NATIONAL ACADEMY OF SCIENCES

HARRY BEEVERS
1924–2004

A Biographical Memoir by

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Biographical Memoirs, VOLUME 86

PUBLISHED 2005 BY
THE NATIONAL ACADEMIES PRESS
WASHINGTON, D.C.

HARRY BEEVERS

January 10, 1924–April 14, 2004

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HARRY BEEVERS'S CAREER of 50 years spanned the emergence of plant metabolism as a discipline, and he was one of its major contributors. The most notable achievement of his research group was the discovery of the glyoxylate cycle in seedlings of plants that store fat in their seed and utilize this fat as a source of energy and for the production of glucose during early seedling growth. These studies culminated in the demonstration that the glyoxylate cycle of fat-storing seeds is located in a specific metabolic compartment, the glyoxysome. In the course of this work he trained a large cadre of Ph.D. students and postdoctoral scholars from around the world, all of whom remember him fondly. He was an excellent and quick-witted public speaker who was always in demand as an after-dinner speaker/entertainer. With his repertoire of songs, the lyrics for many of which he had composed, he was the life of the party. He enjoyed life and was known to muse, "that young scientists shouldn't take themselves so seriously." In addition to being an outstanding researcher, Harry was a rigorous and much beloved teacher both in the classroom and in the laboratory. His achievements and dynamism are all the more remarkable considering he had to cope with diabetes for much of his career.

FAMILY MATTERS AND THE SOURCE OF HARRY'S BIOLOGICAL INSPIRATION

Harry Beevers was born on January 10, 1924, the second of eight children, in Shildon, a small industrial town in County Durham, England. When Harry was six, his family moved to the rural area of Upper Weardale. Although his parents did not have much formal education, they greatly encouraged the education of their children, and six of the eight received university degrees. Harry attended elementary schools at Wearhead and St John's Chapel and later attended the Wolsingham Grammar School (a "public" school in the U.S. sense). Attendance at grammar school required a 30-mile roundtrip, originally by rail and later by bus. While at grammar school, he met Jean Sykes, whom he married in 1949. According to his brother Leonard, Harry initially wanted to become a schoolteacher to instruct in woodworking and arts and crafts, but due to wartime shortages of materials the school lacked the supplies to teach those courses. During his secondary education, Harry was inspired by David Hughes, a dynamic biology teacher who took his students on field trips to study the local ecology of the nearby moors and the relics of the Alpine flora in the Upper Teesdale. Mr. Hughes encouraged independent projects, and with a microscope borrowed from the school, Harry analyzed the fauna and flora of local ponds. This early immersion in biology provided the inspiration for a life of scientific inquiry.

In 1942 Harry entered the accelerated wartime university program and received a B.Sc. first-class honors degree in botany from King's College in Newcastle upon Tyne (then part of Durham University). During the war, he performed nighttime fire-watching duties on the university campus in the company of the resident faculty, which included Profes-

sor Meirion Thomas, who later became his Ph.D. mentor. Harry supplemented his meager student grant by beating grouse on the moors for the local gentry and collecting rose hips that were used to make the vitamin-C-rich syrup that fortified the British wartime diet at a time when fruits and vegetables were scarce. Following the completion of his B.Sc. degree, Harry's military service was deferred, and he started his doctoral research, which he completed in 1946.

THE EARLY YEARS: UNDERSTANDING RESPIRATION

Ever since the work of de Saussure in the early nineteenth century, scientists have used gas-exchange measurements as a way to understand metabolism. Determination of the respiratory quotient—the volume of CO_2 released to the volume of O_2 absorbed—of plant organs allowed plant physiologists to make certain deductions about the metabolic processes involved. With complete oxidation of hexose, the respiratory quotient (RQ) is equal to 1, but respiration of fat results in an RQ value of less than 1. The RQ of the leaves of *Bryophyllum* (a succulent) kept in the dark was known to be less than unity, and Meirion Thomas had suggested that this might be caused by an active process in which CO_2 was converted to organic acids. He came to this idea by examining the literature on the nonphotosynthetic fixation of CO_2 by bacteria. The acidic taste and accumulation of organic acids during the night in the leaves of certain plants was known since Roman times, and the day/night cycle of acid accumulation during the night and its breakdown during the day and interconversion to carbohydrate had been studied in many laboratories. Harry was able to confirm this postulated CO_2 fixation process by growing plants in 5 percent CO_2 and measuring CO_2 uptake volumetrically and acid production by titration. The high

