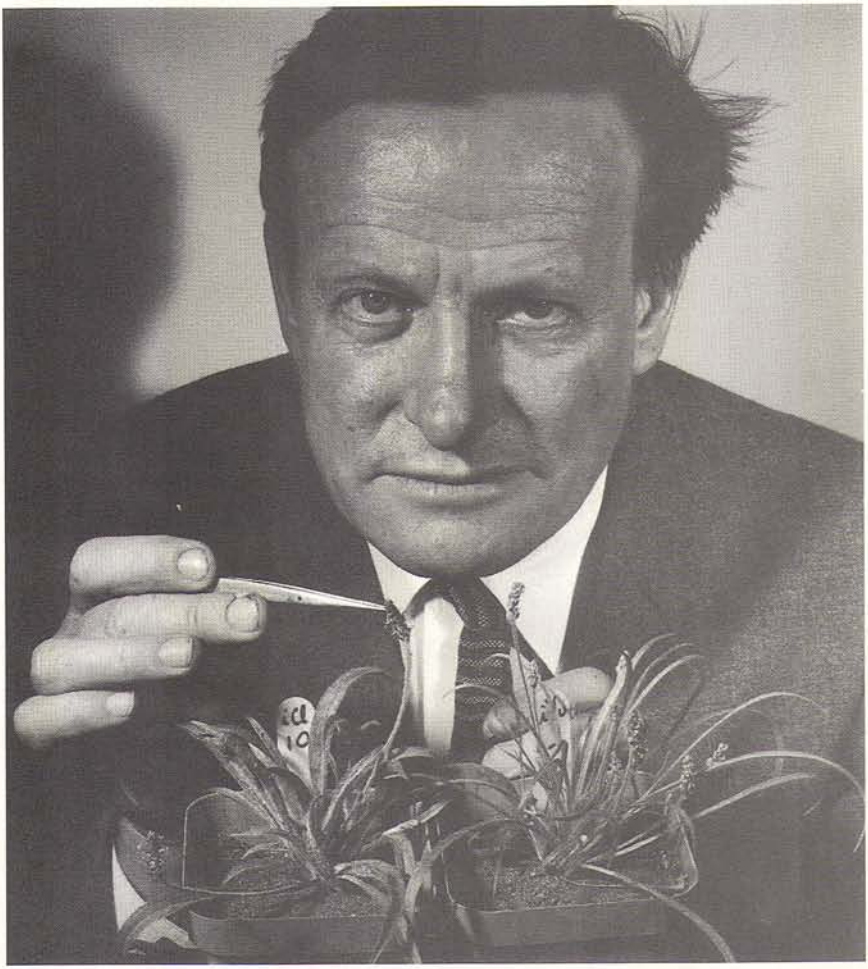

G. LEDYARD STEBBINS

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Annu. Rev. Genet. 2001. 35:803–14
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G. LEDYARD STEBBINS AND THE EVOLUTIONARY SYNTHESIS

Vassiliki Betty Smocovitis
Department of History, University of Florida, Gainesville, Florida 32611; e-mail: bsmocovi@history.ufl.edu

Key Words history of genetics, plant evolutionary biology, evolutionary synthesis, California botany, plant conservation

■ **Abstract** More than any other individual, Stebbins synthesized knowledge from a disparate set of areas that included plant genetics, systematics, and evolution. This work culminated in 1950 with the appearance of his magnum opus, *Variation and Evolution in Plants*. This book gave plant evolution a coherent framework that was compatible with that emerging from the work of Theodosius Dobzhansky, Ernst Mayr, G. G. Simpson, and Julian Huxley, and others associated with establishing the synthetic theory of evolution. For this work he is regarded as the botanical "architect" of the evolutionary synthesis.

