NATIONAL ACADEMY OF SCIENCES

KENNETH BRYAN RAPER

1908—1987

A Biographical Memoir by
ROBERT H. BURRIS AND ELDON H. NEWCOMB

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Kenneth B. Pyle

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July 11, 1908–January 15, 1987

BY ROBERT H. BURRIS AND ELDON H. NEWCOMB

SOME ASSOCIATE Kenneth Raper with the penicillia and penicillin, others with the aspergilli; developmental biologists may remember him most for having introduced *Dictyostelium discoideum* as a superb subject for study. His friends and associates will remember Ken not only as an outstanding, versatile scientist but also as an unusually warm human being.

EDUCATION AND EARLY LIFE

Kenneth Bryan Raper was the seventh child and the sixth son of William F. and Julia Crouse Raper. With the arrival of the seventh son, John—also to become a member of the National Academy of Sciences—the family was completed. The farm in Davidson County, North Carolina, provided—with its tobacco fields and small dairy herd—a satisfying, if not affluent, living.

Each of the Raper children was expected to carry his or her share of the chores, the bright-leaf tobacco requiring a great deal of hand labor. The farm also had two deciduous forests of giant oaks, maples, and hickories, and an area of magnificent mature pines, all of which were sacrificed during the Depression.

Social life in Welcome, North Carolina, centered on the local church and school and entailed a good deal of visiting

among relatives and friends. The Raper family held membership in the Friedberg Moravian and Mount Olivet Methodist churches, favored primarily because of their proximity, though Mount Olivet had also been the church of Ken's father.

Both churches emphasized music. Ken participated in their vocal groups and conceived a lifelong appreciation for music, though he was not among the Rapers who became proficient on an instrument. His brother John, on the other hand, was talented enough on the trumpet to consider music as a career. Education was of prime importance to the family, and despite limited resources, all the Raper children went to college, six earned M.S. degrees, and three completed the Ph.D.—Arthur in sociology, Ken and John in biology.

Ken enjoyed school, did well, and was moved from the sixth to the eighth grade based on a county-wide entrance examination. Before this move he attended a two-room school in Enterprise, travelling the two miles to school on foot, or in severe weather, by horse-and-buggy. The wooden schoolhouse was heated with wood-burning stoves that served as rallying points before classes started. Classes at the front of the room did recitations while other classes at the back mastered their lessons.

Ken retained pleasant memories of his high school years. He was one of twelve in the first class to graduate from Arcadia High School, to the construction of which the Raper family had donated land, lumber, and labor. The school covered grades eight through eleven, and the pupils studied English, French, Latin, algebra, geometry, civics, and some chemistry—but no biology. Ken particularly enjoyed chemistry experiments and the school library, which included the *Book of Knowledge*. He gained recognition in debating and public speaking and as a senior won a gold medal in decla-

mation. He also enjoyed sports, though he never took part in inter-school competitions.

Kenneth's older brothers and sister had gone to college and he assumed he would also. In the fall of 1925 he enrolled at the University of North Carolina in Chapel Hill, where two brothers still in residence helped to ease the transition. But the family had money enough for only the fall quarter, and the problem of how to accumulate enough for the winter and spring loomed large. Ken earned his meals by waiting on table in the college dining hall. He collected suits for a cleaner, delivered the *Daily Tar Heel*, sold felt pennants at ball games, and personalized pillows as Christmas gifts.

At the university Ken enjoyed his classes in English, American history, and mathematics. Then, during his second semester, he met the botanists W. C. Coker, H. R. Totten, and J. N. Couch, who raised his interest in plants and launched him on his scientific career. He was fascinated by his studies, and his enthusiasm impressed his professors sufficiently for them to offer him a $260-a-year undergraduate assistantship. "I have received no offers since," he wrote late in life, "that pleased me more."

