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GOTTFRIED SAMUEL FRAENKEL

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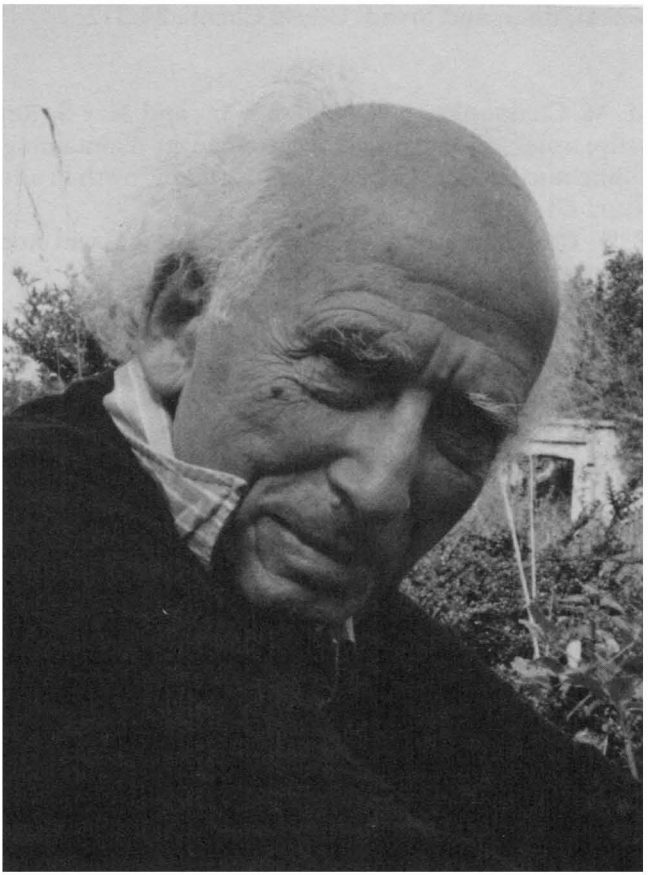
A Biographical Memoir by
C. LADD PROSSER, STANLEY FRIEDMAN,
AND JUDITH H. WILLIS

Biographical Memoir



G. S. Frankel

GOTTFRIED SAMUEL FRAENKEL

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BY C. LADD PROSSER, STANLEY FRIEDMAN, AND JUDITH H. WILLIS

GOTTFRIED FRAENKEL was elected to the National Academy of Sciences in 1968 for his contributions to insect physiology. Although one might attribute his success as a pioneer in diverse areas—behavior, endocrinology, nutrition, insect-plant interaction—to his living in a period with few scientists and many uncharted fields, a reading of this biographical sketch reveals that many of his discoveries came during periods of political upheaval, economic hardship, and conflict with bosses—not conditions generally considered optimal for the advancement of basic research. His published contributions to musicology indicate that he was also adept at finding treasures in well-mined areas. One can only conclude that he was an exceptional person with an uncanny sense of what problems were interesting, important, and solvable.

EARLY LIFE

Gottfried Samuel Fraenkel was born in Munich, Germany. His father was a *Justizrat* and the family typically middle-class Jewish, with interests far from the science that Fraenkel was later to take up so successfully. As a boy he devoted much time to music—both piano playing and singing—but as a young man his major preoccupation was the Zionist cause.

He continued to pursue these activities throughout his life, but in his early years his belief in the Zionist movement was so strong that he made the decision to spend a part of his life living and working in Palestine.

To prepare for this goal, he enrolled in a teaching degree program at the University of Munich. There he attended lectures and engaged in laboratory exercises under R. C. Hertwig, Karl Von Goebel, Richard Martin, Richard Willstätter, Wilhelm Konrad, W. K. Röntgen, and Karl von Frisch.

He became attracted to the field of hydrobiology and—having decided to take a doctoral degree—began to study the life histories of certain leeches on fish. When all of his tank specimens died as the result of a laboratory accident, he took a short trip to the Zoological Station in Naples to obtain fresh material. Once there, he was immediately and irrevocably charmed by the enormous variety and beauty of Mediterranean invertebrate fauna. Already knowledgeable about marine invertebrates from his course with Wolfgang von Buddenbrock at Helgoland he began to experiment, in the short time available, with some jellyfish blown into the Naples harbor by a storm. Within two weeks he worked out and successfully tested his idea that the medusa statocysts functioned as gravity receptors—a theory totally contrary to the dogma of the time. He returned to Munich, and, being advised that his discovery was a suitable dissertation thesis, arranged for Professor O. Koehler to "direct" it.

His talent for quickly defining and completing a project, an ability that was to remain with him throughout his life, was already highly developed at this early stage in his career. Having received his doctorate, he returned to Naples on a Rockefeller Foundation grant and, within a year, produced six publications on various aspects of sensory physiology and orientation of marine invertebrates. He also spent a short period with Alfred Kuhn in Göttingen and found time to

visit the marine stations at Roscoff and Plymouth. The stay with Kuhn resulted in his first paper on insects, a behavioral analysis of the response of bees to color. This predilection for travel and marine stations became a lifelong passion.

