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GEORGE KELSO DAVIS
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A Biographical Memoir by

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George K. Davis

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July 2, 1910–October 27, 2004

BY ROBERT JOHN COUSINS

GEORGE KELSO DAVIS WAS an internationally recognized animal nutritionist whose training in biochemistry and physiology gave him the background to approach applied questions from a fundamental perspective. His pioneering use of trace elements to improve animal performance through diet supplementation was the key to the development of productive cattle industries in Florida and in Argentina. He directed the first use of radioisotopes for nutrition studies in large domestic animals, which led to many seminal findings in mineral metabolism.

George Davis was born in Pittsburgh, Pennsylvania, on July 2, 1910, the son of Ross Irwin Davis and Jennie ("Jeanne") Lovinia Kelso Davis. In 1922 Davis's mother died of pneumonia. George and his brother John went to live with an aunt in Lakewood, Ohio, and a younger brother Robert went to live with an aunt in New York City. His father remarried in 1923 to Constance Sibray, and the family reassembled. His schooling was in the public schools of Pittsburgh. He graduated from the Samuel Pierpont Langley High School and gave the valedictory speech. After taking a business course, he enrolled at the Pennsylvania State College (now Pennsylvania State University) in the fall of 1928,

majoring in dairy science and agronomy. George's interest in agriculture was stimulated by his work, during most childhood summers and vacations, on the farm of his grandfather, George James Davis, located near the mill town of Aliquippa, Pennsylvania.

George said he "was the greenest of green freshmen going to Penn State in 1928." After spending the summer of 1929 in charge of the maternity barn at a dairy farm, he changed his major to agricultural biochemistry. While at Penn State, he was active in the Christian Association (vice president) and was an associate editor of the *Penn State Farmer,* the freshman handbook, and *La Vie*, a campus paper, for which he was fraternity editor. Although he had won his letter in football and other sports in high school, he was much too lightweight (145 pounds at that time) for college football and so, during his college career, he restricted his sports to intramural participation in boxing, tennis, golf, lacrosse, and baseball. George was awarded a number of scholarships as an undergraduate, and these were especially appreciated since this was during the depths of the Great Depression. George realized how good a high school education he had received when he found how easy some of his college courses were. In those days at Penn State the dean of men posted the rank of the students at the end of the semester. During his first year, George discovered that he was third in the freshman class.

George became something of a cynic about the fraternities, realizing that students like him (that is, with good grades) were attractive to fraternities since they helped the fraternities gain a sufficiently high scholastic average to allow social functions, such as dances and house parties. Eventually, during his sophomore year, he was urged by Professor Andy Borland, professor of dairy husbandry, to join the

Alpha Zeta fraternity, which was both honorary (pledging only sophomores) and social (they had a house on campus).

George received the B.S. degree with honors from Penn State in 1932. Owing to the Great Depression, the class of 1932 found a very slim job market. At the urging of his major professor at Penn State, R. Adams Dutcher, Davis accepted a scholarship at Cornell offered by Leonard A. Maynard, a future National Academy of Sciences member. He started his graduate work with Maynard as his mentor in the fall of 1932. George had spent the summer building a house on land inherited by his father. The rental fee from that house would provide a supplemental stipend during his time at Cornell.

Very soon after getting to Cornell on the nine-month scholarship offered by Maynard, another faculty member, L. C. Norris, who was one of Maynard's first graduate students, offered George an assistantship as a chemist to help run studies with poultry, quail, and pheasants. This involved many Kjeldahl nitrogen analyses, but the pay was better than that for the scholarship and it was on a 12-month basis. When it began to look as if George might become a poultry nutrition convert, Maynard stepped in with an assistantship in the animal nutrition laboratory that allowed George to carry out his own graduate research. It should be pointed out that at that time at Cornell, all graduate students in nutrition spent some time working with Maynard, Clive McCay, and Sidney Asdell on projects that these professors had underway. In those depression days, graduate students felt fortunate because, in addition to receiving a stipend, their tuition was waived.

As part of his assistantship, George served as purchasing agent for the Maynard laboratory . He learned a number of lessons in that role that stayed with him over the years. One

lesson was to always have a wish list of needs with accompanying costs available for every opportunity. He also learned to avoid spending all of the funds immediately, just to get rid of the accounting task. During his graduate program, George saw his assistantship stipend increase to $1,400 per year. At the time public school teachers earned about $1,200 annually.

