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CHARLES BIXLER HEISER JR.
1920–2010

A Biographical Memoir by

BARBARA PICKERSGILL AND GREGORY J. ANDERSON

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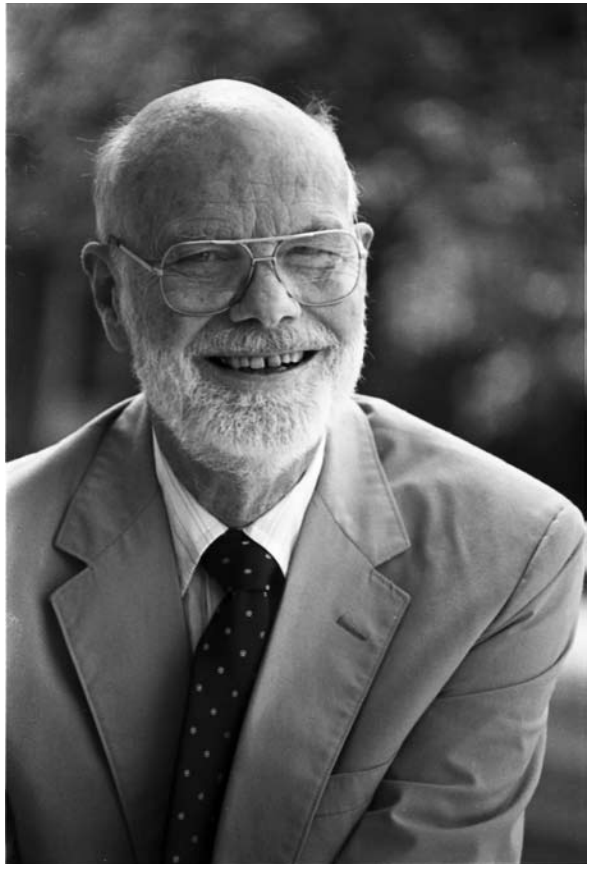
Biographical Memoir



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Charles B. Hurin, Jr.

CHARLES BIXLER HEISER JR.

October 5, 1920–June 11, 2010

BY BARBARA PICKERSGILL
AND GREGORY J. ANDERSON

CHARLES HEISER WAS AN influential figure in the early development of plant biosystematics (also known as experimental taxonomy). Unlike herbarium-based orthodox taxonomy, biosystematics involves study of living plants, in the wild or in experimental cultivation, in order to investigate the causes and consequences of variation within as well as between species and hence to study evolution at the levels of populations and species. This was an exciting field populated by luminaries such as Ledyard Stebbins, Edgar Anderson, Jens Clausen, Verne Grant, and others who influenced, and were influenced by, like-minded colleagues, such as Ernst Mayr and Theodosius Dobzhansky, working in animal biology. The interactions of these and other scientists in related areas of genetics and paleontology gave rise to the Society for the Study of Evolution, and subsequently to a reorganization of government support for biological sciences at the National Science Foundation.

Heiser's contributions to biosystematics grew out of, and fed back into, his equally seminal work on the systematics, evolution, and domestication of the sunflower genus *Helianthus*. He is perhaps best known for his work on the role of interspecific hybridization in generating variation and local adaptation. He also investigated changes in chromo-

some structure and number as barriers to interspecific gene exchange. He had a particular ability to distinguish significant from trivial morphological variation and the patience to persevere with attempts to make difficult interspecific crosses and study chromosome behavior in the resultant hybrids. His work was mostly carried out before the advent of the isozyme and DNA technologies that have revolutionized the study of microevolution, but these new techniques have validated most of Heiser's conclusions.

From sunflowers he extended his studies to other cultivated plants, particularly chile peppers (*Capsicum*) and some of the lesser-known crops of Andean South America, such as pepino (*Solanum muricatum*), naranjilla (*Solanum quitoense*), and quinoa (*Chenopodium quinoa*). In this too he was ahead of his time; in the 1950s and 1960s cultivated plants were not considered appropriate for serious taxonomic study, whereas today they are seen as valuable subjects for investigations of evolutionary responses to selection on a defined and limited timescale.

His work on cultivated plants led to collaborations with archaeologists, and publications in various anthropological and archaeological journals and symposium volumes. His ability to make his expertise intelligible to nonspecialists stood him in good stead here. This talent was especially valuable in his series of popular books that did much to promote botany to the general public. His books also conveyed vividly the enthusiasm for his chosen field that he retained throughout his long life and that led him to continue work and publication well into his ninth decade.

