

NATIONAL ACADEMY OF SCIENCES



THOMAS EISNER

1929-2011

A Biographical Memoir by

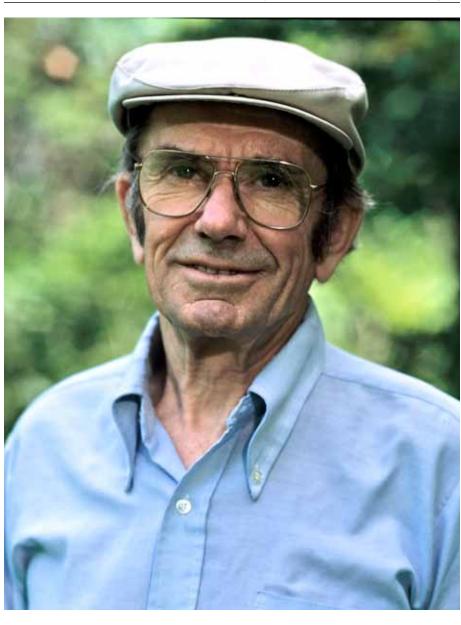
MAY R. BERENBAUM

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June 25, 1929–March 21, 2011

BY MAY R. BERENBAUM

THOMAS EISNER, THE JACOB GOULD SCHURMAN PROFESSOR Emeritus of Chemical Ecology at Cornell University, died on March 25, 2011, three months shy of his 82nd birthday, after a long and courageous battle with Parkinson's disease. Among his many accomplishments, he was widely recognized for founding and developing the field of chemical ecology, an interdisciplinary science that reflected his own broad-ranging interests. On being formally dubbed "Father of Chemical Ecology," however, in characteristically wry fashion he was said to have "shrugged off the 'honor' and demanded a DNA paternity test" (Segelken, 2011). Tom was born in the affluent Charlottenburg district of Berlin, Germany, on June



Thomas Lowe

25, 1929, the child of Hans E. Eisner, a chemist, and Margarete Heil Eisner, an artist and painter. His father, among the last doctoral students of Nobel Chemistry Laureate Fritz Haber, worked with Haber at the Kaiser Wilhelm Institute for Physical Chemistry and Electrochemistry. As the Nazis began to exercise their power and anti-Semitism started to influence government policies, life became increasingly difficult for Jewish scientists.

he Eisner family, whose home and professional lives had been disrupted by Nazi activities, left Germany in April, 1933, and headed to Barcelona, Spain, where Tom's maternal uncle lived with his family and worked for the German film company AGFA. In Barcelona, despite not knowing Spanish, Hans Eisner found employment as a chemist in a pharmaceutical company, the Laboratorios Andrómaco, and the family settled into a rented house overlooking the city. After only three years, however, the outbreak of the Spanish Civil War drove them to pack up and leave again. They departed for France on a freighter rerouted to Barcelona to pick up war refugees. After a short stay in Marseilles the family headed to Paris, where Laboratorios Andrómaco had a subsidiary office. For Tom, going to school in Paris meant mastering French, on top of the Spanish he had learned while in Barcelona. Yet unrest in Europe was spreading; because the pharmaceutical company had

offices throughout South America, the family hoped to leave Europe and relocate there. Tom later (Eisner, 2000) wrote that, of possible South American destinations, Brazil was considered less desirable than the Spanish-speaking counries, because it would have meant learning yet another language. By February 1937, when the family finally left France for Uruguay, he had already "learned to curse Hitler in three languages."

Tom spent a decade in Uruguay, studying English in an international elementary school in anticipation of a career in science, while at the same time receiving German lessons at home from a German rabbi's wife. During this relatively stable interval in his often disrupted childhood, Tom had time to pursue his passions and nurture new interests. He became an accomplished pianist and a spectacular sight-reader, with a particular interest in pieces arranged for four hands. He played with his father, an avid collector of musical scores, throughout his childhood and with fellow musician-scientists throughout his career. He also had the time and opportunity to immerse himself in the rich natural history of the region.

om graduated from high school in Montevideo and, in 1947, in pursuit of better educational opportunities for their son, the Eisners moved again, this time to the United States. They bought a house in Scarsdale, New York, where, after a failed attempt to start a chemical consulting

Tom stayed on at Harvard as a postdoctoral fellow until 1957, when he was hired as an assistant professor at Cornell, one of the schools that had rejected his freshman application. He spent his entire professional career as a member of the Cornell faculty-and kept the old rejection letter framed and hanging on his office wall for the duration.

company, Tom's father established a small but successful company producing chewable vitamins. After running the company for ten years, Hans Eisner sold the operation to a larger company and retired soon thereafter.