level of CO_2 prevented the normal de-acidification during the day and even induced acid formation in the light in plants that had been de-acidified. These discoveries led Harry to a lifelong interest in plant metabolism. This type of carbon dioxide fixation is now known to be part of crassulacean acid metabolism, or CAM, photosynthesis, a form of photosynthesis that is found in many desert plants.

At this point a small digression about Professor Meirion Thomas is in order. Dr. Thomas (1894-1977) was known in his Welsh village as "Thomas the Book" because he wrote a classic textbook entitled *Plant Physiology* that saw five editions between 1935 and 1973. This book inspired generations of British and colonial students of plant biology. He had a very active laboratory where serious experimentation was conducted in an intellectually stimulating environment. Other influential British plant physiologists who were trained there include J. W. Bradbeer, David A. Walker, R. G. Paxton, R. F. Lyndon, and J. M. A. Brown. The lab was apparently a fun place to be in those somewhat drab years immediately after World War II. The Newcastle laboratory group served as an excellent model for the laboratory groups that Harry created later on, first at Purdue University and subsequently at the University of California, Santa Cruz.

From Newcastle, Harry moved to Oxford University, where he was first assistant and then chief research assistant in plant physiology in the medicinal plant research laboratory of W. O. James, an authority on plant respiration. Harry was given the job of looking into the biosynthesis of tropane alkaloids. The biosynthesis of alkaloids involves catechol oxidase, an O_2-consuming enzyme, and this was the subject of some of Harry's work. At that time the available tools were not up to the task of making real progress in understanding the biosynthesis of these complex secondary metabolites. Harry turned his attention to other scientific

problems, including the unusually high rate of respiration of the spadix of *Arum maculatum*. The high rate of oxygen consumption of this organ was found to be resistant to poisoning by cyanide, and Harry concluded that the cytochrome system must not be operational in spadices. Much later it was shown that an "alternative" oxidase, which is cyanide insensitive, shunts electrons to oxygen and that this pathway operates at its highest level when cytochrome oxidase is inhibited by cyanide.

At Oxford, Harry collaborated with Eric Simon on the uptake of weak acids and weak bases by plant organs, and in 1952 they published a paper that would remain useful for years to come. They found that the response of plant cells to weak acids increases when the incubation medium has a pH value below the pK of the weak acid (in other words, when the acid is protonated) and that the reverse held for weak bases, which were more active under mildly alkaline conditions. As many investigations depended on incubating plant organs with inhibitors that were often either acids or bases, these observation proved extremely useful.

Radioactive $^{14}CO_2$ was becoming available in the United States, and several laboratories were beginning to use it to unravel the path of carbon in photosynthesis. Harry recognized the power of this approach to help answer the questions on which he was working after he attended a meeting on CO_2 fixation organized by the Society for Experimental Biology in Sheffield in 1950. He saw that job prospects were limited in postwar England, and R. E. Girton, a plant physiologist from Purdue University, who was spending a sabbatical year in the laboratory of W. O. James, got Harry a one-year appointment as a visiting assistant professor in the Department of Biology at Purdue University. Harry and Jean packed their bags barely a year after being married and set sail for the New World. Soon after arriving in the United

States, Harry attended his first meeting of the American Society of Plant Physiologists (Columbus, Ohio, 1950), and there he met all the important players of the discipline. Throughout his life he remained a staunch supporter of the society and its journal *Plant Physiology*. Eleven years later his younger brother Leonard, who had also become a plant physiologist interested in metabolism, would follow the same route across the Atlantic. Leonard and his wife, Pat, came to the United States in 1961, and he focused his research on nitrogen metabolism, leaving carbon metabolism to Harry. Leonard became a well-recognized plant biochemist in his own right.

