



G. Ledyard Stebbins

GEORGE LEDYARD STEBBINS

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INTRODUCTION

Ledyard Stebbins will be remembered by countless biologists, and more particularly by botanists working in the period immediately after World War II for the remarkable book *Variation and evolution in plants* (11)*, published in 1950. In its preface Stebbins wrote:

The present book is intended as a progress report on the synthetic approach to evolution as it applies to the plant kingdom. ... It does not intend to offer any new hypotheses, except on certain limited phases of plant evolution. ... No attempt has been made to give a final answer to any of the major problems confronting evolutionists, but the information and ideas are presented here in the hope that they will help to open the way towards a deeper understanding of evolutionary problems and more fruitful research in the direction of their solution.

In this synthetic approach Ledyard Stebbins can best be compared with Charles Darwin, and the impact of the book was similar, although of course the basic theory of evolution had by then been well established by the fusion of Darwinism and Mendelism. But the material presented in *Variation and evolution in plants* was so detailed, and made such sense, that botanists suddenly had to realize that plants really did evolve, and that they did this in all sorts of exciting ways, many hardly found in animals and certainly little understood by most evolutionists who, for the most part, were animal oriented.

But all this makes no reference to his many other attributes that made him one of the foremost botanists of the twentieth century, attributes that this memoir will attempt to cover.

* Numbers in this form refer to the bibliography at the end of the text.

EARLY YEARS

Ledyard Stebbins was born in 1906 into a relatively wealthy New York family. His father, George L. Stebbins, was a real-estate developer who helped to develop the posh resort town of Seal Harbor, Maine, and who had been instrumental in helping to create Acadia National Park nearby. As a result Ledyard spent much of his early childhood, especially his summers, in Seal Harbor. By the age of three years he had already developed a fondness for the outdoors, and he soon developed a love of plants and natural history, especially the marine life in tidal pools and the common birds of New England, all readily available to him around Seal Harbor. His interests in natural history were fostered by his family, especially his father.

In the various preparatory schools he attended he remembers the encouragement of teachers in natural history, particularly Ralph Hoffman at Cate School, in Carpentaria, California. After graduating, however, he entered Harvard University in 1924, intending to major in political science with the aim of a career in law. He had no idea of a career in science. However, at the end of his freshman year his interest and love for natural history was apparent, and he spent most of the summer collecting the wild plants of Mount Desert Island, Maine. In this he was encouraged by Edgar Wherry, professor of botany and fern expert at the University of Pennsylvania, who spent his summers in Maine. Immediately after this, taking advantage of the flexibility of the American educational system at Harvard, he took courses in biology, systematic botany and chromosome cytology—hardly preparation for a career in law. Helped by a close friendship with a classmate, Richard Dow, he rapidly became converted to what became his lifelong interest in evolutionary biology and plant taxonomy, and graduated *magna cum laude* in 1928 with a Bachelor of Arts degree,

In all this he seems to have been mostly self-propelled. He records that he could not cite any of his Harvard professors as sources of interest in evolutionary botany, although he admits that he profited greatly from lectures and discussions. However, he was exposed to the teaching of Merritt Lyndon Fernald, and accompanied Fernald on field trips to nearby areas in New England, taking up Fernald's interest in floristics and in the geography of plants in relation to the effects of the ice ages. He was a member of the Harvard Freshman Cross Country Team and an avid hiker and mountaineer, interests that served his botanical work throughout his life. He was also a member of the Harvard Glee Club, singing as second tenor, which allowed him to develop his musical interests, another serious lifetime interest.

He was admitted to the Harvard graduate programme in 1928 and worked closely with Fernald on the New England flora. From this, his first paper (1) was a humble 'Further additions to the Mount Desert flora' followed by 'A revision of some North American species of *Calamagrostis*' (2), both published in *Rhodora*, a journal edited by Fernald. The second paper, on species of grass, usually of little interest to botanists, is not without significance to his later detailed work and love for grasses.

POSTGRADUATE WORK IN A STORMY SEA

Like any ambitious young researcher, Stebbins became interested in new ideas, and in his case new approaches to taxonomy. He was particularly attracted to the use of chromosomes in taxonomic work, an approach that was new at the time, and chose the cytology of the genus *Antennaria* in the Asteraceae (the daisy family) as the subject for his PhD. It was a genus con-

sisting of several closely related species, available nearby but including some with wide distribution. These enabled him to look at geographical variation within species. He sought out the support and advice of E. C. Jeffrey, a morphologist and cytologist, but a very controversial and dogmatic figure, referred to as the 'stormy petrel of botany' (Ames 1979, p. 78). Jeffrey was invited to act as chair for Stebbins's PhD committee. This caused considerable displeasure to Fernald, but he agreed to serve on the committee. Such was the turbulent state of this developing science. However, the young scientist was a somewhat turbulent and independent fellow also, and fell out with Jeffrey—who did not like Stebbins's getting embroiled in the developing subject of genetics—before finishing his PhD. As a result he nearly failed to get their signatures for his thesis.

