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ALFRED EDWARDS EMERSON

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A Biographical Memoir by
EDWARD O. WILSON AND CHARLES D. MICHENER

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SOMETHING ABOUT ants, termites, and other social insects attracts generalists, scholars who begin with a deep interest in basic entomology, or else acquire it, and who restlessly probe far beyond into such fields as evolutionary theory, biogeography, the history of science, and philosophy while conducting otherwise ordinary research. In the eighteenth century it was René Antoine Ferchault de Réaumur; in the nineteenth century, John Lubbock, Auguste Forel, and that famous amateur myrmecologist, Charles Darwin. In our own time William Morton Wheeler has been followed by Karl von Frisch, Caryl P. Haskins, and Theodore D. Schneirla.

Into the last group must be placed Alfred E. Emerson. Until his death he was the leading authority on termites, a restless technical expert who contributed massively to their classification, anatomy, and biogeography. He was also an important contributor to modern ecology, one of the synthesizers of the 1940's and 1950's who brought the large quantities of new data on adaptation, physiology, behavior, and distribution into line with the emerging principles of the "New Synthesis" of evolutionary theory. He was a biogeographer of importance; his detailed knowledge of the world distribution of genera and species of termites helped bring insects into the mainstream of general theory in biogeog-

raphy. And not least, Emerson developed the concept of the superorganism to its extreme degree on the basis of his knowledge of the workings of termite colonies; in the course of this effort he helped to establish the importance of behavioral traits in classification and phylogenetic reconstructions.

Alfred Emerson was born in Ithaca, New York on December 31, 1896, the youngest of four children of a Cornell professor of classical archeology. He moved with his family to Chicago in 1905 when his father became curator of antiquities at the Art Institute of the University of Chicago. His mother was a professional concert pianist and instructor in the history of music at the University of Chicago; his brother and two sisters all enjoyed successful academic careers. One sister, Gertrude, became editor of *Asia Magazine,* settled in India, and was responsible for drawing Emerson into a friendship with Indira Gandhi later in his life.

In the midst of this rich early cultural environment, with its emphasis on the humanities, Emerson flirted briefly with the idea of a career in music. Then, while a student at the Interlaken School in Rolling Prairie, Indiana (1910–1914), he built and ran the school poultry farm—the first odd circumstance in a train of events that led to his career as an entomologist. He was to become the family's scientific "mutant," as he later described himself. Upon reaching college age in 1914, he went to Cornell University with the intention of specializing in poultry science. But the courses were too elementary and dull, causing him to try out the beginning course in each science department of the university in turn. When the time came to choose a major subject in his junior year, Emerson picked entomology, principally—as he once said—because the Department of Entomology was at that time the best of its kind in the world. He became the personal

friend of John H. Comstock and his wife, Anna Botsford Comstock, as well as of James G. Needham, all large figures in the history of the field. The Cornell entomologists stressed depth of training and detailed expertise in individual groups of insects, and Emerson clearly benefited from this experience through all of his subsequent research. At the same time he formed a close friendship with another student, the herpetologist Karl P. Schmidt, who later became curator-in-chief of zoology at the Chicago Natural History Museum and a fellow member of the National Academy of Sciences.

While at Cornell Emerson met his first wife, Winifred Jelliffe, the daughter of Smith Ely Jelliffe, a leading psychiatrist. The couple became engaged in 1918, and soon afterward Emerson left for nine months service in the army (discharged in December, he did not see combat). Next Emerson made a trip to the New York Zoological Station at Kartabo, British Guiana, where, at the suggestion of William Beebe, he began studying termites, and thus began his life's work.

In 1920, as Emerson completed his M.A. at Cornell, he married Winifred and took her on his second trip to Kartabo. A third expedition to British Guiana followed in 1924 and then a six-month sojourn on Barro Colorado Island, Panama, in 1935. The termite collections that Emerson assembled and the experience he obtained during these early visits to the American tropics were a rich source of data and ideas on which he drew during the rest of his life.

In 1921 Emerson accepted an instructorship at the University of Pittsburgh. After completing the requirements for a Ph.D. at Cornell in 1925, he held a Guggenheim Fellowship in 1925 and 1926 and then an associate professorship at the University of Chicago. There he stayed for the remainder of his professional career. The new associations that he formed

at Chicago were decisive in the broadening of his interests and the achievement of theoretical contributions in ecology and behavior.

During the 1920's the Emersons had two children: Helena, who became the wife of Eugene Wilkening, a professor of sociology at the University of Wisconsin; and William Jelliffe Emerson, employed in the Department of Anatomy of the University of Chicago. In 1949, following a summer in which Alfred served as a visiting professor at the University of California, Berkeley, Winifred died suddenly from the effects of a heart defect acquired during childhood. In 1950 Emerson married Eleanor Fish, whom he had known for years and with whom he had collaborated on a children's book, *Termite City* (1937). Those of us who knew this couple in later years were impressed by the closeness and warmth of their marriage.

