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VINCENT GASTON DETHIER
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A Biographical Memoir by

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THOMAS EISNER

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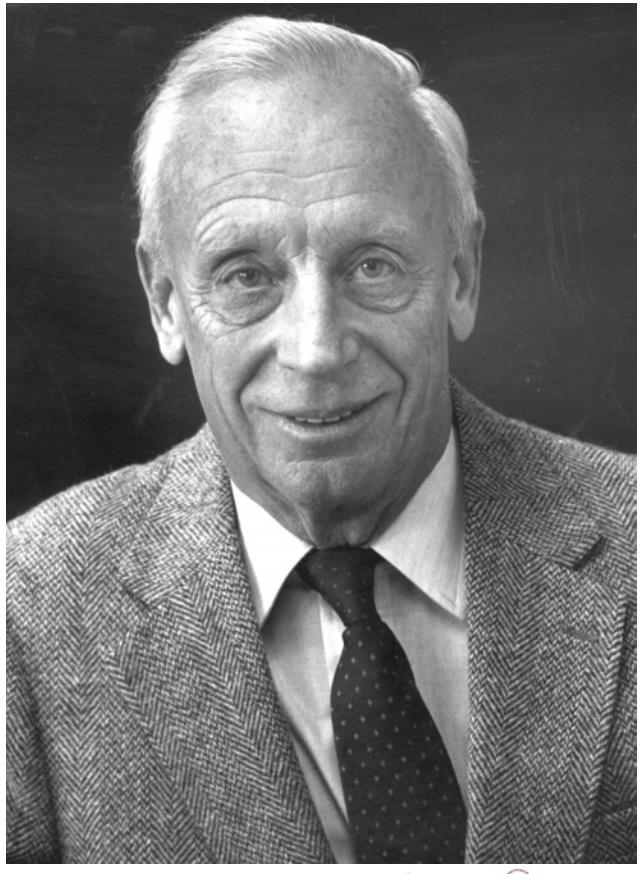
Biographical Memoirs



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VINCENT GASTON DETHIER

February 20, 1915–September 8, 1993

BY ALAN GELPERIN, JOHN G. HILDEBRAND, AND THOMAS EISNER

VINCENT DETHIER WAS A man of many facets—scientist, writer, musician, historian, explorer, and paragon of civility. His interests and activities ranged broadly, from the biophysics of chemosensation and the comparative architecture of renaissance cathedrals, to the ecology of natural populations and the tonal structures of baroque cantatas. Just as it takes a village to raise a child, it took a university—nay, several universities—to provide the depth and diversity of colleagues and coworkers to engage fully Vince's varied interests in science and the arts.

Thanks to his exceptional vitality, Vince paid little heed to advancing years. When he was stricken with his sudden, final illness on September 8, 1993, he was in the classroom inaugurating another course for a group of lucky college students, fully 54 years after the start of his teaching career. He was the Gilbert L. Woodside Professor of Zoology at the University of Massachusetts, Amherst, a position that did not carry a teaching responsibility. Even among his friends and colleagues, few could believe that Vince was 78 years old. He had just returned from a summer spent in his beloved family home in East Blue Hill, Maine, where he wrote many of his more than 170 scientific papers and 16 books, as well as numerous short stories.

ORIGINS OF A SCIENTIST

Vince was born on February 20, 1915, on the outskirts of Boston, Massachusetts. His parents conveyed a rich tradition of, and appreciation for, education, scholarship, and music—activities that permeated the family's household. His father had graduated with first prize in piano from the Royal Conservatory of Liège, and then emigrated to America where he became a music teacher and church organist and choirmaster in Norwood, Massachusetts. Vince's mother, who traced her lineage from an Irish royal clan, had taught in public schools in Boston before she married. This rich intellectual, aesthetic, and spiritual nurture, together with his extraordinary innate curiosity, prepared Vince for a fateful encounter with the insect world. He described this epochal event, which took place in a small park called "the oval," in an autobiographical essay (Dethier, 1985):

> My first acquaintance with a live butterfly resulted entirely from the initiative of the butterfly. I had wandered up to the oval late one hot, humid, summer day. The long, slanting rays of the sun illuminated my white shirt. Suddenly, something rocketed across the street, made a few zigzags, and landed on my shirt, just above the pocket. I stood stock-still and slowly lowered my head to see what it was. There with its wings slowly expanding clung a brown butterfly with a red band extending down each wing. This red admiral was the first live butterfly I had ever seen at close range, and I was fascinated.