In their place Stebbins acknowledges great help from the plant morphologist Ralph Wetmore and the new cytologist at the Arnold Arboretum, Karl Sax. Stebbins seems to have flourished in this rather rough environment. He read widely, obviously did not feel tied to the approaches of the Department of Botany and made use of the Bussey Institution, which was oriented to applied research, particularly connected with agriculture, and which housed several geneticists such as E. M. East and W. E. Castle and journals such as *Hereditas*. His thesis was approved in 1931 and he published two papers on the cytology of *Antennaria* in the *Botanical Gazette* in the following year.

CONFIRMING HIS IDEAS

During the last year of his PhD, in 1930, Stebbins was able to go to the International Botanical Congress in Cambridge. This was a great stimulus to the approach he was taking in his developing interest in plant evolution. He met Edgar Anderson, a visiting fellow at the John Innes Horticultural Institute but from the USA, who was already hard at work on the genetics of hybrid populations of *Iris*, particularly concerning the introgression that could be shown between species, and C. D. Darlington (FRS 1941), whose imaginative evolutionary approach to cytology must have attracted Stebbins greatly (though he later had reservations with some of Darlington's theories).

From 1931 he spent four years at Colgate University in Hamilton, New York. He was not happy there because of its emphasis on sport and because of his heavy teaching programme. Nevertheless he began research on the cytology of *Paeonia*, collaborating with Percy Saunders, who hailed from a family of wheat breeders and was based nearby at Hamilton College. It was greatly to Stebbins's advantage that Saunders had already amassed a considerable collection of living material, which he grew in his backyard at home. They worked together and found (with Hicks) that a great deal of structural heterozygosity existed within the chromosomes of the species (3). Significantly he also wrote his first book at Colgate at the young age of 30 years, an introductory biology text (6), which became used by the US armed forces for a long period.

In 1932 he attended the International Congress of Genetics in Ithaca, one more excellent opportunity to have his ideas extended and refined. He records being present at a memorable discussion between Sax and Darlington about the chiasmotype theory of crossing-over, and hearing T. H. Morgan ForMemRS talk on the future of genetics. However, the elegant preparations by Barbara McClintock (ForMemRS 1989) of chromosomes of maize pairing at prophase of meiosis, uncovering the presence of structural differences, particularly caught his

imagination and stimulated Stebbins to look for, and discover, the same thing in *Paeonia* hybrids.

Although he did not publish anything significant on this work until 1938 (4), his reputation as an imaginative investigator reached E. B. Babcock in Berkeley, who invited him to a research post to work in an ambitious programme supported by the Rockefeller Foundation on the genus *Crepis*. This was only a weed similar to dandelion but it was easy to grow, had very visible chromosomes, and had a host of different species. Babcock was hoping that *Crepis* would turn out to be the plant *Drosophila*. To be going to California excited Stebbins very much, not only because of Babcock but because California was becoming a major centre for evolutionary genetics.

His first assignment was to look at the chromosomes of relatives of *Crepis* in the related tribe Cichoriae, but he soon slid into working on *Crepis* (5), more than anything because it seemed to have the same patterns of evolution as he had found in *Antennaria* and in *Paeonia*. This was the beginning of major work with Babcock, which terminated only with the retirement of Babcock and his publishing of a monograph (Babcock 1947) on the American species of *Crepis*. This provided Stebbins with a major insight into polyploidy as an evolutionary force in plants (7), and also the part played by apomixis (8) (the formation of offspring without normal sexual processes) in the species complexes that could result. These findings put plant evolution into a rather different world, in which there are a lot of interesting and extra processes, from that well understood by zoologists in animals. The previously unrecognized concept that he elaborated was that plant genera are made up of a series of distinctive and usually allopatric diploid species that are usually accompanied by a series of species having chromosome numbers that are multiples of the original basic number and have characters that betray their evolution as derivatives of hybrids between different diploids. These can then be preserved, in evolutionary terms, by apomixis, the position in *Crepis* and *Antennaria*, although not in *Paeonia*.

