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DONALD R. FARRAR

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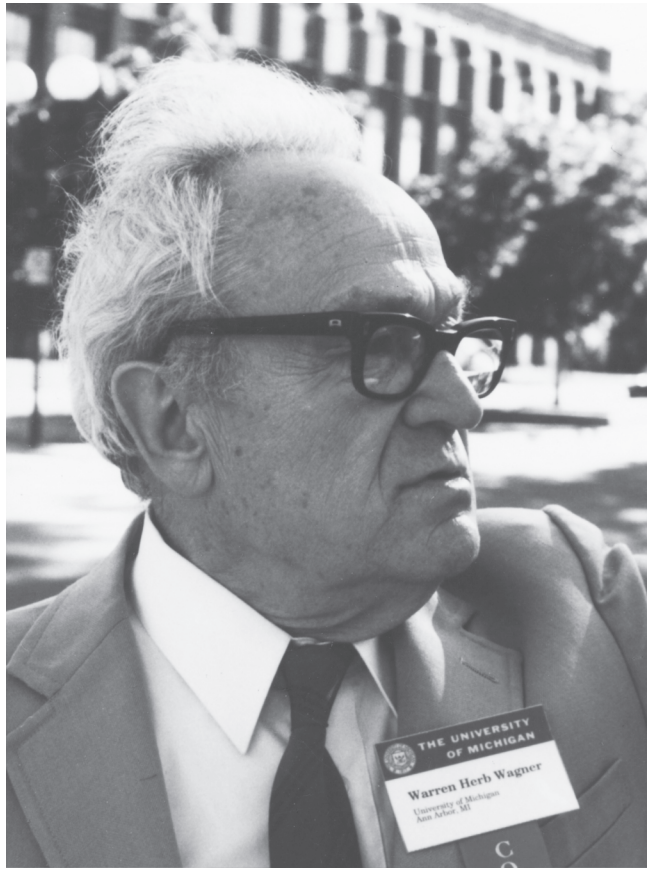

Warren Herbert Wagner

WARREN H. WAGNER, JR.

August 29, 1920–January 8, 2000

BY DONALD R. FARRAR

IN HIS PH.D. RESEARCH Warren ("Herb") Wagner was introduced to classical methods of systematic botany, and found them wanting. He was disturbed by the frequent absence of quantitative data and the generally untestable hypotheses of traditional reconstructions of species' evolutionary relationships. At the time, the latter was based largely on the expert's weighing of the evidence and authoritative statement of an opinion that could be argued but not easily tested. Herb was determined that in his own research monographing the endemic Hawaiian fern genus *Diellia*, he would use evidence from all sources and explicitly state the relative influence of each in an objectively constructed illustration of phylogenetic relationships. The result was the birth of his groundplan divergence index, for which he soon became widely known. Herb's insight and instigation, coupled in ensuing years with computer-assisted analysis of comparative data, revolutionized the fundamental methods and concepts of phylogenetic reconstruction, leading directly to the burgeoning field of cladistic analysis of evolutionary relationships among plants. For his seminal contributions Warren H. Wagner, Jr., is generally considered a founding father of modern plant systematics.

Warren Herbert Wagner, Jr., was born on August 29, 1920, and was raised in Washington D.C., the son of Warren Herbert Wagner and Harriet Claflin Wagner. His early interests in natural history took him frequently to the Smithsonian Institution, where he became acquainted with the experts, including the eminent pteridologists William R. Maxon and Conrad V. Morton and lepidopterist Austin Clark. In college at the University of Pennsylvania he became the enthusiastic field companion of Edgar T. Wherry, author of the *The Fern Guide* (paperback, Dover Publications, 1995). Wherry was a mineralogist who became an expert on fern habitats and the first to point out the important associations of epipetric ferns with particular rock types. This undoubtedly nurtured Herb's enthusiasm for mineralogy; later his extended field trips with students often included a day of mineral collecting. When as a student I brought back an unusual form of cliff-brake fern from Missouri, Herb was anxious to visit the site, not so much for the fern as for the barite crystals I had found there. His fascination with butterflies (he authored or coauthored 20 papers on Lepidoptera)—he called them "flying flowers"[1]—dictated that he carry a butterfly net on field excursions, thus presenting the archetypical layman's image of a biology professor. I vividly recall stopping at a fast-food restaurant in the Missouri Ozarks, where after ordering, Herb headed for a nearby field filled with flowers and butterflies. The curiosity of the restaurant staff was definitely aroused by the spectacle of this man running through the field swinging a net at prey invisible to them. After we explained, our waiter walked into the field to shout, "Hey perfesser, your lunch is ready!"

