THE SCIENTIFIC PAPERS OF G. LEDYARD STEBBINS (1929–2000): SOME HISTORICAL PERSPECTIVES

George Ledyard Stebbins's formal scientific career began in 1929 with the publication of his first article titled "Further Additions to the Mt. Desert Flora" published in *Rhodora*, the journal popular with New England botanists (see Stebbins, 1929a). Though he was a new graduate student in the Harvard botany department at the time (he formally entered in 1928), Stebbins already had extensive knowledge of the New England flora. In particular he was much acquainted with the flora of Mt. Desert, Island, Maine, since it had been the summer retreat for his family. His father, a wealthy New York financier, had actually been a real estate developer for Seal Harbor, where the family owned their summer home. Encouraging a love of natural history, the Stebbins family had exposed their three children to activities out-of-doors and to a community of east coast intellectuals who also retreated to Maine for summer. Stebbins had early fallen under the influence of naturalists like Edgar T. Wherry, the noted expert on ferns. As a result of these favorable circumstances, Ledyard (as he preferred to be called), drew the attention of noted experts on the New England flora like Merritt Lyndon Fernald, while still an undergraduate at Harvard University. It was with Fernald's encouragement and support that he embarked on a career in systematics and the taxonomy of the New England flora. All of his early papers in floristics were thus published in *Rhodora*, the journal that Fernald edited (see for example Stebbins, 1929a, b, c, 1930a, b, 1932a).

From approximately 1926–1929, Stebbins worked under the supervision of Fernald on systematic studies of the New England flora. The 1929 paper published in *Rhodora* consisted of extensions to the former Rand and Redfield flora of Mt. Desert Island, Maine, which Stebbins had purchased as a field guide to use during his summers at Seal Harbor. The extensions described by Stebbins were based on collections that Edward L. Rand had made and deposited with the New England Botanical Club but that had not been included in the Rand and Redfield flora. Using Rand's notes, and his own considerable knowledge of Mt. Desert Island, Stebbins examined some 7,000 specimens and reported over 100 listings in the published paper. In addition to publishing a series of shorter taxonomic studies during this interval of time, Stebbins also completed a major taxonomic revision of *Calamogrostis*, a complex member of the Graminae. Revising T. H. Kearney's work on the genus, Stebbins suggested a major reorganization of the genus based on the examination of less variable characters like glumes and spikelets. The work also began what would be a life-long association with grasses.

Stebbins continued his work with *Calamogrostis*, intending to complete a systematic study of the genus for his doctoral research. As he grew acquainted with the newer literature available in systematics that used chromosome morphology as a taxonomic tool that grew out of a course he took at Harvard with the cytologist Edward Charles Jeffrey, he grew quickly apart from Fernald who preferred the conventional methods of herbarium taxonomy and who held a deep dislike for Jeffrey. Switching his allegiance to Jeffrey, who was acquainted with cytological and microscopical techniques, Stebbins engaged in cytological and taxonomic study of a complex genus, *Antennaria,* completing his doctoral research while still maintaining Fernald as committee member. Jeffrey had recommended the work on *Antennaria*, a complex genus within the Compositae known to have species that reproduced sexually and apomictically with some unusual reproductive patterns; those that reproduced sexually contained equal numbers of staminate plants, while those that were apomictic consisted mostly of pistillate flowers. The added bonus with the genus was that it could be collected from around the Boston area.

The thesis, published as two papers in the *Botanical Gazette* (Stebbins, 1932b, c) was entitled "The Cytology of *Antennaria*." Primarily a descriptive account of the cytological and morphological development of the seed, it explored in detail the cellular divisions in the process of megasporogenesis in the ovules, and microsporogenesis in the pollen grains. It also included observations of the phenotypic variation in various habitats of *Antennaria*. It was approved, but not without some difficulties. During the last stages of the work, Stebbins consulted Karl Sax, the new geneticist at the Arnold Arboretum who recommended that Stebbins revise some of his interpretations of chromosome morphology. Drawing the ire of the chair of his committee who disliked the newer genetics, Stebbins amended the dissertation and relied on the intervention of the chair of the department who kept the graduate committee from arguing among themselves (see Smocovitis, 1997, for a full account of the difficulties; see also Smocovitis, 2001). Though the social environment was not supportive of interdisciplinary endeavors, especially in newer areas of research outside the traditional domains of Harvard botanists, it did provide resources in the way of libraries, specimens, laboratories, and research personnel who could provide extensive assistance to an ambitious researcher. Stebbins took advantage of all the opportunities that Harvard offered and crossed to agricultural institutions at Harvard like the Bussey to obtain journals that introduced him to the newer methods in plant genetics and genecology. Reading widely and energetically, organizing and then retaining this information in his head, were talents that he early manifested as a graduate student working on his dissertation. Later in his career, they were to make possible a staggering number and range of review articles.

