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EDGAR ANDERSON

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A Biographical Memoir by

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BY G. LEDYARD STEBBINS

EDGAR ANDERSON left an indelible impression on the plant science of the twentieth century. His entire life revolved about his love of plants—wild and domestic, in nature and in the garden—and his eagerness inspired students and laymen alike with a similar admiration for and love of the plant world. His research was original in conception, based on precise observations and experiments, and followed by interpretations that were significant and stimulating, even if sometimes incorrect. As a teacher of graduate students, he produced several of the leading evolutionary botanists of our day. His methods of recording variation in populations have been spread by his students and admirers throughout the world and are widely used both by students in classes and by research botanists in their publications. Moreover, as a staff member of two major botanical gardens, he took his relations with plant lovers and gardeners very seriously, whatever their position and interests. He developed this relationship by innumerable visits to private gardens and by personally guiding many visitors through the Arnold Arboretum of Harvard University in Boston and the Missouri Botanical Garden in St. Louis, as well as by publishing a continuous stream of over 300 short popular articles.

Edgar Anderson (if he ever had a middle name or initial, he never used it) was born on November 9, 1897, in Forestville,

New York, the son of A. Crosby Anderson, a private school administrator, and Inez Evora Shannon Anderson, an accomplished amateur musician. At the age of three, he moved with his family to East Lansing, Michigan, where his father became Instructor and later Professor of Dairy Husbandry at Michigan Agricultural College, now Michigan State University. From an early age he exhibited both superior intelligence and a great interest in plants, particularly in cultivating them and watching them grow.

He went to Michigan Agricultural College at the age of sixteen, just before his seventeenth birthday, knowing already that he wanted to be a botanist. He majored in horticulture, and was active in the Horticultural Society, but took part in few other extracurricular activities. After a short interval in the Naval Reserve, he went to Boston in the spring of 1919 to become a graduate student at the Bussey Institution, where he worked under the direction of Edward Murray East. During the 1920s this institution was one of the most unusual and stimulating centers for postgraduate education in biology and was particularly well suited to Anderson's individualist personality. A small group of brilliant biologists—William M. Wheeler and Charles T. Brues in entomology, Oakes Ames and Irving W. Bailey in systematic and morphological botany, Edward M. East and William E. Castle in genetics—were isolated by both distance and temperament from the rest of Harvard and had daily contact with a small group of carefully chosen students. In addition to his research, which was on the genetics of self-incompatibility in *Nicotiana,* he spent much of his time walking through the countryside, learning to identify the native plants, and talking about plant cultivation with members of the staff of the nearby Arnold Arboretum. Harvard botanists whom I knew in the 1930s, particularly Karl Sax, told me that as a graduate student he was not regarded as outstanding, and some of them were later surprised at the success that he achieved.

While at the Bussey Institute he met Dorothy Moore, a fellow botanist, who became a constant companion on botanical hikes through the countryside. They were married in 1923. Her loyal friendship until his death, as well as her modesty and keen intelligence, helped him over many of the rough spots in his life.

After leaving Harvard with his doctor's degree in 1922, Anderson spent nine years at the Missouri Botanical Garden, where he was a geneticist and Director of the Henry Shaw School of Gardening; at the same time he was Assistant Professor, later Associate Professor, of Botany at Washington University in St. Louis. During this period, he developed the beginnings of his highly original and effective methods for looking at and recording variation in plant populations, as well as his keen interest in the needs and progress, both scientific and personal, of students in botany. His training in genetics had given him habits of precision and mathematical accuracy in observing and recording variation in natural populations that were entirely foreign to the taxonomists of that period. Through contacts with Jesse Greenman, Curator of the Garden Herbarium, he became aware of the enormous complexity and extent of the variation present in any large plant genus and of the need for understanding the origin of species as a major step in evolution. On extensive field trips he began to realize that a great amount of genetic variation exists within most natural populations of plants. This realization led him to the conclusion that "if we are to learn anything about the ultimate nature of species we must reduce the problem to the simplest terms and study a few easily recognized, well differentiated species" (*Annals of the Missouri Botanical Garden,* 15[1928]:243).

