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JOSEPH E. VARNER

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A Biographical Memoir by

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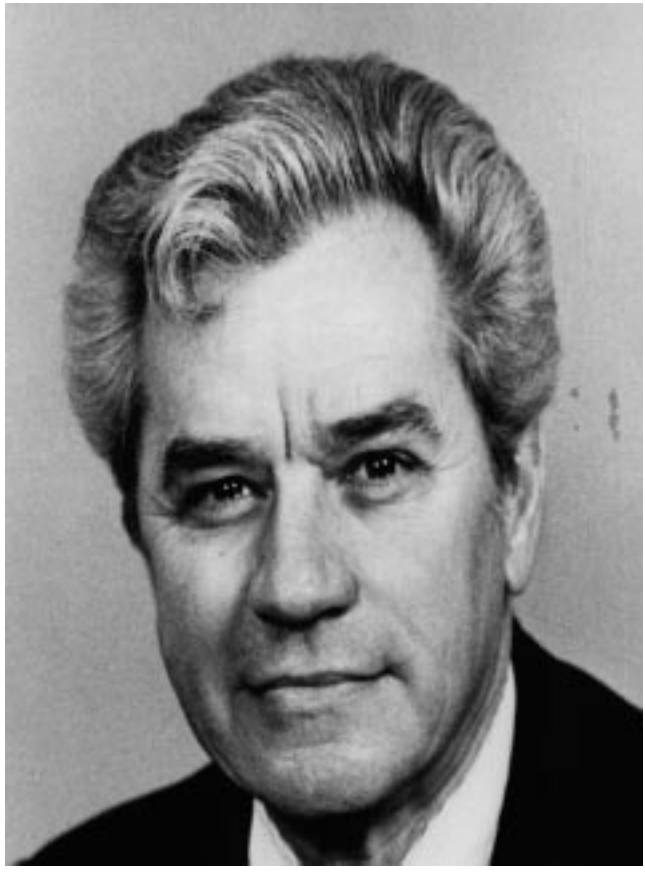
Biographical Memoir



JOSEPH E. VARNER

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BY MAARTEN J. CHRISPEELS

JOSEPH E. VARNER'S fifty-year career (1945-95) spanned the emergence and development of plant biochemistry, and he was one of the major contributors to this field. His most notable research achievements were the definition of cell death as an active process; discovery that the hormone gibberellin regulates the expression of α-amylase in barley aleurone cells at the level of the gene; and cloning of the cDNA for the cell wall protein extensin, which laid the foundation for the study of the role of cell wall proteins in plants. Together with James Bonner, Varner edited *Plant Biochemistry*, which remained the standard single-volume textbook in the field for fifteen years. During the last ten years of his life he was probably the most widely admired and loved plant biologist in the country, the elder statesman of his discipline. He was extremely knowledgeable about biochemistry and whenever he talked to colleagues or students he generously shared his many ideas. He was a tireless promoter of the study of plants and talked about experiments until the final days of his life. In addition, Varner was a sought-after advisor to government, universities, and industry. He was a major supporter of the American Society of Plant Physiologists, which he served as president in 1970-71

and which awarded him its highest honor, the Stephen Hales Prize, in 1990.

GROWING UP IN OHIO AND STARTING A FAMILY

Joe Varner was born and grew up in Nashport, Ohio, on a farm that had been in the family's possession for several generations. He was the second of four sons, one of whom (Robert Varner) carried on the farming tradition; thus, Joe Varner always maintained his ties to the land. His parents, George and Inez Gladden Varner, were both school teachers, and the Varner children were educated first in the rural one-room schoolhouse where their father was the teacher. They later attended the local high school. Inez Varner stayed home to help run the farm and care for her family. Joe's love of science was apparent early on and he won an award for "best student in the county in chemistry and physics." He continued his education at Ohio State University (OSU), where he majored in chemistry and received a bachelor's degree in 1942 and a master's degree in 1943. About his education at OSU he wrote, "It was possible to earn a B.Sc. in chemistry without hearing a single word about physiological chemistry or photosynthesis. It was also possible to sit through an entire year of elementary botany without hearing a single instance of how a chemist might make a contribution to botany."