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G. LEDYARD STEBBINS

G. Ledyard Stebbins, one of the foremost scientists of the twentieth century, died in his home in Davis, California on January 19, 2000. His scientific career spanned most of the twentieth century and included three primary areas of research: botany, genetics, and evolution. He is especially well known for his masterful synthesis of these three areas his 1950 book *Variation and Evolution in Plants* (22). More than any other, this book formed the conceptual backbone of the new science of

plant evolutionary biology and guided an entire generation of plant evolutionists. As a result of writing this book, Stebbins is generally regarded as the botanical "architect" of the evolutionary synthesis, ranking alongside other notable figures such as Theodosius Dobzhansky, Ernst Mayr, G. G. Simpson, and Julian Huxley (11, 14, 16). Much of his original research included studies into the evolutionary genetics of plant species like the genus *Crepis*. He is best known for his work with the Berkeley geneticist E. B. Babcock in articulating the idea of the polyploid complex, a complex of reproductive forms centering on sexual diploids surrounded by polyploids, which may be apomictic as in *Crepis*, and for being the master of the synthetic review article (3).

EARLY LIFE AND EDUCATION

Ledyard (as he preferred to be called) Stebbins began his career with a great love of plants. Like many botanists of his generation, he came from a privileged family who indulged their children's interests. He was born on January 6, 1906, in Lawrence, New York, but spent much of his early childhood going back and forth to the swank seaside resort of Seal Harbor, Maine, where his father was a successful real estate developer. His love of plants and natural history was apparent even as a very small child, a love that he shared with his father, mother, and his elder brother and sister. At the tender age of three, Ledyard had shown not only a marked tendency to enjoy time out of doors, but he had also begun to manifest a behavior pattern for which he later became renowned: a tendency to quick, sudden outbursts of anger, especially as a means to gain attention or win arguments rapidly. As an adult, his temper tantrums became the stuff of urban legends; the best-known story told of Ledyard Stebbins as an adult involved his throwing a typewriter out the window in a fit of anger. The other vestiges of his early childhood that remained with him until the end included a New England "preppie" accent and a schoolboy sense of humor, frequently seen in his love of rhyme and silly verse.

His early academic career was less than stellar, but he enjoyed botanizing and mountaineering. In 1924 he decided to attend Harvard University mostly because his family background dictated his choice of school and because his older brother, Henry, was already enrolled there. Initially without much focus or direction, Ledyard thought that he would pursue a career in law and planned to major in political science, but his love of plants prevailed. By his third year, he decided to major in botany and began courses with the celebrated Harvard faculty, renowned not just for their scientific standing, but also for their contentious and domineering personalites.

He began his graduate work in the botany department in 1928. While comedic with hindsight, his experience in graduate school shaped his subsequent research style. He had a life-long tendency to move from one vital area of research to another as the science demanded, even when this meant overcoming political obstacles and difficult personalities. He initially worked in floristic botany with the foremost

eastern systematist, M. L. Fernald, in the Gray Herbarium, but quickly lost interest in Fernald's outdated taxonomic methods and inflexible personality. Instead of the static herbarium taxonomy practiced by a person whom he derided as one of the "eminent exsiccatae in the Gray Herbarium," Ledyard chose instead the newer and more exciting cytological study of reproductive processes in plants. For his doctoral research he began anatomical and cytological studies of megasporogenesis in the ovule and microsporogenesis in the pollen of the plant genus *Antennaria*. He was able to collect *Antennaria* easily in the nearby environs so that he could also study geographic variation in the genus. Unfortunately, he chose as his doctoral advisor the eminent morphologist and cytologist, E. C. Jeffrey. Jeffrey, also known as "the stormy petrel of botany," hated with a vengeance any of the work emerging from the school of genetics associated with Thomas Hunt Morgan. He preferred instead to contemplate the idiosyncratic hybridization theories made popular by J. P. Lotsy (9). Jeffrey actively campaigned against Morgan's genetics and vigorously discouraged Ledyard from pursuing it.

