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BERNARD ORIN PHINNEY
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A Biographical Memoir by
ANN M. HIRSCH

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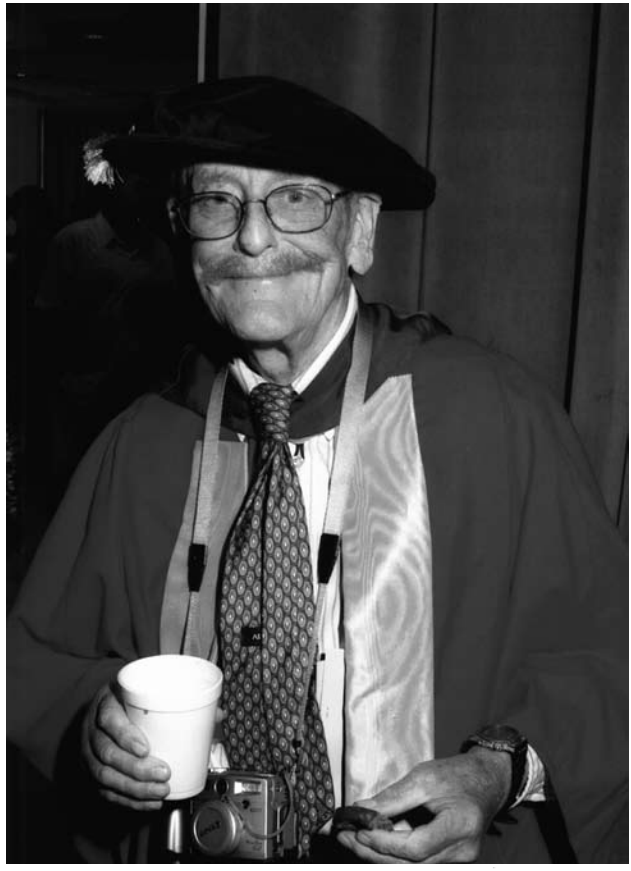
Biographical Memoir



Bernard O'Kane

BERNARD ORIN PHINNEY

July 29, 1917–April 22, 2009

BY ANN M. HIRSCH

BERNARD ORIN PHINNEY WAS well known to the plant biology community for his pioneering research on the plant hormone gibberellin. Phinney was one of the new "biochemical geneticists" who matriculated from the California Institute of Technology following World War II. His almost 70-year scientific career (1940-2009) led to the elucidation of the pathway of the biosynthetic interconversions of gibberellins in maize and other plants. Phinney's research laid the groundwork for the current generation of molecular biologists who examine the mechanism of plant hormone action.

OVER HILL AND UNDER MOUNTAIN: EARLY YEARS IN MINNESOTA, WISCONSIN, AND CALIFORNIA

Bernie, known as "Junior" when he was very young, was born on July 29, 1917, in Superior, Wisconsin, to Franc Maud Lawrence and Bernard Orin Phinney. Apparently he was a surprise because his parents were unaware that Bernie's mother was pregnant with twins. His sister, Susan, was born first and Bernie then joined the family, which also included an older brother, Lawrence ("Larry"). The city of Superior, located on the shores of Lake Superior, and its sister city, Duluth, Minnesota, and surroundings exhibit the extremes of seasonal variation. Although no real mountains, just hills, exist

in northwestern Wisconsin, it was here that Phinney picked up skiing (on wooden skis), an activity that he actively pursued until two years before his death. Phinney also loved plants from an early age and had a garden at his family's summer cottage, which in spite of the fact that northern Wisconsin has almost as many lakes as Minnesota, was not situated on a lake. Phinney must have missed spending summers at the lake as a child because later in life he spent most summers in his wife's family cottage on a lake in Vermont, fishing and enjoying nature.

As a youngster Phinney studied the flute and won prizes for solo flute playing at both the district and state levels as a high school student. A photograph of Phinney as a high school student and the second place winner in the solo flute division in the Wisconsin State Music Festival appeared in the local newspaper. He also won first place in the district festival in Rice Lake, Wisconsin, and later was part of the university band. Phinney played the flute sporadically throughout his life, but he rarely let people know how accomplished he was as a musician. Music was one of the many loves that Phinney carried throughout his long life.