After these academic adventures, Fraenkel concluded that it was time to fulfill his Zionist commitment. With the small amount of money remaining from his fellowship, he boarded a ship for Palestine. Upon arrival he called on the distinguished entomologist F. S. Bodenheimer, who immediately offered him a job as his assistant at the newly founded Zoology Laboratory of the Hebrew University in Jerusalem. There were not many young, vigorous, and experienced zoologists at that time ready to work under the conditions prevailing in Palestine. While visiting friends in the period before the job began, he met—and shortly thereafter married—the Lithuanian-born Rachel Sobol, daughter of a family of well-known and politically active settlers. As he later put it, the family was not overly impressed with this scientist and "latecomer" to Palestine.

It was during this sojourn in Palestine that he became involved with the animals he would study the rest of his working life. In those days Jerusalem was considered a "long distance" from the sea, and Fraenkel was attracted to the only water around—the papyrus pond on the grounds of the university—and to its myriad insect visitors. This pond provided subject matter for a number of fundamental studies on insect tracheal respiration, but it was a major invasion of locusts in 1929 that finally determined Fraenkel's fate. All of the research in the zoology laboratory was turned toward the problem of locust control, and Fraenkel's work in the desert on locust behavior and sensory physiology became the basis of attempts to hold locusts in check. The investigations are classics of their kind and are still widely quoted today. The work also resulted in a falling out with Bodenheimer over author-

ship, finally ending in Fraenkel's departure from his job and from Palestine.

BRITAIN

He returned to Germany in 1932 when the Nazis were already on the rise. Fraenkel felt himself fortunate to find a position as *Privat Dozent* in Frankfurt's Zoology Department. But as soon as Hitler came to power in 1933, he was dismissed. Fortunately, his reputation was already sufficiently established that he was offered a position in England. It is worthy of note that this was one of the many positions awarded to German refugee scientists through the Academic Assistance Council, funded by contributions from English scientists out of their meager, depression-level wages. Fraenkel never forgot this help and often spoke about it as having saved his family. He came to University College, London, as a research associate in 1933. His life and future scientific activity were immediately influenced by the fly, *Calliphora erythrocephala*, that he saw come in through an open window and deposit its eggs on a small piece of meat. He watched the larvae emerge from the eggs and grow and—amid all the difficulties of a new language, a new culture, a new family, almost no salary, and using the most primitive tools—conceived the idea that, within a period of two months, resulted in the discovery of the blood-borne factor we now know to be the insect molting hormone, ecdysterone. He submitted his paper on this to *Nature* and it was printed three weeks later—his first paper in English. (Twenty-one years after Fraenkel's discovery, the structure of the molting prehormone was identified by Peter Karlson using Fraenkel's bioassay method.)

Fraenkel's encounters with British scientists during these early years led to three seminal cooperative ventures. He and John Pringle showed that the halteres, which replace the sec-

ond pair of wings on the adult fly, actually function as miniature gyroscopes, or balance organs. Fraenkel and the physical chemist Kenneth M. Rudall analyzed the strange changes occurring in the cuticle of the larval fly at pupariation, using, among other methods, X-ray diffraction. This study provided the basis for work on insect cuticle that continues to this day, forty years later. Finally, at a chance meeting with a behaviorist, Donald L. Gunn, Fraenkel found a willing audience for his data and ideas on insect behavior—information that would eventually appear in their classic text, *The Orientation of Animals*, published in 1940.

By 1936, Fraenkel's reputation was such that he was offered a post in insect physiology—perhaps the first full-time teaching position ever established in this discipline—in the Department of Zoology and Applied Entomology at Imperial College of the University of London. When World War II came, the Department was evacuated to Slough, and, to aid the war effort, the Pest Infestation Laboratory was created.

Professor J. W. Munro wanted Fraenkel to work on insecticides, but Fraenkel chose to take the view that understanding stored-grain pests would develop the intelligence with which to deal with them successfully. Published as a series of detailed diet studies, his findings showed that insects have the same nutritional requirements as man, except for the beetle *Tenebrio molitor*, that needed an additional but as yet undefined component in its standard diet. By war's end Fraenkel could conjecture that he had found a new vitamin. It is doubtful whether Fraenkel's work contributed directly to ending the war, but his experiments and their results shaped the fields of insect nutrition and applied entomology for years to come. His nutritional expertise, furthermore, extended well beyond insects. As a member of a committee organized by the Fabian Society, he investigated problems of British agriculture after the war and wrote the chapter on

Britain's nutrient requirements in the committee report. He also gained a certain notoriety in Britain as one of the designers of the British National (bread) Loaf—the size, shape, and composition of which were standardized during World War II.

AMERICA

In 1947 Fraenkel paid his first visit to the United States as a lecturer at the University of Minnesota. In 1948, after meeting with various American entomologists, he accepted an offer of a position in the Department of Entomology at the University of Illinois. After his experiences with restrictions on research in Palestine and Slough, he later confided, the freedom to pursue his own objectives in and of itself justified the move to Illinois.