Joe joined the U.S. Marine Corps in 1944, and while he was in the service he found a book on physiological chemistry (Hawk, Oser, and Summerson) at the Santa Ana Public Library that opened his eyes to new possibilities for research. "Wouldn't it be nice to do that sort of thing with plants," thought Varner. In 1945 Joe married Carol ("Ray") Dewey and together they raised a family consisting of son Lee and daughters Lynn, Karen, and Beth. Joe was first employed as an analytical chemist by the Battelle Memorial

Institute, but after a year he returned to OSU to work on his doctorate supported by the G.I. Bill. He wanted to know "how plants work" rather than "what they are made of," and he was awarded a Ph.D. in biochemistry in 1949.

THE FIRST TEN YEARS: FROM ORGANIC ACIDS TO ENZYME SYNTHESIS

Varner started his career when plant biochemistry was emerging as a new branch of experimental plant biology. At that time plant physiology concerned itself with mineral nutrition of plants, the environmental stimuli that induce plants to flower, and the idea that hormones control plant development. The availability of radioactive CO_2 led to the study of plant metabolism and in the late 1940s and early 1950s understanding metabolism was seen as an important step in elucidating the control of plant growth and development.

Varner's doctoral dissertation, carried out under the guidance of Prof. Robin C. Burrell and presented in 1949, dealt with the metabolism of organic acids in *Bryophyllum calycinum*, a plant that fixes carbon dioxide into malic acid during the night, then breaks down the malic acid again during the day to re-fix the released CO_2 with ribulose bisphosphate oxygenase. For this study Varner used radioactive CO_2 supplied by the Oak Ridge National Laboratory. No one at OSU had any experience with ^{14}C, so Joe used his own money to go to Oak Ridge for a thirty-day training course in radioisotopes. Later in his career he would continue to use isotopes in very clever ways.

During his first three years as an assistant professor of biochemistry at OSU, where he was appointed to the faculty in 1950, Varner continued to work on organic acids and he developed a method for their separation by chromatography. However, after spending a year (1953-54) at

the California Institute of Technology in the laboratory of James Bonner, Varner changed his research direction quite dramatically. In the 1950s Caltech was a hot place for plant biology with three active laboratories, those of James Bonner, Arthur Galston, and Frits Went. James Bonner's laboratory was a magnet for plant biochemistry with graduate students and postdocs, such as Sam Wildman, George Laties, Bernard Axelrod, Robert Bandurski, George Webster, and many others who went on to make major contributions to this new field. By all accounts the research environment was enormously stimulating. Ideas flowed freely between genetic, structural, and biochemical laboratories, and the sky seemed the limit. The young scientists could hardly wait to answer all of plant biology's pressing questions. The year at Caltech had a profound impact on Varner's career, and his lifelong friendship with James Bonner resulted in the joint editing of *Plant Biochemistry*.

After returning to OSU from his sabbatical at Caltech, Varner convinced George Webster to join him there. Together they started working on the biosynthesis of glutamine, asparagine, and glutathione. They saw the tripeptide glutathione as a simple model to study peptide synthesis. This work is evidence of Varner's desire to get beyond metabolism and to look at how processes in living organisms are controlled. When Varner arrived at Caltech, Watson and Crick had just published their model of the structure of DNA, and soon after he returned to OSU different laboratories started reporting that proteins could be synthesized in vitro. Furthermore, the one-gene-one-enzyme theory of Beadle and Tatum was much talked about, although the discovery of mRNA, the connection between DNA and protein, was still ten years away. The work on glutathione biosynthesis was important in its own right, but it did not lead

to a better understanding of protein synthesis, because no mRNA template is required to order the amino acids.

Webster went on to work on in vitro protein synthesis, but Varner turned his attention to the role of oxidative phosphorylation and protein synthesis in development (fruit ripening) and senescence (pea cotyledons). His main contribution here was to define cell death as an active process that requires respiration and the synthesis of new enzymes. His work on the synthesis of enzymes in pea cotyledons during seedling growth followed closely on the heels of work by Harry Beevers who demonstrated the induction of glyoxylate cycle enzymes in castor bean endosperm, another senescing tissue. In 1961 Varner published "Senescence in plants," a major review on this topic in the *Annual Review of Plant Physiology*. In the *Plant Biochemistry* textbook, edited with James Bonner in 1965, he devoted an entire chapter to "death." Those who recently "discovered" apoptosis in plants can profit from reading it. Subsequently, Varner's lab found that a diffusible factor from the axis regulates cotyledon senescence.