EARLY YEARS IN INDIANA AND ILLINOIS

Charles Bixler ("Charley") Heiser was born on October 5, 1920, in Cynthiana, Indiana, to Charles Bixler Heiser Sr. and Ines Metcalf Heiser. He liked to say that you could tell that

he came from rural southern Indiana by his accent: he was right. His father worked in insurance but his Heiser grandparents were farmers, and visits to their farm were highlights of the year for the young Charley, to such an extent that he later took his new wife there, by bus, for their honeymoon. His experiences on his grandparents' farm probably gave him the interest in and skill at growing plants that lasted throughout his long professional career and into retirement. At the height of his career, in the spring planting season, he could often be found helping his graduate students to plant out their field experiments, and even in retirement he made almost daily visits to the Indiana University glasshouses and experimental field. He enlisted his grandchildren to help him move around heavy pots when they became too much for him, and he continued his work right up to the day that he suffered a massive stroke. His enthusiasm for growing plants, and the unique data that come from experimental studies with living plants, stimulated all who worked with him to follow his lead.

During his childhood, the family moved frequently within southern Indiana, including in the early 1930s a period in Bloomington, where Charley became acquainted with the Indiana University campus and developed an ambition to return to Indiana University as the football coach. The family moved on to Belleville, Illinois, where Charley graduated from high school after serving as president of his senior class. After his parents moved yet again, to St Louis, Missouri, he entered Washington University.

Given Charley's height (about 6 ft 4 in), it was probably inevitable that his sporting achievements would center on basketball, which together with football, remained a passionate interest throughout his life. He lettered in basketball both in high school and at Washington University, where he noted that he played against only two or three people taller

than himself. There, after obtaining his master's degree, he combined the posts of instructor in botany and interim basketball coach (there was a shortage of coaching personnel during the Second World War). His mentors at Washington University, Edgar Anderson and Robert Woodson, thought that this gave a whole new image to botany.

WASHINGTON UNIVERSITY AND THE INFLUENCE OF EDGAR ANDERSON

Charley entered Washington University in 1939 on a half scholarship because a relative on his mother's side had fought in the Civil War. He was then considering majoring in journalism or in English. He had edited the high school newspaper and covered high school sports for the Belleville daily newspaper. During high school he had written poems and short stories for both children and adults but never had any accepted. However, when still a graduate student, he had two articles accepted (and paid for) by *Natural History* magazine: "Gold is the Sunflower" (published in 1946) and "Peppers: Some Like It Hot" (published in 1951). This presaged what was to become a lifelong interest in these two crops, and in using his writing skills to explain his scientific work to the general public. Later in his life these writing skills resulted in a series of books well received by both fellow botanists and the general public. These treated topics such as the nightshade (potato) family, gourds, the story of human food, and, of course, the sunflower. In 2002 he was honored with the Raven Outreach Award from the American Society of Plant Taxonomists for his contributions to popularizing botany. In 2004 his book *Weeds in My Garden* (2003) received the Garden Globe Award from the Garden Writers' Association "for best talent/writing."

As part of his undergraduate science requirement at Washington University, Charley took the freshman botany course taught by Robert E. Woodson. This course, and the

slides (Kodachromes) of diverse plant life in the tropics of Panama used by Woodson to illustrate his classes, fired Charley with a desire, realized in his first sabbatical, to go to Latin America to work on tropical plants. Woodson's course thus proved a life-changing experience, and Charley eventually majored in the unusual combination of English and botany. This unconventional mixture left him no time for courses in statistics or chemistry, which he later regretted. However, this did not prevent him from publishing with some of his graduate students an early study on the application of numerical taxonomy to the taxonomically difficult *Solanum nigrum* complex and on the use of flavonoids as taxonomic characters in *Luffa*. He was a very strong student and was elected to Phi Beta Kappa. Other honors were election to Omicron Delta Kappa, Thurtene, and Sigma Xi.

In his senior year Charley became acquainted with Edgar Anderson, who was subsequently a mentor, friend, and major influence on Charley's botanical career. Charley had planned to take Woodson's advanced taxonomy course, but Woodson was asked to give a geography course to army veterans, so Anderson volunteered to teach the taxonomy course in his stead. Anderson devoted the whole semester to one plant family, the Asteraceae, starting with sunflowers. Sunflowers fascinated Anderson, particularly the weedy ones that grew in disturbed areas (e.g., along the railroad tracks in St. Louis), and on one field trip he told Charley that if someone looked into sunflowers carefully he would discover something very significant: a remark that Charley said stuck with him. He was later to prove the truth of it.