He first selected *Iris versicolor,* the common blue flag, because he believed it to be clearly defined, and it was common and easily observed. Initially, this appeared to be a mistaken choice, since he soon found that *I. versicolor* of the taxonomic manuals was actually two species, which, after preliminary

analysis, he could easily tell apart. He then set himself the task of finding out, by a careful analysis of populations throughout their geographic areas, how one of these species could have evolved from the other. He recorded several morphological characters in more than 2,000 individuals belonging to 100 populations, data far more extensive than those that any botanist had yet obtained on a single species.

In order to enable these data to be easily visualized and compared, he constructed the first of his highly original and extremely useful series of simplified diagrams or ideographs. By examining them, he reached the conclusion that the variation within each of his two species was of another order from the differences between them; no population of one species could be imagined as the beginning of a course of evolution toward the other. He therefore concluded that speciation in this example was not a continuation of the variation that gave rise to differences between populations of one species, and started to look for other ways in which it could have taken place. The current literature offered a possible explanation: hybridization followed by chromosome doubling to produce a fertile, stable, true-breeding amphidiploid. To apply this concept to *Iris,* he had to find a third species that would provide an alternate parent for one of those studied. Going to the herbarium, he found it: an undescribed variety of *Iris setosa,* native to Alaska.

All of his data, including counts of chromosome numbers, agreed with the hypothesis that *Iris versicolor* of northeastern North America had arisen as an amphiploid, one parent being *I. virginica* of the Mississippi Valley and the Southeast Coast and the other being *I. setosa* var. *interior* of the Yukon Valley, Alaska. He then found geological information to support his hypothesis: *I. versicolor* occurs almost entirely in territory that was covered by ice during the Pleistocene glaciation, while *I. virginica* occurs chiefly south and *I. setosa* var. *interior* northwest of the glaciated area. This was one of the earliest demon-

strations that a plant species can evolve by hybridization accompanied or followed by chromosome doubling. Moreover, it was the first one to show that amphiploid or allopolyploid species can be used to support hypotheses about past distributions of species. Anderson's research on *Iris* began his use of all of the techniques that led to success in his later work: careful examination of individual characters on plants growing in nature and progeny raised in the garden; reduction of this variation to easily visualized, simple terms by means of scatter diagrams and ideographs; extrapolation from a putative parental species and supposed hybrid to reconstruct the alternative parent; and development of testable hypotheses by synthesizing data from every possible source.

Another species studied during this period, *Aster anomalus*, had a completely different pattern of variation. Selected because it is an easily recognized, clearly defined species with a restricted geographic distribution, in a genus that contains many difficult species complexes, it turned out to contain as much variation in any single population as in the entire species. By growing plants under controlled conditions, he showed that variation with respect to leaves, stems, and other vegetative characteristics was due largely to phenotypic modification, but that reproductive characters were remarkably constant for a genotype and exhibited a large amount of genotypic variation within populations. Moreover, each individual plant proved to be highly heterozygous; its progeny from open pollination exhibited almost the entire range of variation found in the species. Population geneticists have in recent years shown by more refined, precise methods that this condition exists in many other species of both plants and animals. Anderson was a true pioneer in the study of genetic variation in natural populations.

The *Iris* research was Anderson's chief accomplishment during his first period at the Missouri Botanical Garden. Toward the end of this period, in 1929–1930, he received a National

Research Fellowship for study in England. There he was guided chiefly by J. B. S. Haldane, but he also studied cytology under C. D. Darlington and statistics with R. A. Fisher. Haldane introduced him to the mutants of *Primula sinensis,* which he analyzed in collaboration with Dorothea De Winton. Their joint research was the first effort in plant material to relate pleiotropic gene action to growth processes.

In 1931 Anderson went to Harvard, where he stayed until 1935, as arborist at the Arnold Arboretum. During this period, much of his important research was in collaboration with Karl Sax, who made him more aware of the importance of chromosomal variation in the origin of species. He supplemented Sax's research on meiosis and pollen development in *Tradescantia* with a cytological monograph of the genus, published jointly, and a taxonomic monograph, published in collaboration with his former student Robert Woodson. The *Tradescantia* research led to two of his most important contributions to evolutionary botany: the concept of introgression and that of "hybridization of the habitat."