The assistantship allowed him to spend more time in the Botany Department, and Professor Couch gave him space to help in a study of the symbiotic relationship between scale insects and fungi of the genus *Septobasidium*. He always considered it a great privilege to have worked with John Couch. Ken's undergraduate minor was history; later he sometimes wished it had been chemistry.

As a junior Ken Raper took a mycology course from W. C. Coker, who was interested in the water molds, Saprolegniaceae. Ken recovered several genera of water molds from surrounding field and forest areas. His descriptions impressed Coker, who urged him to publish. At the age of

twenty, K. B. Raper's first paper appeared in the September 1928 issue of the North Carolina Academy of Sciences's journal, *The Journal of the Elisha Mitchell Scientific Society.*

WASHINGTON, D.C.: THE DEPARTMENT OF AGRICULTURE'S DIVISION OF SOIL MICROBIOLOGY

Before graduating in 1929 Raper took a competitive civil service examination for a position as junior mycologist with the U. S. Department of Agriculture. When Charles Thom, a mycologist with USDA, visited Chapel Hill, he sent word ahead to Couch and Coker that he wanted to meet this Kenneth Raper. Thom was starting a federal Division of Soil Microbiology, and he signed Raper up to come to Washington immediately after graduation. He arrived at Thom's office at the USDA building near the Washington Monument on July 5, 1929. Thereafter the two collaborated closely until Thom's death in 1956.

Although Thom was a crusty character, Raper found working with him at an adjacent desk to be a marvelous experience. Thom was both knowledgeable and willing to share his vast experience of mycology. He also knew almost everyone in the field, and Ken had the opportunity to meet them when they dropped in. Acting on Thom's suggestion, Ken enrolled in evening courses in bacteriology and biology at George Washington University and completed his M.S. degree within two years.

The mycology laboratory was next to the Mall and the Smithsonian museums, and Ken thoroughly enjoyed a quick museum visit at noon and more leisurely tours on weekends. Washington offered many lectures and concerts, and Ken found Rock Creek Park a great place in which to hike. But most of all he remembered Washington as the place where he met and married Louise Montgomery Williams, whom he

affectionately characterized many years later as his "beloved companion, counsel, and benevolent critic."

Thom assigned Raper the task of maintaining and becoming familiar with a large collection of molds. In Ken's earlier experience the penicillia and aspergilli had been treated as weeds, but in the Thom collection they were dominant, and he had to develop an appreciation for them.

Thom then suggested that Ken complete his graduate education by studying at Harvard. After receiving a tuition fellowship and the assurance that his position with the Department would be kept open, Raper moved to Harvard in 1933 to work with William H. Weston.

During a brief summer vacation in North Carolina before entering Harvard, Raper had collected some forest leaf-mold while hiking in the Appalachian Mountains. From litter collected at a site in western North Carolina's Craggy Mountains, he isolated a remarkable new species of cellular slime mold belonging to the genus *Dictyostelium*. He realized that a number of the unusual structural and behavioral features exhibited by this species made it especially attractive for experimental work.

HARVARD YEARS (1933–1935)

At Harvard, Ken showed Weston cultures of his new species of *Dictyostelium* and asked whether he could do his thesis work on it. Though Weston was unfamiliar with the organism, he agreed.

Ken named the new species *Dictyostelium discoideum* and described it in an article in the *Journal of Agricultural Research* in 1935. He then began a two-year exploration of the behavior of the new slime mold. In an extensive series of ingenious experiments, he laid the groundwork for the later adoption of this organism as a model system in which the sorts of intercellular communications and controls that operate in mul-

ticellular organisms could be investigated on a more primitive, approachable level.

Ken found his years at Harvard both demanding and rewarding. His researches were highly successful and he established many helpful friendships. Like so many others, he found "Cap" Weston to be an excellent teacher and counselor. Ken also discovered that Weston rarely assumed authorship of papers and preferred for students to publish under their names only.

In 1936, armed with his Ph.D., Ken returned to Washington with a promotion from junior to assistant mycologist and a $200-a-year raise. The leveling experiences of the Great Depression are difficult to appreciate today.