Phinney attended the University of Minnesota, earning a B.A. degree in 1940 and a Ph.D. degree in 1946, with the botanist Ernst C. Abbe as his adviser. Phinney spoke highly of Abbe, who always encouraged him to get an advanced degree. Abbe was also responsible for Bernie's longtime relationship with *Zea mays*. In his thesis Phinney studied leaf development with the goal of comparing it in normal and dwarf maize. Two papers were published describing external and internal maize leaf development.

While a Ph.D. student, Phinney heard George W. Beadle present a seminar that so inspired him that he went to Caltech to work with Beadle when he finished his doctoral degree. Phinney was a postdoctoral researcher from 1946 to

1948, and worked on *Neurospora* as did many of the other geneticists at Caltech, but he did not forget *Zea mays*. He accumulated a large number of maize mutants, including more dwarfs. Later, James Bonner gave Phinney a sample of gibberellin.

In 1948 Phinney was asked by Flora Murray Scott to teach her course in beginning plant anatomy at the University of California, Los Angeles, while she was on sabbatical. Thus began Bernie's lifelong residence at UCLA. During that time, Phinney commuted between Caltech and UCLA by motorcycle. These were said to be relatively wild rides but were probably related to Phinney's need to be efficient and save time on commuting. Phinney was hired as an instructor at UCLA and taught courses in genetics and microtechnique. Mary Ritzel Corcoran, an undergraduate at UCLA who was to become one of Phinney's first Ph.D. students and later professor at California State University, Northridge, remarked that Phinney was a dynamic teacher with a passion for his subject. Later, when Phinney was living in West Los Angeles, he commuted by bicycle to work. One day he rode over a storm sewer grating the wrong way, and the wheel got caught between the bars of the grate. Phinney went flying. Luckily he was not seriously hurt in that nothing was broken, although he had accrued a large number of skin abrasions. This was one of many hair-raising experiences that Phinney underwent during his early years at UCLA. Once, while watering his corn plants in an outdoor field with a garden hose, he forgot to turn off the water and the resulting flood got into a subterranean electrical conduit, causing a short and an electrical blackout at Hershey Hall, the women's dorm. Phinney was also involved in another flood. He set up a still to run over the weekend to generate deionized water, but a piece of paper towel blocked the drain, and the water flowed out of the sink. As luck would have it, there was a hole in his lab's

floor because of a plumbing repair earlier in the week. During the weekend, the water silently spilled from the hole in the ceiling into the physics library located one floor below and finally went all the way down to the basement.

THE FELLOWSHIP OF THE GIBBANE RING

Phinney's research is intimately tied to the history of gibberellin. He was a strong believer in the power of biochemical genetics and was the first to propose that gibberellin-like substances functioned as endogenous hormones in plants. The history of gibberellin actually began at the end of the 19th century with the discovery by Shotaro Hori that "foolish seedling or silly seedling disease" (bakanae) of rice was due to a fungus infection. The seedlings elongated so much they fell over (i.e., they lodged) and the mature plants produced very little fruit. Hori found that the causative agent of the disease was the fungus, *Gibberelia fujikuroi*, as it is known in the perfect or sexual stage, or *Fusarium moniliforme* in the imperfect or vegetative stage. Kenichi Sawada in Taiwan (then called Formosa) was first (in 1912) to propose that the plant's response was due to a compound produced by the fungus. In 1926 Eiichi Kurosawa, who went to work with Sawada, published a paper about his discovery of a fungal-derived substance secreted into culture medium that caused bakanae. Later, Teijiro Yabuta and Takeshi Hayashi tested the Kurosawa-produced fungal extracts on a diversity of plants; they named the active component "gibberellin." Yabuta and Yusuke Sumiki in a 1938 publication reported that from crystals obtained from the culture filtrate they identified two compounds, gibberellin A and B; A was inactive, but B was active. However, the exact structure of these molecules could not conclusively be demonstrated because the crystals were not pure. In 1941 the letter designations were exchanged

(B became A), and the active compound became known as gibberellin A, or GA.

