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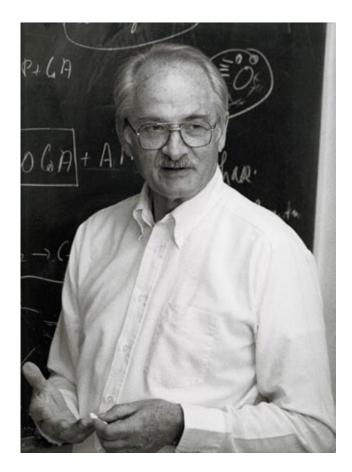
PAUL KARL STUMPF 1919-2007

A Biographical Memoir by ERIC E. CONN

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Biographical Memoir

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PAUL KARL STUMPF

February 23, 1919—February 10, 2007

BY ERIC E. CONN

PAUL STUMPF WAS A WORLD LEADER in the field of plant biochemistry, especially in the subject of plant lipid metabolism. Others have written,

His research accomplishments elucidating the synthesis and metabolism of fats and lipids are too numerous to list here. His discovery in plants of the pathway for degrading fatty acids by alpha-oxidation stands as a singularly important achievement as it provided the understanding of the biochemical basis for a class of human genetic defects, including adult Refsum disease, an inability to metabolize phytanic acid. His research provided a basic understanding of fatty acid and lipid biosynthesis in plants. Paul's approach to science was perhaps reflected by his admiration of Impressionist paintings. He was interested in providing the science that formed the picture, without concern for minute detail. He saw research as Nobel Laureate Albert Szent-Gyorgyi did, whose quotation we all saw when facing Paul in his office: 'Research is seeing what others have seen, but thinking what no others have thought.' Paul was a visionary, foreseeing the impact of genetic engineering on plant research back in the 1970s, when gene cloning was still a decade in the future. Research results produced in his lab laid the foundation for genetic modification of oilseeds to alter their fatty acid composition.¹

Paul was born in New York City on February 23, 1919, under rather tragic circumstances. Two months before Paul's birth his father, Karl S. Stumpf, committed suicide in New York City, leaving his mother without her husband, and her one-year-old child, Felix, without a father.

Paul's father was born in 1884 in the small village of Blankenberg, Germany. For many years his family had worked in the local paper mill. Because of an emerging musical talent, Karl Stumpf left Blankenberg at the age of 14 to study his chosen instrument, the clarinet. As a professional musician—his instrument was the bass clarinet—Karl was for some years a member of the Staatsoper Unter den Linden in Berlin. In 1907 Karl Muck, conductor of the Boston Symphony Orchestra, invited Paul's father, at that time only 23 years old, to join the orchestra as its bass clarinetist. His father accepted the position and together with 17 other German orchestra members became an integral part of the Boston Symphony. Karl Stumpf made frequent professional and personal trips to Germany. On October 2, 1914, en route to New York on the SS Noordam he met his wife-to-be, Annette Schreyer, who was a passenger on the same ship. The young couple entered into a shipboard romance, which culminated in their marriage in Boston on November 7, 1914.

When the United States entered World War I in 1917, a violent anti-German antagonism spread throughout America. One of its victims, Karl Muck, was arrested and jailed as a German spy on March 27, 1918, and by June 24, 1918, eighteen German members of the Boston Symphony Orchestra, including Karl Stumpf, were dismissed. Without an income and any hope of securing a similar position with an American orchestra, and with a growing family (Paul's brother Felix had been born on February 10, 1917, and Annette Stumpf was pregnant with Paul) his father became withdrawn and greatly depressed until on the evening of December 13, 1918, he committed suicide. Ironically, on December 14 his mother received a letter addressed to her husband from Walter Damrosch, then conductor of the New York Symphony Orchestra, inviting Karl Stumpf to join the orchestra as its bass clarinetist.

In 1920 Annette Stumpf decided to move her family to Germany in an attempt to escape from the anti-German feelings that still existed in Boston. She planned to raise her sons in the close presence of her husband's parents and the more familiar environment of postwar Germany. However, after three years in Blankenberg, she decided to return to America since she believed that the future of Germany was bleak.