At this time Varner was also working on oxygen exchange reactions. He investigated the transfer of oxygen from ^{18}O-labeled arsenate in the arsenolysis of glutamine. Throughout his career Varner used isotopes in many creative ways, not only for metabolic labeling but also for exchange reactions, density labeling, protein turnover, and *in planta* enzyme assays. Joe's older brother David was a successful inventor, and Joe had a touch of the same creative streak. In 1952 he published a paper entitled "An automatic constant volume fraction collector" in the *Journal of Chemical Education*.

CAMBRIDGE UNIVERSITY AND THE RESEARCH INSTITUTE FOR ADVANCED STUDIES

In 1959 Joe took his family to England for a sabbatical leave at Cambridge University. After returning to Columbus he became dissatisfied at OSU. He told the dean he was underpaid and unappreciated (Varner apparently had not yet been promoted to associate professor). The dean replied that if Varner thought he was worth more money, he should find an employer willing to pay more. By his own account, Varner promptly wrote a letter of resignation and somewhat later found a position with the Research Institute for Advanced Studies (RIAS), a division of the Martin Marietta Corporation. RIAS was housed in a large suburban property in Baltimore and consisted of a small community of physicists, chemists, mathematicians, and a few biologists. The biology group was led by Bessel Kok, a feisty, brilliant Dutchman (later elected to the National Academy of Sciences), who, like Bonner, had a profound impact on Varner's career. RIAS housed a lively group of scholars; ideas and experiments were hotly debated in the cafeteria and at social gatherings. Kok and Varner, along with George Cheniae and Dick Radmer, constituted a true debating society. Varner's critical thinking skills were sharpened by these lively exchanges. During four productive years at RIAS, Varner poured his creativity into two scientific problems: hormonal control of enzyme synthesis (see below) and the detection of life on Mars. The work on the detection of life on Mars was triggered by a call for proposals from NASA to design a 10-lb instrument that could detect "life" (not just life as we know it). With his background in chemistry and his interest in exchange reactions Varner argued persuasively that we should not look for metabolism (e.g., CO_2 assimilation or release), but rather measure exchange reactions. About this

time it was discovered that phosphoryl/phosphate group transfers resulted in $H_2{}^{18}O$ formation when ^{18}O-phosphate-labeled substrates were used, and Varner suggested that such exchange between water and oxy-anions (phosphate, sulfate, nitrate) could possibly constitute the simplest reactions of "life," whether on Earth or elsewhere. These ideas were published in an article in *Science* in 1967, but the probe that was eventually built (but not used because of NASA budget constraints) relied on the "sniffing" of gases and their analysis by a 10-lb mass spectrometer.

HORMONAL CONTROL OF ENZYME SYNTHESIS

The research for which Varner is best known was his demonstration that the plant hormone gibberellin induces cereal aleurone cells to synthesize massive amounts of α-amylase through the action of the hormone on gene activity. I had the good fortune to join this project as a postdoc in his laboratory. This work finds its origins in the independent observations by L. G. Paleg and H. Yomo that addition of gibberellin to barley grains, from which the embryo had been removed, greatly enhanced the release of sugars and the production of amylolytic enzymes. Varner, who was fully conversant with recent developments in molecular biology, suspected that gibberellin was inducing α-amylase release (activation or synthesis) probably by a process of gene activation. He quickly adopted the barley endosperm system as a model to study the genetic basis of hormonal control of enzyme synthesis, and in 1964 he published a seminal paper on this topic in the *Proceedings of the National Academy of Sciences* (the paper was communicated by James Bonner). Using the available tools, inhibitors of protein synthesis (amino acid analogs) and RNA synthesis (actinomycin D), he was able to conclude that "the effect of gibberellic acid is therefore upon the expression of the genetic informa-

tion which controls α-amylase production." The paper also demonstrated that incubation of endosperm tissue with radioactive amino acids resulted in the production of radioactive α-amylase, suggesting de novo synthesis of the enzyme. A major point of discussion at the time was whether the appearance of enzyme activity in storage organs of seeds during seedling growth resulted from the activation of an inactive enzyme precursor (zymogen) or from de novo synthesis of the enzyme.