Vince never lost that childhood fascination. From that time on, he collected, reared, and studied butterflies and developed a love for living creatures and their behavior. In his early butterfly-rearing efforts, Vince found that all went well when he knew which plant was the insect's preferred food. He was struck by his observation that some caterpillars starved to death rather than eat nutritious but nonpreferred plants, and he wondered why. As a teenager, he performed simple behavioral experiments that led him to

conclude that butterfly larvae possessed keen senses of smell and taste that were vital to their food plant selection. These observations gave early evidence of an independence of spirit and ability to draw important conclusions from simple and elegantly designed experiments. This ability was a recurring theme throughout his scientific career. Captivated by his early observations on caterpillar food selection, Vince found his calling even before he entered Harvard College, where he majored in biology with the expectation of becoming a high-school teacher.

THE HARVARD YEARS

Vince's interest in the natural world survived Harvard's tedious biology courses (rote memorization was *de rigueur*) and close contact with pickled, rank specimens delivered for dissection. Harvard's tutorial system made all the difference. It was Vince's good fortune to have as his tutor the physiologist T. J. B. Stier. Stier not only encouraged his interest in caterpillar food-plant selection but also encouraged Vince to prepare his findings for publication. The result: a pair of papers ("Gustation and Olfaction in Lepidopterous Larvae" [Dethier, 1937a] and "Cannibalism among Lepidopterous Larvae" [Dethier, 1937b]) that went counter to the established belief that creatures with supposedly simple nervous systems like caterpillars could not possibly possess sophisticated chemosensory abilities. Vince—typically, as time would prove—broke new ground that would eventually draw whole contingents of insect sensory physiologists following in his tracks.

When Vince reminisced about his Harvard years, though, it was the adventures with fellow students that he related, not his scientific accomplishments. He and his friends loved, for example, to spend winter break hiking up the sloping backside of Mount Washington, carrying skis and lunch. It

took most of the day to reach the summit. Once there, they exchanged snowshoes for skis, untied and loosened the laces of their boots (there were no safety bindings at that time), and schussed down the steep front slope. Vince reported, with typical humility, that he never made it all the way down without a near-catastrophic spill.

Vince stayed at Harvard for graduate studies (Ph.D. in 1939), during which he pursued his commitment to the study of host-plant selection by lepidopterous larvae. His advisor, C. T. Brues, was an expert on insect feeding habits. One of us (A.G.) recalls Vince commenting that one of Brues's most attractive features was that he required progress reports only once a year, thereby giving Vince the freedom to exercise his judgment on how best to proceed with his experiments. This mentoring style suited Vince perfectly in the heady atmosphere of the Harvard biology community of the 1930s. When Vince and his fellow graduate students needed to learn insect physiology and found no courses on the subject, they organized themselves and taught each other. Among the cadre of fellow students at Harvard at that time were luminaries including Carroll Williams, who were to become leaders in the world of insect study.

One of us (A.G.) profited greatly from Vince's non-authoritarian mentoring style, first in graduate school as Vince's doctoral student and later as Vince's junior colleague on the faculty at Princeton.

At the time when Vince, at Harvard, was studying the chemical senses of caterpillars, no insect chemoreceptor had been functionally identified. His behavioral and morphological studies showed him how difficult it was to overcome the technical problems inherent in the study of insect chemoreceptors. After learning of Adrian's achievements in electrophysiological exploration of sense organs, Vince approached C. Ladd Prosser at Clark University, who was

applying such techniques to the study of earthworms, on how one might go about obtaining recordings from insect chemoreceptors. Despite his best efforts during a stimulating summer in Prosser's laboratory, Vince was unable to achieve the necessary technical breakthroughs. In fact, it would be more than 15 years before it became possible to record action potentials from the primary chemoreceptor neurons of insect chemosensillae. The breakthroughs came none too soon for Vince, who had already decided at the time of receipt of his Ph.D. to make the study of insect chemoreception his lifetime passion.