THE DISCOVERY OF THE GLYOXYLATE CYCLE IN PLANTS

At Purdue, Harry took up the problem of respiration again. At that time (1950) it was not at all clear that the tricarboxylic (TCA) cycle was operating in plants as part of respiration. The reason for this doubt was that malonate, a well-known inhibitor of the TCA cycle in animals, often did not inhibit respiration in plant organs. Having studied the entry of weak acids into plant cells, Harry lowered the pH of the incubation medium allowing malonate to enter the cells, and under those conditions respiration was inhibited. Pyruvate consumption in the TCA cycle was prevented, and pyruvate was diverted to ethanol. Some of these experiments were carried out with Martin Gibbs (later also elected to the National Academy of Sciences) and involved ^{14}C precursors. Gibbs had been hired by the Biology Department of the Brookhaven National Laboratory with the charge of producing ^{14}C-labeled metabolites that could be used by others (and by himself) in research. Harry spent the summer of 1953 with his family in Brookhaven and worked with Gibbs. By using labeled sugars they dispelled doubts that both plants and yeast use the same oxidative pathway that

animal cells use. In a later collaboration with Gibbs, labeled sugars were used to demonstrate the operation of the pentose phosphate pathway in plants. With labeled precursors Harry's group pioneered the demonstration of pools of metabolites later shown to be attributable to subcellular compartments in the plant cell.

It was about this time that Harry decided to work on the conversion of fat to sugar in castor bean seedlings. It had been known for some time that castor beans store fat and that they have a low RQ and quantitatively convert fat to sugars (which accumulate primarily as cell walls in the seedling). This quantitative conversion of fat to carbohydrate had been shown 20 years earlier by the work of J. R. Murlin (*J. Gen. Physiol.* 17[1933]:283-302). The unknown metabolic pathway intrigued Harry, and the availability of ^{14}C-labeled compounds made it possible to investigate the problem. Although castor bean may seem an odd choice of experimental material in this day and age of molecular genetics on the one hand and national security on the other, castor beans were a major crop then and readily available. Harry purchased them from the Baker seed company in Vernon, Texas. Initial work centered on feeding labeled precursors to castor bean endosperm and analyzing the products, and on isolating mitochondria and studying their metabolic properties. This work was carried out by two visitors to the lab: David A. Walker and Takashi Akazawa.

Akazawa recalled that every morning he would prepare mitochondria using the only preparative Beckman ultracentrifuge then available on the Purdue campus and carry the preparation to Harry's lab for further studies using a Warburg apparatus. Although others had reported the isolation of plant mitochondria as early as 1951 (Adele Millerd in James Bonner's laboratory at Caltech), the soft castor bean endosperm proved to be a much superior tissue for the isola-

tion of fragile organelles. Somewhat surprisingly, the labeling patterns produced by feeding various labeled compounds to tissue slices or isolated subcellular fractions of castor bean endosperm were not always readily interpretable by, or consistent with, the then-established metabolic pathways.

The "aha!" moment came when Harry was on sabbatical leave in 1956-1957 at Oxford University, where Hans Krebs occupied the chair of biochemistry. According to Hans Kornberg, Harry met Hans Krebs socially at a college function and explained to him his interest in the conversion of fat to carbohydrate; Krebs then suggested that Harry should collaborate with Kornberg. This was the time when the glyoxylate cycle was being formulated in bacteria. Hans (Kornberg) and Harry then collaborated to demonstrate that the two enzymes that characterize the glyoxylate cycle (malate synthase and isocitrate lyase) are indeed present in the endosperm of castor beans. This discovery set the direction of Harry's career for the next 25 years. To prove that the cycle was operating in castor bean endosperm, David Canvin examined the fate of C1- and C2-labeled acetate, and the labeling patterns he obtained were in agreement with the postulated pathways: Succinate produced from acetate served as a precursor for glucose by a reversal of glycolysis. Canvin's work provided the rigorous "proof of the pudding" that Harry loved!