Though his publication career was off to a good start with the work on *Antennaria*, it was temporarily thwarted after graduation in 1931 when he joined the faculty of Colgate University. The teaching load there was very demanding and Stebbins had the added personal burden of raising his young family (he married in 1930). Nonetheless, Stebbins continued some of his taxonomic studies of *Antennaria*, publishing the report of a new species in *Rhodora* (Stebbins, 1935b) and some floristic studies based on field work in locations such as the Bruce Peninsula in Ontario, Canada (Stebbins, 1935a). He also co-authored his first book with his colleague at Colgate, Clarence Young in the psychology department, entitled *The Human Organism and the World of Life* (Stebbins & Young, 1938). This was an unusual textbook that combined biology with psychology at the introductory freshman level. The book was successful in the late 1930s and 1940s and was adopted by the American armed forces.

By far, however, most of his scientific life between 1931 and 1934 while at Colgate was occupied with his growing interest in genetics, especially plant genetics and systematics and how the methods of genetics could be used to understand phylogenetic processes in plants. His research interests were already veering more heavily to genetics with the friendship of Karl Sax, still at the Arnold Arboretum. He had also begun what became a life-long friendship with Edgar Anderson who shared some of the same interests in genetics, systematics and plant evolution. They had met in 1930 while Anderson was still a fellow at the John Innes Horticultural Institute. Anderson was just about to begin his efforts to detect and measure variation patterns in frequently hybridizing species like in *Iris*. This work culminated with Anderson's pioneering studies on hybridization in plants and his recognizing the phenomenon of introgressive hybridization in the 1940s. Anderson's friendship and intellectual influence on Stebbins manifested themselves later in the 1940s and 1950s as his interests turned more to hybridization and plant evolution.

More immediately influential, however, was A. P. Saunders (known as "Percy" Saunders, of the celebrated Canadian Saunders family of wheat-breeders) at Hamilton College nearby who began a brief, but intense collaboration with Stebbins. Saunders was a keen collector and breeder of peonies. They were good organisms for cytogenetic study because they had few numbers of chromosomes which tended to be large and because the large number of cells in the anthers made the newer cytological squashing techniques easy. Saunders had additionally collected many species native to the old world, had performed countless crosses, and had kept track of hybrids between the various old world forms and crosses with the new world forms beginning in 1916. Many of the hybrids showed chromosomal abnormalities including inversions and translocations that were perfect for cytological investigation.

Stebbins's first paper on the genus *Paeonia* appeared in 1934 in the *American Journal of Botany* and was co-authored with G. C. Hicks (Hicks & Stebbins, 1934). It was primarily a descriptive paper that examined the meiotic behavior of the chromosomes with an eye to determining chromosome behavior such as fragmentation. Though he was the first author in the paper, Hicks had little to do with its writing. As a former student of Jeffrey's he had prepared slides on the *Paeonia* material that Saunders had made available. Hicks was collaborating with Saunders, but had died suddenly, leaving the slides and preparations with him. At the suggestion of both Saunders and Jeffrey, Stebbins had examined the meioitic configuration patterns in this genus, eventually publishing his observations giving Hicks full senior authorship of the paper in 1934.

Though he continued taxonomic and phytogeographic studies into genera like *Lactuca* and *Prenanthes*, the *Paeonia* work signaled the beginning of Stebbins's turn to plant genetics nearly full time. When Stebbins began the *Paeonia* work, he was little more than a conventional taxonomist counting chromosomes or studying their morphology for taxonomic purposes. He published primarily in journals like *Rhodora* and the *Botanical Gazette*. As his experience with cytogenetics increased, however, his interests turned more and more to the larger issues of the underlying genetic mechanisms that could account for the origin, distribution, and relationship of plants like *Paeonia*. Stebbins thus began to affiliate himself more and more with geneticists and began to publish in journals like *Cytologia*, *Genetics* and *Journal of Heredity*.