Having inherited a considerable amount of money from an uncle, Annette unfortunately invested part of it in stocks prior to the disastrous collapse of the stock market in 1929. In the fall of 1930, with the remains of her inheritance, she purchased a small summer resort hotel near Bridgeton, Maine, where her sons attended the local high school, which had a total enrollment of 126 students. With little competition Paul achieved high grades in his classes. In 1932 he read *Microbe Hunters* by Paul De Kruif, a small volume of 12 chapters that briefly described the lives of such giants of microbiology as Pasteur, Koch, Lister, and other scientists of the 19th and early 20th centuries. Reading these chapters was indeed inspirational to a 13-year-old boy and led Paul to decide that he must set as a future goal an advanced degree in the biological sciences.

In the fall of 1934 Paul's brother, Felix, was accepted as a student at Harvard College in Cambridge, Massachusetts. Consequently Annette Stumpf sold the resort hotel and established a boarding house in Cambridge. After the family moved, Paul entered Cambridge High and Latin School with an enrollment of more than 4,000 students. What a contrast from a student body of 126 to one of over 4000! He survived, won a competitive Silver Medal and Science Prize in his senior year and after graduation spent one additional year at the high school to round out his education. He then entered Harvard College in 1937. At Harvard, Paul Stumpf had three exceptional experiences. The first was taking Chemistry 2, the highly regarded organic chemistry course taught by Professor Louis Fieser, a gifted lecturer. Paul did very well in the course and also won the competitive laboratory contest called the "Martius Yellow Competition," in which the top 20 students in Fieser's lecture course had to synthesize seven compounds from α -naphthol in five hours. The second highly rewarding experience was taking Biology 3, General Physiology, taught by Professors A. Redfield and George Wald. This course gave Stumpf greater insight into the structure and functions of living systems. The third experience occurred when, as a senior honors student, Paul was required to carry out a research project.

He had become interested in the new field of enzyme chemistry although at that time Harvard College had no one who could be identified as an enzyme chemist. In the fall of 1940 Stumpf made an appointment to see Professor A. Baird Hastings, chair of the Department of Biological Chemistry at Harvard Medical School, who had published several papers in this field. At the appointment Hastings informed Paul that he no longer was active in this field, but he said that a young, bona fide enzyme chemist had just arrived from England to spend a year in the department; Hastings suggested that it would be worthwhile for Paul to meet him. Hastings took Stumpf downstairs to meet David E. Green, who was occupying a small, dark laboratory with a single wooden bench and enormous soapstone sink, essentially devoid of any equipment. After a short series of questions, Green accepted Paul and put him to work purifying a new enzyme, potato starch phosphorylase. His research resulted in a publication with Green (1942). Paul graduated from Harvard College in June 1941 with an A.B. magna cum laude.

In the fall of 1941 Green was appointed assistant professor in the Department of Medicine in the College of Physicians and Surgeons at Columbia University in New York City. Stumpf applied for graduate work in its Department of Biochemistry with the understanding that his mentor would be Green as he began his research for a doctoral degree, a study of the oxidation of pyruvic acid by *Proteus vulgaris*. At first Green and his coworkers occupied a small laboratory, but in short order he acquired another laboratory adjacent to his research space that Sarah Ratner, her technician Marian Blanchard, and Paul occupied. During the period from 1941 to 1946, Stumpf participated in research that led to eight publications, and had the good fortune to meet giants (or giants-to-be) in biochemistry: Ochoa, Lipmann, Meyerhof, Racker, Bloch, Shemin, K. Meyer, Gunsalus, Leloir, and Heidelberger.

At that time Lipmann had isolated a pyruvic dehydrogenase from *Lactobacillus delbrueckii* that oxidized pyruvic acid in the presence of inorganic phosphate to carbon dioxide and acetyl phosphate, a potentially active acetate compound. The enzyme that Stumpf had isolated possessed none of these properties since it did not require inorganic phosphate, and the end product was free acetic acid. Although Lipmann's discovery aroused considerable interest, numerous biochemists searched for similar systems in animal tissue with no success. With the discovery of the nonphosphate-requiring system in *Proteus vulgaris*, it became clear that the Lipmann system was unique to the *Lactobacillus* species.

In the spring of 1944 Stumpf was ordered to enlist in the U.S. Navy in Boston. Green immediately contacted Washington and requested that Paul be deferred since he was conducting research on an important Quartermaster Corps contract that Columbia University had with the U.S. Army. The research involved determining the action of chlorine on bacteria, a rather critical study since the routine practice in the armed forces was to add chlorine tablets to questionably

safe drinking water. With only one day left before Paul had to return to Boston, Green received a telegram from the Quartermaster Corps officials in Washington deferring Paul for the rest of World War II. Thus he was able to complete his thesis and receive his Ph.D. in 1945. The research in Paul's Ph.D. thesis was entitled "Pyruvic Oxidase of *Proteus vulgaris*" (1945).