Because these were the war years, classes were small. The idiosyncratic advanced taxonomy course that Anderson taught had just two students: Charley Heiser, who had been rejected for active service on medical grounds, and Dorothy

Gaebler, who in 1944 became Dorothy Heiser. They had three children: Lynn, Cynthia, and Charles Bixler.

Charley obtained his A.B. in 1943 and remained at Washington University for his master's degree, directed by J. M. Greenman and awarded in 1944. Although Charley had suggested sunflowers as a topic, his master's thesis was actually on a different genus of Asteraceae, *Psilostrophe*. Nevertheless, encouraged by Anderson, Charley assembled a collection of sunflowers and started making morphological comparisons and experimenting with hybridization. Anderson also secured funds from the Missouri Botanical Garden to send Charley to the Museum of Northern Arizona for a week to learn about the Hopi sunflower. Gas rationing prevented Charley from getting all the way to the Hopi Reservation, but the weedy sunflowers growing near the museum included *Helianthus annuus*, *H. petiolaris*, and some unusual variants that Charley found also in St. Louis wherever these two species grew in close proximity. Charley recognized that these variants were hybrids, much to the excitement of Anderson, who was then pioneering studies on the occurrence, detection, and significance of interspecific hybridization in plants and whose ideas were summarized in a seminal book, *Introgressive Hybridization*, published in 1949. Much later a population of *H. petiolaris* collected by Charley near St. Louis provided the source of cytoplasmic male sterility that was used to develop F_1 hybrid breeding programs in sunflower. For this and his many other contributions to sunflower research, Charley received in 1985 the highest award of the International Sunflower Association, the Pustovoit Award.

After he had completed his master's degree, Anderson and Woodson felt that Charley should spend a year away from the Midwest to broaden his experience before returning to Washington University to complete his Ph.D. He never did return.

UNIVERSITY OF CALIFORNIA: STEBBINS AND MORE SUNFLOWERS

Anderson and Woodson sent Charley to the University of California, Berkeley, where Anderson advised Charley to contact his friend and colleague, G. Ledyard Stebbins; Anderson continued to mentor Charley's activities by mail. As Charley told it, Anderson thought that revisionary work on *Stephanomeria*, which Charley and Stebbins were viewing as a possible Ph.D. problem, would result in just another conventional research publication, whereas with *Helianthus* he would uncover an entire new field of work. Charley wrote back, "If I am uncovering an entirely new field of work…I wish you would let me in on what it is." He evidently found out: *Helianthus* sustained not only his own Ph.D. and the theses of some of his early graduate students but also provided the background for his two classic reviews of hybridization and introgression, the first in 1949, followed 24 years later by an update (1973,2). Together these reviews provided a framework for his research and influenced that of many others (both his own students and his botanical colleagues) for close to half a century.

Soon after his arrival in California, Stebbins took Charley on a field trip and they found several populations of *H. annuus* and *H. bolanderi* growing together, with apparent interspecific hybrids in nearly every mixed population. This determined the topic of Charley's Ph.D. thesis, conducted in the Botany Department, not the Genetics Department. Thus, his doctoral research was nominally under the direction of Herbert Mason, not Stebbins. However, Stebbins remained a major influence and a kindred spirit with whom Charley shared the excitement of research. Lincoln Constance reputedly commented that their influence on each other would make them both nervous wrecks.

Charley completed his Ph.D. in 1947, in the astonishingly short time of two years, despite accepting a teaching

position at the University of California, Davis, in his second year. He was then offered the opportunity to continue on the faculty at Davis but decided instead to accept an offer from Indiana University.

INDIANA UNIVERSITY: A JOB FOR LIFE

Charley's attachment to his Midwestern roots was one of the factors in his decision to accept a position at Indiana University. Others were that Charley felt that botany at Indiana University appeared to have a great future and that he would have a freer choice of research topics than at Davis. The Botany Department was then led by Ralph E. Cleland, a cytologist internationally renowned for his work on *Oenothera*. Cleland was succeeded by Marcus M. Rhoades, an equally distinguished scholar who worked on maize cytogenetics. Indiana University was a center of genetics at the time, with Tracy Sonneborn and the Nobel Prize winner Herman J. Muller, both on the faculty in the Zoology Department. As a consequence, Indiana University provided an excellent environment for the combination of studies in taxonomy, cytology, and evolution that Charley and others were then pioneering and that constituted the relatively new field of biosystematics. In spite of his fundamental commitment to Indiana University and Indiana, as late as the 1970s Charley used to point to some very dusty boxes under one of the lab benches and say that he had not fully unpacked because he was not sure that he would stay; in fact, he remained there and continued to be active in research through his retirement. His work at Indiana University thus covered a span of more than 60 years. He moved quickly through the ranks, from assistant professor in 1947 to associate professor (1951), professor (1957), distinguished professor (1979), and finally distinguished professor emeritus in 1986.