BROADENING THE TRAIL

Later, Stebbins developed these ideas in several articles, and his 1947 review 'Types of polyploids: their classification and significance' (10) became a classic synthesis of evolution involving polyploidy. But before we go as far as that, it must be recorded that by the mid-1930s Stebbins suffered a disappointment when he was not given the faculty post replacing W. L. Jepson in the Botany Department. He was considered too interested in genetics and as a result would not put enough energy into the curatorial work that the department required. With the benefit of hindsight it was almost certainly a wise decision. However, in 1939 he was offered instead a faculty post in Berkeley as assistant professor in the Genetics Department, almost certainly because of the influence of Babcock, who was impressed with his drive and energy. In fact, because of Stebbins's burgeoning interest in the processes of evolution in plants it was a very good appointment.

In the mid-1930s the San Francisco Bay area had become a powerhouse, growing out of the previous activity in genetics, for work on evolution, particularly at Stanford University and the University of California, Berkeley. However, there was also the unique group at the Carnegie Institution of Washington at Stanford, containing Jens Clausen, David Keck and William Hiesey appointed to work on 'biosystematics', to continue the work started by Harvey

Monroe Hall dedicated to improving existing methods of plant taxonomy. This work included the sampling of populations of single plant species and transplanting them into enclosed plots in different environments in an altitude transect from the California coast to the vegetation limit of the higher Sierras. This work started in the 1920s and blossomed in the 1930s, and revealed the great amount of genetic and ecological diversity existing within plant species, a topic in which Stebbins, particularly from his work on *Crepis*, was already very interested, although he had never performed any transplant work himself.

So there was plenty to think about, and the different people concerned with biosystematics and evolution formed a group they named the 'Biosystematists' that met every month somewhere in the Bay area to share their ideas and findings. Stebbins became an active member and was instrumental in inviting speakers. His own work remained concentrated on cytotaxonomy and particularly on the role of polyploidy and apomixis in plant evolution, about which he published several significant papers. It is clear from his list of publications that his interest in the wider aspects of evolutionary genetics grew, and he was appointed Professor of Genetics at Berkeley in 1946.

During the war period Stebbins was required to work on war-related matters. This included the improvement of guayule and various forage grasses. He became involved in hybridization programmes that, although they did not seem to produce any useful practical material, gave the ever-alert Stebbins an opportunity to understand the potential role of hybridization in plant evolution and to get back to work on grasses, which he duly published (for example in (9)).

A significant figure in the development of his ideas during this period was the outstanding evolutionary geneticist Theodosius Dobzhansky (ForMemRS 1965). He first met Stebbins in 1936 at the California Institute of Technology, California, where Dobzhansky had been working on the genetics of populations of the fruitfly *Drosophila* under the supervision of Thomas Hunt Morgan. There were further meetings when Dobzhansky came to visit his friend Michael Lerner, a pioneer of animal population genetics, working in the Department of Poultry Husbandry at Berkeley. These visits were filled with discussion, and Stebbins became more and more attracted to what he saw that modern genetics could contribute to an understanding of evolution.

THE BIRTH OF *VARIATION AND EVOLUTION IN PLANTS*

Dobzhansky moved across the country to Columbia University in New York in 1940. Soon afterwards, L. C. Dunn, at the suggestion of Dobzhansky, invited Stebbins to give the Jesup Lectures. This was a prestigious lecture series sponsored by Columbia University. The previous contributor, in 1941, had been the distinguished zoological taxonomist Ernst Mayr (ForMemRS 1988), whose lectures appeared in a substantial (334-page) book, *Systematics and the origin of species* (Mayr 1942), a synoptic view of species and species formation, but only in animals; Edgar Anderson had given the plant side of the lectures but had not completed any manuscript for a book. Stebbins was therefore given the task of coming up with a synthetic view of plant evolution. He must have been attracted by the invitation because his own thinking was at a critical, though mature, stage and part of the invitation was that the lectures would be published as a book by Columbia University Press in the series not only containing that by Mayr but also two previous ground-breaking books on evolution, *Genetics and the origin of species* (Dobzhansky 1937) and *Tempo and mode in evolution* (Simpson 1944). Here

was a unique opportunity for Stebbins to sort out the conflicting evidence about plant evolution. Many funny (peculiar) things seemed to go on in plant evolution, such as polyploidy, apomixis and vegetative reproduction, along with hybridization, not to mention the fact that plants do not have legs to run about on—they have to sit there and accept what comes. Taken as a whole the situation seemed rather confusing.