The growing interest in genetics took on a life of its own, however, especially since plant genetics, systematics, and evolution and the zones of contact between the three were becoming exciting new areas of research in the 1920s (6, 7). Stebbins traveled to the library of Harvard's Bussey Institution to keep up with the genetics journals like *Hereditas* and *Genetica*, which contained articles by A. Müntzing and C. Leonard Huskins. He sought out geneticists at the Bussey such as E. M. East and took courses with W. E. Castle but found that Castle's mammalian genetics was not immediately helpful. His growing interest in the genetical literature became serious after he began to work with the noted plant geneticist Karl Sax, then just appointed to the Arnold Arboretum. His growing collaboration and friendship with Sax, one of the leaders of plant genetics in his generation, did not, however, sit well with his thesis advisor, Jeffrey. When Sax located a serious error of interpretation in Stebbins's chromosomal studies in his doctoral research, Jeffrey threatened to resign from the thesis committee in retaliation for what he viewed as intrusion into his direction of a student. The thesis was eventually amended so many times to meet the demands of a squabbling committee that it bore numerous scissors and paste marks masking the "offending" passages. It still stands in the Harvard archives as a testament to the contentious Harvard personalities in the botany department. Ledyard's experiences there were nonetheless positive. He completed his dissertation in 1931 and published it as two papers in 1932 (17, 18). This was in addition to publications on the New England flora, especially that of Mt. Desert Island, Maine, that he had published earlier with the assistance of Fernald in his journal *Rhodora*.

THE SHIFT TO GENETICS

In 1931 Stebbins was appointed to Colgate University, where he was required to teach introductory biology. He wrote a textbook with his colleague in the psychology department, Clarence Young, for this course (30). It was an unusual mixture

of biology and psychology that was adopted for use by the American armed forces in the late 1930s and 1940s. Despite a heavy teaching load, Ledyard found time for genetics, spending nearly all his spare time on chromosomal studies of plants. He worked in close collaboration with Percy Saunders (of the Canadian Saunders family of wheat-breeders), at nearby Hamilton College. Saunders was a keen collector and breeder of peonies; his backyard was a profusion of these beautiful plants, some of which could still be seen in 1987, when I visited the house. With Stebbins, Saunders engaged in chromosomal studies in the species hybrids of *Paeonia*, of both old world and new world forms and found numerous interesting deviations from the normal pairing relationships. Stebbins and Saunders spent many evenings working on these studies in a makeshift laboratory in the basement of the Saunders' house.

With Saunders, Ledyard took the important step of attending the 1932 meetings of the International Congress of Genetics in nearby Ithaca, New York. At those meetings Stebbins recalled seeing the famous exhibit that Sewall Wright had set up displaying his shifting balance theory of evolution, but not understanding what they represented. He attended one particularly memorable session that featured Sax and the English cytogeneticist C. D. Darlington. At the climax of an especially heated exchange between Sax and Darlington over the chiasmatype theory, two of the omnipresent stray Cornell dogs broke into the room and engaged in a fight precisely in front of Sax and Darlington. This sent the audience into a paroxysm of laughter over the simultaneity of the two dogfights.

Ledyard listened closely to Thomas Hunt Morgan's famous address on the future of genetics. He also studied John Belling's exhibit demonstrating the existence of chromomeres, which he had mistakenly identified as genes. Most exciting of all, however, was Barbara McClintock's presentation of some of her cytological studies in maize. Using her squashing technique, McClintock showed the linear pairing of parental chromosomes at mid-prophase or pachytene. The paired chromosomes clearly showed the effects of crossing over and demonstrated beautifully the effects of inversions and translocations in their characteristic configurations. Shortly thereafter, he replicated some of the same studies in his *Paeonia* material and was the first to detect ring formation in this genus. The work was hardly groundbreaking, but it did confirm what McClintock and others had been describing concerning chromosome behavior (29).

His interest in genetics was reinforced further when he began a life-long intense friendship with the botanist Edgar Anderson, who was a fellow at the John Innes Horticultural Institute at the time of their meeting. In scientific interests and even in a colorful personal style, Anderson most closely approximated Stebbins. The two had met at the Fifth International Botanical Congress in Cambridge, England, in 1930. Anderson was about to begin his work on detecting and measuring variation patterns in plants like *Iris*, which were frequent hybridizers. He eventually went on to pioneering work on hybridization and was the first to articulate the notion of introgressive hybridization, a phenomenon seen often in plants (8).