By then Stumpf was eager to establish his own research career and was exploring several opportunities, although still associated with David Green. Professor Severo Ochoa asked Stumpf to join his group, which he did not accept since it would have meant working on Ochoa's problems. Professor Fritz Lipmann also offered Paul a position in Lipmann's laboratory in Boston, but he did not accept that offer for the same reasons. A friend of Stumpf's in New York City indicated that her uncle, Professor Thomas Francis, chair of the Department of Epidemiology at the University of Michigan, Ann Arbor, was interested in appointing a biochemist. Paul contacted Professor Francis to indicate he would be interested in the opening and would initiate research in the biochemistry of virus reproduction. On July 1, 1946, Stumpf accepted Francis's offer and, as a bachelor, moved to Ann Arbor to establish his laboratory. He soon met a colleague in the department, Jonas Salk, who was carrying out research on the influenza virus at that time.

A few months after Paul arrived in Michigan, he received a letter from Professor H. A. Barker, who at that time was located in the Department of Plant Nutrition in the College of Agriculture at the University of California, Berkeley. Barker's letter explored the possibility of Paul's joining the department as a plant biochemist but noted that there was no position open at that time. Barker did inquire whether Stumpf would be interested if a position developed. Paul replied stating that he had just accepted the Michigan position and felt duty bound to remain in Ann Arbor for a year. But, if a position did open up in Berkeley, Paul said that he would be interested in exploring the position further, in part because at that time his mother and his brother were living in San Francisco. In December 1946 Stumpf traveled to the Bay Area and met with Professors H. A. Barker and William Z. Hassid on the Berkeley campus.

In July 1947 Paul received another letter from Barker stating that a position was now available for the academic year of 1947-1948. Although his research in virus biochemistry was proceeding fairly well, Stumpf realized that the role of enzymes, as they related to viral growth and function, was very primitive at that time and that success in this field would be difficult. In the meantime Paul had met Ruth Rodenbeck, who was working for a master's degree in chemistry and was also an assistant housemother at a women's dormitory on the campus. They were married on June 13, 1947, with one of their ushers being Salk. The couple briefly struggled with the prospect of moving to Berkeley, and in September 1947 Paul informed Professor Francis of his decision to accept an assistant professorship on the Berkeley campus. Francis accepted the decision but was annoyed at Stumpf's departure from Ann Arbor. After 18 months in Michigan, the Stumpfs purchased a second-hand Plymouth and late in December 1947 left wintry Ann Arbor for the delightful climate of the Bay Area, where Paul began his career as a plant biochemist on the Berkeley campus of the University of California.

Stumpf was delighted with his new colleagues as well as the challenge of initiating a program in plant enzymology. Although he had neither a laboratory nor an office, he did receive \$5,000 in start-up funds as well as bench space in Professor Barker's laboratory. Within six months of his arrival Paul completed and published a paper on the purification and characterization of pea aldolase (1948). This was the first paper in a series on glycolytic enzymes in plant tissues. Their appearance resulted in an invitation to write his first review in *Annual Review of Plant Physiology* (1952). Nearly half a century later a former postdoctoral scholar with Paul, Curtis Givan, authored a review of glycolysis and dedicated it to Stumpf (Givan, 1999).

In 1950 James Bonner's first edition of *Plant Biochemistry* (Bonner, 1950), with its very brief chapter on lipid metabolism, made an impression on Paul. In that chapter Bonner noted that little was known about the β -oxidation of fatty acids in plants, and that nothing was known about the biosynthesis of fatty acids. He strongly urged that research be initiated to improve on the contents of this chapter in future editions. Stumpf undertook this challenge and his resulting research proved so successful that he authored the chapters on plant lipids in the second and third editions of Bonner's book.

In 1951 Professor Barker, whose research interests were in the field of microbial metabolism, accepted Eldon Newcomb (elected to the National Academy of Sciences in 1988) to do postdoctoral work in his lab. Barker soon realized that Newcomb, a Guggenheim fellow from the University of Wisconsin, was more interested in plants than microbes, and therefore suggested he work with Paul Stumpf.