George stated, "Dr. Maynard always insisted that investigations into the nutritional requirements should be repeated on more than one species," and so, in carrying out his doctoral research on the effect of fatty acids on muscle function, he developed diets that were fed to guinea pigs, lambs, goats, and calves. By incorporating cod liver oil into the diets of these herbivores to supply vitamins A and D, Davis found that a muscle dystrophy developed that involved both heart and other striated muscles. Because of the heart damage Davis observed, he and his colleagues had the idea of running electrocardiographs on the animals. The goats were not always cooperative. He discovered that soaking a piece of cheesecloth in salt water and letting the goats suck on it would keep them still long enough to get the EKG.

George was involved in Presbyterian activities on the Cornell campus. One of the programs the Presbyterian student pastor developed to interest students was that of theatrical productions. One such play, called *LoMo*, had two lead characters played by Ruthanna Wood and George. As Ruthanna recalls it, she realized on stage that George's eyes were blue and completely forgot her lines. After Ruthanna graduated in 1934, she left Cornell for her dietetics internship at Columbia Presbyterian Hospital in New York City. George traveled there to visit her as often as he could. George Davis and Ruthanna Wood were married on January 25, 1936, in East Orange, New Jersey, after she had completed her training as a dietitian.

While George was a graduate student, a major project at Cornell was what they called "the old age project." Maynard and McCay had observed that rats kept on a restricted diet from a short time after weaning appeared to live much longer than rats that were allowed to eat *ad libitum*. The logical research question was, "What was the basis for this occurrence?" Special care was taken to see to it that the diets contained all the required nutrients, and multiple observations were made on the activity and body changes that occurred. Experiments to explain the influence of caloric restriction on longevity have continued into the early part of the twenty-first century but without definitive biochemical explanation. George's travels to New York City resulted in some problems for him as a student involved in this project, as he was on occasion tardy in his duties. Nevertheless, based on a narrative that George wrote in his later years, it was clear that he had an eventful and useful graduate experience that was accentuated by the personalities of Maynard, McCay, Norris, and others.

Davis's Ph.D. final examination went smoothly, with Maynard, Dye (physiology), and Olafson (pathology) participating. Following Davis's successful defense, E. B. Forbes of Penn State offered George an academic position, as did George Brown of Michigan State University. A pharmaceutical company in Des Moines, Iowa, also offered him a position. This success at securing employment was very impressive, as job openings during the Depression were scarce. He accepted a position as assistant professor and research chemist at Michigan State in the Experiment Station's Chemistry Department. There he worked with Vern Freeman on swine nutrition, particularly with the problem of necrotic enteritis, as well as with other faculty on projects involving horses, sheep, and beef cattle. Davis remained at Michigan State

for five years and made significant contributions in the areas of nutrition related to disease in animals. These included the water-soluble B vitamins and *Salmonella* infections in swine; riboflavin and vitamin C in "moon blindness" in horses; trace minerals and enterotoxemia in lambs; and vitamin C as a factor in the sterility of bulls. The Davis family grew in East Lansing with daughters Dorothy Jeanne, twins Mary Ellen and Ruth-anna Marie, and Virginia Kay being born there.

His trace element studies led in 1942 to an invitation to join the faculty at the University of Florida as a professor of nutrition and animal nutritionist in the Florida Agricultural Experiment Station. He was hired by A. L. Shealy, head of the Animal Industry Department, and Wilmon Newell, provost of agriculture. After the Davis Family moved to Gainesville, they added two sons, Robert Wyatt and George William Ross.

During World War II, when special emphasis was placed on food production, Davis was challenged by the abundant nutrition-related problems facing the cattle industry of Florida. Most notable of these was "salt sick." In this condition animals that were on pasture for more than three months would rapidly become ill and die even though the pastures produced tremendous tonnages of forage. The philosophy at the time was that purebred cattle could not survive the environmental conditions in Florida. Faculty members Wayne Neal, whom George succeeded, and Raymond Becker suspected cobalt deficiency might be involved, based on research done in Australia and New Zealand. Shortly after he arrived, Davis noticed that this particular problem was unique to specific regions in Florida. Consequently, one of his first projects was to try to analyze forage from "salt sick" and healthy areas for, among other things, iron, copper, and

cobalt. He soon discovered that the chemical methods for analysis of cobalt were not sensitive enough to detect cobalt in any of the samples of forage. This led him to contact colleagues in agronomy at the university, who had a working spectrograph, asking them to run some analyses. They reported that the forages contained 0.04 ppm cobalt plus or minus 200 percent.