Graduating from the University of Pennsylvania in 1942, Herb entered the U.S. Navy Air Corps, serving first in the Atlantic, then in the Pacific Fleet, where he was a naval air navigator. In the Pacific islands he spent his off-duty hours

collecting ferns and butterflies, later publishing (with David Grether) "Pteridophytes of Guam" as well as articles on the pteridophytes and butterflies of the Admiralty Islands. During this time he also flew into California, taking his specimens to E. B. Copeland, renowned expert on Philippine ferns, at the University of California, Berkeley. This was the beginning of an association that would bring him back to Berkeley for graduate study. While in the Navy, he also began what was to become a lifelong study of the ferns of the Hawaiian Islands.

At Berkeley in 1945 Herb joined an exceptional group of graduate students returning from World War II that formed fertile grounds for growth of new concepts in botany, evolution, and systematics. His student colleagues from 1945 to 1950 included Charles Heiser, Ernest Gifford, Jack Rattenbury, Isabella Abbot, Frank Ranzoni, Verne Grant, Art Krukeberg, and Ed Cantino. Their teachers included Melvin Calvin, Richard Goldschmidt, Curt Stern, G. Ledyard Stebbins, and Herb's major professor, Lincoln Constance. Copeland, though retired, was still active and served on Herb's Ph.D. committee.

Also among Herb's student colleagues was Florence Signaigo, who was studying the systematics of red algae with George Pappenfuss. Herb and Florence were introduced by fellow student Charles Heiser in the elevator of the herbarium. Florence recalls,

> Herb and I used to go over to San Francisco, to various bars, where we would order a beer, and after a while Herb would ask the bartender if it was all right if he played the piano. Sometimes the bartender would show up later at the piano with two free beers. Once one had to ask Herb to stop playing a piece because it was making a woman at the bar cry. And once he was offered a job as a piano player.

Herb and Florence were married in 1948. They had two children, Warren Charles Wagner (b. 1953) and Margaret

Frances Wagner (b. 1957). Florence switched her allegiance from algae to ferns and together she and Herb comprised a formidable research team both in the lab and in the field. Their home in Ann Arbor was a busy and warm environment, frequently hosting receptions for visiting botanists and on holidays wonderful dinners for any of his graduate students who were in town. Herb continued to delight audiences in informal gatherings and sometimes at bars with the flamboyant piano playing that reflected his personality. It was always fun to watch the bar manager's expression change from skepticism to astonishment as Herb began to play. Once, after several evenings of this in a hotel bar, Herb was refused permission to play because the house pianist, embarrassed by the contrast with his own lackluster style, was threatening to quit.

Herb actively pursued his research and teaching until just weeks before his death on January 8, 2000, at the age of 79 from sudden cardiac arrest. He had experienced symptoms of heart failure for a few years before his death, but not enough to incapacitate him. Although officially retired, he had continued teaching his courses on woody plants and plant systematics and maintained a rigorous schedule of invited lectures to institutions around the world as well as national and international meetings and symposia. In the summer preceding his death Herb and Florence conducted field work in Alaska and in southwestern Canada, from both places returning with, of course, new species of *Botrychium*.