At Indiana University he taught courses on Survey of Vascular Plants, Systematics of Flowering Plants, Economic Botany or Ethnobotany, and a graduate-level biosystematics course. His research initially centered on continued study of sunflowers. He produced a series of papers on variation, interspecific hybridization, and evolution in both annual and perennial species of *Helianthus*, and in 1969, with some of his former graduate students, he published a substantial monograph of the North American species of the genus. His work established the extent and potential importance of hybridization as a creative force in evolution for all organisms, not just plants, and set a new standard of scientific rigor in plant systematics. His biosystematic studies and his seed collections from wild species have proven to be valuable resources for sunflower breeding. For example, *H. paradoxus*, a rare species that he discovered in saline wetlands in west Texas, has been a source of salt tolerance genes. For his exemplary work in taxonomy and biosystematics he received in 1969 the Gleason Award from the New York Botanical Garden. It is perhaps fitting that his last three papers, written in his 88th year, and fortunately published before his stroke, focused on the origin and domestication of the sunflower in North America.

Helianthus is a temperate genus and, inspired by Woodson's lectures at Washington University as noted previously, Charley was keen to visit tropical America. As a means to this end he started work on peppers (chile peppers, in the genus *Capsicum*, not black pepper, in the genus *Piper*, though as a result of a misunderstanding by the editors of the *Encyclopaedia Britannica*, he contributed the article on black pepper and relatives to the 15th edition). His early work on *Capsicum* was in collaboration with Paul Smith, a pepper breeder at the University of California, Davis, who had made extensive collections of chile peppers throughout

Andean South America but needed these collections to be studied taxonomically.

The first of Charley's own visits to the tropics was to Costa Rica in 1953, as a Guggenheim fellow, and was significant not only for his encounters with many tropical crops in the markets there but also for the start of his friendship with two Ecuadorians, Jorge Soria (later to complete his Ph.D. under Charley's direction) and Jaime Diaz (a plant pathologist), both then students at the Instituto Interamericano de Ciencias Agricolas in Turrialba, Costa Rica. Both helped later with arrangements for Charley's first (1962) and second (1969) sabbaticals in Ecuador, which Charley regarded as among the greatest experiences of his life; so much so that he wished for his cremated remains to be scattered in Ecuador.

Charley was later able to repay some of his debt to Ecuador and his colleagues there through his work on the origin and relationships of the naranjilla, or lulo, (*Solanum quitoense*), a fruit little known outside the tropics but very popular in Ecuador and Colombia. He carried out a numerical taxonomic analysis of morphological variation, investigated reproductive biology (using an electric razor to simulate buzz pollination), made interspecific crosses and investigated the cytology of species and hybrids. The naranjilla has potential for export as juice but suffers from soilborne nematodes. Charley bred a nematode-resistant hybrid between naranjilla and cocona (*S. sessiliflorum*), a related species cultivated in Amazonia. This hybrid became widely grown in Ecuador. The initial interspecific cross and the chromosome doubling of the resultant hybrids were carried out at Indiana University, while Jorge Soria oversaw the field trials in Ecuador. For this work Charley was selected as an honorary member of the Instituto de Ciencias Naturales of Ecuador and later awarded a plaque from INIAP (the national institute of agricultural research in Ecuador), which was presented to him in 1997

at a meeting to celebrate his 50 years at Indiana University. In 1998 in Colombia the Corporación de Investigación Agropecuaria announced the release of 'Lulo La Selva,' a root-knot nematode-resistant lulo based on hybrids of *Solanum quitoense* and *S. hirtum* (a wild species in which Charley had discovered resistance) that Charley had sent to Colombia some years before. Charley hoped that cultivation of this hybrid in Colombia might provide small-scale farmers with an alternative to growing coca (for cocaine production) or marijuana.