After World War II, the research on gibberellins that had gone on in Japan became known in the West, and several laboratories began investigating these hormones in the 1950s, including the USDA Northern Regional Research Lab in Peoria, Illinois, headed by Frank Stodola, the Chemical Corps Biological Lab in Camp Detrick, Maryland, led by John Mitchell, as well as a basic research laboratory set up by Imperial Chemical Industries (ICI) at Akers in the United Kingdom, where Percy Brian, Jake MacMillan, John Grove, Brian Cross, Philip Curtis, and T. P. C. ("Paddy") Mulholland worked. Sumiki came to the West at this time and gave fungal cultures to several labs although there were some false starts before the cultures were established. Most of the research at this time, in the early 1950s, centered on the fungal-derived gibberellins. Very few people were looking for the evidence that gibberellins were produced in plants. One of these people was Phinney and the other was Margaret Radley at the ICI Akers Research Labs.

Phinney began his quest for gibberellins or gibberellin-like substances, as he called them, in plants by first developing a bioassay utilizing the single-gene dwarf-mutant plants he had accumulated. The bioassay procedure was based on his findings published in 1956 that adding gibberellin to the recessive dwarf mutant plants restored them to normal height. His plan next was to find a plant extract that would rescue the dwarf phenotype and then use chromatography to identify one fraction among the many. At this time chromatography was a very new technique, and many chemists were applying it in their research. Phinney was using seeds of the common bean, *Phaseolus vulgaris*, as a source of gibberellins, and he and Charles West determined that two compounds with gibberellin activity could be isolated from common

bean using paper chromatography. West was the first of two chemists who were major collaborators with Phinney. West came to UCLA in 1952 with expertise in chromatographic methods, but he was drafted into the army after one semester at UCLA, and thus the collaboration with Phinney did not begin until he returned. At the same time Radley of ICI was looking for gibberellins in plants. She used dwarf peas in a bioassay developed by the ICI group. Her results, demonstrating that higher plants contained gibberellin-like substances, were published in 1956 and 1957.

The next steps undertaken by both the UCLA and ICI groups involved extracting plant material, analyzing the extracts by paper chromatography, and bioassaying the individual components to find the active fraction. In 1958 MacMillan from the ICI Labs was the first to identify a gibberellin from a plant, specifically from the immature seeds of *Phaseolus multiflorus*, now known as *P. coccineus*, the scarlet runner bean. West and Phinney published in 1959 their results on two crystalline substances from common bean: bean factor I and bean factor II, now known as GA_1 and GA_5, respectively.

Later, Flora Murray Scott recommended that Phinney test the liquid endosperm of the plant *Marah macrocarpus* (wild cucumber or manroot), a California native that grew in the nearby Santa Monica Mountains and had been worked on extensively by Scott in her studies of embryogenesis and seed formation. The endosperm of this plant was very active in the dwarf corn bioassay. Collecting *Marah*, however, had its share of adventures, including encounters with rattlesnakes, poison oak, and a police helicopter. Nevertheless, masses of *Marah* endosperm were taken back to UCLA, extracted, and frozen for future use.

JAPAN—THERE AND BACK AGAIN

Many Japanese scientists continued with the analysis of gibberellins produced by the fungus. Nobutaka Takahashi and Saburo Tamura, using the original crystals obtained from Yabuta and Sumiki, published a paper in 1955 that showed that gibberellin A actually contained three components: GA_1, GA_2, and GA_3. The latter, also known as gibberellic acid, is a tetracyclic-dihydroxy-lactonic acid that had been previously identified by British and U.S. scientists researching the fungal gibberellins. Takahashi and colleagues in 1957 also isolated a new gibberellin, GA_4, as a minor constituent of the culture filtrate. This was only the beginning of the identification of over 120 different structures of gibberellin from both plants and fungi.

In 1957 Phinney visited Japan for the first time to attend an International Genetics Symposium in Kyoto, and thus began a long-lasting collaboration with the Japanese scientists working on gibberellins. The first was Jiro Kato, who was a gibberellin physiologist. In 1959 Phinney invited Kato to his laboratory, where Kato discovered a new gibberellin-like substance in an extract from bamboo growing in the UCLA Botanical Garden. Tamura's group at Tokyo University later identified this substance as GA_{19}. Kato also identified gibberellins in other plants, including a tree fern. Once Kato returned to Japan, he recommended that Masayuki Katsumi apply for graduate study in the Phinney lab. Katsumi was awarded a Fulbright Travel Grantee fellowship and came to the United States in 1961. During this time, Katsumi found by feeding experiments that d_5 and d_1 mutants of maize responded to different kaurene derivatives that are structurally related to gibberellins. Thus, experiments into the investigation of the GA biosynthetic pathway were initiated. Yutaka Murakami also came to UCLA as a research fellow at this time, and found that dwarf rice mutants equivalent to d_5 and d_1 responded

in the same way. Together these findings led to the further development of the GA bioassay methods. Katsumi finished his Ph.D. in 1964 and took a position at the International Christian University near Tokyo.