Seeking a method that would enable them to determine whether cobalt was a factor in "salt sick," Davis, at the point when chemical determination of cobalt content failed, considered the possibility of using radioactive tracers. He purchased a Herbach and Radiman Geiger counter (one of the earliest gamma counters), and started a search for someone who could provide the Florida research team with radioactive cobalt. Davis had been aware of reports of the work on radioisotope production with cyclotrons, and he wrote to six people working with cyclotrons, asking them to collaborate and supply his lab with radioactive cobalt. Those who replied indicated that they could not consider helping, but two noted that they thought the Massachusetts Institute of Technology might be able to help. He called John Irvine at MIT and was told that they were 110 percent booked with their cyclotron. Irvine also said, "Why don't you come see us and we can discuss what can be done?" The invitation from Irvine led to a trip by rail to Boston, where George experienced typical wartime travel difficulties.

The conference went smoothly, and Irvine indicated that MIT would supply the cobalt by bombarding stable iron and separating out the radioactive cobalt. Of course, Davis was interested in cost, having a $300 budget. Irvine just laughed. About three weeks later, the first shipment arrived in Jacksonville, Florida. It was enough radioactive cobalt for 1 cow and 100 rats; but the half-life was limited and

they had to work rather fast. Two weeks later, they got a larger supply that was enough for a year. Davis later stated:

> What I did not know at the time, but learned after World War II, was that these people were working on the atomic bomb. The people in Washington, D.C., were so concerned with secrecy of the Manhattan Project that they reasoned that, 'Normally, if a professor at a university asks for collaboration from a professor at another university, it will be given if at all possible.' The folks at MIT were told to collaborate, and the atomic weapons budget would pick up the costs.

The Florida team was the first to use radioactive isotopes in large animals. As pioneers, they had limited equipment and were learning a lot about both the design of experiments using radioisotopes and protection from radiation exposure as they went along. Cyril Comar and Davis isolated a number of cobalt-labeled compounds from the rumens of the cows given the isotope. Davis later commented, "No doubt one of them was vitamin B_{12}."

The success of the Florida team's research on cobalt led to experiments on the metabolism of other minerals (calcium, copper, iodine, magnesium, phosphorus, and zinc). These radioisotopes were supplied by Irvine. At the close of World War II, George's $300 collaboration with MIT ended. Fortunately, Oak Ridge National Laboratory continued to supply Florida with the necessary isotopes. At a conference to discuss the availability of isotopes from Oak Ridge, Davis stated that it was clear from the presentations made that of all the universities that received radioisotopes during World War II, only the University of Florida's program produced results. Between 1942 and 1960, about 700 scientific papers were published from the nutrition lab at Florida. Davis was an author on 250 of those papers.

Subsequent to starting the cobalt research, George and his coworkers evaluated the poor performance of cattle on ranches in the Ocklawaha region of north-central Florida.

They observed some signs of copper deficiency, so Davis recommended applying copper sulfate (initially 50 pounds per acre) to the pasture. Following the application of copper sulfate to the pasture land, cattle that, when placed on pasture prior to market had averaged gains of six pounds per animal, improved to an average gain of 156 pounds per animal, with an increase in grade. Practical improvements such as these literally built the cattle industry in Florida, with lasting commensurate financial rewards.

During the 1960s, George Davis was very active in nutrition research in South and Central America. Much of this effort was localized in Argentina and focused on the condition in cattle and horses called "enteque seco." The problem at the time was thought to be related to a phosphorus deficiency and had resulted in a decades-long stagnation in beef production. Davis coordinated funding through the Food and Agriculture Organization of the United Nations and Instituto Nacional Technologico Agricultural (Argentina), after being turned down by another U.N. funding group. George's group found that the problem was not phosphorus deficiency. Instead, they observed that in affected animals, elastin-rich tissues (e.g., the lungs and diaphragm) were calcified, an atypical situation. Working with Argentinean counterparts, the research team concentrated on the plant *Solanum malacoxylin* after extensive evaluation of the forage available for these cattle. During the dry months, which coincided with severity of the condition, cattle foraged heavily on this plant,. Excess vitamin D_3 was known to produce the same metastatic calcification in cattle. Davis sent material to Hector DeLuca at Wisconsin and Bob Wasserman at Cornell, both future National Academy of Sciences members. With their help and that of others, the active principal was established as a water-soluble glycoside of the hormonal form of vitamin D_3. Through bypassing usual control

for production of this hormone through oral consumption of the plant, excess calcification occurred. Davis was particularly proud of this international team effort. In autobiographical information, he wrote:

> I shall always be proud of the group that we assembled for the FAO-INTA project. They tackled a problem that had limited animal production. It had been described in their literature for many years, but never systematically approached until this work, and in five years we had not only solved the puzzle but in addition had shown that green growing plants can produce an active form of vitamin D.