PEORIA (1940–1953)

During Ken's absence, Thom had delayed several projects he wished to finish, and Ken once again took up the study of the aspergilli and penicillia. Together they concentrated on the various molds described as species of *Aspergillus glaucus* and *A. nidulans* and clarified the nomenclature and descriptions of the two groups. With the taxonomy of these and several other troublesome groups clarified, they were able some years later to publish their *Manual of the Aspergilli* (1945).

During this period Raper also worked on *D. discoideum* and wrote up his thesis work for publication, papers that, a few years later, sparked great interest in this slime mold.

The thirties in America were marked not only by the Great Depression but also by substantial surpluses of farm products in some parts of the country. Seeking ways to use these surpluses, Congress authorized the construction of four regional USDA research laboratories. The Northern Regional Research Laboratory (NRRL) in Peoria, Illinois, was assigned the task of exploring the fermentation of farm com-

modities to produce valuable new derivatives, and a large proportion of the USDA fermentation laboratory staff in Washington was transferred to Peoria.

The Thom collection of microorganisms was to serve as the nucleus of a collection at Peoria to be explored for their potential in the production of citric, gluconic, lactic, and itaconic acids. In 1940 Kenneth Raper was asked to organize and supervise the collection.

The Rapers arrived in Peoria before any laboratory equipment had been installed, and the USDA group had to improvise benches before they could continue the work begun in Washington on itaconic acid. In the first recorded case of an attempt to improve the product yield of a mold by mutation, Alexander Hollaender sent them—from Bethesda, Maryland—irradiated cultures of *Aspergillus terreus* whose best mutants gave somewhat increased yields. Ken Raper, however, isolated a strain from Texas soil that surpassed even the mutants.

Penicillin

Within the first year of operation of the Peoria laboratory, its focus shifted to the production of penicillin. At Oxford University in England, Florey and Heatley had been isolating penicillin. In animal and (very limited) human experiments, they had demonstrated spectacular therapeutic success.

In the summer of 1941 the two British researchers came to the United States to enlist aid in improving yields of penicillin, which from surface cultures at that time were about two Oxford units per ml. Not receiving an enthusiastic welcome from the pharmaceutical firms, they turned to the National Academy of Sciences, which sent them to Dr. Thom. Thom suggested the new laboratory at Peoria as having the requisite flexibility and expertise in fermentation technology and the willingness to start studies on penicillin production

immediately. Penicillin certainly must have sounded more exciting and challenging than itaconic acid!

At Peoria and across the country the search was on for ways to improve the medium for penicillin production, to produce penicillin in submerged cultures, and to develop more productive strains of the mold. Since only Fleming's strain of *P. notatum* was known at that time to produce penicillin, and it produced it only in surface culture, Raper's laboratory concentrated on finding more productive strains.

This work on penicillin was an unusually successful example of cooperative research. Though the NRRL played the leading role, there was a remarkable sharing of information among industrial laboratories, laboratories at Cold Spring Harbor, the University of Wisconsin, the University of Minnesota, and elsewhere. A newsletter distributed the latest information, and the collaborating laboratories met all three of their goals. Before D-Day, the Allies had an adequate supply of penicillin on hand to treat their casualties.

Growing the Fleming strain in surface culture was very cumbersome, but the strain did not produce penicillin in submerged culture. When NRRL strain 832 (from the Peoria culture collection) was shown to produce some penicillin in submerged culture, a wider search was sparked to find a more effective organism. Cultures from many laboratories were tested in Peoria. But the best strain, NRRL 1951, came from a moldy cantaloupe brought to the laboratory by a Peoria housewife in July 1943.