This elegant work, which was initiated at RIAS in Baltimore, drew the attention of more classically oriented plant physiologists such as Anton Lang, who had just been named director of the newly created Atomic Energy Commission Plant Research Laboratory at Michigan State University (MSU), and Lang offered Varner a position at MSU. Varner left RIAS in the spring of 1965, and much of the work on the barley system was done in the next eight years at MSU by his graduate students (U. Melcher, W. Evins, and D. C. Koehler) and postdocs (J. V. Jacobsen, G. R. Chandra, and myself). Nevertheless, it was ten years before David Ho, another Ph.D. student, showed that gibberellin induces the synthesis of α-amylase mRNA, primarily because the molecular tools to answer that question were not available until then.

Varner combined his penchant for devising simple yet elegant techniques and his love affair with isotopically labeled metabolites to measure, in collaboration with Philip Filner, protein synthesis using density labeling. They used heavy water ($H_2{}^{18}O$) to demonstrate that the increase in α-amylase activity induced by gibberellin in aleurone layers was due to de novo synthesis of the enzyme. Varner reasoned that the ^{18}O would be incorporated into amino acids during hydrolysis of the reserve proteins of the endosperm and would then appear in all newly synthesized proteins.

Newly synthesized proteins should, therefore, have a greater density than did pre-existing proteins, and the technique would settle the zymogen activation question. The proteins were fractionated on isopycnic CsCl gradients in an adaptation of the Meselson-Stahl experiment demonstrating the semi-conservative replication of DNA; the average density of α-amylase synthesized in the presence of 80% $H_2{}^{18}O$ was found to be 1.1% greater than that of the enzyme synthesized in the presence of $H_2{}^{16}O$. The whole experiment was conducted with two aleurone layers and 100 µl of water! The so-called density labeling technique was widely applied in many plant biochemistry laboratories to demonstrate *de novo* enzyme synthesis. However, because of the expense of $H_2{}^{18}O$, D_2O was used for most experiments.

Gibberellin not only turns on the expression of the genes for α-amylase (and other hydrolytic enzymes) in aleurone cells, but also induces the formation of the endoplasmic reticulum, the site of synthesis of these secreted enzymes. Plant cells were known to possess isoforms of enzymes that remain inside the cell, as well as isoforms that are secreted. Varner coined the terms "inzymes" and "outzymes" for such isoforms and discussed with his associates at length his idea that there must be subtle differences in protein structure between the two that allow them to be routed to these two different destinations. We now call these structural differences "targeting signals." My Ph.D. thesis in the laboratory of John Hanson at the University of Illinois on changes in microsomes during cell elongation and my postdoctoral research in Varner's laboratory on α-amylase secretion led to a career in plant cell biology and a study of protein targeting signals and the role of the Golgi apparatus in glycosylation. Varner remained interested in secretion, and in 1971-72 he took a sabbatical leave at the University of Washington to become more familiar with yeast (*Saccharomyces cerevisiae*)

because he thought that it might be a more suitable system for studying this process.

In 1973 Varner left the Plant Research Laboratory and moved to the Biology Department of Washington University in St. Louis. At Washington University he started with a small research group, but he had plans for his new department. Soon after arriving in St. Louis, he convinced the then chancellor William Danforth that he could build a first-rate plant biology program if the department were given additional faculty positions. Varner clearly saw that plant biology was nearing a new takeoff point and he wanted Washington University to be part of it. He attracted a number of first-rate junior plant biologists to the department, including Roger Beachy, Mary Dell Chilton, William Outlaw, and Virginia Walbot. Subsequently, additional plant biologists joined this group. Soon after coming to St. Louis, Varner met Jane E. Burton and in 1976 they were married. They spent twenty happy years together, and he was a caring stepfather for her two children. Scores of plant biologists from all over the world enjoyed the hospitality Joe and Janie provided in their lovely home on Kingsbury Avenue. At Washington University he carried on with the work on gibberellin and aleurone cells for a few years and started his research on cell wall proteins and cell wall architecture.