In moving towards cytogenetic methods in the use of constructing phylogenies and in understanding mechanisms of evolution, Stebbins was following the lead of other biologists at the time. The 1930s as a whole saw the maturation of classical genetics which was understanding the mechanism of Mendelian heredity through model organisms like *Drosophila melanogaster* at the hands of workers like Thomas Hunt Morgan. It was also the critical interval of time that saw the birth of the population genetic models of workers like R. A. Fisher and J. B. S. Haldane in England and Sewall Wright in the United States. Most importantly for botanists, it was the golden age of cytogenetics, that saw the chromosome theory of heredity combined with innovative microscopical and cytological techniques to understand genetics at the chromosomal level. The 1930s saw the pioneering work of cytogeneticists like John Belling, C. D. Darlington, and Barbara McClintock all of whom took advantage of plants to derive understanding of the principles of heredity at the chromosomal level.

Wishing to be informed in what was obviously an important and exciting area of biology, Stebbins and his collaborator Saunders took the important step of attending the famous 1932 meetings of the International Congress of Genetics which was taking place only a short distance away in Ithaca, New York. Together they gave a paper and held a formal exhibit on their recent efforts. Mostly, they attended many of the special sessions that were given by Darlington and Morgan and studied the famous demonstration by Sewall Wright with the adaptive peaks diagram. He met briefly the Berkeley geneticist E. B. Babcock who presented work on the genus *Crepis*. He was excited especially by the work on chromosome abnormalities that Barbara McClintock displayed in maize which he hoped to emulate in his own researches on *Paeonia*. Though some of his work on *Paeonia* did not live up to his expectations, it eventually led to a series of publications culminating with the report of chromosome ring formation in the known North American native *P. brownii* (Stebbins & Ellerton, 1939b). The latter paper was written with Sidney Ellerton, a cytologist from Darlington's laboratory.

As is evident from the sequence of publications, however, the *Paeonia* studies did not appear until well after Stebbins had begun the study of the chromosomes of this genus. The publications were in fact put aside for four or five years as Stebbins shifted his research interests to a more promising genus for cytogenetic and systematic study. The new research project was part of a new position Stebbins accepted as "junior geneticist" to E. B. Babcock, the noted Berkeley geneticist. At the recommendation of Sidney F. Blake, an expert on Compositae with whom he had consulted on his *Antennaria* studies, Stebbins left Colgate in 1935 to take a full-time research position as assistant to Babcock. By the mid-1930s, Babcock had assembled what amounted to a well-organized team of workers to understand the systematics of this complex genus. As one of the leaders of American genetics generally, and agricultural genetics in particular, Babcock had launched the *Crepis* work in the nineteen-teens. The *Crepis* project was an extremely ambitious project to understand the systematics of the genus and its relatives by using the new knowledge and methods gleaned from cytogenetics. In its original intent, the project was designed to rival the research program established by Morgan and his fly-group; it was to be the "planty" equivalent of *Drosophila*. By the mid-1930s, the *Crepis* project was at its peak activity with a number of research assistants, technicians, and graduate students in Babcock's group.

Stebbins's next set of major publications reflected his growing importance in the *Crepis* project. Originally assigned to perform routine chromosome counts on some of the nearest relatives of *Crepis* in the tribe Cichorieae, his interest rapidly shifted to Babcock's own project on the New World species which appeared to demonstrate polyploidy, apomixis and hybridization in ways reminiscent of *Antennaria* and *Paeonia*. In 1937 Stebbins published his first major monograph titled "The Genus *Youngia*" with the Carnegie Institution of Washington. But by far, the major publication of what became a six-year collaboration with Babcock on *Crepis* appeared in 1938 as a monograph "The American species of *Crepis*: Their interrelationships and distribution as affected by polyploidy and apomixis." This monograph laid the foundation for understanding polyploid complexes and the role of apomixis in the formation of some them. For this reason, they first termed the American species of *Crepis* an agamic complex. They recognized that certain plant genera consisted of a complex of reproductive forms that centered on sexual diploids and that had given rise to polyploids; sometimes as in *Crepis*, these were apomictic polyploids. Polyploids that combined the genetic patrimony of two species usually had the wider distribution pattern. Babcock and Stebbins's articulation of the polyploid complex, and their elucidation of its existence in the American species of *Crepis* was considered pathbreaking work at the time. Not only did it demonstrate the complex interplay of apomixis, polyploidy, and hybridization in a geographic context, but it also offered insights into species formation, polymorphy in apomictic forms and knowledge of how all these complex processes could inform an accurate phylogenetic history of this genus in particular and other similar genera in general. Reviewing the 1938 monograph, the distinguished Swedish botanist Åke Gustafsson described it as "the most important work on the formation of species" published in the modern period and described their conclusions regarding the phylogeny of the genus as "bold" (Gustafsson, 1947, p. 6). Genetic evolutionary processes responsible for evolution in this genus were later compared to general insights in evolution in an article that appeared in 1942 in *American Naturalist* with coauthors Babcock and James Jenkins (a *Crepis* genetics coworker) as "Genetic Evolutionary Processes in *Crepis*" (Babcock & al., 1942; for the article and introductory comments see Part IV: *General and Plant Evolution*).

