In response to the invitation from Dunn, therefore, Stebbins took the extensive 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 1950 under the title *Variation and Evolution in Plants* (Stebbins, 1950d). It followed on the heels of not just Dobzhansky and Mayr's previous synthetic books, but also G. G. Simpson's synthesis of paleontology with the newer genetical theory published in 1944 as *Tempo and Mode in Evolution*. Taken as a whole, these books provided the backbone of what Julian Huxley had termed "the modern synthesis of evolution" which incorporated insights from a range of disciplines with evolutionary genetics (Huxley, 1942; Smocovitis, 1996).

Stebbins's book incorporated much of the literature of plant evolution within the wider synthetic framework. He upheld the importance of most of the tenets emerging as part of the new consensus on evolution and followed Dobzhansky's framework fairly closely. He stressed the centrality of natural selection as the dominant mechanism driving evolutionary change, but also left plenty of room for random genetic drift and nonadaptive evolution. He upheld the new notion of the biological species concept that Dobzhansky and Mayr had articulated in their books, but struggled to incorporate phenomena like polyploidy, apomixis and hybridization within this view. Most original in the book was the discussion on genetic systems (a notion he borrowed from C. D. Darlington) which showed how polyploidy, apomixis and hybridization could be conceived as systems which themselves were subject to selection (this work was later extended in Stebbins, 1960a). Though some of the discussion on the biological species concept was difficult, and later subject to revision, the book was effective in putting an end to a range of counterproductive discussions in evolution including the belief in Lamarckian evolution or "soft inheritance." At 643 pages in length and with over 1250 citations, it was an impressive synthetic tome; in fact it was the longest and perhaps the most technically substantive of the set of books associated with the event that increasingly came to be called as "the evolutionary synthesis." It was so comprehensive in scope that it opened up an entire new field of research for younger scholars who began to recognize the field known as "plant evolutionary biology." Assessing the book in a historical article, Peter Raven described it famously as "the most influential single book in plant systematics of this century" (Raven, 1974). The book remains a heavily cited text.

With the appearance of *Variation and Evolution in Plants*, Stebbins earned himself the status of "botanical architect" of the evolutionary synthesis (Mayr & Provine, 1980), but was also catapulted into the front ranks of leading American biologists. His publication record beginning in the early 1950s reflected his leadership status in American biology and then international biology. In addition to maintaining his traditional interests in plant evolutionary biology, and general evolution, Stebbins published widely on current issues of vital political concern to biologists. He was a staunch opponent of Lysenkoism in the Soviet Union, and a fierce advocate of international research (Stebbins, 1950a, 1956d). His international stature was reflected in the fact that he published widely in non-English written journals, and actively sought to apply principles from his studies on breeding forage grasses to increasing food sup-

ply in developing nations (Stebbins 1957g, h and see the earlier Stebbins 1951c, 1956f).

With the publication of what was his *magnum opus*, Stebbins's career took additional new directions. He became active in a number of societies, including serving as charter member in the first international Society for the Study of Evolution. His stature as leader of evolutionary biology was recognized in 1948 when he became the third president of the young society. The same stature in evolution may have had its down side, however. The Berkeley genetics group was taking new directions, especially with the retirement of Babcock in 1947, who remained Stebbins's strong supporter. Although Stebbins actively engaged the genetics literature, and his original research in the 1940s and 1950s delved into polyploidy and plant breeding, his primary research questions in genetics remained defined by evolutionary concerns. Never seriously engaged in research outside such an evolutionary framework, Stebbins's interest in genetics was different from many of his colleagues in Berkeley who were interested in pure genetical mechanisms. As his colleagues began to pursue more recent areas in physiological and biochemical genetics, Stebbins may have felt less at home in Berkeley. As well, he may have felt possible friction with R. E. Clausen, the new chair. Thus, in 1950s, when the invitation came from the University of California administration to help create a new genetics unit on the growing agricultural campus at Davis, Stebbins eagerly accepted the new position and moved to Davis, where he remained until his death. He chaired the new department of genetics there until 1963.