THE WAR YEARS

After a brief appointment as a junior faculty member at John Carroll University in Cleveland, Ohio, Vince joined the Army Air Corps in the Africa-Middle East theater of operations during World War II. Turning adversity into opportunity, he wrote his first book (Dethier, 1947) in the bomb bay of a B-25 using a captured Italian typewriter. Once, while stationed at an isolated airport, Vince hit upon a stratagem for keeping boredom at bay. Through military channels and for no reason other than to see what might happen, he put through a requisition for "anhydrous water." In a matter of weeks the requisition came back, enriched by a whole stack of appended forms, plus a request that he specify the concentration at which the chemical was needed. "Ninety-nine-point-nine percent" was Vince's reply, which prompted a further query. "What kind of container should be used?" "Stainless steel," was Vince's answer, and so the exchange continued, growing in absurdity and in bureaucratic involvement each step of the way. Vince was sure that he had stirred into action a sizeable fraction of the Army Air Corps.

Vince later became liaison officer to the chief of the Chemical Warfare Service in Washington, D.C. This brought him into contact with Kenneth Roeder, arguably the leading insect physiologist in America at the time. On visits to Roeder's laboratory at Tufts University, Vince saw that great strides were being made in insect sensory electrophysiology and realized that he would himself have to make use of the techniques involved.

In 1946 Vince returned from active duty and joined a research group at the Army Chemical Center at Edgewood, Maryland, working with chemicals that affected insect behavior. This group included D. Bodenstein, L. Chadwick, H. Frings, and C. C. Hasset. Their early attempts to relate chemical structure to stimulating effectiveness matched Vince's interests perfectly. At Edgewood he began his research partnership with the black blowfly, *Phormia regina*, and continued his quest to understand the transduction mechanism of insect chemoreceptors. Stimulating the tarsal taste hairs of a hungry *Phormia* elicited reflex proboscis extension, which then served as a quantitative index of stimulating effectiveness of a taste solution. By using very large series of sugars, alcohols, acids, and inorganic salts, Vince began to define the molecular requirements for the binding sites on the chemoreceptors providing input to the proboscis extension reflex. These molecular insights from behavioral studies would later prove invaluable when it became possible to make electrophysiological recordings from the taste cells that populate fly taste hairs.

THE HOPKINS YEARS

After his brief but inspiring research stint at the Army Chemical Center, Vince accepted a professorship of zoology and entomology at Ohio State University. A year after establishing himself in Columbus, he startled his friends by

resigning this tenured position to accept a nontenured post as associate professor at Johns Hopkins University. The years at Hopkins (1947-1958), he later said, were among the most productive, educational, and adventuresome of his career. He was part of a group of neuroscientists and physiological psychologists who shared his broad perspective and appreciation for multiple approaches to animal behavior and its neural mechanisms. Notable among these Hopkins colleagues was Eliot Stellar, who later moved to the University of Pennsylvania and spearheaded a successful drive to lure Vince to Philadelphia.

A major breakthrough in the study of insect chemoreceptors occurred when Vince's first graduate student, E. S. Hodgson, during a postdoctoral stint with K. D. Roeder and with assistance from J. Lettvin at the Massachusetts Institute of Technology, developed an electrophysiological technique for recording the responses of single chemosensory neurons to aqueous stimuli applied to the tip of the taste hair (Hodgson et al., 1955). This tip-recording method led to a seminal series of papers characterizing the responses of single cells in taste hairs of *Phormia* and later, with L. Schoonhoven, of caterpillars. Vince had shown in behavioral experiments with *Phormia* that a taste solution elicited the proboscis extension reflex only when the tastant contacted the tip of the taste hair. Now he could listen in on the neural responses of the small set of contact chemoreceptor neurons associated with dendrites in the hollow channel of taste hairs.