His researches into *Crepis* were vital to Stebbins's career; many of the insights first articulated with the *Crepis* work were extended in subsequent work over the next decades of his life. His ideas on polyploidy and apomixis were extended in papers he wrote in 1940 and 1941 (Stebbins, 1940a, 1941c). Especially notable for its synthetic overview of the subject was his 1947 paper, "Types of polyploids: their classification and significance" (Stebbins, 1947b). It subsequently became a classic review article read widely by workers interested in plant evolution and constituted what is probably one of his most important contributions to the understanding of plant evolution (for the paper and additional comments, see Part III: *Chromosomes and Polyploidy*). His interest in polyploidy and chromosome biology culminated in 1971 with the publication of *Chromosomal Evolution in Higher Plants* (Stebbins, 1971i). An earlier notable article assessing chromosomal evolution appeared in *Science* in 1966, and as late as 1980, Stebbins was still assessing the importance of polyploidy in plants in the widely read reference book on polyploidy edited by Walter Lewis (Stebbins, 1966a, 1980d; both are included in this volume in Part III).

Hybridization, its occurrence and its evolutionary significance, also continued to occupy his interest throughout the 1940s and especially the 1950s. Some of his publications exploring hybridization grew directly out of his later research program on breeding forage grasses (Stebbins, 1957f; this article is included in this volume in Part II: *Hybridization*; for a complete list of the grass work see the list of references beginning with Stebbins & Love, 1941a). Another notable publication on hybridization as an evolutionary stimulus was a widely read article that he wrote with his close friend and coworker Edgar Anderson in 1954 in the journal *Evolution*. Using examples from both artificial and naturally occurring hybridization, they argued that it could accelerate evolution appreciably (Anderson & Stebbins, 1954c; see the article and introductory comments in Part II: *Hybridization*). Some of his insights into hybridization and its role in evolutionary processes in plants were synthesized in a major review article that appeared in a volume specially designated to celebrate the centenary of the publication of Darwin's *Origin* (Stebbins, 1959a; see article in this volume in Part II: *Hybridization*).

Equally important as determining the trajectory of Stebbins's research program, the *Crepis* work also established Stebbins as an authority in plant evolutionary genetics in a relatively short period of time. Babcock was so impressed with Stebbins's energy, industry and contributions to the project that in 1939, he was instrumental in assisting Stebbins to secure for himself an assistant professorship in the genetics division at the University of California, Berkeley. This appointment was especially opportune: although his work on *Crepis* was motivated by concerns in the systematics of the genus, his work was increasingly removed from the concerns of classical taxonomists, many of whom were rejecting the methods associated with the "new systematics" and with the application of tools and insights from genetics and ecology (see Smocovitis, in manuscript, for discussion of this). In 1937 Stebbins had been passed over as the replacement for Willis Linn Jepson in the Berkeley botany department and Lincoln Constance was hired instead. Although he continued to make himself at home in the botany department, Stebbins's interests were squarely within genetics; his colleagues in the botany department did not feel he was sufficiently focused on the curatorial and taxonomic work that the position demanded. The vacancy of a position in genetics that required the candidate to teach the general course of evolution was opportune for Stebbins, whose areas of interest shifted towards the new, exciting areas of evolutionary study. The new movements in evolutionary study were synthesizing Darwinian selection theory with some of the newer insights emerging from Mendelian genetics. In preparation for the course Stebbins read voraciously from the new literature in evolution that was emerging with an eye to selecting readings that would be helpful to his course taught out of the College of Agriculture at Berkeley. His growing interest in general evolution was fueled by two additional factors: his interactions with a unique group of biologists in the San Francisco Bay area called "The Biosystematists," all of whom were concerned with new evolutionary approaches to systematics, and his special friendship with the Russian émigré evolutionist, Theodosius Dobzhansky.

