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INVITED SPECIAL PAPER

G. Ledyard Stebbins, Jr. and the evolutionary synthesis (1924–1950)[1]

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This is an historical paper examining the scientific background of George Ledyard Stebbins, Jr. (b. 1906), one of the foremost botanists of this century and one of the architects of the evolutionary synthesis, the intellectual event that brought together genetics and selection theory in the interval between 1920 and 1950. It considers his scientific influence and research, beginning with his Harvard education in 1924 and ending in 1950 with the publication of his book *Variation and Evolution in Plants.* The paper also more broadly assesses the contributions of other botanists to the evolutionary synthesis, including discussion of the work of Edgar Anderson (1897–1967) and others. It also traces the larger historical patterns of American botany, which saw a shift from East Coast botany as exemplified by Harvard botany, to West Coast botany, as exemplified by California botany.

Key words: Anderson, Edgar; California botany; Dobzhansky, Theodosius; evolutionary synthesis; Harvard botany; history of botany; Stebbins, G. Ledyard, Jr.; *Variation and Evolution in Plants.*

George Ledyard Stebbins, Jr. is one of the foremost botanists of the 20th century. He is known for his contributions to plant evolutionary biology and genetics, but especially for his book *Variation and Evolution in Plants,* a synthetic work that brought disparate knowledge from ecology, genetics, systematics, biogeography, and evolution to bear on understanding of plant evolution (Solbrig et al., 1979; Fig. 1). Its publication in 1950 won him recognition in company with Theodosius Dobzhansky, Ernst Mayr, and George Gaylord Simpson as one of the architects of the evolutionary synthesis of the 1930s and 1940s. This synthesis was an event of ''first-order magnitude'' in the history of the biological sciences (Mayr and Provine, 1980). Arising in the years between 1920 and 1950, it brought together research in systematics, paleontology, genetics, and cytology, reconciling the opposing views of laboratory-oriented geneticists and naturalist-systematists within a common evolutionary framework (Provine, 1971; Mayr and Provine, 1980; Mayr, 1982, 1993). The ''modern synthesis,'' as Julian Huxley termed it in 1942, made Darwin's theory of evolution by means of natural selection the centerpiece of evolutionary studies. From that point on, the ''evolutionary synthesis,'' and the new discipline of ''evolutionary biology,'' became an increasingly unifying influence in the biological sciences (Smocovitis, 1996).

In this article, I examine Stebbins's background in the critical period leading to the publication of *Variation and Evolution in Plants.* I chart the development of his ideas and researches from his studies at Harvard University beginning in 1924 until 1931 to the publication of his magnum opus and endeavor to assess Stebbins's role as the principal botanical architect of the evolutonary synthesis, but also, more broadly, the part played by botanists in that epochal historical event.

GEORGE LEDYARD STEBBINS, JR.: EARLY SCIENTIFIC BACKGROUND

George Ledyard Stebbins, Jr. entered Harvard University in 1924, at the age of 18 (he was born on January 6, 1906 in Lawrence, New York), having come from a wealthy New York family, keen on natural history (Fig. 2). His father, a businessman and lawyer, had been instrumental in launching the conservation movement resulting in Acadia National Park on Mt. Desert Island, Maine. Although Stebbins was an avid naturalist who had grown up botanizing, horse-back riding, and mountain-climbing (his very early influences included the fern expert Edgar T. Wherry [1885–1982]), he chose to major in political science at Harvard with the ultimate goal of seeking a law career. His major shifted in his junior year following exposure to the charismatic teacher of botany, Merritt Lyndon Fernald (1873–1950), then preparing the eighth or centennial edition of Gray's *Manual of Botany.* Taking Fernald's ''Botany 7'' course, ''The Flora of New England and the Maritime Provinces of Canada,'' Stebbins accompanied Fernald on field trips to nearby areas, impressing his teacher with his knowledge of the New England flora. Stebbins emulated Fernald, who initially served as something of a hero to him, and studied floristics. He quickly fell under the influence of Fernald's controversial ''nunatak theory'' (a biogeographic theory

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Fig. 1. George Ledyard Stebbins, Jr. Smithsonian photograph by Dane A. Penland, 1982. Negative number: 82-704-18A.

based on the distribution of glacial relicts), which presaged his life-long interest in phytogeography.

Shortly thereafter, in 1928, Stebbins entered the Harvard graduate program to study botany (Fig. 3). From approximately 1926 until 1929, Stebbins worked closely with Fernald on the taxonomy of the New England flora. A fellow classmate, John Fogg wrote the following reminiscence describing Fernald's strong influence, and proximity, to his students:

> *Stebbins and I occupied adjoining tables in the New England Botanical Club wing, and as Fernald in his resonant tones read portions of his manuscript to each new visitor, we came to know sections of the work almost by ear. Indeed, so familiar were we with the text that when Fernald was interrupted or halted for breath, Stebbins and I would continue to intone, verbatim, the ensuing sentences and paragraphs.*
>
> —Fogg (1951, p. 42)

Stebbins's first paper ''Further additions to the Mt. Desert Island Flora,'' and his second paper, ''A Revision of Some North American Species of *Calamagrostis*'' were published in *Rhodora,* the journal edited by Fernald.

The relationship with Fernald cooled, however, as Stebbins became interested in newer taxonomic methods, which involved detailed study of chromosome morphology and which were unpopular with Fernald. Stebbins's interest in chromosomes and the use of chromosomes in taxonomic study resulted in a falling out with Fernald, whose systematics remained fundamentally conservative until his death in 1950. Fernald was especially displeased that his student sought the company of the controversial cytologist Edward Charles Jeffrey (1866–1952). Jeffrey had such dogmatic preferences, and had engaged in so many altercations with colleagues, that he had even drawn the attention of President Charles Eliot. He was referred to as the ''stormy petrel of botany'' by botanist Oakes Ames in *Jottings of a Harvard Botanist 1874–1950* (Ames, 1979, p. 78).

Working with chromosomes as systematic tools seemed an intellectual imperative to Stebbins, who switched his allegiance to Jeffrey, in so doing incurring some opprobrium from Fernald. With Fernald agreeing to serve on the committee, but with Jeffrey serving as the chair, Stebbins undertook his doctoral research on the cytology of *Antennaria.* This genus was especially suitable for study because it bore several apomictic species. It was also easy to collect in nearby locations. In addition to studying the cytological and morphological development of the seed in *Antennaria* (Stebbins explored in detail the processes of megasporogenesis in the ovules and microsporogenesis in the pollen grains), he also took advantage of easy collecting to examine geographic variation in the genus.