Tom's pursuit of higher education in the United States got off to a rocky start. Shortly after his arrival, he volunteered for a summer job with Charles Michener, a bee biologist at the American Museum of Natural History. Michener encouraged him to study entomology. Despite Michener's assistance and encouragement, Tom was turned down by every college to which he applied. To improve his academic skills, he attended secretarial school for a few months. He then applied and was accepted into a two-year program at Champlain College, in Plattsburgh, New York. There he took his first college courses, in chemistry and in comparative anatomy. (*Campbell Biology* interview, 6th edition) (http://bio2.shtechclub.org/cd/bc_campbell_biology_7/0,7052,4168824-,00.html).

Upon completing the program at Champlain, Tom was accepted at Harvard University. His first formal course in entomology at Harvard was pivotal in his decision to major not in chemistry, his father's area of expertise, but in biology. He graduated with a B.A. in that field in 1951. That same year, he met and began courting Maria Löbell, an exchange student from nearby Simmons College in the Graduate School of

Social Work. The couple married in June 1952, and she became both a life partner and a research partner for Tom, assisting him with laboratory and field experiments for more than a half-century. Maria was also his piano duet partner from their first year of marriage until their last. An expert electron microscopist, she produced many of the memorable images that appeared in many of the 40-plus papers they coauthored over the course of their life together.

Tom remained at Harvard to earn his doctoral degree in 1955, working with famed ant systematisttaxonomy specialist-William L. Brown. A fellow student in the program, Edward O. Wilson, who not only shared Tom's early interest in ants but ultimately rose to be the world's foremost authority on these insects, became a lifelong friend. Among Tom's first publications was a study he did with Wilson on the morphology of the ant proventriculus and its function in social feeding (Eisner and Wilson, 1952). Tom stayed on at Harvard as a postdoctoral fellow until 1957, when he was hired as an assistant professor at Cornell, one of the schools that had rejected his freshman application. He spent his entire professional career as a member of the Cornell faculty and kept the old rejection letter framed and hanging on his office wall for the duration.

At Cornell

Tom rose steadily through the faculty ranks at Cornell, promoted to associate professor in 1962, full professor in 1966, and Jacob Gould Schurman Professor of Chemical Ecology in 1976. Cornell proved to be a fertile place for advancing his scholarly interests; in addition to attracting outstanding graduate students, it put him in a position to begin a legendary collaboration and longtime friendship with chemistry professor Jerrold Meinwald. His new friend was an ideal partner for Tom—superbly skilled as a natural products chemist but, unlike the vast majority of equally skilled colleagues, able to see the impact of ecological interactions and evolutionary history on unusual and distinctive chemicals synthesized by living organisms. Over their years working together, Meinwald and his students and collaborators enriched Tom's biological work by contributing novel structures, new syntheses, innovative methods for isolating and identifying complex structures produced in tiny quantities, and chemical explanations for mechanisms of natural defense in organisms.

Because biologically informative chemicals often occur in complex mixtures and possess unusual structures, Meinwald had to explore new approaches to characterizing unstable compounds in mixtures and to devise stereospecific syntheses. These two colleagues, who also became perfect musical partners, with Tom at the piano and Meinwald playing the flute or recorder, ultimately

coauthored over 150 papers, making up about a quarter of all of Tom's publications and spanning from 1960 to 2008. Chemical classes subjected to their twin talents ranged from one-carbon hydrogen cyanide released from oozing glands of millipedes (Eisner et al., 1963) to the 4-carbon isobutyric acid in the repugnatorial secretions of caterpillar defensive glands (Eisner and Meinwald, 1965) to the 200-plus-membered rings of the azamacrolides in the glandular hairs of Mexican bean beetles, among the largest nonprotein natural products known (Attygalle et al., 1993).

om's early work on morphology—the form and structure of organisms—foreshadowed an important dimension of his approach to research: he possessed an uncanny ability to identify distinctive structural features and to intuit their potential significance in the life of the organism. Chemical signals are, of course, not visible; recognizing their existence by their morphological signposts became Tom's forte. Over the years he demonstrated via elegant and compelling experimentation the functions of anatomical folds, wrinkles, and projections that systematists had meticulously described without ever attempting to characterize them functionally.