The move to Davis also provided him with the incentive to move into newer areas of research in the late 1950s. The tendency to move into new promising areas of research was a life-long characteristic that became very evident in his mid-career choice to move into the newer areas of developmental biology and molecular biology. At a time when his contemporaries like Ernst Mayr and G. G. Simpson were taking sides in the growing rift between what came to be called "organismic biology" versus the newer "molecular biology," Stebbins was already beginning to develop techniques and insights to bridge the two with examples from the plant world. He read voraciously in the newer molecular biology, but also in biochemistry and in plant physiology. Although he continued to work on artificially inducing new polyploid forms of grasses, he began to move into the newer area of developmental morphology and developmental genetics beginning in the late 1950s that was exploring the interface between genetics and morphogenesis. Exploring the "gene to character" transformation in plants like barley became his primary research focus and with the aid of some 35 graduate students and researchers, Stebbins launched an ambitious research program that incorporated newer methods and insights from molecular biology that continued until his retirement as Emeritus Professor of Genetics in 1973 (see papers beginning with Stebbins 1959d, 1965c, g and others). Stebbins's contributions to the field that is now being defined as evolutionary developmental biology ("evo-devo") is only now gaining recognition. His articulation of "phyletic phenocopies" (Stebbins & Basile, 1986b), ways in which species could be induced to phenocopy morphological features of distantly related but extant taxa, is proving a useful notion

in understanding general evolutionary developmental biology (Stearns, 2002).

Although he was identified with the plant world, Stebbins always kept a comparative perspective in mind. The staggering breadth of his intellectual engagements across molecular biology, organismic biology at all levels of evolution can be seen in a highly theoretical paper he co-wrote with R. C. Lewontin in 1971 assessing comparative evolution (Stebbins & Lewontin, 1971h). The comparative perspective also allowed him to endorse and promote a view of transpecific evolution. Such an understanding of transpecific evolution was possible if organisms could be studied at basic levels such as the genic or biochemical level. Working in such a way Stebbins believed that "bridges could be built across" a range of biological disciplines to incorporate genetics and paleontology (Stebbins, 1974b). Diversifying his range of expertise to encompass animal bodies in 1973, he published an article in *Systematic Zoology* on the origin of form in early multinuclear organisms (Stebbins, 1973c). Transpecific evolution and the role that adaptive radiation played was developed further in Stebbins (1975a).

His growing reputation continued into the 1960s and 1970s and his publication record reflected the demands placed on a visible spokesperson for evolution, botany, and biological science. He continued to publish on international biological research and traveled extensively as part of his position as secretary-general to the International Union of Biological Sciences (Stebbins, 1962a, b). Promoting and directing research in botanical science and the plant sciences generally also became an interest (see Stebbins, 1964a, 1967c; 1972c). How science could also be used to shape persistent problems with food supply, overpopulation and determining science policy also generated more publications (Stebbins, 1968b, 1970a, b). As American creationists under the guise of "scientific creationism" began to launch a series of attacks against the teaching of evolutionary biology in the classroom, Stebbins also published extensively defending and promoting the teaching of evolution with the idea that it was the central unifying feature of the modern biological sciences (Stebbins, 1973a; and see Stebbins, 1984e). To help teach evolutionary understanding he wrote a very popular introductory textbook of evolutionary biology that went into three editions titled *Processes of Organic Evolution* (first edition 1966; second edition 1971; third edition, 1977). Along these lines he completed an even more substantive textbook of evolutionary biology with his colleagues Dobzhansky, Francisco Ayala, and James Valentine titled simply enough, *Evolution* in 1977. Then in 1982, well into his retirement, he completed the popular book, *Darwin to DNA: Molecules to Humanity*. He was also active in assisting the writing and dissemination of a series of high school biology textbooks known as the Biological Sciences and Curriculum Study series (or the BSCS) that featured evolution centrally within a unified vision of modern biology.

