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G. Ledyard Stebbins (1906–2000) — An Appreciation

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Ledyard Stebbins, born January 6, 1906, was deeply fond of nature all his life, starting with his experiences around Seal Harbor, Maine, at about four years old. When he was still young, his mother contracted tuberculosis, and the family moved west to try to find a more healthy climate for her—first to Pasadena, then to Colorado Springs. An important formative period of Ledyard's life was spent at Cate School, in Santa Barbara, where he studied for four years. During those years, he was, by his own account, shy and relatively unpopular; but he learned to ride horseback, explored the Santa Ynez Mountains, and fell under the influence of the botanist Ralph Hoffmann, who taught him much about the plants and natural history of that lovely area.

Enrolling in Harvard University in 1924, Ledyard at first had difficulty defining his major, but the summer between his freshman and sophomore years was spent investigating the plants around Bar Harbor, Maine, the family home, and brought him into contact with Edgar T. Wherry, professor of botany from the University of Pennsylvania and a specialist in ferns, who encouraged his botanical interests. When he enrolled for the fall semester of 1925 at Harvard, he had decided to pursue a botanical career. But during his time at Harvard, his love of classical music, which was to be an important element for the remainder of his life, was awakened and nourished, as he participated in music classes and

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choruses, and was encouraged by some powerful and encouraging faculty members and students. Continuing on in the Harvard Graduate School, Ledyard was caught in the cross-fire between those, like Merrit Lyndon Fernald, who took a classical view of botany and plant classification, and the more modern approaches of Karl Sax, who was applying cytogenetic principles to developing a deeper understanding of plants. Thanks to judicious efforts by Paul Mangelsdorf and others, his dissertation was finally approved; but it was a struggle; he graduated in 1931.

One of the key events in Ledyard's early career was his attending the International Botanical Congress at Cambridge, England, in 1930; there he met Edgar Anderson, who was to become a lifetime friend and colleague; Irene Manton; and C.D. Darlington, whose classical "Recent Advances of Cytology," was still in the future. These and other contacts greatly encouraged his interest in and enthusiasm for botany and botanists, which was to be sustained for the rest of his life.

After he obtained his Ph.D., Ledyard Stebbins spent the years 1931–1935 at Colgate University, which he described years later as unhappy years, but it is not clear why this was the case. With an associate, Professor Percy Sanders, he undertook the cytogenetic study of Paeonia, which was the first of a series of essentially biosystematic investigations of diverse plant groups that were to characterize the remainder of his research career. During this time, he discovered complex structural heterozygosity in the western North American species of the genus, an exciting find that was to fuel his enthusiasm for further cytogenetic investigations.

In 1935, Professor Ernest Brown Babcock of the University of California, Berkeley, offered Stebbins a research position in connection with his investigations of the genus Crepis, which he accepted with alacrity. Met at the train station by his fellow Harvard student Rimo Bacigalupi, he plunged into this project with enthusiasm. Also at Berkeley, he began his lifetime preoccupation with Democratic politics, working actively in the 1936 Roosevelt election, and from there onward. After four years on Professor Babcock's grant, Stebbins was appointed to the faculty at Berkeley, and began to teach a course in the principles of evolution, which helped him to generalize his thoughts and finally to his preparing the classical work, "Variation and Evolution in Plants," whose 50th anniversary we are celebrating in this symposium.

In his research efforts, Ledyard began investigating the American species of Crepis (most species of the genus are Eurasian, but there are some very interesting offshoots in North America), outlining the evolutionary features of this group as a pillar complex of polyploids, with the base chromosome number 2n = 22, but widespread polyploids, characteristically apomictic, linking their more narrowly-distributed diploid pro-

genitors. He also began investigating grasses, first Bromus and then Triticeae, with the objective of developing perennial grasses that would provide forage on the dry rangelands of California, and which eventually led to his extensive studies of the genus Dactylis, which he pursued throughout its native range in western Eurasia and North Africa in the decades to follow. Never successful, this quest nonetheless led Stebbins to many interesting discoveries, and broadened the scope of his knowledge of the details of evolution in plants in such a way as to expand the coverage of and insights provided in his landmark book.

In the early 1940s, Stebbins began working actively with Carl Epling on the genetics of Linanthus parryae, an annual of the Mohave Desert in which the prevalence of white or blue flowers in individual populations was held at the time to have resulted from random drift. He also started an active association with Theodosius Dobzhansky, centering around Dobzhansky's efforts at Mather; he regarded Epling, Dobzhansky, and Edgar Anderson as his closest and most influential professional associates.

In 1947, Ledyard Stebbins spent three months at Columbia University in New York, delivering the Jesup Lectures; and these lectures, expanded and elaborated, became *Variation and Evolution in Plants,* the most important book on plant evolution of the 20th century. I first met him in 1950, on a Sierra Club outing, and he was as encouraging to me at the age of 14 as I could have imagined. It seemed to me later that his own rather unhappy and lonely childhood led him naturally to an appreciation for young people, a lifetime interest in connection with which he made significant contributions to the lives of many young scholars. I maintained a strong friendship with him for the remaining half-century of his life.

The first period of Ledyard Stebbins' botanical life extended from 1925, when his serious interest in plants was kindled at Harvard, to 1935, when he arrived at Berkeley; the second, highly productive period, from there to 1950, when "Variation and Evolution in Plants" was published. In that same year, he answered an invitation from the University to establish a department of genetics at the Davis campus, and entered the third period of his professional life. And my, how he loved Davis, its growth, its variety, and its accessibility to all. He was proud of his work at Davis, proud of the growing campus as it matured, pleased with his own contributions, and always contented living there. In 1971, after Dobzhansky's retirement from Rockefeller University, he was influential in recruiting both Dobzhansky and his associate Francisco Ayala, to Davis, where they made outstanding contributions. With retirement, he traveled widely, for example, teaching in Chile during the time of the 1973 coup, and visiting Australia, Africa, Europe, and other parts of the world in teaching, visiting with his colleagues, and, as always, enjoying students.

Variation and Evolution in Plants and Microorganisms

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