Flanges along the elytra, or front wings, for example, are a defining characteristic of paussine ground beetles in the family Carabidae. Tom demonstrated that these flanges function as part of the launching apparatus that directs and deflects quinone-rich secretions discharged at boiling-hot temperatures against predators. Moreover, he pointed out the similarity of this ground beetle wing design to the technology familiar to aviation scientists as the Coanda effect—the tendency of a jet of liquid to be attracted to a nearby surface (Eisner and Aneshansley, 1982c). In another classic example, starburst-like feathery projections everted from the terminus of the abdomens of male bella moths and queen butterflies (called, respectively, coremata and hair pencils) proved to be elaborate delivery devices for plant-derived aphrodisiacs used for courtship and mating (Eisner and Meinwald, 1985).

Other odd anatomical features that yielded their secrets to Tom included the long stalks of lacewing eggs, which are coated with toxins that deter egg predators, the grappling hooks on the dorsum of lacewing nymphs, which provide an anchor for waxy secretions expropriated from their aphid prey; the whip of the whip scorpion, which precisely directs an acidic discharge at a predator; the osmeterial gland of swallowtail caterpillars, which is everted to release noxious substances in the presence of a predator; and the spongy feet of the palmetto beetle, which attach tightly via an oily liquid to the leaf surface and thereby thwart attempts by predators to pluck the beetles off the plants.

Color, too, is an important morphological signpost for chemical communication. Many chemically defended insects advertise their nasty taste with bright colors. Tom thus worked with some of Class Insecta's most colorful members. Cochineal scale (*Dactylopius* spp.), for example, had been used as a source of brilliant red pigment since Aztec times, but Tom was the first to document that the bitter-tasting pigment deters predators of the sedentary and otherwise vulnerable scale insects (Eisner et al., 1980).

ollectively, Tom and his students and collaborators provided fascinating explanations for bizarre and mystifying things in nature—why catnip smells the way it does, what makes stinkpot turtles stink, why seemingly defenseless and immobile eggs and pupae are left alone by predators, and why fireflies can glow at night without being caught and eaten, among others. The collaborative work of Tom and Meinwald, in solving these mysteries of the natural world, yielded remarkable new chemical structures, analytical approaches, and biosynthetic pathways, including the first demonstration of combinatorial chemistry practiced by an insect (Schroeder et al., 1988).

Founding a New Field of Biology

Over four decades of astonishingly productive and ingenious work, Tom and Meinwald merged two hitherto disparate disciplines—evolutionary biology and chemistry—into productive harmony. Tom actively

promoted the growth of the new discipline of chemical ecology. In 1970, with former Harvard mentor William L. Brown and Cornell colleague Robert H. Whittaker, he published a paper expanding the vocabulary of the new discipline, coining the terms "allomone" and "kairomone" to provide a classification system for interspecific chemical signals to complement the existing vocabulary for describing pheromones, which are intraspecific chemical signals (Brown et al., 1970).

Also in 1970, Tom authored a chapter on arthropod chemical defense that appeared in the edited volume edited by E. Sondheimer and J. B. Simeone titled "Chemical Ecology," the first (and for over a decade the only) definitive text in the field (Eisner, 1970). He was also instrumental in designing and offering at Cornell one of the first classes in chemical ecology. He was present at the first Gordon Conference on Plant-Herbivore Interactions in 1980, organized by his Cornell colleague Paul Feeny jointly with University of Kentucky biochemist Gerald Rosenthal, a meeting that ultimately led to the creation of the International Society of Chemical Ecology. With Meinwald in 1990, he founded the Cornell Institute for Research in Chemical Ecology (CIRCE), dedicated to exploring chemical interactions among organisms to expand basic knowledge, conserve biodiversity, and find innovative solutions to environmental and health challenges. CIRCE was the first academic institute dedicated to chemical ecology,

anticipating by six years the founding of the Max Planck Institute for Chemical Ecology in Jena, Germany. Tom's influence on the Max Planck Institute was evidenced by the fact that the founding director of the institute, Ian Baldwin, had been a doctoral student in his laboratory. n 1993 Tom and Meinwald partnered to organize a symposium at the National Academy of Sciences called "Chemical ecology: the chemistry of biotic interactions," the content of which was published in the Proceedings of the National Academy of Sciences and subsequently made available as a book in 1995 (http://www. nap.edu/openbook.php?isbn=0309052815). In 2008, Tom and Meinwald commissioned a second series of papers on chemical ecology in the Proceedings, illustrating how the field had diversified in the intervening 13 years (http://www.pnas.org/cgi/collection/chemical ecology).