In subsequent years the press perpetuated many stories—mostly apocryphal—about "Moldy Mary," but it is fact that the housewife's strain of *Penicillium chrysogenum* immediately proved equal to the best surface strains and was superior in submerged culture to NRRL 832, the strain generally adopted in industry. An even better subculture, NRRL 1951-B25, produced around 250 as compared with the earlier 2

units per ml. and was immediately put to industrial use. Before the war ended, X-radiation at the Carnegie Institution in Cold Spring Harbor and testing at the Universities of Minnesota and Wisconsin had given rise to strains producing 1,000 units per ml. in submerged culture, allowing for a drop in price from twenty dollars to three cents (wholesale) per 100,000 units. The pharmaceutical industry later took over efforts to raise yields and brought them to their present levels of some 50,000 units per ml.

UNIVERSITY OF WISCONSIN AT MADISON (1953–1987)

After the war priorities were rearranged at Peoria and a number of investigators, responding to the emerging interest in antibiotics other than penicillin, left for positions in the pharmaceutical industry. In 1946 Ken Raper welcomed an invitation to teach a course in industrial microbiology as a visiting professor in the botany department of the University of Illinois. Though it involved driving to Urbana on Saturday mornings, the students were mostly veterans who worked hard, and Ken enjoyed teaching them.

After retiring in the early forties, Dr. Thom had been appointed collaborator at the NRRL, where he came each year to work. He and Raper completed their book on the aspergilli and, in 1949, published their comprehensive *Manual of the Penicillia*—especially noteworthy, since the success of penicillin had raised the lowly penicillia to an exalted status.

The NRRL culture collection also acquired prominence, as individual researchers and pharmaceutical firms sought new antibiotics. Also the ruling of the patent office that cultures of patented organisms had to be deposited in support of claims caused many of these to be placed in the NRRL collection.

Although officially Ken had no time at Peoria to work on

Dictyostelium, he was able to search for cellular slime molds by routinely scanning the plates that had been seeded with soil for the recovery of penicillia. He then used lyophilization to preserve spores of the slime molds for later examination.

In 1952 Kenneth Raper accepted a joint appointment in bacteriology and botany at the University of Wisconsin and in January 1953 moved to Madison with Louise and their son Charles. He shared a course in industrial microbiology in the Department of Bacteriology and also taught a jointly listed course in mycology. He and Louise promptly became confirmed "Badgers."

Ken Raper found it easy to make the transition to academic life at the University of Wisconsin. He had known E. B. Fred, president of the University, for many years, and had worked closely with a number of the faculty during the years of joint research on penicillin, including J. F. Stauffer, Myron Backus, W. H. Peterson, M. J. Johnson, and Elizabeth McCoy.

Though teaching left him less time for research, Ken enjoyed the freedom to choose his research problems and the stimulus of working with graduate students. He now put his primary research emphasis on the cellular slime molds, which were becoming increasingly prominent in developmental biology. Since his old book on the aspergilli with Thom was by now both out of date and out of print, he undertook to modernize the treatment of the group, especially by incorporating information on the phenomena of heterokaryosis and heterothallism on which he and his colleagues had worked.

As for the cellular slime molds, no contemporary, comprehensive coverage of these organisms had yet been published. Attention had been focused primarily on *D. discoideum*, yet Raper had collected a number of other species that invited detailed examination.

He and his colleagues soon recognized that the Acrasi-

omycetes were not homogeneous but included two distinct subclasses, the Acrasidae and Dictyostelidae. Both had independent amoeboid cells that aggregated to form fruiting bodies, but the two groups differed in mode of aggregation, nuclear structure, and form of pseudopodia. Although Raper concentrated on the Dictyostelidae, he and his graduate student, Ann Worley Rahn, also examined and described several new members of the Acrasidae. Among these, the species *Fonticula alba* was of particular interest, because it appeared to span the two subclasses in some of its characteristics.

Raper and his colleagues sought to isolate slime molds related as closely as possible to the original strains described in the literature. They placed special emphasis on isolating organisms from soil, the source of many of the species originally described. Collaborators worldwide sent cultures for examination. A number of known species were recovered, while new species were also isolated and described.