With the completion of the project near, Stebbins took his thesis to the new geneticist at the Arnold Arboretum, Karl Sax (1892–1973). Sax promptly found a serious error in the work: the slides that Stebbins had thought indicated pairs of heteromorphic sex chromosomes were, according to Sax, two similar chromosomes one in side view and the other in end view. Jeffrey's resistance to newer microscopical techniques (he did not use a binocular microscope) had nearly led to a fatal error of interpretation. In addition to correcting this interpretation in the thesis, Sax requested that Stebbins remove disapproving remarks in the text on the work of controversial cytogeneticist Cyril Dean Darlington (1903–1981), remarks that Stebbins had ''parroted'' from Jeffrey. No friend to genetics and geneticists, Jeffrey hated Darlington and berated his theoretical work (see Smocovitis [1988] for full discussion of Jeffrey and modern genetics). Sax's suggestions for revision were viewed as unacceptable by Jeffrey, who refused to sign the amended thesis. For support in mediating the conflict, Stebbins turned to developmental morphologist Ralph Wetmore (1892–1989), for whom he had served as teaching assistant. Largely through Wetmore's intervention with Ames, then chair of the factious department, Jeffrey agreed to sign the amended thesis, but was so angry that ''for two days, Jeffrey wouldn't speak to anybody'' (Stebbins, 1986, p. 17). Despite Jeffrey's refusal to serve as Chair of the committee at the very last stage, and Fernald's deciding that he was not interested in cytology, Stebbins obtained their required signatures in time to receive the Ph.D. from Harvard University in 1931. The next year,

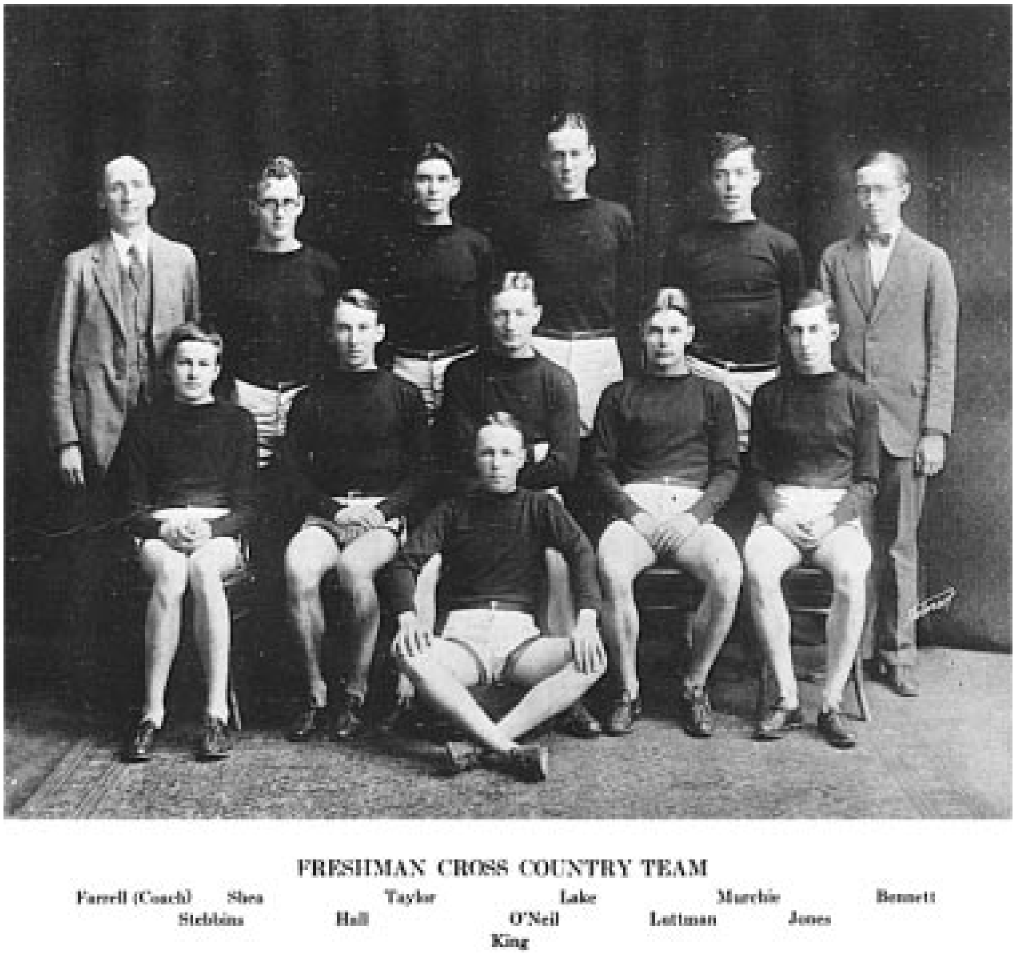
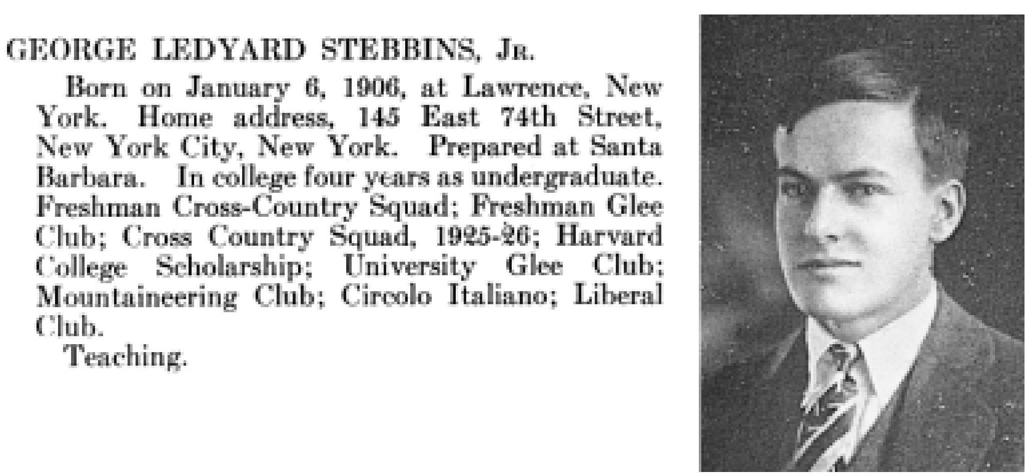


Fig. 2. Harvard Yearbook of 1923–1925. Photograph of the freshman cross-country team. G. Ledyard Stebbins, Jr. is in the front row, seated on the far left. Reproduced with permission from the University Archives at Harvard University.

his research on the cytology of *Antennaria* appeared in the *Botanical Gazette* as two separate papers.