After receiving his Ph. D. in 1950 Herb spent a year as a Gray Herbarium fellow at Harvard, then moved to the University of Michigan in 1951, where he remained throughout his career. From 1966 to 1971 Herb served as director of the University of Michigan's Matthaei Botanical Garden. He chaired the Department of Botany in the Division of

Biological Sciences from 1974 to 1977, and chaired many additional department and college committees, including the University of Michigan's Tropical Studies Committee from 1983 through 1997. He was chairman or president of nine professional societies, including the American Fern Society, American Society of Plant Taxonomists, and the Botanical Society of America, and council member, trustee, or advisor to dozens of organizations. He was in demand as an external reviewer of departments of biology and botany across the country. He served as an editor for the University of Michigan Press, *The Indian Journal of Pteridology,* and *The Flora of North America* (coediting "Pteridophytes" in volume two [1993]). He reviewed countless journal manuscripts and grant proposals. To these causes and many more he gave freely of his time while continuing to teach and while maintaining a research program that generated over 250 publications. He was elected to the National Academy of Sciences in 1985. His official retirement in 1991 proved to be only a formality, as his research and teaching continued unabated.

One of Herb's first endeavors as a young professor at the University of Michigan was probing the origin and relationships of the Appalachian *Aspleniums,* a confusing group of ferns to which he had been introduced years earlier by E. T. Wherry. The keys to solving this puzzle of starkly different species with a seemingly complete array of intermediates lay in (1) examination of chromosome numbers and their pairing behavior in meiosis; (2) relating this chromosome data to spore abortion and intermediate morphologies; and (3) appreciation of the fact that fertility could be restored to "sterile" species hybrids through allopolyploidy, a simple doubling of the basic number of chromosomes (1954). Thus the now well-known Appalachian *Asplenium* triangle was resolved into three diploid species (the corners

of the triangle), three fertile allotetraploid species (originating as hybrids between the three diploids), and numerous backcross hybrids that occurred wherever a tetraploid and diploid species grew together. Subsequently verified through artificial crosses, flavonoid chemistry, and allozymes, this model of reticulate evolution quickly became the basis for making sense of similar species complexes in other fern groups and in seed plants.

Revolutionary in its time, attributing an important role to species hybrids in plant evolution (1968, 1969) contradicted the long-held notion of species hybrids being evolutionary dead-ends. Herb's studies demonstrated that plant species hybrids could in fact be the initial step in the formation, through allopolyploidy, of new species that continued to participate in subsequent evolution of the genus (1980).

Sterile F_1 hybrids also proved to be much more common in plants than in animals, and Herb was on a mission to spread the news. His seminar presentations always worked in a series of hybrids demonstrating wider and wider crosses, ending with a wildly misshapen fern that he proclaimed to be a cross between a wood fern and a red oak! Such exaggerations drove home the point that hybrids were to be expected in nature and recognized as a component of the flora at any given time and place. Although most of these hybrids might be sterile dead-ends, their presence constituted part of the "evolutionary noise" (his term) through which the systematist must trace "signal" lines and processes leading to long-term persistence and divergence (1970).

A part of Herb's diatribe on hybrids was that they were easy to detect, because they were invariably intermediate between their parents. Because development of most morphological traits would be under the control of a set of genes representing a combination of the two parents, not

only could one predict the morphology of hybrids but given a hybrid and one parent, one could also predict the other parent. In the case of allotetraploid species that may have formed in the ancient past, it was possible that one or both of the diploid "parents" might now be extinct. This was Herb's conclusion relative to the wood-fern genus *Dryopteris,* which seemed to lack an extant diploid needed to form two of the allotetraploid species (1970). His naming of this extinct species was hard to accept by many and led to a decade of alternative proposals designed to avoid postulation of a missing species. As with the *Asplenium* triangle, subsequently derived molecular evidence supported Herb's conclusion.