E. B. BABCOCK, *CREPIS*, AND BERKELEY GENETICS

In 1935, Stebbins took a giant step in his turn to genetics by accepting a position as junior geneticist to the noted Berkeley geneticist E. B. Babcock. With the aid of a Rockefeller grant, Babcock hired Stebbins to assist him in an enormous undertaking to understand the genetic basis of evolutionary change in the plant genus *Crepis*. Stebbins was recommended for the position by the Washington-based expert on the Compositae, Sidney F. Blake, and was hired even after Ledyard's father, who was a close friend of the Rockefellers (Ledyard had been a playmate of Nelson's), nearly undermined Ledyard's chances with Babcock by attempting to leverage a higher salary for the appointment. Babcock was not pleased by the attempted intervention using the Rockefeller connection.

Babcock was engaged in an ambitious team-oriented project to find a plant equivalent of *Drosophila*. Very much eclipsed by his contemporary Thomas Hunt Morgan at the California Institute of Technology, Babcock was one of the most important figures in establishing and institutionalizing genetics within the Agricultural College at Berkeley. It became one of the first departments of genetics in the country, thanks to the efforts of Babcock, who was convinced that genetics generally, and agricultural genetics in particular, was a vital part of the mission of the University of California. Babcock's vision for genetics at Berkeley was that it would rival the success of the Morgan school's project with *Drosophila melanogaster*. He chose the genus *Crepis* to be the plant equivalent of *Drosophila* even though it was a weed and not an important crop plant, mostly because he felt the genus with its diverse geographic variation patterns could be used to understand the genetic basis for evolutionary change, which could then form the basis for a taxonomic study (1). Preliminary work had begun as early as 1917–1918, but the project continued into the late 1940s and ended only with Babcock's retirement. Babcock considered his monograph on the genus *Crepis* to be the centerpiece of his life's work (2).

Stebbins's assignment assisting Babcock was in performing chromosome counts in some of the nearest relatives of *Crepis* in the tribe Cichorieae. He quickly developed an interest in Babcock's own research, which was in understanding some of the New World species of *Crepis*, because he recognized patterns of evolution that resembled those in *Antennaria* and *Paeonia*. Like these other genera, *Crepis* was a commonly hybridizing group that displayed polyploidy and could reproduce apomictically. In 1938, Babcock and Stebbins jointly published a monograph on the American species of *Crepis*. It laid the foundation for understanding polyploid complexes and the role of apomixis in the formation of some of them; for this reason, they first termed the American species of *Crepis* an agamic complex. They recognized clearly 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, they also showed, usually had the

wider distribution pattern. Babcock and Stebbins's articulation of the polyploid complex, and their clear elucidation of its existence in the American species of *Crepis* was considered pathbreaking work at the time. Not only did it demonstrate in detail 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 the genus. Stebbins extended these ideas further with subsequent breeding studies in forage grasses and published a series of important articles in 1940, 1941, and 1947 (19–21). The latter article, entitled "Types of polyploids: their classification and significance," became a classic review that synthesized knowledge bearing on polyploidy in plants and constituted probably one of his most important contributions to understanding of plant evolution.

Stebbins worked closely with Babcock for six years. In 1939, he was successful in securing a position as assistant professor in the Berkeley genetics department. Babcock, who was impressed with Ledyard's energy and industry, was instrumental in making the appointment. Earlier, Stebbins had a significant disappointment in that he had failed to obtain the replacement position for Willis Linn Jepson in the botany department. Although he made himself at home with the botanists at Berkeley, Stebbins's interests were considered so heavily genetical that his colleagues in botany did not feel he was sufficiently focused on the curatorial work the position demanded. The position was offered to Lincoln Constance instead. The vacancy of a position in the genetics department, which required teaching of the general course on evolution, was opportune for Stebbins, whose interests were shifting to the exciting areas in evolutionary study opening in the late 1930s. He read voraciously in preparation of the course and quickly realized that there was a serious shortage of books in evolution helpful to him and to his course, which was taught out of the genetics department in the College of Agriculture. His growing interest in evolution was fueled by two additional factors: his interactions with a unique group of biologists all concerned with evolutionary approaches to systematics who called themselves "The Biosystematists," and his special relationship with the Russian émigré Theodosius Dobzhansky.