A neuroethologist by instinct, Vince considered at every turn the nature of the stimuli encountered by fly chemoreceptors in the natural world. This led him to use as taste stimuli a wide array of substances, many derived from leaf surfaces, rather than just the salt, sweet, sour, and bitter compounds commonly used in studying vertebrate chemore-

ception. As the range of chemostimuli broadened, the picture of the taste code became more complex, even as viewed from the limited repertoire of sensory cells in a single *Phormia* taste hair. Vince grappled with the complexities of chemosensory coding with characteristic concern for the Umwelt or sensory world of the fly. (The issue of taste coding in insects is still an active area of research and debate, as it is in mammalian taste coding.)

THE PHILADELPHIA YEARS

Vince moved to the University of Pennsylvania in 1958, joining several of his former Hopkins colleagues in the Institute of Neurological Sciences in the School of Medicine. While Vince's primary appointment was in the biology department, the interdepartmental and interdisciplinary assemblage of behavioral scientists, neuroscientists, and physiological psychologists gathered in the Institute of Neurological Sciences was a lively and intense group that provided each participant with widely ranging perspectives and technical approaches. In this milieu, Vince and his colleague Eliot Stellar wrote the landmark book, *Animal Behavior* (1961), which appeared in three editions and ten languages.

Among the issues with which Vince and others grappled during weekly seminars was motivation. Was it a useful concept? Was it a general concept? Do insects have motivation? Some argued that this behavior separated invertebrates from vertebrates, thereby providing a basis for excluding insects, but in due course Vince performed experiments showing clearly that insects had that key feature. While some of Vince's colleagues found this exasperating, their mutual respect overcame their disagreements. These heated exchanges were educational for the cadre of graduate students in attendance, who learned from the debates that

disagreements in the realm of science need not in any way affect the bonds of friendship.

Vince was renowned for his wit and charm. At a memorably bombastic departmental faculty meeting, passions ran high over opinions strongly held. Among the actors in this drama was the department chair, whose normal speaking voice could reverberate across campus, and who reportedly had the shortest fuse in the history of the university. As the verbal exchange heated up, Vince (himself quite feisty) couldn't resist a few rapier thrusts. "Vince, only an ass would say that," the chairman bellowed. "Yes, Mr. Chairman, I know that," replied Vince, "but I thought you were about to say it, and I wanted to save you the embarrassment." The meeting erupted in laughter and the two men departed the best of friends.

The Philadelphia years marked advances in understanding the response properties of fly gustatory receptors and the regulation of feeding in the fly. The students involved in this work included Frank Hanson, Joseph Larsen, Margaret Nelson, and many others, including one of us (A.G.). The work on *Phormia* was collected in Vince's magnum opus, *The Hungry Fly*, published in 1976, which makes clear that our understanding of fly feeding behavior is more complete than for any other species then under study. (While this is still the case, the mammals are advancing.) With postdoctoral associates Louis Schoonhoven from the Netherlands and Tibor Jermy from Hungary, Vince was able at last to carry out a detailed electrophysiological analysis of caterpillar chemoreceptors, as he had long yearned to do.

THE PRINCETON YEARS

Vince moved to the biology department at Princeton University in 1967, to take up an endowed chair. There, his electrophysiological investigations of flies and caterpillars

continued apace, yielding evidence of the importance of both labeled-line and across-fiber coding in the gustatory pathways of insects. Vince's devotion to insect-plant interactions and chemosensory function was undiminished after more than 30 years of work.

When one of us (A.G.) joined the biology faculty of Princeton in 1968, Vince was as supportive as he had been as a "doctor father," even as his former student's research turned from insects to mollusks. Vince, as so many were to learn on their own, was in every respect an ideal colleague.