HYDROXYPROLINE-RICH GLYCOPROTEINS AND EXTENSIN

While on sabbatical leave at Cambridge University, Varner met Derek Lamport who was then a Ph.D. student of D. H. Northcote. Lamport had just discovered that the most abundant amino acid in a hydrolysate of purified sycamore cell walls was hydroxyproline and had postulated that the cell wall contained a structural protein, which he called extensin. Varner was fascinated by the idea and invited Lamport to become an independent postdoc in his laboratory at RIAS.

Later, he persuaded Anton Lang to appoint Lamport an assistant professor at the AEC Plant Research Laboratory, where they both moved in 1965. While at MSU, Varner and Lamport worked in adjacent laboratories and interacted on a daily basis. Lamport continued the biochemical characterization of extensin, proving its existence to early skeptics.

After Varner moved to Washington University he sensed that aleurone layers and gibberellic acid had run their courses, at least in his laboratories, and after some hesitation he moved to the cell wall protein problem. The hesitation probably stemmed from a reluctance to compete with his long-time friend. However, he knew better than anyone else that Lamport was too set in his biochemical ways to utilize the new molecular tools to push the analysis of extensin into new terrain. Varner's lab used two approaches to get at the extensin protein: the purification of a precursor protein before it becomes covalently linked to the cell wall matrix and the cloning of a cDNA. He switched to the aerated carrot disk system used in my laboratory because we had shown in the late 1960s that wounding (when the disks are cut) induces massive synthesis of hydroxyproline-rich glycoproteins (HRGP, Varner's new term for extensin). They made several attempts to obtain the extensin cDNA. Realizing that a Hyp-rich protein should have a cytosine-rich message, David Stuart attempted to use polyG columns to isolate the message using in vitro incorporation of amino acids. They also devised a way to identify clones that have proline-rich and leucine-poor translation products. These approaches failed, and the cDNA clone for extensin was finally obtained through a library screen by Jychian Chen, a graduate student from Taiwan.

The findings were published in the *Proceedings of the National Academy of Sciences* and were communicated by Varner

himself, having been elected to membership in the Academy in 1984. They confirmed the work of Lamport and showed that the pentapeptide $Ser(Pro)_4$ was repeated 25 times in the derived amino acid sequence of 306 amino acids. TyrLysTyrLys and ThrProVal were also found as other major repeating units. This first cloning of extensin opened up the whole field of cell wall structural proteins. Other students and postdocs worked on many different aspects of HRGP biosynthesis, including insolubilization in the wall, structure of the protein, and the induction by pathogens. With Gladys Cassab, a Ph.D. student from Mexico, he described an entirely new glycine-rich cell wall protein, which he referred to as plant silk. As a result of these important contributions Varner was asked to write a review on cell wall architecture for *Cell*.

While in St. Louis, Varner became a consultant for Monsanto and initiated a joint research project with Jake Schaeffer and others to investigate nitrogen metabolism (glycine and asparagine utilization and protein turnover) in soybean using ^{15}N and ^{13}C NMR. Again, he cleverly used isotopically labeled metabolites, this time coupled to a high-tech analytical technique.

In 1977, in recognition of Joe's numerous contributions to plant biochemistry, the University of Nancy awarded him a doctor *honoris causa* degree. Together with Jane he traveled to France and enjoyed the French hospitality.

TISSUE PRINTING, LIGNIN BIOSYNTHESIS AND CELL DEATH (REPRISE)

As noted earlier, Varner had a penchant for simple yet elegant techniques designed to answer interesting questions. In 1986, with Gladys Cassab, he revived the technique of tissue printing. The question they wanted to answer was whether cell walls of different cell types differ in their mac-

romolecular constituents. If mesophyll cells and bundle sheath cells have different cytoplasmic structures, do they also have different cell walls? Tissue printing had been used off and on to detect enzymes on substrate films (e.g., gelatin), but Varner turned to the nitrocellulose sheets already in common use for immunoblotting to make tissue prints. When a thin tissue slice, especially from a stem, is pressed against nitrocellulose paper, the hard cell walls make a slight indentation, and the proteins that are not covalently bound to the wall are transferred to the nitrocellulose (as are the cytoplasmic proteins). The proteins can then be detected by relying on their enzymatic activity (e.g., peroxidase) or with antibodies (as with immunoblotting). Using side illumination and a low-power light microscope, Varner obtained amazingly beautiful images. Getting good results is not as easy as it sounds, but Varner and a few of his students (Gladys Cassab and Rosannah Taylor) became experts and published several articles demonstrating the utility of the technique in showing cell wall differentiation.