Beginning in the mid-1930s, the San Francisco Bay area became a hotbed for evolutionary activity. 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, and the California Academy of Sciences, in addition to the University of California, Berkeley. Calling themselves "The Biosystematists," the group met at alternating locations every month to share in the new methods that were characterizing the "new systematics" as a whole. Ledyard was a prominent member of the group nearly from the start. He was active in inviting speakers, some of whom included visitors from other states like his close friend Edgar Anderson, from the Missouri Botanical Garden in St. Louis, and his fellow plant systematist at the University of California at Los Angeles, Carl Epling.

The critical players among the Biosystematists were the interdisciplinary Carnegie team 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 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 factors in plant evolution. In particular, they studied patterns of variation of plants as they adapted along steep altitudes in the Californian landscape. Their work is considered pioneering in understanding the mechanisms responsible for plant adaptation along varying altitudinal gradients. Ledyard followed this work closely and visited the team in their experimental sites all through the 1940s.

Also in the mid-1930s, Stebbins began a close friendship with the evolutionary geneticist, Theodosius Dobzhansky. Stebbins met Dobzhansky on a visit to the California Institute of Technology in the spring of 1936 when Dobzhansky was just beginning to turn to his work on the genetics of natural populations using *Drosophila pseudoobscura*. The two interacted further when Dobzhansky frequented the Berkeley campus to see his close friend, the geneticist I. Michael Lerner, then in the Poultry Husbandry Department. Stebbins had interacted with Lerner in a fortnightly journal club called Genetics Associated. Even though Lerner and Dobzhansky frequently spoke to each other in Russian, Ledyard enjoyed listening to them discuss their mutual interests in evolutionary genetics. The friendship with Dobzhansky was to prove absolutely critical to Ledyard as his own interests were shifting more and more to evolutionary genetics, thanks to the teaching demands made by the evolution course. Dobzhansky, who published his own path-breaking synthesis of evolutionary genetics under the title *Genetics and the Origin of Species* in 1937, began to foster Ledyard's evolutionary interests (4). Through the 1940s they came in closer contact when they met for field work at the Carnegie Institution's field site at Mather, California. Both were avid horseback riders and frequently collected hybrids from the back of a horse.

Dobzhansky played the single most important influence in Stebbins's career as an evolutionist. In 1945, thanks to Dobzhansky's recommendation, L. C. Dunn at Columbia University invited Stebbins to deliver the prestigious set of Morris K. Jesup Lectures at Columbia University. One reason why Stebbins had been selected was the need for a comprehensive synthesis of plant evolution. In 1941, Edgar Anderson had co-delivered the Jesup Lectures with the zoologist Ernst Mayr. While Mayr subsequently published his set of lectures under the title *Systematics and the Origin of Species from the Viewpoint of a Zoologist*, Anderson never completed the publication of his set of lectures (10). The viewpoint of the botanist was therefore needed in what was emerging as the new synthesis of evolution launched by Dobzhansky. In response to the invitation, Stebbins took the course notes he had been using for his evolution class and converted them to the Jesup Lectures. The published version of the lectures appeared with Columbia University Press in their Columbia Biological Series in 1950 under the title *Variation and Evolution in Plants*. It was published in the same series as Theodosius Dobzhansky's

1937 *Genetics and the Origin of Species*, Ernst Mayr's 1942 *Systematics and the Origin of Species*, and G. G. Simpson's 1944 *Tempo and Mode Evolution* (13). Taken as a whole, these books provided the backbone of the modern synthesis of evolution, which incorporated insights from a range of disciplines with evolutionary genetics. As far as botany went, Stebbins upheld the importance of most of the tenets emerging as part of the new consensus on evolution and followed his friend Dobzhansky, who had drawn more heavily from animal examples, closely. He stressed the centrality of natural selection but left plenty of room for random genetic drift and nonadaptive evolution. He also upheld Dobzhansky's and Mayr's notion of the biological species concept (BSC), though it took much explaining. (He subsequently backpedaled on the BSC'S application in botany.) The book also effectively killed any serious belief in alternative mechanisms of evolution like Lamarckian evolution or soft inheritance. At 643 pages in length and over 1250 citations, *Variation and Evolution in Plants* was the longest and the last of the books associated with the evolutionary synthesis. The book received instant recognition for its ambitious synthesis of a broad range of areas. It was so comprehensive that it opened a new field of research for younger scholars who recognized themselves as plant evolutionary biologists. Assessing the book, Peter Raven described it as "the most influential single book in plant systematics this century." It remains a heavily cited text (12).