During his research, Barker had accumulated a number of ¹⁴C-labeled fatty acids including (1 and 3^{-14} C)-palmitic acids, which he made available to the Stumpf laboratory. Newcomb and Stumpf decided to initiate their study on lipid metabolism with a very simple experiment. Using a Warburg flask, which allowed them to trap any ¹⁴CO₂ formed, they added a homogenate of cotyledons of germinated peanut seeds to a mixture of (1-¹⁴C)-palmitic acid and all the components required for the β -oxidation of fatty acids in animal tissues. A second flask, which contained only (1-¹⁴C)-palmitic acid and the homogenate, was prepared as a control. After the reac-

tions had gone to completion, the trapped carbon dioxide was recovered from both flasks and counted for radioactivity. To their great surprise and pleasure a considerable amount of ${}^{14}\text{CO}_2$ was found in both cups. The ${}^{14}\text{CO}_2$ observed in the control could not be due to β -oxidation system since the system was independent of the usual cofactors required for β -oxidation. Because the system they had discovered was unknown in the literature, this first experiment eventually led to the elucidation of what they termed an " α -oxidation system." Although the system turned out to be a minor mechanism for fatty acid oxidation in plants, 50 years later the system is now known to be involved in plant pathogen responses (Hamberg et al., 1999).

The existence of the α -oxidation system for fatty acids in humans became very important in understanding the mechanism of Refsum disease, a rare, inheritable disease in humans. Normally phytanic acid, formed by the oxidation of phytol, an alcohol component of chlorophyll found in all leaf tissues, is further oxidized by the liver to CO₂ and water. Patients with Refsum disease lack the α -oxidation enzyme system and thus accumulate high levels of phytanic acid in their serum lipids. The discovery of the α -oxidation system in plants has helped to explain the absence of this critical enzyme system in livers of patients with this disease.

In the early work on the α -oxidation system Newcomb and Stumpf observed that dialysis of the homogenate resulted in a total loss of activity but that the addition of boiled homogenate to the dialyzed system fully restored the activity. Paul Castelfranco was given the task of identifying the nature of this unknown compound as his Ph.D. thesis. He soon discovered that the unknown material was glycolic acid, a well-known organic acid in plants. Glycolic acid is rapidly oxidized to glyoxylic acid and H₂O₂ by the enzyme glycolic acid oxidase. By adding any enzyme-substrate combination that could generate H_2O_2 , such as glucose and glucose oxidase, the requirement for glycolic acid disappeared, and suggested that any system that generated H_2O_2 should function in the α -oxidation process. However, the direct addition of H_2O_2 was inactive.

The final part of the story was the characterization of a possible intermediate in the system. While spending his first sabbatical leave in Bernie Horecker's laboratory at the National Institutes of Health in 1954-1955, Stumpf visited the laboratory of William McElroy at Johns Hopkins University. McElroy had studied in some detail the enzyme luciferase obtained from Achromobacter fischeri. In the presence of flavin phosphate and a long chain aldehyde, fluorescence occurred as a function of the concentration of the long chain aldehyde. Here then was a specific system for measuring the amount of a long chain aldehyde that might be formed in Stumpf's α -oxidation system. When this fluorescence assay was employed in the α -oxidation system, Stumpf observed that a long chain aldehyde was indeed formed. In 1974 further work on the α -oxidation of plant fatty acids by W. E. Shine in Stumpf's laboratory greatly clarified the mechanism of a rather complex series of reactions (1974).

In 1954 I was privileged to join the Berkeley Department of Agricultural Biochemistry, which now housed Paul Stumpf, H. A. ("Nook") Barker and W. Z. ("Zev") Hassid as its only members in the Biochemistry and Virus Laboratory. Nook and Zev, both members of the National Academy of Sciences (in 1952 and 1958, respectively), were wonderful, supportive colleagues but very senior to me, and so it was not surprising that Paul and I became especially good friends and colleagues. I recall one early conversation in which Paul remarked that if one continued to work in the same area that had been their thesis research, it would be difficult for outsiders to discern their accomplishments from those of their Ph.D. supervisor. While I knew that opinion was friendly advice to me as a young assistant professor in the department, it may also have been a factor in his changing his research area a few years earlier.