Herb's persistent proclamation of hybrid intermediacy set up a straw man easily knocked down by later studies showing transgressive hybrid morphologies in traits controlled by one of a few genes. This didn't phase Herb. His goal was always to understand and promote the "big picture," the principles that explained most of nature and natural processes. His procedure though was to study the knowable details. Through accumulation of details the big picture would emerge. Thus he produced exhaustive studies of foliar dichotomy (1952), heteroblastic leaf morphologies (1957), paraphyses (1964), spore structure (1974), and vein reticulation (1979). He compiled detailed floristic analysis of the areas in which he worked—the southern Appalachians (1963, 1970), Hawaii (1999)—and distributional analyses of species and genera he studied. From the latter he became convinced that pteridophytes, despite their ease of dispersal by spores, for the most part showed the same distribution limitations as seed plants (1972). Subsequent research demonstrating the general out-breeding nature of ferns provided the explanation—two or more spores germinating in interactive proximity being required for sporophyte production and thus for migration of most diploid species.

Although I had taken Herb's course in plant systematics and had been exposed to his philosophy for several years, I didn't come to appreciate his truly comprehensive knowledge of pteridophytes until 1967, when Herb participated in the offering of a fern course for graduate students in Costa Rica. For two weeks he lectured daily, not only on the morphology and systematics of tropical ferns but also on the ecology, distribution, and occasionally the physiology of the thousand or more species we were likely to encounter, all seemingly without resort to notes. My feeling then and now was that one could hope to contend with Herb's analysis of the big picture only with a similar comprehensive knowledge of the parts.

Though a comprehensive Wagnerian treatment of the pteridophytes was not produced during his lifetime, Herb's influence on pteridology in the last half of the twentieth century was enormous, through his own studies and those of his students and their students. He was coeditor of the "Pteridophyte" volume of *The Flora of North America* (1993) and author or coauthor of treatments on Ophioglossaceae, Lycopodiaceae, Schizeaceae, Aspleniaceae, and *Dryopteris*. At the time of his death Herb and Florence Wagner had largely finished "The Pteridophyte Flora of Hawaii" (it is now being completed by Florence Wagner). That flora, in its treatment of the remarkable evolutionary patterns of Hawaiian pteridophytes, will reflect their lifetime accumulation of knowledge of pteridophyte biology.

Herb had a passion for studying the small. In 1963 with Aaron J. Sharp he published a paper in *Science* describing "a remarkably reduced vascular plant"—the fingernail-size gametophyte of the fern genus *Vittaria*. The reduction to which the paper referred was not the size of the gametophyte plant itself but its failure to ever produce a sporophyte, the larger and more familiar phase of the fern life cycle. Though

well documented in bryophytes, indefinite persistence of the supposedly ephemeral gametophyte phase through vegetative reproduction was an unheard of phenomenon in ferns. Furthermore, these independent gametophytes were very common in the southeastern United States, covering square meters of moist cliff surfaces much the same as bryophytes. The paper in its initial submission was titled "The Most Reduced Vascular Plant," but the reviewers cautioned that still greater reduction might be found. True to this prediction Wagner and Robert Evers shortly thereafter described from the canyons of southern Illinois the gametophyte of *Trichomanes*—another independent gametophyte, this one reduced to a mere branching filament of cells.

I arrived in Ann Arbor just at the time of these discoveries and was fascinated to find, on my first trip with the Wagners to southern Ohio and Kentucky, both genera of independent gametophytes growing in luxuriant abundance. With Herb's enthusiastic encouragement and my own love of exploring cliffs and rockhouses, I was powerless to resist a lifelong enchantment with the evolution and ecology of these plants. The existence of independent fern gametophytes is now well documented in North America, Hawaii, and Europe and probably occurs worldwide as a natural result of the preadaptation of certain tropical species for vegetative reproduction and dispersal in the gametophyte stage, a habit evolved to promote cross-fertilization in epiphytic habitats.

The other small plants to attract a disproportionate amount of Herb's attention were the moonworts, diminutive plants of the genus and subgenus *Botrychium*. Generally less than 10 cm tall, these plants produce but one leaf per year of very simple (reduced) morphology, usually well hidden among associated vegetation. When Herb first turned his attention to this group, six species were recognized worldwide, five in North America. With Florence's expertise in

cytology and their combined ability to coax hoards of students and amateurs to crawl through meadow vegetation on hands and knees they began detection of a much larger complex of species than ever imagined.[2] Their uncanny ability to discern subtle morphological differences revealed a diversity of diploid, tetraploid, and hexaploid species now totaling 30[3] and illustrating as well as any organisms the concepts of cryptic speciation (1983).