In 1960 Davis assumed the additional responsibility of Director of Nuclear Sciences at the University of Florida. He was responsible for the construction of the nuclear sciences building and programs in the Departments of Chemistry, Physics, Radiation Biology, and Nuclear Engineering. He spearheaded a Center of Excellence development grant from the National Science Foundation, which, with matching funds from the State of Florida, provided over $10 million for the upgrading of programs in theoretical engineering, chemistry, physics, and radiation biology. In 1965 Davis was made director of biological sciences, with responsibilities for microbiology, botany, zoology, biological sciences, and biochemistry.

In 1970 Davis became director of all sponsored research at the university. During his tenure in that position (1970-1975) sponsored research support grew rapidly, particularly in the new Health Science Center. In accord with University of Florida policy of the time, he resigned as director at age 65 and returned to the laboratory as a professor, carrying out research on the relationships of organic compounds that influence the availability of minerals from feed components.

One of George's major activities upon retirement was serving as president of the twelfth International Congress of Nutrition, held in San Diego in August 1981. Four years of planning went into the congress, which was sponsored in part by the International Union of Nutritional Sciences, at that time affiliated with the National Academy of Sciences. Along with his colleagues responsible for the Congress, Davis raised about $100,000, a significant sum for an international congress at that time. An excess of about $50,000 remained, which continues today as a source of funding that allows younger scientists to attend these international congresses. An additional post-retirement activity for George was service to the U.S. Department of Agriculture in the late 1970s as program manager for the competitive grants program in human nutrition. He served as the first director of this program, which is now part of the National Research Initiative of the USDA.

George Davis received over 30 honors and awards. These included, at the national level, the Borden Award of the American Institute of Nutrition, the Herbert A. Spencer Award of the American Chemical Society, the Eli Lilly Lectureship, the Burroughs-Wellcome Lectureship, and election as a fellow of the American Institute of Nutrition. He was honored as a Distinguished Alumnus of Penn State in 1982. At the University of Florida he received the Senior Faculty Award of Gamma Sigma Delta and Faculty Award of Florida Blue Key Honorary, among other honors. His honorary societies included Alpha Zeta, Gamma Sigma Delta, and Sigma Xi. He was a member of over 10 professional organizations, and served as president of the American Society of Animal Science, American Institute of Nutrition, and Society for Environmental Geochemistry and Health. He served on about 50 national committees and 20 international committees or panels.

In 1976 Davis was elected to the National Academy of Sciences, the first scientist from the University of Florida to be so honored. The University of Florida granted him the title of Distinguished Professor of Nutrition Emeritus in 1979, and further honored him in 1996 with its Distinguished Achievement Award.

George and Mrs. Davis were members of the First Presbyterian Church of Gainesville for over 60 years. The church was an important part of their lives, as George taught a Sunday school class for most of that time. They had 6 children, 11 grandchildren, and 14 great-grandchildren. The Davises remained active in University of Florida affairs until they both passed away. Ruthanna Davis died on May 25, 2002. An endowment established through the University of Florida Foundation in 1993 to support graduate education in nutrition across the campus serves as a lasting legacy of their commitment to the University. The George K. and Ruthanna W. Davis Scholarship Fund provides graduate students selecting nutritional sciences as a graduate major with a $5,000 annual salary supplement. Thus far, over 10 students have benefited from the generosity of the Davises.

George Davis died at age 94 on October 27, 2004. When asked to comment on his work, I made the following statement to summarize his research philosophy. “Much of his work addressed fundamental questions, but he always tried to balance it with applied research. He wanted to do work that offered a tangible benefit to society.” I believe that George Davis would have agreed with that summary.

I WISH TO THANK THE Davis family for providing the information upon which this memoir is based. That included considerable autobiographical text that George prepared in his later years. Much of this is available in the University of Florida archives at http://web.uflib.ufl.edu/spec/archome/MS24.htm. That information includes his mention of numerous colleagues at the University of Florida with whom George worked very productively over his long career at this university.

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