THE DAVIS YEARS

With the publication of his magnum opus, Ledyard's life began to take different directions. He was already emerging as a leader in evolutionary biology. He was an active member of the first international society for the study of evolution, the Society for the Study of Evolution, and in 1948, he was elected as its third President. But his interests in evolution may have left him at odds with some of the members of his own department. By the 1940s, the Berkeley genetics department had become world-class and was leading the way in new areas of genetical research. Older areas like plant cytogenetics were becoming replaced with the newer physiological and biochemical genetics. With the retirement in 1947 of Babcock, who had served as chair of the department and was Ledyard's greatest supporter, Ledyard was increasingly becoming the odd one out. While publishing both original research and longer review articles in genetics journals and actively reading the literature, his own researches in genetics were always designed with the aim of understanding the mechanisms of evolutionary change. He was never really concerned with the mechanisms of gene action outside such an evolutionary framework. My sense is that Ledyard was increasingly beginning to feel uncomfortable in his own department and that there may have been tension building between him and R. E. Clausen, who succeeded Babcock as chair. Thus, in 1950 when the invitation came to move to the expanding Davis campus of the University of California and to organize a new department of genetics, Stebbins accepted the invitation enthusiastically. He explicitly told me several times that he liked the idea of being a "big fish in a small

pond." In 1950, therefore, Ledyard moved to Davis, California, which became his home until the time of his death. He was instrumental in launching the genetics department there and stayed as its chair until 1963.

After his move to Davis, his research shifted once again to incorporate newer areas like developmental morphology and genetics in crop plants such as barley. He also became active in training graduate students, nearly all of whom were in developmental biology or plant developmental genetics. Ironically, the only students associated with Ledyard's primary area of research in plant evolutionary biology dated back to his Berkeley days. They were Verne Grant and Charles Heiser Jr. Ledyard had, however, only served as a committee member and not chair of their graduate committees. Other notable students included Ghurdev Khush and Michael Zohary.

From all indications, Ledyard was a popular and engaging teacher, especially at the undergraduate level. His undergraduate evaluations were consistently favorable. He frequently took students on day-trips that showed them California's unique flora. His claim to fame was that he could tell precisely the elevation of his whereabouts by identifying the plants closest to him. Students warmed to his energy, enthusiasm, and love of natural history. His graduate students speak favorably of working with Ledyard, but my sense is that he did not have the patient personality to supervise complex dissertations closely (see below). One recurring description of Ledyard as advisor concerns his legendary sloppiness and complete lack of dexterity in the laboratory: Graduate students and technicians usually prepared two sets of every important slide that they gave to him because he was likely to break it once it got into his hands.

Ledyard cared deeply about the teaching of evolution, and in the early and mid-1960s he worked as one of the faculty in the Biological Sciences and Curriculum Study to institute the teaching of evolution in American high schools. He echoed Dobzhansky closely in stating repeatedly that "nothing in biology makes sense except in the light of evolution." He actively fought the rise of "scientific creationist" groups in California and in the nation. Between 1960 and 1964 he served as secretary-general to the International Union of Biological Sciences. He was active in numerous societies and served as President for nearly all of them.

In the 1960s, his interest in evolution continued to grow. In 1965, he and Herbert Baker edited a collection of papers that came out of an Asilomar conference in a volume entitled *The Genetics of Colonizing Species* (28). His second most important book appeared in 1974 as *Flowering Plants: Evolution Above the Species Level*, following the Prather Lectures he gave at Harvard (26). His other books included a widely adopted textbook of evolution, *Processes of Organic Evolution*, which went through multiple editions (23). He also wrote *Chromosomal Evolution in Higher Plants*, which was also adopted as an advanced textbook, and *The Basis of Progressive Evolution* (24, 25). Along with Dobzhansky, Francisco Ayala, and James Valentine, he wrote the textbook *Evolution* in 1977 and in 1982 he completed his semipopular *Darwin to DNA: Molecules to Humanity* (5, 27).