In the 1960s his primary research program was the morphogenetic study of the hooded barley gene, but he also continued his interests in general evolution, speciation, and plant evolution. He published extensively on subjects like adaptive radiation (see for example Stebbins, 1967d) and its relationship to speciation (Stebbins, 1971a). Keeping up with the newer literature in evolution, he and his colleague Herbert Baker

edited a volume of papers that came out of an Asilomar conference on colonizing species. Appearing in 1965 and titled *The Genetics of Colonizing Species*, it became a widely read, heavily cited and influential collection of papers (Stebbins's contribution is included in this collection in Part One: *Genetic Variation and Speciation*). His second most important scholarly book, appeared in 1974 as *Flowering Plants: Evolution Above the Species Level*, which was based on the Prather Lectures that he delivered at Harvard. He also completed the smaller *Chromosomal Evolution in Higher Plants*, which was also adopted as an advanced textbook, and then *The Basis of Progressive Evolution*, which was an informal collection of papers that grew out of the John W. Harrelson Lectures at North Carolina State. The lectures were a summary of his general view of evolution. In 1970 he revisited the subject of his *magnum opus*, variation and evolution in plants, in a subtantive review article in honor of Theodosius Dobzhansky (Stebbins, 1970d).

Throughout his life, Stebbins continued to play a leadership role as botanical architect of the evolutionary synthesis. In the late 1970s and early 1980s, as the synthetic theory of evolution received a series of challenges to its status, autonomy and validity as scientific theory, Stebbins served as its staunch defender. With his fellow University of California colleague, Francisco Ayala, he wrote a widely read paper that appeared in *Science*, defending the synthetic theory of evolution (Stebbins & Ayala, 1981e; this paper is reprinted in Part IV: *General and Plant Evolution*). Similar assessments of the synthetic theory appeared in 1982b, 1982f, 1983a, and 1987b. In the middle of the debates and challenges to the evolutionary synthesis, Stebbins and Ayala contributed a very popular article surveying Darwinian thought for a special issue of *Scientific American*, that was devoted to the recent debates in evolution (Stebbins & Ayala, 1985b). The questioning and rethinking of the processes of speciation led to a series of other papers and articles that concentrated on plant examples. Stebbins was frequently drawn upon to consider evolution and mechanisms of speciation from the plant world. Two of the more widely read recent papers on plant speciation are included in this collection (Stebbins, 1982d, 1989; Part I: *Genetic Variation and Speciation in Plants*).

After moving to UC Davis, Stebbins also became active in conservation studies and worked closely with both professionals and amateurs, especially in preserving the California flora. He led innumerable public field trips to explore the California flora and led a political campaign to preserve a place he called "Evolution Hill," a strip of beach on the Monterey Peninsula that supported rare and endangered species. He was also instrumental in helping to form the California Native Plant Society. Some of his papers on plant conservation and the rarity of species from a genetic perspective are included in this volume (Part V: *Rare Species and Conservation*).

Towards the end of his life, Stebbins also made some notable contributions to understanding the history and philosophy of biology. He made a significant contribution on a volume on reductionism in biology by examining adaptive shifts and evolutionary novelties (Stebbins, 1974c). Another article in *American Naturalist* took on a recent philosophical critique of evolution as being tautological (Stebbins, 1977a); Stebbins defended the legitimate status of evolutionary theory as a proper scientific

theory. Another philosophical article explored species concepts (Stebbins, 1987a). Substantive historical articles included his reflections on the contributions of botany to the synthetic theory of evolution (Stebbins, 1980f), and the history of plant evolution generally (Stebbins, 1979a), two commemorative pieces assessing the contributions of Edgar Anderson (Stebbins, 1972e) and Göte Turesson (Stebbins, 1995a), an article on the history of biological revolutions (Stebbins, 1994), and a lighthearted personal recollection of his relationship with Dobzhansky (Stebbins, 1995b). Yet another article allowed him to explore the interplay of science and religion; he came down firmly on the side of science (Stebbins, 1984e). One of his last publications which he unofficially titled his "swan song" reflected on his ideas in evolution; it was published in the *American Journal of Botany* (Stebbins, 1999a).

Over the course of his long career that spanned much of the twentieth century Stebbins published important articles and books on a stunning range of areas beginning with systematics, genetics, evolution, developmental biology, molecular biology and conservation biology. By the end, he had listed nearly 300 publications in all these diverse areas of research that included books or articles that were comprised of original research, synthetic or review pieces, directional guides to the profession, critiques, commentaries and reviews, and a set of and popular and semi-popular accounts of evolution and botanical science for a wide audience of readers. This was an impressive achievement indeed, and all the more so because it seemed to closely reflect the development of biology as a whole in the twentieth century.

For all Stebbins publications cited here see *The complete list of publications for G. Ledyard Stebbins (1929–2000)*. For all other citations see *Literature cited*.