In 1955 when Stumpf returned from his sabbatical leave at NIH, Harry Wellman, at that time vice-president of the University of California, proposed to Paul the possibility of transferring to the Davis campus in 1958. A new building, Hoagland Hall, was under construction on the Davis campus, and he and colleagues could easily be housed in that facility. The reason for this move was an urgent need to form a new Department of Biochemistry on that growing campus. Paul discussed this possible move with his wife as well as with his colleagues in the small Department of Agricultural Biochemistry in the College of Agriculture on the Berkeley campus. Neither Barker nor Hassid indicated that they would like to move to Davis, but I was very enthusiastic about the move. It seemed an ideal environment for two plant biochemists to take root, and it offered a great opportunity to get to know faculty members in fields other than science. The campus had only 2,300 students at that time; the population of Davis was 5,000. Our experience over the subsequent years has never given us reason to regret the move.

An agreement was soon reached that both Paul and I would move to Davis by late summer of 1958 in order to offer an introductory course in biochemistry. The move was accompanied by the addition of two new faculty hires, Lloyd Ingraham from the Western Regional Research Lab in Albany, and Sterling Chaykin, who had just completed a postdoctoral position with Konrad Bloch at Harvard University.

By this time Paul had initiated his studies on the β -oxidation of long chain fatty acids that had been demonstrated early on with labeled substrates. This work then logically evolved into an examination of the biosynthesis of fatty acids in plants, including the formation of the physiologically important unsaturated fatty acids, for which there is no analogous work in animal systems. Ohlrogge and I have written:

These studies included the identification of the many component enzymes, their subcellular localization, and the discovery of the prokaryotic nature of enzymes of fatty acid synthesis and of the chloroplast acetyl-CoA carboxylase. The discovery of acyl-ACP thioesterases led to a description of "CoA track" versus "ACP track" reactions that was a conceptual precursor to the prokaryotic and eukaryotic two-pathway hypothesis that has underpinned much of modern plant lipid research.²

We've also written,

In addition to his fundamental research contributions, results from the Stumpf lab laid the foundation for the genetic modification of oilseeds to improve their fatty acid composition. Paul was a key early advisor and consultant for Calgene, the successful biotech company founded in Davis. Much of the early success of Calgene in transgenic modification of the fatty acid composition of canola rested on the groundbreaking characterization and purification of acyl-ACP desaturases and thioesterases that were carried out in Paul's lab.²

Paul has written an interesting "autobiography" describing his perspectives on his 50 years of active lipid research (Stumpf, 1994).

We have also written,

Professor Stumpf trained more than 60 students, postdocs and visiting scientists, many of whom went on to become leaders in plant biochemistry research. Throughout his career he maintained a close connection with bench work. He trained every new arrival in the lab on the use of the gas chromatographs and their radioisotope detectors, and when an instrument needed maintenance, Paul provided hands-on repairs. He was also creatively engaged in each research project, making many suggestions for experiments, while allowing students and postdocs the freedom to follow their own intuition. Many of those who trained with Paul have fond memories of the atmosphere in the Stumpf lab as an excellent place to do science, and of the relaxed social interactions that included trips to the Stumpf cabin near Lake Tahoe.²

Turning from his research, Professor Stumpf was a highly respected citizen of the UC Davis community, and a strong advocate for faculty governance at the University of California. He served on and chaired numerous academic senate committees, including the Committee on Committees, the Committee on Privilege and Tenure, the Academic Freedom Committee, and the Budget Committee. Paul was especially interested in campus planning and served many years on the Academic Senate Campus Planning Committee and the Physical Planning Advisory Committee under Chancellor Mrak. With an extensive collection of photographs, Paul carefully documented the buildup of the campus from a student enrollment of 2,300, when he came to Davis in 1959, to over 19,000 at the time of his retirement in 1984. Paul was also the founding president of the UC Davis Emeriti Association, chair of the UC Davis Academic Senate Emeriti Committee, and secretary of the Council of University Emeriti Associates. Paul also served on numerous review and advisory panels for the National Institutes of Health, the National Science Foundation, and the U.S. Department of Agriculture.