After he moved to Davis, Ledyard became increasingly active in conservation work both with amateur and professional groups. He led innumerable public field trips to explore the California flora and effectively led a political campaign to prevent the destruction of a place he called "Evolution Hill," a strip of beach on the Monterey Peninsula that supported rare and endangered plants. He was instrumental in helping to form the California Native Plant Society and in contributing both scientific and popular articles on the subject of California native plants.

In the course of his long career, Ledyard Stebbins won numerous awards and honors in multiple areas of research. His greatest recognition was receiving the National Medal of Science from President Carter in 1979. In 1973 he became Emeritus Professor of Genetics.

BOTANIST, GENETICIST, OR EVOLUTIONIST: STEBBINS AS SYNTHESIZER

In science as in everything, small-scale synthesizers usually get credit from all constituent parties, but truly great synthesizers can fall between the cracks in the cycle of scientific credit. Ledyard Stebbins was in the latter category; neither fish nor fowl, he frequently failed to receive credit for work in some areas, usually at the hands of narrower colleagues. Systematists felt that he concentrated too heavily on genetics and too little on taxonomic studies, whereas geneticists felt that his work was too evolutionary, natural history–oriented and did not concentrate sufficiently on the mechanisms of gene action. Few, however, have challenged his contributions to plant evolutionary biology, nor questioned his ability to synthesize disparate literature into a coherent framework. This was a work style that he repeatedly demonstrated. His publication list at just over 260 articles bears a striking number of pieces that qualify as synthetic reviews. His ability to read quickly, recognize novel insights, digest new material, and then integrate the knowledge were the hallmarks of his scientific work style. He was a masterful synthesizer and master of the review essay or synthetic thought piece.

THE PERSONAL AND THE PROFESSIONAL: REFLECTIONS ON STEBBINS

Ledyard had such a strong personality, that it could not help but spill over into his professional life. He displayed a strangely predictable form of nonconformism. My sense is that this stemmed from a rebellious attitude toward his family. He suffered from the classic "latter-born son as rebel" syndrome that historian and psychologist Frank Sulloway described in his *Born to Rebel* (31). He considered himself a staunch liberal and a life-long supporter of the Democratic Party, but that was also a reaction against his father, who was a Republican. Though his family was Episcopalian (his father was an avid participant in the church at Seal Harbor),

Ledyard was never much of a believer, but in later years, after marriage to his second wife in the 1950s, he did become an active Unitarian.

Like many creative people, his strengths were simultaneously his weaknesses. He was industrious, intensely focused, and always enthusiastic. He seemed constantly excited by a some new insight that usually came out of his voracious reading. The new insight usually made its way into his latest project almost immediately. He loved following the work of younger people and supported them generously. At times, he seemed almost desperate to please people who mattered to him. At other times, however, he could be self-absorbed, petulant, and completely insensitive to the thoughts and wishes of the people around him. This latter behavior, combined with the tendency to "blow his top" (his expression), did not always make him an easy colleague. Many of his contemporaries dreaded collaborative work, committee work, or even spending an evening with him (he loved to speak in long, perfectly constructed paragraphs that gave little opportunity for conversations). Barbara Monaghan Stebbins, his second wife, best described Ledyard to me once as a "child." I think what she meant to convey with this description was his childlike wonder with the world, his fundamental belief in the goodness of people around him (he was never able to carry a grudge or remain angry for very long), but also his tendency to self-absorption and insensitivity to others. I think this may help explain the fact that no matter how much people may have been frustrated by Ledyard, nearly all admired his accomplishments and spoke of him with admiration, amusement, and affection.

Ledyard loved classical music passionately, frequented art shows with Barbara, and was fond of reading popular books of science. He especially loved to watch cultural programs on PBS. Toward the end of his life, with his eyesight failing, he would sit quietly listening to books on tape such as *Ancestral Passions*, the popular biography on the Leakey family. He absolutely loved having books read to him, and I was happy to read to him sections from David Quammen's *Song of the Dodo*. But though aged and infirm and in pain from a tumor growing on the side of his face, he was still capable of throwing a temper tantrum or two. Good liberal that he was, he did not discriminate against his target of momentary rage (15). To his end, he denied ever throwing that typewriter out the window.

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