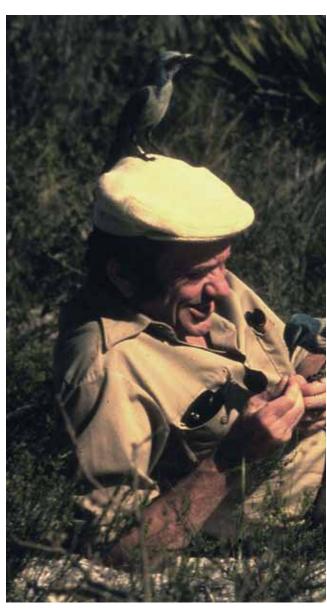
Ardent Conservationist

Over decades of productive work, Tom succeeded in interpreting chemical signaling, the principal sensory mode relied upon by the vast majority of organisms for communication. In the process, he did more than create a new discipline—he demonstrated the importance of natural history in identifying chemical diversity, the value of bioassay in demonstrating and quantifying biological activity, and the enormous benefit of

characterizing chemicals produced by living organisms within the context of their behavior and ecology. Thus, he was a remarkably articulate and persuasive advocate for biodiversity conservation in the context of chemical prospecting (Eisner and Beiring, 1994).

Tom's rich and rigorous research provided clear and compelling chemical arguments to aid those who argue to protect the earth's biotic resources because of their untapped value to humans. He was active in promoting the passage of the Endangered Species Act, testifying before Congress in 1981 (Eisner, 1982), and in garnering support for preservation of natural areas on Lignumvitae Key in Florida, in the Big Thicket region of east Texas (Eisner, 1973 a,b) and in the Emerald Necklace in Tompkins County, New York. He served on boards of many of the major conservation organizations, including the World Resources Institute Council, the Union of Concerned Scientists, and the National Audubon Society, and was a member of the National Scientific Council of the Nature Conservancy. For 14 years, he served as president of the Xerces Society for Invertebrate Conservation, during which time he was a frequent contributor to its magazine, Wings.

Beyond simple advocacy, Tom and Meinwald were instrumental in brokering a unique partnership between Merck & Company, at the time the nation's largest pharmaceutical firm, and Costa Rica's National Biodiversity Institute (INBio), to facilitate chemical prospecting of



Florida scrub jays getting their lunch. Photo courtesy Maria Eisner.

that tropical nation's rich biodiversity resources. Because royalties generated by drugs developed from natural products may not be realized for decades, Merck agreed to pay INBio \$1 million up front and to commit to the institute a share of future profits from any products that might result from the partnership. For its part, INBio pledged 10 percent of its initial payment and half of all subsequent royalties to biodiversity conservation.

hroughout his life, Tom remained a citizen of the world; among his visiting appointments were stints at Wageningen University, the Netherlands; the Smithsonian Tropical Research Laboratory, Barro Colorado Island, Panama Canal Zone; the Max Planck Institut für Verhaltensphysiologie (behavioral psychology) in Seewiesen, Germany; the Division of Entomology, C.S.I.R.O, Canberra, Australia; and the University of Zürich, Switzerland. Closer to home he conducted research at the Marine Biological Laboratories, Woods Hole, Massachusetts; the University of Florida, Gainesville; and the Hopkins Marine Laboratory at Stanford University.

During his first summer as an assistant professor, Tom discovered the Archbold Biological Station in Lake Placid, Florida, and continued regularly to visit and draw inspiration from this site for the rest of his career. Archbold's remarkable flora and fauna including stick insects, ant lions, tortoise beetles, carrion beetles, bombardier beetles, queen butterflies, pipevine swallowtail butterflies, bella moths, golden silk spiders, and ladderweb spiders, along with such plant oddities as sensitive plants and carnivorous sundews—inspired some of his most iconic studies. He described several of these projects in an article for *Bioscience* in 1982 (Eisner, 1982b), making a compelling case for incorporating natural history into biology education, a credo he lived by throughout his career. Among the last classes he taught at Cornell was a wildly popular course on natural history.