Of Herb Wagner's many contributions to plant systematics, he is most widely known for his early conceptual contributions to cladistic methods of analysis and representation of phylogenetic relationships, now the method of choice for research into evolutionary relationships among organisms. After first conceiving and applying his groundplan divergence index method in his dissertation work,[4] Herb spent the next two decades analyzing, perfecting, and promoting it, while applying it to more and more complex systematic problems (1964, 1969). Ultimately he convinced most of his colleagues that his objective and testable methods yielded results more satisfying than the subjective judgments of experts, and with their adoption by the new breed of computer-savvy systematists, "cladistics" was off and running. Later reflecting on the struggles of this period, he commented that "most active taxonomists are so busy that they have little time to contemplate the philosophical foundations of their calling. They are too preoccupied with the act of classification to be burdened with the ideas behind it or to devote themselves to developing a consistent theory" (1969).

Asked to review his development of the groundplan divergence index (1969, 1980), Herb acknowledged that no one part was new and that his thinking was initially influenced by the writings of Benedictus Danser[5] regarding detection of the ancestral form or "groundplan" of phylo-

genetic groups. Herb's contribution was putting philosophy and method together to yield a diagrammatic depiction of phylogenetic relationships based on explicit data and assumptions. Herb's method consisted of five steps: (1) identifying the taxa to be considered; (2) selecting characters that showed evolutionary trends; (3) determining the ancestral state for each character; (4) finding the degree of advancement of each taxon; and (5) connecting taxa by their degree of shared derived characters. Each of these steps required careful objective analysis with no *a priori* assumptions. "Homology is a conclusion and not a datum. . . . Only trends and patterns shown by the data themselves can be applied" (1969). Most basic was the use of in-group and out-group comparisons to objectively determine ancestral character states and the Occam's razor principle of assuming an overall diagram (tree) requiring the fewest character changes (steps) as being the most likely. Herb's method was soon computerized to produce "Wagner trees" as they became known.[6,7] With many subsequent modifications and increasing sophistication, Wagner trees continue to appear in systematic literature. Along with the awards for Herb's many contributions to systematic botany (Willi Hennig fellow, National Academy of Sciences, American Academy of Arts and Sciences fellow, Asa Gray Award of the American Society of Plant Taxonomists), the Wagner tree inscription appropriately recognizes his profound influence on modern phylogenetic reconstruction.

Herb emphasized that a major goal of his groundplan divergence index was to teach concepts in systematic botany. It "forces us to investigate the nature of character states and to evaluate all of the available characters." He admonished that "the systematist should not simply 'plug in' his data set and allow the computer to come up with the cladogram. He should think it out himself, and this, scien-

tifically, may be one of the most useful rewards of following each of the procedures of the Groundplan-divergence Method" (1980). He did more. He *created* an entirely new family of plants, the Dendrogramaceae (also known as the Wagneraceae), to teach the principles involved. The species (illustrated on 5 × 7 cards) demonstrated evolution from normal to fleshy stems, simple to compound leaves, free to fused petals (or possibly the reverse of all of these) as well as other variations. In the classroom these "plants" stimulated hours of discussion (sometimes fierce arguments) over the direction and pattern of their evolution and which was the most parsimonious solution. The exercise proved so effective that through the 1960s new species of Dendrogramaceae continued to be discovered (as well as fossil ancestors). They also reproduced vigorously and dispersed, ultimately achieving much the same distribution as Herb's students and grandstudents. Publications appeared analyzing their systematic relationships using an array of computerized methods. They became as well recognized and as important in systematic lore as real plant families.

