–60°C and the biological implications of their presence in this heated environment. The cultures of fungi went back to Berkeley with Emerson, and not long after that he and a student, Donald G. Cooney, set about gathering together existing cultures and isolating new cultures of all the previously known thermophilic fungi. With Emerson's usual apologies for publication so long delayed, Cooney and Emerson published their definitive book on thermophilic fungi in 1966. This monograph gave a detailed analysis of the morphology, development, systematics, and cultural behavior of this highly specialized segment of the fungal world. It is surprising that more people who heard Emerson's exciting lectures on microbial thermogenesis didn't take up the subject. Michael Tansey, however, a student in the late 1960s, pursued the role of fungi in causing spontaneous combustion of sawdust piles in Northern California and continues an active research program on the biology of thermophilic fungi.

FERMENTATIVE WATER MOLDS

Cantino (1979) has eloquently described Emerson's passion for and methods of baiting with caged apples to isolate *Blastocladia* and related fungi. Emerson had learned the basics from Weston, who had been taught by Thaxter. Wherever you went, you baited for and isolated water molds. Emerson had a real fondness for those organisms that turned up in the more foul habitats or were contained in bacterium-filled pustules on the baits. The organisms he located in such places were commonly members of the Blastocladiales and Leptomitales. Early attempts to grow these fungi in pure culture were frustrating. Although thalli and spores that were free of bacteria could be obtained, they only grew for a short time on agar media before turning black and dying. Working with Edward C. Cantino, Emerson would learn why these organisms were dying. Most of these fungi, whether growing in an atmosphere of 21 percent oxygen, or under conditions where oxygen was all but absent, were pumping out large quantities of lactic acid that killed them if the cultures were not neutralized. Subsequently, lactic acid production would be discovered in a wide range of aquatics by Emerson and his students: E. C. Cantino, John Ingraham, Jean M. Crasemann, Clarence G. Golueke, Frank H. Gleason, and Richard A. Nolan.

In 1957 Emerson rediscovered the remarkable fungus, *Aqualinderella fermentans*, that was originally found by David H. Linder, and later by Emerson's teacher, Weston. For years Emerson kept this fungus alive by growing it on sand pears in water in gallon jugs where he had burned a candle. With student Abraham A. Held, he would discover the reasons for this "witchcraft" in the growing of *Aqualinderella. Aqualinderella* was obligately fermentative in its metabolism and would grow without oxygen (leuco methelene blue) but grew better with carbon dioxide supplemented air. At the time of his death he was still involved with explaining the role of CO_2 in the metabolism of facultatively anaerobic fungi. Had Emerson lived, I am sure his curiosity would have resulted in his studying rumen chytrids, a group of obligately anaerobic "water" molds being discovered at the time. Emerson's final paper, to be published with his last student Donald A. Natvig and entitled *Adaptation of Fungi to Stagnant Waters*, was presented in a symposium on the fungal community at the Second International Mycological Congress in Tampa, Florida, in August of 1977. Through his systematic and meticulous pursuit of these acid producing fungi, Emerson had put together a contribution that will be as much of a landmark of fungal ecology as his work on the systematics of *Allomyces* is in fungal taxonomy.

TEACHING—PERFORMING FUNGI

Emerson was an outstanding teacher of mycology. Although his colleagues throughout the world regarded him as an expert on aquatic fungi, he was remarkably well informed and fascinated by all fungi, and particularly by their biological activities. When he taught mycology, he made certain that students studied living fungi performing as they would in nature, but with fewer distractions. As a student in his courses, it was easy for one to take the parade of living organisms for granted. In fact, much research had gone into learning how to make the fungi students observed perform on schedule. Many theses had their beginnings in this collection of living fungi that had been assembled for teaching. Furthermore, much that we know and take for granted with respect to making the aquatic fungi perform in the laboratory was first worked out by Emerson in conjunction with his teachings.

In conclusion, although many would say that Emerson was so renowned as a teacher that it overshadowed his reputation as an investigator, I would disagree and argue that his teaching and research were inseparable. He was a missionary in a sense, and he delighted in sharing his curiosity about the biology of fungi. All one needed to do was listen, and those of us who had that opportunity benefited enormously from Ralph Emerson. Mycology is a more exact and more exciting field today because of his contributions to it.

TO MRS. MERLE EMERSON, our former colleagues at Berkeley, and others, I am grateful for the help provided in putting together this and my earlier contribution on Ralph Emerson.

HIGHLIGHTS IN THE CAREER OF RALPH EMERSON

1933	B. S., Harvard University
1934	M. A., Harvard University
1935	Photographer, Fleischman Expedition
1937–39	National Research Council Fellow in Botany, Cambridge University
1939–40	Research Fellow in Biology, Harvard University
1940	Instructor in Botany, University of California, Berkeley
1944	Assistant Professor, University of California, Berkeley
1944–46	Microbiologist, Emergency Rubber Project, USDA
1948	Associate Professor, University of California, Berkeley
1948–49	Guggenheim Fellow, Harvard University
1950	Special Lecturer, London University
1952	Elected to membership, American Academy of Arts and Sciences
1953	Professor, University of California, Berkeley
1955–56	Special Assistant to the Chancellor, University of California, Berkeley
1956	President, Mycological Society of America
1956–57	Guggenheim Fellow, Costa Rica
1963–64	Research Professor, Miller Institute for Basic Research, University of California, Berkeley
1963	Citation for Excellence in Teaching, University of California, Berkeley
1964	Merit Award, Botanical Society of America
1967	President, Botanical Society of America
1967–71	Chairman, Department of Botany, University of California, Berkeley
1970–79	Coeditor, *Archives of Microbiology*
1970	Elected to membership, National Academy of Sciences
1971	Vice President, British Mycological Society
1977	Faculty Research Lecturer, University of California, Berkeley
1977	Executive Vice President, Second International Mycological Congress

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