Human Rights Advocacy

Tom's personal history ingrained in him an acute awareness of the power of political regimes to jeopardize science and scientists, which impelled him to advocate tirelessly for academic freedom and human rights. At Cornell he served on its Committee on Restrictions on Academic Research and the National Interest. At the national level he served with distinction on the National Academy of Sciences Committee on Human Rights and on the AAAS Committee on Scientific Freedom and Responsibility, chairing its Subcommittee on Science and Human Rights for eight years. He was fearless in addressing threats to science policy and was outspoken and articulate on such diverse subjects as the biological effects of nuclear war, population control, and global climate change.

Scientist as Artist

The power of Tom's scientific discoveries was often amplified by remarkable visual images. Accompanying his publications for the duration of his career, these images are both biological and technical marvels. Understanding the power of a picture in illustrating a concept, Tom partnered with professionals, including engineers, to capture and preserve images that are now iconic, not only because of the scientific principles they illustrate but because of their inherent beauty.

Perhaps most famously, Tom worked out the mechanism by which the aptly named bombardier beetle (*Brachinus* spp.) explosively discharges its defensive secretion of quinones at boiling-hot temperatures (Aneshansley et al., 1969). To capture the millisecond bursts of bombardier beetle defensive spray required inventing entirely new equipment; that image is now familiar to generations of students and even appears on a few creationist websites. In October 1999, when the U.S. Postal Service issued a commemorative sheet of 33-cent stamps with images of insects and spiders selected for their "educational value and interest to children", the bombardier beetle was one of the 16 insects selected (http://arago.si.edu/index.asp?con=1&cmd=1&cmd=1&cmd=2&pg=2&tid=2043022).

In another example of his relentless resourcefulness in capturing images, to illustrate the range of the whip



Bombardier beetle spraying. Photo by Thomas Eisner and Daniel Aneshanley, Cornell University.

■

scorpion's whip, Tom posed the whip scorpion on pH indicator paper, so that the footprint of every droplet of acidic secretion was brilliantly visible. With his refined aesthetic sense and amazing technical skills, he captured images of chemicals at work—sprays emanating from arthropod orifices, toads spitting out distasteful beetles, spiders paralyzed by millipede alkaloids, fecal shields brandished by tortoise beetle grubs, and hundreds more, vividly rendering chemical communication visible to a broad audience.



Whip scorpion on PH indicator paper. Photo by Thomas Eisner, Cornell University.

om could find and capture beauty even in the most seemingly ordinary insects. *Pieris rapae*, the imported European cabbageworm, is

likely the most familiar butterfly in North America, with a range spanning the continent. An invasive species, it feeds as a caterpillar on plants in the family Brassicaceae and thus is an economic pest of cabbage and other cole crops. On the cuticle of this otherwise thoroughly well-studied species, Tom noticed glandular hairs of unknown function. With Meinwald and others, Tom demonstrated that these caterpillars produce a novel class of linolenic acid-derived natural products (Smedley et al., 2002). Accompanying the article reporting these results was a greatly magnified image of a lowly cabbageworm with, as Tom determined, defensive hairs glistening like Christmas ornaments, perhaps the most beautiful image of this species ever appearing in print.

Always a masterful photographer, Tom found new forms of artistic expression when Parkinson's disease robbed him of the precise motor control needed for photography. His use of a color photocopier to capture images of artfully arranged flowers, leaves, and shells made the "Science Times" section of the *New York Times*. In the article, Tom made the case that a color photocopier "might be useful for children, for adults in nursing homes, or for anyone who has limited mobility and access to the natural world" (Gorman, 2006). Nor did his condition prevent him from teaching classes and writing books; three of his nine books were written in the last decade of his life.



Cabbage worm, with "defensive hairs glistening like Christmas ornaments."

Photo by Thomas Eisner, Cornell University.

Accolades

Tom's work was recognized with virtually every kind of academic award—election as a fellow of the American Academy of Arts and Sciences, the American Association for the Advancement of Science, the Entomological Society of America, the Animal Behavior Society, and the Explorers Club, as well as election to the National Academy of Sciences (1969) and the American Philosophical Society. Internationally, he was elected as a member of the Deutsche Akademie der Naturforscher Leopoldina and as a foreign member of the

Royal Society of London and the Academia Europaea. He received the first Karl-von-Frisch Medal from the Deutsche Zoologische Gesellschaft.