The completed dissertation, heavily amended, with numerous deletions and additions pasted into the typewritten pages, still stands as proof of the dissonance that divided Harvard botany—and its botanists—in the 1920s and the 1930s (Fig. 4). So notorious were the feuds among Harvard botanists, that by the 1930s the very President of the university, A. Laurence Lowell, was rumored to have said: ''What is it about pretty little flowers

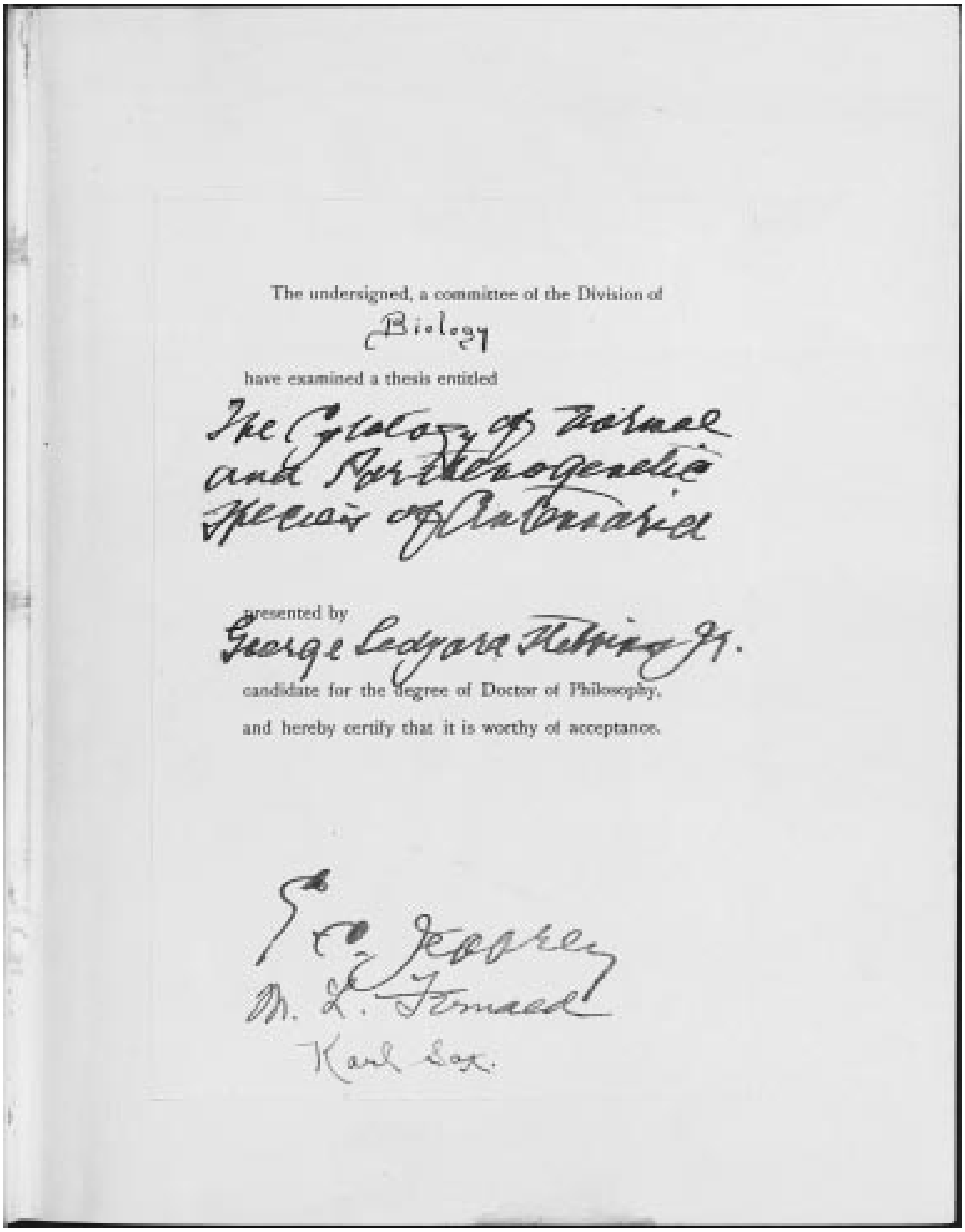


GEORGE LEDYARD STEBBINS, JR.

Born on January 6, 1906, at Lawrence, New York. Home address, 145 East 74th Street, New York City, New York. Prepared at Santa Barbara. In college four years as undergraduate. Freshman Cross-Country Squad; Freshman Glee Club; Cross Country Squad, 1925-26; Harvard College Scholarship; University Glee Club; Mountaineering Club; Circolo Italiano; Liberal Club.

Teaching.

Fig. 3. The Harvard graduate, class of 1928. Reproduced with permission from the University Archives at Harvard University.



The undersigned, a committee of the Division of

Biology

have examined a thesis entitled

presented by

George Ledyard Stebbins Jr.

candidate for the degree of Doctor of Philosophy,

and hereby certify that it is worthy of acceptance.

Karl Sax.

Fig. 4. Signature page of George Ledyard Stebbins's Ph.D. dissertation dated 1931 at Harvard University. Reproduced with permission from the University Archives at Harvard University.

that makes the botanists hate each other so?'' The troubles of the department of botany clearly played themselves out in the education of the graduate students, and for the most part had negative consequences on graduate education, especially with respect to encouraging cross-disciplinary work (Hall, 1990). Yet, extraordinarily enough, Stebbins was one of the few to make the most from this same environment. Reading widely—and in fact voraciously—Stebbins made his way to the nearby Bussey Institution, which housed journals like *Hereditas.* The Bussey was located in Jamaica Plain, Massachusetts and devoted itself to applied branches of biology like agricultural genetics. Although it was a Harvard affiliate, it was also an independent institution far away from most of the other biological institutions at Harvard. Despite the physical and intellectual distance, Stebbins took advantage of available resources at the Bussey. He sought out quantitative agricultural geneticist Edward Murray East (1879–1938), but the two managed only the briefest of interactions. Stebbins, did, however, take a full course with the noted geneticist William Ernest Castle (1867–1962), but the emphasis on mammalian systems was not as immediately helpful to him. Thus, despite the personal, institutional, and scientific divisions that he encountered, Stebbins made the most out of the opportunities offered at Harvard. Most important, the Harvard environment had selected for an independent, resourceful, and strong-willed individual, whose research, even as a fledgling low in the scientific and administrative hierarchy, could not be stopped by personalities, administrative hurdles, or even rifts between botanical fields.

THE GENETICAL TURN, 1931–1935

In the next four years following graduate work, Stebbins pursued his interest in cytogenetics as well as continuing taxonomic and field studies of *Antennaria*. Obtaining a position at Colgate University, which demanded heavy teaching, Stebbins worked in his spare time on a tractable and easily obtainable organism, *Paeonia*. With the assistance of plant breeder Arthur Percy Saunders (1869–1953) at nearby Hamilton College, Stebbins obtained numerous backyard varieties of peonies, most of which were hybrids that Saunders had carefully created and whose detailed genealogy Saunders had tracked. For Stebbins, the numerous hybrids involving both Old World and New World forms proved to be nearly perfect for study of plant evolution using a combination of cytogenetic methods. In the first of the formal *Paeonia* publications in 1934 he wrote:

> *. . .the original aim—that of studying the meiotic behavior of the entire series of species and hybrids, and thereby correlating cytological, genetic, and taxonomic evidence of the relationships between species in order to determine the course, and so far as possible, the mechanism of evolution within the genus—is still in view.*
>
> —Hicks and Stebbins (1934, p. 228)

Other influences continued to reinforce his growing interest in the genetics of the evolutionary process. Continuing his relationship with geneticist Sax, Stebbins studied closely the work of Darlington, John Belling (1866–1933), and C. Leonard Huskins (b.1897). He also continued correspondence with a new friend, Edgar Anderson (1897–1967), whom he had met at the International Botanical Congress in Cambridge, England in 1930. Anderson was then on leave from the Missouri Botanical Garden on a Research Council Fellowship at the John Innes Horticultural Institution and at Rothamstead Experimental Station, and engaged in his own critically important study on the variation of *Iris*.