At Princeton, Vince returned to his interest in learning in flies. The lack of evidence for learning in these insects led Vince to speculate in a remarkable paper entitled "Microscopic Brains" (Dethier, 1964) that perhaps flies could not learn. Two developments were later to prove otherwise. In 1974 Chip Quinn, Bill Harris, and Seymour Benzer published a demonstration of odor-conditioned behavior in *Drosophila* (Quinn et al., 1974). About 10 years later, T. Fukushi showed reliable and robust one-trial color-food conditioning in walking flies (Fukushi,1985). Ironically, the walking flies learned the food-color association as they did the search "dance" that Vince described in his 1964 paper. The molecular dissection of fly learning continues to be a major research topic in neuroscience.

Vince also tested the idea that polyphagous caterpillars would be more likely to show food-aversion conditioning than monophagous caterpillars, a suggestion one of us (A.G.) made in a paper on comparative aspects of food-aversion conditioning. Vince found that one species of polyphagous caterpillar did show such conditioning, while a species of monophagous caterpillar did not.

The phenomenon of learning completes a picture in which food selection behavior comprises three-tiers: (1) a peripheral system, sensitive to multiple chemical stimuli;

(2) an internal chemosensory system that measures the quality and quantity of absorbed food constituents and which may modify the insect's behavior via its input to the central nervous system; and (3) a modifiable integrative center in the central nervous system that decodes sensory patterns and commands the feeding motor-control center, integrating feedback from previous postingestive consequences associated with responses to a chemosensory code.

Vince was at the forefront of the scientific endeavor to unravel food selection behavior in herbivorous insects. He set his enduring mark on the basics of the first two components of the three-tiered system. The third component, the brain, remains even now terra incognita. Analyzing it will not be an easy task, although recent progress in unraveling key aspects of how insects process olfaction, vision, and audition provides encouragement.

THE AMHERST YEARS

Vince increasingly heard the call of two of his lifelong passions—his beloved summer home in East Blue Hill, Maine, and his avocation as a creative writer. He dreamed of early retirement, of living in Maine and building on his already-established success as a celebrated writer. But with Jehan and Paul, the children of his midlife marriage to Lois Crow, still in college, it was not to be. Instead, in 1975 Vince made a last move, this time to assume the Gilbert L. Woodside Professorship of Biology at the University of Massachusetts in Amherst.

Established in his new laboratory, joined by postdoctoral associates Elizabeth Bowdan, Mary Behan, and Roberto Crnjar, and reunited with Martha Yost, who had been his first research assistant at Hopkins and who now lived in Amherst, Vince redoubled his efforts to crack the gustatory code in caterpillars. His prefatory chapter in the *Annual*

Review of Neuroscience for 1990 summarizes his long history of work in chemosensory neuroscience during a time of transition from descriptive to functional studies, along with more philosophical comments on the nature of reality and comprehension made possible by our sensory receptors and filtered by our contemporary intellectual ambience (Dethier, 1990).

His new position was a research professorship, and Vince intended to focus exclusively on his research program, but events distracted him from unfettered focus on research. The university needed his leadership and humanitarian touch—first to serve as founding director of the new Neuroscience and Behavior Program, and later, during a particularly unsettled period in the university's history, to chair the Chancellor's Commission on Civility (Dethier, 1984). At the same time, the university began a series of courses heavily emphasizing writing skills. Appealing to his love of clear and elegant exposition, Vince found that teaching was a commitment he couldn't break.

To acknowledge his accomplishments on the Commission on Civility and his strong commitment to civility issues generally, the university established posthumously the Vincent Dethier Award for the faculty member who best exemplifies the ideals to which Vince aspired. For an academic whose civility was intrinsic to his very nature, this may indeed be the ultimate accolade.

BEYOND THE REALM OF SCIENCE

Vince wrote a number of evocative and lyrical books on natural history, including *To Know a Fly* (1976), *The Tent Makers* (1980), *The Ecology of a Summer House* (1962), and *Crickets and Katydids, Concerts and Solos* (1992). He also wrote celebrated books for children (*Fairweather Duck* [1970] and *Newberry, The Life and Times of a Maine Clam*

[1981]) and satires (including *Buy Me a Volcano* [1972] and *The Ant Heap* [1979]).