Around 1990, when Zeng-hua Ye came to his laboratory, Varner combined his interest in cell wall architecture with a much older interest in programmed cell death. Together they started working on lignin biosynthesis in differentiating xylem elements of cultured *Zinnia elegans* mesophyll cells. With this cell system, developed in Japan by H. Fukuda and A. Komamine, they studied O-methyltransferases in xylogenesis. Their intention was to use the tools of molecular biology to unravel this intriguing developmental program in which the cell first elaborates a complex cell wall and becomes fully functional in water transport after it dies.

MENTORING

Joe Varner was an unusually effective mentor of young scientists. He was the advisor for three masters students,

seventeen doctoral students, and forty-six postdocs and sabbatical visitors. His influence was felt beyond his own laboratory because the impromptu scientific discussions around the coffee table or at lunch attracted graduate students and postdocs from many other laboratories. Together they would dissect a scientific question and illuminate it from different angles. How can enzymology, cell biology, biophysics, chemistry, and structural biology help us get an answer? His favorite term was "brain candy," the reward the brain gets for thinking up clever solutions to difficult problems. At a symposium held in Varner's honor at the time of his retirement in 1993 the many participants referred to the influence that Varner's ideas—his brain candy—had on their research.

PUBLIC SERVICE

Throughout his career Varner was a sought-after advisor who contributed substantially to government, industry, and academic advisory groups. He was a member of the National Science Foundation's Developmental Biology Panel (1968-71) and the Genetic Mechanisms for Crop Improvement Panel of the U.S. Department of Agriculture (CRGO) (1982-85). Realizing the importance of the Department of Agriculture's competitive research grant organization, he volunteered to serve as a program manager (1984-85) and as chief scientist (1986-87). In this last capacity he persuaded the Department of Agriculture to start a postdoctoral grant program. He served as chair of the Scientific Council of the Plant Gene Expression Center of the Department of Agriculture's Agricultural Research Service in Albany, California (1985-90), and was on the visiting committee of the Department of Plant Biology at the Carnegie Institution of Washington in Palo Alto, California (1981-86). For sixteen years he was an associate editor of *Plant Physiology* (1967-84)

and for five years served on the editorial board of the *Annual Review of Plant Physiology* 1970-75). He was sought for these positions because of his renown for fairness and absolute integrity. The betterment of plant biology was his only agenda.

Varner was an engaging lecturer who on eight occasions took a month from his busy schedule to give an upper division/graduate course in plant biochemistry at other universities, including the National Taiwan University (1960), National University of Mexico (1976), University of California, Riverside (1978 and 1982), University of California, San Diego (1979), University of Chile (1981 and 1983), and North Carolina State University (1984). I had the good fortune to attend the 1979 course at San Diego. Several hours of reading and preparation went into each lecture and the chemical basis of all phenomena was explored in depth. During these extended visits he always took the time to share his extensive biochemical knowledge with his colleagues.

In the late 1980s he became concerned that plant biochemistry was being neglected. "Soon, every graduate student will know how to clone a gene, but no one will know how to investigate function" was his rationale for approaching the granting agencies for support for a national plant biochemistry course. The course has been held annually in different locations and has attracted students from everywhere.

Varner's death from cancer at the age of seventy-four was an enormous loss for plant biology. An excellent and generous scientist, he was universally admired by his colleagues. He was a tireless promoter and spokesman for his discipline and a mentor and friend to many, especially the young.

THE FOLLOWING PEOPLE HELPED me by providing details or reading the finished manuscript: Roger Beachy, Jane Burton, Joe Chappell, James Cooper, George Cheniae, Jack Hanson, David Ho, Hans Kende, Frank Salisbury, and Paul Saltman.

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