In 1932, Stebbins was introduced to even newer developments in genetics when he attended the Sixth International Congress of Genetics in nearby Ithaca, New York. Historians now recognize these meetings as a landmark in the history of both genetics and evolution as they were the first indication that a synthesis was beginning to take place between Darwin's selection theory and the newer science of genetics (Provine, 1986). Even though the meetings were intended for geneticists, no less that five of the 18 morning (the major) sessions were devoted to evolutionary themes. Most of the representatives who played an active role in the history of genetics and evolution gave important papers. Among these were: Thomas Hunt Morgan (1866–1945), R. A. Fisher (1890–1962), Richard B. Goldschmidt (1878–1958), J. B. S. Haldane (1892–1964), and Nikolai Ivanovich Vavilov (1887–1942). These were the meetings in which Sewall Wright (1889–1988) presented his ''adaptive peaks'' diagrams that represented his shifting balance theory of evolution, and that drew the attention of his future collaborator, Theodosius Dobzhansky (1900–1975) (Provine, 1986). These were also the meetings where Barbara McClintock (1902–1992) presented her cytological studies of maize. Using the squashing technique, McClintock revealed the linear pairing of parental chromosomes at mid-prophase or pachytene. The paired chromosomes showed the effects of crossing over, and in particular they showed the effects of inversions and translocations and their characteristic configurations.

Although he presented a summary of his work on *Paeonia* with Percy Saunders, and exhibited new hybrids of *Paeonia* at the floricultural exhibit, Stebbins contributed little of historical importance to the conference. He did, however, receive a great deal of inspiration as well as information from other contributors. He noticed Wright's posters and recognized the importance of the adaptive peaks, but was baffled by the details of what they represented, and by the mathematics that he could not decipher. He attended notable panel discussions, one of which discussed the controversies over the chiasmatype theory and pitted two rivals, Darlington and Sax. He also attended the presidential address by Thomas Hunt Morgan, which he later recalled as a landmark in the history of genetics for its insightful directives for future research, and was excited by John Belling's exhibit demonstrating clearly chromomeres, parts of which Belling had mistakenly interpreted as being the genes. But the most exciting work was revealed to him by McClintock, whose work on maize led him to recognize similar chromosomal configurations in *Paeonia*.

Returning to his work quickly with McClintock's chromosomal configurations in mind, Stebbins published a series of papers on the cytogenetics of *Paeonia*, demonstrating ring formation in one of the known native North American species, *P. brownii*. The studies in *Paeonia* turned out to be hardly of the ground-breaking sort that he saw presented in Ithaca, but they were important contributions to genetics, validating arguments presented by cytogeneticists like Belling and McClintock. Equally as important as their scientific merit, the studies also served to convert Stebbins into a full-blown geneticist. While still preserving a naturalist's sensibility and the taxonomist's aims and utilitarian philosophy, Stebbins had also assimilated the geneticist's rigor and experimental methods. All these were brought to bear in his increasing interest in evolution, which began to occupy the center stage of his research during the interval of time between 1935 to the publication of *Variation and Evolution in Plants* in 1950.

THE EARLY CALIFORNIA PERIOD (1935–1939)

One of the most important turns in Stebbins's intellectual development, was his decision to move to the West Coast of the United States. In a relatively short period of time following his arrival there in 1935, his work shifted toward the evolutionary study of plants, combining approaches that he had already assimilated from systematics, cytogenetics, and biogeography. The turn towards full-blown evolutionary study of plants was due to three things: his work on the genus *Crepis* and its relatives; his exposure to like-minded evolutionists in the San Francisco Bay area; and the geographic variation patterns, and other advantages, that the California flora offered.

The move to the West Coast came as the result of strong recommendations by the Washington-based expert on the Compositae, Sidney F. Blake (1892–1959), who recommended him to geneticist Ernest Brown Babcock (1877–1954) at the University of California, Berkeley. Babcock, a pioneer in plant breeding (he created the 'Babcock' peach), required a junior research associate in genetics for his new project funded by a Rockefeller Foundation grant. The project in question was a detailed yet comprehensive taxonomic study of the genus *Crepis* and some of its relatives using knowledge and methods gleaned from cytogenetics. The genus *Crepis* had drawn Babcock's attention largely through the efforts of Russian geneticist Michael Navashin (1857–1930), who thought it would make a splendid ''planty'' equivalent to *Drosophila.* Although the position was only that of a research assistant to the project, and only offered a modest salary, Stebbins jumped at the opportunity of engaging in research full-time. He joined the genetics department at Berkeley in 1935 with the immediate task of performing chromosome counts on some of the nearest relatives of *Crepis* in the tribe Cichorieae. His interest soon shifted to Babcock's own project on New World species of *Crepis,* which appeared to resemble *Antennaria* and *Paeonia* in demonstrating the complex interplay of polyploidy, apomixis, and hybridization. With Babcock's blessings, Stebbins divided his research time between his own work on the relatives of *Crepis,* and Babcock's work on the New World species, beginning in the spring of 1936.

Although *Crepis* failed to live up to the expectations of being the perfect model organism for genetical study (the generation times were too long, and the plant had considerable space requirements), the work on the genus was nonetheless critically important, especially for evolutionary study. In the course of their six-year comprehensive study of the genus and its relatives, Babcock and Stebbins published a series of important articles and monographs, the most significant of which was published cojointly in 1938 as *The American species of Crepis: their interrelationships and distribution as affected by polyploidy and apomixis.* Articulating the notion of an ''agamic complex'' (or what came to be known as the polyploid complex), a complex of reproductive forms centering on sexual diploids surrounded by apomictic polyploids, the monograph was the most complete analysis of the interplay of polyploidy and apomixis with geographical considerations in any genus. Reviewing this work, the Swedish botanist Åke Gustafsson (b.1908) wrote: ''The most important work on the formation of species that has seen the light of day during this period was published by Babcock and Stebbins (1938). Although their conclusions respecting the phylogeny of the *Crepis* genus are rather bold, they present here the first modern treatment of an >>agamic complex>> and, with this as a starting point, discuss species formation and polymorphy in apomicts in general'' (Gustafsson, 1947, p. 6).

While Babcock continued his work on the genus well into the 1940s, publishing his monumental, comprehensive study *The Genus Crepis,* parts I and II in 1947, Stebbins's own interests were appreciably widening by the late 1930s. One reason for this was increasing freedom to pursue his own scientific problems. Assisted by Babcock's support (the result of Babcock being favorably impressed with Stebbins's industry), his position was changed to that of an assistant professor in the genetics department in 1939. By the end of the collaboration with Babcock, Stebbins had secured for himself a position as geneticist at Berkeley, at the same time that he began to establish himself as a formidable presence in systematics and cytogenetics. At this time too, the opportunity of teaching the undergraduate course in evolution presented itself. Viewing it as the chance to immerse himself in the recent literature on evolution, Stebbins used the course to familiarize himself with the latest insights into the evolutionary process.