He returned to the Missouri Botanical Garden in 1935 and remained there for the rest of his life. Continuing the research on *Tradescantia,* he recorded variation patterns in populations of this genus in relation to the physical factors of the environment and the results of sympatric occurrence of two different species. He found that whenever two species having very different ecological adaptations grew near each other in the absence of an intermediate habitat they remained completely distinct, and hybrid plants could not be found. If, however, intermediate or disturbed habitats were present, these would often be occupied by apparent hybrids. Their hybrid nature was confirmed by reproducing them through artificial hybridization. If an intermediate kind of habitat graded into that typical for one of the parental species, apparent backcross plants could be found. Furthermore, in the case of partly allopatric species, he

found that the variation pattern of one species, "species A," is greater in a region of overlap with another, "species B," than in regions where it grows by itself. This variation is always in the direction of species B. He named this phenomenon introgressive hybridization, or introgression, a term that is firmly fixed in the vocabulary of plant systematists and evolutionists.

Returning to a study of the genus *Iris,* he analyzed, with several students, the complex variation pattern of populations found in the Mississippi delta region. He found hybrids between species to be most abundant in habitats greatly disturbed by human activity and particularly in those that showed recombinations of the physical characteristics to which the parental species were adapted. If, for instance, one parental species was adapted to well-drained soil and shaded woodland, while the other grew in poorly drained soil and open sun, poorly drained areas that were shaded or well-drained places in full sun would support hybrids or introgressive backcross derivatives. These new habitats he characterized as "hybridized habitats." He recognized that "hybridization of the habitat" through human disturbance is one of the principal factors responsible for the establishment in nature of plant hybrids and their progeny.

This research led to two of Anderson's most important and widely cited publications: the book *Introgressive Hybridization* and a paper on the same subject in *Biological Reviews.* Research in this field continued with studies of several other genera, and a general paper, "Hybridization as an Evolutionary Stimulus," was published jointly with this biographer in 1954.

The appearance in 1939 of a revolutionary paper by Paul Mangelsdorf and Robert G. Reeves on the origin of Indian corn, or maize, stimulated Anderson to apply his methods to the study of this crop plant. Largely in collaboration with W. L. Brown, who was first his student and later a research worker and coordinator of research for the Pioneer Hi-bred Corn Co., he applied his methods to the comparative study of corn varieties. Among

the most important results of this research was the demonstration that the most valuable Corn Belt hybrids owe their success to particular combinations of characters derived on the one hand from northern flint varieties that were grown in the northeastern states from colonial times and earlier and on the other from the southern dents, which are related to Caribbean and other tropical varieties. Similar studies of Mexican races, conducted largely by Anderson alone, served as a valuable basis for later classifications that other workers completed. During his work with corn, Anderson refined his previously used methods of scatter diagrams and ideographs, which resulted in the technique of the pictorialized scatter diagram. It has proved to be of great value in analyzing populations of hybrid origin, or natural hybrid swarms.

As Anderson's interest in corn developed, he made increasing contacts with geographers, anthropologists, and archaeologists and wrote several papers on the relationship of maize cultivation to the migration and culture of primitive people, in both the Old World and the Americas. These interests were stimulated by a Rockefeller Foundation grant that brought him for a year's collaboration with Carl Sauer, the distinguished geographer at the University of California, at Berkeley, and a Guggenheim award for a study of maize in Mexico. In that country, as well as in Central America, he did much more than look at cornfields. He talked with farmers, learned about local cultures, studied the arrangement and organization of home gardens, and became acquainted with primitive varieties of several different indigenous crops, such as the avocado.

Anderson integrated these new experiences with past memories, popular accounts of his methods of research, and his general philosophy of life in the book *Plants, Man and Life,* published in 1952, which has become a favorite among students and botanists alike. It is a combination of scientific knowledge, folklore of Latin American and other countries, and Andersonian comments on early herbalists and the habits of taxonomists and

botany professors, plus a bit of philosophy. One of his chief contributions to plant science, the pictorialized scatter diagram, is presented for the first time in its final form in a chapter entitled, characteristically, "How to Measure an Avocado." Another gem is a diagrammatic map of an orchard garden in Guatemala, showing how a community of cultivated plants can be made compact and harmonious. His method of studying the origin of cultivated plants and the complexities involved are set forth in his chapter on sunflowers. Sprinkled through the book are thumbnail sketches of personalities—living, historical, and partly fictional. That which appealed to me most was of the mediaeval herbalist Leonhard Fuchs, whom he pictures as a "big, broad-shouldered Henry-the-Eighth sort of man with handsome clothes and a general air of getting things done." This characterization, either consciously or unconsciously, may be in part a wishful self-portrait.

