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GEORGE BROWNLEE CRAIG, JR.

1930—1995

A Biographical Memoir by
EDDIE W. CUPP

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July 8, 1930–December 21, 1995

BY EDDIE W. CUPP

GEORGE B. CRAIG, JR., Clark distinguished professor of biological sciences at the University of Notre Dame, died quietly in his sleep on December 21, 1995, at the age of sixty-five. He was attending a national meeting of the Entomological Society of America when he passed away. He is survived by his wife, Elizabeth (Pflum) Craig, two daughters, Patricia Craig and Sarah Craig Peterek, and his son, James Craig.

Craig had been a member of the National Academy of Sciences since 1983. He was born in Chicago, Illinois, on July 8, 1930, the son of George Brownlee Craig and Alice Madelaine McManus Craig. He attended the University of Chicago Laboratory School, graduated from the University of Indiana in 1951 with a B.A. in zoology and received both M. S. and Ph.D. degrees in entomology from the University of Illinois in 1952 and 1956, respectively.

Craig was an internationally recognized expert on the biology and control of mosquitoes, particularly species belonging to the genus *Aedes*. As a young scientist, he pioneered the study of mosquito genetics using *Aedes aegypti*, the yellow fever mosquito, as the subject of his investigations. His work resulted in the recognition that this species exhibited a wide variety of genetic traits that could be mapped

to specific chromosome locations and also indicated that mosquitoes might be well suited for control measures using genetic means independent of the use of insecticides. During his career, he and colleagues from his laboratory participated in 485 journal articles, technical pamphlets, and abstracts devoted almost exclusively to the biology of aedine mosquitoes. Craig was author or co-author of 182 scientific publications.

His dissertation research was conducted at the University of Illinois in the laboratory of William R. Horsfall, a distinguished entomologist and eminent mosquito biologist. As a graduate student, Craig focused on the sculptured patterns of the chorion of *Aedes* eggs and utilized the uniqueness of these surface designs to develop taxonomic keys for identification of this particular stage in the mosquito's life cycle (1956). As a result, field research on a large group of mosquitoes previously considered intractable became possible by collecting eggs from soil samples and identifying them to the species level. These findings greatly assisted control programs aimed specifically at temporary pool mosquitoes and related species that plagued much of the Midwest and parts of Canada during spring and early summer.

Craig served in the military as a first lieutenant with the U.S. Army Preventive Medicine Detachment at Ford Meade, Maryland, in 1954 and as a research entomologist with the U.S. Army Chemical Center in Maryland from 1954 to 1957, splitting time between these duties and his work as a graduate student. He received his Ph.D. in entomology in 1956 and joined the biology faculty at the University of Notre Dame in 1957.

It was here that he accomplished so much as both researcher and teacher during his brilliant thirty-eight-year career in academia. He chose *Aedes aegypti* for study not only because of its historical prominence and medical im-

portance but because it was also easy to rear and maintain in the laboratory. The result was the establishment of the Mosquito Genetics Project at Notre Dame, which quickly evolved into the Vector Biology Laboratory (VBL). From this scholarly haven he successfully directed over forty Ph.D. students and mentored thirty-nine postdoctoral fellows.

Following the premise that ". . . workers [do] not appreciate the value of genetic knowledge [of mosquito vectors] in studies of disease relationships and public health . . . .," Craig began to isolate mutants of the yellow fever mosquito and by 1962 he and his students had described nine inherited factors affecting color and thirty factors causing modification of body structures. In a 1967 landmark publication, Craig and his colleague, W. A. Hickey, expanded this list to eighty-seven mutants based largely on a systematic program at the VBL of inbreeding different populations of *Aedes aegypti* to uncover recessive alleles in the heterozygous condition. Approximately half of these mutants were useful as genetic markers. In addition, linkage maps placing about twenty-eight mutants on the three chromosome pairs of this mosquito were presented.

While this summary clearly demonstrated the richness of genetic variability in *Aedes aegypti*, it also had several other significant effects that greatly influenced Craig's career, as well as others in the field. *Aedes aegypti* began to rival *Drosophila melanogaster* as a laboratory animal in terms of knowledge of its genetics. Thus, this information also provided a detailed scientific background for non-mosquito specialists and stimulated several to investigate the biochemistry, physiology, and developmental biology of the yellow fever mosquito, thereby introducing to the field of vector biology a group of scientists with a very different research background and orientation (1967, 1968). This is a process that continues today and has helped energize the discipline of vector

biology—the study of insects and related arthropods that transmit disease-causing organisms.