At Illinois, with its strong chemistry department, he began a collaboration with Herbert Carter on his new "vitamin" that led to the isolation, crystallization, and identification of the *Tenebrio* growth factor. He was disappointed when the "vitamin" turned out to be a molecule—carnitine—that had been isolated and identified fifty years earlier from mammalian muscle. Still, no biological role had been assigned to it in the interim, and the work of Fraenkel and his collaborators succeeded in establishing its universality of occurrence and its importance in Coenzyme A transfer reactions. It is worth noting that Fraenkel himself was never satisfied that the full spectrum of its action had yet been elucidated.

Continuing to mine the vein of insect nutrition, he next posed an important question. If, as he had shown, all insects had the same dietary requirements, and if, as was well known, plant leaves generally contained all of the required compounds, why were so many insects restricted in the plants they would eat? By 1958, he had examined enough of the literature to recognize that the so-called "secondary" plant

compounds, of many different structures, might provide a clue to the evolution of host selection. For years, botanists and chemists had been isolating different classes of these compounds associated with different plant families but were unable to establish functions for most of them. Fraenkel opened a new field—insect-plant coevolution based upon chemical and sensory interactions. He described the *raison d'être* of secondary plant compounds "as only . . . to repel and attract insects." Some regarded this as a flash of insight, but it is, as documented in his 1959 *Science* paper, the result of a long, thoughtful process tempered by extensive experience in nutrition and behavior. In a comment made much later, when this paper was chosen as a Citation Classic in 1984, he described the initial resistance to his idea as follows: "Perhaps it seemed implausible that such a simple explanation could be virtually new and at the same time correct."

In 1961, when this idea was beginning to cause ferment in ecological circles, Fraenkel received one of the few Research Career Awards ever given in his field by the U. S. Public Health Service. In collaboration with a number of his students, he then examined the chemical basis of host selection, solidifying the theory.

Fraenkel's early work with flies still intrigued him. Using modern techniques developed long after those halcyon days of string and wax, he reexamined the tanning of adult flies after emergence from the puparium, and promptly discovered a new hormone, bursicon, which was proven responsible for post-ecdysial activities. Interest in this hormone grew, and by 1968 much of Fraenkel's work had been corroborated and extended to other insects. He was elected to the National Academy of Sciences in that year.

By the time he retired in 1972 he had also vindicated his old *Calliphora* assay. Responding to a challenge by Carroll M. Williams and associates, Fraenkel and a Czech colleague, Jan

Zdarek, discovered additional factors that accelerate puparium formation.

Thanks to the enlightened policy of the University of Illinois in supporting the continued research of emeritus professors, Fraenkel embarked upon a research program after his retirement that included such topics as interactions among nutritional states, developmental hormones, behavioral changes accompanying metamorphosis, and aging. Over the next twelve years he worked with a number of senior colleagues but most often employed bright undergraduate students as his hands. In this way he helped train a number of disciplined investigators. Throughout that time Fraenkel's manual Smith Corona typewriter continued to pound out research articles on diverse topics. He also maintained a steady flow of correspondence with far-flung colleagues until only a few weeks before his death at age eighty-four.

CLOSING REMARKS

Fraenkel's travels, both to meetings and for research purposes, took him all over the world. He studied inter-tidal snails on Bimini, leather pests in Yemen, rice leaf folders in Sri Lanka, and silkworm nutrition in Japan. He had a collector's eye for art objects and—with his love of music—the decorative title pages of sheet music. In 1968 he published a book deriving from this avocation, *Decorative Music Title Pages* (Dover Press). He also turned up a rare and instructive edition of Hector Berlioz's *Les Troyens* and published a paper on its significance. He was a skilled pianist and made a practice of seeking other musicians wherever he went.

But Fraenkel's first love was biology—a love he communicated to his two sons. Gideon Fraenkel is now professor of chemistry at Ohio State University and Dan, professor of microbiology and molecular genetics at Harvard Medical

School. Their father died a few months after the death of his devoted wife of fifty-six years, Rachel Sobel Fraenkel, herself an accomplished sculptor.

Gottfried Fraenkel had that rare ability to recognize important questions and solve them with direct and simple techniques. Ever ready to exploit the materials at hand, his work was seminal to diverse areas of insect biology that have since become major fields of study.

WE WISH TO THANK Robert Metcalf for his help in discussing Professor Fraenkel's scientific contributions.

HONORS AND DISTINCTIONS

1926–1927	Fellow, International Education Board, Rockefeller Foundation
1955	Honorary Fellow, Royal Entomological Society, London
1962–1972	Research Career Awardee, U. S. Public Health Service
1968	Member, National Academy of Sciences
1972	Fellow, American Association for the Advancement of Science
1980	Honorary Doctor, François Rabelais University, Tours
1982	Honorary Fellow, The Linnean Society, London
1984	Honorary Doctor, The Hebrew University, Jerusalem

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