A NEW METABOLIC COMPARTMENT: THE DISCOVERY OF GLYOXYSOMES

The next breakthrough came when Bill Breidenbach joined the laboratory as a postdoctoral researcher. It had been assumed that the glyoxylate cycle was operating in mitochondria, because three of the five enzymes needed for the cycle occur in mitochondria. However, there was circumstantial evidence to indicate that a different subcel-

lular compartment might be involved. Widmar Tanner, a graduate student, had found numerous single-membrane-bounded organelles in his electron micrographs of castor bean endosperm, and compartmentation of the glyoxylate cycle in distinct organelles had been observed in Kornberg's lab in *Chlorella* and *Tetrahymena.* Breidenbach applied his expertise with linear sucrose gradients to endosperm homogenates, and in a paper published in 1967 he showed that mitochondria banded at a sucrose density of 1.19 g/ml, whereas the two glyoxylate cycle enzymes banded in a different organelle fraction at 1.25 g/ml. This fraction also contained the other three enzymes needed to complete the cycle (and also found in mitochondria). Examination by microscopy showed them to be similar to the organelles observed by Tanner. Beevers and Breidenbach called these organelles glyoxysomes. The announcement by Harry that he had discovered a new class of organelles in plant cells was made at the opening of the new facilities of the Atomic Energy Commission Plant Research Laboratory at Michigan State University in the spring of 1967.

Because glyoxysomes constituted a new metabolic compartment, they became a hot research topic. The race was on to understand their biogenesis, and to define other pathways that might be found in them. The laboratories of Paul Stumpf and Harry Beevers discovered simultaneously that glyoxysomes contain the enzymes for the β-oxidative breakdown of fatty acids. Leaves had been shown to possess structurally similar organelles termed peroxisomes, and Edward Tolbert's laboratory discovered that these contain glycolate oxidase, an enzyme essential for photorespiration. Glyoxysomes and peroxisomes were found to contain catalase, an enzyme that efficiently disposes of the hydrogen peroxide generated in the β-oxidation and photorespiration pathways. These findings raised questions of the rela-

tionship between the organelles. Are they discrete but related structures or did they evolve one into the other?

In the mid-1960s the study of peroxisomes in mammalian cells was initiated and propelled by Christian de Duve, a future Nobel laureate, but the research had stalled: The organelle was thought to be an evolutionary remnant of a primitive respiratory compartment in which substrates were oxidized without the benefit of ATP production. The discoveries made by Beevers and others that this was an important metabolic compartment in plant cells resuscitated research on mammalian peroxisomes. It was not until 1973 that the presence of fatty-acid β-oxidation was reported in mammalian peroxisomes. In mammalian cells peroxisome formation is induced by hypolipidemic drugs, and defects in peroxisomal enzymes or biogenesis are the basis of a number of human genetic diseases.

In 1969 Harry Beevers was elected to the National Academy of Sciences. That was also the year that Professor Kenneth Thimann, a member of the Academy, persuaded Harry to leave the shores of the Wabash and his weekly cheering of his favorite Boilermakers football team and join the biology faculty of the new campus of the University of California at Santa Cruz. Harry and Jean packed their bags once more and departed for the redwoods. There, Harry continued the study of metabolic compartmentation in plant cells.