Recognition of both the size and scientific quality of his work on the formal genetics of *Aedes aegypti* also firmly placed George Craig in the pantheon of mosquito geneticists with other internationally recognized luminaries such as G. Frizzi, J. B. Kitzmiller, and H. Laven. Craig's influence as a scientist and thinker was expanded to the global playing field and, with this prominence, he began to shape the policy and operations of a variety of domestic and international institutions that touched virtually every aspect of his discipline. A further charge—the World Health Organization International Reference Center for *Aedes*—was added to the VBL in 1969, and he readily accepted this responsibility and opportunity to collect and house the many exotic strains of medically important *Aedes* mosquitoes from around the world.

Because of his deep concern that results from the VBL be translated into useful public health programs aimed at vector control, Craig and colleagues devoted a great deal of their research planning to developing genetic control schemes that could function with little or no use of insecticides (1967). As a result, he and his students identified genes from *Aedes* spp. that controlled susceptibility to parasites causing malaria as well as important eco-physiological traits such as autogeny, diapause, host choice, and sex ratio distortion (1968, 1969). If manipulated into a vector population, these genetic factors might compromise the ability of a mosquito to successfully transmit a pathogen or even cause the insect population to go out of existence. Concurrent with the genetic work, he and members of the VBL described the physiological basis for such critical pre- and post-mating processes as female receptivity (1968) and refractoriness, reinforcing his earlier description of matrone, a male-pro-

duced factor that induces monogamy in female mosquitoes following insemination. Not surprisingly, a great deal of the information discovered during those halcyon days remains valuable today as vector biologists attempt to construct transgenic mosquitoes using methods in molecular biology instead of laboratory crosses.

In 1969 Craig was selected as a scientific advisor and member of the research faculty of the International Center of Insect Physiology and Ecology (ICIPE) in Nairobi, Kenya. This appointment, which required a considerable time commitment away from the VBL, provided the first real opportunity to conduct field research on *Aedes aegypti* in the biological environment of its native origin. He directed the Mosquito Biology Unit (MBU, an acronym that means both "mararia" and "mosquito" in one East African dialect) for the next eight years and focused a great deal of his attention primarily on the population biology of *Aedes aegypti* and its control using genetic means. Working almost exclusively from a field laboratory in Mombasa, Craig and colleagues investigated the population genetics of this mosquito using electrophoretic surveys as a means to measure and compare genetic distances between resident and nonresident populations and to demonstrate sympatric subspecies in East Africa. Other studies measured vector competency for yellow fever virus and host-seeking behavior and movement of female mosquitoes both within and between villages. Attempts at area-wide control by using genes introduced via translocations were largely unsuccessful, however, leaving Craig dissatisfied with that aspect of the project. He left Africa with a much greater appreciation of the population genetics of this species and the belief that control of mosquitoes through genetic means alone would be an extremely daunting task.

The occurrence of La Crosse virus in the eastern United

States and the danger of encephalitis posed by this arbovirus led Craig and his colleagues to develop a multi-faceted program centered on the mosquito vector, *Aedes triseriatus*. This phase of his career, in many ways, mirrored his earlier efforts with *Ae. aegypti*. *Ae. triseriatus* has a similar biology to *Ae. aegypti*, using natural cavities such as rot holes in deciduous trees and other plants that temporarily hold water to lay its eggs; it is in this aqueous environment that the immature stages develop.

Spurred on by observations made primarily by scientists at the University of Wisconsin in the early 1970s, Craig and his colleagues at the VBL mapped the genetic differences in vector competence of *Ae. triseriatus* to La Crosse virus as a first step to understanding its endemic distribution. The results, published in 1977, demonstrated a high degree of variability for this trait in populations collected over most of the eastern United States and opened the way for a long-running series of laboratory and field studies. Over the next five years, the VBL's preoccupation with *Ae. triseriatus* (and its sibling *Ae. hendersoni*) led to fundamental knowledge of the population genetics of this species (1978, 1980), patterns of interspecific hybridization (for *Ae. triseriatus* and *Ae. hendersoni* and two other siblings found primarily in the western United States), linkage maps, cytogenetics, and formal genetics of diapause, an important phenological trait since La Crosse virus is transovarially transmitted (1980).