Such was Herb Wagner's talent for getting students immersed in systematics and plant science in general. He had little sympathy for those who complained of the difficulties of academia or who did not pursue their studies with a strong, honest effort. For students displaying genuine interest in their research discoveries he quickly multiplied that interest through his own. His clear excitement over discoveries large and small was the genius of his inspirational leadership. He could make hard work not only palatable but also fun. My recollection of lunchtime discussions among Herb and us students is that always there was the sense of examining breaking news at the forefront of scientific discovery. Importantly, it was the science behind those discoveries, rather than the people, that was the focus. He

cultivated the attitude that all research was worthwhile and that the goal was advancement of knowledge, not personal glory. He applied this philosophy to encourage reluctant students to publish their work, saying that they "owed it to science" to communicate their findings. This particular ploy worked to keep me in school when I was contemplating taking time out for a stint in the Peace Corps.

Herb received well-deserved awards for and acknowledgements of his gift for teaching both inside and outside the classroom, but his influence certainly was not limited to the classroom. In addition to numerous research field trips, Herb seldom made a seminar visit to a new or botanically interesting area without insisting on an accompanying field trip. These trips invariably included a retinue of local amateur botanists as well as students and academic professionals. From their "Wagner experience" hundreds of students, professionals, and amateurs became hooked on science, not because they wanted to please Herb, although that was always fun, but because they became genuinely infused with the excitement of scientific discovery. Herb's ability to inspire others through his interest in their studies and their knowledge not only fostered independent research but also created a legion of professionals and amateurs eager to contribute data to Herb's projects as well. The total productivity of this synergism, though unquantifiable, remains hugely visible.

Herb's distinguished career at the University of Michigan included chairmanship or cochairmanship of over 45 doctoral committees and membership on more than 235. He taught a variety of courses, including systematic botany and biology of woody plants, both of which he continued to co-teach after "retirement" in 1991 through the fall of 1999. Teaching was as much a joy to Herb as it was to the students who continued to pack his courses. His outrageous performances and exaggerations delighted his audiences. It was always of

great interest to his teaching assistants to see who among the students did and who didn't believe that *Rafflesia* was pollinated by elephants, *Wolffia* by mosquitoes, and *Podophyllum* by turtles. Herb's public lectures and seminars were equally popular. Few biologists have been in such demand as a visiting speaker. His curriculum vitae list of invited lectures totaled 169—after retirement!

Warren H. Wagner, Jr., will be remembered as a wonderful teacher and inspirational leader whose legacy lives on in hundreds of individuals whose lives he touched. His command of the principal subjects of his research, his beloved ferns, was excelled by none. He used intimate knowledge of detail to synthesize big-picture principles that withstood the scrutiny his flamboyant style invited. His contribution to plant systematics and evolution and to the biology of ferns profoundly influenced the direction of these fields into the twenty-first century.

Additional biographic information on W. H. Wagner, Jr., with more complete bibliographies has appeared in obituary publications in *Taxon* (49[2000]:585-592) and *American Fern Journal* 92[2000]:39-49). The photograph and information on early years were graciously provided by Florence Wagner. Factual information is taken from Herb Wagner's 1999 curriculum vitae. Other anecdotes and observations extend from my long association with the Wagners, as a graduate student in Ann Arbor and in many subsequent field trips and discussions of plants, people, and philosophy.

NOTES

1. W. H. Wagner. 1996. Flying flowers! Butterflies and their foodplants. *LSA Bulletin* (published by the College of Literature, Science, and the Arts, The University of Michigan) 9:4-9, cover.

2. W. H. Wagner and F. S. Wagner. 1998. Moonwort madness: A

reply. *Am. Fern Soc. Bull. (Fiddlehead Forum)* 25:30-31. The Wagners recount how they became interested in *Botrychium* and some of their adventures in searching for these reclusive plants.

3. This number includes several species not yet officially published.

4. W. H. Wagner, Jr. The fern genus *Diellia*: Structure, affinities, and taxonomy. *Univ. Calif. Publ. Bot.* 26(1)(1952):1-212.

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6. A. G. Kluge and J. S. Farris. Quantitative phyletics and the evolution of anurans. *Syst. Zool.* 18(1969):1-32.

7. J. S. Farris. Methods for computing Wagner trees. *Syst. Zool.* 19(1970):83-92.

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