His growing interest in evolution was also encouraged and informed by the growing number of biologists interested in evolution and the ''new'' systematics beginning to make its way to the San Francisco Bay area. Unlike the biologists at Harvard who were divided by their fields, institutions, and personalities, biologists at newer institutions like Berkeley cotaught courses, actively collaborated on their research, and consulted one another in both formal and informal contexts (although some noteworthy personal animosities between botanists had arisen at Berkeley; see Constance [1978] for note of the William Albert Setchell and Willis Linn Jepson rift). Botanists at Berkeley, for instance, were closely tied to geneticists, as a result of the botany department's inclusion into the College of Agriculture in the 1930s. The proximity of Stanford University, the Stanford-based Carnegie Institution of Washington, and the California Academy of Sciences also created a critical mass of a diverse group of colleagues, and the fact that the institutions were actively hiring and building in the interwar period brought younger, energetic researchers into the area. The growing numbers of plant geneticists and evolutionists were also drawn to the California flora, which revealed a stunning range of variation patterns, and offered the perfect natural environment for critical study of plant evolution.

The most important of these groups with a focus on efforts to understand mechanisms of plant evolution was the Stanford-based Carnegie Institution of Washington. Beginning in 1918–1919 through the pioneering efforts of Berkeley taxonomist Harvey Monroe Hall (1874–1932), in collaboration with Carnegie-based ecologist Frederic Clements (1874–1945), the Carnegie Institution began to mount a large-scale project to understand plant evolution from a cross-disciplinary study involving ecological parameters along California's varied altitudinal gradients. By the late 1920s, the Carnegie Institution under the direction of Hall (he had since split from the collaboration with Clements largely as a result of irreconcilable differences) had established formal experimental gardens at three locations: one at 9.2 m (30 feet) at Stanford, one at 1373 m (4500 feet) at Mather, and a subalpine Station at Timberline, at 3050 m (10000 feet). The goal had been to draw on the work of European genecologists like the German Anton Kerner von Mari-

Fig. 5. The Biosystematists in the Bay area circle. Group photograph taken at Placerville Forest Genetics Station in May, 1946. Standing: H. E. McMinn (Mills), G. F. Ferris (Stanford), E. G. Linsley (Berkeley), H. Graham (Mills), L. Adams (Stanford), C. Y. Chang (unknown), E. B. Babcock (Berkeley), W. E. Castle (ex-Harvard), R. H. Weidman (station), R. Goldschmidt (Berkeley), G. S. Meyers (Stanford). Kneeling: R. C. Miller (California Academy of Sciences), G. L. Stebbins (Berkeley), C. O. Sauer (Berkeley), H. L. Mason (Berkeley), I. L. Wiggins (Stanford), L. Constance (Berkeley), N. Mirov (station), P. Stockwell (station), W. Cummings (station), and H. Kirby (Berkeley). The members of the Carnegie Institution of Washington group, J. Clausen, D. D. Keck, and W. Hiesey, were not present at that meeting. Photograph courtesy of Lincoln Constance.

laun (1831–1898), the Frenchman Gaston Bonnier (1853–1922), and more recently by Göte Turesson (1892–1970) in Sweden and William Bertram Turrill (1890–1961) in England, all of whom performed transplant experiments along altitudinal gradients or used different soil conditions to gauge genotypic and phenotypic variation in designated plant species. In 1932 Hall died unexpectedly and was replaced by the Danish geneticist Jens Clausen (1891–1969) as leader of the team; the remainder of Hall's interdisciplinary team included the taxonomist David Keck (1903–1995) and the physiologist William Hiesey (b. 1903). Together, the Carnegie team of Clausen, Keck, and Hiesey launched the first large-scale interdisciplinary attempt to understand evolution in plants using a combination of approaches that involved ecology, genetics, and systematics (Hagen, 1982, 1984). The team oversaw a series of large-scale experiments through the 1930s and the 1940s, publishing a series of monographs through the Carnegie Institution, culminating with the publication in 1951 of Jens Clausen's Messenger Lectures at Cornell University as *Stages in the Evolution of Plant Species.*

The San Francisco Bay area had thus seen a considerable growth of interest in what were then regarded as newer and bolder interdisciplinary approaches to the ''new'' systematics (the term was actually suggested to Julian Huxley by Darlington; see Huxley, 1940). One result of the growth of interest in cross-disciplinary understanding of systematics was the creation of an informal society in the Bay area with the name of the ''Biosystematists'' (the term ''biosystematics'' was coined by Wendell H. Camp and Charles L. Gilly in 1943; see Camp and Gilly, 1943; Fig. 5). The organizational push had come from Babcock at Berkeley, who enrolled zoologists in the group, and Clausen at Stanford. Although the exact founding date is uncertain (David Keck wrote that it was founded in 1935 in one source; interviews with Stebbins and Lincoln Constance point to 1937; see Smocovitis, 1994 for fuller discussion of organizational activity in evolutionary studies), the group met informally (and continues to do so) on a monthly basis at alternating Bay-area scientific institutions. At these meetings interested workers (anywhere from 20 or 30 or more individuals) attended a lecture either by one of the Bay-area members, or by a visiting lecturer (these included visitors like Edgar Anderson). Creating a collegial atmosphere where scientific knowledge could flourish, the group shared their latest insights and data on an unusually broad range of organisms from an interdisciplinary perspective with colleagues. They often shared literature and kept informed on the varied new approaches used by biologists.

Since arriving in the Bay area, Stebbins had actively sought like-minded individuals, many of whom shared his interest in combining cytogenetics and systematics in the attempt to understand plant evolution. At Berkeley, he had belonged to the Genetics Associated, a fortnightly journal club that included the young geneticist I. Michael Lerner (1910–1977), a Russian émigré, then beginning graduate work in Poultry Husbandry at Berkeley. He was an active member of the Biosystematists, and in fact assisted Babcock's efforts to help draw in zoologists to the group. He attended the very first meeting of the group in October 1937 at the Carnegie Institution of Washington at Stanford. The first speaker in the series had been David Keck, who gave a lecture on Alfred Wegener's theory of continental drift, then a highly controversial theory. Stebbins quickly made the acquaintance of the Carnegie team, and visited their experimental gardens as often as he could. He was greatly impressed with the comprehensive scope of their project and followed the experimental results closely.

THE EVOLUTIONARY PERIOD 1939–1950

But the most critically important influence on Stebbins at this time was his meeting and subsequent close association with the evolutionist Theodosius Dobzhansky. At the time, Dobzhansky was working in Morgan's new laboratory of genetics at Pasadena's California Institute of Technology. The two met in the spring of 1936 when Stebbins was invited to give a seminar at Cal Tech. He recalls that he met both Dobzhansky and his wife Natasha while they were working on translocations in *Drosophila* (most probably *D. melanogaster*) (Oral History Interviews, 1987). The two met once again on Dobzhansky's frequent visits to the Bay area to visit his close friend, Lerner.