The result, *Variation and evolution in plants* (11), was the largest of the four books in this series, with 643 pages and no less than 1250 references; it was published in 1950. It was a most distinguished piece of writing, because of its logic, its ideas and its coverage. To those who were young at the time, it seemed to be a miraculous lifeboat in a confused sea. Stebbins had had time to mull over and sort out the many processes that contribute to evolution in plants, and give them proper perspective. Although Stebbins was well acquainted with the animal side of evolution (especially the recent synthetic literature), he included few examples from animals. The book took into account the processes of evolution in the animal world, but with an eye to a comparative spirit of inquiry that concentrated on plants.

The unique contribution of the book was to bring together an enormous variety of research and place it in a completely neo-Darwinian evolutionary perspective. Those already familiar with the subject were entranced with the depth of the material and evidence that Stebbins had assembled. ‘Stebbins killed any serious belief in alternative mechanisms of evolution for plants, such as Lamarckian evolution or soft inheritance, which were still upheld by some botanists’ (Smocovitis & Ayala 2004). A second part of his preface needs to be quoted:

There is now no need for seeking hidden causes of evolutionary diversification or evolutionary progress, except in regard to certain specific processes, like mutation. Instead, the attention of scientists has been [should be] focussed on evolution as a series of problems in dynamics. The direction and speed of the evolution of any group of organisms at any given time is the resultant of the interaction of a series of reasonably well-known factors and processes, both hereditary and environmental.

He argued, in the preface, for a very simple, logical approach. Evolution must be considered on three levels: first, that of individual variation within an interbreeding population; second, that of the distribution and frequency of this variation; and third, that of the separation and divergence of populations as the result of the building up of isolating mechanisms leading to the formation of species. He does not mention natural selection there, probably because he thought it too obvious. But the fourth chapter of the book contains a remarkable review of the evidence available at the time on natural selection in plants, containing references to work, particularly that in Russia on cornfield weeds (Sinskaia & Beztuzheva 1931), in Sweden on pasture plants (Sylvén 1937), and in California on crop varieties (Harlan & Martini 1938), overlooked by most evolutionists. He had even found a completely overlooked example of recorded historic changes in the genetic composition of a plant population growing in a pasture (Kemp 1937). He built up a unique picture of the power of natural selection, which was substantiated only by later work. But it has to be said that it remained disappointingly overlooked for many years by zoologists.

It is by this single book that Stebbins made his reputation, although by being based at Berkeley he had the opportunity to interact with many people, especially geneticists, who appreciated his sharp mind and flow of ideas, as well as his encyclopaedic knowledge of plants and the local flora. He also established himself as a great promoter of the study of plants, even to the extent of having fierce arguments over what should be the balance between plants and animals in the papers of the new journal *Evolution* of which Mayr was the editor (Smocovitis 1997).

Part of the strength of Stebbins's work came from his taxonomic and related morphological background, which runs through a lot of his work. One example in the 1950s is a small but significant paper (16) on morphological evidence for the origin of the B genome of wheat. At the same time he could publish on the influence of aridity on evolution (12), the evolution of cultivated plants and weeds (13) and hybridization as an evolutionary stimulus (15). But he followed his taxonomic interests, for instance in papers on a new classification of the tribe Cichorieae (14), and on taxonomy and the evolution of genera in the Gramineae (17). This was a remarkably productive period.

This omnivorous approach to the problems of plant evolution continued through the 1950s and 1960s. However, although Stebbins embraced many topics, he did not run through them superficially but assessed them carefully and published definitive papers to record his judgments. His all-round abilities were recognized by his appointment as Secretary General to the International Union of Biological Sciences, for the years 1960–64. During this period he was responsible, with Herbert Baker, for a remarkable conference, 'The Genetics of Colonizing Species', held at Asilomar. The proceedings were subsequently published (20), and remain one more ground-breaking synthesis produced by Stebbins.

SPREADING HIS INTERESTS

At the end of this period it might seem that Stebbins ran out of steam, because his productivity in his ground-breaking analyses diminished. It was true that by 1965 he had reached his 60th year. But anyone who knew him could only have been impressed by his endless vigour, his delight in going into the field, and his remarkable knowledge of the Californian flora. An expedition with Ledyard was an inspiration, provided that you were not too terrified by his driving, especially by his capacity to stop suddenly when he spied some plant or habitat of interest. But he had not really lost steam. It was rather that he had become caught by the need, and the possibility of understanding, how genes worked, and how those genes coded for particularly important characters—in plants, of course. He seemed to be driven to this by the enthusiasm that surrounded him, first for developmental genetics, and then for the molecular genetics that was beginning to dominate genetics departments. He began to work on various aspects of developmental genetics, especially as manifested in the effects of the hooded gene (18) in barley, and then of other genes (19).