Following Phinney's marriage in 1965 to Jean Swift, the couple took a yearlong (1966-1967) sabbatical, which was based in the Katsumi lab. During this sabbatical year, Phinney and Jean took several long road trips exploring the Japanese countryside. Phinney bought a used Nissan sedan and in the autumn they traveled by car through northern Honshu to Hokkaido often staying at old Japanese inns (ryokan). In the spring they traveled for another six weeks through southern Honshu, Shikoku, and Kyushu. Phinney had a sign on the car in Japanese that roughly translated to "I am an American professor looking for bakanae-diseased rice plants." With this sign and a few words in Japanese, Phinney was able to collect a large sample of rice seedlings infected with the fungus. By his own count he collected 1,500 strains of *Fusarium monoliforme*. During this time, he also met with Sumiki's and Tamura's research groups. These were memorable times for the Phinneys not only in terms of research but also because as a couple they established a lifelong love of Japanese culture, food, prints, and architecture. Their house in Brentwood was very Japanese in both style and architecture.

Phinney frequently returned to Japan visiting scientists at Riken and also meeting with Takahashi, who had earlier elucidated the structure of the gibberellins from the fungal extract. These meetings resulted in fruitful collaborations that led to the identification of a large spectrum of endogenous gibberellins in various plants and with the help of MacMillan and colleagues the elucidation of the gibberellin biosynthetic pathway in maize. In addition, they led to a steady stream of graduate student and postdoctoral researchers from Japan who

came to Los Angeles to work in the Phinney lab, including Hisakazu Yamane, Shozo Fujioka, Masatomo Kobayashi, and Yoshihito Suzuki. Many of these Japanese scientists have fond memories of working at UCLA with Phinney and his colleagues. Indeed, everyone in Japan with whom Phinney was associated liked him very much.

THE TWO POWERS—ELUCIDATING THE BIOSYNTHETIC PATHWAYS

At about the same that Phinney was working with Takahashi and Katsumi, he and MacMillan decided to join forces. Phinney had throughout his career maintained close ties with a chemist, first with West at UCLA and then with MacMillan, who at this time had moved to the University of Bristol. Phinney saw the importance of interdisciplinary research long before it became fashionable, and throughout his career promoted these types of interactions.

MacMillan met Phinney for the first time in 1957 at a gibberellin meeting at Stanford. Here Phinney told MacMillan about his and West's work on gibberellins in bean seeds. MacMillan lamented in a later article "Reflections of a Bio-organic Chemist" that to his shame he could not tell Phinney that they were working on the same project. They interacted again in 1969 at the International Botanical Congress in Seattle, where MacMillan got excited about a paper presented by Phinney and his Ph.D. student Machi Dilworth (née Fukuyama), and invited both to Bristol to do research in the summer of 1970. From 1976 onward the two scientists spent almost every summer together either in Bristol or Los Angeles, working on papers or planning future research. This led to numerous sabbaticals and summers at each other's institutions. Later the two scientists, Phinney and MacMillan, in collaboration with a cadre of postdoctoral researchers and collaborators (many former graduate students from the Takahashi lab but also from Bristol, including Peter

Hedden, Clive Spray, and John Bearder) deduced the details of the metabolic pathway of gibberellin synthesis in maize as well as the difference in GA_3 biosynthesis in maize versus the fungus. At UCLA Hisakazu Yamane synthesized various GAs and their precursors, which were double labeled with [^{3}H] and [^{14}C]. Using these compounds as internal standards, postdocs in UCLA extracted and purified the endogenous GAs from maize. The purified GAs were sent to Gaskin and MacMillan for identification and quantification by GC-MS. The labeled compounds were also used for the metabolic studies at UCLA that were also supported by the U.K. group. An enzyme preparation from *Marah* seeds helped in this study.