In the mid-1930s, Dobzhansky was actively formulating his synthesis between the newer science of genetics with knowledge of adaptation and biological diversity through his long-distance collaboration with mathematical theorist Wright. A keen naturalist, who was sensitive to the geographic variation and distribution of organisms, Dobzhansky was equally skilled in the laboratory with a broad knowledge of the fly-room cytology and genetics that he had learned from Morgan's ''fly'' group. Choosing to study the inversion frequencies in the giant salivary chromosomes in wild populations of *Drosophila pseudoobscura,* Dobzhansky had been inspired by the mathematical formulations of Wright and his ''shifting-balance'' theory of evolution, which he had first seen visually displayed at the International Congress of Genetics in Ithaca (Provine, 1986). In 1936, at the invitation of Leslie Clarence Dunn (1893–1974), Dobzhansky gave the Morris K. Jesup Lectures at Columbia University, which contained his synthesis of evolutionary theory. While recovering from a fractured knee-cap as a result of a horseback-riding accident that winter, Dobzhansky converted his lectures into a comprehensive text, which was titled *Genetics and the Origin of Species.* It was subsequently published, in a remarkably quick fashion, the summer of 1937. It is now generally regarded as the first such comprehensive text, ushering in the new synthesis of evolution (Provine, 1995). Stebbins had therefore met Dobzhansky at his most active—and critical—stage in formulating his modern synthesis of evolution.

The interactions between Stebbins and Dobzhansky steadily increased with time, especially as Stebbins read the evolutionary literature and followed Dobzhansky's work closely. It was during these interactions that Stebbins grew to appreciate developments in evolutionary theory that included the insights of the ill-fated Russian school of population genetics, as well as the insights of not only Wright, but also R. A. Fisher and J. B. S. Haldane, who were using mathematical models to examine the relative importance of the factors of evolution. He eagerly read Dobzhansky's 1937 book, and closely followed his subsequent work on the genetics of natural populations in *Drosophila pseudoobscura.* During what would become a life-long relationship, Stebbins and Dobzhansky shared numerous collecting trips, many of which were on horseback, at favorite locations like Mather in California. At breakneck speed on their horses, they stooped to collect interesting specimens along the way, which Stebbins termed ''horseback hybrids,'' all the while carrying on animated conversations on evolution (Oral History Interviews, 1987). Their relationship intensified between the years 1944 and 1946 when both were frequent visitors at the Carnegie Institution of Washington at Mather, with Dobzhansky staying at the Carnegie Institution's cabin at the north edge of Yosemite National Park (Fig. 6). Unfortunately, the precise content of these interactions cannot be reconstructed as little or no historical documentation exists.

In the early 1940s their interactions, along with some of their evolutionary activity, were hindered temporarily by Dobzhansky's move to Columbia University, but also by the entry of the United States into the Second World War. While many biologists like the paleontologist George Gaylord Simpson (1902–1984) left for active service, others were forced into wartime-related activities. Stebbins found himself in a project to breed guayule. Although that project contributed little of consequence, his other projects on the breeding of various kinds of forage grasses, begun in the late 1930s and carried over during the war years, continued to enhance his understanding of cytogenetics, especially of polyploidy. This resulted in more publications elaborating the ''polyploid complex,'' the most comprehensive of which appeared in 1947 (Stebbins, 1947). His work on the polyploid complex was to prove one of his major contributions to 20th century botany.

Despite such minor interruptions, Stebbins continued his scientific research largely unhindered. He was active

Fig. 6. G. Ledyard Stebbins, Jr. and Theodosius Dobzhansky at Mather, California. Photograph dated approximately 1965, courtesy G.L.S.

with the Biosystematists, who continued to meet during the war years, playing a greater and greater role in shaping evolutionary activity at the national level. In 1943 they were instrumental in assisting the organization of evolutionary activity by holding a meeting of interested evolutionists on the west coast; at the same time a group of New York-based workers held a similar meeting with the goals of helping to organize a society for the study of evolution. Both groups had been trying to revive an interest in the formal organization of systematics and evolution, which had lain dormant since the Society for the Study of Speciation, founded in the late 1930s, had ceased (see Smocovitis, 1994 for fuller discussion of the organization of evolutionary study). By 1943 the Biosystematists, a significant number of whom were botanists, were assisting the coordination of efforts to organize evolutionary study, working closely with what remained of the Society for the Study of Speciation, and the National Research Council-backed Committee on Common Problems of Genetics, Paleontology, and Systematics. As part of their activity, members of the Committee produced mimeographed bulletins edited by the systematist Ernst Mayr, which were distributed widely to evolutionists in the United States as a way of facilitating information transfer among systematists, paleontologists, and geneticists working on a range of organisms.

In addition to publishing reviews, news, and notices of interest to evolutionists, the bulletins also included letters of exchange concerning critical issues in evolution common to all. Perhaps the most noteworthy inclusion in the bulletins were the numerous exchanges among botanists, which rival if not exceed the contributions by other evolutionists. So noteworthy were these exchanges that from them one quickly surmises that the evolutionary study of plants was generating data that could not be readily reconciled with the understanding of evolution gained from animal systems. The exchanges reveal the extent to which botanists like Babcock, Carl Epling (1894–1968), Ralph Chaney (1890–1971), and Herbert Mason (1896–1994) were actively seeking understanding of plant evolution commensurate with the evolutionary views propounded through animal examples. Active members of the Committee who were botanists and whose names appeared on the mailing list at the back of the bulletins include: Edgar Anderson, E. B. Babcock, Ralph Chaney, Carl Epling, Herbert Mason, and Stebbins. All were west coast botanists located at Berkeley, with the exception of Anderson and Epling, who was located at the University of California, Los Angeles. All were also active participants in meetings of the Biosystematists, which even Epling and Anderson occasionally attended. Out of a total of 29 names listed on the mailing list of the bulletins, seven of them, nearly one-quarter, belonged to California botanists. The importance of the west coast botanists was thus notable in efforts to organize evolutionary study in the 1940s.

Although he was not one of the original signatories to the founding document of what became the international Society for the Study of Evolution (the SSE) at the 1946 St. Louis meetings (Anderson, Babcock, and Epling were some of the notable botanists among the signatories), it is evident that by the mid-1940s, Stebbins had emerged as one of the leading botanical representatives active in the SSE. In 1947 he celebrated with fellow evolutionists from all over the world at the Princeton meetings of the new evolution society. Just one year later, in 1948 he was elected the third President of the society, following the presidencies of Simpson and John T. Patterson, verterbrate paleontologist and *Drosophila* geneticist, respectively. The only other botanist on the executive committee up to that date had been Babcock, who served as one of the three first vice-presidents. It is clear from existing correspondence deposited at the American Philosophical Society that the early leaders of the SSE, like Mayr and Simpson as well as Dobzhansky (who had actually played a significantly smaller role in the organizational side of evolutionary biology), relied heavily on Stebbins for general counsel; possibly this was because of Babcock's advancing age.