But this time he had chosen a topic that turned out to be more difficult than those he had undertaken before, and although he applied his powerful mind to the problems, there were not the tools available, as others also found. There was also the problem that he did not have the necessary biochemical background, although he sought the aid of collaborators and graduate students. The result was that despite several thoughtful papers on the topic (for instance (22)), none had the quite the impact of his earlier evolutionary work, although some of this work is being assessed by those interested in evolutionary developmental biology (or 'evo-devo') at this time.

This applied also, but in a slightly different manner, to his second major book, *Flowering plants: evolution above the species level* (23), which was based on the Prather Lectures he gave in Harvard. Here he was trying to take evolution on beyond where he had stopped before. The problem was that the techniques for doing this, which we now realize to be molecular, had not then been developed. How different, and how startling, would have been the book if he

could only have written it 20 years later. But it was well received and widely used; it was exciting to younger people and especially to graduate students.

He wrote an undergraduate textbook, *Processes of organic evolution* (21), which was very successful. Its attraction was the way in which it concentrated, as its title implies, on the processes of evolution in a very logical manner. In 1977, in collaboration with Dobzhansky, Ayala and Valentine, he followed this with a more advanced textbook (24), intending to catch up with the array of techniques available to evolutionary biologists. In their preface the authors, because of this, admitted to the need for several authors, and suggest that 'Perhaps this is the last time that a reasonably comprehensive account of the theory of evolution can be encompassed in a single volume'. Despite its truth, what a pity this was so for a subject of such importance to understanding our place in the world.

During this period Stebbins continued to produce papers on evolutionary problems—always interesting, often synoptic, but never as far-reaching as those he had written earlier. He was continuously in demand to visit overseas institutions, such as the University of Chile at Santiago in 1973, the Australian National University and CNRS Montpellier in 1974, and the Soviet Union in 1975, as well as being Visiting Professor to many local universities. He was elected to the National Academy of Sciences in 1952, to the American Philosophical Society 1953, the Royal Swedish Academy of Arts and Sciences, and the Linnean Society (by whom he was awarded its Gold Medal) in 1973, and was awarded an Honorary Doctorate of the University of Paris in 1962. In 1979 he was awarded the National Medal of Science by President Carter. In 1980 the University of California named a nature reserve in his honour, as the Stebbins Cold Canyon Reserve, which delighted him greatly. In 1999, at the 16th International Botanical Congress, he was honoured by a banquet at which, together with his old zoological colleague Ernst Mayr, he was given the Institute of Biological Sciences Distinguished Service Award.

Right through into his 80th and 90th years he continued to write perceptive papers, noticeably returning to his early love for grasses. In 2000 a colloquium sponsored by the National Academy of Sciences was held at Irvine, California, entitled 'Variation and Evolution in Plants and Microorganisms: Toward a New Synthesis 50 Years after Stebbins' (Ayala *et al.* 2000). Although very frail, Stebbins had fully intended to be present, but alas he died two weeks before the symposium was held.

As a teacher Stebbins was lively and attractive, even though when asking him questions you had to risk being demolished rather fiercely, whether you were undergraduate or post-graduate. He did not suffer fools gladly, and admitted that he was too able 'to blow his top'. He was haunted by a story that one day in a fit of frustration he had thrown his typewriter out of the window of his lab and then gone down to pick it up, weeping. But perhaps the story is apocryphal; he never would admit to it. He was married twice, first to Peggy, with whom he had three children, and then to Barbara, who gave him a stepson. Barbara was a great support for this sometimes unworldly enthusiast in his later years. Her influence on Ledyard was extensive, as she introduced him to the Unitarian Church, which they attended, and to art collecting and other cultural activities, which they shared together until the end.

In the field he was just a delight, so very happy to act as expositor for some interesting evolutionary situation which he had taken his audience to see. One of his colleagues, Francisco Ayala, records how, when he gave his last lecture in 1973 before his retirement, he received a long standing ovation (Smocovitis & Ayala 2004). He worked closely with other biologists in the Biological Sciences Curriculum Study developing better teaching of evolution in schools.

He fought against the rise of creationism. He was a great character. It is remarkable in a country where such clear thinking has been available for so long that creationist arguments are so rife at the present time. As a good liberal, he was of course a lifetime democrat.

ACKNOWLEDGEMENTS

This memoir owes a great deal to the several people who have gone before in writing accounts of Ledyard Stebbins and his most interesting life. In particular the first author would like to acknowledge the dedicated work of his co-author, who took Stebbins and his role in our understanding of evolution as the subject of a detailed biography (Smocovitis 1997, Crawford & Smocovitis 2005), which should be consulted for further information.

The frontispiece photograph was taken in about 1988.

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