Paul and I coauthored five editions of our popular textbook *Outlines of Biochemistry* from 1963 to 1986. The use of Outlines in the name of our text was a follow-up from another textbook, *Outlines of Enzyme Chemistry*, that he had coauthored with John B. Neilands in Berkeley, which ran for two editions. Both were published with John Wiley and Sons. Paul and I also coedited the 16-volume treatise of *Biochemistry of Plants* (Stumpf and Conn, 1980-1990). He frequently cited this treatise as an example of the rapid growth of the literature in plant biochemistry over the 30 years since James Bonner's first edition of *Plant Biochemistry* appeared in 1950. Professor Stumpf was elected to membership in the National Academy of Sciences in 1978 and would sometimes recall the way he was informed of this honor. He was lecturing to approximately 450 students in general biochemistry on a Tuesday in late April 1978. Just before going to class his secretary reported that someone was trying to reach him by telephone. He said that he would return the call after class and hurried over to the classroom. He had begun his lecture when Professor Emanuel Epstein entered the classroom and asked permission to make an announcement. Paul gave him permission and Emanuel announced that Paul had just been elected to the National Academy of Sciences. Whereupon Paul responded by saying, "Well, I'll be _____," much to the delight of his students. Only later did Paul learn that Professor Epstein had also been elected that morning.

Paul Stumpf served as president of the American Society of Plant Physiologists in 1980 and chaired its Board of Trustees from 1986 to 1990. He had earlier received the Stephen Hales Prize from the society in 1974. Then in 1992 he was awarded the Charles Reid Barnes Life Membership by the society. Another award was the Lipid Chemistry Prize from the American Oil Chemists Society in 1974. His sabbaticals were facilitated by a Senior Scientist Award from the Alexander von Humboldt Foundation of Germany (in 1976) and two Guggenheim Foundation Fellowships (in 1962 and 1969). Paul was elected to the Royal Danish Academy of Sciences in 1975.

A few years after Paul Stumpf retired, the Board on Agriculture of the National Research Council issued a report in which it analyzed the persistent inadequate funding of research in the agricultural sciences and recommended that Congress greatly increase its annual appropriation from \$40 million to \$500 million. J. Patrick Jordan, administrator of the Competitive State Research Services of the U.S. Department of Agriculture, asked Paul to help develop its existing Competitive Grants Program into the National Research Initiative Competitive Grants Program. In 1988 Paul was appointed chief scientist responsible for the conversion. (Although this appointment was normally for one year only, Stumpf was reappointed two more times and served until 1991.) The Board on Agriculture report was supported by the George H. W. Bush administration and enacted into law by Congress in September 1990. It then became Paul's responsibility to oversee the implementation of this report and its new funding in 1990 to the level of \$70 million, and to \$100 million in 1991. Unfortunately, even now the recommended support of \$500 million has not been achieved.

During those three years in Washington, Stumpf thoroughly enjoyed the drastic change from being an academic to heading an important federal organization, which provided research funds for many agricultural scientists. Besides dealing with scientists and solving minor problems that would arise in the program, Paul also had the responsibility of explaining the programs to members of Congress. He frequently commented to his colleagues in Davis that for a significant number of Congress persons, their efforts were mainly divided between funneling funds to their districts and getting reelected. On one occasion Paul made a courtesy call to a powerful Congressman from Massachusetts and during their conversation the Congressman asked what district Paul was from in Massachusetts. When Stumpf replied that he was not from Massachusetts but from California, the courtesy call ended abruptly.

Ohrogge and I have noted:

Twenty two years of retirement permitted the Stumpfs to enjoy numerous trips around the world. They loved to travel and participated in approximately 50 Elderhostel programs, including one to Antarctica. Golf bags were frequently packed on these trips, as Paul had what one daughter has described as a 'hate-love' relationship with that sport.²

In order to support education and research in the department he had founded, he and his wife, Ruth, endowed the Paul K. and Ruth R. Stumpf Professorship in Plant Biochemistry in the Section of Molecular and Cellular Biology at UC Davis in 1999.

Paul Stumpf died February 10, 2007, at his home in the University Retirement Community at Davis. He was 87 and had been ill for some time. He is survived by his wife of 59 years, Ruth Stumpf, five children, and their spouses: Ann Shaw (Michael), Kathryn Fruh (Bill), Margaret Noonan (Mark), David Stumpf (Susan), and Richard Stumpf (Patrice), 11 grandchildren, and one great grandchild.

NOTES

1. T. A. McKeon and R. A. Moreau. A tribute to Paul K. Stumpf. *INFORM* 18(3)(2007):193-194.

2. E. E. Conn and J. B. Ohlrogge. Paul Karl Stumpf obituary. Am. Soc. Plant Biol. Newsl. 34(3)(2007):23-24.

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