As first editor of the journal *Evolution,* Mayr had solicited manuscripts from all relevant branches of evolution and had been careful to include botanical papers, but there were simply not enough suitable manuscripts initially submitted by botanists for inclusion. At least two instances of friction took place between Stebbins and Mayr concerning the paucity of botanical manuscripts making their way to final publication in *Evolution.* In one instance Stebbins heatedly wrote to Mayr: ''Many of us on the plant side are beginning to feel that 'Evolution' is favoring animals too much, and our interest in the journal and society is starting to decline'' (Stebbins to Mayr, April 21, 1949, Ernst Mayr Papers, SSE, Box St.-Z, Library of the American Philosophical Society). Another point of friction was over the unsuitability of a manuscript submitted by Stebbins that had too many half-tone plates for inclusion (Mayr's estimate stands at ~50). Stebbins wrote to Mayr: ''It seemed to me that you were discriminating against the higher plants, except in cases like Verne Grant, where the information was of great interest to zoologists'' (Stebbins to Mayr, October 12, 1950, Ernst Mayr Papers, SSE, Box St.-Z, Library of the American Philosophical Society). The disputed manuscript never appeared in *Evolution,* as it would have probably ''bankrupted'' (in Mayr's terms) the journal, but the exchange did increase pressure to include more botanical manuscripts. More broadly, these exchanges also indicate that by the late 1940s Stebbins had begun to take more of a leadership role in defending the proper inclusion of botany in the new journal for the new discipline of evolutionary biology.

Although Stebbins had emerged as a leader in the new discipline by being an active member and a promoter of his field, what made his leadership possible, and in fact inevitable, was the publication of his magnum opus, *Variation and Evolution in Plants.*

VARIATION AND EVOLUTION IN PLANTS (1950)

It was through his contact with Dobzhansky that the opportunity to draw together all of his knowledge of plant evolution in one comprehensive text arose. In 1945 at the suggestion of Dobzhansky, and with his constant encouragement, Stebbins accepted the invitation from the Board of Regents and Dunn to deliver the Morris K. Jesup Lectures at Columbia University. Stebbins was keen to accept the honor since part of the arrangement involved a contract with Columbia University Press to publish the lectures in book form. His lectures would become part of the Columbia Biological Series, which had included Dobzhansky's book, as well as Mayr's *Systematics and the Origin of Species* (1942) and Simpson's *Tempo and Mode in Evolution* (1944). All had appeared by the time that Stebbins received the invitation so that the series had established itself as being the vehicle for the texts in evolution that were incorporating biological fields into the new synthetic framework on evolution.

The inclusion of a botanical work in the series was critically important, especially as the first attempt to do this had failed miserably. In the proper spirit of synthesis, the Jesup Lectures of 1941 delivered in the spring of that year had been given by Mayr, a zoologist, and by Anderson, a botanist, whose assignment it was to explore the new systematics in both zoology and botany. While Mayr delivered his lectures and quickly produced the required manuscript for Columbia University Press, Anderson delivered his lectures, but failed to complete his portion of the manuscript. Reasons for this are unclear, but there is considerable evidence indicating that Anderson often failed to complete longer projects (see Smocovitis [1988] for further discussion on Anderson). Anderson's failure to produce his half of the lectures worked ultimately to Mayr's advantage as Mayr was invited to double the length of his manuscript. This led to Mayr's 1942 *Systematics and the Origin of Species,* which ushered systematics into the synthesis, and became one of the pivotal works of the period. The botanical counterpart, which would have complemented Mayr's contribution, would have been the perfect opportunity to explore the newer work in plant cytogenetics and systematics, and could have addressed critical differences between animal and plant evolution, thus never appeared. Sadly, the manuscript, and the content, of Anderson's lectures have vanished, leaving his comparative discussion between animal and plant evolution, and the tantalizing differences between the two, largely out of the historical record.

The opportunity for a botanical synthesis was thus overdue by the time that Stebbins received the invitation for his set of lectures. In 1945 he began to compile his notes, graphs, and slides in preparation for the lectures, which he delivered in 1946. By January of 1947 he had begun to convert his lectures into book form, taking approximately one and a half years to finish the project. When it appeared in 1950, it was 643 pages long and included ~1250 citations; this was the longest of all the texts in the Columbia Biological Series.

The synthetic cast of the volume and the fields whose knowledge was brought to synthesis were readily apparent by its organization, which fell into approximately four parts: morphology, biosystematics, cytogenetics, and (paleo-) biogeography. In each of these areas, Stebbins covered an impressive range of the botanical literature that had accumulated. Especially noteworthy was the synthesis of recent perspectives from biosystematics, drawn from Clausen, Keck, and Hiesey, Turesson, and others, and cytogenetics drawn from Darlington, Sax, Huskins, and others. From the work of such biosystematists, Stebbins pointed out that the distinction between phenotypic and genotypic variation in plants could be determined. The work also silenced, once and for all, belief in Lamarckian inheritance, which had long been an obstacle in understanding plant evolution. Biosystematics also contributed to a dynamic population-oriented view of the plant world, one that would make possible more rigorous experimental and statistical approaches. Contributions from cytogenetics had made possible the sorting of the confusing interplay of hybridization, apomixis, and polyploidy, which, through the work of Darlington, had been reconceived as ''genetic systems,'' themselves subject to selection. This was the subject of Chapter V, possibly the most important and original of the chapters.

In its specific formulation of evolutionary theory, the book bore close resemblance to Dobzhansky's own *Genetics and the Origin of Species.* For example, Stebbins stressed natural selection acting at the level of individual differences, even though he left enough room for nonadaptive evolution and random genetic drift. Dobzhansky's notion of the biological species concept, the ''BSC,'' was also applied to plants, although Stebbins later recalled that this was possibly the most difficult problem to reconcile with Dobzhansky's framework (Oral History Interviews, 1987). Also in keeping with Dobzhansky's evolutionary vision, Stebbins espoused a progressive view of evolution. In short, the methods, goals, and the ultimate understanding of evolution in plants were rendered consistent with the view of understanding in animal systems like birds and insects. *Variation and Evolution in Plants* thus functioned as what philosophers of science call a ''consistency argument,'' which attempted to make consistent the pattern and mechanisms of plant evolution with the perspective Dobzhansky had made popular. It also became a conceptual framework for reorganizing general knowledge of plant evolution so that the new field of plant evolutionary biology became a possibility (see Smocovitis, 1988 for further discussion).