Other investigations produced in-depth biological knowledge of these two mosquitoes and were useful in understanding the sweeping epidemiology of La Crosse virus. These included the impact of larval nutrition in affecting the ability of the adult female mosquito to transmit the virus, the presence in *Ae. hendersoni* of a salivary gland barrier to virus transmission, the spatial distribution in wood lots of immature and adult *Ae. triseriatus* and average survivorship of the

adult female, and the ability of *Ae. triseriatus* to move to the periphery of urban environments (including South Bend, Indiana) and readily establish itself in tree holes found in domestic settings and discarded tires. The latter study was significant and prescient since it foreshadowed another major chapter in Craig's career—his studies of the Asian tiger mosquito *Aedes albopictus*.

The emphasis by Craig and his group on studying all aspects of the vector biology of *Ae. triseriatus* also advanced a fundamental understanding of the tree-hole habitat in which the immature stages of this mosquito occurs. Over a ten-year period, a series of papers were published from the VBL characterizing the ecology of this niche and describing its influence on mosquito biology. In recognition of these contributions, a major workshop was held in 1984 and the resultant proceedings, published in 1985, were dedicated to Craig. Of the thirty-three papers presented at that workshop, over half specifically addressed the ecology of tree-hole or container-breeding mosquitoes.

It was also in 1985 that *Aedes albopictus* entered the United States through the port of Houston, Texas. This mosquito, given the common name of the Asian tiger mosquito, quickly became the center of attention at the VBL. Immediately sensing its potential medical importance as a vector of viruses, Craig and his colleagues at the VBL and elsewhere demonstrated that this invader species could transmit not only dengue viruses (if one or more strains of this exotic virus were introduced into the United States) but also medically important indigenous viruses such as La Crosse and eastern equine encephalitis (EEE). In a masterfully simple series of studies using photoperiodic sensitivity and cold-hardiness of the egg stage, members of the VBL demonstrated that the probable introduction of *Ae. albopictus* was in tire casings shipped to the United States from temper-

ate-zone Asia and not from a tropical location (1987). They predicted (quite accurately) that this species would be able to spread into the Midwest since the egg stage can diapause and withstand the rigors of winter. This has since come to pass.

Working with collaborators from the Centers for Disease Control, Craig later demonstrated that EEE virus occurred in naturally infected mosquitoes in Florida and that a geographic strain of the mosquito from that location was fully able to transmit the virus (1992). This report not only highlighted the broad host selection of blood feeding exhibited by *Ae. albopictus* (EEE typically circulates in avian populations) but it alerted the public health community to yet another threat—the potential hazard of a particularly virulent form of encephalitis associated with this introduced species.

As with *Ae. aegypti* and *Ae. triseriatus*, the members of the VBL characterized the Asian tiger mosquito from a variety of biological and genetic perspectives and over the ensuing years this species was the subject of dozens of journal and other technical articles, including a critical summary of information for the hemisphere (1995). Even in the months preceding his death, Craig refused to yield to the physical discomfort of heart disease and continued his usual exuberant pace. Having recognized the epidemiological significance of the diapause capability of *Ae. albopictus* for the eastern and mid-western United States, he and his colleagues published on the importance of this phenomenon (1995). He coordinated a field trip in the summer of 1995 along the Texas-Mexico border to assess the dengue situation and evaluate the relative roles of *Ae. aegypti* and *Ae. albopictus* as vectors. Ever the teacher and mentor, he and his VBL colleagues had just finished making six presentations at the

national meeting of the Entomological Society of America in Las Vegas when he passed away.

George Craig was an exceptionally strong-willed person who took great pride in his occupation. He loved academia and the intellectual possibilities that it offered both society and his profession. He also loved the University of Notre Dame and once stated jovially that the only other job perhaps better than his was being a U.S. senator. Then, after a dramatic pause, he retorted, "No, being a full professor at Notre Dame is the absolute best job of all."

He placed immense demands on himself to excel as a scientist and required the same of his VBL colleagues. The result was a career filled with awards and numerous professional acknowledgements. Chief among them was the Walter Reed Medal of the American Society of Tropical Medicine and Hygiene, an award shared by a veritable elite of tropical public health. He was also posthumously awarded the Hoogstraal Medal by the American Committee for Medical Entomology, a subgroup of that society. Fittingly, an earlier recipient of this medal had been W. R. Horsfall.

Craig was an inspirational figure to many in the profession because of his willingness to use his international stature and position in science as a bully pulpit for support of vector biology. Indeed, his advocacy for this area of science became a major preoccupation during the five years prior to his death as he labored to increase funding opportunities for field-oriented, ecological, and epidemiological research to strike a balance with the burgeoning laboratory investigations emphasizing molecular biology. He was also deeply devoted to his students and postdoctoral fellows and often toiled persistently on their behalf after they had left his laboratory. He was a loyal friend to many and a fierce partisan to a few.