Later in his career Charley became increasingly passionate about making directly applicable contributions to agriculture and humankind—as represented by this work (as well as his sunflower work). In addition, Charley took pleasure in having introduced into cultivation two ornamental plants: a peperomia (*Peperomia* 'Tena') collected near Tena, Ecuador, and the ball loofah (*Luffa operculata*). He also made a number of contributions to the horticultural diversity of bottle gourds (another of his research interests). He was proud to receive recognition from regional organizations in addition to his many national and international professional honors. For instance, The Indiana Gourd Society recognized his bottle gourd work with the Roll of Honor Award in 1999, and The Indiana Academy of Science recognized him with a Distinguished Scholars Award in 1997.

Charley's first research students worked on the taxonomy of various genera of Asteraceae (e.g., *Tagetes, Viguiera, Bidens*). Charley used to say that anyone purporting to be a taxonomist owed it to the subject to publish at least one monograph or revision during their professional life. He practiced what he preached by publishing, with some of his research students or colleagues, not only a monograph of all the North American species of *Helianthus* but also a revision

of the section of *Solanum* that includes the naranjilla and a taxonomic treatment of the American species of *Luffa*.

Charley's interests and the topics of his graduate students' theses soon broadened from the Asteraceae to the taxonomic and biosystematic problems posed by cultivated plants, particularly some of the crops of the Andean region: pepino (*Solanum muricatum*), uvilla (*Physalis*), amaranth (*Amaranthus*), quinoa and its Mexican counterpart huauhzontle (*Chenopodium quinoa* and *C. berlandieri)*, and of course chile peppers and naranjilla. His taxonomist's eye enabled him to disentangle parallel variation resulting from human selection during cultivation from the often more subtle differences that indicate that different species of the same genus were domesticated in different parts of the Americas for the same purpose. Thus, he reduced the taxonomic inflation represented by recognition of 50 species of *Capsicum* in the 19th century to just five domesticated taxa, paving the way for more detailed studies of their origins, evolution, and archaeological record. With Hugh Wilson he showed that the domesticated chenopods of Mexico and the Andes are distinct species more closely related to weeds in their respective areas than to each other and thus an example of independent domestication not, as had been previously suggested, pre-Columbian crop dispersal between Middle and South America. He demonstrated that the domesticated sunflower originated in the eastern United States, not the Southwest or Mexico: something that has since been validated by molecular studies and that he was promoting vigorously in an ongoing debate in print just before his stroke. This demonstration helped to establish eastern North America as one of the regions in the world in which agriculture arose independently. For those interested in the origins of crops domesticated in the Americas and inter-American crop dispersals, his reviews are still useful starting points.

From crop dispersals within the Americas Charley moved to the more contentious question of early human transoceanic dispersals of cultivated plants. He published a substantive paper on one of the classic problem genera in this context, the bottle gourd (*Lagenaria siceraria*), as well as a consideration of botanical and other aspects of the wearing of gourds as penis sheaths in New Guinea and South America. He acquired and grew samples of *Scirpus* reeds from the Andean region and Easter Island and concluded that although these belong to the same species, there was no evidence to suggest that the species was spread to Easter Island by humans in prehistoric times, as Thor Heyerdahl had suggested. He showed that an Asian species in the taxonomic section of *Solanum* that contains naranjilla probably resulted from a post-Columbian introduction by the Spanish of an American species, but he was unable to explain satisfactorily the presence of another species, *S. repandum*, very similar to the Amazonian domesticate *S. sessiliflorum*, as a weed and domesticate in Oceania.

He built up a wide correspondence with other scientists, and also missionaries, diplomats, Peace Corps volunteers, and nationals of various countries who might help him obtain seeds of the often rather obscure species in which he had become interested. His own travels were principally in Latin America. Although he greatly enjoyed seeing new places and new plants, he could be a nervous traveler. At coffee time in the herbarium at Indiana University before a major trip he would bequeath the various genera he was then working on to whichever of the assembled company he felt would best look after them. It was therefore with a mixture of incredulity and amusement (after all had ended well) that the coffee group learned that Charley and his family had been hijacked to Cuba while on a flight in Ecuador in 1969.

His studies on this wide range of species in turn paved the way for his more general papers on systematics and

the origins of cultivated plants, biochemical systematics, cytogenetics and evolutionary change under domestication, unconscious selection, and his thoughts on the role of religion in the origin of agriculture. These were usually prepared as invited contributions for conferences. Charley was a superb speaker, frequently called upon not just for keynote papers at conferences but also for more lighthearted banquet addresses, of which his tributes to Edgar Anderson are excellent examples.