The book received favorable reviews in a wide range of botanical, genetical, and general science journals. Anderson wrote that the book was ''a brilliant demonstration of what may be done by one who understands how to integrate facts about the germplasm'' (Anderson, 1951, p. 170). Other colleagues wrote him personal letters of praise. Jens Clausen called it ''grand'' and was especially impressed by the ''wealth'' of literature discussed (letter from Clausen to Stebbins, August 15, 1950; in author's possession). Dobzhansky, who was instrumental in producing the book wrote the following to Stebbins:

> *As you know I consider it not just a good book, but a great book, one of a kind which are published once in a long while. It will mark a turning point in evolutionary thought and of course in botany as well. Of course this is not to say that I agree with all you say there, but science progresses because contradictions are resolved by more work and more thinking! Anyhow, the light of evolutionary genetics now should penetrate the musty shadows of the grass-roots botanical systematics!*
>
> —Letter from Dobzhansky to Stebbins, 27 August 1950 (in author's possession)

Although it would be an exaggeration to suggest that the book transformed *all* botanical practices and practitioners, many of whom remained untouched by evolutionary or genetical perspectives, it was read widely, and was especially influential in turning younger botanists to formal study of plant evolution. This was certainly Peter H. Raven's assessment of the book, which he thought was ''the most influential single book in plant systematics of this century'' (Raven, 1974, p. 168). It remains one of the most commonly cited items that appear in leading journals like *American Journal of Botany.*

G. LEDYARD STEBBINS, JR. AND THE EVOLUTIONARY SYNTHESIS: CLOSING THOUGHTS

From this brief scientific biography of the architect who brought botany into the synthesis, it is apparent that Stebbins had an unusually broad set of interests that developed sequentially, much as the history of each field did, feeding ultimately into the synthetic perspective: taxonomy, morphology, cytogenetics, biosystematics, and finally evolutionary biology. Even in his institutional move from the northeast to the west coast, he followed the intellectual shift that saw the growth of botany in the west coast take a more dynamic, interdisciplinary direction. Few of his contemporaries shared the breadth of interests in each field, or were able to keep up with the literature growing in evolution. Fewer still appeared to possess the personal characteristics required to complete the onerous task, which required the will, determination, and ability to focus and reconcile an extraordinarily diverse body of literature. The personal encouragement and professional support of no less a central figure than Dobzhansky also played a critical role.

Another group that could have and arguably should have written a major synthetic work was the Carnegie Institution team of Clausen, Keck, and Hiesey. Despite the resources that were available to them, and despite the success of their project, Clausen, Keck, and Hiesey published surprisingly little, though it was of high quality. According to Stebbins this was due to Clausen's ''perfectionistic'' approach to the publication of scientific papers (Oral History Interviews, 1987): rather than publishing as the data were generated, Clausen preferred instead to wait until data had accumulated to his satisfaction. His own synthesis, *Stages in the Evolution of Plant Species* (1951), was an influential book widely cited by younger workers, but could not compare with the comprehensive or ambitious scope of *Variation and Evolution in Plants.*

Anderson, Stebbins's close friend and coworker, was one of the few botanists in a similar position to perform a synthesis. An energetic, imaginative individual, Anderson not only shared many of the same interests but had a similar background (he was a graduate of the Bussey Institution; see the special volume commemorating Anderson in *Annals of the Missouri Botanical Garden* 59 [1972]; and see Kim Kleinman, ''Edgar Anderson and the evolutionary synthesis,'' unpublished data). During his visit to England in the early 1930s, furthermore, he came under the immediate influence of the mathematical theorists, Haldane and Fisher. His work on *Iris* had also drawn on a combination of ecological, genetical, and systematic approaches, giving him a synthetic perspective. Most importantly he was invited to publish his insights cojointly with Mayr in 1941. His failure to produce the botanical analog to *Systematics and the Origin of Species* was clearly a disappointment to the history of botany, as it would have possibly energized study of plant evolution as early as 1942 (when Mayr published his book). Whether or not he could have written a book comparable to *Variation and Evolution in Plants* is subject to historical discussion, given that Anderson's views of plant evolution, and specifically his upholding of introgressive hy-

Fig. 7. Three of the architects of the evolutionary synthesis: G. Ledyard Stebbins, Jr., George Gaylord Simpson, and Theodosius Dobzhansky (Mayr is not pictured), photograph taken in the early 1970s, courtesy G.L.S.

bridization and reticulate evolution, would have been at odds with animal evolutionists like Mayr.

The space left by Anderson was filled within four years by Stebbins whose specific goal had been to reconcile evolutionary understanding from the animal world with the plant world, and to do this within Dobzhansky's evolutionary framework. That alone would have made for a more influential and synthetic work that would speak to a wider audience of biologists. From 1945, Stebbins labored to produce first the lectures and then the text. Given the wealth of literature covered, the range of botanical fields contributing to a synthetic picture of plant evolution, and the sheer technical difficulty of the synthesis, the book was actually produced in a timely fashion. Here, it should be noted that *Variation and Evolution in Plants* was one of the more technical of the Columbia Biological Series (if not the most technical), covered the widest possible range of subjects, and performed the intellectually onerous feat of creating a consistency argument with Dobzhansky's book. In short, its completion was nothing short of a monumental feat.

Botanists themselves contributed constructively to the literature feeding directly into *Variation and Evolution in Plants*, and also served as key players in the organization of evolutionary biology in the mid-1940s. As suggested here, West Coast American botanists were especially active through the Biosystematists and served as organizational, as well as intellectual, leaders in helping to organize the Society for the Study of Evolution. Further historical inquiry into the contributions of botanists during this century and across national contexts of their activities (this analysis has concentrated on American efforts) will contribute to a fuller understanding of the history of 20th century biological sciences.

G. LEDYARD STEBBINS, JR. 1950–PRESENT

Ledyard Stebbins was only 44 years old when his magnum opus appeared. His botanical career continued to flourish, as it expanded into still newer areas of biological research like developmental biology and molecular genetics. In 1950 he moved to the University of California, Davis, where he was instrumental in building the Department of Genetics. At this time, Stebbins began to collaborate with graduate students, seeing some 35 students receive their degrees. Many went on to distinguished careers of their own. During the 1969–1970 academic year, he was instrumental in appointing his retired friend Dobzhansky to the same department; the two remained warm friends until Dobzhansky's death in 1975. By then, both Stebbins and Dobzhanksy, along with George Gaylord Simpson and Ernst Mayr had been recognized as ''architects'' of the evolutionary synthesis and for their leadership roles in the discipline of evolutionary biology (Fig. 7).

In the early 1960s Stebbins served biology additionally as secretary-general to the International Union of Biological Sciences. One result of this was a conference at Asilomar, California in 1964, whose proceedings were edited in collaboration with Herbert Baker (1920–1994) as *The Genetics of the Colonizing Species* in 1965. He also served as president of the following societies: American Society of Naturalists (1969), the Botanical Society of America (1962), and the California Native Plant Society (1966–1972), in addition to the SSE in 1948. Other honors included: two Guggenheim awards, one in 1954, and one in 1960. He was elected to the National Academy of Sciences, and in 1979–1980 he received the National Medal of Science from President Carter.

Most important were his numerous publications, which continue to the present. Six other books followed *Variation and Evolution in Plants: Processes of Organic Evolution* (first edition 1966, second edition 1971, third edition 1977); *The Basis of Progressive Evolution* (1969); *Chromosomal Evolution in Higher Plants* (1971); and his influential *Flowering Plants: Evolution Above the Species Level* (1974). Along with Dobzhansky, Francisco Ayala, and James Valentine, he wrote the textbook: *Evolution* (1977), and he completed his popular book *Darwin to DNA, Molecules to Humanity* (1982).

In 1973 he became Emeritus Professor of Genetics at the University of California, where he remains. Ledyard Stebbins continues to read widely, following closely the latest developments in the understanding of plant evolution. On January 6, 1997 he turned 91 years of age.

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