Other aspects of dictyostelids examined by Raper and his colleagues included the development of macrocysts, methods for axenic culture of the slime molds, the phenomenon of cell aggregation, and the phototaxis of pseudoplasmodia.

By the time of his official retirement in 1979, Raper felt that he and his students had accumulated enough information to justify a book on the Dictyostelidae. His early "retirement" years were spent in producing *The Dictyostelids,* published in 1984 in collaboration with Ann Worley Rahn. Part I covers the biology of the cellular slime molds; Part II is devoted to the systematics of the dictyostelids.

HONORS AND PUBLIC SERVICE

Kenneth Raper was elected to the National Academy of Sciences in 1949 and was a member of its Council when the Academy met with President Kennedy in celebration of its

hundredth anniversary. He served on the NAS Committee on Science and Public Policy and on several committees of the National Research Council, including the executive committee of the Division of Biology and Agriculture, and the Merck and National Science Foundation Postdoctoral Fellowship Boards.

He served on a committee to strengthen the American Type Culture Collection, an assignment that required substantial effort since the ATCC, barely surviving, was housed in different institutions. In 1950 Ken signed a contract on a residence in Washington, D.C., to which the collection was moved. The importance of the American Type Culture Collection has become much more apparent in recent years. Ken Raper was pleased to establish it firmly in Rockville, Maryland, where it continues with a diverse home collection of 40,000 cultures and 70,000 distributed cultures a year.

Kenneth Raper also played a major role in *Biological Abstracts*' struggle to survive, serving for five years as a trustee and one year (1969) as vice president. A survivor of hard times, BIOSIS today publishes a number of abstracts journals and runs computer-operated retrieval services.

For several years Ken was associated with the International Union of Biological Sciences. He served as national chairman from 1962 to 1965 and was a member of the U. S. delegation at four General Assemblies abroad. As an outgrowth of the IUBS experience he was asked to chair the organizing committee for the XI International Botanical Congress held in Seattle in 1969. This involved several years of planning and put him in direct contact with prominent biologists from many countries.

CONCLUSION

Although his early scientific endeavors were not in academia, at the University of Wisconsin Ken taught for many years at the undergraduate and graduate levels. He found

teaching both challenging and enjoyable and was particularly fond of laboratory courses, where he could observe the blossoming interest of the students. Supervision of graduate students afforded him the opportunity to watch young investigators develop into productive scholars and lifelong friends.

Ken Raper always found time to participate actively in professional societies. Working as he did at the interface between plants and animals, between eukaryotes and prokaryotes, he interacted with microbiologists, mycologists, and botanists. Ken sometimes thought he might have spread himself too thin, but he also recognized that his interdisciplinary efforts gave him unusual insight as a "naturalist." By any standard, his was an interesting, satisfying and unusually productive career.

Kenneth Raper once listed what he considered to be his seven major contributions to science. These were:

(1) the isolation of better penicillin-producing molds during World War II, culminating in the isolation of NRRL 1951, the parent of virtually all strains of *Penicillium chrysogenum* used in the production of penicillin;
(2) the publication of authoritative books on the aspergilli and the penicillia;
(3) the establishment and initial direction of the Northern Regional Research Laboratory culture collection;
(4) the use of lyophilization to preserve the spores of filamentous fungi and of cellular slime molds;
(5) the discovery of *Dictyostelium discoideum*, a unique cellular slime mold, followed by pioneering investigations on the growth, morphogenesis, and cellular differentiation of this microorganism, which seemingly bridges the gap between the plant and animal kingdoms;
(6) sustained investigations of the cellular slime molds, culminating in publication of *The Dictyostelids* summarizing what is known of the natural history and systematics of the class Acrasiomycetes; and
(7) the help that he was able to give to students and associates in their development of a broader vision of the microbial world.

Kenneth Raper lived a full and happy life. In his later years he was alert and productive until stricken by a heart

attack. His death a week after the attack left his friends saddened but appreciative of having been able to share even a small portion of his life. We can only hope that there will be others with his high intelligence, insight, compassion, sense of duty, and zest for life.