MacMillan was elected to the fellowship of the Royal Society of London in 1978 and Phinney was elected to the National Academy of Sciences in 1985. Both scientists garnered numerous awards for their discoveries during their long careers. Phinney was awarded a Research Medal from the International Plant Growth Substances Association (1982), and the Stephen Hales award from the American Society of Plant Biologists (ASPB) (1984). He received a Certificate of Merit for "meticulous research in plant physiology" (1986) and a Centennial Award from the Botanical Society of America (2007). Phinney was elected as an honorary foreign member of the Japanese Society of Chemical Regulation of Plants (1988). He was elected and served as the president of the ASPB from 1989 to 1990 and was honored as a member of the inaugural class of ASPB fellows in 2007. In 1989 Phinney was awarded an honorary D.Sc. from the University of Bristol in the United Kingdom, and from then on, he wore his bright-red honorary robe and black tam o'shanter to every UCLA graduation. In 1991 he received another award, a research fellowship from the Japanese Society for the Promotion of Science.

GIBBERELLIN A_1—ONE RING TO RULE THEM ALL

The experience of hearing Beadle talk about the power of biochemical genetics led Phinney to do the experiments that contributed in a major way toward understanding the function and metabolism of gibberellins. His observations were among the first to show that this class of plant hormones, which affect such critical developmental phenomena as seed germination, stem elongation, and fertilization, could be understood using a biochemical genetics approach. His research linked chemistry to biology. Early on, he showed that gibberellins could rescue the maize dwarf phenotype and research done in collaboration with West led to the identification of GA_1, the only gibberellin in the GA pathway that is active in the control of stem elongation in maize. His later work with MacMillan and collaborators, Japanese colleagues, and postdoctoral researchers led to the deduction of the gibberellin biosynthetic pathways in maize and other plants. Phinney spent his entire scientific career working with this group of plant hormones, but gibberellin A_1 was probably his favorite. Indeed, he long had a VW camper with the license plate GIBB A1. MacMillan said that one of the most enjoyable parts of their long-term collaboration was attending many international meetings together, often on the road in the GIBB A1-labeled VW camper.

During his long career, Phinney maintained the seed stocks of the various maize mutants used in his research. He also sent them to others upon request. Phinney was not just a research adviser, he actively participated in the lab doing greenhouse experiments, growing maize in the fields at UCLA and elsewhere. Phinney attended numerous scientific meetings and was also deeply interested in the research of others, often going to seminars outside his field. He supported junior scientists and helped numerous postdoctoral researchers and Ph.D. students. Often he worked behind the scenes suggesting

junior colleagues as speakers for conferences and financially supporting people working in his lab. He and Jean Phinney established a Graduate Fellowship in Plant Molecular Biology at the University of Minnesota.

Phinney had many interests in life in addition to his research on gibberellins—music, fast cars, orchids and ferns, skiing, and Japanese art and culture. Curiously, Phinney never flaunted his knowledge or his skills (except for still skiing at age 90). Indeed, he usually downplayed his expertise and experiences. For example, few people knew he played the flute and that he knew a great deal about music. Often Phinney would give people the impression that he had a bad memory because he carried a small book with him that he called his "brain" in which he would jot down names and addresses and various facts that he picked up at seminars. Phinney always found what he was looking for in his "brain" even though it was filled with scribbles and appeared to others as being completely disorganized. He also had the habit of losing his "brain" as well as his wallet, his keys, and all sorts of things, oftentimes in the most unexpected places.

Of his many interests Phinney probably loved science most of all. Well into his nineties and up to about two months before he died, Phinney spent hours in the UCLA Plant Growth Center, testing an extract of *Marah* on nongibberellin-responding dwarf mutants of *Arabidopsis*. He wanted to make one more discovery before he hung up his beret.

His wife, Jean; four children, Scott Phinney, Katcha Burnett, Peter Phinney, and David Phinney; and eight grandchildren survive him.

MANY PEOPLE HELPED ME write this obituary by supplying me with various details of B. O. Phinney's life and science. I am grateful to Jean S. Phinney, Charles A. West, Mary R. Corcoran, Masayuki Kasumi, Machi Dilworth, Jack MacMillan, Masatomo Kobayashi, Art Gibson, and Clive Spray. Thanks also to Nancy A. Fujishige for her editorial input. All generously gave of their time, their anecdotes, and their memories to help me write about a person who will be difficult to forget.

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