The ontogenetic relationship between glyoxysomes and peroxisomes could readily be investigated in the cotyledons of certain fat-storing seeds such as cucumbers. When cucumber seedlings grow, they metabolize fat (just as castor beans do) but when exposed to light, they become photosynthetic and produce peroxisomes that contain the enzymes of photorespiration. Are these peroxisomes produced *de novo*, as proposed initially by Harry, or do they evolve from glyoxysomes by the simultaneous export/degradation

of certain enzymes and the import of new ones. The question was hotly debated and eventually resolved in favor of a gradual change in enzyme composition. Resolving this question required the use of biochemical techniques as well as immunocytochemistry to study the enzymic complement of both peroxisomes and glyoxysomes in greater detail, work carried out by Anthony Huang, Roland Theimer, and Takashi Kagawa in Harry's laboratory.

MORE METABOLIC COMPARTMENTS: PLASTIDS AND VACUOLES

Harry's interest in the subcellular compartments that contribute to the conversion of fat to carbohydrate led him to study the role of both plastids and vacuoles in this process. With respect to plastids, he was interested in finding out whether the gluconeogenic process occurred in the plastids or in the cytosol. His interest in vacuoles stemmed from earlier work by David MacLennan, who showed in his laboratory that in roots, malate formed by the dark fixation of carbon dioxide ends up in vacuoles with very different kinetics compared with malate formed by feeding acetate into the glyoxylate cycle. (Remember that Harry worked on malate synthesis during his doctoral research.) Such anomalies tweaked Harry's interest in the role of the vacuole as an active metabolic compartment. Because chloroplasts and vacuoles are large organelles and fragile as well, they are notoriously difficult to isolate even if plant organs are chopped with razor blades rather than ground in a mortar. Working in Japan, Mikio Nishimura had developed a technique that permitted the isolation of organelles from protoplasts, which were obtained by digesting small pieces of plant organs with cellulolytic enzymes. Harry became aware of this technique while a visiting professor in the laboratory of Takashi Akazawa. After Nishimura came to Santa Cruz, he applied his technique to castor bean cotyledons and was

able to isolate a pure preparation of plastids and protein storage vacuoles (then called protein bodies). The research with isolated plastids led to the conclusion that gluconeogenesis occurs in the cytosol. The work with isolated protein storage vacuoles led Nishimura in a different direction. Although vacuoles had been known (from the early work of Philippe Matile) to contain certain hydrolytic enzymes, the research of Nishimura and Beevers provided the first biochemical demonstration that they contain a host of hydrolases and that vacuoles can digest the proteins stored within. During seedling growth, the matrix of the protein storage vacuoles is digested and the vacuoles, which initially are quite dense, become light and translucent.

Another plant metabolism strand that runs through Harry's work in the 1970s concerns the biosynthesis of phospholipids and the relationship between the endoplasmic reticulum—the site of many lipid biosynthetic enzymes—and glyoxysome biogenesis. Electron micrographs of both plant and animal cells published at that time suggested that microbodies arose by budding of the endoplasmic reticulum (ER), and research in the Beevers lab was aimed at providing biochemical evidence for this process. Michael Lord decided to look at the intracellular site of phosphatidyl choline synthesis because this is the major lipid of the endomembrane system of the plant cell. He identified the ER as the site of the final catalytic step in the synthesis of this phospholipid and in the process he developed the magnesium shift technique that has been useful to ER researchers ever since. When two lots of tissues are homogenized in parallel, one in a medium with 1 mM EDTA and the other in a medium with 2 mM magnesium chloride and when the homogenates are fractionated on parallel sucrose gradients, the ER turns out to have a very different density in the presence of EDTA, because ribosomes are removed from

the ER. This work led to many insights into the metabolism of lipids in plants, but the budding hypothesis could not be confirmed. Harry's interest in compartmentation and metabolism extended to mechanisms of metabolite transport both intracellularly (import into mitochondria, for example) and between tissues or organs (absorption of metabolites by the cotyledons from the self-digesting endosperm). In the mid-1980s Nick Kruger in Harry's laboratory extended work done by others on the role of fructose 2,6-bis phosphate in carbohydrate metabolism. Basically, Harry loved metabolic biochemistry. The great thing about biochemistry, he used to say, was that you could really nail something, in contrast to a field like, say, nuclear physics. "That's NUClear, not UNClear physics!" he would explain.