By his own testimony, Alfred Emerson's principal contribution to science was the more than one hundred articles that added vastly to our knowledge of the systematics, phylogeny, distribution, and natural history of termites around the world. In fact, he may well have been the most productive researcher on this subject who ever lived. By 1969, 1,914 species of termites had been described by termitologists. Emerson's collection, which was donated to the American Museum of Natural History, contained about one million specimens representing 1,745 species, or 91 percent of the known world fauna. No less than 80 percent of the species are represented by primary type specimens. His personal library on termites is virtually complete to the late 1960's, constituting an important bequest to future investigators. Emerson remained active right through the later years of his life, as evidenced by his excellent review of the Mastotermitidae (1965), description of the first Mesozoic termite (1967), reviews of the fossil Kalotermitidae (1965) and Rhinotermiti-

dae (1971), and analysis (with Kumar Krishna) of the rare and little known Serritermitidae. Emerson's carefully researched and cautious studies are the most authoritative sources of information on the classification and evolutionary biology of the termites. His monographs on the termites of Kartabo and the Belgian Congo (Zaire) and Cameroon remain after many years the most valuable field guides for entire tropical faunas. They are so well written and illustrated as to be useful to anyone with an elementary knowledge of entomology.

In 1949 Emerson coauthored the major synthetic work on ecology to that time, *Principles of Animal Ecology*, an influential textbook known lightly among students and other biologists as the "The Great AEPPS"—after the initials of the authors' last names (W. C. Allee, A. E. Emerson, Orlando Park, Thomas Park, and Karl P. Schmidt). This massive work collected much of what was known about animal ecology at that time, making full use of current evolutionary theory and the still fragmentary principles of population biology. Emerson's main contribution was to summarize knowledge of the social insects, demonstrating with numerous examples the diverse and often bizarre ways that features of social behavior adapt species to particular challenges in the environment. In general, *Principles of Animal Ecology* stimulated a great deal of rigorous research in ecology and helped set the stage for the surge in population and community ecology that occurred during the 1950's and 1960's. (A commentary on Emerson's eminence as an ecologist was published by T. Park in 1967 [*Bulletin of the Ecological Society of America*, 48: 104–7].) Emerson's scholarly treatment of the social insects was the best since the monographs by W. M. Wheeler twenty years previously, and they helped to keep these creatures in the midst of developments in the major topics of ecology and the remainder of evolutionary theory.

On top of Emerson's cumulative work concerning termites, his most striking single contribution, in the opinion of many, was his use of behavioral traits as taxonomic characters. Emerson referred to the structure of termite nests as "frozen behavior" that could be weighed and sketched with the same reliability and quantity of information as many anatomical traits. He showed that certain species of *Apicotermes* can be distinguished more readily by the architecture of their nests than by the anatomy of the termites themselves. His case seems exceptionally strong today, because termites have relatively complex, stereotyped behavior, and as subsequent investigators have shown, these insects use nest structure to regulate the microclimate of the colony. It is fair to say that what Konrad Lorenz and other vertebrate ethologists did for the use of behavior in bird systematics, Emerson helped to accomplish for the use of behavior in the systematics of termites and other social insects.

Alfred Emerson is also well known for his espousal of the superorganism concept, in which the castes and functions of the insect colony are compared with the anatomical and physiological features of single organisms. This method of analogy, first put in concrete form by Wheeler and highly popular in the first half of the century, was perhaps carried to its extreme by Emerson. He saw in the social insects the exemplification of "dynamic homeostasis," which he believed to be a new unifying principle of evolutionary theory. This part of Emerson's thought has had relatively little impact, principally because during the period of his most assertive articles (1952–1958) the pendulum had begun to swing away from holistic conceptualization and toward piecemeal, experimental analysis of individual physiological mechanisms and patterns of behavior. But at the very least, however much out of focus, and even during this period of its waning, the superorganism concept remained a stimulating distant goal toward

which many younger entomologists felt themselves to be working.

In spite of being a hard-working scholar in an exacting specialty, Emerson was a gregarious man, exceptionally generous with his energies and time. He was friendly not only with his intellectually gifted associates, but also with less gifted persons with whom he willingly discussed everyday topics. He wrote long letters of advice and encouragement to younger entomologists, never displaying the protectiveness or hardening of opinion that afflicts some established scientists. In different years he served as president of the Ecological Society of America, the Society for the Study of Evolution, and the Society for Systematic Entomology and was a vice-president of the Entomological Society of America. Among his honors were an honorary D.Sc. from Michigan State University in 1961, received after his service as a distinguished visiting professor in 1960, and the Eminent Ecologist Award for 1967 from the Ecological Society of America. He was elected to the National Academy of Sciences in 1962.

On Sunday, October 3, 1976, Alfred Emerson died of a heart attack near his summer home at Huletts Landing, on Lake George, New York. He will be remembered for the magnitude and rigor of his scholarship, his uncompromising and lifelong devotion to science, his interest in the relevance of science to humane learning, and, especially by those who knew him best, the largeness and generosity of his spirit.

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