In 1954 Anderson became Director of the Missouri Botanical Garden, but he found full-time administration frustrating and in 1957 resigned and resumed his career of teaching and research. The last years of his life, however, did not bring forth any outstanding new creative effort. During the 1960s he was plagued by illness, and his productivity in basic science declined. His principal contributions during that period were a steady flow of popular articles on trees, shrubs, and other plants of the garden, on improved methods for amateur gardeners, on miscellaneous garden lore, and on reviews of both scientific and popular books. After his death in 1969, his admirers assembled a volume of the *Annals of the Missouri Botanical Garden* (vol. 59, no. 3, 1972) dedicated to his memory and containing a biographical sketch and full bibliography, as well as reminiscences by former students and friends and research papers that had been inspired by his knowledge and work.

Anderson was elected to the National Academy of Sciences in 1954. Other honors were: membership in the American Academy of Arts and Sciences, the Darwin–Wallace Medal of

the Linnean Society of London, a Golden Jubilee Award of Merit from the Botanical Society of America, and the Order of the Yugoslavian Crown. He was President of the Botanical Society of America, the Herb Society of America (which he helped establish), and the Society for the Study of Evolution.

Edgar Anderson, more than most scientists, was a man of extraordinary contrasts. He had the brilliance to produce some of the most original and fruitful ideas in modern plant science, but occasional lapses of intellectual discipline led him to publish some hypotheses that must now be regarded as just plain foolish. As an observer and recorder of variation, he was extremely precise and careful, but he was also casual and sometimes negligent when it came to performing experiments that were necessary for verifying his hypotheses. He had a wide knowledge and understanding of botanical literature but could sometimes overlook references that would have been highly relevant.

In his personality, he had the humility that led him early in life to become a Quaker, and he remained faithful to and conscientious in observing that religion throughout his life. At the same time, he was aggressively ambitious and scornful of other scientists whom he considered to be intellectually inferior. He could be rudely abrupt with either his scientific opponents, his acquaintances, or even his closest friends. On the other hand, he could never hold a grudge or hurt people intentionally. His warmth and friendliness were, above all, showered lavishly upon younger scientists who, in his opinion, were intelligent and ambitious enough to warant his attention. He reveled in his unconventionality. He could never resist the temptation of exercising his keen wit at someone else's expense. Nevertheless, he was highly sensitive to the needs and motives of others. For many of his former students and friends, the exciting days spent in the company of Edgar Anderson are remembered as among the brightest of their lives.

IN PREPARING this memoir, I have had available a large amount of material obtained from the staff of the Missouri Botanical Garden. I wish to acknowledge with thanks the assistance of Dr. David Gates, former Director, Dr. Duncan M. Porter, and Dr. Erna R. Eisendrath for this material. Many of the facts of Anderson's life were taken from the biography by John J. Finan (*Annals of the Missouri Botanical Garden,* 59[1972]:325–45). The Bibliography is abridged and edited from that prepared by Dr. Eisendrath (*ibid.,* 346–51). Some of my comments are repeated from my article on recollections (*ibid.,* 373–79). The photograph of Dr. Anderson was supplied through the kindness of Dr. Peter Raven, Director, Missouri Botanical Garden.

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KEY TO ABBREVIATIONS

Am. J. Bot. = American Journal of Botany
Am. Nat. = American Naturalist
Ann. Bot. = Annals of Botany (London)
Ann. Mo. Bot. Gard. = Annals of the Missouri Botanical Garden
Bot. Gaz. = Botanical Gazette (Crawfordsville, Indiana)
Bull. Torrey Bot. Club = Bulletin of the Torrey Botanical Club
Chron. Bot. = Chronica Botanica (Lancaster, Pa.)
J. Arnold Arbor. = Journal of the Arnold Arboretum, Harvard University
J. Hered. = Journal of Heredity
Natl. Res. Counc. Publ. = National Research Council Publication
Proc. Natl. Acad. Sci. USA = Proceedings of the National Academy of Sciences of the United States of America

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