Harry constantly took exception to the intrusion of teleology into science. One of his pet peeves related to the assignment of strategies to plant functions. In a departure from the majority of his research, which was dependent upon subcellular fractions of plant cells, Harry used whole plants to refute the purported functions of plant transpiration. In a series of experiments Widmar Tanner and Harry demonstrated that illuminated whole corn plants under nontranspiring conditions did not overheat and die and still took up and transported mineral nutrients. Thus transpiration may not function to cool the plant and transpiration is unnecessary for mineral transport.

Throughout these many years at Purdue University, UC Santa Cruz, and later in retirement, Jean remained Harry's steadfast companion, and she survives him, living in Carmel, California. Harry is also survived by his son, Michael, born in West Lafayette in 1951. Like Harry, Jean also held a B.Sc. degree from King's College, Durham University, but as was customary in those days, she did not pursue a career after marriage. She provided the warm welcome and the hospi-

tality for all the U.S. and the many foreign Ph.D. students and postdocs who passed through Harry's lab. I can only imagine what those lab parties must have been like at the Beeverses' home with Harry dipping into his large repertoire of songs. With love and affection Jean tirelessly met the demands of Harry's diabetic condition and the health consequences of the prolonged treatment.

No account of Harry's contributions to science would be complete without the lyrics of at least one of his scientific songs. Indeed, he used these songs not only to liven up parties or conferences, but also in his lectures, as they made important points about scientific techniques or results. The lyrics below were composed by Bernie Axelrod and Harry in the summer of 1951 and refer to the use of a Warburg apparatus in combination with a culture of *Leuconostic mesenteroides.* This microbe allows one to determine the distribution of radioactivity in the various carbon atoms of glucose. The counter referred to is an early radioactive decay counter in which a light flashed with each decay event that was registered. The lyrics are set to the tune of "Clementine."

> Leuconostoc in the side arm, glucose in the center well
> Tip it in with phosphate buffer, carbon 1 comes off like hell
> Through the use of Leuconostoc we have carbons 1 through 6
> Pure and unadulterated, they don't mingle, they don't mix.
>
> Refrain:
>
> To the counter, to the counter, to the counter like a shot!
> Turn the switch on, see the lights flash! Is it cold or is it hot?

Like all scientists of some distinction, Harry did his fair share of administrative work and science reviewing and evaluating. Notable in this regard is that he was elected president of the American Society of Plant Physiologists, serving

in 1961-1962. His most important act that year was to appoint Martin Gibbs as the editor of *Plant Physiology*, the society's journal. In 1970 the society awarded Harry its highest honor, the Stephen Hales Prize, "in recognition of his outstanding studies of glyoxylate metabolism and glyoxysomes."

ACKNOWLEDGEMENTS AND NOTES

I knew Harry quite well, but I could not have written this piece without the information supplied by quite a few of Harry's friends and collaborators, including David Walker, Hans Kornberg, Martin Gibbs, Widmar Tanner, Nick Kruger, Anthony Huang, Michael Lord, Takashi Akazawa, Mikio Nishimura, and Joe Chappell, and by Harry's brother Leonard and his UC Santa Cruz colleague Lincoln Taiz. Harry wrote a prefatory chapter published in the *Annual Review of Plant Physiology* and *Plant Molecular Biology* (44[1993]:1-12) that contains many interesting details of his career. Another useful source of information is an article written by Tom ap Rees in *Molecular Approaches to Compartmentation and Metabolic Regulation* (A. H. C. Huang and L. Taiz, eds., pp. 22-29, 1991, American Society of Plant Biologists). An interesting source of Harry's early work with Martin Gibbs is recorded in "The Summer of '51" (M. Gibbs, *Biochem. Biophys. Res. Comm.* 312(2003):81-83).

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