Beginning in the mid-1930s, the San Francisco Bay area had become a hotbed for evolutionary studies (Hagen, 1984). A new generation of systematists who incorporated insights from genetics and ecology had taken root in the Bay area at institutions like Stanford University, the Carnegie Institution at Stanford University, the California Academy of Sciences, and at the University of California, Berkeley. Unlike biologists at older institutions like Harvard who were divided by their fields, institutions and personalities, biologists at newer institutions on the west coast actively collaborated with each other. As the institutions grew, so too did the number of younger workers; many of them were also drawn to the California flora, which revealed a stunning range of variation patterns, and offered an ideal natural environment for the study of plant evolution. A group of these mostly younger workers organized in the mid-1930s into an informal organization known as the "Biosystematists" which met informally at alternative locations every month to share in the new methods that were characterizing what was coming to be called "the new systematics" (Huxley, 1940). Stebbins was a prominent member from the start, organizing lectures and inviting speakers like Edgar Anderson and Carl Epling from the University of California, at Los Angeles. Also important was the interdisciplinary team at Stanford's Carnegie Institution that included the Danish genecologist Jens Clausen, the taxonomist, David Keck, and the physiologist William Hiesey. By the mid-1930s, the team was engaged in a series of long-term systematic studies that incorporated knowledge of genetics, ecology, and taxonomy to understand patterns of evolution in plants, initially to distinguish environmental from genetic facts in plant evolution. In particular, they studied patterns of variation of plants as they adapted along steep altitudes in the Californian landscape. Stebbins followed their work closely and visited the team in their experimental sites all throughout the 1940s.

The second major intellectual push towards pursuing general evolutionary studies came as a result of Stebbins's growing friendship with Dobzhansky. Stebbins had met Dobzhansky on a visit to the California Institute of Technology early in the spring of 1936. Dobzhansky at the time was turning to the study of the genetics of natural populations in *Drosophila pseudoobscura*. Stebbins had the opportunity to get to know Dobzhansky further when the latter visited his friend the poultry geneticist I. Michael Lerner at Berkeley. The growing friendship with Dobzhansky proved critical to Stebbins as his own interests were shifting more and more to evolutionary genetics, aided by the demands placed on him to teach the course in evolution. Dobzhansky, who published his own pathbreaking synthesis of evolutionary genetics in 1937 titled *Genetics and the Origin of Species* encouraged those interests and in turn also gave him insights into animal evolution. In the 1940s, Stebbins and Dobzhansky frequently interacted as they visited common field sites like those at the Carnegie Institution's site at Mather. Both were avid horseback riders and collected hybrids while on horseback.

All of these interactions fueled Stebbins's interest in general evolution and from the early 1940s on, his publication career tended to show a bifurcation in general categories of publications. In addition to publishing narrower articles based on his original research, he increasingly began to write large scale synthetic or review pieces not just on plant evolution, but also general evolutionary studies. Although his original research efforts continued to be fruitful, spawning a range of projects into areas like understanding applied aspects of the genetics and breeding of grasses like *Bromus*, *Dactylis*, *Sitanion*, and *Elymus* (see Stebbins, 1957f as an example of this work; reprinted in this volume in Part II: *Hybridization*), his claim to fame increasingly after the mid-1940s was as the spokesman for synthesizing the broad range of literature in plant evolution that was accumulating and in a way that made it compatible with understanding mechanisms of evolution in other organisms. By the mid-1940s his knowledge of general mechanisms of evolution was far broader than many of his contemporaries not just in botany, but also in zoology (see as an example Stebbins, 1959e). In 1945, for example, he engaged in a small controversy with zoologist Ernst Mayr over a monograph published by Theodosius Dobzhansky and Carl Epling which studied rates and patterns of evolution in natural populations of *Drosophila pseudoobscura*. Writing a spirited defense of Epling in particular who had been criticized by Mayr, Stebbins demonstrated a thorough familiarity with not only plant evolution, but also the *Drosophila* research program made famous by Dobzhansky (Stebbins, 1945d).

Stebbins's mastery of the general evolution literature and how plant evolution fit into this wider body of literature did not escape Dobzhansky. At his recommendation, Stebbins was invited by L. C. Dunn to deliver the prestigious set of lectures known as the Morris K. Jesup Lectures at Columbia University in 1945. Part of the contract with Columbia was the publication of the lectures as part of the book series known as the Columbia Biological Series, which had included Dobzhansky's *Genetics and the Origin of Species*. One reason Stebbins had been selected, was the need for a comprehensive synthesis of plant evolution. His friend Edgar Anderson had delivered the Jesup Lectures with the zoologist Ernst Mayr in 1941, but while Mayr published his lectures as what became a famous synthesis of animal systematics titled *Systematics and the Origin of Species. The Viewpoint of a Zoologist* in 1942, Anderson did not complete the writing of his lectures in manuscript form to provide the much needed viewpoint of the botanist (Kleinman, 1999).