George Craig was also an outstanding teacher who worked

tirelessly to be effective in the classroom, laboratory, and the field. Inspired throughout his professional life by the teaching example set by Professor Horsfall, he aspired to be as successful in the academic arena as in research. In the classroom, he had an effective, almost charming way of disarming students and creating a relaxed but challenging atmosphere, both in undergraduate colloquia and graduate seminars. One of my fondest recollections of Craig is watching him sit very casually in the VBL insectary, dissecting mosquitoes, and chatting in a light-hearted way with an undergraduate student. Over a period of an hour, the topics the two discussed ranged from the methodological approaches used in formal genetics to how to design a meaningful experiment. The student left, committed to becoming a biologist. He often said that his most treasured prize was the Distinguished Teaching Award given by the Entomological Society of America; he was selected as the first recipient in 1975.

Craig's service contributions were legion. He gave his time freely to an almost endless number of organizations, committees, and causes. Never content to remain in the ivory tower, he was particularly devoted to mosquito control. Having worked summers from 1951 to 1953 as a student in the Des Plaines Valley (Illinois) Mosquito Abatement District, he remained interested in this vocation his entire professional life, faithfully attending meetings for mosquito workers in the state, the region, and nationally. He was made a charter member of the Indiana Vector Control Association in 1976 and served as the director of the mosquito abatement program in his county from that year until his death. In 1988 he became president of the American Mosquito Control Association, one of the largest professional groups of its kind in the world. He also assisted other scientific societies, governmental agencies, and inter-

national organizations in a variety of committee and governing capacities. Conscious of his civic responsibilities and the importance of teaching nature to young minds, he was a merit badge counselor to both the Girl Scouts and the Boy Scouts of America. He advised numerous conservation organizations and was an ardent defender of the environment, retreating annually to his cabin in Michigan to vacation and reflect on his work.

His love for collegiate sports was renowned. Having been a wrestler at the University of Indiana, he followed that sport closely and often coordinated his spring speaking schedule to coincide with seminar invitations at institutions hosting NCAA wrestling finals or located within easy driving distance of that venue. As a member of the University of Notre Dame's athletic board, he reveled in the football team's success and the opportunities to attend post-season bowl games. At the same time, he was committed to maintaining the high academic achievements expected of Notre Dame's scholar athletes and expected only the very best from them both on and off the field of competition.

The contributions made by Craig to medical entomology are almost incalculable. During his prodigious career, his work and that of his VBL colleagues consistently joined laboratory and field research, thereby leading to the rapid development of promising leads that could be verified shortly after their discovery. This approach, with its commitment to deriving "real world" answers required by vector control professionals promulgated a much-needed trend in this area of entomology. The diversity and amount of biological information developed for the major aedine mosquito species studied by Craig and associates is enormous and, because of its fundamental nature, largely remains useful. As alluded to earlier, key aspects of the genetic information on *Ae. aegypti* are currently being used in an attempt to

transform the genome of that and related species by introducing favorable traits into mosquitoes. The field ecology findings for the three major *Aedes* species studied by the VBL will also be extremely important as attempts are made to release transgenic mosquitoes into natural populations to insert and maintain genes that modulate vector efficiency.

During his tenure at Notre Dame, Craig recruited and trained an enormous number of students and postdoctoral fellows and he assisted dozens of scientists visiting the VBL for sabbaticals or short-term sojourns. His scientific accomplishments and engaging personality inspired students and professionals at other institutions to pursue vector biology. Thus, in the context of achievements during his career, this living legacy of scientific talent and commitment to vector biology is his greatest contribution and the one of which he would be most proud. When Craig's obituary appeared in *The New York Times*, it noted his passing by announcing that he was an entomologist "feared by mosquitoes." This pronouncement would also give him great satisfaction.

I THANK MORTON FUCHS, University of Notre Dame, for sharing biographical information and providing a photograph of Craig taken by the University of Notre Dame's Publications and Graphic Services in 1989. This photo appeared in the 1990 faculty directory. I particularly want to thank Leonard Munstermann, Yale School of Medicine, who contributed valuable bibliographical information denoting VBL publications from 1959 to 1996. Other sources of information included *The New York Times* (December 23, 1995), *The Washington Post* (December 24, 1995), and an obituary written by Bruce Eldridge, University of California, that appeared in the *Journal of Vector Ecology*.

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