THE INFORMATION in this sketch was taken almost entirely from an unpublished autobiography written by Kenneth Raper and submitted to the Academy in July 1986. It is available upon request in the Academy archives.

HONORS AND DISTINCTIONS

DEGREES

1929	A.B.	University of North Carolina, Chapel Hill
1931	A.M.	George Washington University, Washington, D.C.
1935	A.M.	Harvard University, Cambridge, Massachusetts
1936	Ph.D.	Harvard University (Austin Fellow)
1961	D.Sc.	University of North Carolina, Chapel Hill

PROFESSIONAL APPOINTMENTS

1929–1936	Junior mycologist, Bureau of Chemistry and Soils, USDA, Washington, D.C.
1936–1940	Assistant mycologist, Bureau of Plant Industry, USDA, Washington, D.C.
1940–1953	Microbiologist, senior microbiologist, and principal microbiologist, Northern Regional Research Laboratory, USDA, Peoria, Illinois
1946–1953	Visiting professor of botany, University of Illinois, Urbana
1953–1966	Professor of bacteriology and botany, University of Wisconsin, Madison
1966–1979	William Trelease Professor of Bacteriology and Botany, University of Wisconsin, Madison
1979–1987	Professor emeritus, University of Wisconsin, Madison

ACADEMIES AND LEARNED SOCIETIES

1949	National Academy of Sciences; Council, 1961–1964; Committee on Science and Public Policy, 1962–1966
1949	American Academy of Arts and Sciences
1958	American Philosophical Society
1954	Wisconsin Academy of Sciences, Arts and Letters

BOARDS AND COMMITTEES

AMERICAN TYPE CULTURE COLLECTION

1948–1962 Trustee
1952–1955 Chairman, Executive Committee

BIOLOGICAL ABSTRACTS (NOW BIOSCIENCES INFORMATION SERVICE)

1959 Vice president
1964–1969 Trustee
1966–1969 Executive Committee

NATIONAL RESEARCH COUNCIL

1953–1957 Merck Fellowship Board, National Science Foundation
1956–1961 Executive Committee, NRC Division of Biology and Agriculture

NATIONAL SCIENCE FOUNDATION

1961–1964 Selection Committee for Senior Postdoctoral Fellowships
1966–1969 Chairman of Biological Sciences

XITH INTERNATIONAL BOTANICAL CONGRESS (IBC)

1965 U.S. National Committee
1966–1969 Chairman, Executive Committee

INTERNATIONAL UNION OF BIOLOGICAL SCIENCES (IUBS)

1958 Chairman, American Delegation, XIIIth General Assembly, London
1961 American Delegation, XIVth General Assembly, Amsterdam
1964 Chairman, American Delegation, XVth General Assembly, Prague
1967 American Delegation, XVIth General Assembly, Montreux

MEMBERSHIPS

American Association for the Advancement of Science; Council (1970–1975)
American Institute of Biological Sciences

American Society for Microbiologists; Council (1954–1958)
American Society of Naturalists
American Society for Cell Biology
American Academy of Microbiology
Botanical Society of America
Mycological Society of America (charter member); President (1951)
Society for Developmental Biology
Society for General Microbiology (Great Britain)
Society for Industrial Microbiology (charter member); President (1953)

HONORS

1929 Phi Beta Kappa
1936 Sigma Xi
1946 Lasker Award (to Peoria Penicillin Team, NRRL)
1947 USDA Distinguished Service Award (to Peoria Penicillin Team, NRRL)
1957 George Ives Haight Traveling Fellowship for travel in France, Holland, and the United Kingdom
1960 Certificate of Merit, Botanical Society of America
1967 Charles Thom Award, Society for Industrial Microbiology
1981 Distinguished Mycologist Award, Mycological Society of America
1983 Honorary member, American Society for Microbiology
1984 Honorary member, British Mycological Society