Tom also won high honors from practically every scientific society to which he belonged, including the Founder's Award from the Entomological Society of America, the Newcomb Cleveland Prize from the AAAS, the Procter Prize from Sigma Xi, the Distinguished Service Award from the American Institute of Biological Sciences, and the Silver Medal from the International Society of Chemical Ecology. In 1990 he received the Tyler Prize for Environmental Achievement, and in 1994 he was awarded the National Medal of Science. He also received honorary degrees from the University of Würzburg, the University of Zürich, the University of Gothenburg, and Drexel University.

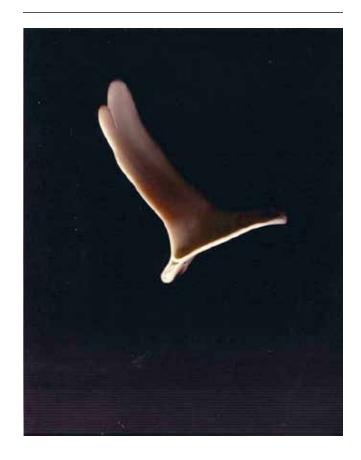
Beyond the scientific community, Tom also won recognition for his efforts in promoting public understanding of science. Of six films by or about him, "Secret Weapons," produced with the BBC, won the Grand Award in the Science Category of the New York Film Festival. This film, for which he served as both writer and presenter, also won the Best Science Film at the British Association for the Advancement of Science and the Scientific Award at the Wildscreen Festival. His book *For Love of Insects* (Eisner, 2003) was designated the Best Book in Biological Sciences that year by the Professional and Scholarly Publishing Division of the



Above and opposite: images which Eisner made by arranging natural materials on a color photocopy machine.

Photo by Thomas Eisner, Cornell University.

American Association of Publishers, and in 2005 he won, from Rockefeller University, the Lewis Thomas Prize for Writing about Science. Entomological colleague Louis Roth conferred a unique form of immortality



upon Tom in 1994 by naming a new genus of beetlemimicking cockroach *Tomeisneria* in his honor (Roth, 1994).

Tom was survived by his wife of 58 years, Maria Löbell, along with three daughters—Yvonne, Vivian, and Christina—six grandchildren, a sister, Beatrice Gil Zorrilla, and nephews and nieces. In his memory a fund was started to create an endowment at the Archbold Biological Station. Despite his extraordinary creativity, astonishing insight, and unflagging enthusiasm, his almost 82 years were not sufficient to allow him to explain all of the mysteries in this rare pocket of biodiversity, and the endowment will ensure that natural history will continue to inspire and motivate lovers of insects (and every other kind of organism) for years to come.

In Tom's honor, the Department of Neurobiology and Behavior at Cornell University has established the Thomas Eisner Memorial Fund. The fund was established with the aim of providing extra support for new assistant professors in the department who are doing work that continues the tradition of excellent research and teaching in behavioral biology established by Tom Eisner. From time to time, when appropriate, one new assistant professor will be honored with the title of "Thomas Eisner Fellow", a title that s/he will hold for the period of the assistant professorship.

Irrespective of its paternity, the field of chemical ecology owes its existence to the insight, the creativity, and the energy of Tom Eisner. A check of the membership list of the International Society for Chemical Ecology reveals that, as biological subdisciplines go, the field has remained relatively small. Far greater in number, however, are the thousands of people, in biology classes hearing lectures describing Tom's work or

at home watching Tom's films or reading Tom's books, who have been intrigued and inspired by his research, teaching, and service, and who have gained a greater appreciation of the scientific enterprise, and a greater admiration of Class Insecta, as a result.

Acknowledgments

I thank Maria Eisner and Jerry Meinwald for sharing their memories with me and for checking for accuracy this necessarily incomplete account of Tom's rich and remarkable life. Maria Eisner supplied the photographs appearing in this memoir.

Disclaimer

Parts of this essay appeared in two previous memoirs:

Berenbaum, M. R., 2011. Retrospective. Thomas Eisner: Interpreter extraordinaire of nature's chemistry. *Proc. Natl. Acad. Sci. U.S.A.* 108:19482-19483.

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