In *Newberry* Dethier showed his talents as a storyteller par excellence. During summers with the family in Maine, he observed and absorbed in great detail the world of creatures on the surrounding coastal shores. He portrayed this world with warmth and wit in the daily adventures of a clam named Newberry, to whom a local doctor gave a purple woolen muffler to tie around his long neck to cure an ache. Newberry's adventures and involvements bring alive, and charmingly so, the essential biology of many shore creatures, from clams and starfish to sandpipers and gulls.

Vince's short story "The Moth and the Primrose" (Dethier, 1980) was selected for inclusion in *The Best American Short Stories of 1981*, one of several awards Vince received for his varied works of fiction. In part a poetic lesson in insect-plant interactions, the story is a moving tale of Old Prout, a clam digger, "one of the least of all creatures" who did "great good simply because he did no harm. Yet in simply living his life he affected the lives of all others." Prout built a road across a peninsula or, rather, "by use he had created the road. Although he did not know it, with the road he had made possible a whole cosmos. He had made possible the primroses. Without the road, there would have been none because they grew nowhere else. Without the primroses, there would have been no moths because they too could exist nowhere else." In this bittersweet tale, Vince portrays the interwoven lives of Prout, the primroses, and the moths. No account here could possibly capture the depth of understanding for the flowering and ebbing of life nor the pathos expressed in this story. Prout died one night in a violent storm; without him, the road gradually disappeared, and with it went the primrose and the moths. At the burial the parson pondered the meaning of the old

hermit's life. Being ignorant of the interplays of nature Prout made possible, the parson would not understand that "in some unfathomable manner Prout was perfected in the being of the moth and the primrose. Perhaps it was right that all these things ceased in time to exist after the old man had gone. For nothing really survives the man . . . a trace perhaps, a pyramid, a web; but these must be empty symbols."

Particularly notable among these works that intertwine literature and philosophy is *Ten Masses*, in which Vince gives voice to his personal philosophy and the role of faith in his life. Vince could have been a poster child for Stephen Jay Gould's Principle of NOMA—"Non-Overlapping Magisteria." Critical scientific thought and religious faith belong to distinct "magisteria," or domains of knowledge, Gould says; they are not mortal enemies. We do not know what Vince would have said on this issue, but his life and writings are a testament to the potential creative synergy of these two magisteria.

Vince's exceptional qualities as a scientist of breadth, insight, and creativity, as an inspiring and beloved teacher, as a masterful writer, and as a gentleman of good humor, generosity, and uncommon yet natural civility endeared him to everyone who knew him and brought him richly deserved recognition. Among his many honors were election to the American Academy of Arts and Sciences (1960), The National Academy of Sciences (1965), and the American Philosophical Society (1980); membership in the Explorers Club; and fellowship in the Royal Entomological Society of London. In 1993 he received the John Burroughs medal for distinguished nature writing.

Of the many honors he received and meetings he attended, the yearly gathering of fellows of the American Philosophical Society, rich with artists, authors, musicians, and

scientists, held a special attraction. At his inaugural meeting in 1980, he found great delight in having lunch with a fellow inductee, the opera singer Beverly Sills. His address to the members, "Sniff, Flick and Pulse: An Appreciation of Interruption" (Dethier, 1987), was vintage Vince, weaving together how the principles of sensory perception and biophysics, elucidated in the realm of odor perception, are directly tied to human perception and the appreciation of art, architecture, and music.

Vincent Gaston Dethier was loved—and is remembered—for his passion for nature, his elegant science, his deep desire to understand, and his dedication to lucid and esthetic communication of that understanding; for his friendly manner, keen wit, lively sense of humor, and love of family; and for his humanity. In her contribution to the Festschrift honoring Dethier on his seventieth birthday, Miriam Rothschild gave voice to these feelings in her own perfect and inimitable way. Referring to a painting by Van Gogh, she wrote:

> Two White butterflies twirling in freedom and winged delight. For me they are the symbol of daydreaming—the poetry that Vince Dethier insinuates so cunningly into our factual information and knowledge. For the gift, of these special white butterflies—along with all your official and unofficial students, past, present, and future—Vince Dethier, I tender you my most heartfelt and grateful thanks (Chapman et al., 1987).

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