UNIVERSITY COMMITTEES AND POSTS, UNIVERSITY OF WISCONSIN

1959–1960 Cancer Research Committee
1959–1960 Plant Science Colloquium
1960–1962 Secretary, Executive Committee, Faculty Biological Division
1970–1974 Executive Committee, Faculty Biological Division
1959–1965 Research Committee, Graduate School
1970–1971 President, Wisconsin Chapter of Sigma Xi
1971–1975 University Senate
1974–1975 President, Wisconsin Chapter of Phi Beta Kappa
1974–1977 Press Committee
1976–1979 Faculty Rights and Responsibilities Committee

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1928

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1932

With C. Thom. The arsenic fungi of Gosio. *Science* 76:548–50.

1935

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1937

Growth and development of *Dictyostelium discoideum* with different bacterial associates. *J. Agric. Res.* 55:289–316.

1940

Pseudoplasmodium formation and organization in *Dictyostelium discoideum*. *J. Elisha Mitchell Sci. Soc.* 56:241–82.

1941

With C. Thom. Interspecific mixtures in the Dictyosteliaceae. *Am. J. Bot.* 28:69–78.

1943

The culture collection of the Northern Regional Research Laboratory. *Chron. Bot.* 7:340–41.

1944

With D. F. Alexander and R. D. Coghill. Penicillin II. Natural variation and penicillin production in *Penicillium notatum* and allied species. *J. Bacteriol.* 48:639–59.

1945

With A. Hollaender and R. D. Coghill. The production and characterization of ultraviolet-induced mutations in *Aspergillus terreus*. I. Production of the mutations. *Am. J. Bot.* 32:160–65.

With D. F. Alexander. Preservation of molds by the lyophil process. *Mycologia* 37:499–525.

With C. Thom. *Manual of the Aspergilli*. Baltimore: Williams & Wilkins. 273 pp.

1949

With C. Thom. *Manual of the Penicillia*. Baltimore: Williams & Wilkins. 878 pp.

1952

A decade of antibiotics in America. *Mycologia* 44:1–61.

1953

With D. I. Fennell. Heterokaryosis in *Aspergillus*. *J. Elisha Mitchell Sci. Soc.* 69:1–29.

1954

With W. B. Cooke. The 1950 foray of the Mycological Society of America. *Mycologia* 46:670–79.

1957

Microbes—man's mighty midgets. *Am. J. Bot.* 44:56–65.

1958

With M. S. Quinlan. *Acytostelium leptosomum*: a unique cellular slime mold with an acellular stalk. *J. Gen. Microbiol.* 18:16–32.

1961

With T. M. Konijn. Cell aggregations in *Dictyostelium discoideum*. *Dev. Biol.* 3:725–56.

1962

With H.-R. Hohl. Nutrition of cellular slime molds. III. Specific growth requirements of *Polysphondylium pallidum*. *J. Bacteriol.* 86:1314–20.

1965

With J. C. Cavender. The Acrasieae in nature. III. Occurrence and distribution in forests of eastern North America. *Am. J. Bot.* 52:302–8.

With D. I. Fennell. *The Genus Aspergillus*. Baltimore: Williams & Wilkins. 686 pp.

1973

With G. W. Erdos and L. K. Vogen. Mating types and macrocyst formation in *Dictyostelium discoideum*. *Proc. Natl. Acad. Sci. USA* 70:1828–30.

The Acrasiomycetes. In: *The fungi*, eds. G. C. Ainsworth, F. K. Sparrow, and A. S. Sussman, vol. IV-B, pp. 9–35. New York: Academic Press.

1978

The penicillin saga remembered. *Am. Soc. Microbiol. News* 44:645–54.

1979

With A. C. Worley and M. Hohl. *Fonticula alba*: a new cellular slime mold (Acrasiomycetes). *Mycologia* 71:746–60.

1984

The dictyostelids. Princeton: Princeton University Press. 453 pp.