In 1987 Charley was accorded one of the top honors available to U.S. scientists: election to the National Academy of Sciences. The citation emphasized his significant research on the evolution and domestication of such important crop plants as sunflowers and peppers and his perceptive investigations into the nature of hybridization in plants that laid the foundation for our modern understanding of the way plant populations are related.

He was a mentor to 29 doctoral students and uncounted (he couldn't remember how many) master's students, and he influenced many more. The work he guided covered at least 14 plant families, over 30 genera, and nearly 40 topical or conceptual areas. He was a sympathetic and understanding supervisor, giving his students latitude to follow their own instincts about the direction that their research should take but applying pressure when necessary. He was generous in promoting his students' interests, introducing them at scientific meetings to senior figures in the field, who were usually his personal friends. Unusual by today's standards, he did not insist on coauthorship of papers resulting from theses that he had supervised, thereby provoking much introspection in more than one student who had hoped that his name would attract attention to a first publication and, when he declined coauthorship, was left wondering whether that meant that the paper was unworthy. The Department of Plant Biology

at Indiana University set up the Charles B. Heiser Graduate Fellowship in memory of his role in training and mentoring students. This role is also commemorated in the Charles B. Heiser Jr. Mentor Award of the Society for Economic Botany, proposed by their Student Network Committee.

HONORS, AWARDS, AND OFFICES HELD

Several of Charley's honors and awards have already been mentioned, but a more complete list is given here for ease of reference. He received a Guggenheim Fellowship in 1953, a National Science Foundation Fellowship in 1962, and a Senior Post Doctoral Fellowship from the same source in 1975. He was elected president of the American Society for Plant Taxonomy in 1967, president of the Society for the Study of Evolution in 1974, president of the Society for Economic Botany in 1977-1978, and president of the Botanical Society of America in 1980. He received the Gleason Award of the New York Botanical Garden in 1969; the Merit Award of the Botanical Society of America in 1980, followed by their Centennial Award in 2006; the Pustovoit Award of the International Sunflower Association in 1985; the Asa Gray Award of the American Society of Plant Taxonomists in 1988 and their Peter Raven Award in 2002; the Distinguished Scholars Award of the Indiana Academy of Science in 1997; the Roll of Honor Award of the Indiana Gourd Society in 1999; and the Garden Writers' Association Award for Best Writing/Talent in 2004. He was the Indiana Academy of Science's Speaker of the Year in 1985. He was elected to the National Academy of Sciences in 1987. In 1997 he received a plaque from the Instituto Nacional Autónomo de Investigaciones Agropecuarias of Ecuador for contributions to the improvement of the naranjilla, *Solanum quitoense*.

EPILOGUE

In November 2008 Charley suffered a severely disabling stroke. He died on June 11, 2010, of the ensuing complications. Studies of sunflowers and hybridization still continue at Indiana University, building on Charley's pioneering work. Following Charley's retirement in 1986, Loren H. Rieseberg was appointed to the faculty and has since been elected a foreign fellow of the Royal Society of the United Kingdom; this recognition arises in part for the increased understanding of evolution, hybridization, and domestication of sunflowers gained from application of molecular genetics to many topics initially studied by Charley. Charley and Loren enjoyed numerous productive discussions about sunflowers and hybridization. Although new techniques have necessitated modification of some of Charley's interpretations, others still stand. His publications are still much cited and remain a monument to a professional lifetime spent on what a former Ph.D. student described as "never work—more like a full-time hobby."

IN WRITING THIS MEMOIR we have drawn extensively on the following sources:

- Heiser's delightful part-autobiographical tribute to Edgar Anderson: Student days with Edgar Anderson, or how I came to study sunflowers. *Ann. Mo. Bot. Gard.* 59(1972):362-372.
- His curriculum vitae updated to July 2010 and on file at Indiana University.
- An incomplete autobiography that he started writing for his children but mailed also to G. J. Anderson (fall 2006).
- Our own tributes to him: B. Pickersgill and G. J. Anderson. Travels with Charley—sunflowers and beyond: An appreciation of the life and work of Charles B. Heiser, Jr. (1920-2010). *Econ. Bot.* 64(2010):281-286. G. J. Anderson. Charles B. Heiser Jr., 1920-2010. *Plant Sci. Bull.* 56(3)(2010):115-117).

We have also drawn on our memories of our time as his Ph.D. students and our continuing interaction and friendship with him throughout our professional careers. We thank especially Cyndi Roberts (daughter) and other members of the Heiser family, as well as Susan Kephart (former student), Loren Rieseberg and Jeff Palmer (colleagues) for discussions, comments, and background information as we prepared this document.

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